Limitation of plant water use by rhizosphere and xylem conductance: results from a model

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ABSTRACT

Hydraulic conductivity (K) in the soil and xylem declines as water potential (Ψ) declines. This results in a maximum rate of steady-state transpiration (Ecrit) and corresponding minimum leaf Ψ(Ψcrit) at which K has approached zero somewhere in the soil–leaf continuum. Exceeding these limits causes water transport to cease. A model determined whether the point of hydraulic failure (where K = 0) occurred in the rhizosphere or xylem components of the continuum. Below a threshold of root:leaf area (A R: A L), the loss of rhizosphere K limited Ecrit and Ψcrit. Above the threshold, loss of xylem Ψ from cavitation was limiting. The A R: A L threshold ranged from > 40 for coarse soils and/or cavitation-resistant xylem to < 0·20 in fine soils and/or cavitation-susceptible xylem. Comparison of model results with drought experiments in sunflower and water birch indicated that stomatal regulation of E reflected the species’ hydraulic potential for extracting soil water, and that the more sensitive stomatal response of water birch to drought was necessary to avoid hydraulic failure. The results suggest that plants should be xylem-limited and near their A R: A L threshold. Corollary predictions are (1) within a soil type the A R: A L should increase with increasing cavitation resistance and drought tolerance, and (2) across soil types from fine to coarse the A R: A L should increase and maximum cavitation resistance should decrease.

Key-words: drought responses; hydraulic conductance; rhizosphere conductance; root–shoot ratio; soil–root interface; water relations; water transport; xylem cavitation.

INTRODUCTION

As postulated by the cohesion-tension theory, the flow of water from soil to leaf represents a ‘tug-of-war’ on a hydraulic rope. If the hydraulic continuum breaks, the plant cannot access atmospheric CO2 without desiccating to death. There are two weak spots in the continuum: at the rhizosphere where steep water potential gradients may create dry non-conductive zones (Newman 1969), and in the xylem where cavitation can eliminate water transport (Zimmermann 1983). While earlier studies have considered the limitation of water uptake by one or the other of these processes (Newman 1969; Bristow, Campbell & Calissendorff 1984; Tyree & Sperry 1988), it is an open question how rhizosphere and xylem properties interact to limit water uptake. In this paper, we answer this question with a model.

The theory of hydraulic limits on water uptake begins with Darcy’s law, which can be applied to steady-state flow through the soil–plant hydraulic continuum:

\[ E = -K \frac{d \Psi}{dx}, \]

where E is the transpiration rate (per leaf area), dΨ/dx is the water potential gradient driving flow, and K is the hydraulic conductivity expressed per leaf area (Table 1 lists symbols, definitions, and units). Figure 1 shows the steady-state relationship between E and leaf Ψ for a constant bulk soil Ψ(Ψs = the Ψintercept). If K is a constant, E is directly proportional to the decrease in leaf Ψ and there is no hydraulic limit to E or leaf Ψ (dashed line 4 in Fig. 1).

Hydraulic limits arise because K is not constant, but instead decreases in xylem and soil as a function of decreasing Ψ. In the xylem, the decline in K is caused by cavitation, and the K(Ψ) function is described by a ‘vulnerability curve’ (e.g. Fig. 3). In the soil, the decrease in K occurs by the same mechanism causing cavitation in xylem: the displacement of water-filled pore space by air as capillary forces fail (Hillel 1980; Pockman, Sperry & O’Leary 1995). The K(Ψ) function for soil depends largely on soil texture, with more sensitive functions for coarser soils (Hillel 1980).

When Ψ-dependent K is incorporated into Darcy’s law, there is no longer a directly proportional relationship between E and Ψ (Fig. 1, curves 1–3). Instead, increases in E are associated with progressively disproportionate decreases in Ψ because of declining K. The E reaches a maximum (Ecrit) at the corresponding minimum leaf Ψ(Ψcrit). At these critical values, K(Ψ) has approached zero somewhere in the hydraulic continuum (Appendix). As Ψs decreases, Ecrit declines (Fig. 1, compare curves 1–3). When Ψs = Ψcrit, the plant cannot transport water.

If stomata allow E to exceed Ecrit long enough for steady-state conditions to develop, the positive feedback

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between decreasing $K$ and $Y$ becomes unstable: a phenomenon dubbed ‘runaway cavitation’ when it occurs in xylem (Tyree & Sperry 1988). Runaway cavitation breaks the hydraulic rope and eliminates water transport by driving $K$ to zero. A model by Tyree & Sperry (1988) predicted an $E_{\text{crit}}$ that was only slightly greater than actual maximum $E$ in four diverse tree species, suggesting stomatal regulation of $E$ was adaptive in avoiding hydraulic failure of the xylem. The gas exchange capacity of plants may have hydraulic constraints.

The Tyree and Sperry model, however, did not incorporate the $K (Y)$ relationship for the soil. Transpiration-driven decreases in $Y$ soil are accentuated in the rhizosphere because of the cylindrical geometry of water uptake (Cowan 1965; Newman 1969; Bristow, Campbell & Calissendorff 1984), and ‘runaway cavitation’ can potentially occur at the soil–root interface. Rhizosphere limitations should be especially important for coarse soils and plants with less absorbing root area relative to their transpiring leaf area (Newman 1969). Although variable rhizosphere conductance has been incorporated in water uptake models (Cowan 1965; Bristow et al. 1984), none have incorporated variable xylem conductance. It is not clear whether below-ground hydraulic constraints are more or less important than those of the xylem.

The model presented in this paper shows how three causal factors – (1) cavitation resistance, (2) root:leaf area ratio ($A_R / A_L$), and (3) soil type (specifically, soil texture) – interact to set hydraulic limits on water transport. The analysis of cavitation resistance includes the influence of root xylem, which is more vulnerable than canopy xylem in many species (Sperry & Saliendra 1994; Alder, Sperry & Pockman 1996; Hacke & Sauter 1996; Mencuccini & Comstock 1997). The purpose of the model is to obtain a

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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<tr>
<td>$A_L$</td>
<td>leaf area</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$A_R$</td>
<td>absorbing root area</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$a$</td>
<td>fraction of plant volume</td>
<td>–</td>
</tr>
<tr>
<td>$b$</td>
<td>soil texture parameter</td>
<td>–</td>
</tr>
<tr>
<td>$c$</td>
<td>Weibull function parameter</td>
<td>–</td>
</tr>
<tr>
<td>$C$</td>
<td>capacitance (per $A_L$)</td>
<td>mmol MPa$^{-1}$ m$^{-2}$</td>
</tr>
<tr>
<td>$d$</td>
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<td>$E_{\text{crit}}$</td>
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<td>$F$</td>
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</tr>
<tr>
<td>$i$</td>
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<tr>
<td>$K_s$</td>
<td>maximum soil conductivity</td>
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<tr>
<td>$k_s$</td>
<td>maximum element conductance</td>
<td>mmol s$^{-1}$ MPa$^{-1}$ m$^{-1}$</td>
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<tr>
<td>$L$</td>
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<tr>
<td>$r$</td>
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<td>$W_s$</td>
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<td>mmol m$^{-3}$</td>
</tr>
<tr>
<td>$X$</td>
<td>soil conductance factor</td>
<td>m</td>
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Greek symbols

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<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Units</th>
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<tr>
<td>$\phi$</td>
<td>matric flux potential</td>
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<td>$\psi$</td>
<td>water potential</td>
<td>MPa</td>
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<td>$\psi_s$</td>
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<td>MPa</td>
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<td>$\psi_{\text{crit}}$</td>
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<td>MPa</td>
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Table 1. List of major symbols and their definitions. Units are those used in equations. Values cited in text or figures may have different units.
better understanding of biophysical limits on water uptake and their relevance to physiological responses of plants to water availability.

