

Water deficits and hydraulic limits to leaf water supply

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ABSTRACT

Many aspects of plant water use – particularly in response to soil drought – may have as their basis the alteration of hydraulic conductance from soil to canopy. The regulation of plant water potential (Ψ) by stomatal control and leaf area adjustment may be necessary to maximize water uptake on the one hand, while avoiding loss of hydraulic contact with the soil water on the other. Modelling the changes in hydraulic conductance with pressure gradients in the continuum allows the prediction of water use as a function of soil environment and plant architectural and xylem traits. Large differences in water use between species can be attributed in part to differences in their ‘hydraulic equipment’ that is presumably optimized for drawing water from a particular temporal and spatial niche in the soil environment. A number of studies have identified hydraulic limits as the cause of partial or complete foliar dieback in response to drought. The interactions between root:shoot ratio, rooting depth, xylem properties, and soil properties in influencing the limits to canopy water supply can be used to predict which combinations should optimize water use in a given circumstance. The hydraulic approach can improve our understanding of the coupling of canopy processes to soil environment, and the adaptive significance of stomatal behaviour.

Key-words: drought responses; hydraulic architecture; plant–soil interactions; stomatal regulation; water relations; water transport; xylem cavitation.

INTRODUCTION

In this review, we consider how the stomatal response to water stress is influenced by stress-induced changes in the hydraulic conductance of the soil–leaf pathway. We evaluate the thesis that stomatal regulation (and longer-term leaf area regulation) of gas exchange is necessary to preserve hydraulic continuity of the soil–leaf continuum, and that without such regulation, the advantages of vascular tissue and root systems for mining soil water could not be fully exploited (Tyree & Sperry 1988; Jones & Sutherland 1991; Sperry *et al.* 1998; Sperry 2000).

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The function of stomata in water relations (not considering additional CO₂ and light responses) is like a pressure regulator. A pressure regulator limits pressure changes by controlling flow rate, and the stomata limit the variation in plant water potential (Ψ) with soil moisture and evaporative demand by controlling transpiration. In this way, the plant avoids damaging drops in Ψ . To function as a pressure regulator, the stomata must be capable of sensing or predicting plant Ψ as it changes with conditions. Fortunately, the details of the sensing process (which are the subject of much investigation; Jones 1998; Nardini & Salleo 2000) are of no direct concern to our topic. What is important is the fact that some form of Ψ regulation exists. It is also not implied that the regulation of Ψ need be perfect, or ‘isohydric’, only that if plant Ψ does drop in response to drought, as in anisohydric species, the drop is regulated.

Given the pressure regulator mode of stomatal function, it is inevitable that changes in hydraulic conductance of the soil–leaf pathway, soil moisture, and evaporative demand will *indirectly* drive changes in stomatal conductance and transpiration (Saliendra, Sperry & Comstock 1995; Fuchs & Livingston 1996; Comstock & Mencuccini 1998; Hubbard *et al.* 2001). Thus, the analysis of soil–plant hydraulics can be used to explain and predict patterns of plant water use with respect to the soil and atmospheric environment, and the large differences between species and cultivars. This has been a goal of research on the soil–plant–atmosphere continuum (SPAC) for over four decades (Gardner 1965; Philip 1966). The earlier work tended to emphasize soil hydraulics, because flow in the soil is a physical process and can be readily quantified, whereas plant hydraulics were less well understood. Here we emphasize the important similarities between flow in soil and flow in xylem. The incorporation of soil and xylem dynamics can improve the treatment of plant hydraulics in SPAC models and set a physical constraint on the stomatal regulation of transpiration (E) and Ψ .

We begin with an overview of the theoretical linkage between water transport and transpiration. This is followed by a discussion of the behaviour of hydraulic conductivity along the soil–leaf continuum, with an emphasis on the similarity of soil and xylem pathways. A final section considers examples of how the hydraulic approach has been used to predict plant water use and the limits to gas exchange. We conclude with a discussion of the approach and prospects for future research. For simplicity, we focus on the influence of soil moisture on plant water use. A similar approach that

emphasizes the evaporative gradient is given in Oren *et al.* (1999).

THEORY

If one could make a plant transpire at any rate E from zero to infinity while holding the bulk soil water pressure constant, the trajectory of E versus leaf Ψ (at steady state), could look like Fig. 1a. When E is zero, the leaf Ψ would equal the bulk soil Ψ (ignoring gravitational effects). As E was increased there would be a corresponding drop in leaf Ψ . The E versus Ψ trajectory will not be a straight line because the hydraulic conductance of the flow path will not be constant with Ψ . For at least two well-understood reasons, the hydraulic conductance will decline as Ψ becomes lower with elevated E , creating a curved trajectory wherein Ψ must drop disproportionately with increasing E . These two reasons are a loss of soil conductivity in the rhizosphere between bulk soil and root surface (Newman 1969), and cavitation in the xylem (Tyree & Sperry 1989). Although there may be additional changes in conductance with E , such as variable aquaporin activity in root or leaf membranes (Henzler *et al.* 1999; Clarkson *et al.* 2000), or variable KCl concentration in xylem sap (Zwieniecki, Melcher & Holbrook 2001), the Ψ -dependence of these factors is not well characterized, as opposed to the inevitable physical processes of rhizosphere drying and xylem cavitation.

The theoretical E versus Ψ trajectory cannot go to infinity, but has a maximum steady-state E -value, E_{crit} (Fig. 1a, solid line, open symbol) with an associated Ψ_{crit} . Any higher steady-state rate of E is impossible, because the drop in pressure drives the remaining hydraulic conductance in the bulk soil–leaf pathway to zero, breaking apart the hydraulic continuum. The critical values of E and Ψ describe a physical boundary to gas exchange with respect to soil and plant hydraulics. Transpiration and plant Ψ must be regulated to stay within these physical limits or else canopy desiccation will occur.

The existence of a hydraulic limit means that pulling harder on the water column does not necessarily provide more water to the leaves. Oil workers are aware of this concept, knowing that to extract the maximum oil volume from a single well, pumping rates must be moderated to maintain fluid contact as flow resistance increases with fluid withdrawal. Plants may need to regulate their rate of water uptake to stay within the hydraulic limits of their supply line.

The E versus Ψ trajectory can be replicated for any bulk soil moisture. A drier soil will have a lower pressure intercept and a flatter E versus Ψ trajectory with a lower E_{crit} (Fig. 1a, dashed line, open symbol) than a wet soil because the starting hydraulic conductance (i.e. at $E = 0$) is reduced under drier conditions. The drier the soil, the more restrictive are the hydraulic limits to steady-state transpiration.

