

# Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata*

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## ABSTRACT

As soil and plant water status decline, decreases in hydraulic conductance can limit a plant's ability to maintain gas exchange. We investigated hydraulic limitations for *Artemisia tridentata* during summer drought. Water use was quantified by measurements of soil and plant water potential ( $\Psi$ ), transpiration and leaf area. Hydraulic transport capacity was quantified by vulnerability to water stress-induced cavitation for root and stem xylem, and moisture release characteristics for soil. These data were used to predict the maximum possible steady-state transpiration rate ( $E_{\text{crit}}$ ) and minimum leaf xylem pressure ( $\Psi_{\text{crit}}$ ). Transpiration and leaf area declined by ~80 and 50%, respectively, as soil  $\Psi$  decreased to  $-2.6$  MPa during drought. Leaf-specific hydraulic conductance also decreased by 70%, with most of the decline predicted in the rhizosphere and root system. Root conductance was projected to be the most limiting, decreasing to zero to cause hydraulic failure if  $E_{\text{crit}}$  was exceeded. The basis for this prediction was that roots were more vulnerable to xylem cavitation than stems (99% cavitation at  $-4.0$  versus  $-7.8$  MPa, respectively). The decline in water use during drought was necessary to maintain  $E$  and  $\Psi$  within the limits defined by  $E_{\text{crit}}$  and  $\Psi_{\text{crit}}$ .

Key-words: *Artemisia tridentata*, drought stress, sagebrush, water transport, xylem cavitation.

## INTRODUCTION

*Artemisia tridentata* Nutt. (sagebrush) dominates much of the landscape in the Great Basin region of the USA. This region is a particularly harsh environment for plant life because plants are exposed to large seasonal fluctuations in temperature and water availability. The Great Basin is a cold desert (Caldwell 1985) with temperatures frequently dropping below freezing during the winter months. Precipitation primarily occurs as snow during the winter and amounts range from 160 to 420 mm per year, depending on elevation (West 1983). The seasonality of precipitation results in a prolonged summer drought period that typically occurs from July to September. *A. tridentata* is capable of withstanding the harsh climate of the Great Basin, and remains evergreen during the driest of summers and the coldest of winters.

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Although characterized as an evergreen shrub, *A. tridentata* functionally has a semi-drought deciduous habit. Large ephemeral leaves are produced in spring on the elongating shoots. These leaves remain on the plant throughout the spring, and then abscise with the onset of water stress (Miller & Shultz 1987). A second cohort of leaves is produced in the axils of the ephemeral leaves in the late spring. These leaves are smaller, and a fraction of them persist through winter (~20%; Kolb, unpublished results). The evergreen nature of *A. tridentata* suggests that it has the capacity for photosynthesis during the winter or early spring when conditions are favourable; however, photosynthetic activity is probably not substantial during the winter months (Caldwell 1979).

The peak of photosynthetic activity for *A. tridentata* occurs in the spring when conditions are most favourable (DePuit & Caldwell 1973), yet gas exchange continues during the summer despite the development of low water potentials. In a greenhouse study, DeLucia & Heckathorn (1989) found that photosynthesis occurred at leaf water potentials below  $-5$  MPa. Although greenhouse studies do not always reflect behaviour under natural conditions, several studies have reported similarly low xylem pressures ( $< -5$  MPa) for native *A. tridentata* during the summer (Branson & Shown 1975; Branson, Miller & McQueen 1976; Campbell & Harris 1977; Everett *et al.* 1977; DeLucia, Schlesinger & Billings 1988; Evans & Black 1993). This suggests that *A. tridentata* is able to tolerate the seasonal development of low xylem pressures and may remain physiologically active during the summer drought period. One explanation for the frequently measured low xylem pressures is that the shrubs are not particularly deep rooted, and their ability to access water deep in the soil profile is restricted. Maximum rooting depth has been reported to be ~2 m (Richards & Caldwell 1987; Reynolds & Fraley 1989), with 60% of the rooting mass located in the top 0.6 m of soil (Sturges 1977; Sturges 1979; Abbott, Fraley & Reynolds 1991).

Despite the low water potentials experienced during the summer, inflorescences of *A. tridentata* develop and mature during this period. Importantly, the addition of water during the height of the summer drought was found to significantly increase floral biomass (Evans, Black & Link 1991). This suggests that although *A. tridentata* can tolerate low xylem pressures, the level of water stress it experiences may limit productivity and impact plant fitness.

The success of *A. tridentata* within the Great Basin may be tied to its ability to partition soil water resources and adjust water usage. *A. tridentata* was the first species in

which hydraulic lift was discovered (Richards & Caldwell 1987). Hydraulic lift describes the nightly relocation of water from deep within the soil profile through the roots to the dry, shallow layers where it is then available for plant uptake the following morning (Caldwell & Richards 1989). *A. tridentata* also adjusts the amount of water used during the drought period by stomatal closure (Evans & Black 1993) and decreasing transpiring leaf area (Black & Mack 1986).

The purpose of this study was to evaluate the hydraulic limitations to water use in *A. tridentata*. As drought develops, hydraulic conductance of the soil and xylem declines. In soil, the decline in conductance depends on soil texture (Hillel 1980). In xylem, the loss of conductance depends on resistance of the xylem to cavitation (Tyree & Sperry 1989). The manner in which these conductances decline sets limits on transpiration and xylem pressure (Sperry *et al.* 1998). This research tests the hypothesis that changes in transpiration and leaf area during drought are coordinated with hydraulic limits on water transport in *A. tridentata*.

This hypothesis was tested on one population of *A. tridentata* followed through four summer drought periods. Water use was quantified by measurements of leaf area and transpiration rate, and plant and soil water status were estimated from xylem pressure and soil water potential. To assess the capability of *A. tridentata* to maintain water transport during drought, the vulnerability to water stress-induced xylem cavitation was quantified for both root and shoot xylem. These parameters were then used to estimate hydraulic limitations using a model of the soil–plant continuum that incorporated variable soil and plant hydraulic conductances (Sperry *et al.* 1998; Appendix).

## MATERIALS AND METHODS

### Study site

The study population of *A. tridentata* was at the Tintic Range Experimental Station, Tintic, Utah (39°55' W, 112°03' N, elevation 1775 m). Measurements were made from May to September for the years 1993–1996. The site is on loam soil with 36, 44 and 20% sand, silt and clay fractions, respectively ( $n = 3$  soil samples at 0.3 m depth analysed by Utah State Analytical Laboratory, Logan, Utah, USA). No grazing occurred at the site during the study period or for the previous five years.

Based on ploidy level (tetraploid,  $n = 18$ ) and ultraviolet fluorescence tests (McArthur, Welch & Sanderson 1988), the sagebrush at the site was characterized as *A. tridentata* ssp. *wyomingensis* introgressed with tetraploid ssp. *vaseyana* (E.D. McArthur, personal communication). Although ssp. *vaseyana* is typically diploid, autopolyploidy is common in the subgenus *Tridentatae* of *Artemisia* (McArthur, Pope & Freeman 1981; McArthur *et al.* 1998).

