Plant, Cell and Environment (1993) **16**, 279–287

Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*

J. S. SPERRY & W. T. POCKMAN

Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA

ABSTRACT

The extent to which stomatal conductance (g_s) was capable of responding to reduced hydraulic conductance (k) and preventing cavitation-inducing xylem pressures was evaluated in the small riparian tree, *Betula occidentalis* Hook. We decreased k by inducing xylem cavitation in shoots using an air-injection technique. From 1 to 18 d after shoot injection we measured midday transpiration rate (E), g_s, and xylem pressure ($\psi_{p\text{-}xylem}$) on individual leaves of the crown. We then harvested the shoot and made direct measurements of k from the trunk (2-3 cm diameter) to the distal tip of the petioles of the same leaves measured for E and g_s. The k measurement was expressed per unit leaf area (k_l, leaf-specific conductance). Leaves measured within 2 d of shoot injection showed reduced g_s and E relative to non-injected controls, and both parameters were strongly correlated with k_l. At this time, there was no difference in leaf $\psi_{p\text{-}xylem}$ between injected shoots and controls, and leaf $\psi_{p\text{-}xylem}$ was not significantly different from the highest cavitation-inducing pressure ($\psi_{p\text{-}cav}$) in the branch xylem (−1·43 ± 0·029 MPa, n=8). Leaves measured 7–18 d after shoots were injected exhibited a partial return of g_s and E values to the control range. This was associated with a decrease in leaf $\psi_{p\text{-}xylem}$ below $\psi_{p\text{-}cav}$ and loss of foliage. The results suggest the stomata were incapable of long-term regulation of E below control values and that reversion to higher E caused dieback via cavitation.

Key-words: Betula occidentalis; Betulaceae; birch; hydraulic conductance; xylem cavitation; water stress; transpiration; stomatal conductance.

INTRODUCTION

Xylem pressure ($\psi_{p\text{-}xylem}$) is limited by cavitation in xylem conduits. Cavitation refers to the breakage of the water column and occurs when decreasing $\psi_{p\text{-}xylem}$ draws air through inter-conduit pit membranes (Crombie, Hipkins & Milburn 1985; Sperry & Tyree 1988, 1990). The result is a vapour and/or air-filled (embolized) conduit that no longer conducts water. Plants vary by an order of magnitude in the least negative $\psi_{p\text{-}xylem}$ required to cause cavitation ($\psi_{p\text{-}cav}$): from −1·0 MPa in the tropical tree *Schefflera morototoni* (Tyree *et al.* 1991) to −10.0 MPa in the chaparral species *Ceanothus megacarpus* (Kolb & Davis 1991).

The range of xylem pressures that cause cavitation in a plant is perhaps the most unambiguous definition of its critical water stress: pressures within and below this range reduce or eliminate water transport. Many plants regularly develop $\psi_{p\text{-}xylem}$ approaching $\psi_{p\text{-}cav}$, suggesting that cavitation is limiting not only in theory, but also in reality (Tyree & Sperry 1988; Sperry & Sullivan 1992). This is further supported by models which predict catastrophic cavitation for transpiration rates only slightly higher than the actual maximum measured in the field (Tyree & Sperry 1988). More recent models incorporating stomatal conductance (g_s) also predict how optimal (maximum) g_s is constrained by cavitation (Jones & Sutherland 1991).

The possibility that plants operate with a minimal safety margin against cavitation suggests there may be interaction between $\psi_{p\text{-}cav}$ and the components of the plant that influence $\psi_{p\text{-}xylem}$. The xylem pressure in a branch is a function of the soil water potential (ψ_{soil}), the flow rate (F), and the hydraulic conductance (k) from the soil to the branch:

$$\psi_{p\text{-}xylem} = \psi_{soil} - F/k \qquad (1)$$

For steady-state conditions, F can be approximated by the product of the transpiration rate per leaf area (E) and the leaf area (A_l) supplied by the branch xylem. Expressing E as a function of stomatal conductance to water vapour (g) and the difference in mole fraction of water vapour between leaf and air (Δw), Eqn 1 becomes:

$$\psi_{p\text{-}xylem} = \psi_{soil} - [(g\Delta w)\,(A_l/k)] \qquad (2)$$

If plants operate with $\psi_{p\text{-}xylem}$ slightly above $\psi_{p\text{-}cav}$ during peak gas exchange, then a decrease in ψ_{soil} or an increase in Δw must be countered by appropriate alteration of A_l, k, or the stomatal component of the leaf conductance (g_s) in order to prevent a drop in $\psi_{p\text{-}xylem}$ leading to cavitation. Adjustments in g_s would be the only means of avoiding cavitation over the short term, while long-term adjustments could involve A_l and k.

These predicted responses are consistent with recent evidence of changes in g_s to maintain constant leaf water

Correspondence: J. S. Sperry, Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA.

