Leaf Hydraulics

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Abstract
Leaves are extraordinarily variable in form, longevity, venation architecture, and capacity for photosynthetic gas exchange. Much of this diversity is linked with water transport capacity. The pathways through the leaf constitute a substantial (≥30%) part of the resistance to water flow through plants, and thus influence rates of transpiration and photosynthesis. Leaf hydraulic conductance ($K_{leaf}$) varies more than 65-fold across species, reflecting differences in the anatomy of the petiole and the venation architecture, as well as pathways beyond the xylem through living tissues to sites of evaporation. $K_{leaf}$ is highly dynamic over a range of time scales, showing circadian and developmental trajectories, and responds rapidly, often reversibly, to changes in temperature, irradiance, and water supply. This review addresses how leaf structure and physiology influence $K_{leaf}$, and the mechanisms by which $K_{leaf}$ contributes to dynamic functional responses at the level of both individual leaves and the whole plant.
INTRODUCTION

The role of the hydraulic system in constraining plant function has long been recognized (15, 37, 135), but until recently the hydraulic properties of leaves had received little sustained attention. This is somewhat surprising given that the leaf constitutes an important hydraulic bottleneck. Research in previous decades focused on the question of the major pathways for water movement across leaves (14, 38). Current research on leaf hydraulics continues to elucidate these pathways, as well as seeks to understand the influence of the water transport pathways on gas exchange rates, the coordination of hydraulic design with leaf structural diversity, and the dynamics of leaf hydraulic conductance, diurnally, over the leaf lifetime, and in response to multiple environmental factors (Figure 1).

\[ K_{\text{leaf}} \]: leaf hydraulic conductance (units mmol m\(^{-2}\) s\(^{-1}\) MPa\(^{-1}\))

LEAF HYDRAULIC CONDUCTANCE

\[ K_{\text{leaf}} \] is a measure of how efficiently water is transported through the leaf, determined as the ratio of water flow rate \( (F_{\text{leaf}}) \) through the leaf (through the petiole and veins, and across the living tissues in the leaf to the sites where water evaporates into the airspaces) to the driving force for flow, the water potential difference across the leaf \( (\Delta \Psi_{\text{leaf}}) \). \( K_{\text{leaf}} \) is typically normalized by leaf area (i.e., \( F_{\text{leaf}} / \Delta \Psi_{\text{leaf}} \)). Hydraulic conductance is the inverse of resistance, \( R_{\text{leaf}} \). \( K_{\text{leaf}} \) is the more commonly used metric. However, because resistances are additive in series, \( R_{\text{leaf}} \) is used in discussion of the leaf as a component of whole-plant resistance, or when partitioning the resistances within the leaf.
Why does $K_{\text{leaf}}$ have such a strong influence on water movement through the whole plant? The resistance of open stomata to vapor diffusion out of the leaf is typically hundreds of times greater than the hydraulic resistance to bulk flow of the liquid moving through the plant (37). Transpiration rates are thus dictated by this diffusion process, which in turn depends on the stomatal and boundary-layer conductances and the difference in vapor pressure between the intercellular air spaces of the leaf and the atmosphere (Figure 1). However, the maintenance of open stomata depends on having a well-hydrated leaf interior, i.e., a high leaf water potential ($\Psi_{\text{leaf}}$). From the Ohm’s law analogy for the soil-plant-atmosphere continuum (52, 135),

$$\Psi_{\text{leaf}} = \Psi_{\text{soil}} - \rho g b - \frac{E}{K_{\text{plant}}},$$

where $E$, $\Psi_{\text{soil}}$, $\rho$, $g$, $b$, and $K_{\text{plant}}$ represent, respectively, transpiration rate, soil water potential, the density of water, acceleration due to gravity, plant height, and the whole-plant hydraulic conductance. Thus, at a given soil water supply, $\Psi_{\text{leaf}}$ declines with higher $E$, with a sensitivity that depends on $K_{\text{plant}}$. For a leaf to sustain $\Psi_{\text{leaf}}$ at a level high enough to maintain stomata open (i.e., for the leaf to maintain a high $g_s$), $K_{\text{plant}}$ must be sufficiently high. Consequently, $K_{\text{plant}}$ strongly constrains plant gas exchange. As shown in the following, $K_{\text{leaf}}$ is a major determinant of $K_{\text{plant}}$.

**Relation to Whole-Plant Hydraulic Conductance**

Leaves contribute a majority of the hydraulic resistance to water flow in shoots, and form a substantial part of the hydraulic resistance in whole plants (80, 132, 146). For 34 species of a range of life forms, the leaf, including petiole, contributed on average $\approx$30% of $K_{\text{plant}}$ ($R_{\text{plant}} = 1/K_{\text{plant}}$) (99). However, there are cases in which the leaf is reported to contribute up to 80% to 98% of $R_{\text{plant}}$ (23, 80). Notably, the contribution of $R_{\text{leaf}}$ will vary with time of day; early in the day, when there is net water movement from stem storage (48, 123), leaves are likely to constitute a higher proportion of resistance than when water is obtained directly from the soil (Figure 1). Additionally, $R_{\text{leaf}}$ changes with temperature, water supply, and irradiance, and as leaves age.
ψ_leaf: leaf water potential (units MPa)

