Hydraulic constraints on plant gas exchange

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Abstract

Stomatal conductance (g_s) and transpiration (E) are often positively correlated with the hydraulic conductance of the soil–leaf continuum (k_{s-l}). Interaction between g_s and k_{s-l} helps regulate water potential (Ψ) of leaves. When soil and plant Ψ decreases during water stress, k_{s-l} decreases. A well-documented cause of the decrease in k_{s-l} is xylem cavitation. The interaction between k and Ψ in xylem creates physical limits on the range of Ψ and E over which gas exchange can occur. Differences in drought tolerance between species correlate with hydraulic limits. Safety margins from complete hydraulic failure are often small enough to require stomatal regulation of Ψ and E. While stomatal regulation avoids complete hydraulic failure, controlled decreases in plant k can be substantial during drought. Decreasing plant k amplifies the effect of water stress on the leaves and effectively increases the sensitivity of the stomatal response to drought. Increased stomatal sensitivity may promote drought survival. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

In response to water stress, plants regulate their transpiration by decreasing their stomatal conductance. Although this reduces their photosynthetic potential, they do this to avoid dehydrative damage to their cells and tissues. Mutants lacking the stomatal closure response wilt and die under stress conditions that are readily survived by wild type (Tal, 1966). Water stress is relative; a water potential that induces stomatal closure in one species may have little effect on another. This is presumably because dehydrative damage occurs at different water potentials in different plants. At present we lack a clear understanding of exactly what physiological processes drive stomatal regulation of gas exchange and how they differ between plants of different drought tolerances (Meinzer, 1993).

There would be several benefits of knowing with greater precision the adaptive significance of stomatal closure induced by water stress. On an ecological scale, this knowledge would increase our understanding of vegetation patterns with respect to water availability, and allow better predictions of how vegetation will respond to environmental change. In agriculture, our ability to model and predict the response of crops to water deficits would improve. Perhaps most significantly, knowing the most limiting processes for gas exchange would allow us to progressively remove those limits through directed breeding. The result could be more drought tolerant crops and less dependence on irrigation.

There are many physiological functions that could be driving the stomatal response to drought. Considerable attention has focused on cell physiology and biochemistry. While cell growth in shoots can be very sensitive to water deficits, its cessation is not limiting for gas exchange because it can cease at water poten-

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tials much higher than those triggering stomatal regulation of water loss (Hsiao, 1973). Enzyme activity is influenced by decreasing water potential and accompanying increases in ion concentrations (Kramer and Boyer, 1995). However, water potentials that cause stomatal closure in most species can have little effect on cellular respiration (Huang et al., 1975) which argues against any fundamental interaction between enzyme function and the physiological range of water potentials. In many mesic and/or herbaceous species, stomatal regulation appears necessary to maintain leaf water potentials above the turgor loss point, and osmotic adjustment can translate into corresponding adjustment of stomatal regulation (Morgan, 1984). However, in desert and chaparral species with sclerophyllous leaves, the association between turgor maintenance and gas exchange is ambiguous (Saruwatari and Davis, 1989).

The potential resiliency of the plant cell in response to extreme dehydration is evident from 'resurrection' plants whose cells can survive air drying (Gaff, 1981). These plants are best represented among the non-vascular, and more primitive vascular, plants. The same tolerance of desiccation is seen among the algae, where some species can continue metabolism at water potentials that would kill a sunflower plant (Kramer and Boyer, 1995). It is curious that the evolution of higher vascular plants was associated with the loss of the seemingly innate potential of lower plants to survive desiccation (the exception being at the seed stage of the life cycle). Perhaps new physiological processes associated with the evolution of a larger and more complex plant body became more limiting to gas exchange than those occurring within individual cells.

The vascular tissue itself represents a vital whole-plant process which is impaired by water stress: the supply of water to the photosynthetic tissue. The supply is needed to sustain the transpiration associated with carbon uptake through the stomata. As water deficits develop, events in plant and soil make it increasingly difficult to keep the hydraulic pipeline between soil and leaf intact. The transport characteristics of this pipeline impose physical limits on the rate at which water can be supplied to the leaves, and on the potential rate of transpiration allowed by stomata (Tyree and Sperry, 1989).

In this paper, I will consider to what extent the necessity for vascular plants to maintain hydraulic contact with soil water constitutes a limiting process that is protected by stomatal regulation of transpiration. These limits to water supply are independent of the dehydration limits of individual cells. It is tempting, but naive, to assume there will be a single process driving stomatal regulation of water status. The intent of this paper is not to determine which processes are most limiting to gas exchange, but to explain the limits imposed by one function, water transport, so that ultimately its importance can be placed in proper context.

