DIVERSITY OF HYDRAULIC CONDUCTANCE IN LEAVES OF TEMPERATE AND TROPICAL SPECIES: POSSIBLE CAUSES AND CONSEQUENCES

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TYREE, M. T., SOBRADO, M. A., STRATTON, L. J. & BECKER, P. 1999. **Diversity of hydraulic conductance in leaves of temperate and tropical species: possible causes and consequences.** Liquid-flow-pathway hydraulic conductances (K_L) were measured in leaves of 24 species of temperate and tropical plants. The leaves had specific leaf areas (SLA) ranging from 0.05 to 0.5 m^2 g^{-1}. Leaves with low SLA were typically sclerophylls and leaves with high SLA were typically malacophylls. No correlation was found between K_L and SLA. Whole shoot conductances were measured by transient (K_t) and quasi-steady state (K_q) methods. In the transient method, pressure (P) was increased at a rate of 3 to 5 $kPa\,s^{-1}$, whereas in quasi-steady state measurements, P was held constant for about 15 min. Flow (F) through leaves during transient measurements was a linear function of P and passed through the origin (F = 0 at P = 0) indicating that K_t was a first order rate constant ($F = K_t P$). At low conductances, K_t was up to 9.3% more than K_q. This difference is tentatively ascribed to polarisation of solutes across membranes during quasi-steady state measurements. Implications of low leaf conductances on the measurement of xylem pressure potential with a Scholander-Hammel pressure bomb are also discussed.

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TYREE, M. T., SOBRADO, M. A., STRATTON, L. J. & BECKER, P. 1999. Kepelbagaian pengaliran hidraulik dalam daun bagi spesies yang terdapat di kawasan iklim sederhana dan iklim tropika: sebab-sebab dan akibat yang mungkin berlaku. Pengaliran hidraulik laluan-aliran-cecair (K_L) disukat dalam daun 24 spesies pokok di kawasan iklim sederhana dan iklim tropika. Daun-daun tersebut mempunyai luas daun yang khusus (SLA) berjulat daripada 0.05 hingga 0.5 m^2 g^{-1}. Daun yang mempunyai SLA yang rendah lazimnya sklerofil dan daun dengan SLA yang tinggi lazimnya malakofil. Tiada kaitan didapati di antara K_L dan SLA. Keseluruhan aliran pucuk disukat dengan kaedah sukatan alihan (K_t) dan kaedah keadaan-kuasimantap (K_q). Dalam kaedah alihan, tekanan (P) bertambah pada 3 hingga 5 kPa s^{-1} manakala dalam sukatan keadaan-kuasimantap, P dibiarkan secara tetap selama 15 min. Aliran (F) melalui daun semasa sukatan alihan ialah fungsi linear bagi P dan melalui (F=0 pada P=0) yang asal menunjukkan bahawa K_t adalah kadar tertib pertama yang tetap (F=K_t P). Pada aliran yang rendah, kaedah K_t didapati sehingga 9.3% lebih tinggi daripada kaedah K_q. Perbezaan ini mungkin disebabkan oleh pengutuban zat terlarut menerusi membran sewaktu sukatan keadaan-kuasimantap. Kesan aliran daun yang lemah terhadap sukatan potensi tekanan xilem dengan bom tekanan Scholander-Hammer juga dibincangkan.

Introduction

The introduction of the high pressure flow meter (HPFM) has permitted the rapid determination of conductance to liquid water flow in roots, stems and leaves (Tyree *et al.* 1994, Tyree *et al.* 1995). Early studies revealed low hydraulic conductances (K_L) in leaves. The K_L of several *Quercus* species is so low that the drop in water potential from the base of the petiole to the evaporative surfaces of the lamina is 0.9 to 1.5 MPa (Tyree *et al.* 1993b). In *Acer saccharum* and *A. rubrum*, leaf resistance (inverse conductance) to water flow equals the total hydraulic resistance to water flow from the ground to the branch tips of adult trees (Yang & Tyree 1994).

The K_L measured with a HPFM will include vascular and non-vascular components. The vascular component of K_L will include the vessels of the petiole and veins of the blade. Leaves with few vessels of small diameter and long veins will have lower vascular conductances than leaves with many vessels of large diameter and short veins.

