

HYDRAULIC CONDUCTIVITY, XYLEM CAVITATION, AND WATER POTENTIAL FOR SUCCULENT LEAVES OF *AGAVE DESERTI* AND *AGAVE TEQUILANA*

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Axial hydraulic conductivity (K_h) was measured for fresh, dehydrated, and rehydrated leaves of the Crassulacean acid metabolism (CAM) leaf succulents, *Agave deserti* and *Agave tequilana*. Dehydration of leaves at 35°C for several hours caused K_h to decrease, with a 50% decrease occurring at a leaf water potential of -2.37 MPa for *A. deserti* and at -1.72 MPa for *A. tequilana*. When leaves were rehydrated in water, the decrease in K_h was completely reversible, indicating that the decrease under dehydrated conditions was caused by xylem cavitation. During extended drought of potted plants, leaves of *A. deserti* dehydrated less rapidly than those of *A. tequilana*, resulting in leaf water potentials of -1.96 MPa and -3.42 MPa, respectively, at 100 d of drought. Also, transpiration decreased 87% at 40 d of drought for *A. deserti* compared to 97% for *A. tequilana*. Based on leaf water potentials during drought and leaf vulnerability to cavitation, *A. deserti* and *A. tequilana* would experience 41% and 80% decreases in K_h , respectively, at 100 d of drought. The difference between the two species was primarily caused by the higher leaf water potentials of *A. deserti* compared to *A. tequilana*, rather than by differences in vulnerability to cavitation. A model of whole-plant axial hydraulic conductance for *A. deserti* indicated that, under well-watered conditions, the leaves had a lower axial hydraulic conductivity than the roots. After 60 d of drought, however, the root hydraulic conductivity was lower than that of the leaves, a phenomenon that would aid in restricting water loss from the plant to the soil during extended drought.

Keywords: *Agave*, embolism, transpiration, water relations.

Introduction

Hydraulic conductance is often used to quantify xylem flow rates and to predict the influence of specific components in the water transport pathway on water movement (Zimmermann 1983; Gartner 1995). Woody trees have been used as model organisms for such studies of branches and roots (Sperry et al. 1998; Zott et al. 1998). Recently, studies on roots of succulent plants have shown that the leaf succulent *Agave deserti* maintains root regions of high and low hydraulic conductance that minimize the loss of water from a plant to the soil during drought, while allowing rapid water uptake when drought ceases (North and Nobel 1998). In addition, the roots of *A. deserti* and the stem succulent *Opuntia ficus-indica* are highly vulnerable to xylem cavitation and have low water transport rates during the initial stages of drought because of their high root-water potentials (Linton and Nobel 1999). Despite these and other studies concerning root hydraulic conductance of succulent plants (*A. deserti* [North and Nobel 1991], *Ferocactus acanthodes* [North and Nobel 1992], *O. ficus-indica* [North and Nobel 1996]), almost nothing is known about the hydraulic conductance of the succulent shoots for such plants.

Xylem cavitation lowers hydraulic conductance by blocking xylem conduits with air or water vapor (Tyree and Sperry

1989), resulting in decreased downstream plant water potentials and stomatal closure that further limits water loss (Linton et al. 1998). Xylem cavitation is caused by air seeding through interconduit pit membranes (Sperry and Tyree 1988), with the extent of cavitation (usually measured by the influence of cavitation on hydraulic conductivity) increasing as the xylem pressures decreases. The relationship of xylem pressure to the decrease of hydraulic conductance, termed a “vulnerability curve,” has been measured for a variety of roots, shoots, and petioles of temperate and tropical trees (Cochard 1992; Alder et al. 1996; Hacke and Sauter 1996) using centrifugation, air-injection, and air-drying techniques (Alder et al. 1997). Cavitated conduits can refill, a process that has been observed visually (Utsumi et al. 1998; McCully 1999) and measured hydraulically (Zwieniecki and Holbrook 1998; Tyree et al. 1999), although the mechanism of such refilling is largely not understood (Holbrook and Zwieniecki 1999). Recovery from embolism is also known to occur in roots of *A. deserti* (North and Nobel 1998), but whether it occurs in the succulent leaves is unknown.

The species used for this study, *A. deserti* and *Agave tequilana*, are monocotyledonous leaf succulents. *Agave deserti* is native to the Sonoran Desert of the southwestern United States and northwestern Mexico (Shreve and Wiggins 1964). It can tolerate up to a year without precipitation via water conservation inherent to Crassulacean acid metabolism (CAM) and storage of water in its massive leaves (Nobel 1976). *Agave tequilana* is a larger agave that is commercially grown in restricted regions of Jalisco, Mexico, for the production of te-