2. Premise

Much of what I will be considering follows from a simple premise: that the ability of the plant to supply water to the leaves will correspond with the ability of the leaves to lose water. As water supply capability becomes threatened, stomatal regulation will insure that water use will not exceed supply. In physiological terms, this premise states that the hydraulic conductance of the soil–leaf continuum will be functionally linked to stomatal conductance of the leaves.

I will consider some evidence for this premise, and some hypotheses for how hydraulic and stomatal conductances are linked. Most space, however, will be devoted to the implications of this premise for stomatal regulation.

3. Stomatal and hydraulic conductances

The capability of the water uptake and transport system can be quantified by its 'hydraulic conductance' (k) which is the change in flow rate of liquid water through the system per change in hydraulic pressure driving the flow. Hydraulic conductance is often expressed per leaf area. As explained by the cohesion–tension theory, the pressures driving bulk flow of water from soil to leaf are negative. They are generated by capillary forces arising in cell wall pores as water evaporates from the wall surface (Pickard, 1981). The water pressure of the transpiration stream usually approximates its total water potential (Ψ) because the xylem water is dilute enough to have a negligible osmotic potential.
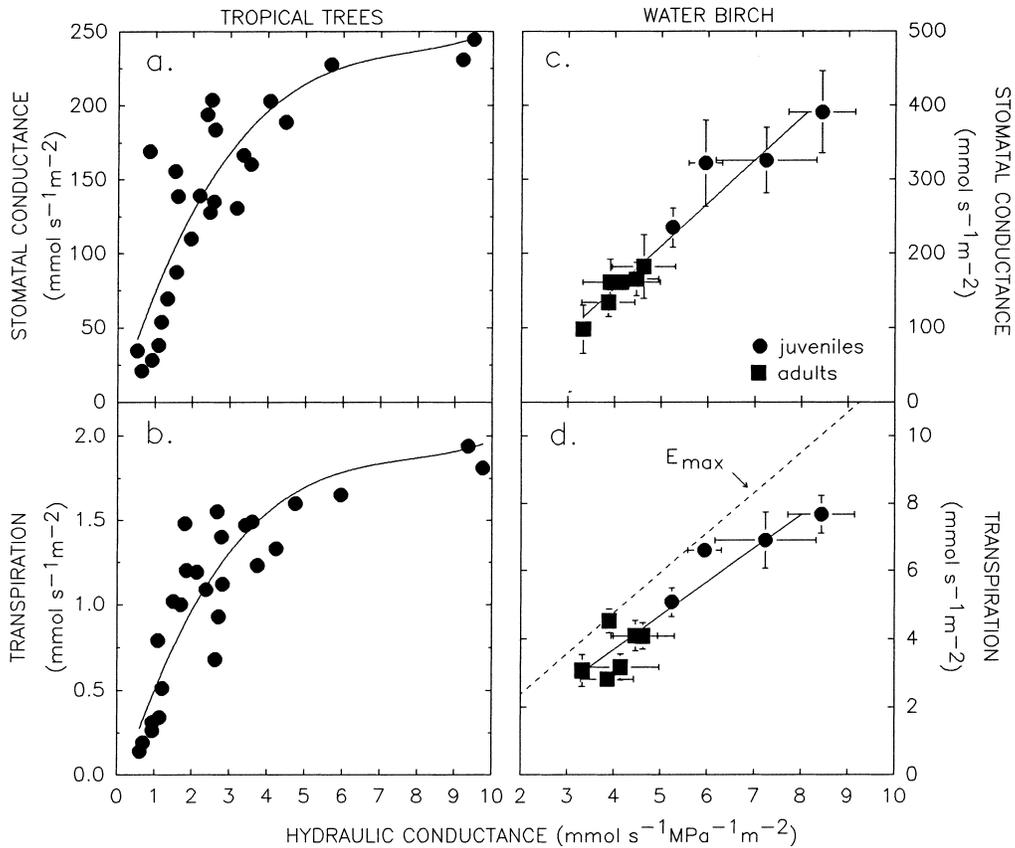
Fig. 1. Stomatal conductance (a, c) and transpiration rate (b, d) vs. hydraulic conductance from bulk soil to leaf. (a, b) Tropical trees (from Meinzer et al., 1995); (c, d) water birch (*Betula occidentalis*) juveniles and adults (from Saliendra et al., 1995); dashed line in (d) represents an estimate of E_{max} (Fig. 5, Eq. (2)) based on the cavitation response of *B. occidentalis* stem xylem.