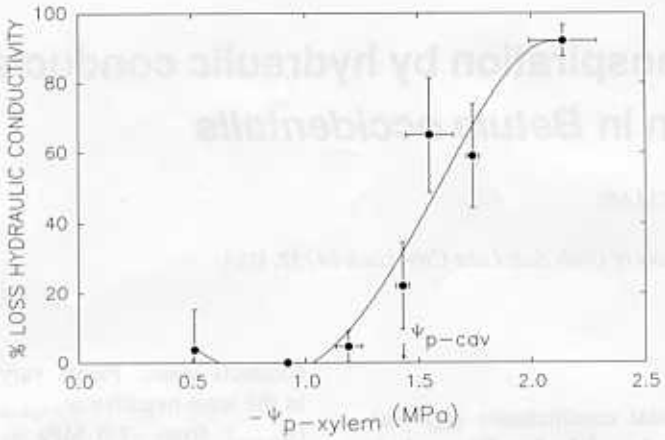

Figure 1. Percentage loss in hydraulic conductivity by xylem embolism as a function of $\psi_{p\text{-}xylem}$ in *Betula occidentalis*. Embolism is the mean of three to eight segments (diameter 0·5–0·9 cm) from the same branch: $\psi_{p\text{-}xylem}$ is the mean of three readings per branch; error bars are 95% confidence limits (modified from Sperry & Sullivan 1992). The highest xylem pressure capable of inducing cavitation ($\psi_{p\text{-}cav}$) is −1·43 ± 0·029 MPa.

balance in response to reduced ψ_{soil} (Davies & Zhang 1991), and in response to reduction of k/A_l by root pruning or increase in k/A_l by defoliation (Meinzer & Grantz 1990). Moreover, reduction in k/A_l as plants grew in size was associated with reduced E keeping $\psi_{p\text{-}xylem}$ from causing significant cavitation (Meinzer *et al.* 1992). The ratio k/A_l has been termed the 'leaf-specific hydraulic conductance' (k_l; Zimmermann 1978) and is a useful parameter because of its importance in determining the pressure drop along the transport pathway (Eqn 2; see also 'Methods').

The purpose of this paper is to present a preliminary evaluation of the response of E, g_s, and $\psi_{p\text{-}xylem}$ to experimentally reduced k in field-grown *Betula occidentalis* Hook. (water birch). This work is part of an effort to determine how the parameters determining $\psi_{p\text{-}xylem}$ are integrated to maximize gas exchange while minimizing cavitation and dieback in response to stress. We chose *Betula occidentalis* for these initial experiments because it is a small riparian tree growing along perennial streams. This results in a constant and high soil water potential throughout the growing season and simplifies the interactions in Eqn 2. Previous work at the same field site used in this project showed that the branch xylem of *B. occidentalis* cavitates in response to water stress over a relatively narrow range of xylem pressures: as $\psi_{p\text{-}xylem}$ was decreased, loss of hydraulic conductivity resulting from cavitation was detected at −1·43 ± 0·029 MPa ($\psi_{p\text{-}cav}$) and was complete by ca -2·1 MPa (Fig. 1; Sperry & Sullivan 1992).

MATERIALS AND METHODS

All of our experiments used *Betula occidentalis* trees in the Red Butte Canyon research area in the Wasatch Mountains bordering Salt Lake City, Utah, USA. This tree grows in clumps of multiple shoots that reach ca. 13 m in height. Shoots of a clump are connected at the base and presumably represent one individual. We completed the experiments during August and early September 1991 using the shoots of two adjacent clumps. Shoots used were of similar heights (ca. 5–6 m).

Induction of cavitation

We decreased k in individual shoots of a clump by inducing cavitation. We injected air into cut side-branches of otherwise intact shoots in the field and raised the air pressure until air was forced across intervessel pits. In theory, cavitation will occur when the pressure difference between xylem and air equals or exceeds $\psi_{p\text{-}cav}$ (−1·43 MPa; Fig. 1). To evaluate this, we made daytime injections (6 h duration) to determine the minimum air pressure required to induce cavitation when $\psi_{p\text{-}xylem}$ was at a minimum, and then used the same pressure for an overnight injection when $\psi_{p\text{-}xylem}$ was at a maximum to see if no cavitation was induced as expected. We also made overnight injections at air pressures in excess of 1·5 MPa which should cause cavitation regardless of $\psi_{p\text{-}xylem}$.

We used a pressure-tight collar equipped with a compressible gasket to inject the trees (Fig. 2; see also Salleo *et al.* 1992, for description of a similar device). We chose this method over other techniques of decreasing k such as freezing and thawing (Hammel 1967), or imposing water stress (Schultze & Mathews 1988), because it minimized direct damage to living tissue.

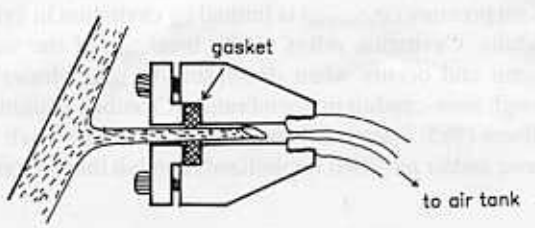

Figure 2. Device for injecting air into cut side branches and inducing cavitation by forcing air across intervessel pits.

We measured cavitation by how much it reduced hydraulic conductivity in excised stem segments from the shoot. Hydraulic conductivity (k_h) is defined as the flow rate per pressure *gradient* and thus, is independent of the length of the pathway being measured. It differs from hydraulic conductance (k) which is defined as the flow rate per pressure *difference* across the pathway being measured and is dependent on path length (Tyree & Ewers 1991). We cut segments 10 cm in length underwater and attached them to a tubing system designed to measure the hydraulic conductivity under gravity-induced pressure gradients of ca 0·07 MPa m^{-1}. Conductivity measurements were constant over the measurement period (3–10 min) even in obviously embolized segments, indicating no significant re-filling by these pressures. After the initial measurement we re-filled embolized vessels by using high-pressure (1·75 MPa m^{-1}) flushes until the hydraulic conductivity reached a maximum value. We calculated the amount of embolized (cavitated) xylem in the segment as the per cent the initial conductivity was below the maximum value (Sperry, Donnelly & Tyree 1987).

