

LOSS OF WATER TRANSPORT CAPACITY DUE TO XYLEM CAVITATION IN ROOTS OF TWO CAM SUCCULENTS¹

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Loss of axial hydraulic conductance as a result of xylem cavitation was examined for roots of the Crassulacean acid metabolism (CAM) succulents *Agave deserti* and *Opuntia ficus-indica*. Vulnerability to cavitation was not correlated with either root size or vessel diameter. *Agave deserti* had a mean cavitation pressure of -0.93 ± 0.08 MPa by both an air-injection and a centrifugal method compared to -0.70 ± 0.02 MPa by the centrifugal method for *O. ficus-indica*, reflecting the greater tolerance of the former species to low water potentials in its native habitat. Substantial xylem cavitation would occur at a soil water potential of -0.25 MPa, resulting in a predicted 22% loss of conductance for *A. deserti* and 32% for *O. ficus-indica*. For an extended drought of 3 mo, further cavitation could cause a 69% loss of conductance for *A. deserti* and 62% for *O. ficus-indica*. A model of axial hydraulic flow based upon the cavitation response of these species predicted that water uptake rates are far below the maximum possible, owing to the high root water potentials of these desert succulents. Despite various shoot adaptations to aridity, roots of *A. deserti* and *O. ficus-indica* are highly vulnerable to cavitation, which partially limits water uptake in a wet soil but helps reduce water loss to a drying soil.

Key words: *Agave deserti*; embolism; hydraulic conductance; *Opuntia ficus-indica*; vessel anatomy; water relations; xylem physiology.

Xylem cavitation due to water stress occurs via “air-seeding,” as shown for many trees and shrubs (Zimmermann, 1983; Sperry and Tyree, 1988; Sperry et al., 1996). According to this mechanism, when the negative hydrostatic pressure within a xylem conduit is sufficient to overcome the capillary forces at the air–water interface in a pit membrane, an air bubble can be pulled into a water-filled conduit from an adjacent air-filled conduit. This air bubble is a “seed” for vaporization of the metastable water; expansion of the air bubble results in a vapor-filled conduit that is hydraulically dysfunctional. The pressure at which an air bubble is drawn through a pore in the pit membrane is a function of the pore diameter (the capillary equation; Nobel, 1991). Experimentally, a positive air pressure applied to the outside of the water-filled xylem can force air across a pit membrane, having the same cavitation effect as a negative hydrostatic pressure within conduits in root and stem segments (Cochard, Cruiziat, and Tyree, 1992). Recently, centrifugal force has also been used to cause cavitation by generating negative hydrostatic pressure within the xylem of excised plant segments (Alder et al., 1997). These two methods agree well for branches of various temperate trees (Pockman, Sperry, and O’Leary, 1995; Alder et al., 1997), but their application to roots is limited to a single species, *Betula occidentalis* (Alder et al., 1997).

A comparison of 60 temperate, tropical, and Mediterranean trees and shrubs shows a weak positive correlation of xylem conduit diameter with vulnerability to cavitation

(Tyree, Davis, and Cochard, 1994). Within an individual species, vulnerability to cavitation can increase with xylem conduit diameter, such as for *B. occidentalis* (Sperry and Saliendra, 1994) and *Populus balsamifera* (Hacke and Sauter, 1996) but not for others, such as *Acer grandidentatum* (Alder, Sperry, and Pockman, 1996) and *Alnus glutinosa* (Hacke and Sauter, 1996). Vulnerability to cavitation can also increase with xylem tissue diameter or plant segment diameter (Cochard, 1992; Sperry and Ikeda, 1997), despite the prediction of the air-seeding hypothesis that vulnerability to cavitation due to water stress should depend on the diameter of the pores in pit membranes.

Although a low xylem pressure can cause xylem water to cavitate, it also provides a larger driving force for water uptake from the soil. However, as xylem pressure decreases, as generally occurs during drought, complete loss of conductance will ultimately occur. The trade-off between an increasing driving force for water uptake and increasing cavitation results in a maximum water flow rate that occurs just before the complete loss of conductance (Sperry et al., 1998). If excessive transpiration permits xylem pressures to decrease below the xylem pressure at which the rate of water flow is maximized, the subsequent complete loss of conductance will cause failure of the hydraulic system (Jones and Sutherland, 1991). Hydraulic models for trees (Tyree and Sperry, 1988) predict that plants will maximize water uptake by allowing xylem pressures to approach the critical xylem pressure.