The non-vascular conductance will be determined by the tissues that water must pass through from the minor veins to the mesophyll air-spaces. Water will pass from veins to bundle sheath cells and will disperse in various directions to palisade, mesophyll and epidermal cells. Water will flow through extracellular pathways (cell walls parallel to the cells) and through transcellular pathways (in and out of cells through cell walls and membranes). The conductance of the extracellular pathway will depend on the porosity of the cell walls, the cross-sectional area of cell walls and the total path length. The transcellular conductances will depend on the number of cells passed and on the permeability of the plasma membranes to water flow.

Not enough is known about the relationship between K_l and leaf anatomy. In some cases the non-vascular conductances can be less than the vascular conductance in leaves (Tyree & Cheung 1977, Yang & Tyree 1994), so we might expect leaf thickness or SLA (an inverse index of the number of cells water must pass through) to correlate with K_l. The correlation will be very good if all leaves had cell walls of similar porosity and membranes of similar permeability to water. Lignification of cell wall will reduce porosity and decrease conductance of the extracellular pathways. Thus we might expect sclerophylls to have lower extracellular conductances to water flow and this would decrease overall K_l. But differences in leaf anatomy that might affect the pathway and path length of water flow in leaves might make K_l quite independent of leaf thickness and cell wall lignification.

The HPFM permits the examination of the dynamics (= time dependence) of water flow through tissues. The dynamics could be quite different for transcellular versus extracellular pathways of water movement. Water flow through extracellular pathways will be driven totally by pressure differences, whereas flow through transcellular pathways will be driven both by pressure differences and osmotic potential differences across cell membranes. When flow is initiated by a rapid increase in pressure across a membrane, flow will be high initially and then decline with time, because as water passes through the membrane solutes are swept up to the membrane on the upstream side and swept away from the membrane on the downstream side (see discussion). The solute sweep will cause a counter osmotic force reducing the rate of water flow. The HPFM can be used to measure both transient flows and quasi-steady state flows of water (see methods). Our hypothesis was that unlignified tissues should transport water mostly by extracellular pathways, whereas lignification of cell walls should reduce the amount of extracellular transport and increase the amount of transcellular transport. The symptom of this diversion of water to a transcellular pathway should be a divergence between transient values of leaf conductances versus quasi-steady state values of conductance as overall leaf conductance declines.

Sclerophylls are immediately distinguished from malacophylls (Cowling & Campbell 1983) by texture. Sclerophylls are tough, hard and stiff (Turner 1994b); they resist mechanical damage (fracturing, tearing and indenting) more than malacophylls (Lucas *et al.* 1991, Choong 1992, Turner 1994a). The anatomical bases for sclerophyllous properties are: thick cuticles, thick outer epidermal walls, lignification of secondary walls, and abundant sclerification, particularly of the vascular bundle sheaths and the leaf margins (Esau 1977, Fahn 1982, Napp-Zinn 1984). Sclerophylls are generally small and thick (Grubb 1986, Turner 1994a). The leaf thickening involves all tissues in the leaf blade and the frequent presence of a hypodermis. Leaf toughness is caused by sclerification of vascular bundles in leaves; the vascular bundles can be 20–30 times tougher than the other lamina tissues (Lucas *et al.* 1991, Choong *et al.* 1992). There is no quantitative measure of sclerophylly, but it correlates with a number of interesting features. Sclerophyllous leaves tend to have a low specific leaf area (SLA, m^2 of leaf area per g dry weight), which in turn is strongly, negatively correlated with lamina thickness (Turner 1994a). Readers interested in the potential adaptive advantages of sclerophylly

may refer to an number of papers (Chabot & Hicks 1982, Coley 1988, Koike 1988, Coley & Aide 1991, Reich *et al.* 1991, Reich *et al.* 1992, Turner 1994a).

The purpose of this study was to conduct a survey of K_t in a wide range of taxa in order to (1) get an idea of the diversity of K_t values in a large number of temperate and tropical species, (2) see if there is evidence of enhanced water transport through transcellular pathways as leaf conductance declines, and (3) see if there is any correlation with SLA (an inverse measure of sclerophylly).