Maximum Leaf Hydraulic Conductance Across Species and Life Forms

Measurements of leaf hydraulic conductance for hydrated leaves (K_{leaf}^max), made with several methods (103), indicate a dramatic variability across the 107 species so far examined (Figure 2). K_{leaf}^max ranges 65-fold from the lowest value (for the fern Adiantum lunulatum; 0.76 mmol m^{-2} s^{-1} MPa^{-1}) to the highest (for the tropical tree Macaranga triloba; 49 mmol m^{-2} s^{-1} MPa^{-1}). K_{leaf}^max is highly variable within a life form, varying by tenfold among coexisting tree species (104), and on average tends to be lowest for conifers and pteridophytes, higher for temperate and tropical woody angiosperms, and highest for crop plants (Figure 2). The model species Arabidopsis thaliana and Nicotiana tabacum have moderate values of 12 and 26 mmol m^{-2} s^{-1} MPa^{-1}, respectively (68, 115). Interspecific variation in K_{leaf}^max reflects differences in the anatomy of the petiole and venation, as well as pathways beyond the xylem through living tissues to sites of evaporation.

PATHWAYS OF WATER MOVEMENT IN THE LEAF

Water Movement Through Leaf Xylem: Petiole and Venation

On entering the petiole of a dicotyledonous leaf, the vascular bundles in the leaf traces reorganize, differentially supplying midrib bundles, which branch into the second- and third-order veins (42, 58). Water exits the major veins into the surrounding tissue, or into the minor veins, the tracheid-containing fine veins embedded in the mesophyll (5, 27). In dicotyledons the minor veins account for the preponderance of the total vein length (e.g., 86%–97% in temperate and tropical trees) (91, 100). Thus, the bulk of transpired water will be drawn out of minor veins, resulting in the major and minor veins acting approximately in series (99, 146).

Leaf vein systems are enormously variable in many aspects: in vein arrangement and density; and in the number, size, and geometry of the vascular bundles in the veins; and of the xylem conduits within the bundles (97). These structural characteristics play a critical role in how water is distributed across the leaf, and thus an increasing number of studies focus on the relationship of K_{leaf}^max to venation architecture. K_{leaf}^max correlates with the dimensions of conduits in the midrib (1, 3, 79, 100), and for ten species of tropical trees, correlated strongly with the midrib conductivity calculated from the Poiseuille equation for the xylem conduits (100). This correlation does not imply that the midrib is a substantial constraint on the conductance of the xena, or on K_{leaf}^max, but rather implies a scaling of hydraulic resistances throughout the leaf (see below) (100). Higher minor vein density in

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Figure 2

Leaf hydraulic conductance averaged for contrasting life forms (for hydrated whole leaves, including petiole, and when possible for fully illuminated sun leaves; data pooled across plant age and habitat; pteridophytes, 4 species, 19, 24; conifers, 6 species, 7, 24, 133; temperate woody angiosperms, 38 species; 1, 24, 34, 47, 63, 64, 81, 83, 92, 99, 102, 106, 130–133, 146; tropical woody angiosperms, 49 species, 7, 16–20, 24, 41, 104, 118, 131, 133; crop herbs, 7 species, 65, 82, 115, 117, 124–126; all species average for 107 species also includes 2 grass species, 19, 66; and Arabidopsis, 68) Error bars = 1 SE.
general corresponds to a higher supply capacity (or $K_{\text{max}}^\text{leaf}$), not by increasing the conductance through the vein xylem system per se (34), but rather primarily by increasing the surface area for exchange of xylem water with surrounding mesophyll, and reducing the distance through which water travels outside the xylem (97, 100). By contrast, the arrangement and density of major veins is not related to $K_{\text{leaf}}^\text{max}$ (100). However, major vein arrangement plays an essential role in distributing water equitably across the lamina (97, 150), and redundancy of major veins could buffer the impacts of damage and/or cavitation (discussed below).

Water Movement Outside the Xylem: Bundle Sheath and Mesophyll

Water movement pathways outside the xylem are complex and potentially vary strongly across species that diverge in leaf mesophyll anatomy. Important progress has been made on this critical topic, although a full understanding will likely require new approaches.

Once water leaves the xylem, it enters the bundle sheath, made up of parenchymatous cells wrapped around the veins (42). A number of early studies concluded that water exits the xylem through cell walls, moving around the bundle sheath protoplasts, because membranes were thought to be too resistive to occur in the transpirational pathways (e.g., 12, 13). However, the presence of aquaporins and the high surface area for water transport across the membranes of bundle sheath cells means that intercellular water movement is, in fact, plausible (53, 68, 102, 112). Indeed, in some species, water seems constrained to enter bundle sheath cells by suberized perpendicular walls, a barrier analogous to the root Casparian strip (60, 136). Dye experiments suggest movement into the bundle sheath cells; in leaves transpiring a solution of apoplastic dye, crystals form in the minor veins (27). Other evidence comes from the temperature response of measured $K_{\text{leaf}}$ (69, 102) and the recently demonstrated role of aquaporins (82, but see 68), both consistent with crossing membranes (see below). The bundle sheath cells may be a “control center” in leaf water transport, the locus for the striking temperature and light responses of $K_{\text{leaf}}$.