The curves in Fig. 1a are the basis for predicting plant water use from soil moisture and xylem properties. If the underlying hydraulic conductance changes are properly

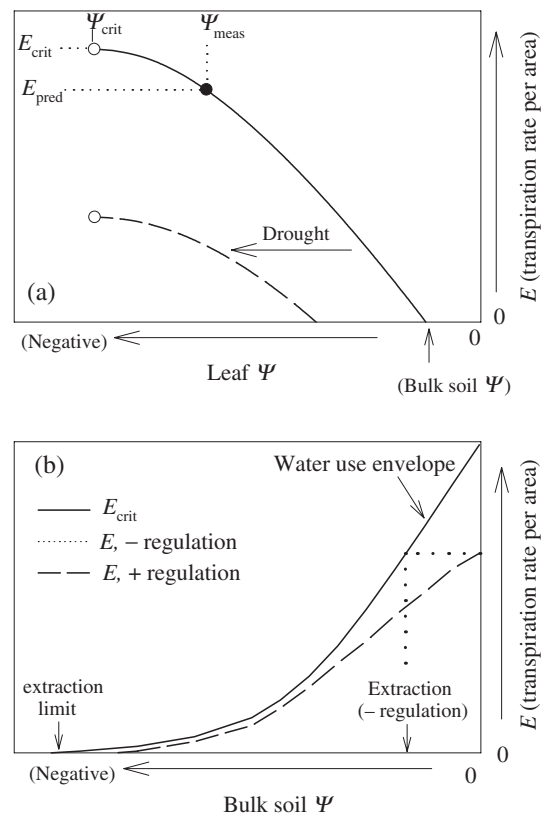


Figure 1. Definition of hydraulic limitations in the soil–leaf hydraulic continuum. (a) Theoretical steady-state trajectory of transpiration (E) versus leaf water potential (Ψ). When $E = 0$, leaf $\Psi = \Psi$ of the bulk soil. The disproportionate drop in leaf Ψ with increasing E results from the progressive Ψ -induced loss of hydraulic conductance in the continuum. The maximum permissible steady-state E is E_{crit} ; any higher transpiration rate drives the hydraulic conductance to zero. E_{crit} is associated with corresponding leaf Ψ_{crit} . Actual E can be predicted (E_{pred}) from this trajectory from measured or estimated leaf Ψ (Ψ_{meas}). As bulk soil Ψ becomes more negative (drought), the E versus Ψ trajectory flattens (dashed curve) and hydraulic limits become more severe. (b) The trajectory of E_{crit} for the soil–leaf continuum versus declining bulk soil (Ψ). The E_{crit} curve is the plant's 'water use envelope' and defines the upper boundary for steady-state water transport as a function of soil Ψ . The 'extraction limit' is the bulk soil Ψ at which E_{crit} becomes negligible and water cannot usefully be extracted from the soil. The extraction potential (Fig. 4b) is the area under the envelope. Shown also are hypothetical patterns of actual E with (+) and without (–) stomatal regulation. Without regulation (dotted line), once E surpasses E_{crit} there is no further water uptake, and the ability of the plant to extract water is compromised (extraction, – regulation). Regulation of E (dashed line) is necessary for the plant to stay within its hydraulic limits and fully exploit its potential for soil water uptake.

characterized, the theoretical curve will include the actual E and Ψ of the plant for steady-state conditions. If there is any information on leaf Ψ for steady-state conditions – either from a direct midday measurement, or an assumption of isohydric or anisohydric regulation of midday Ψ (Fig. 1a, Ψ_{meas}), the midday E can be predicted from the trajectory (E_{pred}), and the safety margin from E_{crit} estimated.

The day-to-day stomatal response to soil drought can be predicted by calculating the E versus Ψ trajectory for any soil moisture value, and locating the plant on the curve based on its manner of Ψ regulation.

A convenient way of summarizing the prediction of water use from soil and plant hydraulics is illustrated in Fig. 1b. This figure plots the E_{crit} and E derived from individual curves like those in Fig. 1a against the bulk soil Ψ (= Ψ intercept) for each trajectory. The solid line in Fig. 1b shows how E_{crit} declines to zero as soil moisture declines. We refer to this as the 'water use envelope' because it defines the maximum hydraulically possible rate of water use as a function of soil moisture. The minimum bulk soil water potential allowing any gas exchange is referred to as the 'extraction limit', analogous in a sense to the permanent wilting point.

The thesis that stomatal regulation is required to preserve hydraulic contact between soil and canopy and thereby maximize the soil water extraction by vascular plants, is illustrated by the dotted line in Fig. 1b ('- regulation'). This shows what would happen if there was a constant midday stomatal conductance as soil dried, assuming a constant evaporative gradient and E . The plant would reach E_{crit} at a relatively high value of bulk soil Ψ , prematurely desiccating the canopy. The plant's actual extraction in the absence of any stomatal response ('extraction, - regulation') would be much less than the hydraulically defined extraction limit. In contrast, the plant Ψ regulation that results from stomatal action (dashed line, '+ regulation') can allow the plant to 'push the envelope' while not exceeding it, thereby maximizing gas exchange without interrupting water conduction. For the plant to accomplish this, the stomata must always keep the midday Ψ less negative than Ψ_{crit} as soil moisture declines.

The analysis shown in Fig. 1 is attractive, because to the extent it is valid, it can be used to explain and predict differences in maximum gas exchange capacity and water use between different soil moisture regimes, soil types, root systems, and xylem types. It can be used to predict plant traits that should optimize water extraction from a particular soil environment for a given investment in roots and xylem. However, to undertake such an analysis, the hydraulic conductance in the soil-leaf continuum must be characterized as a function of Ψ in the continuum. This requires taking the continuum apart to characterize the Ψ responses of each important component, and then putting it back together again to estimate the response of the entire continuum.

Ψ -DEPENDENT HYDRAULIC CONDUCTIVITIES IN THE CONTINUUM

In analysing the components of the soil-leaf continuum, it is useful to distinguish conductance (k) from conductivity (K):

$$k = Q/\Delta\Psi \quad (1)$$

$$K = -Q/(d\Psi/dx) \quad (2)$$

The Q is the volume flow rate, Ψ is the component of water potential driving the flow (pressure in soil and xylem), and x is distance along the flow path. In tissues where more than one Ψ component participates in driving Q there will be additional terms (e.g. pressure and osmotic components in extra-xylary root tissue; Steudle 1994). The k can be measured directly, or derived from the integration of K with respect to x along the flow path. The k is thus a function of flow path length, whereas K is independent of length. In addition, k and K are usually expressed relative to an area transverse to the flow path, which can be designated by subscript. Here, we use a subscript s for soil area (e.g. K_s), r for surface area of absorbing roots (e.g. K_r), and x for xylem cross-sectional area (e.g. K_x).