Materials and methods

Plant material

Nine species were selected from mixed hardwood forests and wetlands in Burlington, Vermont, United States of America, to reflect the range of sclerophylly characteristic of the region. The species measured were *Alnus rugosa* (Du Roi) Spreng., *Betula alleghaniensis* Britton, *B. lenta* L., *Carpinus caroliniana* Walter, *Fraxinus americana* L., *F. nigra* Marsh, *Ilex verticellata* (L.) Gray, *Ostrya virginiana* (Mill.) K. Koch and *Quercus velutina* Lam. In order to increase the range of specific leaf areas (SLA), 15 additional species were collected from primary tropical heath forest, secondary heath shrubland, and primary dipterocarp forest in Brunei, Borneo. The species measured were *Agathis borneensis* Slooten, *Aglaia glabrata* Teijsm. & Binn., *Dacryodes* sp., *Dillenia suffruticosa* (Griff.) Martelli, *Syzygium bankense* (Hassk.) Merrill & Perry, *S. muelleri* (Miq.) Miq., *Gonocaryum minus* Sleumer, *Horsfieldia polyspherula* (Hook. *f.*) J. Sinclair, *Myristica malaccensis* Hook.*f.*, *Pouteria maingayi* (C. B. Clarke) Baehni, *Ploiarium alternifolium* (Vahl) Melch., *Rhodomyrtus tomentosa* (Aiton) Hassk., *Sindora coriacea* (Baker) Maingay *ex* Prain, *Xanthophyllum flavescens* Roxb. and *Xerospermum laevigatum* Radlk.

Shoot collection

Shoots were collected in the field and stored in air-tight plastic bags with small amounts of water added to keep the shoots hydrated. They were transported back to the laboratory and measured within three days. Cut surfaces of stems were kept under water whenever possible. Shoots of all temperate species were collected in summer (June and July) and shoots contained mature leaves of one to three months age and in some cases were in continuous flush (having a mixture of mature and immature leaves). Shoots of tropical species were collected from understory trees and were generally cut using pole pruners at a height of 5 to 7 m. Tropical shoots always contained mature leaves of unknown age and sometimes contained some immature leaves.

Leaf areas and specific leaf weights

After measurement of absolute conductances as described below, all leaves were harvested and leaf areas were determined on a Li-Cor Model 3100 leaf area

meter (Li-Cor Inc., Lincoln, Nebraska, USA). Leaf blade subsamples were collected by cutting lamina free from thick veins. The leaf area of the subsample was measured on the Li-Cor 3100 and then dried at 60 to 70 °C for $\geq$ 48 h. Dry weights were then determined and SLA ($m^2 g^{-1}$) calculated from (leaf area) / (dry weight).

The high pressure flowmeter

Hydraulic conductances reported in this paper were normalised to leaf surface area. The absolute hydraulic conductance is the ratio of the water flow rate through the leaf (F, kg s^{-1}) to the pressure difference causing flow (ΔP in MPa). The absolute conductance increases as leaf area (A, m^2) increases because a large leaf has more parallel pathways for water movement. Thus the normalised leaf conductance is $K_l = F/(A \Delta P)$.

Shoot and leaf conductances were measured using an HPFM as described previously (Tyree *et al.* 1995). Functionally, the HPFM is an instrument that permits rapid measurement of water flow (F, kg s^{-1}) while controlling water pressure. The flowmeter is connected to the base of a shoot with a water-tight seal and water is perfused into the base of the shoot with an applied pressure (P) of 0.5 to 0.7 MPa. Leaves were viewed as having conductances in series with stems. Inverse conductances (= resistances) are additive in series, so leaf conductances were determined by the difference in resistances. First the resistance of the shoot is measured with leaves,

$$R_{+L} = P/F_{+L}, \qquad\qquad (1A)$$

then the leaves are removed and the shoot resistance measured again without leaves,

$$R_{-L} = P/F_{-L}. \qquad\qquad (1B)$$

Then the absolute leaf resistance is calculated from

$$R = R_{+L} - R_{-L}. \qquad\qquad (1C)$$

All R values were measured on shoots with basal stem diameters of 3 to 7 mm and leaf areas of 0.005 to 0.03 m^2 except for species with very large leaves when 2 to 5 leaves had combined areas of up to 0.2 m^2. Five to seven shoots were measured for each species.