The CAM succulents *Agave deserti* and *Opuntia ficus-indica* used in this study maintain high root water potentials during extended drought (Nobel, 1988), and water uptake by their roots occurs mainly from wet soils (Nobel and Lee, 1991; Nobel and Cui, 1992). Cavitation occurs in the roots of *A. deserti* and *O. ficus-indica* at relatively high xylem pressures (Ewers, North, and Nobel, 1992; North and Nobel, 1996), limiting water uptake from the

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soil to the first few weeks of drought and thereafter reducing water loss from the succulent shoots back to a drying soil (Nobel and Cui, 1992). In the present study, the loss of root hydraulic conductance due to cavitation accompanying decreasing xylem pressure (a vulnerability curve) was quantified using both air-injection and centrifugal methods. Because of its more mesic habitat (Nobel, 1988), roots of *O. ficus-indica* were hypothesized to be more vulnerable to cavitation than those of *A. deserti*. Correlations between xylem dimensions and vulnerability to cavitation were also examined for each species. Vulnerability curves were used to predict the extent of cavitation that the roots would experience in a drying soil and to determine relative flow rates in the xylem under varying root xylem pressures. It was hypothesized that although appreciable cavitation could occur in these roots, the extent of the cavitation would be minimized through maintenance of relatively high root xylem pressures by the nearby succulent shoot tissue.

MATERIALS AND METHODS

Plant material—Plants of *Agave deserti* Engelm. (Agavaceae) were collected at "Agave Hill" in the University of California Philip L. Boyd Deep Canyon Research Center (33°38' N, 116°24' W, 850 m elevation) near Palm Desert, California; they were transplanted into 20-L rectangular pots and watered weekly with 0.05% Hoagland's solution supplemented with micronutrients. Irrigated 7-yr-old plants of *Opuntia ficus-indica* (L.) Miller (Cactaceae) growing at the University of California Agricultural Research Station, Riverside, California, were sampled in the field. For both species, nonbranching root segments >30 cm in length were removed at soil depths of 10–40 cm and immediately wrapped in plastic bags to minimize dehydration.

Xylem anatomy—Transverse sections were taken at midsegment from the excavated roots and stained with 0.05% toluidine blue O. The average area of vessel lumens was determined by tracing individual vessels with a digitizing tablet (Kurta, Altek Corp, Silver Spring, Maryland) using a camera lucida attached to a light microscope. For *A. deserti*, all vessels in a transverse cross section were measured. For *O. ficus-indica*, transverse sections were divided into four 90° radial sectors and 50 randomly selected vessels were measured from each sector, after which the number of vessels in an entire root cross section was determined. Vessels were nearly circular for both species, allowing vessel diameter to be calculated readily from vessel area.

Cavitation study—Two techniques were used to induce cavitation in the root xylem: an air-injection method (Cochard, Cruiziat, and Tyree, 1994) and a centrifugal method (Holbrook, Burns, and Field, 1995; Pockman, Sperry, and O'Leary, 1995). For measurements using the air-injection method, a root segment was trimmed under water to 20 cm in length and then inserted into a cylindrical pressure chamber with an opening at each end. The root was sealed within the chamber with rubber stoppers and compression fittings that allowed the ends of the root segment to protrude from both ends of the chamber (Sperry and Saliendra, 1994). To expel any embolisms that had occurred in the soil or during transport, 100 kPa of water pressure was applied to the distal end for 20 min, after which the water pressure on the distal end was reduced to 5.0 kPa. The volumetric flow rate of water (Q_v , in cubic metres per second) was then measured at the proximal end by collecting and weighing the extruded water in vials filled with cotton wool. The axial hydraulic conductivity (also called a conductance per unit length) of the root segment (K_h , in metres to the fourth power per megapascal per second) was calculated from

$$Q_v = K_h \frac{\Delta P}{\Delta x} \quad (1)$$

where Δx (in metres) is the root segment length, and ΔP (in megapascals) is the water pressure difference that caused flow along the root axis. After determination of the initial K_h , the air pressure in the chamber was increased to 500 kPa for 10 min to allow time for the pressurized air to enter the xylem conduits, after which the chamber pressure was reduced back to zero and K_h of the root segment was measured again. This process was repeated with progressively higher air pressures (in 500-kPa increments) until <5% of the initial K_h remained. The value of Q_v under no pressure difference was always <0.5% of Q_v under ΔP . In addition, due to the small values of ΔP used to cause flow (5–7 kPa), K_h was approximately constant along a root during a measurement.