What happens to water once it passes out of the xylem into the bundle sheath and beyond? Although this is clearly a question of great importance, current evidence remains indirect. A large portion of the mesophyll volume is airspace, with limited cell-to-cell contact, but spongy mesophyll cells are in contact to a far greater degree than palisade cells, and thus would seem better suited to conduct water (142, 143). The epidermis has substantial cell-to-cell contact, and water could move directly there from the minor veins, in species with bundle sheath extensions—tightly packed, chloroplast-free cells that connect the bundle sheath that surrounds the minor veins to the epidermides in many species (70, 145). In those species, the epidermis can remain hydrated despite having little vertical contact with the photosynthetic mesophyll (59, 138). In species lacking bundle sheath extensions, water must move across the mesophyll. Whether water moves principally apoplastically (i.e., in the cell walls), transcellularly (i.e., crossing membranes), or symplastically (i.e., cell-to-cell via plasmodesmata) is not yet known, and probably differs among species and conditions. The first experimental studies on sunflower suggested that apoplastic movement dominates during transpiration, and that water crosses mesophyll membranes only during rehydration or growth (13, 139). However, other experiments showed that movement through symplastic routes was plausible (129, 134); the cell pressure probe has indicated significant symplastic water transport among mesophyll cells in succulent Kalanchoë leaves (77).

Finally, there is the question of where in the leaf water evaporates, important because the resistances in the pathways to those sites will determine overall $R_{\text{leaf}}$. Mathematical and physical models predict that evaporation inside the leaf will occur principally
near the stomata—from surrounding epidermal cells, and/or from the mesophyll directly above the stomata, and/or from the guard cells themselves (71, 134). However, such models do not account for the fact that in at least several species, the cuticle extends into the substomatal cavity, potentially reducing evaporation (90 and references therein). An alternative scenario is that most water evaporates deep within the mesophyll, close to the veins (13, 14). Circumstantial support for this idea comes from the fact that the measurement of resistance to helium diffusion across an amphistomatous leaf equaled about twice that of water vapor out of the leaf—which travels half the distance (43), suggesting that water begins its diffusion deep within the leaf (14). A third scenario is that water evaporates relatively evenly throughout the mesophyll (87). This scenario predicts a vapor diffusion pathway similar to that of CO₂ assimilated during photosynthesis (though opposite in direction). Indeed, the computation of intercellular CO₂ concentration using typical photosynthesis systems relies on this assumption (44), as does the use of the pressure bomb to estimate the driving force for transpiration (103, 146). Where water principally evaporates within the leaf is not clear; the data from modeling, dye studies, biophysics, and gas exchange measurements do not provide a coherent story. A definitive answer is likely to require new approaches, such as the use of in vivo imaging to track changes in cell dimensions within transpiring leaves (e.g., 111).

A complete understanding of water flow pathways will illuminate several important aspects of leaf function, including the enrichment of oxygen isotopes (6), and the response of stomata to leaf water status. Guard cells can respond within seconds (93, 95, 98, 114); their movement depends on cell water potential and turgor pressure, which in turn depends on where precisely the bulk of water evaporates in the leaf, and on the hydraulic conductances from the veins to epidermis and guard cells (e.g., 26, 45). Quantifying these parameters should help explain the onset of patchy behavior of stomata at small scales (76).

Partitioning the Leaf Hydraulic Resistance

How is \( K_{\text{leaf}} \) determined from these complex pathways of water movement? This question is especially important because the way in which the leaf hydraulic resistance \( (= 1/K_{\text{leaf}}) \) is partitioned between the xylem and across the extraxylem pathways will strongly influence the responsiveness of \( R_{\text{leaf}} \) to changing conditions. If the resistance of the leaf xylem \( (R_{\text{xylem}}) \) is a major component of \( R_{\text{leaf}} \), then the enormous variation in venation architecture across species could reflect strong differences in \( R_{\text{leaf}} \). That would be very unlikely, however, if \( R_{\text{xylem}} \) were negligible relative to the extraxylem resistance \( (R_{\text{outside xylem}}) \); in that case, even large relative differences in \( R_{\text{xylem}} \) among species would have little impact on overall \( R_{\text{leaf}} \). Additionally, the larger \( R_{\text{xylem}} \) is, relative to \( R_{\text{outside xylem}} \), the greater the effect on \( R_{\text{leaf}} \) of changes in \( R_{\text{xylem}} \) due to environment (e.g., drought-induced cavitation; see 72). Thus, substantial discussion surrounds the issue of where the major resistances to water flow occur within leaves (e.g., 34, 47, 82, 102, 104). Some of this controversy resulted from methodological differences, including the failure to take into account the effect of irradiance on \( R_{\text{leaf}} \) (see below) and the use of treatments to determine \( R_{\text{xylem}} \) that opened up pathways for water to move out of low-order veins, bypassing conduit endings and higher-order veins that contain higher resistance; using those methods resulted in estimates of \( R_{\text{xylem}} \) as 27% of \( R_{\text{leaf}} \), averaged for the ten species tested (12, 34, 109, 125, 128–130, 146). Recent studies conducted under high irradiance, in which only minor veins were severed, found \( R_{\text{xylem}} \) to be 59% of \( R_{\text{leaf}} \), averaged for 14 species (47, 82, 102, 104).

