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Co-ordination of vapour and liquid phase water transport properties in plants

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ABSTRACT

The pathway for water movement from the soil through plants to the atmosphere can be represented by a series of liquid and vapour phase resistances. Stomatal regulation of vapour phase resistance balances transpiration with the efficiency of water supply to the leaves, avoiding leaf desiccation at one extreme, and unnecessary restriction of carbon dioxide uptake at the other. In addition to maintaining a long-term balance between vapour and liquid phase water transport resistances in plants, stomata are exquisitely sensitive to short-term, dynamic perturbations of liquid water transport. In balancing vapour and liquid phase water transport, stomata do not seem to distinguish among potential sources of variation in the apparent efficiency of delivery of water per guard cell complex. Therefore, an apparent soil-to-leaf hydraulic conductance based on relationships between liquid water fluxes and driving forces *in situ* seems to be the most versatile for interpretation of stomatal regulatory behaviour that achieves relative homeostasis of leaf water status in intact plants. Components of dynamic variation in apparent hydraulic conductance in intact plants include, exchange of water between the transpiration stream and internal storage compartments via capacitive discharge and recharge, cavitation and its reversal, temperature-induced changes in the viscosity of water, direct effects of xylem sap composition on xylem hydraulic properties, and endogenous and environmentally induced variation in the activity of membrane water channels in the hydraulic pathway. Stomatal responses to humidity must also be considered in interpreting co-ordination of vapour and liquid phase water transport because homeostasis of bulk leaf water status can only be achieved through regulation of the actual transpirational flux. Results of studies conducted with multiple species point to considerable convergence with regard to co-ordination of stomatal and hydraulic properties. Because stomata apparently sense and respond to integrated and dynamic soil-to-leaf water transport properties, studies involving intact plants under both natural and controlled conditions are likely to yield the most useful new insights concerning stomatal co-ordination of transpiration with soil and plant hydraulic properties.

Key-words: Hydraulic architecture; leaf water potential; plant hydraulic conductance; stomatal regulation; transpiration.

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INTRODUCTION

The pathway for water movement from the soil through plants to the atmosphere can be represented by a series of liquid and vapour phase resistances (van den Honert 1948). It is a well-known axiom in plant water relations that the physically limiting resistance to water loss must be in the vapour phase. If the liquid phase, or hydraulic, resistance were physically limiting, the leaves would quickly desiccate. Nevertheless, the operating range of vapour phase resistance is ultimately constrained by the requirement for stomata to balance transpiration with the physiologically limiting total hydraulic resistance of the soil/leaf pathway. When stomatal regulation of vapour phase resistance balances transpiration with the efficiency of water supply to the leaves, leaf desiccation is avoided at one extreme, and unnecessary restriction of carbon dioxide uptake at the other, both of which inhibit plant carbon gain.

In addition to the aforementioned general balance between vapour and liquid phase water transport properties in plants, there is mounting evidence that stomatal regulation of vapour loss is exquisitely sensitive to short-term, dynamic perturbations of liquid water transport. The objectives of this synthesis are to review examples of dynamic stomatal co-ordination of transpiration with changes in apparent soil-to-leaf hydraulic properties, evaluate evidence concerning the types of signals involved, and to identify and discuss important components of dynamic variation in liquid phase water transport properties relevant to stomatal regulation *in situ*. Conductance terminology is typically used in discussions of regulation of liquid and vapour phase water transport because water flux is a linear function of conductance at a given driving force. However, resistance terminology is more convenient for assessing the consequences of changes in the properties of components of the water transport pathway that are arranged in series. Therefore, both resistance and conductance terminology will be used as appropriate in the following discussion.

DYNAMIC CO-ORDINATION OF VAPOUR AND LIQUID PHASE RESISTANCE

Numerous studies of stomatal regulation contain descriptions of stomatal behaviour from which active co-ordination of vapour and liquid phase water transport properties can either be inferred or documented directly. Co-ordinated changes in root permeability to water and stomatal conductance of individual sunflower, barley and maize plants subjected to a wide range of evaporative demand and water flux resulted in bulk leaf water potential (Ψ_L) remaining nearly constant, leading Aston & Lawlor (1979) to conclude that stomata were responding to conditions in the root rather than directly to Ψ_L. On a larger scale, co-ordinated adjustments in stomatal conductance, canopy transpiration and tree allometry and hydraulic resistance in stands of *Pinus sylvestris* grown at different spacings led to homeostasis of Ψ_L (Whitehead, Jarvis & Waring 1984). These types of compensatory adjustments at the tree and stand level were predicted by a model proposed earlier by Whitehead & Jarvis (1981) and discussed further by Whitehead (1998). Not all species exhibit isohydric behaviour, the maintenance of nearly constant Ψ_L over a wide range of conditions. Hubbard *et al.* (2001) proposed that isohydric behaviour should be associated with a linear relationship between stomatal conductance (g_s) and whole-plant leaf-specific hydraulic conductance (G_t), whereas anisohydric behaviour should be associated with a curvilinear relationship between stomatal and hydraulic conductance in which the decline in g_s with declining G_t is at first gradual, and then becomes increasingly steep as G_t continues to decline.