### Soil and plant water status, leaf transpiration

Measurements of pre-dawn shoot xylem pressure (pre-dawn  $\Psi_x$ ) were used as a proxy for bulk soil water status.

Pre-dawn xylem pressure was measured with a pressure chamber (P.M.S. Instruments, Corvallis, Oregon, USA) between 0500 and 0600 h. Plant water status was determined from measurements of midday shoot xylem pressure (midday  $\Psi_x$ ) which was measured between 1300 and 1400 h. In each case, leafy shoots were collected from five plants with three replicates per plant, sealed in a darkened plastic bag that contained a moist paper towel, and measured immediately. From measurements of pre-dawn and midday  $\Psi_x$ , we could calculate the *in situ* pressure difference across the soil–plant continuum (pre-dawn  $\Psi_x$  – midday  $\Psi_x$ ) and estimate the ‘mid-path xylem pressure’ (mid-path  $\Psi_x$ ) as the xylem pressure midway between pre-dawn  $\Psi_x$  and midday  $\Psi_x$ . The mid-path  $\Psi_x$  was used to relate  $\Psi_x$  to changes in xylem conductivity from cavitation. Mean  $\Psi_x$  per sampling date was used in all analyses.

Soil water potential was also measured independently from soil psychrometers installed at the study site in April 1994 to quantify the extent of soil drought for the study site. Two trenches were dug and four soil psychrometers (Wescor PST-55-30-SF, Wescor Inc., Logan, Utah, USA) installed horizontally in the wall of each trench following the methods of Brown & Chambers (1987). The psychrometers were installed at depths of 0.3, 0.7, 1.1 and 1.5 m. Measurements of soil water potential ( $\Psi_s$ ) were made at pre-dawn, when thermal gradients in the soil are minimized, by cooling the junction for 30 s and measuring the output with a microvoltmeter (Wescor PR-55, Logan, Utah, USA).

Leaf transpiration rate ( $E$ ) was measured for five plants (three replicates per plant) between 1100 and 1300 h using a null-balance porometer equipped with a cylindrical chamber to accommodate the leafy shoots of *A. tridentata* (LI-1600, LICOR Inc., Lincoln, Nebraska, USA). Porometry alters the boundary layer and evaporative gradient (McDermitt 1990) leading to errors in transpiration measurements. However, for *A. tridentata*, porometer measurements are less problematic because under natural conditions the small leaf size (0.26–1.23 cm<sup>2</sup> individual leaf area; Shultz 1986) results in a high boundary layer conductance compared to stomatal conductance. Potential errors arising from altered or inaccurately measured air temperatures were reduced because of the low ambient humidities (< 25% relative humidity) recorded during most measurements. Mean  $E$  per sampling date was used in all analyses.

### Measurements of hydraulic conductance and leaf area

Leaf-specific conductivity ( $k_l$ ) was calculated for the soil-to-leaf pathway to characterize changes in transport capacity as the summer drought progressed. Pathway  $k_l$  was calculated from measurements of midday  $E$  and  $\Psi_x$ :

$$k_l = E / (\text{pre-dawn } \Psi_x - \text{midday } \Psi_x) \quad (1)$$

We used pre-dawn  $\Psi_x$  as a proxy for  $\Psi_s$  in our calculation of  $k_l$  because psychrometer measurements may not accurately reflect  $\Psi_s$  for all areas within the study site due to heterogeneity in water availability.

Branch hydraulic conductance ( $k$ ) and native percent embolism were measured periodically during the growing season using the method of Kolb, Sperry & Lamont (1996). Branches were excised from the plant, and brought to the laboratory where they were re-cut under water. Re-cutting removed air emboli that resulted from harvesting techniques or during transport. The base of the branch was connected to a reservoir of filtered, degassed HCl that was located on a balance. The remaining portion of the branch was placed into a vacuum chamber. Five partial vacuum pressures were applied, and the rate of solution uptake calculated as the slope of the uptake rate versus pressure relationship to account for non-zero flow intercepts (Kolb *et al.* 1996).

The ratio of leaf area to shoot basal area was quantified for excised branches collected from adult plants between 1994 and 1996. Leaf area was estimated by collecting all leaves from an excised branch and oven-drying them for at least 24 h. The dry weight was then measured and used to calculate leaf area using a linear regression of the relationship between leaf area and dry weight. To calculate shoot basal area, stem diameter was measured and the transverse area calculated assuming that the stem was circular in cross-section. Changes in the ratio of leaf area to basal area reflect changes in leaf area since xylem production in *A. tridentata* was mostly complete before the initiation of seasonal measurements, and stems selected were consistent in size.

### Vulnerability to cavitation

We measured the vulnerability to cavitation for both shoot and root xylem by constructing 'vulnerability curves' (Tyree & Sperry 1989) with the centrifugal force method (Pockman, Sperry & O'Leary 1995; Alder *et al.* 1997). A vulnerability curve describes the relationship of percentage loss in hydraulic conductivity (% embolism) as a function of xylem pressure ( $\Psi_x$ ).

To measure stems, we collected branches from the field, brought them to the laboratory, and then cut the stems under water to 0.257 m. The segments (6–8 mm diameter) were then placed in a tubing manifold similar to the one described in Sperry, Donnelly & Tyree (1988), with the exception that the entire apparatus was submerged to eliminate evaporation from the segment. The segments were flushed with pressurized (100 kPa), degassed HCl solution (pH  $\approx$  2) to remove any air emboli induced naturally or during harvesting. The acid was used to minimize microbial growth in the tubing system. Previous studies showed no effect of acidification on hydraulic conductivity or cavitation resistance (Sperry & Saliendra 1994; Alder *et al.* 1997). Since this work was completed we have switched to filtered water as our measuring fluid, and disinfect the tubing system every week or so with bleach to control microbial growth. Flow rate through the stem segment was measured gravimetrically at a hydraulic head of  $\sim$  7 kPa. Hydraulic conductivity ( $k_h$ ) was calculated as the flow rate of solution per pressure gradient.

To improve resolution of the low  $k_h$  typical of *A. tridentata*, we measured the flow rate under zero pressure before and after applying the hydraulic head. This 'background' flow rate was averaged and subtracted from the flow under pressure to obtain the net flow rate caused by pressure. Background flows were typically negative, meaning water was absorbed by the segment.

Following measurement of the initial  $k_h$ , segments were placed in a centrifuge rotor designed to keep the ends immersed in water. Segments were spun in a centrifuge (Sorvall RC-5C, DuPont Instruments, Wilmington, Delaware, USA) for 3 min and then inserted into the tubing manifold. The  $k_h$  for each segment was remeasured, and '% embolism' calculated as the percentage  $k_h$  had dropped below the initial value. This process was repeated, spinning the segments to progressively lower  $\Psi_x$ , until  $k_h$  was essentially zero.