The potential for water loss from the leaves is quantified by 'leaf diffusive conductance' (g_l) which is the change in transpiration rate (E) per change in vapor pressure difference between leaf and air (Δw). Leaf conductance consists of stomatal conductance (g_s) and boundary layer conductances in series. When boundary layer conductance and Δw are constant, g_s and E are proportional. Both g_s and E are usually expressed per leaf area.

A number of observations have demonstrated a correlation between the liquid phase conductance from soil-to-leaf (k_{s-l}; per leaf area), and g_s or E (Fig. 1, Meinzer and Grantz, 1990; Meinzer et al., 1995; Saliendra et al., 1995). The correlation results from an active response of stomata to k_{s-l} because when k_{s-l} is experimentally changed there is an almost immediate

change in g_s. When k_{s-l} per leaf area was increased by partial defoliation or shading, g_s of the untreated foliage increased. When k_{s-l} was decreased by root pruning or stem notching, g_s decreased (Meinzer and Grantz, 1990; Sperry et al., 1993; Whitehead et al., 1996; Pataki et al., 1998).

The stomatal response to k_{s-l} has the consequence of moderating changes in leaf water status that otherwise would occur. For example, a 65% decrease in k_{s-l} caused by notching the stem xylem would have caused a corresponding decrease in leaf Ψ at steady-state conditions. However, in response to this treatment, stomatal closure reduced E by 50% resulting in no change in bulk leaf Ψ (Sperry et al., 1993). Near homeostasis in mid-day leaf Ψ was also observed as a result of the proportionality between k_{s-l} and g_s through plant

development (Meinzer et al., 1992; Saliendra et al., 1995).

What is the mechanism coupling g_s to k_{s-l}? One hypothesis is that as hydraulic conductances change during plant development, associated changes in xylem sap composition and concentration are sensed in the leaf and result in corresponding changes in g_s (Meinzer et al., 1991). It is not clear, however, how this explains the very rapid (<15 min) response of stomata to experimental changes in k_{s-l} (Sperry et al., 1993; Saliendra et al., 1995; Fuchs and Livingston, 1996). Another explanation is that stomata respond to changes in Ψ of the leaf caused by alteration of k_{s-l}. It has long been recognized that a negative feedback between leaf Ψ and g_s could be the basis for stomatal regulation of Ψ. The link between leaf Ψ and the stomatal response could be via a turgor-mediated release of abscissic acid (Raschke, 1975).

There is experimental support for the importance of leaf Ψ in mediating the stomatal response to decreasing k_{s-l}. The stomatal closure that occurred after k_{s-l} was decreased by stem notching, was completely reversible by increasing leaf Ψ via pressurizing of the root system. Negative feedback between g_s and leaf Ψ was sufficiently sensitive to maintain bulk leaf Ψ constant (Saliendra et al., 1995; Fuchs and Livingston, 1996). This result emphasizes the fallacy of assuming that regulation of constant bulk leaf Ψ cannot be achieved by a stomatal response to leaf Ψ (e.g. Davies and Zhang, 1991). The apparent paradox of stomata responding to a constant variable is resolved if the stomata are not responding to *bulk* leaf Ψ (which is constant) but to spatial and temporal variation in Ψ of individual cells or populations of cells.

The interaction between hydraulic and stomatal conductances becomes important under water stress conditions because k_{s-l} declines as Ψ declines. The interaction between k and Ψ sets limits to the plant's hydraulic transport capacity and exerts a significant influence on stomatal regulation of water use during drought.

4. The hydraulic conductance–water potential interaction

The k versus Ψ relationship under drought conditions can be introduced with an example from the literature. Blizzard and Boyer (1980) measured k_{s-l} in soybean plants during a controlled drought. The total k_{s-l} was divided into two components: soil-to-root cortex and root cortex-to-leaf.

The soil-to-root component dropped considerably during the drought, as was expected (Fig. 2a, solid circles). As the soil dries, capillary forces holding water in pore spaces are overcome by the decreasing hydraulic pressure in the soil water. Air displaces water from the pore space causing a decline in the hydraulic conductance of the soil (Nobel, 1991; Campbell, 1985).