For the centrifugal method (Alder et al., 1997), a root segment was trimmed under water to 27 cm in length and attached to tubing that led to an analytical balance at the proximal end and to a water pressure source at the distal end while submerged. After expelling embolisms as above, the water pressure was reduced to 5.0 kPa. To account for flow that could occur without any pressure difference across a submerged root, the measurement of K_h at a particular pressure (Eq. 1) was preceded and followed by a measurement of Q_v under no pressure difference, which was subtracted from the Q_v under a pressure difference to give the actual Q_v for the calculation of K_h . After the initial (maximal) K_h measurement, the root was placed in a specially designed centrifuge rotor and spun about its longitudinal axis. The root ends were contained in water-filled L-shaped reservoirs that submerged them during centrifugation. The most negative pressure (P_{xylem} , MPa) experienced by the root xylem (at its center) equaled

$$P_{\text{xylem}} = -0.5\rho\omega^2r^2 \quad (2)$$

where ρ is the density of water (in kilograms per cubic metre), ω is the angular velocity (in radians per second), and r (in metres) is the distance from the center of the spinning root to the surface of the water that submerged the root tip. After spinning the root for 5 min at the desired negative pressure, K_h was measured within 5 min, which avoids refilling of the vessels (Alder et al., 1997); this was repeated for progressively higher angular velocities until <5% of the initial K_h remained.

Vulnerability curves for both the air-injection and the centrifugal methods, which represent the cumulative percentage loss of K_h (Tyree and Sperry, 1988), were expressed relative to the hydraulic conductance at the maximal pressure that the xylem of these roots experiences in wet soil (–0.25 MPa for *A. deserti* and –0.29 MPa for *O. ficus-indica*; Nobel and Lee, 1991) and were fit with an exponential equation. The mean cavitation pressure was determined by plotting the percentage conductance loss per unit pressure change (rather than plotting the cumulative loss of conductance, as for a vulnerability curve) and taking the mean of this distribution based on the midpoint of each pressure change. For the analysis of the vulnerability curves in the following model, the osmotic pressure was assumed to be negligible so that the root xylem pressure (P_{xylem}) could be replaced by the root xylem water potential (Ψ_{xylem} ; Nobel, 1991; Tyree, 1997).

Data were statistically analyzed by Student's *t* test and are presented as means \pm 1 SE.

Model—Axial water movement along root xylem can be described by the equation (ignoring radial flow)

$$Q_v = -K_h \left(\frac{d\Psi}{dx} \right) \quad (3)$$

where $d\Psi/dx$ (in megapascals per metre) is the water potential gradient along the xylem. Recognizing that Q_v is a constant along the xylem and that K_h depends on Ψ [$K_h(\Psi)$], as represented by a root vulnerability curve, Eq. 3 can be integrated from $x = 0$ to $x = \Delta x$ after multiplying both sides by dx (Sperry et al., 1998)