Plant and soil K -values are not constants, but depend on a number of factors ranging from temperature, ionic strength of the transpiration stream, cell membrane composition, and the driving force itself. The curves of Fig. 1 are the result of interactions between K and Ψ , and we confine ourselves to this source of variation in K in the next two sections.

Soil and xylem

Together, the soil and xylem account for probably over 99% of the total length of the flow path from soil water source to evaporating surface in the leaf even in the smallest vascular plants. The $K(\Psi)$ functions of soil and xylem are the most unambiguous cause of the hydraulic limit to plant water use as defined in Fig. 1, and they have the same physical basis (Fig. 2). Bulk flow in both media occurs through pores and is driven by a gradient in pressure, usually a negative pressure (included in the 'matric potential' for soil). The pores in soil are the highly irregular spaces between the individual soil particles (Fig. 2a) whereas pores in xylem are organized into the relatively wide lumina of the xylem conduits alternating with the narrower channels of the connecting pits (Fig. 2b). The saturated K of both media (K at Ψ near 0 with all pores filled with water) is a function of the pore dimensions. Coarser textured soils with larger particle sizes have larger pores and higher saturated K_s than finer soils (Jury, Gardner & Gardner 1991). Similarly, xylem with larger diameter and longer conduits has greater K_x than xylem with narrower and shorter conduits (Zimmermann 1983). The permeability of the pits also influences the saturated K_x (Petty & Puritch 1970; Calkin, Gibson & Nobel 1986). As might be expected based on the differences in pore structure, saturated xylem K_x tends to be greater (e.g. $500 \text{ mol s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$ for diffuse-porous *Betula occidentalis*, Sperry & Saliendra 1994) than saturated soil K_s (e.g. $22 \text{ mol s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$ for a loam; Campbell 1985).

As the pore water pressure becomes more negative in soil and xylem, air is sucked into the pore space, displacing the water, ultimately reducing the K from relatively large values at saturation to near zero. In soil, the air spreads through the continuum of irregular pore space (Fig. 2a), and the nature of the $K(\Psi)$ function depends on soil tex-

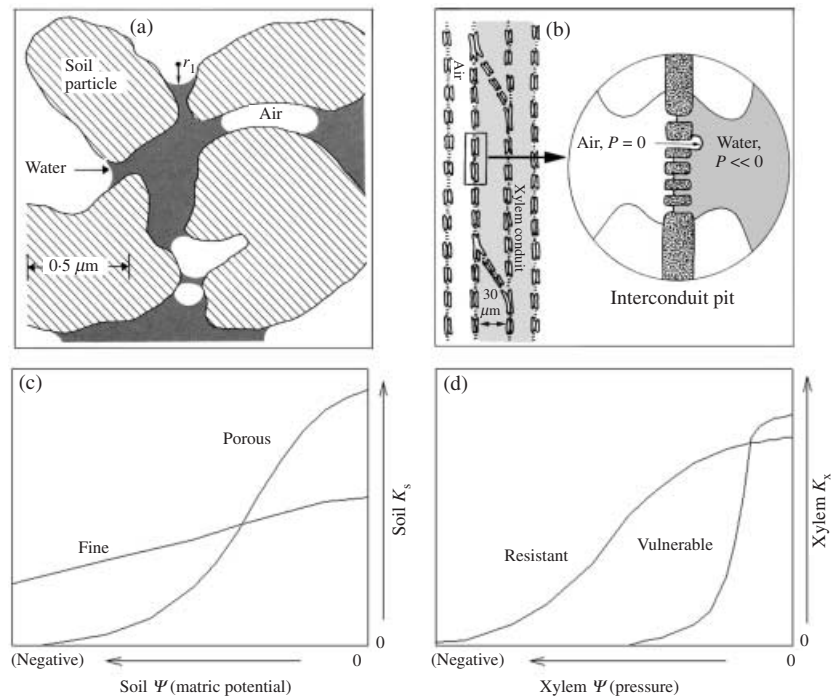


Figure 2. Basis for variable hydraulic conductivity (K) in soil and xylem. (a) Water (shaded) held in soil pore space under negative pressure (Ψ , ignoring osmotic potential) by capillary forces. As the Ψ becomes more negative, air displaces the water-filled pore space as capillary forces yield (from Nobel 1991). (b) Water (shaded) is held in xylem conduits under negative pressure (P) by capillary forces in pores of the conduit walls. Some conduits are inevitably air filled owing to ageing, abscission of parts, and damage. As P becomes more negative, air spreads to adjacent conduits as capillary forces yield in the interconduit pits (inset). Air entry nucleates cavitation and reduces xylem conductivity (modified from Cruiziat & Tyree 1990). (c) Declining soil conductivity (K_s , per soil area) as a function of increasingly negative soil Ψ . Porous soils have greater saturated K_s , but more precipitous $K(\Psi)$ functions than finer soils because their larger pore spaces empty abruptly at less negative Ψ . (d) Declining xylem conductivity (K_x , per xylem area) as a function of increasingly negative Ψ (pressure) of xylem water. Vulnerable xylem loses K_x at less negative Ψ than resistant xylem because of leakier interconduit pits. Any trade-off between cavitation resistance and saturated K_x is minimized by the potential uncoupling of conduit lumen size from pit structure.

ture. Coarse soils with large pore spaces and high saturated K_s tend to show a much more abrupt decline in K_s with Ψ than finer-textured soils with lower saturated K_s (Fig. 2c; Jury *et al.* 1991). In the xylem, the air spreads conduit-by-conduit through the limiting membranes of the interconduit pits (Fig. 2). The air 'seeds' cavitation in a conduit as it is sucked across the pit membrane – the details of the seeding process depending on variations in pit structure between angiosperms and conifers (Crombie, Hipkins & Milburn 1985; Sperry & Tyree 1988; Sperry & Tyree 1990; Jarbeau, Ewers & Davis 1995; Sperry *et al.* 1996). The pressure at which the K_x declines in xylem depends on the permeability of the pits rather than on the dimensions of the conduit lumina: cavitation-resistant xylem has less permeable pits than cavitation-susceptible xylem (Figs 2b & d). Because the size of the conduit lumina can be uncoupled from pit structure, there is no necessary relationship between saturated K_x and the cavitation resistance (Fig. 2d), although this can occur in some cases (Tyree, Davis & Cochard 1994a). The $K(\Psi)$ function of xylem is often referred to as a 'vulnerability curve'.

Living tissues of root and leaf

In terms of distances involved, the living tissues of root and leaf are trivial components of the soil–leaf pathway. These short distances are a good thing for the plant because the K_r for the radial flow path from soil to xylem of absorbing root tissue (approximately $0.0025 \text{ mmol s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$, estimated from Steudle & Heydt 1997) is seven to eight orders of magnitude less than the saturated K_x of xylem or K_s of soil.