More interesting was the root-to-leaf component. Under well-watered conditions, the root-to-leaf conductance was lower than that of the soil-to-root pathway (Fig. 2a, open circles). Wet soil generally has a very high hydraulic conductance because of the considerable amount of water-filled pore space. Notably, however, the root-to-leaf component did not remain constant as the soil dried. This was contrary to the common assumption of constant plant k, adopted mainly for convenience and for lack of information to the contrary (e.g. Cowan, 1965). Root-to-leaf conductance declined during drought and as a result remained the lower of the two conductances over the entire range of soil water potentials (Fig. 2a, open circles).

The fact that the root-to-leaf conductance can remain smaller than the soil-to-root conductance throughout a drought indicates that it will have the greater influence on leaf water status during the drought under transpirational conditions. For this reason, I will focus on the interaction between k and Ψ within the plant as the basis for illustrating the hydraulic constraint on gas exchange.

4.1. Mechanisms of declining plant k

Blizzard and Boyer (1980) speculated that much of the decline they observed in root-to-leaf k was owing to xylem cavitation, because the xylem composed most of the measured pathway. Alder and Sperry (unpublished) estimated the loss of k resulting from cavitation in the xylem of soybean shoots using an air-injection method (Sperry and Saliendra, 1994). The correspondence with the data of Blizzard and Boyer (Fig. 2b, compare open circles and solid squares) indicates that much of the decline in root-to-shoot k in soybean can in fact be explained by xylem cavitation.
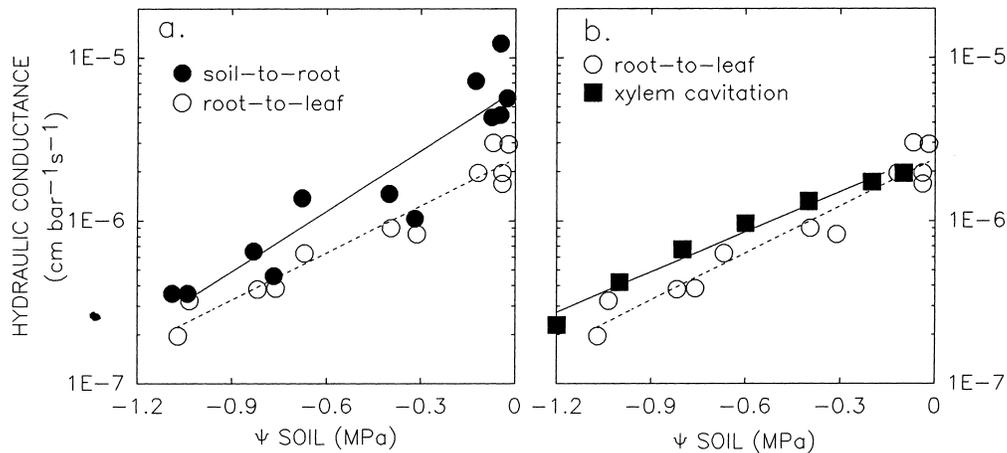
Fig. 2. Hydraulic conductance (log scale) vs. Ψ soil in soybean. (a) Soil-to-root and root-to-leaf hydraulic conductances (from Blizzard and Boyer, 1980) and (b) root-to leaf data from Blizzard and Boyer (1980) compared with the loss of hydraulic conductance in soybean shoot xylem from cavitation (Alder and Sperry, unpublished). Cavitation data was scaled relative to the mean well-watered conductance obtained by Blizzard and Boyer (i.e. conductances at Ψ soil >−0.2 MPa).

The transpiration stream also flows in extra-xylary pathways in the root and leaf where cavitation does not occur. Changes in root and leaf tissues during water stress can have important consequences for plant k. The root has been particularly well-studied in this regard (Steudle, 1994). However, with few exceptions (Nobel and North, 1993), the changes extra-xylary k across a wide range of Ψ encountered during a drought have not been well documented. Furthermore, the mechanisms responsible for these changes are not fully understood.

In contrast, the mechanism of cavitation is relatively well known. According to the 'air-seeding' hypothesis (Zimmermann, 1983), cavitation occurs when xylem pressures drop low enough to aspirate air into water-filled conduits from neighboring air spaces. The air seeding pressure depends on the magnitude of the capillary forces holding air–water menisci in the conduit wall pores. The smaller the pores, the greater the pressure difference required to pull air through the wall. A number of studies show strong support for the air-seeding hypothesis, and indicate that the site of air-seeding is at the pit membrane pores of inter-conduit pits (Crombie et al., 1985; Jarbeau et al., 1995; Pockman et al., 1995; Sperry et al., 1996).