Transpiration and xylem pressure measurements

We used a total of five injected shoots to assess the response of g_s and E to injection. These shoots were left for 1, 2, 7, 15 and 18 d after injection before being measured for g_s, E, and k. We measured E and g_s (Li-cor 1600, Li-cor Inc., Lincoln, NE, USA) on 15–30 leaves spaced evenly throughout the injected shoot. Two non-injected shoots served as controls. To simplify the comparison of g_s and E data taken on different days we only used measurements made on days with similar Δw (30–40 kPa MPa^{-1}). At least three measurements were made on each leaf spanning the hours from approximately 1030 to 1300 h. Diurnal observations indicated this included the period of maximum gas exchange. We calculated the average midday E and g_s for each leaf by integrating both with respect to time to obtain cumulative water loss and conductance, respectively, and then dividing by the measurement period. Shoots were in full sun during the measurements.

Transpiration rates measured with the porometer overestimated the *in situ* rate by less than 13% based on estimates of minimum boundary layer conductance (g_b; McDermitt 1990) and assuming the porometer did not alter the Δw around the leaf. Calculations assumed a 0·5 ms^{-1} or greater wind speed and an effective leaf length of 0·03 m ($g_b \geq 980$ mmol $m^{-2}s^{-1}$).

We measured leaf xylem pressure at least three times during the midday observation period using a pressure chamber. The water potential of the main trunk of the shoot was estimated using a temperature-corrected stem psychrometer (Plant Water Status Instruments, Guelph, Ontario, Canada) attached to a de-topped side-branch. This stopped any flow through the branch and reduced fluctuations in temperature gradients caused by flowing xylem sap. The side branch was located immediately below the part of the shoot used in the k measurements (see below). Pre-dawn measurements of leaf xylem pressure were made periodically during the 4 weeks of experiments.

k measurement

We measured k and A_l for the same leaves measured with the porometer. The k measurement was intended to incorporate the region of the soil-to-leaf pathway altered by the injection treatment. To allow comparison of k measurements made on different shoots, we measured it on shoots of similar basal diameter. Immediately following the midday field measurements, we cut the shoot near the base and brought it into the laboratory in plastic bags. We re-cut the shoot base underwater (to remove vessels embolized by the initial cut) to a basal diameter between 2 and 3 cm. This diameter was approximately 3–3·5 m above ground level. The cut end was shaved smooth with a razor blade, and attached to a plastic bag filled with filtered (0·2 μm) treated water. All the leaves were then cut from the shoot at the base of the lamina using razor blades. The petioles of leaves used in the transpiration measurements were labelled and the area of the lamina measured.

We connected the base of the shoot to a pressurized source of filtered (0·22 μm) 10 mol m^{-3} oxalic acid solution (used to prevent microbial growth; see Sperry *et al.* 1987) and forced solution into the shoot at ca. 0·05 MPa; the actual pressure was measured using a bubble manometer. During the first 5 min following pressurization, we collected water coming out of the marked petioles in tared vials filled with cotton wool. Evaporation from the vials was minimized by inserting petioles through small openings in the vial lids. We removed the vials from the petioles after the measurement, put them in a plastic bag to minimize evaporation, and began weighing them immediately. We calculated k as millimoles of water collected per unit time and pressure. Repeated 5-min measurements on the same shoot gave similar k values indicating there was no significant re-filling of embolized vessels under pressure.

Estimation of xylem pressure drop

The physiological significance of hydraulic conductance is the pressure drop it induces under transpirational conditions. For this reason, it was useful to express it per unit leaf area (k_l, leaf-specific conductance). The pressure drop (ΔP) across the portion of the pathway represented by the k measurement can be readily calculated from E and k_l:

$$\Delta P = E\,(1/k_l) \qquad (3)$$

This assumes steady-state flow and represents a maximum possible value.

The pressure drop was calculated from the trunk to the distal end of the petiole because this was the portion of the pathway where k was measured. The calculated pressure drop was compared with an independent measurement

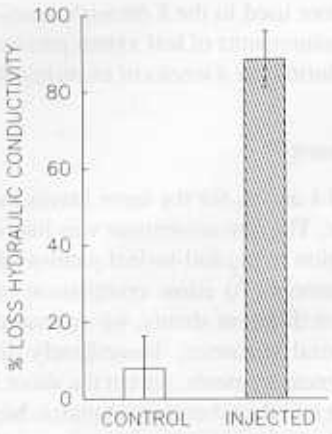

Figure 3. Percentage loss in hydraulic conductivity by embolism in a control shoot (n=7 branch segments) and a shoot injected at 1·75 MPa overnight (n = 8 segments). Error bars are 95% confidence limits.

obtained by subtracting the average trunk $\psi_{p\text{-}xylem}$ measured with stem psychrometers, from the average leaf $\psi_{p\text{-}xylem}$ measured with the pressure bomb. The measured value was expected to be greater than the calculated estimate because the calculation did not account for the pressure drop within the lamina. Calculated values in excess of measured values were evidence of a large deviation from steady-state flow resulting from use of stored water.