Measuring roots required modifications to the above protocol. The longer and wider vessels in roots (see Results) of the size we measured (3–5 mm diameter) forced us to use a hydraulic pressure head no greater than 3 kPa because otherwise air would be pushed out of embolized vessels running through the segment. When we flushed root segments, we found there was a substantial loss of hydraulic conductance after they were spun to the modest  $\Psi_x$  of  $-0.5$  MPa, a pressure to which they were routinely exposed in the field. Presumably this represented conduits refilled during the flushing procedure but embolized under natural conditions. We suspected that these were older conduits long since gone out of function and no longer able to sustain any significant negative pressure. This was not a problem in stems because the older conduits are physically unable to refill because they become plugged and are walled off from the current year's xylem by a cork layer. To ensure the vulnerability data on roots reflected currently functioning xylem, we did not flush them prior to measuring, but instead collected them underwater in the field to avoid inducing cavitation during harvesting. Furthermore, we scaled the vulnerability curves for roots relative to the hydraulic conductance at  $\Psi_x = -0.5$  MPa.

### Xylem vessel anatomy

Vessel diameter distributions were calculated for stem and root segments. Diameters were measured for the current year's xylem from stem segments that were used to construct vulnerability curves. We also measured vessel diameters for root segments, but the segments were different from those used for the root vulnerability curve. Transverse sections were made from each segment with a razor blade, and the vessel lumen area and maximum diameter measured with a digitizing tablet (Micro-plan II, DonSanto Corp., Natick, Massachusetts, USA). For each segment, diameter distributions and mean diameter were determined from at least 200 measured vessels using 5  $\mu$ m size classes.

Vessel length distributions were measured for both root and stems using the latex-suspension technique of

Zimmermann & Jeje (1981). Plant material was collected from the field, and brought to the laboratory where the distal end of the main axis was cut under water. The root or branch was then flushed with filtered water ( $0.2 \mu\text{m}$ ) for 30 min to refill any embolized conduits. After flushing, the main axis was supplied with a dilute paint pigment solution (1:200 w/w) that was pressurized for several days at 40 kPa. This procedure is based on the assumption that the pigment particles will flow unrestricted through xylem conduits, but the particles are too large to pass between conduits. In primary roots, pigment particles may not always follow the same pathway as water (Steudle & Petterson 1998); however, in mature woody roots and stems, axial flow of pigment particles is likely to be unimpeded until a vessel end wall is encountered. This results in an accumulation of pigment within a conduit. Following injection, the root or stem was cut into 10 mm sections, the cut ends smoothed with a razor blade, and the number of pigment-filled conduits counted. Vessel length distributions were then determined according to Zimmermann & Jeje (1981).

### Analysis of hydraulic limitations

We used a transport model (Sperry *et al.* 1998; Appendix) to solve Eqn 1 for the steady-state relationship between  $E$  and leaf  $\Psi_x$  at a given pre-dawn  $\Psi_x$ . The model incorporated variable hydraulic conductance in the continuum as a result of soil drying in the rhizosphere and cavitation in the xylem. The maximum possible  $E$  calculated by the model was  $E_{\text{crit}}$ , and the associated minimum leaf  $\Psi_x$  was  $\Psi_{\text{crit}}$ . Any increase in  $E$  beyond  $E_{\text{crit}}$  in theory causes hydraulic failure by driving hydraulic conductance to zero either in the rhizosphere or xylem.

The model was applied to field data using the following seven inputs: (1) root and stem vulnerability curves, (2) soil texture parameters (Appendix), (3) pre-dawn and midday  $\Psi_x$ , (4) midday  $E$ , (5) relative leaf area, (6) maximum  $k_1$ , and (7) root area per leaf area ( $A_r:A_l$ ). The relative leaf area was the fractional change in leaf area during drought estimated from leaf area per basal area measurements (Fig. 2b). The maximum  $k_1$  was the pre-drought  $k_1$  adjusted for the measured change in leaf area. It set the maximum conductance for predicting declines resulting from soil drying and cavitation. The  $A_r:A_l$  was needed to scale plant conductances (determined on a leaf area basis) with rhizosphere conductances (determined by root area, Appendix). The  $A_r:A_l$  was not measured, but solved for by the model as explained below.

For each pair of pre-dawn and midday  $\Psi_x$  measurements, the model provided the following four outputs: (1)  $E_{\text{crit}}$  and  $\Psi_{\text{crit}}$ , (2) the predicted change in  $k_1$  from pre-drought values (also broken down into rhizosphere, root xylem and shoot xylem components), (3) the predicted midday  $E$  corresponding to midday  $\Psi_x$ , and (4) the predicted safety margin from hydraulic failure in terms of  $E$  and  $\Psi$  ( $E_{\text{crit}} - E$ , midday  $\Psi - \Psi_{\text{crit}}$ ).

To solve for the pre-drought  $A_r:A_l$ , we adjusted it to obtain a 1:1 fit between measured and predicted  $E$  and  $k_1$

for the four summers of data. The pre-drought  $A_r:A_l$  was adjusted seasonally based on measured changes in leaf area during the drought (Fig. 2b).

### Pressure–volume analysis

The turgor loss point ( $\Psi_{\text{t1p}}$ ) and the osmotic potential at saturation ( $\Psi_{\text{sat}}$ ) were estimated using the pressure–volume relationship. Terminal shoots were collected following measurement of pre-dawn  $\Psi_x$  in June and August 1996. Two shoots were collected per plant from seven different plants. Evans, Black & Link (1990) showed that rehydration changes the pressure–volume relationship for *A. tridentata* shoots. Consequently, we used different shoots for rehydration than those used for the pressure–volume analysis. The rehydrated samples were supplied with distilled water for 4 h. It was found that after 4 h of rehydration there was minimal change in shoot weight, suggesting that full rehydration had been achieved. Following rehydration, the shoots were weighed, and then oven-dried at  $70^\circ\text{C}$  for over 24 h before measuring the dry weight. The mean fresh weight to dry weight ratios for the rehydrated samples were used to calculate the saturated weight of the samples used in the pressure–volume analysis using the procedure of Evans *et al.* (1990). Shoots used for pressure–volume analysis were briefly supplied with water (less than 15 min), and their initial  $\Psi$  and weight measured. The shoots were allowed to dehydrate by transpiring between measurement intervals (Ritchie & Hinckley 1975). Estimates of the turgor loss point and the osmotic potential at saturation were obtained using a computer program provided by P.J. Schulte (Schulte & Hinckley 1985).