The cavitation response has been measured in the xylem of several species. Typically the response is measured as the loss in k of the xylem (k_x) versus minimum Ψ of the xylem (Fig. 3). Species adapted to well-watered habitats such as riparian *Populus* species, cavitate at much higher Ψ than species adapted to severe droughts, such as *Ceanothus* species of the California chaparral that must endure droughts of 6–8 months and can develop xylem pressures approaching −10 MPa (Fig. 3). Species adapted to intermediate drought, such as great basin sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) are intermediate in their cavitation response (Fig. 3). The variation in cavitation resistance is attributable to differences in air-seeding pressure (Sperry et al., 1996) which in turn is a function of the pore sizes in inter-conduit pit membranes (Jarbeau et al., 1995).

5. Cavitation and the transpiration constraint

The extensive documentation of the cavitation response in plants allows direct analysis of how it limits transpiration (E). According to Darcy's law

$$E = k_{s-l}(\Delta\Psi_{s-l}) \tag{1}$$

for steady-state conditions where $\Delta\Psi_{s-l}$ is the difference in pressure between water in the soil (Ψ_s) and in the leaf xylem (Ψ_l; assuming negligible osmotic
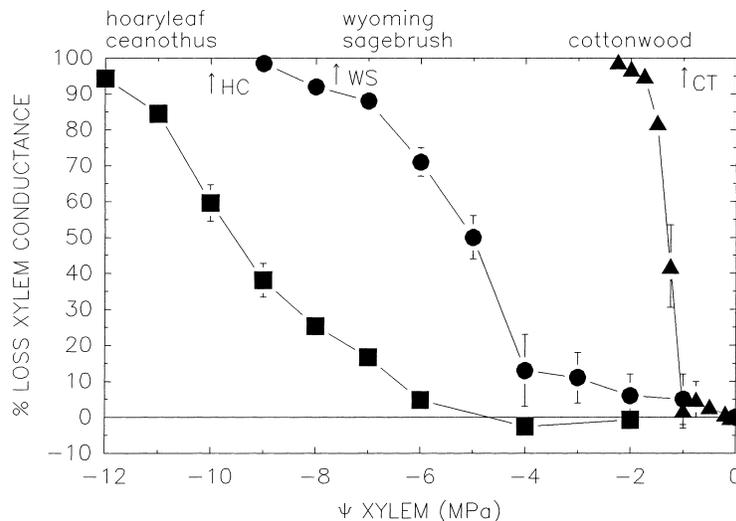
Fig. 3. The percentage loss of hydraulic conductance in stem xylem vs. Ψ xylem in three species of contrasting drought tolerance. Data was obtained using a centrifugal force technique (Alder et al., 1997). The relatively drought-susceptible cottonwood was a hybrid of *Populus trichocarpa×P. deltoides* (Alder and Sperry, unpublished). Hoary leaf ceanothus (*Ceanothus crassifolius*) is a shrub of the california chaparral (Davis and Sperry, unpublished). Wyoming sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) is a small shrub of the intermountain west (Kolb and Sperry, 1999). Arrows on the upper Ψ axis indicate minimum xylem pressures measured in the field for each species (HC: ceanothus, WS: sagebrush, CT: cottonwood; cottonwood pressure based on measurements of *Populus fremontii*; Pockman and Sperry, 2000).

effects). If k_{s-l} is constant, there is no hydraulic limit to E as $\Delta\Psi_{s-l}$ is increased at constant Ψ_s (Fig. 5, dashed line). However, k_{s-l} is not constant, but varies because of cavitation, soil drying, and changes in non-xylary tissues. Assuming that cavitation dominates the changes in k_{s-l} with Ψ (as implied by Fig. 2), Eq. (1) can be re-written as

$$E = [k_{s-l}(\Psi)](\Delta\Psi_{s-l}) \tag{2}$$

where $[k_{s-l}(\Psi)]$ is determined by the cavitation response (Jones and Sutherland, 1991). In Eq. (2), E cannot increase without limit as $\Delta\Psi_{s-l}$ is increased because this requires progressively more negative Ψ which will cause progressively lower k. There is a maximum E for Eq. (2) (E_{max}) which is associated with a minimum critical Ψ (Ψ_{CT}; Fig. 5, solid line).

The Ψ_{CT} corresponds to the Ψ required to cause 100% cavitation. This is still the case even when changes in soil conductivity are incorporated in Eq. (2) indicating that the xylem is more limiting than the soil under most circumstances (Sperry et al., 1998).