The current consensus is that the hydraulic resistance of the leaf's xylem is about the same order as in the extraxylem pathways (47, 79,
that, contrary to empirical data, which showed conduit numbers and dimensions (34). Howterized with measured venation densities and Poiseuille flow through a network parame- mated for dicotyledonous leaves by assuming of biological (and other) networks (e.g., 8, 121). Next generation studies will improve our ability to scale up from anatomical mea- urements to accurate prediction of venation 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation.

82, 102, 104; but see 34), and that species vary in their partitioning. Indeed, among tropical trees, the % of $R_{leaf}$ in the xylem differed significantly between species (ranging from 26% to 89%); species that establish in high-light environments had 70% of $R_{leaf}$ in the xylem on average, whereas those from low irradiance had 52% (104). Despite this variation, across the range of species’ values, $R_{xylem}$, $R_{outside xylem}$ and $R_{leaf}$ were linearly cor- related across species (104). The implications of this finding are that differences in venation architecture reflect strong differences in $R_{leaf}$, and also that $R_{leaf}$ will be sensitive to changes in the conductance of both the xylem and extraxylem pathways. Indeed, the ratio of $R_{xylem}$ to $R_{outside xylem}$ is dynamic. For example, $R_{xylem}$ will increase if vein xylem em- bolizes during drought, whereas $R_{outside xylem}$ changes according to an endogenous circadian rhythm, and also increases under low irr- radiance (82, 101, 131); both resistances in- crease at lower temperatures, with $R_{outside xylem}$ increasing more strongly (69, 102; see below).

Because leaf vein systems consist of water movement through a well-defined arrange- ment of fixed tubes, they should be amenable to quantitative methods used in the study of biological (and other) networks (e.g., 8, 34, 66, 102, 140, 147). In the most anatomically explicit model to date, $R_{xylem}$ is esti- mated for dicotyledonous leaves by assuming Poiseuille flow through a network parameter- ized with measured venation densities and conduit numbers and dimensions (34). However, contrary to empirical data, which showed that $R_{xylem}$ constitutes on average over 50% of $R_{leaf}$ (see above), the model suggested from the xylem conduit measurements that $R_{xylem}$ was only ≈2% of $R_{leaf}$. Thus, anatomical features not included in the model, for example, the resistance to water movement between xylem conduits, must play an important role (34, 121). Next generation studies will improve our ability to scale up from anatomical mea- surements to accurate prediction of venation network $R_{xylem}$.

**COORDINATION OF MAXIMUM LEAF HYDRAULIC CONDUCTANCE WITH LEAF STRUCTURE AND FUNCTION**

The coordination of hydraulics with leaf structure and gas exchange is likely to have played a critical role in the early evolution of the laminate leaf. Lower CO₂ levels and cooler temperatures during the Devonian would have allowed large leaves to avoid overheating, but the higher stomatal densities, which evolved to maintain CO₂ assimilation, would have led to more rapid transpiration (89) and thus required concomitant increases in leaf hydraulic capacity (9–11). The coordi- nation among leaf hydraulic supply and de- mand and leaf form remains a key design ele- ment among modern plants.

**Coordination with Gas Exchange**

Recent work demonstrates correlations across species between liquid phase (hydraulic) conductances of stems, shoots, or whole plants and vapor phase (stomatal) conductance ($g_s$) and maximum rates of gas exchange (e.g., 3, 54, 57, 73, 74, 80, 110). Consistent with this matching of hydraulic supply and demand is the strong coordination across species be- tween $K_{stem}^{max}$ and stomatal pore area per leaf area, maximum $g_s$, and photosynthetic capacity (3, 19, 24, 99, 104).

What is the basis for the interspecific co- ordination of leaf hydraulic properties and gas exchange? The coordination of $K_{stem}$ (and $K_{leaf}$) and maximum $g_s$ and $E$ would arise from convergence among species in $\Psi_{leaf}$, $\Psi_{stem}$, boundary-layer conductance and leaf- to-air vapor pressure difference (see Equation 1 and Figure 1) (104). Given that hydraulic conductances scale through the plant (99), species would converge also in the water po- tential of the stem xylem proximal to the leaf ($\Psi_{stem}$), the water potential drop across the leaf ($\Delta \Psi_{leaf} = \Psi_{leaf} - \Psi_{stem}$), and that across the whole plant ($\Delta \Psi_{plant} = \Psi_{leaf} - \Psi_{soil}$; 74). The linkage indicates a “standard- ization” of water relations among plants of