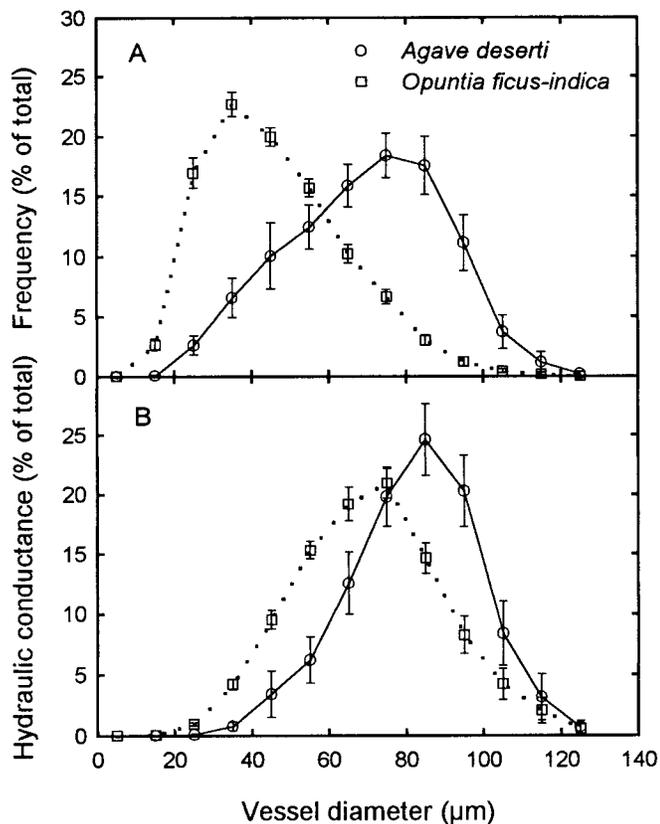


Fig. 1. Frequency (A) and relative hydraulic conductance (B) vs. vessel diameter for *Agave deserti* (○, $N = 17$ roots) and *Opuntia ficus-indica* (□, $N = 28$ roots). Data are grouped into 10-μm-diameter classes and are means ± 1 SE. Hydraulic conductance was assumed to be proportional to (vessel diameter)⁴, as described for cylinders by the Hagen-Poiseuille relation (Nobel, 1991).

$$Q_v \int_0^{\Delta x} dx = Q_v \Delta x = - \int_{\Psi_{\text{distal}}}^{\Psi_{\text{proximal}}} K_h(\Psi) d\Psi \quad (4)$$

where Ψ_{distal} is the water potential at $x = 0$ and Ψ_{proximal} is the water potential at $x = \Delta x$. To determine the influence of cavitation on Q_v , Eq. 4 was solved by holding Ψ_{distal} constant and progressively lowering Ψ_{proximal} until Q_v converged to a constant value; this yielded the critical volume flow rate ($Q_{v\text{crit}}$) at that particular Ψ_{distal} and marks the threshold that will result in complete loss of conductance if it is exceeded (Sperry et al., 1998). Because $K_h(\Psi)$ (represented by an exponential equation) mathematically never reached zero, $Q_{v\text{crit}}$ was taken at 98% loss of conductance. The relation between Q_v and Ψ_{proximal} at a constant Ψ_{distal} obtained from Eq. 4 under conditions of cavitation [decreasing $K_h(\Psi)$ as Ψ decreases] was compared to results obtained in the absence of cavitation [constant and maximal $K_h(\Psi)$ as Ψ decreases].

The relationship between $Q_{v\text{crit}}$ and Ψ_{distal} indicates the maximum Q_v that could occur as Ψ_{distal} varies. Measurements of root xylem water potential (Ψ_{xylem}) in relation to soil water potential (Ψ_{soil}) for these two species (Nobel and Lee, 1991) were used to predict Q_v for actual roots by replacing Ψ_{proximal} with Ψ_{xylem} and Ψ_{distal} with Ψ_{soil} in Eq. 4, substituting the empirical data for the two variables, and solving for Q_v , which was then compared to $Q_{v\text{crit}}$ for that particular Ψ_{distal} .

RESULTS

Xylem anatomy—The ranges in vessel diameter for the two species were similar, but *Agave deserti* had a larger