Quasi-steady state measurements of leaf conductance

Quasi-steady state leaf conductances were measured by first perfusing shoots at 0.5 to 0.7 MPa for about 15 minutes. Water flow into the base of the shoot exceeded the rate of transpiration from the leaves. This was confirmed in most cases by a noticeable infiltration of water into the leaf blade and an approach to constant

conductance. Leaf infiltration was necessary to insure that leaf water potential (Ψ_L) was equal to zero; otherwise it would be necessary to measure Ψ_L and calculate shoot resistance from $R_{+L} = (P - \Psi_L)/F$.

In some cases it was difficult to tell when leaves were infiltrated with water because of the opacity of the leaves, so the quasi-steady state flow was taken as an indication of leaf infiltration, i.e the resistance value was taken when resistance was relatively constant. Leaf conductances per unit leaf area were computed from

$$K_L = 1/(AR_L), \qquad\qquad (2)$$

where A = leaf area.

Transient measurements of leaf conductance

K_L values calculated from measurements of F at a single pressure are meaningful only if the relationship between F and P is linear and passes through the origin. In order to confirm the validity of conductance computed from equations (1A-C), some measurements were determined from the slope of F versus P over a range of pressures. For these measurements P was changed at a constant rate of 3 to 5 kPa s^{-1} while making instantaneous measurements of F every 3 s. Readers should consult Tyree *et al.* (1995) for a discussion of theory and potential sources of error in such measurements.

Results

The quasi-steady state measurements (equations 1A & 1B) assume that there is a linear relationship between F and P. This linear relationship was confirmed by the transient measurements, a typical example of which is shown in Figure 1. Nevertheless, there was a small systematic disagreement between the transient and the quasi-steady state K values, K_t and K_q respectively (Figure 2). The regression in Figure 2 was $K_t = 0.917149 K_q^{0.982695}$ ($r^2 = 0.999$). At high K values (e.g. 4×10^{-3} kg s^{-1} MPa^{-1} m^{-2}) the agreement between K_q and K_t was within 1%, but the disagreement was greater at low K values (e.g. 4×10^{-5} kg s^{-1} MPa^{-1} m^{-2}), where K_t was about 9.3% greater than K_q.

There was no significant relationship (r = 0.021, p = 0.924, n = 24) between SLA and leaf conductance per unit leaf area (Figure 3). The temperate species tended to have higher SLA values and hence were less sclerophyllous than the tropical species. The range of leaf conductances was from 3×10^{-5} to 5×10^{-4} kg s^{-1} m^{-2} MPa^{-1}. The highest and lowest K_L values of temperate species did not differ significantly from the highest and lowest K_L values of tropical species.
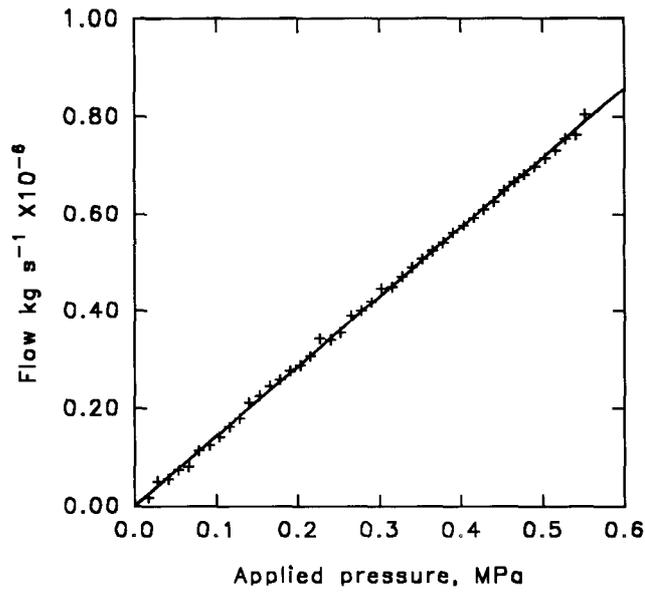
Figure 1. Typical transient measurement measured on a yellow birch shoot (*Betula alleghaniensis*). The applied pressure was increased at the rate of 3.2 kPa s[1]. The flow at each pressure is plotted versus the applied pressure.
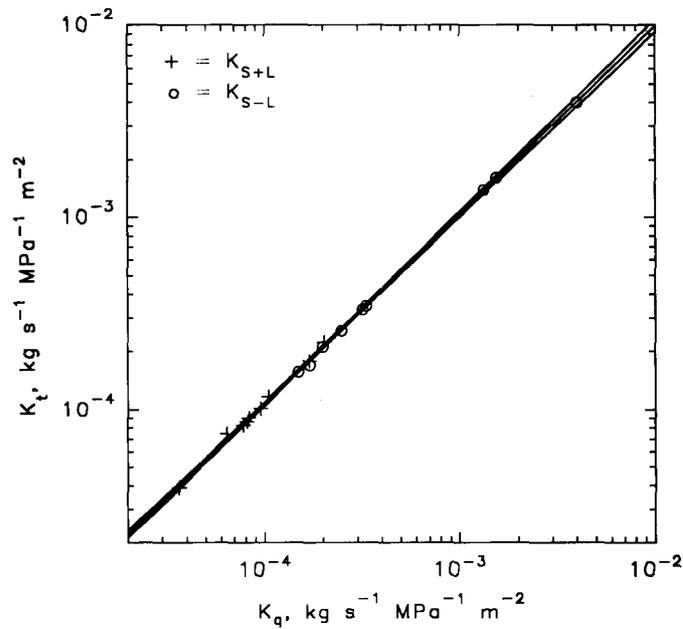