Results of studies conducted with multiple species point to considerable convergence among co-occurring species with regard to co-ordination of stomatal and hydraulic properties. In some cases, two or more species share a single curvilinear relationship between g_s and G_t with g_s clearly becoming asymptotic at the highest values of G_t observed, whereas in other cases a single linear function appears to describe the dependence of g_s on G_t among multiple species. For example, 1–2 m tall individuals of five co-occurring tropical forest gap colonizing species shared a common curvilinear relationship between g_s and G_t (Meinzer *et al.* 1995). Five 18–35 m tall co-occurring tropical forest canopy tree species also exhibited a common curvilinear dependence of g_s on G_t (Andrade *et al.* 1998). Although the two studies were conducted in similar types of forest less than 50 km apart, the dependence of g_s on G_t differed among the two groups of plants with g_s being greater in the canopy trees at a given value of G_t. Shared linear relationships between g_s and G_t were reported for two desert subshrubs (Comstock 2000), four Brazilian savanna woody species (Meinzer *et al.* 1999), and 11 woody species growing in a European botanical garden (Nardini & Salleo 2000). It is not clear whether these examples of apparent curvilinear versus linear relationships between stomatal and hydraulic conductance reflect anisohydric versus isohydric regulation of Ψ_L as suggested by Hubbard *et al.* (2001). Isohydric and anisohydric behaviour may represent the same regulatory process operating at different points along a continuum of hydraulic conductance. For instance, an 'isohydric' species that normally operates at a relatively low range of G_t where g_s changes linearly with G_t, may begin to behave like an anisohydric species if G_t is enhanced by relief from drought or other constraints. Thus, unless the entire operating ranges of g_s and G_t for a species can be established, classification of its behaviour as either isohydric or anisohydric may be potentially misleading.

The high degree of convergence in relationships between stomatal and hydraulic properties among co-occurring species is intriguing, given the probable divergence in their hydraulic architecture and xylem vulnerability to cavitation. Divergence in relationships between stomatal and hydraulic properties obtained in studies carried out in different locations may be partly attributable to differences in measurement procedures and growing conditions. Further convergence in stomatal co-ordination of vapour and liquid phase water transport among diverse plant growth forms growing in different biomes may be revealed when uniform measurement protocols are implemented allowing the data obtained to be normalized for differences in variables such as evaporative demand, light, temperature and leaf boundary layer properties.

POTENTIAL SIGNALS INVOLVED IN STOMATAL CO-ORDINATION OF VAPOUR AND LIQUID PHASE WATER TRANSPORT PROPERTIES

As it seems intuitively reasonable that maximum stomatal aperture should be limited by the water supply to the leaf, the literature is replete with examples of attempts to correlate stomatal behaviour with leaf water status usually expressed as some measure of the water potential of the bulk leaf tissue. Indeed, progressively increasing soil water deficit will eventually displace the operating ranges of both Ψ_L and g_s to lower values. However, during incipient soil drying, daily minimum values of Ψ_L often remain nearly constant as a result of strong reductions in g_s (Bates & Hall 1981). Sharp reductions in g_s in the presence of essentially constant bulk leaf Ψ would require either stomatal sensing of bulk leaf Ψ via a negative feedback loop with extremely high gain, or feed-forward control of g_s with respect to bulk leaf Ψ via feedback sensing of water status in some other portion of the plant such as the roots or even in a localized region of the leaf itself. True feed-forward control would thus allow stomata to limit transpiration in anticipation of potential reductions in bulk leaf Ψ resulting from perturbations in the soil environment or increased soil-to-leaf hydraulic resistance.

Feed-forward behaviour of stomata with respect to regulation of Ψ_L has been attributed to the presence of chemical modulators of stomatal opening in the transpiration stream arriving at the leaf (see Davies, this volume). The control of stomatal opening by chemical signals generated in roots growing in drying soil has been termed non-hydraulic signalling to distinguish it from strictly hydraulic signalling involving transpiration-induced fluctuations in leaf xylem tension and Ψ_L. However, Tardieu & Simonneau (1998) concluded that isohydric behaviour, the maintenance of nearly constant Ψ_L independent of soil water status, is linked to an interaction between both chemical and hydraulic information. In field-grown maize, for example, stomatal sensitivity to abscisic acid in the xylem sap increased with declining leaf Ψ (Tardieu, Zhang & Gowing 1993).