THE MODEL

Flux balance equations and hydraulic conductance functions

The model uses the standard finite-difference approach to solving Darcy’s law for the soil–plant hydraulic pathway (Campbell 1985). The soil–leaf continuum was divided into ‘nodes’ and connecting ‘elements’ (Fig. 2; see below). The soil elements defined a cylindrical rhizosphere adjacent to the absorbing roots. For each node \( i \) (ascending from \( i = 1 \) at the leaves, Fig. 2), we wrote the flux balance, or Richards’, equation (Ross & Bristow 1990) in which the difference in flux of water leaving versus entering node \( i \) equals the change in water content at node \( i \) \( (\Delta W = W_{i+1} - W_{i-1}) \) over time step \( \Delta t \) \( (t_2 - t_1) \). These equations assume the driving forces \( (\Delta \Psi_i = \Psi_{i+1} - \Psi_{i-1}) \) are differences in water pressure (i.e. osmotic effects are ignored):

\[
F_i (\Psi_i, \Psi_{i+1}, \Psi_{i-1}) = k_i \Delta \Psi_{i-1} - k_i \Delta \Psi_i - \Delta W/\Delta t, \tag{2}
\]

where \( k_i \) is the hydraulic conductance of the element sub-tending node \( i \), and \( F_i \) is the mass balance for node \( i \) which equals zero for the correct values of \( \Psi_i \), \( \Psi_{i+1} \), and \( \Psi_{i-1} \). Note that in formulating Eqn 2, hydraulic conductivity \( (K, \text{ Eqn 1}) \), which is a length- and/or area-independent parameter, is converted to conductance \( (k) \) which incorporates the specific geometry of element \( i \) (Table 1).

The water content \( (W, \text{ moles of water per volume of tissue or soil}) \) and hydraulic conductance in Eqn 2 are both functions of \( \Psi \). In the soil we used Campbell’s (1985) equation,

\[
W_i = W_s (\Psi_i / \Psi_s)^{-1/b} \tag{3}
\]

where \( W_s \) is the water content at maximum hydration where \( \Psi_s = \Psi_e \), and \( b \) is a soil-texture parameter that increases with finer texture (Table 2). The value for \( \Psi_e \) in soil was taken as the ‘air-entry’ value, which is also a function of soil texture (Table 2; Campbell 1985). In the plant, \( \Delta W_i \) for Eqn 2 was calculated as:

\[
\Delta W_i = a_i \Delta \Psi_i A_{L} C, \tag{4}
\]

where \( C \) is the whole-plant capacitance or change in water content per change in \( \Psi \) per leaf area, \( A_{L} \) is the leaf area, \( \Delta \Psi_i \) is the change in \( \Psi \) at node \( i \) over the time step, and \( a_i \) is the fraction of the total plant volume with which node \( i \) exchanges water.

The hydraulic conductance function for the rhizosphere elements was taken from Campbell (1985):

\[
k_i = X_i K_s (\Psi_i / \Psi_e)^{(2 + 3/b)}, \tag{5}
\]

where \( K_s \) is the maximum soil hydraulic conductivity at saturation (at \( \Psi_s = \Psi_e \)), \( b \) is the soil texture parameter in Eqn 3, and \( X_i \) is a factor that converts hydraulic conductivity to hydraulic conductance. We assumed a cylindrical geometry for water uptake by roots so that nodes were at progressively greater radial distances from the root centre (Fig. 2). The ‘conductance factor’ for the cylindrical flow geometry of the rhizosphere elements is:

\[
X_i = 2\pi l \ln^{-1} (r_{i+1}/r_i), \tag{6}
\]

where \( l \) is the total length of absorbing roots, and \( r_i \) is the radius of node \( i \) (Campbell 1985).

We used a log transformation (Passioura & Cowan 1968) to set rhizosphere nodes exponentially closer together nearer to the root where \( \Psi \) gradients are largest. This transformation equates to:

\[
r_i = r_{i+1} (r_{\text{max}}/r_i)^{(l - s)/m}, \tag{7}
\]

where \( r_i \) is the radius of node \( i \), \( r_{i+1} \) is the radius of the root surface, \( r_{\text{max}} \) is the radius of the outermost rhizosphere node, \( s \) is the node number of the root surface, and \( m \) is the number

Figure 2. Model organization showing division of the soil–plant hydraulic continuum into 16 nodes and 15 elements. Element conductance is symbolized as variable electrical resistance. Nodes exchange water with a volume of plant or soil. Shoot and root branching was represented by the series conductance of hydraulically equivalent units \( (k_1: \text{leaves}, k_2: \text{shoots}, k_3: \text{transporting roots}, k_4: \text{absorbing roots}) \). Soil node spacing was set by a log transformation of the distance from the root surface to the outermost soil node (Eqn 7). Roots were assumed to exhibit uniform spacing in a defined soil volume. Solution of Eqn 13 gave \( \Psi \) of nodes 1–16 at controlled values of flux from node 1 \( (=E_{A_{L}}) \).
of rhizosphere elements. We assumed the absorbing roots were uniformly aligned in the soil volume such that their associated soil cylinders exhibited closest packing in the soil space. Under these conditions, \( r_{\text{max}} \) is related to root length density of absorbing roots (\( L \): length per soil volume):

\[
r_{\text{max}} = (\pi L)^{-0.5}
\]  
(Campbell 1985).

The hydraulic conductance function for the plant elements was based on a Weibull model fit (Rawlings & Cure 1985; Neufeld et al. 1992) to empirical vulnerability curves (Fig. 3). The Weibull equation includes two curve-fitting parameters \( (d \) and \( c)\):

\[
k_i = k_c e^{-\Psi_i d^c},
\]  
(9)

where \( k_i \) is the hydraulic conductance of element \( i \), \( \Psi_i \) is the xylem pressure at node \( i \) and \( k_c \) is the element’s maximum conductance in the absence of cavitation. Values for \( d \) and \( c \) were obtained using a standard curve-fitting routine. There is no conductance factor in Eqn 9 because \( k_i \) was inputted as conductance rather than conductivity.