Capacitance measurements

As described in the 'Results' section, injected shoots showed considerable leaf death and surviving leaves appeared to be transpiring stored water. We measured the water storage capacity (capacitance) of mostly-defoliated branches by measuring their water loss as a function of $\psi_{p\text{-}xylem}$. We selected three shoots between 0·78 and 0·90 cm in diameter at the base and removed all but a few leaves (9–12% of original leaf area remaining). We measured $\psi_{p\text{-}xylem}$ with stem psychrometers attached near the base of the branch; psychrometers actually measure water potential, but this will equal $\psi_{p\text{-}xylem}$ if the xylem sap is pure water. Water loss was measured gravimetrically. Paired measurements of xylem pressure and shoot weight were made repeatedly until the pressure dropped below –2·5 MPa. Capacitance was quantified as water loss per unit decrease in xylem pressure.

RESULTS

Air injection induced significant embolism throughout birch shoots relative to controls (Fig. 3). Embolism was caused not only in the main axis of the shoot, but in side branches as well; in general, it was highest close to the injection point and dropped off with increasing distance. Not surprisingly, this embolism was associated with considerable dieback that was visible in some cases within a day of the injection. Leaves continued to die for several d following the injection and some shoots ultimately lost over 90% of their foliage.

The minimum injection pressure required to cause embolism in a day-time injection was 0·35 MPa (data not shown) indicating that xylem pressures in the branches were within 0·35 MPa of the cavitation range at midday. The small safety margin from cavitation was also evident from mid-d leaf $\psi_{p\text{-}xylem}$ which was not significantly different from $\psi_{p\text{-}cav}$ in controls (Fig. 7). Although leaf $\psi_{p\text{-}xylem}$ will underestimate $\psi_{p\text{-}xylem}$ in the branches, the fact that controls averaged 8% embolism indicates they fell below the maximum cavitation pressure. Injections at 0·5 MPa overnight caused no reduction in k_l relative to controls (Fig. 4). This was expected because xylem pressures at night were high (–0·10 MPa at pre-dawn) and the injection pressure was not sufficient to force air across intervessel pits and into functional vessels. However, an injection pressure of 1·75 MPa during the night, induced considerable embolism (Fig. 3) as predicted.

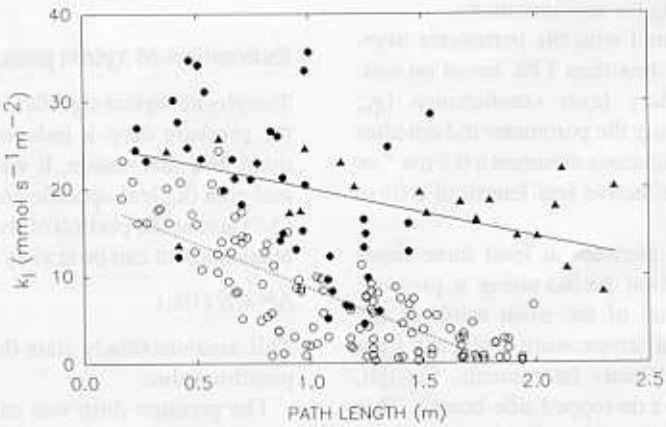

Figure 4. Hydraulic conductance per leaf area (k_l) from the trunk (at 2–3 cm diameter) to distal end of petiole as a function of path length. Shoots injected at 0·5 MPa for ca. 6 h during the day (○) had reduced k_l relative to controls (●) primarily at the distal branch tip (large path lengths). A shoot injected at 0·5 MPa overnight (▲) showed no evidence of reduced k_l.

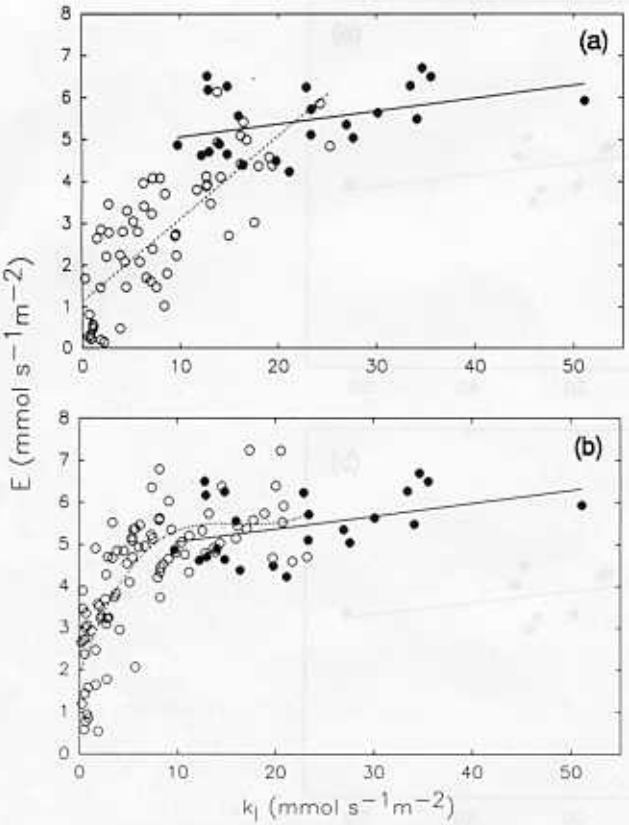

Figure 5. Midday average transpiration rate (E) versus k_l. Leaves on non-injected controls showed no correlation between E and k_l (●, $r^2 = 0{\cdot}17$). (a) Leaves measured 1–2 d following the injection of the shoot showed strong correlation between E and k_l (○; $r^2 = 0{\cdot}62$). (b) Leaves measured 7–18 d following the injection of the shoot had no correlation between E and k_l over control range of k_l; below this range E decreased, but many leaves had values of E approaching those of controls.