Figure 2. Log-Log regression of whole shoot conductances measured by the transient method (K_t) versus the quasi-steady state method (K_q) for shoots of nine temperate species with leaves (K_{S+L}) and without leaves (K_{S-L}). The lines through the data are the linear regression (on log-transformed data) and the 99% confidence interval.
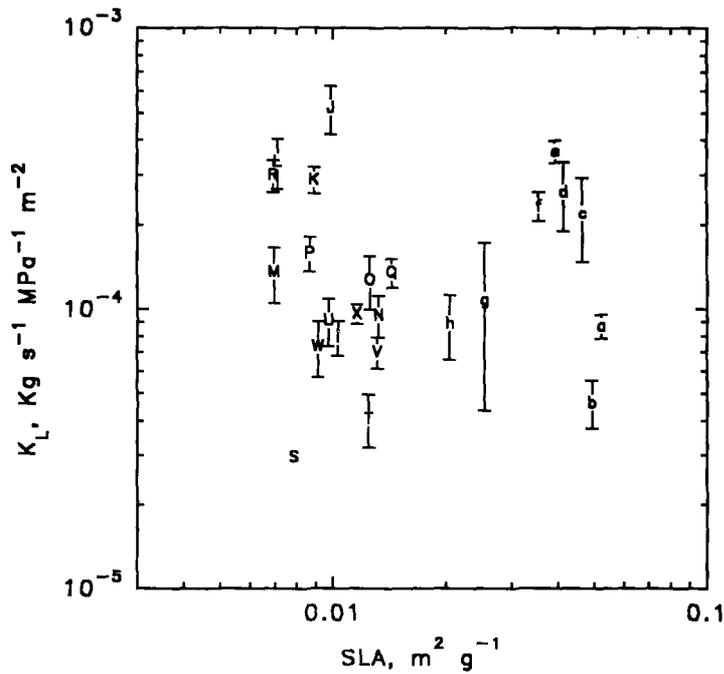
Figure 3. Hydraulic conductance of leaves, K_L, versus specific leaf area (SLA). Values plotted are means ± SEM (when SEM is bigger than the symbol size, n = 5 to 11). Each species is denoted by an alphabetic symbol; lower cases letters are temperate species from Vermont, USA, and upper case letters are tropical species from Brunei, Borneo. Species are: a = *Carpinus caroliniana*, b = *Ostrya virginiana*, c = *Betula lenta*, d = *Betula alleghaniensis*, e = *Ilex verticellata*, f = *Fraxinus americana*, g = *Alnus rugosa*, h = *Fraximus nigra*, i = *Quercus velutina*, J = *Ploiarium alternifolium*, K = *Dillenia suffruticosa*, L = *Rhodomyrtus tomentosa*, M = *Sindora coriaceae*, N = *Syzygium bankense*, O = *Aglaia glabrata*, P = *Syzygium muelleri*, Q = *Dacryodes* sp., R = *Agathis borneensis*, S = *Xerospermum laevigatum*, T = *Myristica malaccensis*, U = *Horsfieldia polyspherula*, V = *Gonocaryum minus*, W = *Xanthophyllum flavescens*, X = *Pouteria maingayi*.