Although the soil–plant continuum has a maximum possible flow rate corresponding to E_{max}, there is no physical reason why the stomata could not allow E to exceed E_{max}. However, if E_{max} is exceeded, the positive feedback between decreasing k and Ψ becomes uncontrolled and so-called 'runaway' or 'catastrophic' cavitation causes a complete loss of hydraulic conductance in the xylem (Tyree and Sperry, 1988). Whether or not this limit matters to the plant depends on the margin of safety the plant exhibits relative to failure of xylem transport.

An estimate of the safety margin can be obtained by comparing the Ψ_{CT} (Ψ at 100% loss of xylem conductivity) with the actual minimum Ψ experienced. For 73 species, there is a significant correlation between Ψ_{CT} and minimum Ψ (Fig. 4, solid line). Plants that are more drought tolerant (experience and survive lower Ψ) are also more resistant to cavitation. The safety margin between minimum actual and possible Ψ for species on the mesic-to-hydric end of the spectrum (minimum actual $\Psi > -1.6$ MPa) in Fig. 4 is 1.04 ± 0.46 MPa ($n=13$). In contrast, minimum pressures in the xeric plants can be several Megapascals
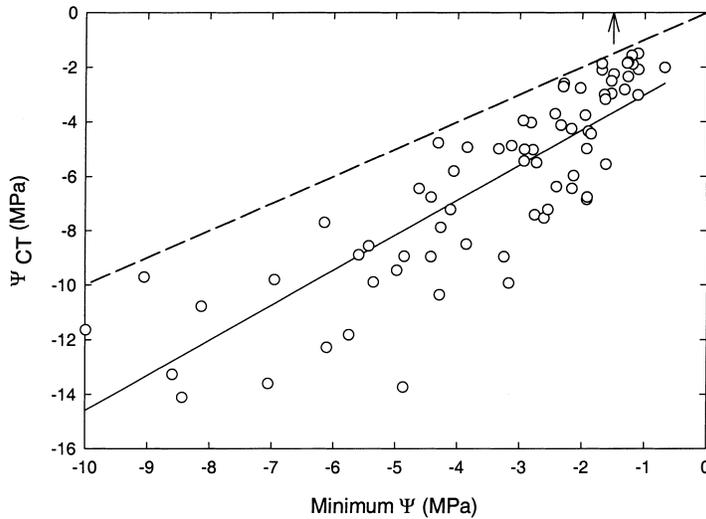
Fig. 4. Minimum possible Ψ xylem based on the cavitation response vs. minimum actual Ψ xylem based on field observations for 73 species. Dashed line is 1:1 relationship. Safety margins from complete hydraulic failure are the '*y*' axis difference between data and the 1:1 line. Species to the right of the arrow at -1.60 MPa minimum actual pressure are on the mesic/hydric end of the drought tolerance scale and average a safety margin of 1.04 ± 0.46 MPa ($n=13$). Species to the left of the arrow are progressively more xeric-adapted and tend to have larger safety margins (average$=3.28\pm1.96$ MPa; $n=60$; Sperry, 1995, Pockman and Sperry, 2000).
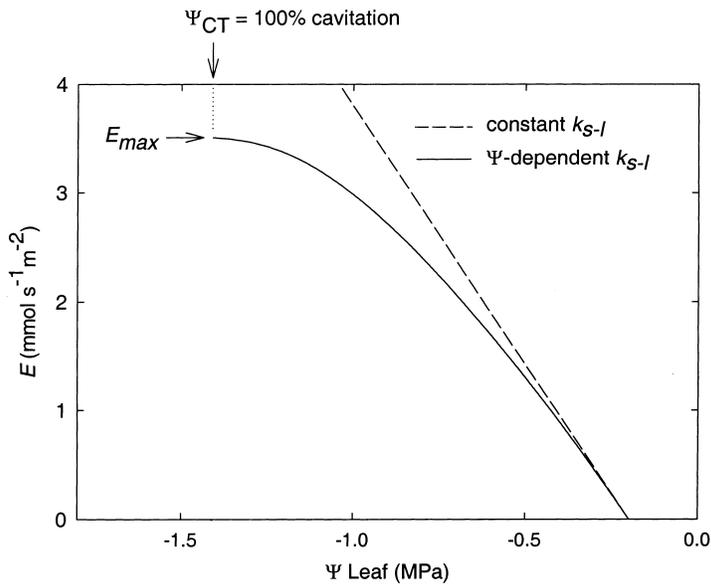
Fig. 5. Transpiration rate (=xylem flow rate at steady state) vs. Ψ xylem for constant Ψ soil. Dashed line is Eq. (1) with constant hydraulic conductance (k) in the soil-to-leaf pathway. Solid line is Eq. (2) with hydraulic conductance as a decreasing function of decreasing Ψ [$k(\Psi)$]. In this example, the k (Ψ) function of xylem in *B. occidentalis* was used (Sperry and Saliendra, 1994). Eq. (2) gives a maximum xylem flow rate (E_{max}) associated with a minimum xylem pressure (Ψ_{CT}). If stomata allow E to exceed E_{max} uncontrolled loss of hydraulic conductance will develop ('runaway cavitation', Tyree and Sperry, 1988).

below those in the mesic plants. A mesic plant in a xeric habitat would be unable to conduct water to its leaves because its safety margin would be exceeded and it would be completely cavitated. Cavitation limits the gas exchange potential of these mesic species during water stress.