Potential hydraulic signals are generated during normal diel fluctuations in transpiration even when soil water reserves have not been significantly depleted. However, there is scant evidence that diel cycles of Ψ_L play an important role in regulating g_s when soil water deficits are minimal. Correlation between g_s and daily minimum Ψ_L within species is generally poor and even negative until a threshold value of Ψ_L is attained (Whitehead, Okali & Fasehun 1981; Syvertsen 1982; Meinzer *et al.* 1988, 1995; Jones & Sutherland 1991). Strong correlations between maximum g_s and declining pre-dawn Ψ_L observed in some studies may actually reflect a response of g_s to hydraulic changes in soil/plant system rather than a direct influence of Ψ_L prior to dawn on maximum g_s later in the day (Reich & Hinckley 1989).

Although the preceding discussion implies a clear mechanistic basis for distinguishing between stomatal responses to so-called hydraulic versus non-hydraulic signals, stomatal responses in intact plants are often ambiguous in this regard. For example, stomatal conductance typically decreases in response to root pruning (Aston & Lawlor 1979; Briggs & Wiebe 1982; Meinzer & Grantz 1990). This manipulation can be interpreted as generating a hydraulic signal in the form of diminished leaf-specific hydraulic conductance following partial root removal. If stomata did not respond by restricting transpiration, leaf water potential would decline. However, stomatal responses to root pruning may also exhibit some feed-forward characteristics when stomata overcompensate causing leaf water potential to be noticeably less negative following root removal than before (Meinzer & Grantz 1990). Similarly, partial defoliation, a manipulation that increases leaf-specific hydraulic conductance, often leads to increased stomatal conductance in the remaining leaves with leaf water potential remaining nearly constant (Meinzer & Grantz 1990; Pataki, Oren & Phillips 1998). Partial shading, an analogous manipulation that results in a decrease in transpiring leaf area and therefore increased leaf-specific conductance, has also been reported to lead to increased stomatal conductance in the unshaded leaves (Whitehead *et al.* 1996). In sugarcane, co-ordination of stomatal conductance and leaf-specific hydraulic conductance as total leaf area increases during growth leads to nearly constant minimum leaf water potentials over a wide range of plant size (Meinzer & Grantz 1990; Meinzer *et al.* 1992). Responses of stomata to root pruning, partial defoliation, partial shading of foliage, and increasing leaf area during growth are consistent with variation in the concentration or delivery rate of chemical promoters of stomatal opening arriving at the guard cells in the transpiration stream.

Recently, Salleo *et al.* (2000) have suggested that cavitation itself may act as a hydraulic modulator of stomatal opening. These authors found that stomatal conductance of laurel shoots increased as leaf water potential declined, then decreased abruptly when Ψ_L reached a threshold value corresponding to the onset of cavitation in the stem. Pulses of cavitation in the stem were also paralleled by decreases in stomatal conductance. Based on these observations, a negative feedback loop involving stomatal conductance and the water potential threshold for cavitation rather than bulk leaf water potential itself was proposed. Regardless of the signals involved, all of the stomatal responses described above exhibit feed-forward characteristics with respect to bulk leaf Ψ because they co-ordinate water loss with changes in leaf area-based hydraulic properties leading to relative homeostasis of bulk leaf water status.

Although the preceding discussion has emphasized co-ordination of stomatal and hydraulic conductances, it must be noted that homeostasis of bulk leaf water status can only be achieved through regulation of the actual transpirational flux. Thus, for a given soil-to-leaf hydraulic conductance, the value of stomatal conductance required to maintain leaf water potential at its daily minimum set point will depend on the atmospheric evaporative demand assuming boundary layer resistance remains constant. Stomatal responses to humidity must therefore be considered in interpreting stomatal co-ordination of vapour and liquid phase water transport. Stomatal sensing of changes in evaporative demand has been studied extensively without a clear consensus concerning the mechanisms involved. In the past decade, a number of studies have reported behaviour consistent with stomatal sensing of the transpiration rate itself rather than the relative humidity or saturation deficit (Mott & Parkhurst 1991; Meinzer & Grantz 1991; Monteith 1995; Meinzer, Hinckley & Ceulemans 1997b). Stomatal sensing of transpiration could involve either the bulk leaf (stomatal) transpiration rate, or epidermal (cuticular) transpiration. Apparent feed-forward regulation of bulk leaf water potential in response to perturbations of hydraulic conductance and evaporative demand is difficult to reconcile with a sensing mechanism involving the bulk leaf transpiration rate. However, sensing of cuticular transpiration, especially if epidermal hydraulic conductance in the vicinity of the guard cells is low, would be compatible with feed-forward regulation of bulk leaf water potential. Consistent with this, Franks & Farquhar (1999) reported that stomatal sensitivity to vapour pressure deficit (VPD) was greatest in species in which estimated epidermal hydraulic conductance and overall hydraulic conductance was lowest.