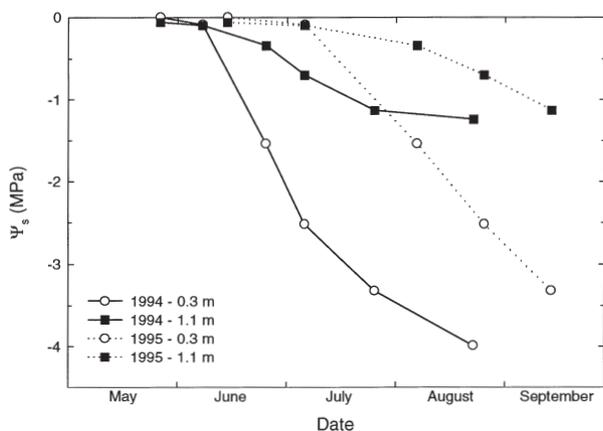
### Statistical analysis

Statistical analysis was performed using JMP software (version 3.1, SAS Institute Inc.) and SSPS (Jandel Scientific Inc.). Student's  $t$  test was used to test differences in slope and intercept of regression lines of measured versus predicted  $E$  and  $k_1$ . Correlation was tested with a Pearson's correlation test. The  $t$  test was used to compare mean xylem vessel diameter for root versus stem material, and to compare the tissue water relations parameters for the June and August 1996 sampling dates.

## RESULTS

### Soil and plant water status during drought

Soil water potential measured with psychrometers declined at all measured depths during the growing season, with some years drier than others (Fig. 1). Figure 1 shows only the  $\Psi_s$  measured at depths of 0.3 and 1.1 m since  $\Psi_s$  measured at these depths was significantly correlated with pre-dawn  $\Psi_x$  ( $r = 0.66$ ,  $P = 0.0095$ , and  $r = 0.59$ ,  $P = 0.0273$ , respectively). As a general trend, pre-dawn  $\Psi_x$  during the height of the summer drought period was more strongly correlated with  $\Psi_s$  measured for the deeper soil (1.1 m



**Figure 1.** Seasonal changes in soil psychrometer measurements of soil water potential ( $\Psi_s$ ) from May to September for 1994 and 1995. The  $\Psi_s$  at 0.3 and 1.1 m were correlated with pre-dawn  $\Psi_x$  ( $r = 0.66$ ,  $P < 0.01$ ).

depth) than the shallow soil (0.3 m depth). This probably reflected the dimorphic rooting pattern described for *A. tridentata* (Sturges 1979; Abbott *et al.* 1991).

Transpiration rate decreased with decreasing  $\Psi_x$  (Fig. 2a). Extrapolating the linear relationship suggested that  $E$  would approach zero at  $-3.2$  MPa. Drought was also associated with a decline in leaf area per basal area, a proxy for detecting changes in plant leaf area (Fig. 2b; data from 1994–1996). There was more than a 50% reduction in leaf area as pre-dawn  $\Psi_x$  dropped from above  $-1$  MPa to below  $-2.5$  MPa.

### Vulnerability to cavitation and xylem anatomy

We observed a shift in the susceptibility of stem xylem to cavitation during the growing season (Fig. 3a). Stems measured in May 1995 were relatively vulnerable to cavitation (99% loss of conductivity at  $-2.8$  MPa based on a Weibull fit). The stems became progressively more resistant until mid-July when they appeared to stabilize (99% loss of conductivity at  $-7.8$  MPa, Weibull fit). There was no evidence for variation in vulnerability between years. A vulnerability curve constructed by air dehydration in July and August 1994 (Kolb *et al.* 1996) was very similar to the centrifuge curve for July 1995 (Fig. 3b, compare open versus solid symbols), despite the fact these years differed in the magnitude of the drought (Fig. 1). Furthermore, a companion study of other sagebrush populations indicated no difference in vulnerability curves obtained in different years by identical methods (Kolb & Sperry, 1999).

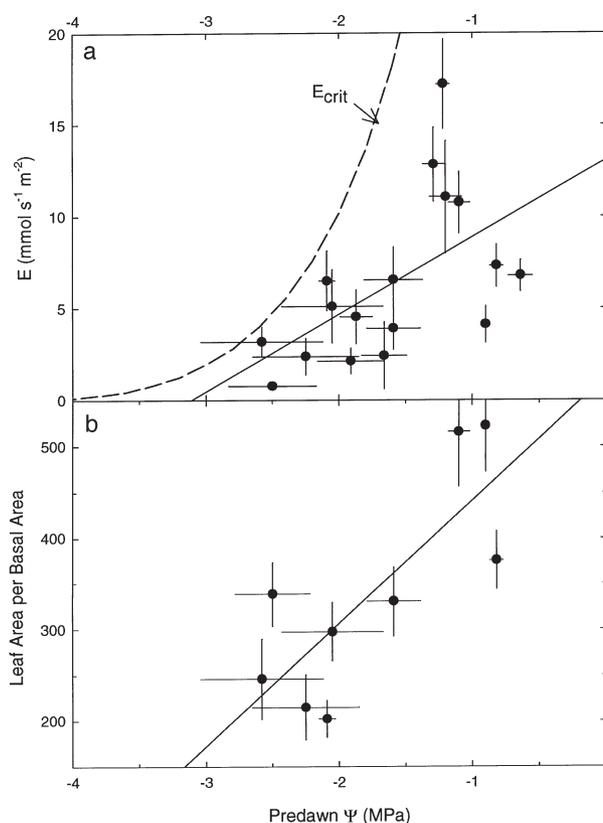
Root xylem was considerably more vulnerable to cavitation and embolism formation than stem xylem (Fig. 3b, solid squares and circles, respectively). Based on the Weibull fit to vulnerability curve data, roots lost 99% of their conducting capacity at  $-4$  MPa, versus  $-7.8$  MPa for July stems (Fig. 3b). The greater susceptibility of roots suggested that during the height of the summer drought, root xylem might limit water transport and gas exchange to

a greater extent than stem xylem. We did not determine whether there was a seasonal shift in the susceptibility of root xylem to cavitation (all root vulnerability curve data were obtained during mid-June 1997).