A preliminary model solved the nodal Richards’ equations (Eqn 2) by converting them to ordinary differential equations (for \( d\Psi_i/dt \)) and integrating with the Runge-Kutta procedure (Press et al. 1989). This proved inordinately time-consuming on the computer because the non-linearity of the \( k \) functions in the equation required extraordinarily small time steps (< 0.001 s) under wet soil conditions. The present version linearized the Richards’ equation using the ‘Kirchhoff transform,’ an integral transform (Ross & Bristow 1990) that substitutes ‘matric flux potential’ (\( \Phi \)) for \( \Delta \Psi \) as the driving force for flow (Campbell 1985). Matrix flux potential is the integral of hydraulic conduc-
tance from \( \Psi = \Psi_i \) to \(-\infty\):

\[
\Phi_i = \int_{\Psi_i}^{\Psi_e} k_i (\Psi) \ d\Psi_i.
\]  
(10)

Integrating Eqn 5 for soil element conductance gives:

\[
\Phi_i = k_i \Psi_i / (1 – 3/b).
\]  
(11)

Equation 9, the Weibull function for plant hydraulic conductance, can only be integrated using numeric methods. The equation was converted to the complement of an incomplete gamma function for which a numerical routine was available (Press et al. 1989):

\[
\Phi_i = k_c \int_{z(\Psi_i)}^{\infty} e^{-z} z^{(h-1)} \ dz,
\]  
(12)

where \( z = (\Psi_i d^c) \), and \( h = 1/c \).

The Richards’ equation (Eqn 2) written in the form of \( \Phi \) gives:

\[
F_i (\Phi_i, \Phi_{i+1}, \Phi_{i-1}) = (\Phi_i - \Phi_{i-1}) - (\Phi_{i+1} - \Phi_i) - (\Delta W / \Delta t),
\]  
(13)

which results in element conductance of unity, linearizes the steady flow equation, and allows it to be integrated for each element using practical time steps of 1 h (the default setting). However, the transient flow problem remains non-linear because of the dependence of \( W \) on \( \Psi \) (Eqn 3). To solve the set of \( i + 1 \) simultaneous equations for \( F_i = 0 \) at each time step, we used the Newton–Raphson method (Campbell 1985). This routine iteratively adjusts each \( \Psi_i \) until \( \Sigma_{i=1}^{n} |F_i| \) converged on zero (where \( n = \) total nodes in model). The model was written in visual basic within the Excel 5.0 spreadsheet application (Microsoft, Inc.).
Discretizing the soil–plant continuum

An important advantage of the Kirchhoff transform (Eqn 13) is that it minimizes the number of nodes required to obtain the steady-state solution of $E_{\text{crit}}$ and associated parameters. With the Richards’ equation (Eqn 2), $E_{\text{crit}}$ estimates converge on the proper solution as the continuum is more finely discretized, and preliminary tests are necessary to determine an acceptable number of nodes. The Kirchhoff transform gives the correct $E_{\text{crit}}$ and $\Psi_{\text{crit}}$, whether the continuum is represented by 1 or 100 nodes (Appendix), as long as the $k(\Psi)$ function is the same along the flow path. To solve for steady-state $E_{\text{crit}}$, discretizing is only necessary if the $k(\Psi)$ functions change through the continuum, as they do within soil because of the changing conductance factor $X_i$ (Eqns 5 & 6), and within the plant because of possibly different values of $d$ and $c$ for the Weibull function (Eqn 9) along the flow path. We applied the same procedures developed by Ross & Bristow (1990) for applying the Kirchhoff transform to a hydraulic continuum across media with different $k(\Psi)$ and $W(\Psi)$ functions.

We divided the soil–leaf continuum into 16 nodes with 15 connecting elements (Fig. 2). The plant consists of four elements: absorbing roots, transporting roots, stems, and leaves. This allowed us to vary the elements: absorbing roots, transporting roots, stems, and 15 connecting elements (Fig. 2). The plant consists of four compartments if desired. In organizing the plant elements, we assume that the axial conductance is infinite, and possibly different values of $d$ and $c$ for the Weibull function (Eqn 9) along the flow path. We applied the same procedures developed by Ross & Bristow (1990) for applying the Kirchhoff transform to a hydraulic continuum across media with different $k(\Psi)$ and $W(\Psi)$ functions.

Node 1 is the evaporating surface of the leaves, and the subtending conductance ($k_1$) is the collective conductance of all laminae from the junction with the petiole to the evaporating surface. This flow path includes both xylem and mesophyll components. Node 2 is the petiole–lamina junction, and its subtending conductance ($k_2$) is the conductance of the xylem of the entire branched stem system, including the petioles. Node 3 is the stem–root junction, and the subtending conductance ($k_3$) is the conductance of the xylem of the non-absorbing root system. Node 4 is the junction between water-absorbing and non-absorbing roots. The associated conductance ($k_4$) is the collective conductance of all absorbing roots from the root surface to node 4. Although the flow path in these roots includes both xylem (axial flow) and non-xylem (radial flow) components, we assume that the axial conductance is infinite, and that the water uptake along the length of an absorbing root will be equal. This is a reasonable assumption for the presumably short (= 100–200 mm) absorbing zones behind root tips (Steudle 1994).

The rhizosphere was more finely discretized than the plant because of the changing $k(\Psi)$ function with distance from the root surface (Eqn 5). The total rhizosphere volume was divided into 10 nodes. However, tests showed that, under conditions when soil properties were determining $E_{\text{crit}}$ and $\Psi_{\text{crit}}$ (see ‘Results’), as few as three nodes were required for these parameters to be within 2% of their value when using a 50 node model. The reason for such efficient discretizing is the log transformation of the nodes which concentrates them close to the root where the limiting conductance develops (Fig. 2; Eqn 7; Passioura & Cowan 1968).

Associated with each node is a volume of plant tissue or soil with which water was exchanged as nodal pressures changed. The total nodal volume was taken as the adjacent half of the element volume above (downstream from) the node plus the adjacent half of the element volume below (upstream from) the node.

Determination of hydraulic limits

The model was applied to finding $E_{\text{crit}}$ and $\Psi_{\text{crit}}$ for the continuum. Boundary conditions for the equation set (Eqn 13) were that $\Psi$ at the outermost soil node ($i = 16$) was set to a constant ($\Phi_{16} = \text{constant}$), as was the product $E_{\text{crit}}$ at the outermost soil node ($i = 16$) (Appendix). As the product $E_{\text{crit}}$, which in terms of Eqn 13 was the flux of element $i = 0$ (substituted for $\Phi_1 - \Phi_0$), initial conditions were that $\Psi$ at all nodes equalled $\Psi_{16}$.