Interaction between stomatal responses to humidity and plant hydraulic architecture was also observed in four tropical forest canopy tree species, each with an apparently distinct relationship between stomatal conductance and VPD (Meinzer *et al.* 1997a). However, when stomatal conductance was normalized by the branch-specific ratio of leaf area to sapwood area, an index of potential transpirational demand relative to water transport capacity, a common relationship between stomatal conductance and VPD for all four species emerged. Taken together, the results implied that at a given combination of leaf area/sapwood area and evaporative demand, the vapour phase conductance, and therefore the transpiration rates on a leaf area basis were identical in all four species.

COMPONENTS OF DYNAMIC VARIATION IN APPARENT HYDRAULIC RESISTANCE

Studies of plant hydraulic architecture have traditionally focused on characterizing the inherent hydraulic properties of various segments of the root-to-leaf pathway and on the mapping of hydraulic constrictions within the plant (Zimmermann 1978; Tyree & Ewers 1991). Barring events such as cavitation, these properties presumably remain fixed over periods of hours to days. Although general correlations between prevailing stomatal conductance and components of hydraulic architecture have been demonstrated (Sperry & Pockman 1993; Kolb & Sperry 1999; Comstock 2000; Hacke *et al.* 2000; Tausend. Meinzer & Goldstein 2000), dynamic aspects of stomatal regulation cannot be deduced from steady-state hydraulic properties of excised plant segments. As the examples cited here suggest, stomata are able to sense and respond appropriately to dynamic variation in leaf area-based apparent hydraulic properties over the course of a day in the absence of changes in the inherent properties of the hydraulic pathway. In co-ordinating vapour and liquid phase water transport, stomata do not seem to distinguish among potential sources of variation in the apparent efficiency of delivery of water per guard cell complex. Therefore, an 'apparent' soil-to-leaf hydraulic conductance (G_t), a measure of whole-plant water transport efficiency based on the liquid water flux per unit driving force *in situ*, seems to be the most versatile for interpretation of stomatal regulatory behaviour that achieves relative homeostasis of leaf water status in intact plants. A whole-plant hydraulic variable defined in this manner integrates intrinsic hydraulic properties of the water transport pathway with dynamic processes that affect delivery of water to the leaves such as exchange of water between storage compartments and the transpiration stream via capacitive discharge and recharge, temperature-mediated changes in the viscosity of water, and fluctuations in the activity of membrane water channels.

Role of capacitance

The role of capacitance in plant–water relations has long been recognized and has been formally incorporated into models of water transport along the soil/plant/atmosphere continuum (e.g. Cowan 1972). Similarly, seasonal courses of discharge and recharge of stored water in intact, large trees have been measured and modelled (Waring & Running 1978; Waring, Whitehead & Jarvis 1979). However, the specific role of short-term cycles of capacitive discharge and recharge in governing daily patterns of stomatal behaviour has not been addressed until recently. The discharge of water from storage compartments into the transpiration stream will transiently increase the apparent soil-to-leaf conductance. The magnitude and duration of this effect will depend not only upon the intrinsic capacitance of the storage compartments, but also upon their absolute volume and their volume relative to the transpiring leaf area served. The intrinsic capacitance of a tissue is typically defined as the ratio of its change in water content to change in water potential. This relationship specifies the absolute volume of water that can be exchanged with storage tissues over the normal operating range of water potential for those tissues in a given species. However, the impact of stored water on diurnal variation in soil-to-leaf hydraulic conductance will be determined largely by the amount of transpiring leaf area in relation to the volume of water available from storage. In trees, for example, the influence of stored water on G_t is expected to increase as the leaf area/sapwood area ratio diminishes. The dynamics of discharge and recharge of storage compartments can be characterized using the lag between changes in sap flow in the upper crown (a surrogate for transpiration) and sap flow near the base of the tree (Phillips *et al.* 1997; Goldstein *et al.* 1998). Consistent with this, Andrade *et al.* (1998) reported a strong correlation ($r^2 = 0{\cdot}73, P < 0{\cdot}05$) between apparent soil-to-leaf hydraulic conductance and the difference between sap flow in the upper crown and at the base of the stem among five tropical forest canopy trees. Apparent hydraulic conductance was highest when sap flow in the crown exceeded that at the base of the tree, indicating that a portion of the water being transpired from the crown was derived from internal storage. Conversely, apparent hydraulic conductance was lowest when sap flow at the base of the tree was greater than that in the crown indicating recharge of internal water stores. The daily course of total vapour phase conductance (crown conductance) in the trees studied by Andrade *et al.* (1998) closely tracked that of the difference between sap flow in the crown and at the base of the tree (Fig. 1), resulting in a highly significant overall correlation between crown conductance and the difference in sap flow between the upper and lower measurement points (Fig. 2). Using a theoretical model, Williams *et al.* (1996) were able to account for the afternoon decline in CO_2 uptake in a mixed *Quercus–Acer* stand on the basis of partial stomatal closure in response to depletion of stored water. The preceding examples indicate that although capacitance does not influence the steady-state hydraulic properties of the root-to-leaf pathway, the dynamic hydraulic variable, G_t, and consequently g_s, can be strongly influenced by daily cycles of capacitive discharge and recharge.