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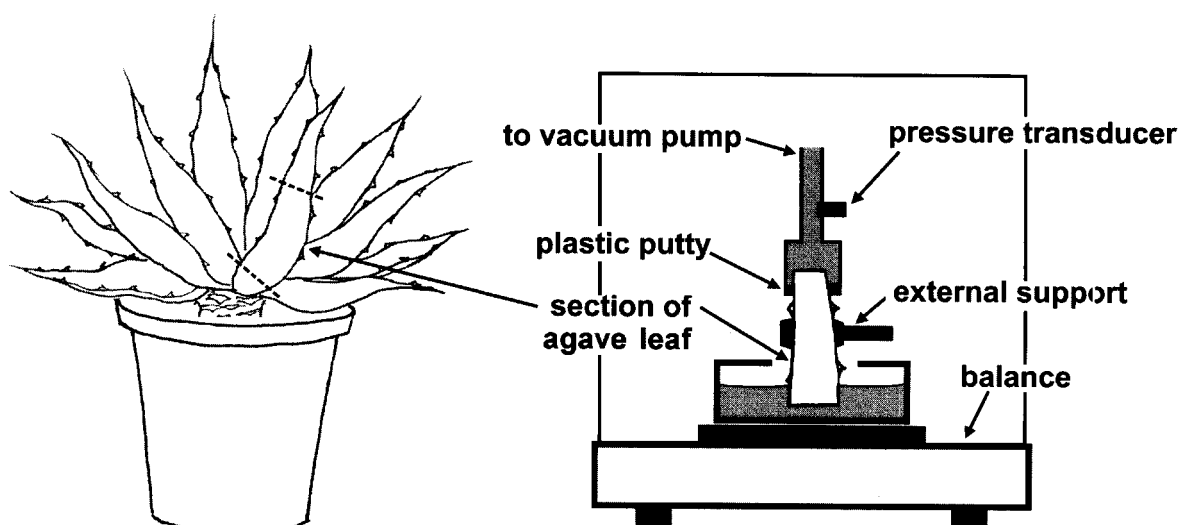


Fig. 1 Schematic of apparatus used to measure hydraulic conductance of agave leaves. Negative pressure was applied to the distal end of the leaf via a vacuum pump and monitored by a pressure transducer. Flow rate through the leaf was measured via the change in mass of the water in the beaker.

quila from its stems and attached leaf bases (Nobel 1994). Leaves of *A. tequilana* are generally longer and thinner than the leaves of *A. deserti*. Both species are almost acaulescent, possessing linear succulent leaves that arise from the reduced stem near the soil surface. Consequently, most of the above-ground axial water movement occurs longitudinally through the succulent leaves.

This study seeks to measure the axial hydraulic conductivity of a succulent agave leaf under well-watered conditions. As leaf water potential decreases, it is hypothesized that extensive cavitation occurs in agave leaves and that the cavitation response of the leaves differs from that of the roots. In addition, it is hypothesized that *A. deserti* and *A. tequilana* differ in their vulnerability to cavitation as a result of their distinct leaf morphologies and that these differences would be reflected in their water relations during drought. These hypotheses were addressed in this study using a technique for measuring hydraulic conductivity (Sperry and Saliendra 1994) that was modified for agave leaves, along with measurements of transpiration, leaf water potential, and leaf water storage during drought.

Material and Methods

Plant Material

Individual plants of *Agave deserti* Engelm. (Agavaceae) were collected at Agave Hill in the University of California Philip L. Boyd Deep Canyon Desert Research Center (33°38'N, 116°24'W, 820 m elevation). Individuals of *Agave tequilana* Weber (Agavaceae) were obtained from a commercial plantation near Tequila, Jalisco, Mexico (20°54'N, 103°50'W, 1160 m elevation). Single plants were transplanted into 20-L pots, transferred to a glasshouse at the University of California, Los Angeles, and watered twice weekly with 0.05% Hoagland's solution. After 2 yr of maintenance under these conditions, *A. deserti* had 10–12 unfolded leaves that were

0.20–0.25 m in length, and *A. tequilana* had 12–14 unfolded leaves that were 0.5–0.6 m in length.

Measurement of Leaf Hydraulic Conductance

A leaf of *A. deserti* or *A. tequilana* was cut from a plant 1 cm from the leaf base and then immediately submerged in water. All water used in the hydraulic conductivity studies was doubly distilled and passed through a 0.2- μ m filter. While submerged, the distal tip was cut off, and the proximal end was recut to remove the tracheids that would have become air filled when the leaf was first cut off the plant. The resulting leaf segment was 12 cm in length and approximately symmetrical about midleaf. The distal end of the leaf was then connected to water-filled vinyl tubing using plastic putty and a hose clamp (fig. 1). The leaf with the attached vinyl tubing was suspended vertically above a Mettler AE100 analytical balance (Mettler-Toledo, Greifensee, Switzerland) with the proximal end of the leaf submerged in a beaker of distilled water that was placed on the balance. After the flow rate had stabilized, negative pressure was applied to the distal end of the leaf via a vacuum pump connected to the tubing, causing water to flow from the beaker into the leaf (fig. 1). The volume flow rate at a specific negative pressure typically stabilized within 10 min and remained constant thereafter. The pressure of the water at the distal end of the leaf was controlled via a needle valve, monitored with a pressure transducer (Validyne PS309, Northridge, Calif.), and recorded at regular intervals by a computer. Mass data from the balance were recorded simultaneously through a cable connection to the computer. The hydraulic conductivity (K_h , $\text{m}^4 \text{s}^{-1} \text{MPa}^{-1}$) of the leaf segment was calculated as follows:

$$K_h = -\frac{\Delta Q_v}{\Delta P} l, \quad (1)$$

where $\Delta Q_v/\Delta P$ ($\text{m}^3 \text{s}^{-1} \text{MPa}^{-1}$) is the difference in the volume flow rate divided by the difference in pressure causing the flow and l (m) is the length of the leaf segment. The value of ΔQ_v was corrected for the effect of leaf buoyancy (the error due to leaf buoyancy is proportional to the ratio of the leaf cross-sectional area to the water surface area in the beaker and was always less than 6%).

After the initial measurement of K_h , the leaf was dehydrated at 35°C in a convection oven for 2–24 h so that K_h could be determined for a range of leaf water potentials. Before placing the leaf in the oven, the leaf epidermis was removed in large strips with forceps, which decreased the amount of time needed to dehydrate the leaf and allowed the leaf to dehydrate evenly along its length, yet resulted in no damage to the underlying mesophyll or vascular bundles. Measurements of leaf K_h were made on a several leaves before and immediately after removal of the epidermis to test for any effect due to the removal of the epidermis, which indicated that the presence of the leaf epidermis had no effect on leaf K_h . After dehydration, a 1.2-cm-diameter leaf core was removed from the leaf 2 cm from its proximal end. The leaf core was quickly blotted with Kimwipe tissue (North and Nobel 1997), placed in a stainless steel cup, and inserted into a Decagon SC10X sample changer (Decagon Devices, Pullman, Wash.). Preliminary experiments showed that a leaf with its cuticle and epidermis removed had little variation in water potential along its length (<0.01 MPa), allowing the sampling of the leaf core from one end of the leaf for the measurement of water potentials and preserving the remaining part of the leaf for the measurement of hydraulic conductance. After allowing 3 h for equilibration, the water potential of the leaf core was measured using a peltier thermocouple psychrometer (Decagon Tru-Psi; North and Nobel 1998). The remaining leaf segment was submerged in water and trimmed at both ends to remove all exposed tracheids that would have become air filled due to the severed ends, after which K_h of the dehydrated leaf was measured as described above. The leaf was then rehydrated by submerging it for 24 h in water that had been adjusted to pH 2.0 with HCl to inhibit microbial growth (Sperry and Saliendra 1994). Following rehydration, the leaf was trimmed at both ends underwater and K_h of the leaf segment was measured again.

For inter- and intraspecific comparisons of hydraulic conductivity, K_h is often expressed per area of stem in cross section, yielding specific conductivity. The cross-sectional area of the stem can be defined to include only the area of the conducting xylem, the entire xylem area, or the whole-stem cross section (Gartner 1995). For this study, specific conductivity was calculated from the area of the leaf in cross section. Since leaves of agave taper along their lengths, the leaf cross-sectional area used for the determination of specific conductivity was calculated from the average of the distal and proximal leaf areas of a single leaf.

Transpiration and Leaf Water Potential

Five individuals of each species were randomly assigned to two environmental growth chambers (model E15, Conviron, Winnipeg, Manitoba, Canada), with 12-h photoperiods and day/night temperatures of 25°/15°C. The photosynthetic photon flux (PPF) in the middle of the plant canopy, as measured

by a Li-Cor quantum sensor (Li-Cor, Lincoln, Nebr.), was 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. After maintaining the plants in the growth chambers for 60 d with twice weekly watering, the plants were droughted by withholding water for 100 d.

After wrapping a pot and the soil surface with multiple layers of polyethylene film, the change in mass of the pot plus the plant was recorded every 10 min for 24 h by computer to indicate transpiration. A similarly wrapped control pot without a plant was also periodically weighed to assure that water vapor was not diffusing through the plastic film. After the 24-h measuring period, the plastic film was removed. The water loss of a plant over 24 h was divided by the total leaf surface area (the sum of the upper and lower surfaces for the crescent-shaped, amphistomatal agave leaves) to obtain the daily transpiration per unit leaf area. For measurement of leaf water potential during drought, leaf cores 1.2 cm in diameter were removed at midleaf. After removing the cuticle plus epidermis, each core was quickly blotted with tissue and inserted into a stainless steel cup for the measurement of water potential as described above. Leaf water potential was measured every 20 d during 100 d of drought.