The model was verified by setting $E$ to permissible values and testing for flux balance. Under these conditions, fewer than 20 iterations were required to make $\Sigma_{i=1}^{16} |F_i| < 0·001$ mmol s$^{-1}$, and cumulative water depletion was within 0·0001% of cumulative transpiration.

To determine $E_{\text{crit}}$, $E$ was incremented in steps of 0·01 mmol s$^{-1}$ m$^{-2}$ from permissible values until $\Sigma_{i=1}^{16} |F_i|$ failed to converge on zero after a maximum of 30 iterations. At each increment, the model was run for enough time steps to achieve steady-state flow ($\Sigma_{i=1}^{16} |\Delta \Psi_i|/\Delta t < 0·001$ MPa h$^{-1}$). We deliberately set liberal requirements for model failure by adjusting the criteria for flux balance to $\Sigma_{i=1}^{16} |F_i| \leq 1$ mmol s$^{-1}$. The $E_{\text{crit}}$ and $\Psi_{\text{crit}}$ were the last permissible values before model failure.

The choice of the $E$ increment can influence the $E_{\text{crit}}$ and $\Psi_{\text{crit}}$ estimates. The prediction of $E_{\text{crit}}$ is less sensitive to the $E$ increment than $\Psi_{\text{crit}}$ because $E$ approaches $E_{\text{crit}}$ in an asymptotic manner, while $\Psi$ decreases abruptly to $\Psi_{\text{crit}}$ (Fig. 1). Mathematically, $\Psi_{\text{crit}} = \infty$ because our soil and xylem $K(\Psi)$ functions never reach zero (Eqns 5 & 9; Appendix). Thus, decreasing the $E$ increment caused the model to converge on $E_{\text{crit}}$, as $\Psi_{\text{crit}}$ became increasingly negative. Our choice of a 0·01 mmol s$^{-1}$ m$^{-2}$ $E$ increment was based on a very conservative estimate of the control sensitivity of stomata. Using this increment, $\Psi_{\text{crit}}$ corresponded to > 98% loss of conductance in the limiting element of the continuum (e.g. Fig. 7).
Model parameters

Plant parameters were based largely on data from woody plants.

Secondary parameters

Secondary parameters were held constant for all simulations except when varied for a sensitivity analysis (Table 3).

Maximum hydraulic conductance in the absence of cavitation ($k_c$ in Eqn 9) was equal for all plant elements and scaled with leaf area to give a leaf-specific conductance of 5 mmol s$^{-1}$ MPa$^{-1}$ m$^{-2}$ for the whole plant. This is a typical value for woody plants (Meinzer et al. 1995; Saliendra, Sperry & Comstock 1995). The equal conductance for shoot and root systems was a realistic approximation based on measurements in a variety of herbaceous and woody plants (Hellkvist, Richards & Jarvis 1974; Saliendra & Meinzer 1989; Meinzer et al. 1992; Sperry & Pockman 1992; Yang & Tyree 1993; Menuccini & Comstock 1997). While there is evidence that leaves ($k_4$) and absorbing roots ($k_3$) have lower conductance than stems and transporting roots (Yang & Tyree 1994; Lopez & Nobel 1991), we set them equal for the sake of simplicity, while conducting a sensitivity analysis to determine the influence of lower conductance in the $k_1$ and $k_2$ components.

For plant capacitance ($C$ in Eqn 4), we used the whole-plant, leaf-specific value of 5 mmol Mpa$^{-1}$ m$^{-2}$ as estimated for apple trees by Landsberg, Blanchard & Warrit (1976). The choice of $a$ in Eqn 4 divided whole-plant capacitance into leaf ($a = 0.4$), stem ($a = 0.5$), transporting root ($a = 0.05$), and absorbing root ($a = 0.05$) components. The choice of $a$ was based on biomass fractions of roots, stems, and leaves reported in Givnish (1995) for 2–6 m trees. The radius of absorbing roots ($r_a$, in Eqn 7), was 0.1 mm; a typical value for fine roots (Caldwell & Richards 1986).

Primary parameters

Primary parameters were the hypothetical causal factors underlying the hydraulic limits: cavitation resistance, root:leaf area ($A_R:A_L$), and soil texture.

Four cavitation resistances were chosen to represent the span of known values (Fig. 3) and to establish the $d$ and $c$ values for the $k(Ψ)$ functions of the plant elements (Eqn 9). On the vulnerable end was water birch (Betula occidentalis, water birch; Alder et al. 1997), representative of obligate riparian trees in the Western United States; on the resistant end was ceanothus (Ceanothus crassifolius, hoary leaf ceanothus; Portwood et al. 1997), a shrub of the California chaparral. Intermediate vulnerabilities were represented by sagebrush, a mesic-adapted Artemisia species (Artemisia tridentata ssp. vaseyana, mountain sagebrush; K.J. Kolb and J.S. Sperry, in review), and boxelder (Acer negundo; U. Hacke and J.S. Sperry, unpublished). All vulnerability data were collected using either the air-injection method (Cochard, Cruziat & Tyree 1992; Sperry & Saliendra 1994) or the centrifugal force technique (Pockman et al. 1995; Alder et al. 1997). Data were from stem segments of between 5 and 10 mm diameter. In water birch and boxelder there were additional data from similarly sized root segments (Fig. 3; dashed curves). No data were available for smaller absorbing roots or for leaf xylem.

For sagebrush and ceanothus simulations where we had no root vulnerability data, all four conductance elements were given the same $k(Ψ)$ function. In water birch and boxelder, the two root elements were given the $k(Ψ)$ function for root xylem and the two shoot elements were given the corresponding function for stem xylem. Although the absorbing root and leaf elements include non-xylem flow paths, without any data on the $k(Ψ)$ function we applied the xylem functions by default.

We ran simulations using $d$ and $c$ values that resulted in no cavitation and constant plant $k$ over physiological values of $Ψ$ ($d > 50, c > 100$). Under these circumstances, the only hydraulic constraint on flux and pressure was in the soil and rhizosphere components of the continuum.

The $A_R:A_L$ was varied from a minimum of 0.24 to 40, a range that includes most measured values (Rendig &

| Table 3. Sensitivity analysis. Parameters tested were capacitance, whole-plant $k/A_L$, percentage of plant resistance in root elements 3 and 4 (% $R$ 3+4; with equal resistance in elements 3 and 4); percentage of resistance in root element 4 (% $R$ 4; with equal resistance for 3+4 and 1+2), percentage of resistance in leaf (% $R_1$, equal resistance for 3+4 and 1+2), root length (l), distance to outermost soil node ($r_{max}$), and $k_4 = k_{d4}$ vs. the same $k(Ψ)$ function as $k_4$. Default and test values of each parameter are shown: %Δ = percentage of increase in test value vs. default; %Δ$E_{crit}$ = percentage change in $E_{crit}$; %ΔΨ$_{crit}$ = percentage change $Ψ_{crit}$.