$g_s$: stomatal conductance to water vapor (units mmol m⁻² s⁻¹)
a given life form and vegetation type during peak transpiration, when soil is moist. There is evidence of strong convergence in water relations parameters $\Psi_{\text{leaf}}$, $\Psi_{\text{stem xylem}}$, $\Delta \Psi_{\text{leaf}}$, and $\Psi_{\text{soil}}$ during peak transpiration for plants of a given system in moist soil during the growing season (23, 24, 55, 80, 123). The typically modest range in these parameters (typically $\pm <0.5 \text{ MPa}$) occurs despite variation within a vegetation type in plant size and age, rooting depth and vulnerability to cavitation, as well as divergence among species in the season during which they manifest peak activity, which would further destabilize the coordination (104). The convergence in $\Delta \Psi$ is analogous to the range of household appliances in a given country being designed to run at a given voltage—from lamps to ovens—with the current through the appliance dependent on the electric conductance, or resistance.

The finding of narrowly constrained water relations in a given vegetation type provides a potentially powerful basis for a general relationship between $K_{\text{leaf}}$ and maximum rates of gas exchange. In addition, increased understanding of how the coordination of $K'_{\text{leaf}}$ and gas exchange shifts across life forms and habitats will allow prediction of performance differences for plants adapted to different zones around the world. One study so far has demonstrated that the coordination between hydraulics and gas exchange varies among vegetation types: Tropical rainforest trees as a group have higher potential gas exchange relative to $K_{\text{leaf}}$ than temperate deciduous trees, consistent with their adaptation to higher $\Psi_{\text{leaf}}$ and $\Psi_{\text{soil}}$, and/or lower VPD during peak activity (104).

### Coordination with Leaf Flux-Related Structural Traits

Leaves vary tremendously in area, thickness, shape, nutrient concentrations, and capacity for gas exchange. The intercorrelation of many traits places some bound on this diversity, for instance among those related to carbon economy, including leaf mass per area (LMA; leaf dry mass/area), leaf lifespan (e.g., 96, 141), and nitrogen concentration per mass and net maximum photosynthetic rate per mass ($A_{\text{mass}}$; 141), and provides a framework for understanding the integrated function of clusters of traits. Similarly, coordination among traits related to water flux through leaves exists for plants of a particular life form and habitat (99) (Table 1). In addition to their higher total maximum stomatal pore area and gas exchange per area (see above; 3, 19, 99), leaves with high $K'_{\text{leaf}}$ tend to have wider xylem conduits in the midrib and higher venation densities (3, 102). $K'_{\text{leaf}}$ correlated

### Table 1  Leaf structural and functional traits, sorted by putative association with maximum water flux per area (and $K_{\text{leaf}}$), leaf mass per area, or drought tolerance\(^a\) across species

| Maximum flux-related traits |  |
|----------------------------|  |
| Leaf hydraulic conductance |  |
| Stomatal pore area         |  |
| Stomatal conductance       |  |
| Net maximum photosynthesis per area |  |
| Leaf midrib xylem conduit diameters |  |
| Mesophyll area/leaf area   |  |
| Thickness of leaf and palisade mesophyll |  |
| Leaf chlorophyll concentration per area |  |
| Leaf nitrogen concentration per area |  |
| Leaf shape (margin dissection) |  |
| Leaf water storage capacitance per area |  |

| Leaf mass per area-related traits |  |
|----------------------------------|  |
| Leaf density                     |  |
| Leaf thickness                   |  |
| Leaf lifespan                    |  |
| Leaf chlorophyll concentration per mass (negatively related) |  |
| Leaf nitrogen concentration per mass (negatively related) |  |
| Leaf water content per mass (negatively related) |  |

| Leaf drought tolerance traits |  |
|-------------------------------|  |
| Cuticular conductance (negatively related) |  |
| Modulus of elasticity (variably related) |  |
| Leaf density (variably related) |  |
| Leaf water storage capacitance per area |  |
| Osmotic potentials at full and at zero turgor |  |
| Resistance to leaf xylem cavitation |  |

\(^a\)Associations are positive except when noted.
with palisade thickness, and palisade/spongy mesophyll ratio for tropical rainforest tree species (100), and with total leaf thickness and water storage capacitance per area for temperate woody species (99). These correlations arose due to structural coordination—the sharing of an anatomical or developmental basis—and/or due to functional coordination—the coselection of characters for benefit in a particular environment (99, 116).

Independence of Maximum $K_{\text{leaf}}$ and Traits Related to Leaf Mass Per Area, or to Leaf Drought Tolerance

Certain leaf traits show a disproportionate number of linkages with other traits (86). $LMA$ is one such “hub” trait (Table 1). However, $K_{\text{max}}$, a hub trait in its own right (being linked with many water-flux traits), is unrelated to $LMA$ (Table 1) (20, 78, 99, 104, 133).