Do Ψ -induced declines in tissue K contribute to a potential hydraulic limitation as for soil and xylem? The short answer is probably not, because there is no evidence for the direct, instantaneous, and inevitable coupling between tissue K and Ψ as seen for K and Ψ in soil and xylem (Fig. 2). There are many reasons why root tissue K will change with transpiration and Ψ , including changes in membrane conductivity, exo- and endo-dermal permeability, cell and root shrinkage (Nobel 1994; Steudle & Peterson 1998). However, these factors are potentially controlled by metabolism, and their linkage to Ψ is poorly characterized and likely to be highly variable with an unpredictable response time.

EVALUATING HYDRAULIC LIMITS IN THE SOIL–LEAF CONTINUUM

To evaluate the Ψ -induced changes in the soil–leaf continuum, the various $K(\Psi)$ functions need to be integrated over the entire flow path. This is where the branching structure, root depth distribution, root : shoot ratio, and overall size of the continuum becomes important. For example, the fact that root tissue K_r is eight orders of magnitude less than xylem K_x and seven orders of magnitude less than saturated soil K_s may suggest that leaf water supply is predominately controlled by root tissue hydraulics. However, in a medium-sized tree the distance that water must travel through xylem and soil is about five orders of magnitude greater than in crossing the root tissue, and owing to the branched structure of the root system, the absorbing root surface area is another several orders of magnitude greater than the transverse sectional area of the xylem draining these roots. Coupled with the substantial decline in xylem and soil K with Ψ , soil and xylem components can exert a major influence on leaf water supply, particularly under drought conditions. The importance of plant size is evident from the observed decline in soil–leaf hydraulic conductance with tree height (Saliendra *et al.* 1995; Mencuccini & Grace 1996); this decline is attributable to increasing xylem flow distances, since the distance across the root cortex or leaf mesophyll is relatively constant for all plants.

Of particular importance in scaling from K values to k values is the root : leaf area ratio ($A_R : A_L$). This influences the relative importance of soil versus plant limitations on water uptake. If one root is supplying the transpiration stream to 1000 leaves, there will be very steep Ψ gradients as soil water funnels down to the limited root surface area, resulting in ‘dry zones’ and very low soil K in the rhizosphere that can limit water uptake (Cowan 1965; Newman 1969; Williams 1974; Caldwell & Richards 1986; Passioura 1988). Rhizosphere dry zones will also be favoured in porous soils with more sensitive $K(\Psi)$ functions (Newman 1969). Water depletion zones around roots have been observed using magnetic resonance imaging methods and computer-assisted tomography (Hainsworth & Aylmore 1989; Macfall, Johnson & Kramer 1990).

Both modelling and empirical approaches have been used to assess changes in continuum k with Ψ . Empirical methods are plagued by the difficulties of measuring conductances in different continuum components without altering them in the process. Two common methods for measuring whole shoot or root system k , the root pressure chamber (Markhart & Smit 1990) and the high pressure flow meter (Tyree *et al.* 1993b), use significant positive pressures over extended time periods. These pressures refill any embolized xylem in the system, and cannot be used to assess Ψ -induced changes in k . An alternative is to estimate conductance components in droughted plants from measurements of Ψ and E at steady state. Using this method, Blizzard and Boyer (Blizzard & Boyer 1980) found that whereas soil and plant hydraulic conductances declined in concert during drought in soybean, most of the decline in

plant conductance was not in the root cortex component, but in the xylem. Independent measurements of the cavitation resistance in soybean are consistent with their data (Sperry 2000).

Modelling approaches can increase the utility of limited empirical data through the generation of well-defined and testable hypotheses. Although there are a vast number of soil–plant–atmosphere models, relatively few incorporate $K(\Psi)$ behaviour throughout the continuum. Earlier models incorporated these functions for the soil, but did not incorporate $K(\Psi)$ functions for plant xylem (Cowan 1965; Newman 1969; Bristow, Campbell & Calissendorff 1984). Milburn was the first to realize that cavitation in xylem could also limit plant water uptake in a fashion analogous to dry zone formation in the rhizosphere (Milburn 1979). The xylem limitation was analysed quantitatively in 1988 (Tyree & Sperry 1988) after methods had been developed to measure vulnerability curves (Sperry 1986). In the 1988 paper it was shown for the first time that xylem cavitation could underlie stomatal regulation of gas exchange in response to transpiration-induced water stress. A model was presented predicting E_{crit} on the basis of vulnerability curves. The maximum E of four tree species closely approached E_{crit} suggesting hydraulic limits on stomatal regulation. A large number of less quantitatively developed studies have since supported this conclusion by showing that excessive cavitation would occur in the absence of stomatal regulation of Ψ (Tyree & Sperry 1988; Meinzer & Grantz 1990; Lu *et al.* 1995; Saliendra *et al.* 1995; Cochard, Breda & Granier 1996; Mencuccini & Comstock 1997; Linton, Sperry & Williams 1998; Sparks & Black 1999; Bond & Kavanagh 1999; Nardini & Salleo 2000; Vogt 2001). The shortcoming of the Tyree and Sperry model (Tyree & Sperry 1988) was that it did not incorporate below-ground constraints which makes it less useful for understanding responses to soil drought.

Recently the above- and below-ground constraints on leaf water supply have been combined in a model that predicts the E versus Ψ trajectory for the entire soil–leaf continuum (Sperry *et al.* 1998; see also Williams, Bond & Ryan 2001). This model incorporates $K(\Psi)$ functions of soil, root xylem, and shoot xylem, and it can account for branched root systems penetrating to different depths, and a branched canopy. For lack of well-defined $K(\Psi)$ behaviour of the living tissues of roots and leaves, these conductances were assumed to vary to the same extent with Ψ as xylem and thus to be neither more nor less limiting. Results obtained from this approach are synthesized from recent publications (Kolb & Sperry 1999; Ewers, Oren & Sperry 2000; Hacke *et al.* 2000a; Jackson, Sperry & Dawson 2000) in the following sections and discussed in relation to empirical investigations.

The water use envelope and plant transpiration

Plotting actual water use envelopes is complicated by the fact that bulk soil Ψ varies within the rooting zone, so there is no single value for the x -axis. For relatively shallow-

rooted plants, the root system can be treated as a single layer, with pre-dawn plant Ψ used as an average bulk soil Ψ for the rooting zone (Sperry *et al.* 1998; Kolb & Sperry 1999). In systems where soil Ψ and root distribution with depth is important and known, E and E_{crit} can be estimated for any soil Ψ depth distribution. However, the results cannot be conveniently plotted as a single water use envelope. In these situations, a reference envelope can be derived for a constant bulk soil Ψ with depth (Ewers *et al.* 2000; Hacke *et al.* 2000a), or the soil Ψ at a particular depth can be used if this is correlated with Ψ at all depths (Jackson *et al.* 2000). Another complication is that if E is expressed per leaf area, variations in leaf area with soil moisture will change the envelope. Depending on the situation, a reference leaf area can be used (Sperry *et al.* 1998; Kolb & Sperry 1999), or E can be converted to ground area or per plant basis (Ewers *et al.* 2000; Hacke *et al.* 2000a).