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<th>Parameter</th>
<th>Default</th>
<th>Test</th>
<th>%Δ</th>
<th>%Δ$E_{crit}$</th>
<th>%ΔΨ$_{crit}$</th>
</tr>
</thead>
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<tr>
<td>Capacitance (mol MPa$^{-1}$ m$^{-2}$)</td>
<td>5</td>
<td>7</td>
<td>+40</td>
<td>0</td>
<td>-3.0</td>
</tr>
<tr>
<td>Whole plant $k/A_R$ (mmol s$^{-1}$ MPa$^{-1}$ m$^{-2}$)</td>
<td>5</td>
<td>7</td>
<td>+40</td>
<td>+7.1</td>
<td>+1.5</td>
</tr>
<tr>
<td>% $R$ 3+4</td>
<td>50</td>
<td>70</td>
<td>+40</td>
<td>0</td>
<td>-1.5</td>
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<tr>
<td>% $R$ 4</td>
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<td>35</td>
<td>+40</td>
<td>0</td>
<td>0</td>
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<td>4200</td>
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<td>$k_{d4}$</td>
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</table>
Taylor 1989; Glinski & Lipiec 1990; Tyree, Velez & Dalling 1997). This ratio also represented the ratio of hydraulic conductance in rhizosphere versus plant because these were proportional to their respective root and leaf areas. The ratio was varied by changing \( A_L \) and/or \( A_R \). The \( A_R = 2\pi r_L V \), where \( V = \) soil volume = 0.3 m\(^3\). We varied \( A_R \) by changing \( L \). This influenced rhizosphere conductance via changes in \( l \) (Eqn 6) and \( r_{\text{max}} \) (Eqn 7). We also analysed the independent effect of changing \( l \) versus \( r_{\text{max}} \).

Several soil types were chosen to span the range of textures from clay through loam to coarse sand (Table 2).

## Controlled drought experiments

A comprehensive comparison between predictions of \( E_{\text{crit}} \) and \( \Psi_{\text{crit}} \) with empirical data awaits experiments designed explicitly for that purpose. However, we were able to make a preliminary comparison using data from controlled drought experiments on sunflower (Helianthus annuus) and water birch (Betula occidentalis).

Potted plants were grown from seed in fritted clay under well-watered greenhouse conditions until they were \( 0.5–1.5 \) m tall. Cylindrical pots were \( 0.15 \) m in diameter and \( 0.76 \) m tall, holding \( 0.014 \) m\(^3\) of soil. Values for soil parameter \( b \) were obtained by best fit of Eqn 3 to moisture release data for fritted clay (van Bavel, Lascano & Wilson 1978: \( b = 5.12 \)). The saturated hydraulic conductivity \( (K_s, \text{Eqn 5}) \) was set to \( 11.1 \text{ mol s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1} \) based on data from van Bavel et al. (1978) and assuming their water content for a drained pot of 0.39 m height.

Vulnerability curve parameters \( c \) and \( d \) (Eqn 9) were the same as reported in Fig. 3 for water birch. In sunflower, they were obtained from the best fit of Eqn 9 to data obtained for mature stems \( (c = 3, d = 2.3; \text{ J. S. Sperry, unpublished results}) \) using the centrifugal force method (Pockman et al. 1995; Alder et al. 1997). The sunflower vulnerability curve was very similar to that for boxelder stem xylem (Fig. 3).

Values for \( k_s \) of the plant elements (Eqn 9) were based on \( k \) measurements of root and shoot systems of well-watered plants using the vacuum canister method of Kolb, Sperry & Lamont (1996). This method gave approximate \( k_s \) values for the two root elements in series and the two shoot elements in series. Conductance was divided equally among the two elements within the root and shoot system.

The \( A_R:A_L \) was not measured. A range was estimated based on published values of root length per leaf area which range from 3900 to 14 000 m\(^2\) (Rendig & Taylor 1989). These correspond to \( A_R:A_L = 2.4–9.1 \), assuming \( r_s = 0.1 \) mm. Measurements of \( A_L \) and a soil volume of 0.014 m\(^3\) allowed us to set a corresponding range of \( L \) (Table 4).

Given the uncertainty of \( A_R:A_L \), and of using \( k_s \) values measured on nonintact plants to represent the \textit{in situ} values, we used the model to estimate a liberal range of \( E_{\text{crit}} \) values as a function of soil \( \Psi (i.e., \Psi_{\text{1d}}) \). The high end was based on maximum \( A_R:A_L \) in combination with a 20% increase in \( k_s \) of each plant element over the measured value; the low end used minimum \( A_R:A_L \) and a 20% decrease of \( k_s \).

To obtain data on how \( E \) varied with soil \( \Psi (\Psi_s) \), water was withheld and periodic measurements of \( E \) and \( \Psi_s \) were made during the drought. The \( E \) was measured in a whole-canopy open gas exchange system as described in Saliendra et al. (1995). The \( E \) measurements were destructive because leaf area was measured by defoliating the plant and using a bench-top leaf area meter (LiCor, Lincoln, NE, USA). The \( \Psi_s \) was measured psychrometrically by removing soil samples from ports in the sides of the pots at 300 mm depth \((n = 3 \text{ samples per pot}) \) and sealing the samples in psychrometer chambers (Merrill Scientific, Logan, UT, USA).

## RESULTS

### Analysis of \( E_{\text{crit}} \) and \( \Psi_{\text{crit}} \)

The dependence of \( E_{\text{crit}} \) on \( \Psi \) is shown in Fig. 4 for loam soil (Table 2). The five xylem types are shown, four with varying cavitation resistance (open symbols) and one with no cavitation (solid symbols). Where the non-cavitating curve shows higher \( E_{\text{crit}} \) and lower \( \Psi_{\text{crit}} \) than the cavitating curves, the xylem was limiting. Where the two curves are the same, the rhizosphere was limiting. For all curves, \( E_{\text{crit}} \) decreased to zero as \( \Psi \) decreased to \( \Psi_{\text{crit}} \) (\( \Psi_{\text{crit}} \) is shown by arrows on the \( \Psi_s \) axis in Fig. 4a).