Role of cavitation

The vulnerability of xylem to cavitation has been the subject of intensive study and discussion during the past decade (Tyree & Ewers 1991; Salleo *et al.* 1992; Alder *et al.* 1997) and xylem vulnerability curves depicting the relationship between loss of hydraulic conductivity and xylem tension have now been characterized for stems and other organs of numerous species (Cochard 1992; Sperry & Sullivan 1992; Tyree *et al.* 1993; Sperry *et al.* 1994; Alder, Sperry & Pockman 1996; Mencuccini & Comstock 1997; Sperry & Ikeda 1997; Kavanaugh *et al.* 1999; Nardini & Pitt 1999). However, it must be emphasized that the impact of

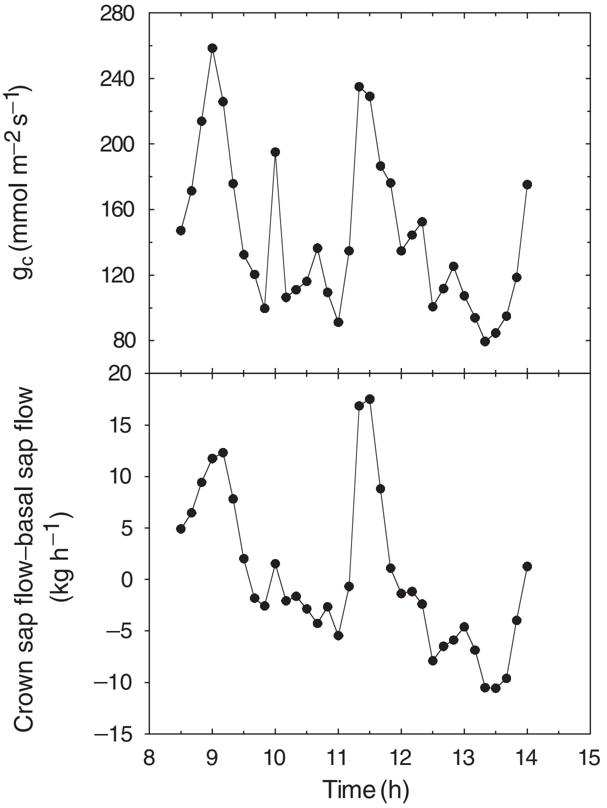

Figure 1. Daily courses of crown conductance (g_c) and the difference between total sap flow in the upper crown and near the base of a 30 m tall, 0·57 m d.b.h. *Ficus insipida* tree growing at the Smithsonian Tropical Research Institute canopy crane site in the Parque Natural Metropolitano near Panama City, Panama. Crown conductance is the total vapour phase conductance of the crown on a unit leaf area basis (Meinzer *et al.* 1993). Sap flow in the upper crown was used as a surrogate for transpiration (Goldstein *et al.* 1998). Differences between sap flow in the crown and at the base of the tree are an index of discharge and recharge of internal water storage compartments located between the points of sap flow measurement.

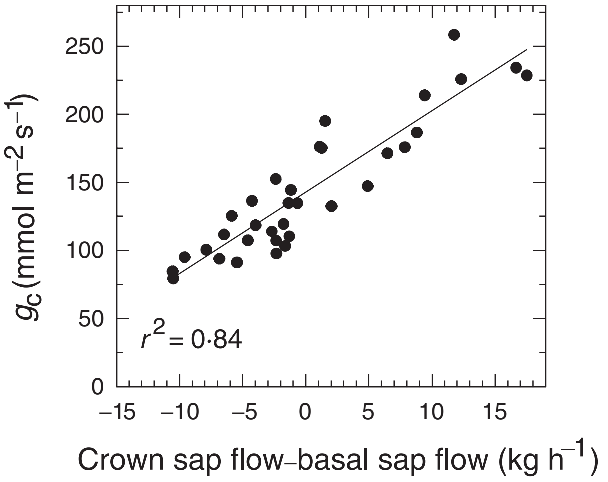

Figure 2. The relationship between crown conductance (g_c) and the difference between crown and basal sap flow obtained from the data shown in Fig. 1.