Leaf thickness was measured with vernier calipers at the beginning and at the end of the drought period. Leaf volume divided by leaf surface area was calculated based on the known geometry for agave leaves. The depth of water available for transpiration was calculated by dividing the leaf volume by the leaf surface area, taking into account an average density for agave leaves of 0.96 g cm^{-3} (Nobel 1988). This ratio of leaf volume to leaf surface area is a useful index for indicating the water storage within a succulent leaf (Nobel 1988). For example, succulent leaves with a large volume and small surface area will have more water available for transpiration compared to leaves with small volumes and of equal surface area. Mathematically, this ratio of leaf volume to leaf area yields the average depth of tissue in which water can be stored per unit surface area where water can be lost. Statistical significance was determined using Student's *t*-test or ANOVA, as appropriate.

Results

Leaf Hydraulic Conductance

For a freshly excised leaf of *Agave deserti*, the volume flow rate increased proportionally as the distal pressure became more negative (fig. 2). The conductance, which equals the negative slope of the regression between flow rate and applied pressure ($\Delta Q_v/\Delta P$; eq. [1]), was $1.39 \times 10^{-11} \text{m}^3 \text{s}^{-1} \text{kPa}^{-1}$ for this freshly excised leaf. After dehydration to a water potential of -3.2 MPa, the conductance decreased to $0.42 \times 10^{-11} \text{m}^3 \text{s}^{-1} \text{kPa}^{-1}$; the flow rate at a pressure of 0 kPa (obtained by interpolation) actually increased compared to the value for the fresh leaf due to the dehydrated status of the leaf. Following rehydration in water for 24 h, the conductance increased to $1.47 \times 10^{-11} \text{m}^3 \text{s}^{-1} \text{kPa}^{-1}$; the flow rates into such a hydrated leaf at a particular applied pressure were less than those of fresh or dehydrated leaves. When multiplied by the leaf length, the above conductances yield the hydraulic conductivity (K_h ; eq. [1]), leading to values of $1.67 \times 10^{-9} \text{m}^4 \text{s}^{-1} \text{MPa}^{-1}$ (fresh),

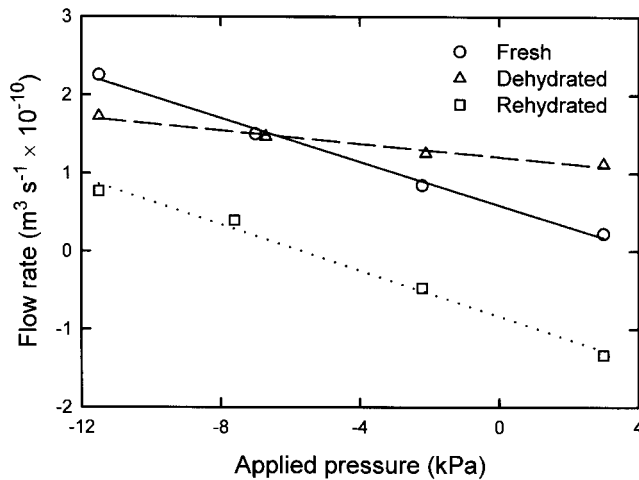


Fig. 2 Pressure applied to the distal end of the leaf versus volume flow rate for a single leaf of *Agave deserti* that was freshly excised (circle), dehydrated at 35°C for 24 h (triangle), and rehydrated in water for 24 h (square). $R^2 > 0.97$ in all cases.

$0.42 \times 10^{-9} \text{ m}^4 \text{ s}^{-1} \text{ MPa}^{-1}$ (dehydrated), and $1.39 \times 10^{-9} \text{ m}^4 \text{ s}^{-1} \text{ MPa}^{-1}$ (rehydrated).

Under wet conditions, freshly excised leaves of *A. deserti* and *Agave tequilana*, which had water potentials of $-0.46 \pm 0.07 \text{ MPa}$ and $-0.64 \pm 0.04 \text{ MPa}$, respectively, had similar K_h per leaf cross-sectional area (fig. 3; $P = 0.76$). Dehydrated leaves of *A. deserti* (water potential of $-3.4 \pm 0.3 \text{ MPa}$) exhibited a lower K_h per cross-sectional area, equaling 26% of the fresh value ($P < 0.001$). Dehydrated leaves of *A. tequilana* (water potential of $-2.6 \pm 0.3 \text{ MPa}$) had a K_h that was 34% of the fresh value ($P = 0.03$; fig. 3). Following rehydration, the decrease in K_h was fully reversible, supporting the premise that the decrease is caused by xylem cavitation; the rehydrated values were 110% of the initial for *A. deserti* (rehydrated to a water potential of $-0.11 \pm 0.05 \text{ MPa}$) and 91% of the initial for *A. tequilana* (rehydrated to a water potential of $-0.09 \pm 0.04 \text{ MPa}$; fig. 3).