Model predictions of the envelope show considerable variation within a species according to species' cavitation resistance (Fig. 3a, solid E_{crit} lines), soil type (Fig. 3b), root : shoot ratio (Ewers *et al.* 2000), and root depth distribution (Jackson *et al.* 2000). In general, vulnerable xylem, porous soils, low root : shoot ratio and shallow root systems result in a much narrower water use envelope (less negative extraction limit) than the converse properties.

The variation in the envelope corresponds with habitat and with mode of stomatal regulation. Importantly, actual plant water use does appear to 'push the envelope', particularly under drought conditions where E_{crit} approaches zero (Fig. 3, compare E_{crit} to E). *Betula occidentalis* (Fig. 3a, water birch) is a small tree of perennially wet riparian habitats where Ψ_{soil} is constant and high. It has a very narrow envelope on account of its vulnerable xylem. It also shows isohydric Ψ regulation, keeping midday Ψ constant and above a Ψ_{crit} of -1.7 MPa despite variations in soil moisture,

humidity, or hydraulic conductance (Saliendra *et al.* 1995). It tends to maintain relatively small margins of safety from E_{crit} , on the order of a few $\text{mmol s}^{-1} \text{m}^{-2}$, even under well-watered conditions (Fig. 3a). This plant simply does not have 'room' for anisohydric Ψ regulation, because it is so limited by its high Ψ_{crit} that is set by the point of complete cavitation in the shoot xylem.

Artemisia tridentata (Fig. 3a, sagebrush) is a shrub of desert regions where soil Ψ can drop below -6 MPa. It has a much broader envelope than *B. occidentalis* owing to much more cavitation-resistant xylem. It also shows anisohydric stomatal regulation: midday leaf Ψ drops as soil moisture declines, at least until midday Ψ approaches Ψ_{crit} during drought (Kolb & Sperry 1999). This anisohydric regulation results in very large safety margins from E_{crit} when soil Ψ is high. Thus, drought-adapted plants with greater cavitation resistance and broad envelopes appear to be over-built under well-watered conditions. This suggests there may be relatively little stomatal control in these plants when soil is wet, with maximum E and minimum leaf Ψ being limited only by maximum stomatal apertures and densities. Interestingly, *A. tridentata* changes its cavitation resistance seasonally, being more vulnerable during the wet spring, and becoming more resistant with the onset of summer drought (Kolb & Sperry 1999). The broadest envelope (based on maximum cavitation resistance) is shown in Fig. 3a, which exaggerates safety margins under wet conditions. At first glance, Fig. 3a seems to imply that sagebrush can potentially use water at a greater rate than water birch under wet soil conditions. Although this is correct at the leaf level, to the extent that sagebrush has a lower leaf area per plant than birch, the difference in E_{crit} on a per plant or stand basis between the species diminishes.

The envelopes in Fig. 3b are for half-sib-related plantations of *Pinus taeda* (loblolly pine), and illustrate the impor-

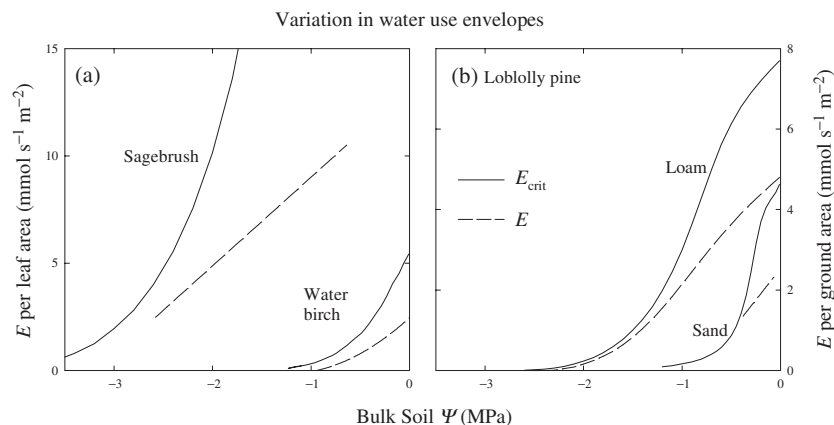


Figure 3. Variation in water use envelopes and actual plant water use. (a) The effect of differences in cavitation resistance between species. Sagebrush plants (*Artemisia tridentata*) with more cavitation-resistant xylem have a much broader water use envelope than vulnerable species like water birch (*Betula occidentalis*). Soil type was similar between both species. Actual water use (dashed lines) converges on hydraulic limits (solid curves), particularly under drought (from Sperry *et al.* 1998; Kolb & Sperry 1999). (b) The effect of soil porosity on envelopes for half-sib loblolly pine (*Pinus taeda*) plantations of equal ages (Hacke *et al.* 2000a). Trees in sand have much narrower envelopes (solid curves) than trees in loam owing to the more precipitous $K(\Psi)$ function for sandy soil. In both soils, actual water use (dashed curves) converged on hydraulic limits during drought.

tance of soil type. Trees growing in sand had a much narrower envelope than those in the finer loam soil because of the more sensitive $K(\Psi)$ function of sand (e.g. Fig. 2c). The actual water use in these plantations was adjusted to stay within the corresponding envelopes, converging on E_{crit} under drought (Fig. 3b, dashed lines). The broader envelope in loam was associated with an isohydric regulation of midday leaf Ψ at approximately -2.1 MPa; the narrower envelope in sand corresponded with a less negative isohydric regulation at approximately -1.6 MPa (Hacke *et al.* 2000a).

Importantly, where model predictions of E have been compared with actual E measurements, the agreement is very good whether for greenhouse plants subjected to short-term rapid drought of days (Sperry *et al.* 1998), sagebrush shrubs subjected to a prolonged monotonic summer drought (Kolb & Sperry 1999), or for loblolly pine trees experiencing irregular drought cycles spanning two growing seasons (Hacke *et al.* 2000a). These results are encouraging, because they suggest that the changes in soil and xylem K with drying are important causes of change in the overall soil-leaf k . If the model can successfully predict E , it also gives more credence to its predictions of E_{crit} , which are more difficult to validate.