We repeated the injections until a protocol was found that only induced embolism in the part of the shoot included in the k_l measurements and that did not kill all of the leaves. Satisfactory results were obtained for a 0·5 MPa midday injection of ca. 6 h duration. This decreased k_l from trunk to petiole primarily for leaves in the distal part of the shoot relative to controls; leaves near the base of the shoot were less affected by the treatment (Fig. 4). This, together with direct embolism measurements made on excised segments, suggested that most embolism was confined to the part of the shoot harvested for the k_l measurements.

The response of E and g_s to reduced k_l caused by the injection treatment was time dependent. In the short term treatment (shoots measured 1-2 d after injection), g_s and E fell below control values and both parameters were positively correlated with k_l (Figs 5a & 6a).

In the long-term treatment (shoots measured 7–18 d after injection), dieback was extensive and surviving leaves had E and g_s values similar to controls for the same range of k_l. At values of k_l below the control range there was sharp decline in E although some leaves maintained relatively high E values (3–4 mmol $m^{-2} s^{-1}$) even at k_l below 2 mmol s^{-1} m^{-2} (Fig. 5b). The changes in E resulted from corresponding changes in g_s (Fig. 6b).

Leaf $\psi_{p\text{-}xylem}$ in the short-term treatment was the same as in controls. In long-term treatments, leaf $\psi_{p\text{-}xylem}$ fell significantly below the control mean and $\psi_{p\text{-}cav}$ (Fig. 7). The drop in xylem pressure was especially pronounced in the distal leaves (Fig. 7) which showed the greatest reduction in k_l relative to controls (Fig. 4).

The calculated pressure difference between trunk and petiole (Eqn. 3) under-estimated the measured value in controls, short-term treatments, and long-term treatments for leaves with k_l in the observed control range ($\geq$ 4·4 mmol $s^{-1} m^{-2}$; Fig. 4). This was expected because calculated values did not account for the pressure drop in the lamina. However, leaves of long-term treatments with k_l below control values had a calculated pressure drop over 1 MPa in excess of the measured value (Fig. 8). This suggested extreme non-steady-state flux and the transpiration of stored water.

Stored water could be supplied by cavitating xylem vessels because of $\psi_{p\text{-}xylem}$ falling below $\psi_{p\text{-}cav}$ (Fig. 7). The capacitance of branches was highest over the range of xylem pressures causing cavitation (Fig. 9, 1·4–2·1 MPa), suggesting that most of the water lost over this range was released from water-filled vessels. Re-filling of cavitated vessels was not observed during the experiments and so the prolonged reliance on xylem conduits as a source of stored water would require progressively higher xylem tensions and an eventual elimination of water transport with consequent death of the foliage.

DISCUSSION

The results suggest that controls were operating near and even somewhat below cavitation pressures (Fig. 7) and that the short-term reduction in g_s in response to experimentally reduced k_l (Fig. 6) prevented xylem pressures from dropping further and causing more cavitation. The mechanism of this stomatal response to k_l is unknown. Several studies have shown adjustments in g_s at constant leaf water potential in response to soil drought or root pruning and it has been proposed that stomata respond to chemical signals released by the root (Davies & Zhang 1991). This is unlikely in the present study because the water potential of the soil in the rooting zone was high and constant throughout the treatments as evidenced from predawn leaf $\psi_{p\text{-}xylem}$ measurements. Perhaps there is a threshold leaf water potential for stomatal closure that coincides with $\psi_{p\text{-}cav}$, as was found for the palm *Rhapis excelsa* (Sperry 1986).

The unknown mechanism linking reduced k_l to a decrease in g_s was a transient one because g_s and E showed a partial return to near control values over time (Figs 5 & 6). This apparently caused the observed decrease in $\psi_{p\text{-}xylem}$ below $\psi_{p\text{-}cav}$ (Fig. 7). The large deviations from