The foregoing observations suggest that hydraulic limits do constrain transpiration, particularly under water stressed conditions. The stomatal response of a number of species conforms to this expectation, although in many studies Ψ_{CT} is not explicitly defined. Adjustments of g_s to developmental or experimental manipulations of k_{s-l} in sugarcane (*Saccharum* spp. hybrid), *Betula occidentalis*, and *Fraxinus excelsior* were sufficient to avoid loss of hydraulic conductance from cavitation (Meinzer et al., 1992; Sperry et al., 1993). Fig. 1d shows the consistently small safety margin between E and E_{max} maintained by *Betula occidentalis* across a range of k_{r-l}. Significantly, in a few instances, stomatal response to experimental reductions in k_{s-l} of *Betula occidentalis* were not fast enough to avoid catastrophic cavitation and shoots died within hours (Sperry et al., 1993).

Stomatal responses to soil drought in *Betula occidentalis*, *Acer grandidentatum*, *Picea abies*, and *Quercus petraea* were also consistent with the need to maintain a safety margin from excessive cavitation (Cochard et al., 1995; Saliendra et al., 1995; Alder et al., 1996; Lu et al., 1996). In the case of *A. grandidentatum*, g_s declined to near zero during a natural drought when Ψ reached Ψ_{CT} of the root xylem. Stem xylem was more resistant to cavitation and still maintained a sizable safety margin from Ψ_{CT} (Alder et al., 1996).

In *Betula occidentalis*, the stomatal response to soil drought, like the response to changing k_{s-l}, was mediated via leaf Ψ as determined from experiments where shoot Ψ was increased by root pressurizing (Saliendra et al., 1995). The same leaf-level response was seen for stomata of *Alnus rubra* and *Psuedotsuga menziesii* (Fuchs and Livingston, 1996). This suggests that the stomatal response to hydraulic conductance, and to drying soil, can both occur via the same leaf-level mechanism. Although there is evidence in other plants for stomatal responses to root water status via xylem-borne chemicals (Davies and Zhang, 1991), clearly this is not the only mechanism by which stomatal responses to drought occur.

6. Controlled cavitation and plant water use

The Ψ_{CT} and E_{max} defined in the previous section represent theoretical limits that the plant cannot exceed without losing all hydraulic transport. However, as the curvature of the solid line in Fig. 5 indicates, substantial cavitation can occur before Ψ reaches Ψ_{CT}. This 'controlled' cavitation reduces k_{s-l} but without triggering runaway cavitation. The extent of controlled cavitation that can occur at a given Ψ_s is dependent on the shape of the $k_x (\Psi)$ function: a steep, threshold cavitation response allows little controlled cavitation whereas a gradual cavitation response allows more (Jones and Sutherland, 1991). Controlled cavitation explains much of the observed decline in k_{s-l} in soybean plants during drought (Fig. 2).

During soil drought, a controlled decline in k_{s-l} will amplify the effect of declining Ψ_s on Ψ_l. This is clear from solving Eq. (1) for Ψ_l:

$$\Psi_l = \Psi_s - \frac{E}{k_{s-l}} \tag{3}$$

where $(\Psi_s - \Psi_l)$ is substituted for $\Delta\Psi_{s-l}$ in Eq. (1). At a typical midday Ψ_l of -1.5 for $\Psi = -0.2$ MPa, the ratio E/k_{s-l} will equal 1.3 MPa. If Ψ_s decreased by 0.8 MPa during a drought and there was no change in E or k_{s-l} then the droughted Ψ_l would be -2.3 MPa. In contrast, if a 0.8 MPa decline in Ψ_s caused a 50% decline in k_{s-l} and E remained unchanged, the droughted Ψ_l would be -3.4 MPa: much more negative than if hydraulic conductance had remained constant. Changes in plant hydraulic conductance (as opposed to soil) would have the dominant amplifying effect as long as conductances were lower in plant than in soil (Fig. 2).