At the relatively high \( A_R:A_L \) of 10 in Fig. 4a, xylem cavitation was limiting (compare open versus solid symbols).

| Parameter | Sunflower measured | Water Birch measured | |
| --- | --- | --- | |
| Whole plant \( k_s \) (mmol m\(^{-3}\) s \(^{-1}\) MPa\(^{-1}\)) | 1.45 ± 0.77 | 2.18 ± 0.76 | |
| \% \( R = 3+4 \) | 85 ± 4 | 52 ± 8 | |
| \( A_L \) (m\(^2\)) | 0.195 ± 0.119 | 0.321 ± 0.1 | |
| \( L \) (mm m\(^{-3}\)) | – | 0.054–0.195 | |

Table 4. Plant parameter settings for sunflower and water birch simulations shown in Fig. 8. Soil settings were for fritted clay (Table 2) using a soil volume of 0.014 m\(^3\). Means are based on \( n = 10 \) plants for sunflower and \( n = 9 \) plants for water birch. Plant parameters were whole-plant \( k_s \) (all four elements in series), percentage of total resistance in elements 3 and 4 (% \( R = 3+4 \), with equal resistances per element), leaf area \((A_L)\) and root length density \((L)\). Settings for \( L \) corresponded to a range of 2.4–9.1 for \( A_R:A_L \). The \( d \) and \( c \) values for the Weibull function (Eqn 9) are given in Fig. 3 for water birch, and were 2.3 and 3, respectively, for sunflower.
more vulnerable the xylem to cavitation, the lower was \( E_{\text{crit}} \) at a given \( Y_s \), and the higher (less negative) was \( Y_{\text{crit}} \). The \( Y_{\text{crit}} \) was sufficient to cause \( \approx 98-99\% \) loss of xylem conductance based on the xylem vulnerability curve (Fig. 3). Decreasing \( A_R:A_L \) from 10 to 5 (Fig. 4b) and 1 (Fig. 4c) caused a gradual transition from xylem cavitation to rhizosphere conductance as the limiting factor for \( E_{\text{crit}} \) and \( Y_{\text{crit}} \). This is evident from the identical \( E_{\text{crit}} \) for ceanothus xylem versus non-cavitating xylem at \( A_R:A_L = 1 \) (Fig. 4c). The same was nearly true for sagebrush. The more cavitation-susceptible xylem types (boxelder, water birch) were still xylem-limited (Fig. 4c). However, as \( A_R:A_L \) was decreased further (data not shown), the rhizosphere became limiting for all xylem types.

Figure 5 extends the findings in Fig. 4 to different soils. It shows \( Y_{\text{crit}} \) as a function of \( A_R:A_L \) for cavitating (solid lines) versus non-cavitating (dashed lines) xylem. Figure 5a is for sandy loam (Table 2). At lower \( A_R:A_L \), the \( Y_{\text{crit}} \) was the same with or without cavitation (overlapping dashed and solid lines) and the rhizosphere was limiting. At higher \( A_R:A_L \), the \( Y_{\text{crit}} \) for cavitating xylem converged on the \( Y \) causing \( \approx 98-99\% \) loss in xylem conductance (Fig. 3) while the \( Y_{\text{crit}} \) for non-cavitating xylem continued to decrease. The threshold \( A_R:A_L \) marking the transition between rhizosphere versus xylem limitation is where \( Y_{\text{crit}} \) values for cavitating versus non-cavitating xylem depart.

It is evident from Figs 4 and 5a that each xylem type had a threshold \( A_R:A_L \) above which xylem cavitation was limiting and below which the rhizosphere conductance was limiting. The \( A_R:A_L \) threshold increased as cavitation resistance increased.

Figure 5b generalizes the results in Fig. 5a across five soil types. The dashed lines again represent \( Y_{\text{crit}} \) in the absence of cavitation, with lines 1–5 indicating soils of

increasingly finer texture from sand to loam (3 is sandy loam from Fig. 5a). The horizontal solid lines represent $\Psi_{\text{crit}} = \Psi$ at 99% loss of xylem conductance. The $A_{R:a_l}$ threshold for a given soil and xylem type is approximated by the intersection of dashed and solid lines. The actual transition was smooth (Fig. 5a) indicating a range of $A_{R:a_l}$ over which the rhizosphere exerted a gradually diminishing influence (compare Figs 5a & b).

The coarser the soil type, the more limiting the soil was to plant fluxes and pressures relative to the xylem, and the higher was the $A_{R:a_l}$ threshold for xylem limitation. For example, the coarsest soil (sand, dashed line 1), limited $\Psi_{\text{crit}}$ in all but the most cavitation-susceptible type (water birch), and then only at the highest $A_{R:a_l}$. In contrast, in the finest soil analysed (loam, dashed line 5), the xylem determined $\Psi_{\text{crit}}$ even in the most cavitation-resistant species. Simulations for soils finer than loam were all xylem-limited.

Increasing $A_{R:a_l}$ above the xylem-limiting threshold continued to influence $E_{\text{crit}}$ up to a second threshold (Fig. 6). The influence is evident in the sagebrush results in Fig. 4: increasing $A_{R:a_l}$ caused $E_{\text{crit}}$ to increase for intermediate $\Psi_r$ (e.g. $\Psi_{\text{crit}} > \Psi_r < 0$). The $E_{\text{crit}}$ was maximized by progressively higher $A_{R:a_l}$ in more cavitation-resistant species (Fig. 6).

The results in Fig. 5 show conditions under which xylem versus rhizosphere conductance is more hydraulically limiting, but they do not indicate in which conducting element $k$ approaches zero at hydraulic failure. When the xylem was limiting, the element with $k \equiv 0$ was in the leaf element, because it has the lowest $\Psi$, and also in the transporting root element, if the root elements were more vulnerable to cavitation than the stem elements (as for water birch and boxelder). Figure 7 shows an example (from boxelder xylem under xylem-limiting conditions (triangles, sandy loam soil, $A_{R:a_l} = 27$). The leaf and transporting root elements (1 and 3) had near-zero hydraulic conductance at $E_{\text{crit}}$ (Fig. 7, solid triangles). Although a substantial reduction in hydraulic conductance also occurred at the root–soil interface, rhizosphere element conductance (e.g. 5, 6 and 7) was still above that in xylem elements 1 and 3. (Note: elements were exponentially shorter as they approached the root; Fig. 2).

When the soil conductance was limiting $E_{\text{crit}}$, the hydraulic bottleneck at the root–soil interface was responsible. Figure 7 also shows boxelder under soil-limiting conditions (circles, sandy loam soil, $A_{R:a_l} = 1$). At $E_{\text{crit}}$, the elements with the lowest conductance were adjacent to the root surface (Fig. 7, solid circles, elements 5, 6 and 7) rather than in the plant.

It should be emphasized that, while $E_{\text{crit}}$ and $\Psi_{\text{crit}}$ are associated with $k$ reaching zero somewhere in the continuum, the total conductance in the continuum may still be substantial. In Fig. 7, for example, the total loss of conductance in the continuum at $E_{\text{crit}}$ was 58% and 86% for xylem- and rhizosphere-limited cases, respectively.