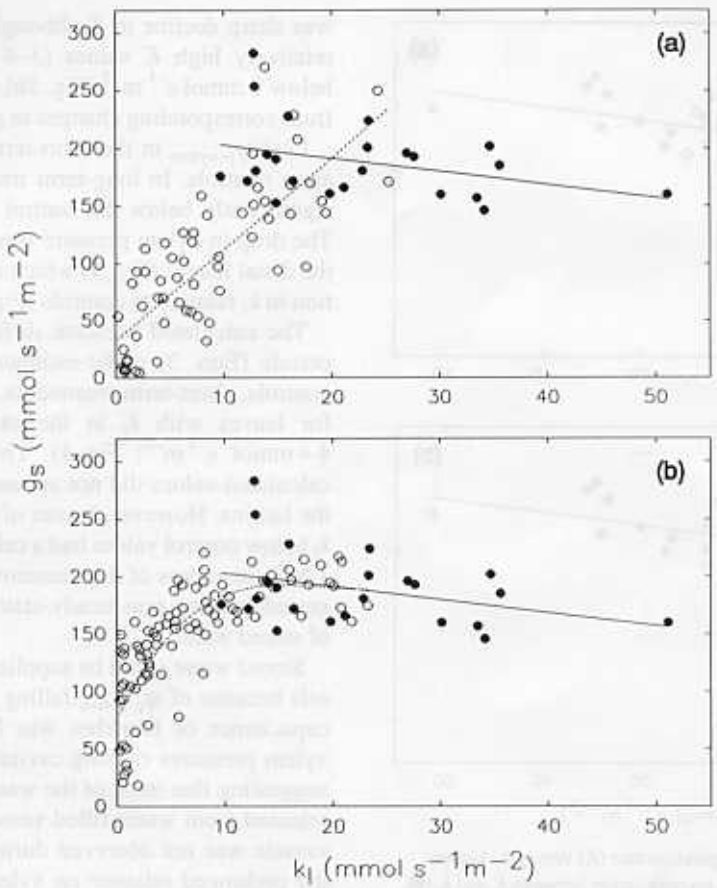

Figure 6. Midday average stomatal conductance (g_s) versus k_l for the same leaves and measurement period as in Fig. 5. As for E in Fig. 5, g_s showed no correlation with k_l for leaves on non-injected controls (●; $r^2 = 0{\cdot}13$). (a) Leaves measured 1–2 d following the injection of the shoot (○) showed a strong correlation between g_s and k_l ($r^2 = 0.62$) indicating the trend in E shown in Figure 5a resulted from stomatal control. (b) Leaves measured 7–18 d following the injection of the shoot showed the same pattern in g_s as they did for E (Fig. 5b), indicating that trends in E resulted from changes in g_s.

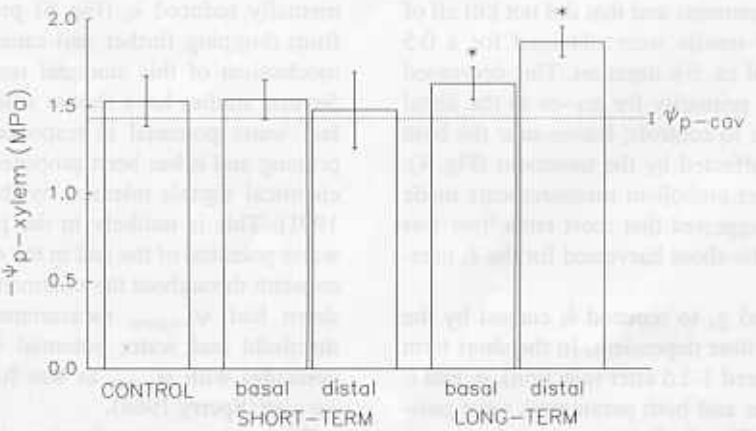

Figure 7. Midday leaf xylem pressures ($\psi_{p\text{-}xylem}$) in controls and injected shoots (n ≥ 8 for each mean). 'Short-term' refers to leaves measured 1–2 d following shoot injection; 'long-term' refers to leaves measured 7–18 d following shoot injection. For injected shoots, means are shown for basal and distal leaves on the shoots. Asterisks indicate means significantly different from $\psi_{p\text{-}cav}$ ('t' test, P=0·01). Only leaves from the long-term treatment developed pressures significantly below $\psi_{p\text{-}cav}$.

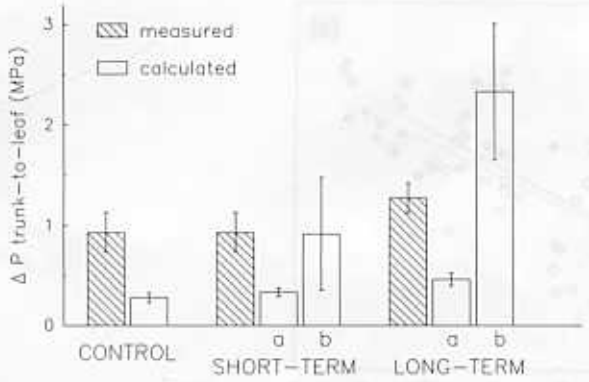

Figure 8. Pressure drops between trunk and leaf. Hatched bars indicate pressure differences obtained by subtracting leaf $\psi_{p\text{-}xylem}$ from trunk $\psi_{p\text{-}xylem}$ ($n \geq 8$). Open bars indicate calculated pressure differences based on data in Fig. 5 and Eqn 3 ($n \geq 23$). 'Short-term' and 'long-term' are defined as in Fig. 7. Bars marked 'a' represent leaves with k_l within the control range. Bars marked 'b' represent leaves with k_l below the lowest control value (4·4 mmol s^{-1} m^{-2}; Fig. 4). Measured values exceed or equal calculated values in all but the long-term leaves with k_l below controls ('long-term, b'); here the calculated value is well above the measured range indicating pronounced non-steady-state flow resulting from the transpiration of stored water.

steady-state flow in leaves with k_l below the control range indicated that they were transpiring water released from storage, including water released from cavitating xylem conduits. These high transpiration rates could only be followed by leaf death once the xylem became completely cavitated.