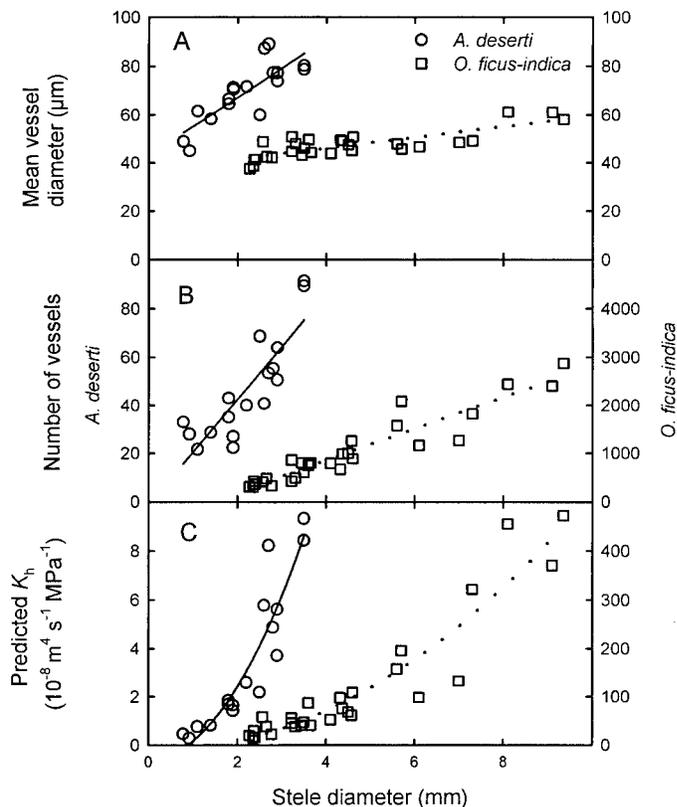


Fig. 2. Mean vessel diameter (A), number of vessels (B), and predicted K_h (C) vs. stele diameter for *A. deserti* (○, $N = 17$ roots) and *O. ficus-indica* (□, $N = 28$ roots). The left ordinate is for *A. deserti* and the right ordinate is for *O. ficus-indica*.

mean root vessel diameter ($70 \pm 3 \mu\text{m}$, $N = 17$ roots) than *Opuntia ficus-indica* ($47 \pm 1 \mu\text{m}$, $N = 28$ roots, $P < 0.001$; Fig. 1A). The mean vessel diameter weighted on the basis of conductance was $82 \pm 3 \mu\text{m}$ for *A. deserti* and $71 \pm 2 \mu\text{m}$ for *O. ficus-indica* (Fig. 1B). For *O. ficus-indica*, only 10% of the vessels were larger than $73 \mu\text{m}$, yet they accounted for 45% of the overall conductive capacity, whereas for *A. deserti*, 10% of the vessels were larger than $96 \mu\text{m}$ and they contributed 21% of the overall conductance.

Mean vessel diameter (by size) increased 62% with increasing stele diameter for *A. deserti* and 38% for *O. ficus-indica* (Fig. 2A), which based upon the Hagen-Poiseuille Law would increase conductance sixfold for *A. deserti* and fourfold for *O. ficus-indica*. Over the range of stele diameters measured, the number of vessels in an individual root increased sixfold, from 12 to 75 for *A. deserti* and eightfold from 291 to 2610 for *O. ficus-indica* (Fig. 2B). Thus, the overall increase in predicted root hydraulic conductance (K_h) with increasing stele diameter was 36-fold for *A. deserti* and 34-fold for *O. ficus-indica* (Fig. 2C).

Xylem cavitation—The injection technique and the centrifugal technique for measuring loss of K_h due to xylem cavitation gave nearly identical results for roots of *A. deserti* (Fig. 3, $P > 0.6$ at all xylem pressures); the mean cavitation pressure was $-0.93 \pm 0.08 \text{ MPa}$ for both

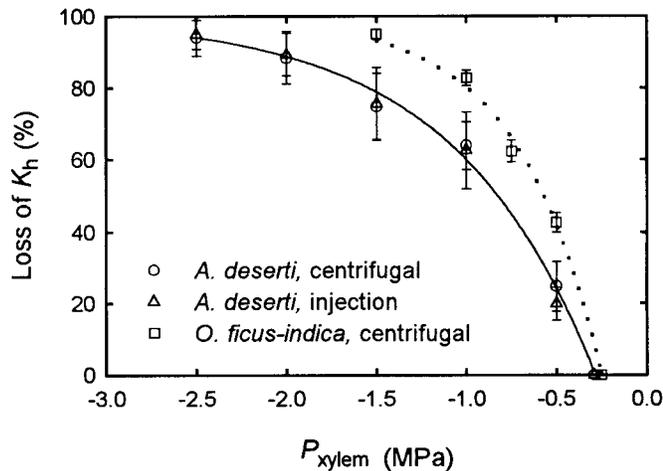


Fig. 3. Loss of root hydraulic conductance (K_h) accompanying decreasing root xylem pressure (P_{xylem}) for *A. deserti* and *O. ficus-indica*. The vulnerability curves for *A. deserti* are from both the centrifugal force method (\circ , $N = 9$ roots) and the injection method (\triangle , $N = 8$ roots) and for *O. ficus-indica* are from the centrifugal force method only (\square , $N = 24$ roots) and are means ± 1 SE. Centrifugal data are fit with an exponential equation [% loss = $100(1 - a e^{P_{xylem} b})$], where a and b are curve-fitting parameters].

techniques. *Opuntia ficus-indica* had a mean cavitation pressure of -0.70 ± 0.02 MPa using the centrifugal technique (Fig. 3). The vulnerability curves of *A. deserti* and *O. ficus-indica* were significantly different at and below -0.5 MPa ($P < 0.05$). Within a species, the mean cavitation pressure was not correlated with either mean vessel diameter or stele diameter (data not shown).