Decreasing $A_{R:a_l}$ transferred the hydraulic limitation from xylem to rhizosphere because it reduced the ‘resting’ (i.e. $E \approx 0$) rhizosphere conductance (Fig. 7; compare open triangles with open circles), therefore causing the rhizosphere bottleneck to create the lowest $k$ values in the continuum as $E$ approached $E_{\text{crit}}$. At high $A_{R:a_l}$, the resting conductance in the rhizosphere was much greater than in the plant (Fig. 7, open triangles); thus, even though a rhizosphere bottleneck developed as $E$ increased, it did not result in the limiting conductance for the continuum. Lower $A_{R:a_l}$ brought the resting conductance closer to those in the plant (Fig. 7, open circles) with the result that rhizosphere conductance became limiting as flux increased. At intermediate $A_{R:a_l}$, the relative limitation of rhizosphere versus xylem was less pronounced, and both components exerted influence, as evidenced by the smooth transition from rhizosphere to xylem limits in Fig. 5a, and the influence of $A_{R:a_l}$ on $E_{\text{crit}}$ under xylem-limited conditions (Fig. 6).

**Sensitivity analysis**

Table 3 summarizes a sensitivity analysis for secondary model parameters under xylem-limited conditions. As

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**Figure 6.** $E_{\text{crit}}$ relative to $E_{\text{crit}}$ at $A_{R:a_l} = 40$. All values are for loam soil at soil $\Psi = 1/3 \Psi_{\text{crit}}$ (xylem-limiting conditions).
expected, $\Psi_{\text{crit}} = \Psi$ at 98–99% loss of xylem conductance regardless of parameter settings.

The $E_{\text{crit}}$ increased 7.1% for a 40% increase in whole-plant $k_i/A_L$ (maximum leaf-specific conductance). The effect of increasing $L$ (and $A_R$) was primarily due to the increase in $I$ (28–6% response) rather than a decrease in $r_{\text{max}}$ (10–7% response), meaning that total root length was more important than density. The $E_{\text{crit}}$ was not influenced by the allotment of $k_i$ among elements; however, it did increase by 9–6% when the absorbing root $k$ was held constant (Table 3).

The $E_{\text{crit}}$ values were for steady-state conditions where $\Psi$ of outermost soil node was held constant. As a result, capacitance had no influence on $E_{\text{crit}}$ (Table 3). In reality, soil $\Psi$ will decrease as water is withdrawn. However, when we modelled the non-steady-state case we found no significant change in the $E_{\text{crit}}$ versus $\Psi$, relationships shown in Fig. 4 (simulations not shown).

**Controlled drought experiments**

Figure 8 shows the comparison between model predictions of $E_{\text{crit}}$ versus $\Psi_{\text{crit}}$ and data from controlled drought experiments. A range of $E_{\text{crit}}$ is shown based on a ±20% deviation in plant $k_i$ from measured values and a 2.4–9.1 range in $A_R/A_L$ (see Table 4 for parameters). Xylem cavitation was limiting for both sunflower and water birch. The greater resistance of sunflower to cavitation than water birch is reflected in the lower $\Psi_{\text{crit}}$ and greater $E_{\text{crit}}$ of sunflower than water birch (Fig. 8).

In both species, stomatal closure during drought was necessary and sufficient to keep $E$ below maximum $E_{\text{crit}}$ and so avoid a predicted hydraulic failure. However, safety margins from the $E_{\text{crit}}$ range decreased substantially as drought progressed. As predicted because of its greater cavitation resistance, sunflower maintained higher $E$ relative to water birch at all soil $\Psi$. If water birch had not restricted $E$ below that of sunflower, the model would predict hydraulic failure, even under well-watered conditions.

**DISCUSSION**

Both rhizosphere and xylem constraints were important for setting the range of possible flux and pressure in plants, but their relative importance depended on conditions. The rhizosphere was limiting for low $A_R/A_L$, coarse textured soils, and species resistant to cavitation. Xylem cavitation was limiting for higher $A_R/A_L$, fine textured soils, and species vulnerable to cavitation (Fig. 5b). The incorporation of the rhizosphere component is a significant improvement over previous attempts to estimate hydraulic limits (Tyree & Sperry 1988; Jones & Sutherland 1991; Alder et al. 1996).

The method of analysis also improves over earlier attempts. Previous models did not employ the Kirchhoff transform (Ross & Bristow 1990), and their accuracy depended on how finely the continuum was discretized (Appendix). Insufficient discretizing resulted in predictions of $\Psi_{\text{crit}}$ much less negative than that which caused 100% loss of xylem conductance (Jones & Sutherland 1991; Alder et al. 1996; Mencuccini & Comstock 1997). While Jones & Sutherland (1991) emphasized that stomatal conductance may be maximized at the expense of some xylem conductance, our model predicts that stomatal conductance (a proxy of $E$) will be maximized at the expense of all conductance at the limiting point in the continuum. According to Fig. 7 this will be in the root and/or leaf xylem under xylem-limiting conditions, or in the rhizosphere. At $E_{\text{crit}}$ the loss of conductance for the entire continuum (soil-to-leaf) may be substantially below 100% (e.g. 59–86% for simulations in Fig. 7).

Assuming a benefit from maximizing leaf area and stomatal conductance while minimizing root biomass and cavitation resistance, plants should operate as close as they can to their hydraulic limits without risking failure. This is consistent with the drought experiments (Fig. 8), and the analysis of Tyree & Sperry (1988). Although the Tyree & Sperry study did not incorporate the Kirchhoff transform or rhizosphere resistances, it was discretized and would match our model predictions under xylem-limiting conditions. A large body of empirical work also supports the existence of small safety margins in plants that are relatively vulnerable to cavitation and likely to be xylem-limited (Sperry & Pockman 1993; Sperry, Alder & Eastlack 1993; Tyree et al. 1993, 1994; Cochard et al.)
Plants with very cavitation-resistant xylem (sagebrush, ceanothus) may only approach their hydraulic limits when $\Psi_c$ drops during drought. At high $\Psi_c$, the $E_{\text{crit}}$ for these xylem types (Fig. 4) was far above typical maximum values for plants ($= 10 \text{ mmol s}^{-1} \text{ m}^{-2}$), and $E$ would probably be limited by other factors such as the maximum diffusive conductance of the leaf-to-water vapour. A decrease in $\Psi_c$ during drought would reduce $E_{\text{crit}}$ well within the physiological range and constrain gas exchange, a prediction borne out by application of the model to field data from sagebrush (Kolb & Sperry, manuscript in preparation) and ceanothus (Portwood et al. 1997).

Being able to predict hydraulic limitations based on interactions between soil type, water availability, $A_R$,$A_L$, and xylem type (Fig. 5b) leads naturally to hypotheses about adaptive combinations of these properties. A set of these hypotheses can be formulated if we assume at the outset that plants operate near their hydraulic limits, at least on a seasonal basis.

The most general hypothesis is that plants will be near the $A_R$,$A_L$ threshold where xylem is limiting. The $A_R$,$A_L$ should be at least as high as the threshold because this minimizes $\Psi_{\text{crit}}$. Increases in $A_R$,$A_L$ beyond the threshold confer progressively diminishing returns with respect to water uptake (Figs 5 & 6), and would represent a waste of root biomass with respect to water uptake.