We can tentatively define a critical k_l for this species below which a leaf would be in danger of dieback by cavitation. This would be the lowest k_l not associated with extreme deviations from steady-state flow and presumed exhaustion of stored water via cavitation. Interestingly, this coincided closely with the lowest control k_l (4·4 mmol s^{-1} MPa^{-1} m^{-2}; Fig. 4). The variation in k_l in controls may represent variation in the safety margin from cavitation: those leaves with higher k_l would have a greater safety margin than those with lower k_l. This was the conclusion drawn from computer simulations of the cavitation response to increased transpiration (Tyree & Sperry 1988).

We can make a more direct evaluation of the safety margin from cavitation in *B. occidentalis* by using Eqn 2 with estimates of the total hydraulic conductance from soil to petiole. We can estimate whole-path k_l by assuming that only the measured component of k_l from trunk to petiole was changed by the injection treatment and that the non-measured component from the soil to the trunk was equal in all shoots. We calculated the k_l from soil to trunk using Eqn 3 where the E value was the average for controls (5·4 mmol s^{-1} m^{-2}; data from Fig. 5), and P was the pressure difference between ψ_{soil} (estimated from pre-dawn leaf $\psi_{p\text{-}xylem}$: –0.10 MPa) and trunk $\psi_{p\text{-}xylem}$ (-0.60 ± 0.210 MPa, n=6). Whole path k_l was obtained from the combined conductance (in series) of k_l from trunk to petiole and k_l from soil to trunk.

Assuming constant soil water potential and Δw, which was approximately true for our experiments, the maximum transpiration rate allowable without $\psi_{p\text{-}xylem}$ dropping below $\psi_{p\text{-}cav}$ in the petiole is linearly related to the soil-petiole k_l (Fig. 10; solid line). If $\psi_{p\text{-}cav}$ in petioles is the same as in branches where it was measured, any data points on or above the theoretical line would represent leaves developing cavitation-inducing xylem tensions.

The correlation between E and k_l for controls and short term treatments is similar to the theoretical line (Fig. 10a) suggesting the xylem was operating at the cavitation limit and experiencing limited cavitation. The correlation between E and k_l in controls and long-term treatments deviates from the theoretical line such that leaves with low k_l are well within the cavitation zone (Fig. 10b). This is consistent with our interpretation of the response to reduced k_l: leaves with critically low k_l are incapable of avoiding large amounts of cavitation because of their inability to maintain a long-term reduction in g_s.

The results suggest cavitation pressure is a variable of central importance in understanding the response of plants to water stress. Although we decreased k_l at constant soil water potential in the present study, we would expect similar results if soil water potential was decreased for constant k_l. In both cases, the maximum possible value of E without cavitation is decreased (Eqn 2) and to avoid cavitation, the plant must reduce water loss by decreasing g_s and/or A_l. While drought-induced changes in stomatal behaviour and tissue water relations have been extensively characterized (Schulze 1986), only recently has there been an attempt to

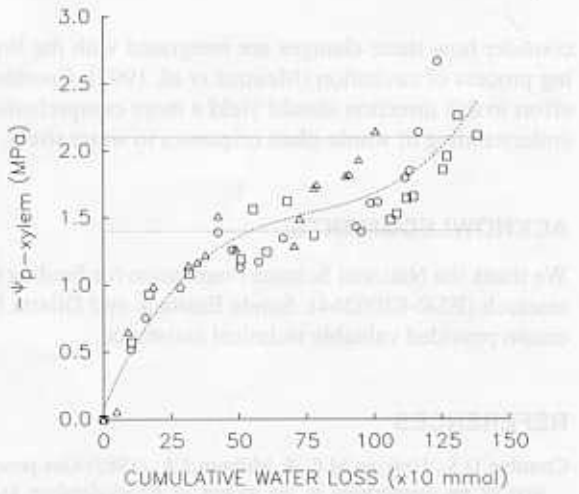

Figure 9. $\psi_{p\text{-}xylem}$ as a function of cumulative water loss in three branches (□, △, ○,) of equal size (basal diameters of 0·78–0·90 cm). Water loss was almost entirely from the stem because branches were mostly defoliated (10–12% original leaf area). The water storage capacitance is given by the inverse of the slope and was greatest over the cavitation range (xylem pressures between horozontal dotted lines, data from Fig. 1).