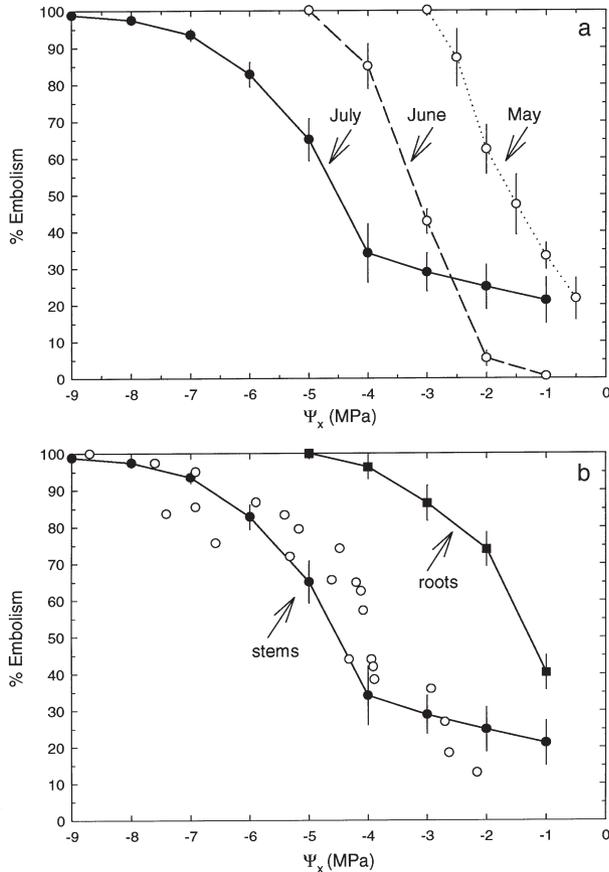
Xylem vessels in roots were much larger than in stems (Fig. 4). Mean diameter ( $\pm$  SE) was  $19.9 \pm 3.0 \mu\text{m}$  for stems versus  $36.5 \pm 3.0 \mu\text{m}$  for roots (Fig. 4a). Similarly, root xylem vessels were much longer than stem vessels (Fig. 4b). We did not detect any stem vessels that were longer than 0.1 m; however,  $\sim 40\%$  of root vessels were longer than 0.1 m. Both the larger vessel diameter and length measured for roots suggested that roots were more efficient at water transport than stems.

### Analysis of safety margins from hydraulic failure

Measured versus predicted  $k_1$  showed a 1:1 relationship for pre-drought  $A_1:A_1$  settings of 10 and 20 (Fig. 5a). A setting of 1 or 5 showed no relationship, with predicted values being too low. Similar results were obtained for  $E$  (Fig. 5b). This indicated that model results were relatively



**Figure 2.** (a) Transpiration rate ( $E$ ) versus pre-dawn  $\Psi_x$  and (b) leaf area per stem basal area versus pre-dawn  $\Psi_x$ . Both  $E$  and leaf area showed a significant decline with decreasing pre-dawn  $\Psi_x$  ( $r = 0.52$ ,  $P < 0.05$ ;  $r = 0.78$ ,  $P < 0.05$ , respectively). The maximum  $E_{crit}$  predicted by the transport model is shown in (a) as a dashed line. Maximum  $E_{crit}$  was based on the largest pre-drought  $k_1$  measured over the four-year study period and minimum seasonal leaf area predicted from (b). Bars indicate standard errors of the means ( $n = 5$  for  $E$  and pre-dawn  $\Psi_x$ ;  $n = 15$  for leaf area/basal area).



**Figure 3.** Vulnerability curves for xylem of roots and stems of *A. tridentata*. (a) Vulnerability curves for stems measured in May, June and July of 1995 showing a progressive shift to more resistant xylem during the growing season. Curves were measured with the centrifugal force method (Alder *et al.* 1997). Error bars are standard errors of the mean ( $n = 4$  for May and June,  $n = 12$  for July with 1 stem per plant). (b) Comparison of stem (July 1995) and root (June 1997) xylem using the centrifugal force method (solid symbols, means and standard errors,  $n = 12$  for stems and roots). The centrifugal force method gave similar results to the air-dehydration technique employed in an earlier study on the same population in July and August of 1994 (open symbols; Kolb *et al.* 1996).

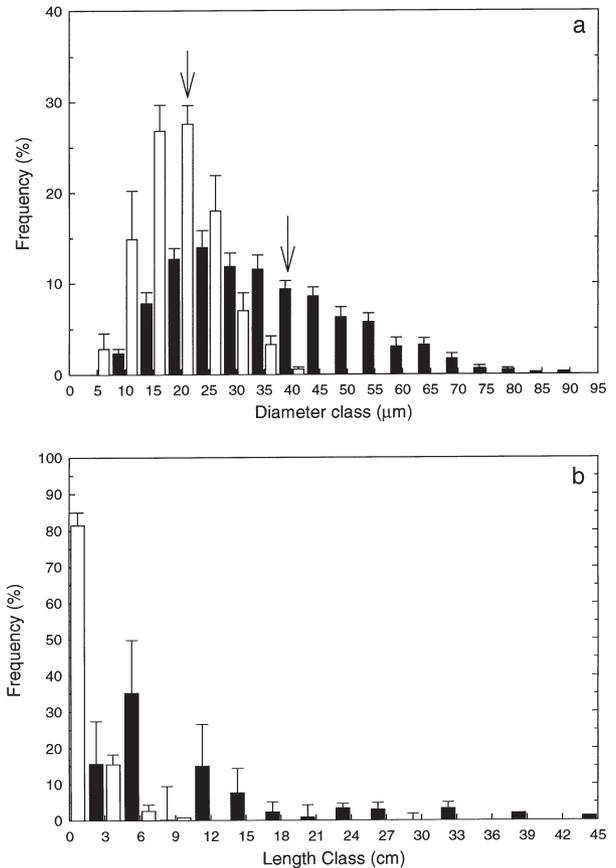
insensitive to  $A_r:A_1$  settings above 5 as compared to lower settings. This also predicted that the actual  $A_r:A_1$  was above 5 which is a reasonable conclusion for a xeric-adapted plant. We used an  $A_r:A_1$  setting of 10 to predict  $E_{crit}$  and  $\Psi_{crit}$  and changes in  $k_1$  during drought (Figs 6 and 7).

As implied by Fig. 5(a) ( $A_r:A_1 = 10$ ), measured and modelled  $k_1$  showed statistically the same decline during the drought (Fig. 6a;  $t$  test of slopes not significant) with a 50–70% loss of  $k_1$  as xylem pressures dropped from approximately  $-1$  to  $-3$  MPa. The decline in leaf-specific conductance under-estimated the decline in hydraulic conductance because of the reduction in leaf area during the drought (Fig. 2b). When leaf area was held constant in the model, it predicted that the loss of hydraulic conductance was localized to the rhizosphere and root xylem components of the continuum, with no change in the shoot xylem