As the leaf water potential was lowered by dehydration, K_h decreased for both species (fig. 4, each data point represents a measurement from a separate leaf). Leaves of *A. deserti* experienced a 25% decrease in K_h at -1.36 MPa , a 50% decrease at -2.37 MPa , and a 75% decrease at -4.10 MPa (fig. 4A, values for decreases in hydraulic conductance are based on the regression line). Leaves of *A. tequilana* (fig. 4B) were more vulnerable to cavitation (reduction of K_h) than were those of *A. deserti* and experienced a 25% decrease in K_h at -0.98 MPa , a 50% decrease at -1.72 MPa , and a 75% decrease at -2.99 MPa .

Leaf Water Potential and Transpiration

For both species, leaf water potential and transpiration decreased substantially during 100 d of drought (fig. 5). During this period, the soil water potential decreased from -0.02 MPa at 0 d of drought to -4.0 MPa at 100 d of drought. Leaf water potentials of *A. deserti* and *A. tequilana* were similar at 0 and 20 d of drought (fig. 5A; $P > 0.06$) but were significantly

different beginning at 40 d ($P < 0.001$). At 100 d of drought, leaf water potentials of *A. deserti* had decreased twofold to -1.96 MPa , and those of *A. tequilana* had decreased sixfold to -3.42 MPa (fig. 5A). At the beginning of drought, daily transpiration per unit leaf surface area of *A. tequilana* was almost twice that of *A. deserti* (fig. 5B). After 10 d of drought, transpiration of *A. tequilana* declined to 25% of its predrought value and at 40 d was 3% of the predrought value. Transpiration of *A. deserti* decreased to 73% of its predrought value at 10 d and at 40 d was 13% of the predrought value. At 20 d, the two species had similar rates of transpiration, a trend that continued during the rest of the 100 d of drought (fig. 5B).

The amount of transpiration (fig. 5B) was also expressed as a depth of water lost averaged over the total leaf surface area. For *A. deserti*, the total depth of water transpired was 1.9 mm from 0 to 40 d and 0.6 mm from 40 to 100 d. During these same periods of drought, *A. tequilana* transpired a depth of water of 1.9 mm (0–40 d) and 0.5 mm (40–100 d). Based on measurements of leaf thickness and width, the total depth of water available for transpiration (the V/A ratio) at the beginning of drought was 43% higher for *A. deserti* than for *A. tequilana* (table 1). During 100 d of drought, the average leaf thickness for *A. deserti* decreased 32% from 10.4 to 7.1 mm and for *A. tequilana* decreased 43% from 5.8 to 3.3 mm.

Discussion

For freshly excised succulent leaves of *Agave deserti*, the leaf-specific conductivity (K_h divided by the distal leaf surface area) averaged $0.19 \times 10^{-6} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$, which is lower than corresponding values for various woody stems. For instance, 2-yr-old branches of poison oak, *Toxicodendron diversilobium*, have a 16-fold greater leaf-specific conductivity ($3.0 \times 10^{-6} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$ [Gartner 1995]), the scrambling vine, *Lonicera sempervirens*, has a 1.3-fold greater leaf-specific

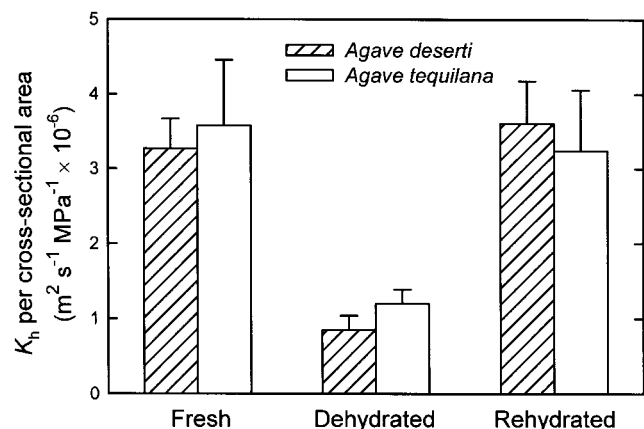


Fig. 3 Hydraulic conductance (K_h) per cross-sectional area for leaves of *Agave deserti* (hatched bars) and *Agave tequilana* (open bars) accompanying varying water status. Individual leaves were freshly excised (fresh), dehydrated at 35°C for 24 h for *A. deserti* and 12 h for *A. tequilana* (dehydrated), and subsequently rehydrated in water for 24 h for both species (rehydrated). Data are presented as means \pm SE ($n = 5$ leaves).