The evidence suggests that most plants are xylem-limited. Measurements of $A_R$,$A_L$ vary tremendously, from 0·24 to over 10 (Tyree et al. 1998; Rendig & Taylor 1989). Even at the low end of this range, all plants would be xylem limited if growing in a loam- or finer-textured soil (Fig. 5b, dashed line 5). Excess of $A_R$,$A_L$ beyond the threshold may reflect requirements for uptake of nutrients rather than water. For a modest $A_R$,$A_L$ of 2, soils would have to be at least as coarse as a sandy loam (Fig. 5b, dashed line 3) to limit fluxes in relatively cavitation-susceptible plants such as boxelder, water birch, and probably most crop species (Sperry 1998). These conclusions are consistent with Newman’s (1969) analysis of the rhizosphere bottleneck, wherein he estimated that, for a sandy loam, $A_R$,$A_L$ less than 0·62 would be necessary for an appreciable rhizosphere resistance to develop. Our results also parallel those of Bristow et al. (1984) where rhizosphere resistances influenced plant water uptake for coarse soils with a $b$ value below 3·5 (Table 2), and other factors constrained uptake in finer soils ($b > 3·5$).

A related hypothesis is that plants growing in drought-prone habitats should be more resistant to cavitation and have higher $A_R$,$A_L$ than plants in wetter habitats. This is true with respect to cavitation resistance (Sperry 1998), and in many instances for root density (Glinski & Lipiec 1990) which may correspond to higher $A_R$,$A_L$.

Superimposed on the hypothetical trend with drought exposure are adaptive trends related to soil type. Plants should be hydraulically compatible with their soil. Plants in finer textured soils would tend to develop the lowest $A_R$,$A_L$ and have the widest range of cavitation resistance. Plants in sandier soils would have the highest $A_R$,$A_L$ and be more uniformly vulnerable to cavitation. Rooting density is known to be higher for certain plants in coarse versus fine soils (Glinksi & Lipiec 1990), and a recent analysis of vulnerability curves of forests in Brunei indicated rather uniformly vulnerable xylem for species of the heath and Dipterocarp forests on relatively coarse soil (Becker, Patino & Tyree 1998).

A caveat to these hypotheses is that an increase in $E_{\text{crit}}$ and/or a decrease in $\Psi_{\text{crit}}$ can have the disadvantage of promoting faster consumption of water and accelerating soil drought. This is the case where a fixed soil volume is available to the roots, as in potted plants. In the ground, however, the total soil volume drained by roots is more ambiguous, and could actually be dependent on the manner in which $E$ is regulated during the drought. Drought simulations incorporating rhizospheric resistances (Newman 1969) and larger soil volumes would be necessary to explore these interactions.

The use of the pipe model leads to an even draining of the soil volume and an even distribution of cavitation among morphologically equivalent units of the plant. This may approach reality for shallowly rooted plants with fibrous root systems and weak apical dominance in the shoot, but otherwise it is an oversimplification. Nevertheless, the prediction of $\Psi_{\text{crit}}$ should not depend on the model’s representation of hydraulic architecture because under xylem-limited circumstances it is constant at near the 100% loss point of the vulnerability curve (Table 3). The $E_{\text{crit}}$, however, may be more accurately predicted by a species-specific representation of morphology. The pipe model also predicts uniform hydraulic failure at $E_{\text{crit}}$ whereas the branched catena approach of Tyree & Sperry (1988) demonstrated a patchwork pattern of canopy dieback with hydraulically favoured branches surviving at the expense of others.

Synthesizing the effects of rhizosphere and xylem conductance on plant water use has led to explicit hypotheses concerning the coordinated evolution of root-shoot ratios and cavitation resistance in response to soil type and water availability. Evaluation of these hypotheses should be accompanied by finer resolution of the $k(\Psi)$ relationships in xylem of different organs (especially roots and leaves), and in non-xylary tissues of roots and leaves, as well as a more quantitative understanding of root architecture and function.

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REFERENCES


APPENDIX

Solution of $E_{\text{crit}}$ and $\Psi_{\text{crit}}$

Equation 1, Darcy’s law, can be expressed in terms of hydraulic conductance between two points in the flow path, where $k(\Psi)$ represents the $\Psi$-dependent leaf-specific hydraulic conductance between those points:

$$E = -k(\Psi) x_l d\Psi/dx,$$

where $x_l$ is the distance between the points. If $k(\Psi)$ represents the conductance between soil and leaf, Eqn A1 can be solved for $E_{\text{crit}}$ by separating variables and integrating over the soil–leaf continuum, yielding:

$$E = -\int_{\Psi_s}^{\Psi_l} k(\Psi) d\Psi,$$

where $\Psi_l$ = leaf $\Psi$ and $\Psi_s$ = soil $\Psi$. $E$ is maximized ($= E_{\text{crit}}$) when $\Psi_l = \Psi_{\text{crit}}$ = limit of $\Psi$ as $k$ goes to zero. The $\Psi_{\text{crit}}$ is independent of $\Psi_s$, and $E_{\text{crit}}$ decreases as $\Psi_s$ decreases.

The Kirchhoff transform and the solution of $E_{\text{crit}}$ and $\Psi_{\text{crit}}$

Transforming Eqn A1 in terms of matric flux potential ($\Phi$) equates to:

$$E = -x_l d\Phi/dx.$$  
(A3)

Separating variables and integrating over the continuum from soil to leaf (as for Darcy’s law, above) gives:

$$E = -(\Phi_l - \Phi_S),$$

where $\Phi_l$ and $\Phi_S$ represent leaf and soil $\Phi$, respectively. From the definition of $\Phi$ in Eqn 10:

$$(\Phi_l - \Phi_S) = \int_{\Psi_s}^{\Psi_l} k(\Psi) d\Psi.$$  
(A5)

Substituting $E$ for $- (\Phi_l - \Phi_S)$ in Eqn A5 gives Eqn A2 as derived from Darcy’s law. $E = E_{\text{crit}}$ under the same conditions as for Eqn A2.

The use of matric flux potential for a single element model (i.e. two nodes, soil and leaf) yields the correct value for steady-state $E_{\text{crit}}$ and $\Psi_{\text{crit}}$ as long as the $k(\Psi)$ function is identical throughout the pathway. Discretizing is only necessary when there is a change in the $k(\Psi)$ function. In contrast, numerically solving Darcy’s law for the same parameters requires extensive discretizing even if the $k(\Psi)$ function is constant in the continuum. For example, assuming a linear $k(\Psi)$ function with a zero intercept, no discretizing caused a 50% underestimation of $E_{\text{crit}}$ and overestimation of $\Psi_{\text{crit}}$. Over 30 elements were required to get within 5% of the correct values.