Discussion

Quasi-steady state versus transient K values

It is not clear whether K_t or K_q is the better representation of the true hydraulic conductance for leaves. This should not be a major concern given the high variance of K values which made the typical SEM 10 to 30% of the mean (Figure 3). But reasons for the K_t being systematically greater than K_q may provide some insights into the physics of water transport in leaves.

If the pathway of non-vascular water transport in leaves involves a transcellular pathway, then we might expect K_q to be less than K_t because of a polarisation of solute concentrations caused by continuous water flow across semi-permeable membranes. At the upstream side of any membrane, the non-permeating solutes would be swept up to the membrane but could not pass through and would be swept away from the plasma membrane on the downstream side. The sweeping of solutes would be countered by a back diffusion from the high- to low-concentration regions. Eventually a steady-state situation would develop in which the rate of diffusion of solutes back equals the rate of mass flow in the direction of the water stream.

The flux density of water, J_w, passing through the membrane would be given by,

$$J_w = L_p \, (P_u - P_d + \pi_u - \pi_d), \qquad (3)$$

where subscripts u and d refer to upstream and downstream sides of the membrane, π is the solute potential (a negative quantity) and L_p is the membrane permeability to water. The sweeping effects would tend to make π_u more negative and π_d less negative than before transcellular flow (J_w) began thus reducing $\pi_u - \pi_d$ and the initial magnitude of J_w. Since F is the membrane surface area times J_w, it follows that F would be reduced during quasi-steady state measurements of K. During transient measurements, P was changed too rapidly for $\pi_u - \pi_d$ to reach the minimum value at any given P when instantaneous values of F were measured, so we might expect K_t values to be greater than K_q values. If solute polarisation is the cause of the difference between K_t and K_q, then K_q values are probably more representative of the 'functional conductances' encountered during quasi-steady state transpiration, but the 'true conductance' would be nearer to K_t.

The 'true conductance' would depend on all the L_p values and cell wall conductance values in series and parallel along the pathway of water flow. But to calculate the true conductance we would need detailed knowledge of both P and π values within the leaf. Functionally, we usually describe water flow though leaves in terms of pressure potentials without knowledge of π values so the value of conductance calculated is a 'functional conductance'.

Cost of low conductance

The K_t values reported in this study range from 4×10^{-4} to 3×10^{-5} kg s^{-1} MPa^{-1} m^{-2}. This study broadens the range of K_t values reported for other temperate species which range from 4 to 5×10^{-5} for several *Quercus* spp. (Tyree *et al.* 1993b) to 1 to 2×10^{-4} for *Fagus, Juglans, Acer* and *Populus* spp. (Tyree & Cheung 1977, Tyree *et al.* 1993a, Tyree *et al.* 1994).

The lowest values of K_t are potentially limiting to the plant if an excessive gradient in water potential within the leaf adversely affects photosynthesis or

guard cell function. The drop in pressure potential, ΔP, from the base of the leaf to the mesophyll air spaces would be given by:

$$\Delta P = E/K_L \qquad (4)$$

where E is the evaporative flux density. Ranges of values of ΔP are shown in Figure 4 for different E and K_L values. Typical E values for leaves in direct sunlight are 1 to 8×10^{-5} kg s^{-1} m^{-2} with moist tropical values tending to be at the high end of the range (Tyree *et al.* 1991, Machado & Tyree 1994) and moist temperate values being at the low end (Yang & Tyree 1993). The range of K_L for temperate and tropical leaves is similar, so both types exhibit great variation in expected ΔP at a given E. Tropical sclerophylls can be expected to have ΔP values of 1 to 2.7 MPa (for $K_L = 3 \times 10^{-5}$ kg s^{-1} MPa^{-1} m^{-2} and E = 3 to 8×10^{-5} kg s^{-1} m^{-2}). Since many moist tropical forest trees can be expected to have midday water potentials in the range of -1 to -3 MPa, the leaf of some species may be the biggest liquid-path resistance in the soil-plant continuum. More work is needed to confirm this tentative conclusion.
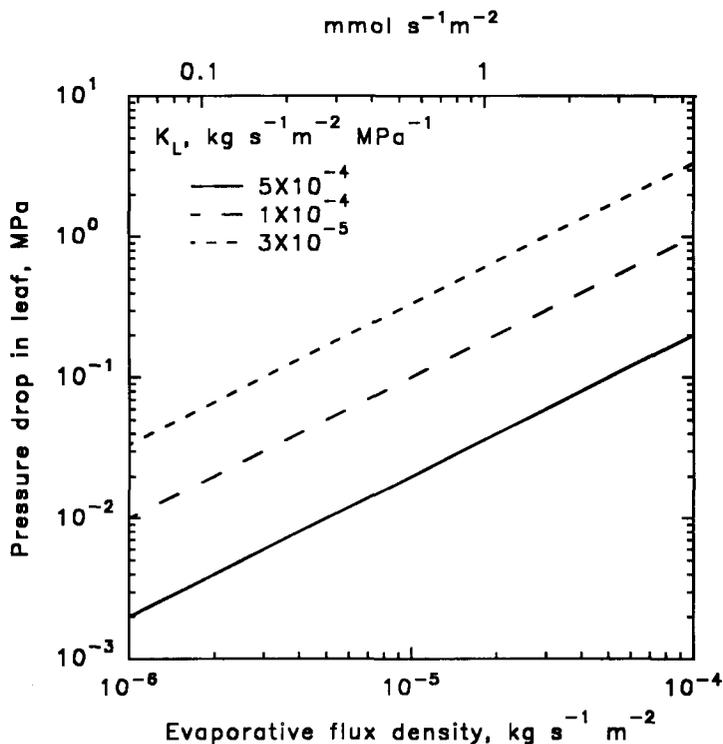

Figure 4. Predicted pressure drops from base of leaf petiole to evaporative surface (y-axis) versus evaporative flux density (x-axis) for various values of K_L. The solid line is for the maximum K_L observed in this study, the long dashed line is for the mean value and the short dashed line is for the lowest K_L values observed in this study.

Water flow pathways

The above conclusions must be tempered by the fact that liquid-path conductances in leaves measured by the HPFM may not be the same as the liquid-path conductance of the transpiration stream. But it can be argued that the HPFM probably overestimates the true conductance. During transpiration water evaporates from air-water interfaces in the mesophyll air spaces of leaves. Water that evaporates is replaced by water flowing from the minor veins to the sites of evaporation. Pathways may differ between perfusion with the HPFM and transpiration, because the boundary conditions at the interface between the intercellular spaces and cells in the leaf may differ.

During transpiration the rate of evaporation from interfaces is rate-limited by the conductance to water vapor diffusion in intercellular air spaces, so the pathway through the non-vascular tissues will not be determined totally by liquid path conductances. Water might evaporate predominately from the peristomatal regions during transpiration (Yianoulis & Tyree 1984) or water may follow the same pathway as CO_2. In the former case transpiration from peristomatal regions will generate Ψ gradients from minor veins to the site of evaporation so that the rate of evaporation equals the flow of water to the site of evaporation. Therefore the liquid pathway will be longer and the conductance lower than in the case of the CO_2 pathway.

The boundary conditions during perfusion with the HPFM are different, because the internal air spaces fill with water during perfusion. Consequently, Ψ is nearly zero at the interfaces, because the pressures required to drive liquid water from the interfaces through intercellular spaces and through the stomates and out of the leaf are likely to be very small. So during perfusion water will tend to follow the pathway of highest conductance from minor veins to interfaces. There will always be some water flowing from minor veins to peristomatal regions during perfusion, but the flow through the pathway will be less than through the shorter pathway from the veins to the nearest interface. So the liquid path conductances might be overestimated during perfusion depending on how closely the pathways for transpiration and perfusion coincide (Yang & Tyree 1994).