Do plants ever exceed E_{crit} and trigger complete loss of hydraulic connection to all or part of the canopy? Fig. 3 suggests that this would be most likely to occur under soil drought situations where E converges on E_{crit} . Transport failure has been associated with foliar desiccation in riparian cottonwoods subject to experimental soil drying or natural drought in floodplains subject to declining water tables (Tyree *et al.* 1994b; Sparks & Black 1999; Rood *et al.* 2000). Drought deciduous behaviour in walnut (*Juglans regia*) has also been attributed to excessive cavitation in the leaves (Tyree *et al.* 1993a). Desiccation by hydraulic failure has also been postulated for chaparral shrubs (*Ceanothus crassifolius*) exposed to more than 6 months of drought and weeks of drying winds (Davis *et al.* 2002; Davis, Kolb & Barton 1998). Seedling mortality in the chaparral has been linked to excessive cavitation (Williams, Davis & Portwood 1997). Recent dry growing seasons in the Great Basin have also caused complete transport failure in roots and foliage loss in desert shrubs (*Chrysothamnus viscidiflorus*, Sperry and Hacke, unpublished). We suspect that more instances of dieback by hydraulic failure will be reported as investigators become more aware of the phenomenon.

Causes of hydraulic limitation

The question of where the limiting hydraulic resistances are in the soil-leaf continuum has long been a matter of debate (Gardner 1965; Newman 1969; Molz 1975; Blizzard & Boyer 1980). The water use envelope is defined by a limiting resistance – a resistance somewhere in the continuum that goes to infinity. Which component is most limiting and under what circumstances? A theoretical answer is provided by Fig. 4, and it suggests that the limiting component can be a number of places depending on the circumstances.

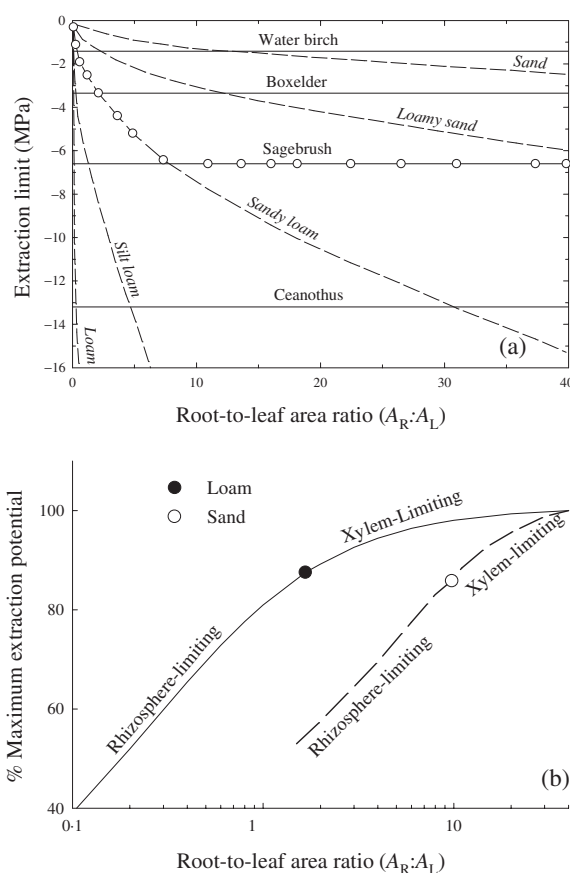


Figure 4. Interactions between soil type, xylem type, and root : leaf ratio on predicted hydraulic limits to plant water use. (a) Extraction limit (bulk soil P at $E_{crit} \approx 0$) versus root : leaf area ratio ($A_R : A_L$). The dashed curves for the indicated soils assume that the rhizosphere alone limits water extraction (i.e. no xylem cavitation). Solid horizontal lines represent the xylem pressure causing 100% cavitation in the indicated species (water birch, *Betula occidentalis*; box elder, *Acer negundo*; sagebrush, *Artemisia tridentata*; ceanothus, *Ceanothus crassifolius*). The extraction limit for a soil plus xylem combination is found by crossing over from the soil curve to the xylem line as $A_R : A_L$ increases (e.g. circles for sandy loam + sagebrush). From Sperry *et al.* (1998). (b) Extraction potential (= area under the water use envelope) versus root-leaf area ratio ($A_R : A_L$) for half-sib related loblolly pines (*Pinus taeda*) in two even-aged plantations. Symbols are measured values of $A_R : A_L$. Extraction limit is shown relative to its value at $A_R : A_L$ of 40, a liberal maximum for woody plants. Low $A_R : A_L$ limits extraction because of hydraulic failure initiated in the rhizosphere. Extraction at high $A_R : A_L$ is limited by xylem cavitation. Trees in sandy soil maintained a similar relative extraction potential as in loam by increasing their $A_R : A_L$ to minimize the rhizosphere limitation (Hacke *et al.* 2000a).

Figure 4a shows the interaction between the extraction limit (\approx 'width' of the water use envelope, or the permanent wilting point) and the $A_R : A_L$ ratio for different soil types (curved dashed lines) and cavitation resistances (solid horizontal lines). The extraction limit for any soil plus xylem combination is found by crossing from the soil curve to the xylem line as $A_R : A_L$ increases (e.g. circles for sandy loam

+ sagebrush xylem). As $A_R : A_L$ increases from zero, the extraction limit decreases because the greater root area for water uptake relieves a hydraulic limitation at the rhizosphere. Above a threshold $A_R : A_L$, there is no further decrease in the extraction limit because at this point the limiting resistance has shifted from the rhizosphere to the xylem as a result of cavitation (Sperry *et al.* 1998). The shift from rhizosphere to xylem limitation is gradual, with an intermediate $A_R : A_L$ range where both are colimiting. As expected from previous analyses (Newman 1969; Bristow *et al.* 1984; Passioura 1988), Fig. 4a confirms that a rhizosphere limitation is probably only a serious factor in soils coarser than a loam. In loam or finer soils, hydraulic limits will be set by cavitation resistance of the xylem for even very low $A_R : A_L$. In these cases, a more negative extraction limit results from a greater cavitation resistance.

The interaction between $A_R : A_L$ and the water use envelope is also shown in Fig. 4b for the loblolly pine (*P. taeda*) stands of different soils shown in Fig. 3b. In this figure, the envelope is represented by the area under the E_{crit} curve ('extraction potential'). The extraction potential is a more sensitive measure of hydraulic limits than just the extraction limit, because it reflects changes in the latter as well as the restriction of E_{crit} within the water use range. This term should not be misconstrued as predicting the potential amount of water extracted. The envelope by itself only predicts the maximum steady-state rate of extraction as a function of bulk soil Ψ . Once again, a threshold $A_R : A_L$ is evident above which further increases do not increase the size of the envelope because once the rhizosphere limitation is relieved, the xylem limitation is not influenced by adding more roots. The $A_R : A_L$ threshold is shifted much higher in sand versus loam soil because the much more sensitive $K(\Psi)$ function in the coarser soil exacerbates the rhizosphere limitation problem. Interestingly, the actual $A_R : A_L$ of these plants was close to the optimal threshold value in both stands (Fig. 4b, symbols on curves), which required a much greater root investment in the sandy soil.