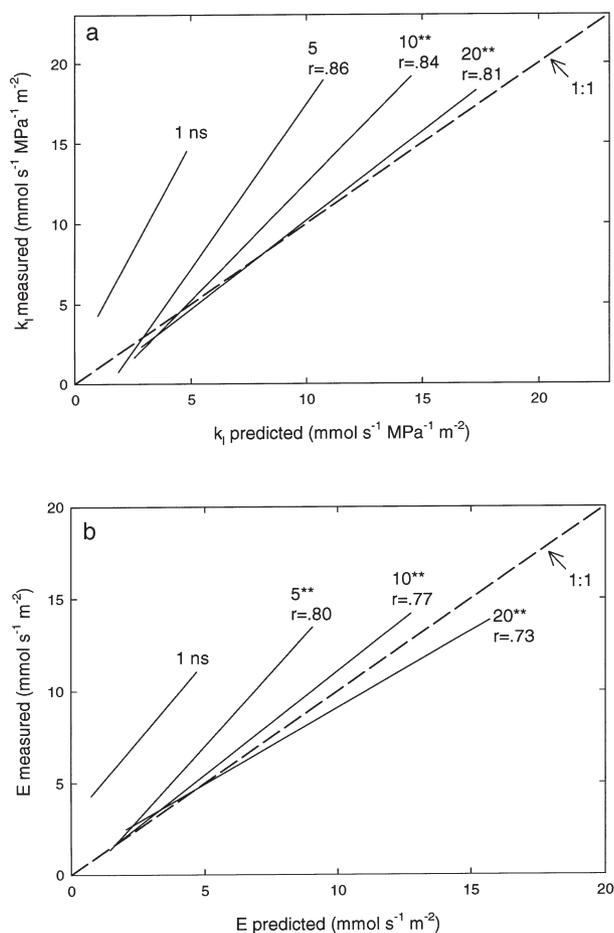
(Fig. 6b). The difference between shoot and root xylem reflected the latter's greater vulnerability to cavitation (Fig. 3b). This result was consistent with measurements of the loss of conductance in branches, which showed no relationship with  $\Psi_x$  during the growing season over four years of study (data not shown).

Safety margins from  $E_{crit}$  diminished as  $E$  declined under drought conditions (Fig. 7a). The decline in  $E$  with drought was necessary to avoid exceeding the modelled  $E_{crit}$  (Figs 2a and 7a). The model predicted that the most liberal estimate of  $E_{crit}$  (based on maximum pre-drought  $k_1$  and lowest seasonal leaf area) would decline to zero as pre-dawn  $\Psi_x$  fell below  $-3.5$  MPa (Fig. 2a, dashed line). This paralleled the extrapolated decline in measured  $E$  with drought.

Safety margins from  $\Psi_{crit}$  also decreased as midday  $\Psi_x$  declined during drought (Fig. 7b). Safety margins based on  $\Psi_{crit}$  appear relatively larger than those based on  $E_{crit}$  because as hydraulic failure is approached, a small increase in  $E$  corresponds to a disproportionately larger decrease in  $\Psi_x$  owing to the decline in hydraulic conductance (Sperry *et al.* 1998). The  $\Psi_{crit}$  estimates clustered around two values. Simulations based on May data (i.e. May



**Figure 4.** (a) Percentage of vessels versus diameter class for stems (open bars) and roots (filled bars). Arrows indicate mean diameters, which differed between roots and stems ( $P < 0.0001$ ). Error bars are standard errors for  $n = 6$  segments. (b) Percentage total vessels versus length class for stems (open bars) and roots (solid bars). Error bars are standard errors for  $n = 4$  segments.



**Figure 5.** Measured versus model prediction of leaf-specific hydraulic conductance for the soil–leaf continuum ( $k_1$ , panel a), and transpiration rate ( $E$ , panel b). Dashed lines are 1:1. Regression lines and  $r$  values are shown for root area to leaf area ratios ( $A_r:A_l$ ) of 1, 5, 10 and 20 ( $n = 17$  sampling dates). Double asterisks indicate that slopes and intercepts of regression lines were not different from 1 and 0, respectively (one-sample  $t$  test,  $P < 0.05$ ). A pre-drought  $A_r:A_l$  of 10 was used for model results in Figs 6 and 7.

vulnerability curve from Fig. 3a and May midday  $\Psi_x$ ) had an average  $\Psi_{crit}$  of  $-2.6$  MPa. This corresponded to the pressure causing 99% loss of conductivity in the stem xylem (Fig. 7b, arrow on upper  $x$  axis), indicating that hydraulic failure occurred in the shoot. The June and July data gave an average  $\Psi_{crit}$  of  $-4.6$  MPa. For the July data (drought conditions), this indicated that hydraulic failure was occurring in the root xylem rather than the stem which did not lose its conductance until pressures dropped below  $-7.8$  MPa (Fig. 7b, arrow on upper axis). Failure in the root under drought conditions was also shown by the fact that root conductance declined during drought in such a manner as to remain the lowest conductance in the continuum (Fig. 6b).

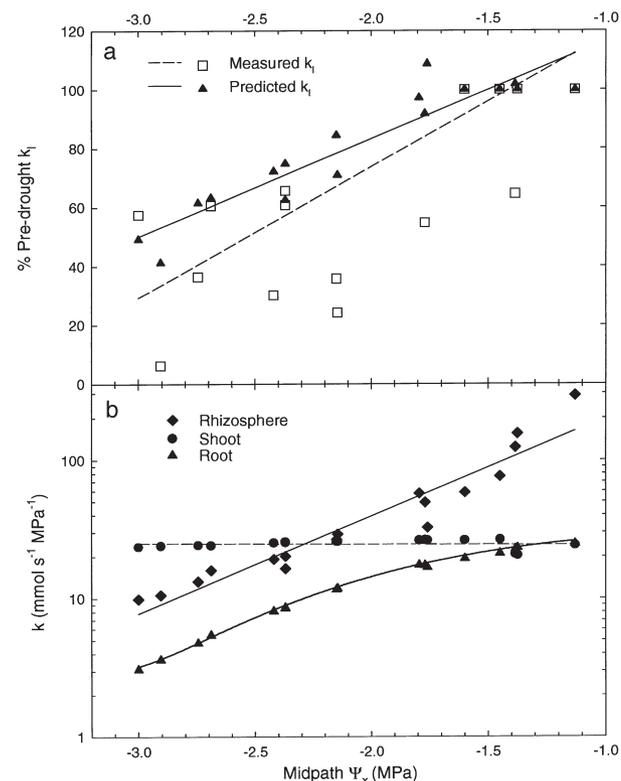
### Pressure–volume analysis

In June, midday  $\Psi_x$  was above the  $\Psi_{tlp}$ , but the plants dropped below the  $\Psi_{tlp}$  in August (Table 1). There was