Because this complex of water flux–related traits is coordinated with net maximum photosynthesis per leaf area, which is equal to $LMA$ in its driving differences in $A_{\text{mass}}$ across species globally (data in 141), and because $A_{\text{mass}}$ generally scales up to whole-plant relative growth rate, water flux–related traits including $K_{\text{leaf}}$ are a potentially fundamental determinant of species performance differences. However, $K_{\text{max}}$ is apparently independent of a partially interrelated complex of traits associated with leaf drought tolerance, i.e., the ability to maintain positive turgor and gas exchange at low $\Psi_{\text{leaf}}$ (Table 1). These traits are evidently coselected by desiccating conditions (85, 107), and include low osmotic potentials at full and at zero turgor, and low cuticular conductance (99, 100).

Responses of Leaf Hydraulic Conductance to Dehydration and Damage

The hydraulic conductance of the petiole ($K_{\text{petiole}}$) and of the whole leaf declines during drought, correlating in vivo with declines in gas exchange (Figure 3a) (17–19, 25, 30, 32, 33, 49, 50, 62, 63, 81, 83, 105, 108, 109, 117, 124, 125, 149). An important factor contributing to the decline of $K_{\text{leaf}}$ at low $\Psi_{\text{leaf}}$ is xylem cavitation (55, 83, 149). Petioles with lower conductance take up dye into fewer vessels (25, 149), and dehydrated leaves take up dye into fewer minor veins in the network (83, 105, 124, 125). The xylem can become increasingly vulnerable with increasing drying iterations—i.e., “cavitation fatigue,” as shown in petioles of Aesculus hippocastanum (50). However, cavitation is not the only potential source of $K_{\text{leaf}}$ decline during dehydration. Dehydrating conifer leaves decline in $K_{\text{leaf}}$ owing to collapse of xylem conduits, which precedes cavitation (21, 33). The potential collapse of xylem conduits in dicotyledous conditions. The dynamics of $K_{\text{leaf}}$ are typically closely correlated with those of gas exchange (Equation 1 and Figure 1) (32, 35, 36, 69, 72). As $K_{\text{leaf}}$ declines (e.g., owing to dehydration), $\Psi_{\text{leaf}}$ will similarly decline, and stomata will close as, or before, $\Psi_{\text{leaf}}$ becomes damaging, leading to reduction of $g_\text{s}$ and $E$ (32, 108). In droughted plants such a mechanism operates in tandem with chemical signals from the roots to close the stomata (36, 39). Associated declines in intercellular CO$_2$ concentration ($c_i$) drive a reduction in photosynthetic rate (46, 69). Declines in $\Psi_{\text{leaf}}$ can also directly reduce photosynthetic rate metabolically (40).

Why is $K_{\text{leaf}}$ dynamic, given that its decline drives such loss of function? $K_{\text{leaf}}$ reduction during water stress would protect the xylem by driving stomatal closure, thus alleviating the tensions in the transpiration stream. Also, membrane channels important in maintaining a high $K_{\text{leaf}}$ require metabolic energy for expression and potentially for activation.

DYNAMICS OF LEAF HYDRAULICS OVER SHORT AND LONG TIME SCALES

$K_{\text{leaf}}$ is highly dynamic, varying over a wide range of time scales, from minutes to months, and according to microclimate and growing
Mean reduction of leaf hydraulic conductance in given conditions

Figure 3
Leaf hydraulic conductance is highly dynamic, as shown by the responses depicted here with respect to controls (color as a proportion of white bars). Note that the averaged responses shown are only indicative—the responses vary strongly in magnitude according to the particular species and ranges of conditions observed. (a) Response to branch dehydration (13 species; 17, 19, 63, 83, 124, 125); (b) response to incident irradiance, during measurement over minutes to hours (14 species; 34, 47, 82, 101, 131); (c) response related to leaf aging (9 tree species; 16, 18, 20, 64, 106); (d) response to growth irradiance, including shade vs sun leaves (4 tree species; 99), and leaves of plants grown in 2% versus 8% daylight (2 species, 41); (e) response to water supply during growth (3 species; 1, 41).

leaves remains to be investigated, as does the additional possibility of decline in conductance of the extra-xylem paths. A strikingly rapid and complete recovery of \( K_{\text{leaf}} \) during rehydration has been documented after rewatering droughted plants or rehydrating partially dehydrated leaves (62, 63, 75, 124). Such short-term increases in \( K_{\text{leaf}} \) result from a diversity of mechanisms. For example, conifers elastically recover their xylem geometry on rewatering (21, 33), whereas rice leaves reverse embolism through root pressure (122). Where root pressure is not operating, an active mechanism may exist for embolism refilling even when xylem tensions exist, involving ion pumping or transient pressures, associated with increasing starch degradation (25, 124, 149).