Fertilizing plants often results in a reduction in the root : shoot ratio (Linder *et al.* 1987; Haynes & Gower 1995; Albaugh *et al.* 1998), which according to Fig. 4b could restrict the water use envelope and render fertilized plants more vulnerable to drought. A fertilizing treatment of the sand-grown loblolly pines shown in Fig. 4b did in fact result in a significant reduction in $A_R : A_L$ whether or not the fertilized stands were also irrigated (Ewers *et al.* 2000). When irrigation was applied in addition to fertilization, there was a substantial narrowing of the water use envelope, predicting that these trees would be relatively sensitive to drought in the event that irrigation was withdrawn. This kind of response may explain greater drought-sensitivity of fertilized stands seen in other studies (Linder *et al.* 1987). Interestingly, the non-irrigated but fertilized trees showed much less of a narrowing of the envelope because the root xylem showed an increase in cavitation resistance that tended to counter the loss of $A_R : A_L$ (Ewers *et al.* 2000).

When the root : shoot ratio is sufficiently high to cause hydraulic failure in the xylem, where in the xylem does it

occur? In the simple, but less realistic, situation where there is one $K(\Psi)$ function for all the xylem from root to leaf, failure will occur only at the distal end of the flow path where Ψ is most negative. Under these conditions, the Ψ_{crit} and the extraction limit are both equal to the Ψ causing complete cavitation in the xylem. However, in many woody plants, the root xylem is substantially more vulnerable to cavitation than shoot xylem (Alder, Sperry & Pockman 1996; Sperry *et al.* 1998; Kolb & Sperry 1999; Ewers *et al.* 2000; Hacke *et al.* 2000a; Hacke, Sperry & Pittermann 2000b). The model predicts that hydraulic failure in this case can occur in the root system (Kolb & Sperry 1999; Ewers *et al.* 2000; Hacke *et al.* 2000a). Roots in the shallowest soil layers will lose transport capacity earliest in a drought, and if these are the only roots supplying the canopy, their failure will trigger failure in the distal shoot xylem as well. In this case, the Ψ_{crit} and extraction limit is the Ψ causing complete cavitation in the more vulnerable root xylem (Kolb & Sperry 1999). If deeper roots are present, failure in shallow roots will simply shift water uptake down to wetter soil layers without necessarily triggering shoot damage.

To some degree, the architecture of the plant may be localizing the point of hydraulic failure to redundant and replaceable points in the continuum, thereby increasing its ability to cope during progressive soil drought and to recover once it is relieved. This was the essence of M.H. Zimmermann's 'segmentation hypothesis' proposed many years ago (Zimmermann 1983). By analogy with an electric circuit, it makes sense for the plant to limit failure to redundant components that are readily replaceable ('hydraulic fuses') rather than to have it disrupt the major transport arteries.

Hydraulic limits and optimal plant water use: testable hypotheses

The above sections suggest that plants have co-ordinated their hydraulic capacity, as quantified in the water use envelope, to match their mode of Ψ regulation. They invest as much in roots and cavitation resistance as is necessary for their particular water use niche, presumably because to invest more would be a waste of carbon. The cost of excess roots is obvious, but what is the cost of excess cavitation resistance? Recently, the cost of cavitation resistance has been mechanistically linked to wood density: denser and stronger wood is necessary to balance the greater negative pressure within the xylem conduits (Hacke *et al.* 2001a). Thus, even if cavitation resistance was not always associated with a reduced saturated xylem conductivity (Tyree *et al.* 1994a), it would exact a price by reducing growth rate through greater xylem density (Enquist *et al.* 1999).

Figure 4, although not cast in units of carbon cost, represents a beginning for quantifying the trade-offs between water extraction capability versus the required plant investment. It allows us to formulate several testable hypotheses for how plants should alter their morphology and physiology to optimize water use under different soil and climatic conditions.

- 1 To the extent that water uptake is the sole driver of $A_R : A_L$, plants should adjust their $A_R : A_L$ to the threshold value where the rhizosphere and xylem are more or less colimiting (Fig. 4b). An $A_R : A_L$ below this threshold would compromise extraction capability, and an $A_R : A_L$ above this threshold would be ineffectual for increased water uptake.
- 2 To the extent that fertilizing reduces $A_R : A_L$, it can reduce water uptake from drying soils and increase drought sensitivity (Ewers *et al.* 2000).
- 3 Across soil types: the more porous the soil, the higher the $A_R : A_L$ will have to be to saturate the extraction limit. In the most porous soils (e.g. Fig. 4a, sand, loamy sand), cavitation resistance should be diminished because the soil dries out at relatively high Ψ regardless of the $A_R : A_L$.
- 4 Within a given soil type: the drier the soil of the rooting zone, the more cavitation-resistant the xylem and the higher the $A_R : A_L$ for saturating the extraction limit.
- 5 For a seasonally dry soil moisture regime: more porous soils will favour greater rooting depth than finer soils because less water will be available for extraction at low Ψ in the shallow layers of a porous versus fine soil (Jackson *et al.* 2000).

Most of these hypotheses have received some support. Figure 4b is evidence for 1 and 3 wherein the $A_R : A_L$ of half-sib loblolly pine plantations (symbols on loam and sand curves) increased by nearly six-fold to stay near the value required to saturate the extraction potential in response to growth in soils of very different porosity. This was also accompanied by a reduction in cavitation resistance of sand-grown versus loam-grown trees (Hacke *et al.* 2000). A follow-up study on fertilizing treatments suggested hypothesis 2, which has not been directly tested (Ewers *et al.* 2000a). Hypothesis 4 has been supported by a number of studies showing a correlation between cavitation resistance and the minimum xylem Ψ experienced by plants in their natural habitats (Tyree & Cochard 1996; Davis *et al.* 1998, 1999; Hacke *et al.* 2000b; Pockman & Sperry 2000), but see (Pinol & Sala 2000). The fifth hypothesis for rooting depth was recently supported in comparisons of rooting depths across soil types in global root databases (Jackson *et al.* 2000).

DISCUSSION

Implementing the theory of hydraulic limitation has been successful in predicting the regulation of transpiration in response to soil moisture and soil type within a plant type, and also the huge differences in water use between species. The Ψ regulation of stomata does appear to be necessary for avoiding hydraulic failure, and thereby maximizing the extraction of soil water. The pattern of Ψ regulation – whether it is isohydric or anisohydric, and the particular thresholds of Ψ that are controlled – have to be tuned to the soil moisture regime and the hydraulic capability of the plant's root system and xylem. The extensive variation in

water use between plants can be attributed in part to differences in their 'hydraulic equipment' that is presumably optimized for drawing water from a particular temporal and spatial niche in the soil environment. Explicit hypotheses for this optimization can be tested in the further evaluation of the hydraulic approach.