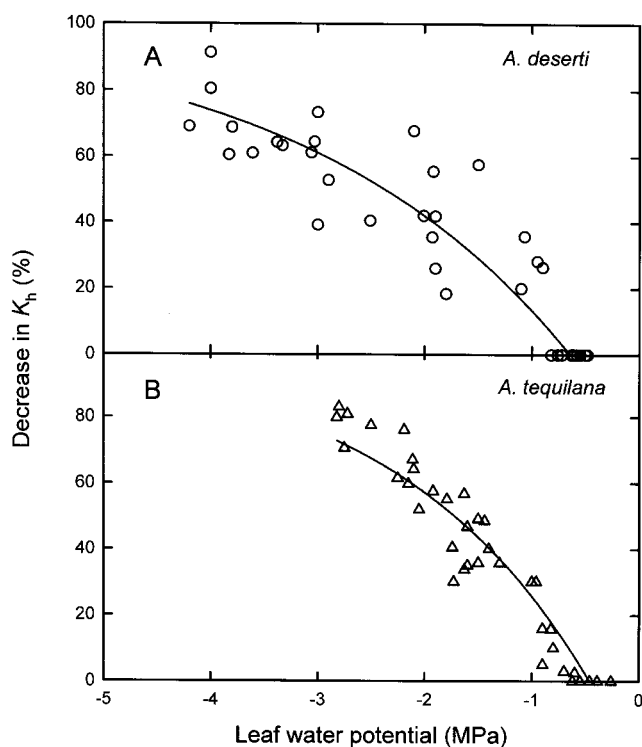


Fig. 4 Percentage decrease in K_h versus water potential for leaves of *Agave deserti* (A) and *Agave tequilana* (B). Each data point represents a measurement from a single leaf. Data are fit with an exponential equation (decrease [%] = $100[1 - e^{a(\psi - b)}]$), where a and b are curve-fitting coefficients (*A. deserti*: $a = 0.40 \text{ MPa}^{-1}$, $b = -0.64 \text{ MPa}$, $R^2 = 0.83$; *A. tequilana*: $a = 0.55 \text{ MPa}^{-1}$, $b = -0.46 \text{ MPa}$, $R^2 = 0.90$).

conductivity ($0.24 \times 10^{-6} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$ [Chiu and Ewers 1992]), and young stems of the coastal sage scrub, *Salvia melifera*, have a threefold greater leaf-specific conductivity ($0.57 \times 10^{-6} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$ [Kolb and Davis 1994]) than the average for leaves of *A. deserti*. These low values of K_h for agave are due to the small diameter of their leaf tracheids (M. J. Linton and P. S. Nobel, unpublished observations) and the low density of the vascular bundles within the leaves (each bundle is separated by approximately eight water-storage parenchyma cells [Smith and Nobel 1986]). Agaves also have much lower maximum transpiration rates (*A. deserti*, ca. $6 \text{ mmol m}^{-2} \text{ d}^{-1}$) than those of woody trees ($33\text{--}94 \text{ mmol m}^{-2} \text{ d}^{-1}$ for a variety of trees at midsummer [Kramer and Boyer 1995]), owing to the nocturnal stomatal opening characteristic of CAM and resulting in a decreased requirement for xylem tissues. Also reducing the need for highly conductive xylem is the large volume of water storage in the succulent leaves of agaves that can provide water during transpiration (Nobel 1988).

The measured flow rate through an agave leaf at a specific applied pressure varied considerably in response to the water potential of the leaf. For dehydrated leaves, the flow rate at small applied pressures (close to 0 kPa) was higher than the corresponding flow rate for fresh leaves, presumably because the dehydrated status of the leaf caused additional water to

flow from the water reservoir into the leaf. After leaves were submerged in water for several hours, negative flow rates (water moving from the leaf back to the water reservoir) were often observed, resulting from water infiltrating the air spaces of the leaf during rehydration and the subsequent movement of this water from the vertically oriented leaf to the water reservoir during the measurement of flow. A similar phenomenon occurs for roots and stems of many species that are centrifuged to induce cavitation, causing desiccation of root and stem parenchyma cells and the artificial inflation of flow rates compared to those of nondesiccated plant segments (Linton and Nobel 1999). Therefore, the measurement of flow rate at two or more different applied pressures is crucial for obtaining an accurate value of K_h for plant segments with substantial parenchyma, such as succulent leaves or young roots (Kolb et al. 1996; Davis et al. 1999; Kolb and Sperry 1999). For woody stems, however, the flow rate under no applied pressure is often zero, and hydraulic conductance can often be calculated from a single measurement of flow at a particular applied pressure (Sperry and Saliendra 1994).

Based on leaf water potentials during drought and vulnerability to cavitation, leaves of *A. deserti* are predicted to have a 2% decrease of K_h at 20 d of drought and a 41% decrease at 100 d, whereas *A. tequilana* would experience decreases of 10% and 80%, respectively. The 95% greater cavitation of *A. tequilana* compared to *A. deserti* at 100 d of drought is apparently attributable to two causes: greater vulnerability to