Because the linkage of \( K_{\text{leaf}} \) and gas exchange is mediated by \( \Psi_{\text{leaf}} \) and species diverge in their \( \Psi_{\text{leaf}} \) responses, the extent to which \( K_{\text{leaf}} \) and \( g_c \) remain coordinated during dehydration varies among species. The distance between \( \Psi_{\text{leaf}} \) at stomatal closure (\( \Psi_{\text{stomatal closure}} \)) and the \( \Psi_{\text{leaf}} \) at which the xylem is irreversibly embolized is termed the safety margin (19, 119, 120). In species with a wide safety margin, the risk is minimal, as stomata close before \( K_{\text{leaf}} \) declines substantially (19, 30, 32, 83). However, in other species, with a narrow safety margin, \( g_c \) declines by half only after \( K_{\text{leaf}} \) or \( K_{\text{petiole}} \) decline by 20% or more (17–19, 25, 62, 63, 80, 105, 108, 125). High safety margins protect the xylem, but lower safety margins allow plants to maintain gas exchange closer to the level of irreversible \( K_{\text{leaf}} \) decline (19, 120). The decline in \( K_{\text{leaf}} \) would confer safety to the whole-plant hydraulic system by augmenting the decline in \( \Psi_{\text{leaf}} \), accelerating...
stomatal closure, which would protect portions of the plant that are less easily replaced (18). The protection conferred will vary according to species, because species differ in whether whole leaves, petioles, and midribs are more (17, 22, 28, 49, 84, 105, 108, 125), equally (33), or less (32, 49, 83, 122) vulnerable to loss of conductance compared with the stem as \( \Psi \) declines (and xylem tensions increase).

One of the most commonly investigated patterns in stem hydraulics is a trade-off between hydraulic efficiency (i.e., maximum hydraulic conductance) and resistance to drought-induced cavitation (135). This pattern is not found in leaves: The vulnerability of \( K_{\text{leaf}} \) to drought is not higher for leaves with high \( K_{\text{leaf}} \). In our analysis of the available data for 13 species of ferns, trees, and herbs varying 42-fold in \( K_{\text{leaf}} \), \( \Psi \) at 50% loss of conductivity ranged from −1.3 MPa to −3 MPa, and was uncorrelated with \( K_{\text{leaf}} \) (\( r^2 = 0.07; P = 0.4 \); data of 17, 19, 63, 83, 124, 125).

\( K_{\text{leaf}} \) is also reduced by herbivory and other forms of mechanical vein damage. The interruption of major veins was classically held to have no effect on leaf function, as leaves often survive with a perfectly healthy appearance (29, 91). However, damage that interrupts primary veins in dicotyledonous leaves immediately produces massive declines in \( K_{\text{leaf}} \), and in \( g_c \) and photosynthetic rates, which persist weeks later, after the wounded tissue has scarred over; in some species, the leaves desiccate (4, 51, 81, 98). Whether major vein disruption leads to tissue death or not would depend at least as much on evaporative demand and on the leaf's ability to reduce water loss (i.e., with an impermeable cuticle) as on the leaf's vascular architecture. However, redundancy in the venation—such as conduits in parallel within each vein, and multiple veins of each order—would buffer \( K_{\text{leaf}} \) against both cavitation and damage, by providing pathways around damaged or blocked veins (29, 51, 84, 97, 137).

**Responses of Leaf Hydraulic Conductance to Changes in Temperature and Irradiance**

\( K_{\text{leaf}} \) increases at higher temperatures, as shown in experiments conducted in vivo, determining gas exchange while manipulating temperature and controlling other microclimatic variables (46). This increase is only partially accounted for by the direct effects of temperature on the viscosity of water. Investigation of the temperature response of water flow through shoots and leaves showed an activation energy of 26–27 kJ mol\(^{-1}\), but when minor veins were severed, so that water was forced through only xylem, the activation energy dropped to \( \approx 17 \) kJ mol\(^{-1}\), which corresponds to changes in the viscosity of water (12, 102, 127, 128). Thus, the viscosity response applies to the xylem pathways, whereas an extraviscosity response applies to the pathways outside the xylem (102), consistent with the flow path crossing membranes (68). The temperature induced changes in \( K_{\text{leaf}} \) can allow \( \Psi \) and \( g_c \) to remain stable even as \( E \) increases due to higher \( VPD \) (46, 69).

\( K_{\text{leaf}} \) responds strongly to irradiance; for many species \( K_{\text{leaf}} \) is much lower when measured at low irradiance than at high irradiance (i.e., at \( < 10 \) \( \mu \)mol photons m\(^{-2}\) s\(^{-1}\) versus at \( > 1000 \) \( \mu \)mol photons m\(^{-2}\) s\(^{-1}\) (Figure 3b) (82, 101, 131). The responses vary across species, and can range up to a several-fold increase from low to high irradiance. The kinetics of the \( K_{\text{leaf}} \) response to irradiance differs sufficiently from that of stomatal aperture to suggest that the light response arises in the hydraulic pathways through the mesophyll (131), and involves activation of aquaporins (53, 82, 131). These same channels apparently follow an endogenous circadian rhythm: In sunflower, \( K_{\text{leaf}} \) increases up to 60% from night to day, and the rhythm can be reversed if photoperiod is switched, and the rhythm continues for days even when plants are kept in constant darkness (82). The response can be removed by treatment with HgCl\(_2\), and recovered by using mercaptoethanol,
implying the agency of aquaporins (82). In sunflower, dark-acclimated leaves show a strong light response, but light-acclimated leaves do not, suggesting that their water channels are already activated (82). The deactivation of aquaporins in the dark would be adaptive, assuming the maintenance of activity requires energy expenditure. For plants kept in the dark for 1 h, or for 4–6 days, $K_{\text{leaf}}$ and shoot hydraulic conductances (measured under high irradiance) were reduced by 20%–75% on average (2, 117). The response of $K_{\text{leaf}}$ to irradiance implies the existence of a previously unknown level of control of a plant’s response to environment; this response would facilitate the increases of stomatal aperture and leaf gas exchange with increasing irradiance by improving water supply to the mesophyll.