Model—Under conditions of no cavitation, Q_v increased linearly as $\Psi_{proximal}$ decreased (Fig. 4). At a Ψ_{distal} of 0.0 MPa but with cavitation, Q_v increased up to a maximum (Q_{vcrit}) at a $\Psi_{proximal}$ of -3.3 MPa for *A. deserti* and at -2.05 MPa for *O. ficus-indica* (Fig. 4A), which were 32 and 34% of Q_v without cavitation, respectively. The value of Q_{vcrit} decreased slightly for a Ψ_{distal} of -0.5 MPa, resulting in a Q_{vcrit} that was 21% of maximum for *A. deserti* and 17% for *O. ficus-indica* (Fig. 4B).

Q_{vcrit} decreased as Ψ_{distal} decreased for both species (Fig. 5), consistent with the decreasing driving force for water uptake. Values of Q_{vcrit} were above zero at a lower Ψ_{distal} for *A. deserti* than for *O. ficus-indica*, owing to the higher vulnerability of *O. ficus-indica* to cavitation. Based on measurements of Ψ_{soil} and Ψ_{xylem} , water uptake was predicted only above a Ψ_{soil} of -0.50 MPa for *A. deserti* and -0.48 MPa for *O. ficus-indica* (Fig. 5). Over the range of Ψ_{soil} that water uptake would occur, Q_v averaged 22% of Q_{vcrit} for *A. deserti* and 30% for *O. ficus-indica*.

DISCUSSION

Xylem conduit diameter was not correlated with mean cavitation pressure in roots of *Agave deserti* and *Opuntia ficus-indica*, consistent with results for roots of *Pseudotsuga menziesii* (Sperry and Ikeda, 1994). Smaller diameter conduits may not cause greater resistance to cavitation under water stress, but a causal link between pit

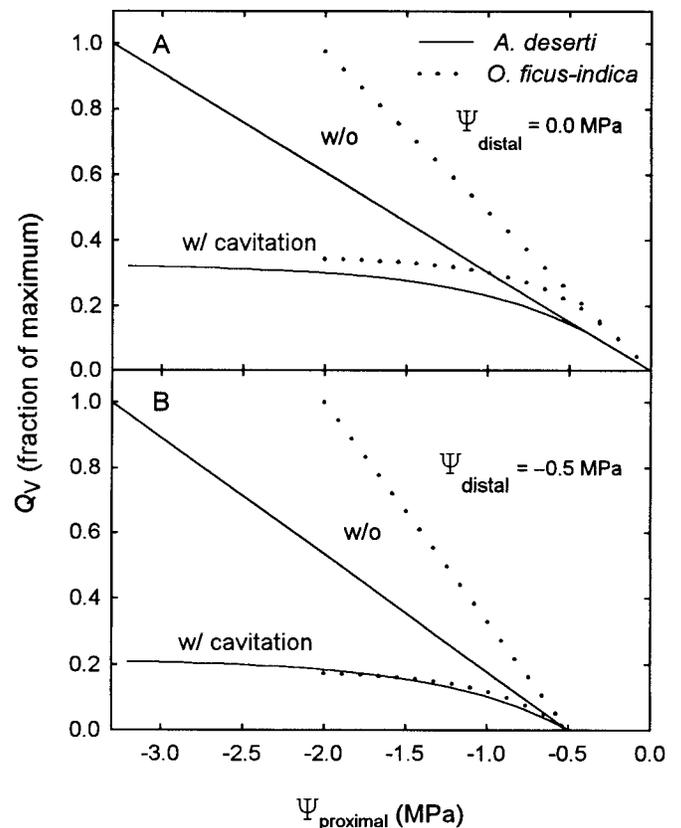


Fig. 4. Predicted volumetric flow rate (Q_v) vs. proximal xylem water potential ($\Psi_{proximal}$) for roots of *A. deserti* and *O. ficus-indica* at a Ψ_{distal} of 0.0 MPa (A) and -0.5 MPa (B). Data are modeled from Eq. 4 and use the root vulnerability curves (Fig. 3); the straight lines represent Q_v without cavitation and the curved lines represent Q_v with cavitation. Values of Q_v are shown relative to the maximum without cavitation (occurring at a $\Psi_{proximal}$ of -3.3 MPa for *A. deserti* and -2.05 MPa for *O. ficus-indica*).