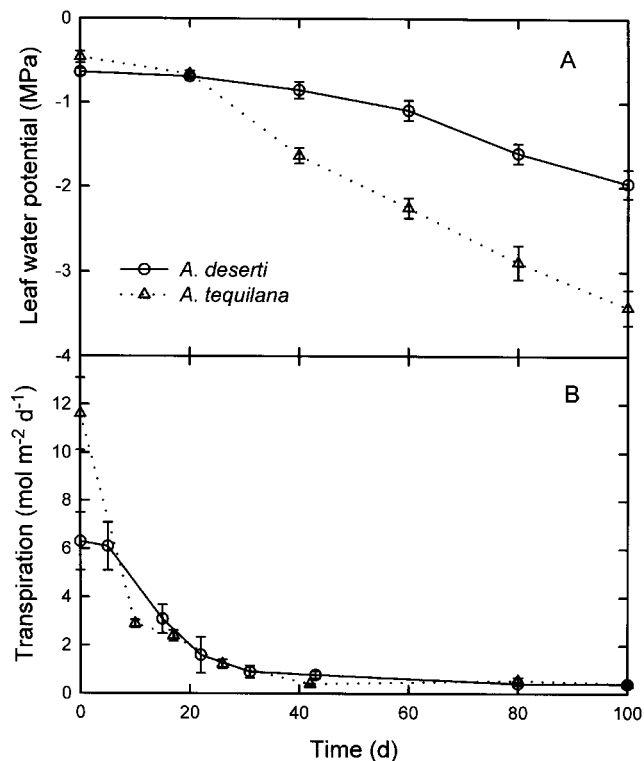


Fig. 5 Leaf water potential (A) and daily transpiration (B) during drought for *Agave deserti* (circle) and *Agave tequilana* (triangle). Data points are averages \pm SE (leaf water potential: $n = 5$ plants; transpiration: $n = 3$ plants).

cavitation and lower leaf water potentials during drought. A comparison of the vulnerability curves indicates that *A. tequilana* was only slightly more vulnerable to cavitation than *A. deserti* (the former averaging 14 more percentage points of decrease in K_h), whereas a comparison of leaf water potential indicates that, from 40 to 100 d of drought, *A. tequilana* leaves averaged 1.17 MPa lower than those of *A. deserti*. Therefore, the primary reason for differences in the decrease of K_h during drought are due to the lower leaf water potentials for *A. tequilana*. Both species had similar leaf water potentials at the beginning of drought, but the thinner leaves and higher initial transpiration rate of *A. tequilana* resulted in more rapid dehydration and subsequent larger decreases in leaf water potential.

The high vulnerability to cavitation of *A. deserti* and *A. tequilana* is consistent with a drought-avoider strategy for coping with extended drought (Levitt 1980). For these species, water uptake occurs only from relatively wet soil, and drought is survived by means of large water stores in the succulent shoot (Nobel 1988; Linton and Nobel 1999). Therefore, xylem that is highly resistant to cavitation would not be particularly advantageous for these desert succulents. However, *Larrea tridentata* is a drought-tolerator shrub of the Sonoran Desert that occasionally co-occurs with *A. deserti*, experiences much more negative xylem pressures during drought, and transpires throughout the dry season (Pockman 1996). By having xylem that is highly resistant to cavitation, *L. tridentata* is able to extract water from a drying soil and maintains efficient water transport during drought.

The mechanism for the reversal of cavitation when the leaves were submerged in water is probably via active secretion of ions or through positive water pressure from adjacent parenchyma (Holbrook and Zwieniecki 1999). Plants of *A. deserti* that are droughted for extended periods resume stomatal opening and carbon fixation within 2 d, processes that reach the predrought value within 7 d (Nobel 1988; Graham and Nobel 1999). For leaf xylem to refill under such conditions, water would need to be transported from the roots through the uncavitated tracheids and rehydrate the leaf parenchyma, which would then presumably participate in the refilling process. This refilling probably requires somewhat longer time periods than the 24 h required for excised leaves but should occur within the first few days following rewetting of the soil in order for maximal transpiration and water movement to occur.

Based on the vulnerability curves for *A. deserti* roots (Linton and Nobel 1999) and this study on leaves, the overall plant

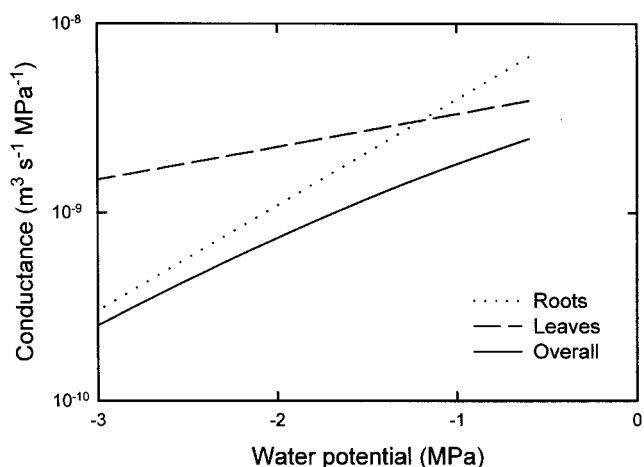


Fig. 6 Model for axial hydraulic conductance of root xylem (dotted line), leaf xylem (dashed line), and the total plant xylem pathway (solid line) for *Agave deserti*. Axial root conductance is based on the root vulnerability curve of *A. deserti* (adapted from Linton and Nobel 1999), and axial leaf conductance is based on the leaf vulnerability curve (fig. 4A). Results are for the axial conductance pathway only and are modeled for a plant having 12 leaves with an average length of 0.25 m and 10 main roots with an average length of 0.30 m (Nobel and Jordan 1983; Nobel 1988). The X-axis represents the root, leaf, or overall water potential, as appropriate. The model does not include nonxylary changes in conductance and is based on a simple two-conductances-in-series analysis, where at any given water potential, the reciprocal of the overall conductance equals the sum of the reciprocals of the constituent conductances (Nobel 1999, p. 308).