cavitation on total hydraulic resistance and ultimately stomatal resistance, if the two are actively co-ordinated, will depend on where cavitation occurs in the root/leaf pathway and on the partitioning of hydraulic resistances among roots, stems and leaves. Root systems often constitute about 50% of the total plant hydraulic resistance (Saliendra & Meinzer 1989; Tyree, Velez & Dalling 1998; Nardini & Tyree 1999). The relative contributions of stem and leaf resistance to the remaining shoot resistance can vary substantially, but leaf resistance often dominates (Black 1979; Küppers *et al.* 1987; Machado & Tyree 1994; Yang & Tyree 1994; Nardini & Salleo 2000). Thus, other colimiting resistances will attenuate the influence on whole-plant water transport of a given loss of stem hydraulic conductivity. These relationships are illustrated in Fig. 3 where the relative total resistance of the root-to-leaf pathway is plotted as a function of percentage loss of stem hydraulic conductivity for various ratios of leaf-to-shoot resistance. Even when shoot resistance is equally partitioned among leaves and stems, a 50% loss in stem hydraulic conductivity results in an increase in total resistance of only 25%. When leaf resistance is more dominant as is often the case, larger losses of stem conductivity can be sustained with a negligible effect on total resistance. These scenarios suggest that although cavitation in stems is often emphasized, its negative influence on whole-plant water transport may be minimal. Because their relative resistances are usually greater, cavitation in roots and leaves may have a greater effect on total resistance and stomatal behaviour than cavitation in stems. It has been proposed that daily cycles of cavitation followed by refilling of xylem elements may even have a positive influence on leaf water balance by transiently releasing stored water into the transpiration stream (Lo Gullo & Sal-

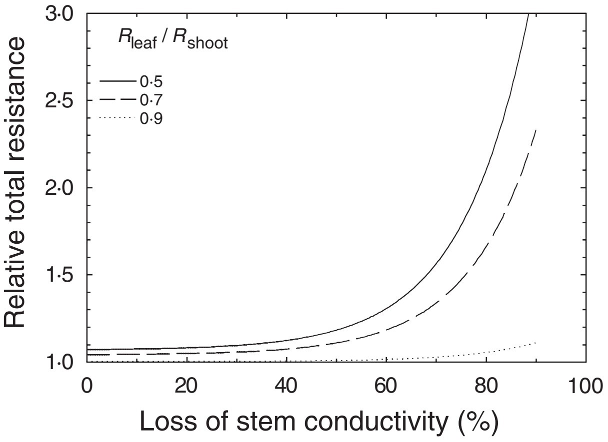

Figure 3. Relative total resistance of the root-to-leaf pathway in relation to percentage loss of stem hydraulic conductivity for various ratios of leaf to total shoot hydraulic resistance.

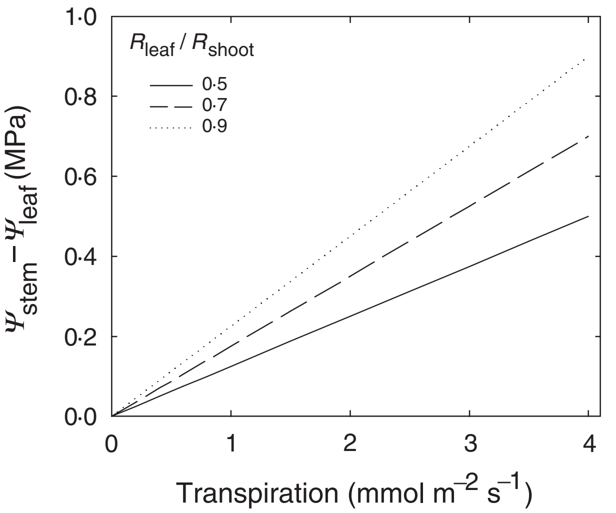

Figure 4. The difference between stem and leaf water potential as a function of transpiration for various ratios of leaf to total shoot hydraulic resistance. Total soil-to-leaf hydraulic conductance was assumed to be 2 mmol m^{-2} s^{-1} MPa^{-1}.

leo 1992). Transient release of water via cavitation in stems would dampen diurnal fluctuations in leaf water potential and partially uncouple total soil-to-leaf hydraulic resistance from soil and root resistances upstream from the points of water release. The net result would be greater apparent soil-to-leaf hydraulic conductance sensed by stomata than in the absence of cavitation, which would allow greater rates of gas exchange to be sustained, or at least extend the period during which gas exchange is maximal.

The partitioning of hydraulic resistance among stems and leaves creates another potential problem in estimating the effect of cavitation in stems on total resistance and therefore on stomatal regulation of transpiration. Traditionally, xylem tension has been inferred from the bulk water potential of transpiring leaves. However, if leaf resistance is relatively large in relation to stem resistance, transpiration can induce a substantial difference in water potential, and therefore xylem tension, between the leaves and the stem (Fig. 4). Indeed, it has long been recognized that large differences in water potential can be observed between adjacent transpiring leaves and covered, non-transpiring leaves (Ritchie & Hinckley 1971; Turner & Long 1980; Saliendra & Meinzer 1989; Melcher *et al.* 1998). Under these conditions, the water potential of a covered, non-transpiring leaf should provide a better estimate of xylem tension in the stem (McCutchan & Shackel 1992; Melcher *et al.* 1998). Use of bulk water potentials of transpiring rather than covered leaves in conjunction with stem xylem vulnerability curves is expected to lead to overestimates of cavitation and loss of stem conductivity *in situ*.