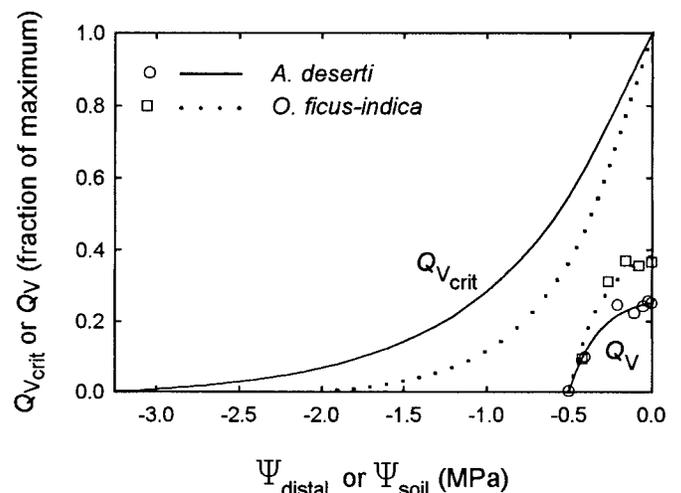


Fig. 5. Critical volumetric flow rate (Q_{vcrit}) predicted by Eq. 4 for *A. deserti* (—) and *O. ficus-indica* (•••) vs. distal water potential (Ψ_{distal}) presented as a fraction of the maximum Q_{vcrit} (which occurs at a Ψ_{distal} of 0.0 MPa). Also presented are predicted values of Q_v relative to the value of Q_{vcrit} at the corresponding Ψ_{distal} for *A. deserti* (\circ) and *O. ficus-indica* (\square) as calculated from empirical root water potentials (Ψ_{xylem}) at decreasing Ψ_{soil} (Nobel and Lee, 1991).

membrane pore size and conduit diameter could explain the frequent correlation of vulnerability to cavitation and conduit diameter (Tyree, Davis, and Cochard, 1994). At a developmental level, xylem conduit diameter typically is related to stele diameter, as the additional water uptake requirements of a maturing plant are met by larger diameter vessels or tracheids. For *A. deserti* and *O. ficus-indica*, the overall relative increase in the hydraulic conductivity K_h with stele diameter was similar, but the relative increase in mean vessel diameter was greater for *A. deserti* and the relative increase in the number of vessels was greater for *O. ficus-indica*. These observations are consistent with the lack of secondary growth in the monocotyledonous *A. deserti* (Carlquist, 1975), which produces larger vessels that permit an increased xylem flow as its roots mature. Secondary growth in the vascular tissues of the dicotyledonous *O. ficus-indica* produces a greater number of vessels as the demand for water uptake increases.

As hypothesized, roots of *O. ficus-indica* were more vulnerable to cavitation than those of *A. deserti*, consistent with the relative habitat preferences and tolerances of low water potentials for these two species. Although the native habitat of *O. ficus-indica* is unknown, this species is found extensively throughout the tropics and subtropics, in contrast to the arid native habitat of *A. deserti* in the northwestern Sonoran Desert (Nobel, 1988; Hickman, 1993). For many species, drought tolerance can be correlated with vulnerability to cavitation (Carlquist, 1975; Tyree, Davis, and Cochard, 1994), such as for *Pinus edulis* and *Juniperus osteosperma* (Linton, Sperry, and Williams, 1998) and three subspecies of *Artemisia tridentata* (Kolb and Sperry, in press).

Within the period of positive water uptake for hydrated plants (when $\Psi_{\text{soil}} > -0.5$ MPa), significant cavitation occurs in these roots, with a predicted 24% loss of conductance for *A. deserti* and 40% for *O. ficus-indica* at a Ψ_{soil} of -0.5 MPa. At this Ψ_{soil} , the difference in cavitation loss of conductance between the two species is almost entirely determined by root vulnerability to cavitation, as the difference in the root xylem water potential (Ψ_{xylem}) between the two species is only 0.02 MPa. At a Ψ_{soil} below -0.5 MPa, water loss from the root to the drying soil is energetically favored, as Ψ_{xylem} remains close to the water potential of the succulent shoot (Nobel, 1988). As drought proceeds, the large cladodes (succulent stem segments) of *O. ficus-indica* maintain higher root and shoot water potentials than the water potential of the less succulent *A. deserti*. For instance, at the end of 3 mo of drought, Ψ_{xylem} is approximately -1.3 MPa for *A. deserti* (North and Nobel, 1998) and -0.7 MPa for *O. ficus-indica* (Goldstein, Andrade, and Nobel, 1991), resulting in similar predicted losses of conductance of 69 and 62%, respectively. Six months of drought cause root water potentials of *A. deserti* to decrease to -2.0 MPa (North and Nobel, 1998), with a predicted 87% loss of conductance. Rewetting of the soil after 30 d of drought partially refills cavitated conduits in both species (North and Nobel, 1995, 1996), providing new lateral roots a hydraulic connection to the shoot. Therefore, although significant cavitation occurs in a wet soil during water uptake, cavitation in these species may be more significant in limiting water