hydraulic conductance decreases with decreasing plant water potential (fig. 6). Under well-watered conditions (a plant water potential of ca. -0.6 MPa), the conductance of the roots for a medium-sized plant of *A. deserti* is $6.65 \times 10^{-9} \text{ m}^3 \text{ s}^{-1} \text{ MPa}^{-1}$, which is 70% greater than the conductance of $3.90 \times 10^{-9} \text{ m}^3 \text{ s}^{-1} \text{ MPa}^{-1}$ for the leaves. This higher conductance of the roots compared to the leaves is consistent with studies of root water uptake for *A. deserti* that indicate a redundancy of roots for daily water uptake under well-watered conditions (Graham and Nobel 1999). Water uptake for *A. deserti* only occurs for the first 7 d of drought, when the plant water potential is greater than ca. -0.7 MPa (Nobel and Lee 1991). Within this range of water potentials (> -0.7 MPa), the leaves have a lower conductance compared to the roots (fig.

Table 1

Leaf Characteristics for *Agave deserti* and *Agave tequilana* under Wet and Droughted Conditions

Species	V/A (0-d drought; mm)	Leaf thickness (mm)					
		0-d drought			100-d drought		
		Leaf base	Midleaf	Leaf tip	Leaf base	Midleaf	Leaf tip
<i>A. deserti</i>	3.3 ± 0.2	17.6 ± 1.0	9.9 ± 0.5	3.7 ± 0.3	11.6 ± 0.7	6.6 ± 0.5	3.1 ± 0.1
<i>A. tequilana</i>	2.3 ± 0.1	10.9 ± 1.0	4.3 ± 0.1	2.2 ± 0.2	6.1 ± 0.1	2.5 ± 0.2	1.3 ± 0.1

Note. Leaf thicknesses at the base and tip were measured 2 cm from the corresponding end. Volume/surface area (V/A, the depth of water available for transpiration) was calculated using known geometry for agave leaves (Nobel 1988) and measurements of leaf thickness and width. Data are means \pm SE ($n = 4$ plants).

6, dashed line compared to dotted line), indicating that the leaves are the limiting organ for axial water movement during the period of water uptake from the soil. As the plant water potential decreases during drought, the greater vulnerability to cavitation of the roots compared to the leaves causes the roots to be the limiting organ for axial water movement at plant water potentials lower than -1.21 MPa (fig. 6), which occurs at ca. 60 d of drought (North and Nobel 1998). The lower axial hydraulic conductance of the roots at water potentials below -1.21 MPa would limit the loss of water from the leaves to the soil during extended drought. Additional resistance to water flow from the plant to the soil during drought is provided by the low hydraulic conductance of the soil and the root-soil air gaps (Nobel and Cui 1992).

The relative vulnerability to cavitation of these two species is consistent with their general habitat preference. *Agave deserti* in the northwestern Sonoran Desert receives ca. 240 mm of annual rainfall (Nobel 1988), whereas *A. tequilana* receives ca. 1000 mm of annual rainfall in Jalisco, Mexico (Gentry 1982). A correlation between vulnerability to cavitation and general drought tolerance has also been found in other species (Tyree et al. 1994), including three subspecies of *Artemisia tridentata* (Kolb and Sperry 1999). In a comparison of two sympatric conifers, *Pinus edulis* and *Juniperus osteosperma*

(Linton et al. 1998), a general correspondence between vulnerability to cavitation and drought tolerance (and subsequent habitat preference) was also found. Although *P. edulis* was more vulnerable to cavitation as water potential decreased than *J. osteosperma*, the two species had similar decreases of hydraulic conductance due to cavitation because *P. edulis* had a greater restriction of transpirational water loss during drought. Therefore, for these two conifers, the most important physiological consequence of differential vulnerability to cavitation was the possibility of cavitation rather than the actual occurrence of cavitation. In this study, *A. tequilana* showed greater reduction in transpiration during drought than *A. deserti*, but the former still had much larger decreases in hydraulic conductance. Accordingly, the occurrence of extensive cavitation in agaves appears to be less detrimental to plant water relations than for other species, as extended drought can be tolerated via leaf water storage.

Acknowledgments

We thank Rebecca M. Linton for her illustration of the agave in figure 1. This research was supported by a Stephen A. Vavra Fellowship to M. J. Linton and a grant from the National Science Foundation (IBN-94-19844) to P. S. Nobel.

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