Temperature/viscosity

The viscosity of water undergoes marked changes over the range of temperature normally experienced by plants. For example, as temperature increases from 10 to 30 °C, viscosity decreases by 39%. In the absence of compensatory influences of temperature on other components of soil/leaf water transport efficiency, the temperature dependence of water viscosity should result in proportional, dynamic variations in hydraulic resistance of the portion of the soil/leaf pathway experiencing given temperature variations. Although the effects of water viscosity on plant hydraulic properties are often taken into account in comparing measurements of hydraulic conductivity of excised plant organs made at different temperatures (Tyree *et al.* 1995), the potential impact of viscosity-mediated changes in hydraulic resistance on the behaviour of intact plants in the field has been largely ignored. Most discussions of the temperature dependence of plant water transport properties have emphasized the impact of low temperatures on membrane permeability, especially in roots growing in cold soils (Kaufmann 1977; Running & Reid 1980; Teskey, Hinckley & Grier 1984). Recently, however, in an ingenious attempt to demonstrate a direct stomatal response to changes in plant hydraulic conductance, Cochard *et al.* (2000) showed that temperature-mediated variations in the hydraulic conductance of roots and shoots of *Quercus robur* seedlings could be explained by the temperature dependence of water viscosity up to ≈35 °C. Furthermore, Ψ_L remained constant as transpiration and whole-plant hydraulic conductance increased linearly with root temperature between 10 and 40 °C. The potential impact of the temperature dependence of water viscosity on plant hydraulic resistance and leaf water status in the field is further illustrated by the simple modelling exercise shown in Fig. 5 (conditions and assumptions specified in figure legend). For a plant growing in a site where the temperature rises from 10 °C at dawn to 30 °C in the early afternoon, the relationship between Ψ_L and transpiration would be linear (i.e. constant resistance) in the absence of a temperature effect on water viscosity (Fig. 5, dotted line). However, if it is assumed that stem and leaf temperature track air temperature (Fig. 5, dashed line), the relationship between Ψ_L and transpiration becomes distinctly non-linear, indicative of decreasing hydraulic resistance with increasing transpiration. Total resistance would decline even more rapidly with increasing transpiration if the temperature of the roots carrying out the bulk of water absorption also tracked air temperature (Fig. 5, solid line). The non-linearity in the relationship between Ψ_L and transpiration would be even more noticeable under more typical non-isothermal field conditions in which stems and leaves are heated above air temperature. In practice, diminishing hydraulic resistance with increasing temperature and evaporative demand might not dampen diurnal fluctuations in Ψ_L under field conditions, but might allow plants to sustain greater maximum transpiration rates, and therefore more gas exchange, for a given daily minimum value of Ψ_L. Reports of an apparent flow dependence of hydraulic resistance in field-grown plants are consistent with an important role for water viscosity in mediating plant responses under natural conditions (Passioura 1984).

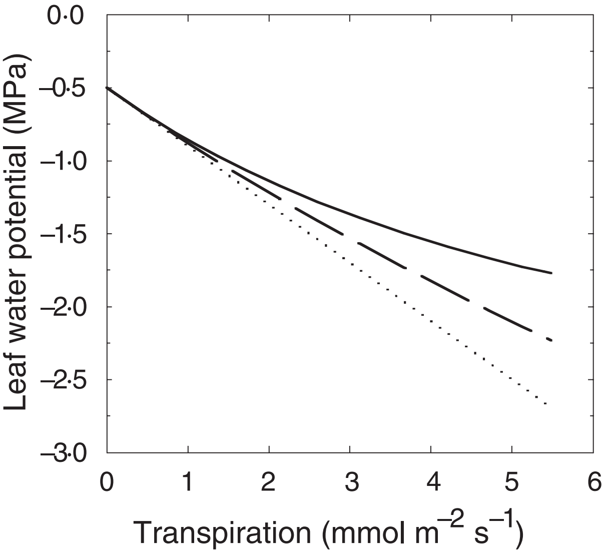

Figure 5. Predicted relationships between leaf water potential and transpiration resulting from different assumptions concerning the impact of the temperature dependence of water viscosity on hydraulic resistance. Assumptions were: no temperature effect on viscosity (dotted line), leaf and stem temperature track air temperature (dashed line), and roots carrying out bulk of water absorption also track air temperature. Conditions for simulation: air temperature rises from 10 to 30 °C, air saturation deficit rises from 0·25 to 3·5 kPa, photosynthetic photon flux density (PPFD) rises from 0 to 2000 μmol m^{-2} s^{-1}, and total vapour phase conductance rises from 0 to 150 mmol m^{-2} s^{-1} over an 8 h period beginning at dawn. Vapour phase conductance was assumed to saturate at approximately 1000 μmol m^{-2} s^{-1} PPFD. Total root and shoot resistances were assumed to be equivalent under isothermal conditions.