loss back to a drying soil, which occurs when Ψ_{soil} becomes less than Ψ_{xylem} (Nobel and Cui, 1992).

Predicted values of Q_v based on empirical data were far below $Q_{v\text{crit}}$, as a consequence of the relatively high Ψ_{xylem} of *A. deserti* and *O. ficus-indica*. From an energy point of view, roots of these species would increase the rate of water uptake from the soil if Ψ_{xylem} were lower. In addition, a lower Ψ_{xylem} would increase the range of Ψ_{soil} over which water uptake could occur, effectively prolonging the period of water uptake as drought progressed. This appears to be the case for *Larrea tridentata*, a ubiquitous shrub of the Sonoran and Mojave deserts, which experiences significant cavitation only at xylem pressures lower than -10 MPa and maintains transpiration throughout the entire year (Pockman, 1996). For CAM succulents, however, high root water potentials are maintained by the succulent shoots. Thus, instead of xylem that is highly resistant to cavitation to allow water extraction during extended drought, these succulents are "drought avoiders" (Levitt, 1980), where water uptake is limited to a relatively wet soil and long periods of drought are tolerated because of water storage in the succulent tissue.

The air-injection and centrifugal methods for measuring cavitation agreed for roots of *A. deserti*, as well as for *Betula occidentalis* (Alder et al., 1997), providing additional evidence that cavitation occurs via air-seeding and strengthening the utility of the centrifugal method for measuring cavitation in roots. Recently, the interpretation of both methods has been challenged in the presentation of a "compensating pressure theory," which has been proposed as the replacement for the cohesion-tension theory of xylem transport (Canny, 1995). In particular, the air-injection and centrifugal methods may cause complete cavitation at much less negative pressures than previously believed and conduits may be refilled by water from xylem parenchyma via a "compensating pressure" while the measurement of K_h is in progress, so that vulnerability curves actually reflect the limit at which parenchyma can refill xylem conduits (Canny, 1998).

This compensating pressure hypothesis proposes that the maximum available "compensating pressure" for xylem refilling equals the osmotic pressure of the xylem parenchyma, leading to the prediction that the negative pressure at which xylem vessels can no longer be refilled corresponds to the osmotic pressure of the adjacent xylem parenchyma (Canny, 1998). This interpretation appears to fit branches of some species (Pockman, Sperry, and O'Leary, 1995; see analysis in Canny, 1998) that experience nearly complete loss of conductance at a threshold of negative pressure that is equal but opposite in sign to the osmotic pressures of the xylem parenchyma. In contrast to branches, many root vulnerability curves show a continual increase in loss of conductance that may become asymptotic as xylem pressures continue to decrease (Sperry and Saliendra, 1994; Alder et al., 1997; Sperry and Ikeda, 1997). The root vulnerability curves for *A. deserti* and *O. ficus-indica* generally follow a rectangular hyperbolic relation, with a high rate of initial loss that gradually decreases with lower xylem pressures. These roots do not appear to have a threshold of conductance loss that corresponds to the osmotic pressure of the xylem parenchyma (mean osmotic pressure of roots for *A. de-*

serti is 0.95 MPa; North and Nobel, 1998) and therefore do not agree with the predictions of the compensating pressure theory. The asymptotic vulnerability curves for *A. deserti* and *O. ficus-indica* may be adaptive by allowing substantial cavitation at xylem pressures immediately below the point at which water uptake ceases ($\Psi_{\text{soil}} \approx -0.5$ MPa), thereby controlling water loss to the soil at high Ψ_{soil} , while maintaining low levels of conductance at low xylem pressures for quicker recovery and refilling after a long drought.

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