In reality, the stomatal response to declining k_{s-l} (e.g. Fig. 1) prevents the potentially disproportionate decline in Ψ_l. What ends up being amplified by decreasing hydraulic conductance is not the change in Ψ_l, but the regulatory response of stomata to drought. Stomatal conductance must be decreased more to achieve the same Ψ_l when k_{s-l} decreases than if k_{s-l} were constant. The greater the decline in k_{s-l}, the more sensitive is the stomatal response to drought.

A simple experiment demonstrates the significance of changes in the plant component of k_{s-l} for the reduction in g_s during drought. When plants are droughted and then rewatered, Ψ_s and the soil component of

k_{s-l} quickly approach pre-drought levels. However, a comparable recovery in g_s is often not seen. Excising a leaf and supplying it with water, however, caused complete recovery of g_s in sunflower suggesting that the after-effect of drought in this case was vascular blockage rather than a biochemical effect at the stomatal apparatus (Boyer, 1971). In a similar experiment with sunflower, simulated root pressure after a drought caused an abrupt increase in g_s. The root pressure promoted refilling of vessels in the root system that were cavitated during the drought (Saliendra and Sperry, unpublished data).

These and other observations suggest that much of the stomatal closure observed during drought is a result of the amplifying effects of declining k_{s-l} in the plant rather than a strictly proportional response to drying soil. There is some evidence that most of the decline in k_{s-l} occurs in the xylem of the root system because roots can be substantially more susceptible to cavitation than shoots (Sperry and Saliendra, 1994; Saliendra et al., 1995). On rewatering, there is the potential for considerable hysteresis in the recovery of k_{s-l} to pre-drought values. Recovery would occur by refilling of cavitated vessels by root pressure (Milburn and McLaughlin, 1974), and by growth of new roots.

While declining k_{s-l} is often considered to be disadvantageous to the plant because it increases water stress on the leaves, it may actually be advantageous. If reduced k_{s-l} does substantially amplify the stomatal regulation of E during drought, the consequence would be a more gradual use of soil water than if k_{s-l} were constant. This would potentially extend the survivable drought period for the plant. While competition for water between species could erase this advantage, there is a limit to how fast water can be extracted from soil before an uncontrolled loss of hydraulic conductance in the soil–root contact zone occurs (Cowan, 1965). Declines in plant k_{s-l} could help 'tune' the plant's water uptake rate to avoid excessive declines in rhizosphere k and in this way draw the most water from the soil over the longest time.

7. Conclusion

The opening premise that a plant's ability to lose water from the leaves during gas exchange will be associated with its ability to supply leaves with water leads to an explicit definition of hydraulic constraints on water use and gas exchange. The interaction between k and Ψ resulting from xylem cavitation creates unambiguous limits on the range of Ψ over which gas exchange can occur (Fig. 3). Gross differences in drought tolerance between species correlate with these hydraulic limits (Fig. 4). In many cases, safety margins from hydraulic failure are small enough that they would be exceeded in the absence of stomatal regulation of Ψ and E (Fig. 1d).

While stomatal regulation avoids complete hydraulic failure, substantial decreases in plant k can occur during soil drought because of cavitation and other processes in the extra-xylary tissues (Fig. 2). Decreases in plant k have the effect of amplifying the water stress and increasing the sensitivity of the stomatal response to drought. Increased stomatal sensitivity could promote drought survival.

Although a basic framework exists for understanding the interactions between changes in plant hydraulic capacity and plant responses to stress, more needs to be learned within this framework. The Ψ dependence of k in the extra-xylary tissues of root and leaf are incompletely understood (Steudle, 1994). The cavitation response of root xylem may be especially important, yet little work has been done on root xylem. Stomatal sensing mechanisms are still debated both in terms of root versus shoot signals and in terms of the molecular mechanisms linking stress to changes in g_s. Modeling studies need to incorporate reasonable $k(\Psi)$ functions for the plant to more accurately predict changes in water use under water limited circumstances. Models also need to test how changes in plant k influence plant water use during drought.

Beyond the focus on hydraulic constraints, we need to know to what extent these constraints influence the overall drought tolerance of plants. As emphasized in Section 1, many other processes may limit gas exchange besides water supply to leaves. A reasonable way to assess the importance of hydraulic properties would be to compare them between crop cultivars with demonstrated differences in drought tolerance. Little work has been done on the cavitation response of crop plants, and in many cases there is as yet no physiological explanation of observed differences in drought tolerance between cultivars.

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