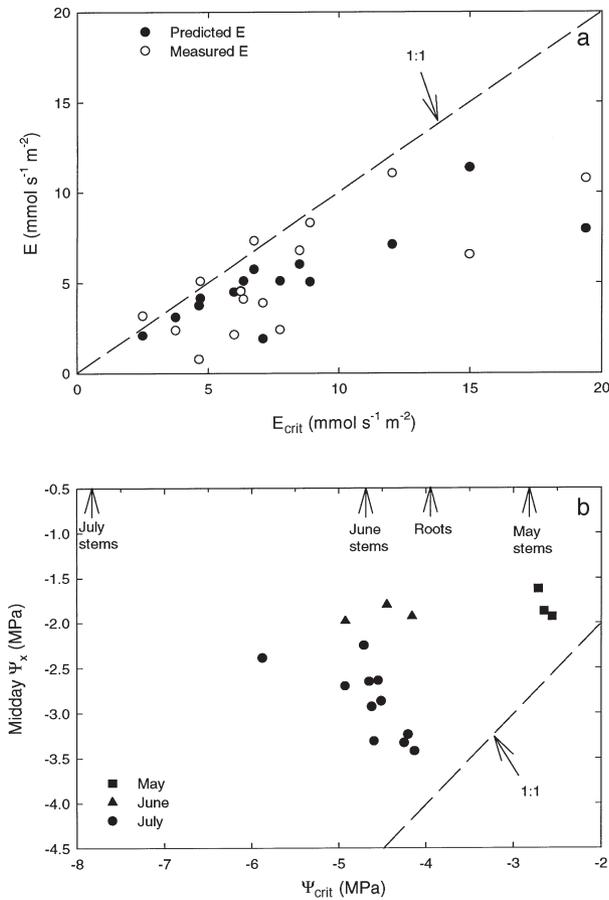
substantial osmotic adjustment, as is evident from the changes in  $\Psi_{tlp}$  and  $\Psi_{sat}$  between June and August, but it was not sufficient to maintain positive turgor during the height of the drought period.

### DISCUSSION

The results supported our hypothesis that a decrease in water use during drought was necessary to avoid hydraulic failure in the soil–leaf continuum, as evidenced by diminishing safety margins from  $E_{crit}$  and  $\Psi_{crit}$  during drought (Figs 2a and 7a). The decline in transpiration and leaf area during drought (Fig. 2) was associated with a 70% drop in the leaf-specific conductance of the whole plant (Fig. 6a), with most of the decline in conductance predicted to occur in the root xylem and rhizosphere rather than in shoot xylem (Fig. 6b). Hydraulic failure under drought conditions was predicted to occur in the root xylem owing to its relative susceptibility to cavitation (Fig. 3b).



**Figure 6.** (a) Measured versus predicted percentage decline in leaf-specific hydraulic conductance for the soil–leaf continuum ( $k_1$ ) with decreasing mid-path  $\Psi_x$ . Declines are shown relative to pre-drought  $k_1$  measured for four successive growing seasons. Both declines were significant ( $P < 0.05$ ) and slopes were not different ( $t$  test). (b) Model prediction of hydraulic conductance of rhizosphere, root and shoot components of the soil–leaf continuum versus mid-path  $\Psi_x$ . The pre-drought conductance used in the model was based on the average pre-drought  $k_1$  measured for four seasons of study. No adjustment was made for declining leaf areas during the season so that changes shown reflect a decline in hydraulic conductance rather than changing leaf area.



**Figure 7.** (a) Measured and predicted transpiration rate ( $E$ ) versus the physical maximum based on limits to hydraulic conductance ( $E_{crit}$ ). Safety margins ( $E_{crit} - E$ ) correspond to the y axis distance between  $E$  and the dashed 1:1 line. (b) Midday  $\Psi_x$  versus the physical minimum leaf  $\Psi_x$  ( $\Psi_{crit}$ ) based on hydraulic limits. Safety margins ( $\Psi - \Psi_{crit}$ ) correspond to the y axis distance between midday  $\Psi_x$  and the dashed 1:1 line. The  $\Psi_x$  corresponding to 99% loss of hydraulic conductance (based on the Weibull function fit to vulnerability curves – Eqn A1) in May stems, roots, June stems, and July stems is shown on the top axis.

Our results join a growing number of studies implying that cavitation in root xylem may be the limiting factor for the maintenance of gas exchange during drought for many woody species (Sperry & Saliendra 1994; Alder, Sperry & Pockman 1996; Hacke & Sauter 1996; Mencuccini & Comstock 1997; Sperry & Ikeda 1997; Linton, Sperry & Williams, 1998). The smaller roots in particular may be the

most vulnerable link in the xylem based on results of Sperry & Ikeda (1997).

One adaptive argument for roots being more vulnerable than stems is that this localizes hydraulic failure to a part of the continuum where hydraulic conductance is most easily restored by new root growth or refilling of embolized conduits. Although we saw no evidence of  $k_1$  increasing during or immediately after the growing season, we did not systematically study short-term changes associated with specific rain events.

As to why any part of the xylem should be hydraulically limiting, it can be argued that the gradual cavitation of xylem can act like a valve to amplify water stress at the leaf level, inducing greater stomatal closure and leaf drop than otherwise. Such a brake on water use could be adaptive in conserving water during a drought. Ultimately, the hydraulic conductance of the soil and rhizosphere puts limits on the potential benefit of greater cavitation resistance for extracting soil water (Sperry *et al.* 1998), and the advantages of greater cavitation resistance together with higher root area per leaf area must be balanced against costs.

The vulnerability of the root system of *A. tridentata* to cavitation may have implications for its ability to conduct nocturnal ‘hydraulic lift’ of water from deep to shallow soil layers. Caldwell & Richards (1989) found that hydraulic lift maximized midday  $E$  and stomatal conductance, but that its magnitude decreased as the summer drought progressed. It is possible that the progressive cavitation of the root system limits the range of soil  $\Psi$  over which hydraulic lift is operable, while at the same time lift would delay the onset of low  $\Psi$  in shallow soil.

In the absence of a measurement of  $A_r:A_l$  for this population, it is impossible to directly evaluate the validity of the transport model used to predict safety margins from hydraulic failure. However, the model prediction of an  $A_r:A_l$  range of 10–20 is within the wide spectrum of published values, which extend from 0.24 to over 14 (Fiscus 1981; Rendig & Taylor 1989; Tyree, Velez & Dalling 1998). Interestingly, the best correlation between measured and predicted  $E$  and  $k_1$  was not associated with a slope of 1, but with a slope greater than 1 (Fig. 5). This suggests that the model was somewhat under-estimating the changes in hydraulic conductance during drought. This trend is also seen in Fig. 6(a) where the measured change in  $k_1$  with  $\Psi$  is less than the predicted slope, although not enough to be statistically significant. It is possible that the small roots (< 3 mm diameter) were even more vulnerable than the size we measured (3–5 mm diameter).

Sampling date	Pre-dawn $\Psi_x$	Midday $\Psi_x$	$\Psi_{tlp}$	$\Psi_{sat}$
June	-1.1 ± 0.1	-1.8 ± 0.1	-2.0 ± 0.2	-1.5 ± 0.2
August	-2.5 ± 0.3	-3.3 ± 0.4	-3.0 ± 0.2	-2.6 ± 0.3

**Table 1.** Water relations parameters for June and August of 1996

All values are given in units of MPa. Pre-dawn and midday  $\Psi_x$  are the mean of five plants ± 1 SE.  $\Psi_{tlp}$  and  $\Psi_{sat}$  are the mean values of six plants ± 1 SE. All water relations parameters measured in August were significantly lower than those measured in June ( $P < 0.0001$ ).