Xylem sap composition

In early reports of hydraulic conductivity measurements on excised stem segments, it was noted that perfusing the segments with tap water or a dilute KCl solution prevented the decline in conductivity that was observed when deionized water was used (Zimmermann 1978). These observations have traditionally been regarded as representing a methodological problem. However, the results of two recent studies suggest that endogenous changes in the ionic composition of xylem sap may play a role in regulating short-term variations in hydraulic resistance in intact plants. Zwieniecki *et al.* (2001) demonstrated rapid, reversible changes in flow rate (hydraulic resistance) when stem segments of several species were alternately perfused with aqueous KCl solutions and deionized water. Among the 27 species studied, ion-mediated flow enhancement ranged from 2·5 times in *Laurus nobilis* to 1·1 times or less in conifers. A split stem experiment was conducted to confirm that the phenomenon occurs *in vivo*. In all cases, flow enhancement was concentration-dependent and near maximal at KCl concentrations representative of the range of total ionic content of xylem sap in intact transpiring plants. It was concluded that the response is mediated by reversible swelling of pectins (hydrogels) located in intervessel pit membranes. Consistent with the observations of Zwieniecki *et al.* (2001), van Leperen, van Meeteren & van Gelder (2000) found that perfusion of chrysanthemum stems with dilute solutions of KCl and other salts raised their hydraulic conductivity. However, the magnitude of the response was generally much smaller than that reported by Zwieniecki *et al.* (2001) and not concentration-dependent. In addition, the enhancement of hydraulic conductivity by ionic solutions appeared to increase with decreasing segment length, and therefore decreasing frequency of vessel ends, leading van Leperen *et al.* (2000) to conclude that the phenomenon was not associated with the presence of intervessel pit membranes. The basis for the discrepancy in the presumed mechanism of ion-mediated changes in xylem hydraulic resistance remains to be resolved.

The ionic composition of xylem sap is known to change seasonally, and in response to changes in the root environment (Ferguson, Eiseman & Leonard 1983; Andersen & Brodbeck 1989; Glavac, Koenies & Ebben 1990; Schurr & Schulze 1995; Schill *et al.* 1996). Elucidation of the role of xylem sap composition in modulating stomatal behaviour via ion-mediated changes in xylem hydraulic resistance will require concurrent measurements of xylem sap composition and stomatal and hydraulic properties in intact plants.

Aquaporins

Because the soil-to-leaf water transport pathway contains points at which water must cross living membrane barriers, it is reasonable to expect that aquaporins (see Steudle, this volume) may play a prominent role in mediating dynamic variations in liquid, and therefore vapour phase, resistance. However, most of the work to date on water channels in plants has focused on their identification, characterization and localization in cells and tissues. At the organ level, $HgCl_2$, a known water channel inhibitor, has been shown to cause a sharp, reversible decline in the hydraulic conductance of detopped root systems (Maggio & Joly 1995; Wan & Zwiazek 1999) and water channels have been implicated in the endogenous diurnal oscillations in root pressure and hydraulic conductivity (Henzler *et al.* 1999). It is reasonable to postulate that stomata would respond to aquaporin-mediated variations in whole-plant hydraulic conductance and evidence to support this has been presented for *Populus tremuloides* seedlings (Wan & Zwiazek 1999) and cotton and tomato plants (Hwang 2000).

CONCLUSIONS AND RECOMMENDATIONS

Because stomata apparently sense and respond to integrated and dynamic soil-to-leaf water transport properties, studies involving intact plants under both natural and controlled conditions are likely to yield the most useful new insights concerning the means by which stomata balance transpiration with changing soil and plant hydraulic properties to achieve homeostasis of bulk leaf water status. Interactions and synergy among features such as capacitance, cavitation, and water viscosity will make the design of definitive experiments a challenge. Interpretation of behaviour observed in intact plants must also rely on a good understanding of hydraulic architecture and its implications for partitioning of resistances along the soil-to-leaf pathway. In plants such as trees that span a large range of size during their lifetimes, dynamic co-ordination of vapour and liquid phase water transport in seedlings and saplings is certain to differ from that in mature individuals. Characterization of the functional consequences of changes in hydraulic architecture during tree growth is therefore essential. Additional multispecies surveys employing standardized methods will be useful in determining the extent to which specific features of stomatal co-ordination of vapour and liquid phase water transport are universal. Appropriate allometric scaling factors such as leaf area in relation to conducting xylem area will be needed to reveal the degree of functional convergence in co-ordination of vapour and liquid phase water transport among phylogenetically and architecturally diverse species.

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