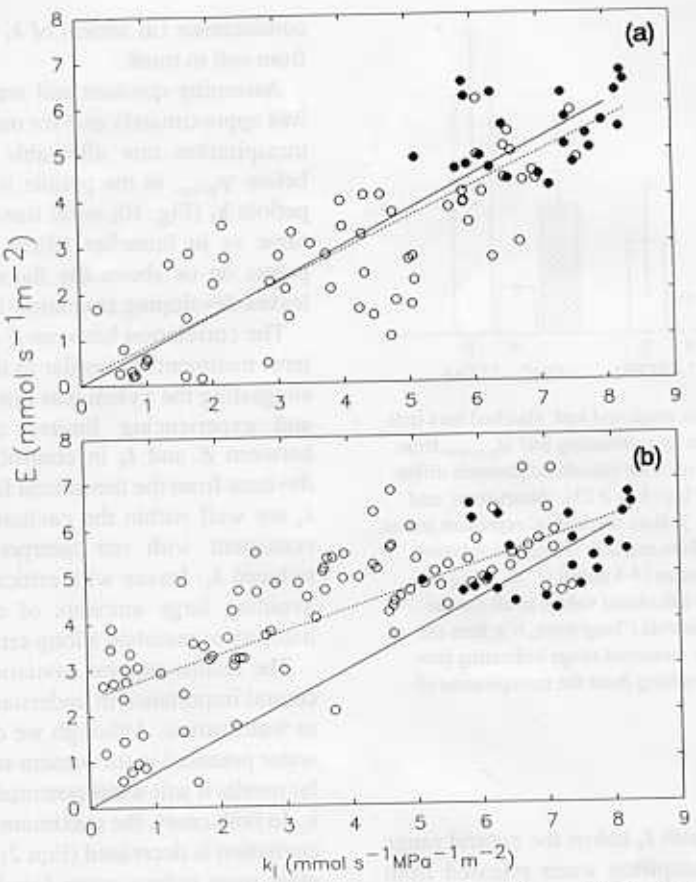

Figure 10. Midday transpiration rate (E) as a function of the estimated whole-path (from soil to petiole) hydraulic conductance per leaf area (k_l). The solid line assumes $\psi_{p\text{-}xylem}$ equals $\psi_{p\text{-}cav}$ (−1·43 MPa) and ψ_{soil} is −0·1 MPa: this is the predicted relationship if the xylem is operating at the brink of cavitation; any leaf on or above this line would in theory be inducing cavitation. (a) Leaves measured 1–2 d following injection of a shoot (○) together with controls (●) show a correlation between E and k_l that is identical to the predicted line. (b) Leaves measured 7–18 d following injection of the shoot (open circles) show an increasingly greater disparity from the predicted relationship as k_l decreases: most leaves at low k_l are well within the cavitation range.

consider how these changes are integrated with the limiting process of cavitation (Meinzer *et al.* 1992). Continued effort in this direction should yield a more comprehensive understanding of whole-plant responses to water stress.

ACKNOWLEDGMENTS

We thank the National Science Foundation for funding this research (BSR-8806264). Sonda Eastlack and Diletta Piccotino provided valuable technical assistance.

REFERENCES

Crombie D.S., Hipkins M.F. & Milburn J.A. (1985) Gas penetration of pit membranes in the xylem of *Rhododendron* as the cause of acoustically detectable sap cavitation. *Australian Journal of Plant Physiology* **12**, 445–453.

Davies W.J. & Zhang J. (1991) Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Molecular Biology* **42**, 55–76.

Hammel H.T. (1967) Freezing of xylem sap without cavitation. *Plant Physiology* **42**, 55–66.

Jones H.G. & Sutherland R.A. (1991) Stomatal control of xylem embolism. *Plant, Cell and Environment* **14**, 607–612.

Kolb K.J. & Davis S. D. (1991) Differential occurrence of xylem embolism between a coastal sage species and chaparral shrub species growing at the same microsite. *Bulletin of the Ecological Society of America* **72** (Supplement), 165.

McDermitt D.K. (1990) Sources of error in the estimation of stomatal conductance and transpiration from porometer data. *Hortscience* **25**, 1538–1548.

Meinzer F.C. & Grantz D.A. (1990) Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell and Environment* **13**, 383–388.

Meinzer F.C., Goldstein G., Neufeld H.S., Grantz D.A. & Crisosto G.M. (1992). Hydraulic architecture of sugarcane in relation to patterns of water use during plant development. *Plant, Cell and Environment* **15**, 471–477.

Salleo S., Hinckley T.M., Kikuta S.B., LoGullo M.A., Weilbony P., Yoon T.M. & Richter, H. (1992) A method for introducing xylem emboli *in situ*: experiments with a field-grown tree: technical report. *Plant, Cell and Environment* **15**, 491–497.

Schultz H.R. & Matthews M.A. (1988) Resistance to water transport in shoots of *Vitis vinifera* L. *Plant Physiology* **88**, 718–724.

Schulze E.D. (1986) Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology* **37**, 247–274.

Sperry J.S. (1986) Relationship of xylem embolism to xylem pressure potential, stomatal closure, and shoot morphology in the palm *Rhapis excelsa*. *Plant Physiology* **80,** 110–116.

Sperry J.S., Donnelly J.R. & Tyree M.T. (1987) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11,** 35–40.

Sperry J.S. & Tyree M.T. (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiology* **88,** 581–587.

Sperry J.S. & Tyree M.T. (1990) Water stress induced xylem embolism in three species of conifers. *Plant, Cell and Environment* **13**, 427–437.

Sperry J.S. & Sullivan J.E.M. (1992) Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology* **100,** 605–613.

Tyree M.T., Snyderman D.A., Wilmot T.R. & Machado J.L. (1991) Water relations and hydraulic architectures of a tropical tree (*Schefflera morototani*). *Plant Physiology* **96,** 1105–1113.

Tyree M.T. & Ewers F.W. (1991) The hydraulic architecture of trees and other woody plants (Tansley review no. 34). *New Phytologist* **119**, 345–360.

Tyree M.T. & Sperry J.S. (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* **88**, 574–580.

Tyree M.T. & Sperry J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology* **40**, 19–38.

Zimmermann M.H. (1978) Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany* **56**, 2286–2295.

Received 18 May 1992; received in revised form 20 July 1992; accepted for publication 7 October 1992