The loss of shoot turgor appears to occur routinely in *A. tridentata* during drought (Table 1). Loss of turgor may be adaptive as a physiological sensor linking water stress to the abscission of leaves and reduction of stomatal conductance as  $\Psi_x$  approaches hydraulically limiting values. There was a suggestive similarity between the minimum seasonal  $\Psi_{\text{up}}$  (−3 MPa, Table 1), the  $\Psi_x$  required to cause > 90% loss of root system conductance (−3.08 MPa, Weibull fit to root vulnerability curve in Fig. 3b), and the pre-dawn  $\Psi_x$  at which  $E$  should approach zero (−3.2 MPa, Fig. 2a). A similar agreement was seen for *Acer grandidentatum* Alder *et al.* 1996). We did not investigate the mechanism of the 1 MPa osmotic adjustment we observed in  $\Psi_{\text{up}}$  (Table 1), but according to Evans *et al.* (1992) it occurs passively in *A. tridentata* as a result of a low volumetric elastic modulus of its leaf cells.

The seasonal shift in vulnerability of stems to cavitation (Fig. 3a) suggests that the vulnerability of xylem to water stress-induced cavitation may be linked to the development and maturation of xylem conduits. Mencuccini & Comstock (1997) found a similar phenomenon when they compared the vulnerability to cavitation of different aged resprouts of *Ambrosia dumosa* and *Hymenoclea salsola*. They found that younger stems were more vulnerable than older, woody stems. In our study, we found that early in the growing season stems were more vulnerable than when measured later in the season. The shift in resistance to cavitation for *A. tridentata* may correspond to the timing of cambial activity and stem elongation. The vascular cambium becomes active in early May for *A. tridentata* (Kolb, personal observation) and stem elongation continues until mid-June (Miller & Shultz 1987). Therefore, our stem vulnerability curves probably reflect different stages of xylem maturation.

Our study indicated a rather close ‘tuning’ of the hydraulic capacity of *A. tridentata* with the range of drought it experienced over a four-year period. Had pre-dawn  $\Psi_x$  dropped 0.5–1 MPa lower, this population would have been unable to conduct gas exchange (Fig. 2a). As a species, *A. tridentata* occupies habitats with a wide range of water availability, from mesic mountain sides to xeric bajadas (West 1983). A companion study of the different subspecies of *A. tridentata* has shown that cavitation resistance varies considerably according to the water availability of the habitat, apparently as a result of genetic differentiation. The xeric-adapted *A. tridentata* ssp. *wyomingensis* is much more resistant to stem cavitation than the high-elevation *A. tridentata* ssp. *vaseyana* (50% embolism at −5 versus −3 MPa in July, respectively; Kolb & Sperry, in press). Furthermore, differences between the subspecies were maintained in a common garden. The population in the present study was intermediate between these subspecies in habitat, morphology, leaf florescence, and also in cavitation resistance, with July stems showing 50% embolism at approximately −4.3 MPa (Fig. 3a). *A. tridentata* seems to have a remarkable ability to adjust its suite of drought tolerance characteristics to different environments, and it is likely that this ability has allowed the species to have a broad geographical and elevational distribution.

## ACKNOWLEDGEMENTS

This work was supported by the National Science Foundation grant IBN931980. We thank Durant McArthur of the USDA Intermountain Shrub Science Laboratory for his help in identifying the subspecific nature of the Tintic population, Nathan Alder and Erin Moore for their assistance with data collection, and John Ayre for his help with root excavations. We also thank the University of Utah Department of Biology for logistical support, and Utah State University for allowing us to conduct this research at the Tintic Experimental Range facility in Tintic, Utah.

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Received 28 September 1998; received in revised form 4 January 1999; accepted for publication 4 January 1999

## APPENDIX

The transport model used a finite difference approach to solve Eqn 1 for steady-state flows and pressures in the soil–plant continuum. The Kirchhoff transform (Ross & Bristow 1990) was employed to limit discretizing to those parts of the continuum differing in their  $k(\Psi)$  functions (Sperry *et al.* 1998). For the plant components, a Weibull function (Rawlings & Cure 1985) was used to fit a curve to the vulnerability data, which gave the following  $k(\Psi)$  function:

$$k = k^* e^{-(\Psi/d)^c} \quad (\text{A1})$$

where  $d$  and  $c$  are curve-fitting parameters of the Weibull function,  $k$  is the hydraulic conductance, and  $k^*$  is the pre-drought conductance based on pre-drought measurements of  $k_1$  as explained in the text. Plant conductance was expressed on a leaf area basis. Vulnerability curves for root and stem xylem were used to represent root and shoot conductances, with 50% of the pre-drought hydraulic resistance in the root system as is representative of a number of woody plant species, including desert shrubs (Mencuccini & Comstock 1997).

The  $k(\Psi)$  function for the rhizosphere assumed a cylindrical geometry of water uptake across a 5 mm distance from bulk soil to the root surface. The radial distance between the root and bulk soil was divided into 11 elements using a log transformation (Passioura & Cowan 1968) to set element lengths exponentially smaller near the root surface where  $\Psi$  gradients are largest. For each element,  $i$ , the  $k(\Psi)$  function was calculated as (Campbell 1985):

$$k_{si} = X_i Ks^* (\Psi_e / \Psi_i)^{(2 + 3/b)} \quad (\text{A2})$$

where  $k_{si}$  is the conductance of element  $i$ ,  $X_i$  is a conductance factor derived from the cylindrical geometry of

uptake,  $Ks^*$  is the saturated soil conductivity ( $11 \text{ mol s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$ ),  $\Psi_e$  is the air-entry potential for the soil ( $-2.2 \text{ kPa}$ ) and  $b$  is a parameter derived from soil texture ( $b = 7.1$ ). Soil parameters were calculated from the sand, silt and clay fraction at the site according to relationships in Campbell (1985). The conductance factor in Eqn A2 ( $X_i$ ) is a function of the absorbing root length ( $l$ ) according to the following equation where  $r_i$  is the radius of element  $i$  (Campbell 1985):

$$X_i = 2\pi l / \ln^{-1}(r_i + 1/r_i) \quad (\text{A3})$$

Rhizosphere conductance was expressed on a root area basis by assuming a root radius of 0.1 mm for absorbing roots. The ratio of root area to leaf area scaled rhizosphere and plant conductance in the continuum.

To run the model,  $E$  in Eqn 1 was incremented from  $0.01 \text{ mmol s}^{-1} \text{ m}^{-2}$  in  $0.01 \text{ mmol s}^{-1} \text{ m}^{-2}$  steps while holding bulk soil  $\Psi$  constant (pre-dawn  $\Psi_x$  in Eqn 1). At each  $E$  increment, the model was solved for steady-state leaf  $\Psi_x$  (midday  $\Psi_x$  in Eqn 1) and  $k_1$ . At  $E_{\text{crit}}$  and  $\Psi_{\text{crit}}$ , the subsequent  $E$  increment caused the model to fail because Eqn 1 could not be solved for any higher  $E$  value.