We can only speculate on how the plant achieves a co-ordination between the stomatal regulation of Ψ and the hydraulic capabilities of the soil–canopy supply line. In an evolutionary sense, it would be achieved by natural selection for the midday leaf Ψ that maximizes gas exchange: a Ψ at a safe distance above Ψ_{crit} . But in a physiological sense, how does *B. occidentalis* (Fig. 3a) 'know' to keep midday leaf Ψ above its Ψ_{crit} of -1.7 MPa that is set by its cavitation resistance, and to thereby stay within its water use envelope (Saliendra *et al.* 1995; Sperry *et al.* 1998)? If the signalling system between living cells and stomata is independent of cavitation there is no physiological reason why midday leaf Ψ in this species could not be regulated near -0.5 MPa or near -2.5 MPa, although either value would be maladaptive – the former by unnecessarily limiting gas exchange, and the latter by causing hydraulic failure. In this case, the observed co-ordination would be through independent adjustments (via natural selection) in stomatal regulation and transport capacity. Alternatively, the co-ordination may be achieved more directly via a physiological link between cavitation and the stomatal signalling system as suggested by Nardini & Salleo (2000).

The accuracy of the predictions of water use and hydraulic limits depends on the accuracy of the $K(\Psi)$ functions along the flow path, particularly of the most limiting component in series. For example, a recent study concluded that cavitation resistance of conifers in the north-western United States did not correlate with water availability in the habitat (Pinol & Sala 2000). However, only stem xylem was considered, which in many conifers and other woody plants is substantially more resistant (and not limiting to water uptake) as compared to root xylem (Sperry & Ikeda 1997; Linton *et al.* 1998.; Hacke *et al.* 2000a,b). The accuracy of soil $K(\Psi)$ functions is critical in more porous soils where a rhizosphere limitation is important. These soil functions are nearly impossible to measure over much of the range of interest for plants in natural communities and must be estimated from other soil properties (Campbell 1985). It has recently been noted that hydraulic limits can be substantially influenced by the length of the xylem conduits as well as their $K(\Psi)$ behaviour. In general, the longer the conduits at the site of cavitation, the more substantial the hydraulic limitation for a given $K(\Psi)$ relationship (Comstock & Sperry 2000).

To predict the response of plants to repeated drying and wetting cycles, hysteresis in the $K(\Psi)$ functions of soil and xylem must be known. Although there is significant hysteresis in soil $K(\Psi)$ behaviour (Philip 1966; Campbell 1985), this is probably much less than for the xylem curves depending on the extent and mechanism of cavitation reversal. The xylem pressure must rise to near atmospheric or above before gases can dissolve (Yang & Tyree 1992),

meaning there should be a substantial hysteresis in the $K(\Psi)$ behaviour of the xylem. Several studies have demonstrated this refilling when xylem pressure is within 30 kPa of atmospheric or above (Sperry *et al.* 1987; Sperry, Donnelly & Tyree 1988; Borghetti *et al.* 1991; Sperry & Sullivan 1992; Cochard, Ewers & Tyree 1994; Sperry *et al.* 1994; Hacke & Sauter 1996; Zhu, Cox & Arp 2000; Cochard *et al.* 2001). In some species, the $K(\Psi)$ function itself can be altered after an embolism and refilling cycle as a result of increased permeability of the vascular system to air entry (Hacke *et al.* 2001b). A further complication is the possibility that xylem conduits may refill even when the prevailing pressure in the transpiration stream is substantially negative (Salleo *et al.* 1996; Canny 1997; McCully, Huang & Ling 1998; Zwieniecki & Holbrook 1998; Holbrook & Zwieniecki 1999; Tyree *et al.* 1999; Zwieniecki & Holbrook 2000). However, these results are equivocal because studies using cryo-SEM techniques to assess embolism reversal have been shown to be subject to artifacts (Cochard *et al.* 2000), and other investigations did not measure xylem pressure *during* the refilling process to confirm that it indeed was low enough to require a novel refilling mechanism (Salleo *et al.* 1996; Zwieniecki & Holbrook 1998; Tyree *et al.* 1999). More information on the refilling process during rewetting cycles is required.

The living tissues of root and leaf are the cause of variable conductances which could have a significant modulating effect on the physical limitations that exist in the soil and xylem components. Although it seems unlikely that these could eliminate hydraulic limitations set by soil and xylem, these plant-mediated effects could significantly alter the shape of the E versus Ψ trajectory (Fig. 1a) over the short-term (Tsuda & Tyree 2000), and cause substantial hysteresis in the recovery of hydraulic conductance after a drought (Nobel 1994). An additional complication are reports of the effects of ion composition of the xylem sap on xylem conductivity (Zimmermann 1978; Ieperen, Meeteren & Gelder 2000; Zwieniecki *et al.* 2001). These ion effects do not appear to influence the cavitation resistance of the xylem (V. Stiller, J.S. Sperry, unpublished data). A final complication linked to radial water movement across roots is the build-up of solutes external to the endodermis in saline and heavily fertilized soils which can reduce water uptake in a manner somewhat similar to dry zone formation at the rhizosphere (Hamza & Aylmore 1992; Stirzaker & Passioura 1996).

The examples we have discussed have been limited to steady-state conditions. It is important also to consider non-steady-state conditions in a spatially explicit soil–root environment (e.g. see Doussan, Vercambre & Pages 1998). This eliminates the somewhat artificial bulk soil versus rhizosphere distinction and incorporates the parahrizal resistances (Newman 1969) that govern long-distance water flow in the soil. In this way, the ‘sphere of influence’ of a particular plant root system can be analysed, along with competitive interactions between plants. Above the ground, the influence of stem capacitance on hydraulic limitations may be important for large trees where the decline

in hydraulic conductance from soil to leaf may be limiting carbon gain (Ryan & Yoder 1997).

The overwhelming limitation on plant productivity is leaf water supply (Kramer & Boyer 1995), and it is logical that factors influencing this water supply play a central role in the adaptation of plants to their terrestrial environment. Leaf water supply is much more complex than simply the water availability in the rooting zone. The process of moving water to the site of evaporation with a minimum of investment is a major factor driving the architecture and physiology of land plants, including the function of stomatal regulation. In this context, the physiological tolerance of cells to water deficits should be expected to match the supply capacity of the system delivering resources to these cells. Interestingly, recent work does show that the sensitivity of leaf cell physiology to Ψ corresponds to the cavitation resistance of the xylem (Brodribb & Hill 1999). The significance of vascular supply to physiology is not lost on the armies of cardiovascular physiologists and modellers. Transport issues appear to be similarly important in the evolution and functioning of plants.

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