Conductance and leaf anatomy

This study demonstrates a high variance in K_L values in the taxa studied, but no correlation with SLA (a measure of sclerophylly). The high variance could be due to two factors: the first factor is differences in the materials in cell walls and membranes that might cause differences in conductance of these materials to water. The second factor is differences in leaf anatomy, e.g. two leaves of the same thickness but one with a thick vascular bundle sheath might have lower K_L than the other without a bundle sheath. Some interesting relationships might be revealed from a study of comparative leaf anatomy seeking correlations with measured K_L values.

These correlations are unlikely to be straightforward. The presence of a thick bundle sheath may be ameliorated by the co-occurrence of bundle sheath extensions, whose frequency is greater in thinner leaves of north temperate deciduous species than the thicker leaves of tropical species (Wylie 1952). An index of vein density increased with height of tropical trees (Högermann 1990), as might be expected from the greater evaporative demand experienced by leaves in the overstory and the presumably higher conductances afforded by increased vein density. Yet the same index of vein density (Högermann 1990, Table 59) was not significantly correlated with either SLA (r = - 0.085, p = 0.667, n = 28) or blade thickness (r = 0.054, p = 0.799, n = 25) for samples from matched canopy levels (Rollet 1990, Appendix 3). Wylie (1946), on the other hand, did find a weak but significant correlation of intervascular interval with blade thickness; the former being much more strongly correlated with the thickness ratio of spongy mesophyll + epidermis to palisade tissue. Finally, the characteristic conductance of leaves is unlikely to have evolved independently of wood anatomy and its consequences for stem and root conductances (cf. Rury & Dickison 1984).

Leaf conductance and the pressure bomb

It has long been known that the pressure bomb (Scholander *et al.* 1965, Tyree & Hammel 1972) measures the xylem pressure potential, P_x, of leaves inside the pressure bomb, i.e. P_x = minus the balance pressure. This is approximately equal to the leaf water potential (Ψ_L) whenever the solute potential of the xylem fluid (π_x) is nearly zero since $P_x = \Psi_L - \pi_x$. Some people have further assumed that P_x of a non-transpiring leaf inside a pressure bomb is approximately equal to the P_x of the transpiring leaf prior to excision, but P_x measured inside the pressure bomb is always less than or equal to P_x in the transpiring leaf. When P_x is much bigger than the pressure drop inside a transpiring leaf, then the assumption is approximately correct. But when the pressure drop is, say, -2 MPa, and P_x = -1 MPa during transpiration, then the value of P_x of a leaf inside the bomb might be - 2 MPa (somewhere between -1 and -3 MPa) after the transpiration-induced gradients in leaf water potential have equilibrated following enclosure of the leaf inside the pressure bomb. While many physiologists have recognised this problem, the magnitude of the problem has not been fully appreciated.

Conclusion

Leaf hydraulic conductances, K_L, were measured in 24 temperate and tropical species. Values of K_L ranged from 3×10^{-5} to 50×10^{-5} kg s^{-1} m^{-2} MPa^{-1} (almost a factor of 20), but were not correlated with specific leaf area, a common measure of sclerophylly. A possible anatomical explanation of differences in K_L between species is worthy of further investigation.

Transient and quasi-steady state measurements of K_L agreed within 1 to 8% of each other. Transient measures of K_L were higher than quasi-steady state measures

at the lowest K_L values, and this is consistent with a transcellular pathway of water transport in leaves of low conductance.

Leaves with low K_L can have substantial drops in water potential from the petiole to the site of evaporation, i.e. up to 2.7 MPa. Stomates are near the end of the water flow pathway in leaves; consequently, large drops in water potential should be taken into account when interpreting the impact of water flux and drought on stomatal physiology. Our interpretation of pressure bomb measurements of xylem pressure potential also needs to be altered in view of the large drop in leaf water potential in leaves with low K_L.

Acknowledgements

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