**Diurnal Rhythms in Leaf Hydraulic Conductance**

$K_{\text{leaf}}$ is dynamic diurnally, and its changes reflect simultaneous responses to multiple factors. As discussed above, $K_{\text{leaf}}$ follows an endogenous circadian rhythm; $K_{\text{leaf}}$ also increases with incident light over the scale of minutes and hours (64, 101, 131). Additionally, $K_{\text{leaf}}$ increases with temperature. By contrast, $K_{\text{leaf}}$ declines as leaves dehydrate under high midday temperatures and VPD. Thus, contrasting trends have been observed for the diurnal response of $K_{\text{leaf}}$. For sunflower, and for four tree species, $K_{\text{leaf}}$ increased by up to two- to threefold over a few hours from morning to midday, as irradiance and temperature increased, and then declined by evening, in a similar pattern as $g$ and $E$ (64, 126). On the other hand, a midday decline in $K_{\text{leaf}}$ by 30% to 50% has been observed for tree species as transpiration increased to high rates by midday (18, 83), apparently as a response to leaf dehydration. Similar diurnal declines in conductance were found for tree petioles and for flow axially across rice leaves (25, 122, 149). In other species no diurnal patterns were observed (31, 149). Such variable patterns in diurnal responses of $K_{\text{leaf}}$ are likely to reflect the particular combinations of irradiance, leaf and air temperature, soil moisture, and VPD, as well as endogenous rhythms. Thus, one would expect $K_{\text{leaf}}$ to increase each morning in response to internal cues, as well as increasing irradiance and temperature; but if $E$ is driven high enough by a high VPD (and/or if soil is dry), low $\Psi_{\text{leaf}}$ would result in significant declines in $K_{\text{leaf}}$ and in $g_s$, recovering by the end of the day.

**Trajectories of Leaf Hydraulic Conductance During Development and Leaf Aging**

$K_{\text{leaf}}$ is also dynamic over the lifetime of the leaf. $K_{\text{leaf}}$ increases in developing leaves as the vasculature matures (1, 20, 67). Weeks or months after $K_{\text{leaf}}$ reaches its maximum, it begins to decline, with reductions of up to 80–90% at abscission (Figure 3c) (1, 16, 18, 64, 100, 106). One factor contributing to this decline of $K_{\text{leaf}}$ is the accumulation of emboli in the vein xylem, and eventual blockage by tyloses (106, 135). $K_{\text{leaf}}$ would decline also owing to reduction of the permeability of cell walls or membranes (see 136). Decreases in $K_{\text{leaf}}$ would cause progressive dehydration, potentially contributing to the observed decline in midday $\Psi_{\text{leaf}}$ as leaves age (16, 65, 106). Reductions in $K_{\text{leaf}}$ are coordinated with age-related declines in other functional traits, including leaf nitrogen concentration, stomatal sensitivity to VPD, leaf osmotic potential, and gas exchange (e.g., 56, 94). Some have hypothesized that the seasonal decline of $K_{\text{leaf}}$ is a trigger for leaf senescence (16, 106).

**Plasticity of Leaf Hydraulic Conductance Across Growing Conditions**

Although most studies of leaf hydraulics have been performed on plants in high-resource conditions, $K_{\text{leaf}}$ is highly plastic across growing conditions, owing to developmental
changes in vein density, conduit sizes or numbers (e.g., 3), and/or in the structure and conductivity of extraxylem pathways. Leaves expanded in shade—or in crown positions liable to shade—have low $K_{\text{leaf}}^{\text{max}}$ relative to sun leaves (Figure 3d) (99, 113), part of the complex of shade leaf characters including lower vein densities, smaller stomata, thinner leaves, less dissected leaf shape, and lower rates of gas exchange (e.g., 61, 144, 148). In mature sunflower plants, $K_{\text{leaf}}^{\text{max}}$ was linearly related to irradiance from basal to apical leaves (65); in this case an irradiance effect combines with an age effect. $K_{\text{leaf}}^{\text{max}}$ is also plastic across plant growing conditions. $K_{\text{leaf}}^{\text{max}}$ and shoot hydraulic conductance were lower for plants grown several months in lower irradiance (Figure 3d) (41), or in lower water or nitrogen supplies (Figure 3e) (1–3, 41). Such plasticity in $K_{\text{leaf}}^{\text{max}}$ runs in parallel with adaptive differences, as sun-adapted species tend to have several-fold higher $K_{\text{leaf}}^{\text{max}}$ than shade-adapted species on average, for temperate and tropical species sets (79, 104). These findings suggest that $K_{\text{leaf}}^{\text{max}}$ plays a potentially important role in determining plant resource responses and also in determining ecological preferences among species.

### SUMMARY POINTS

1. $K_{\text{leaf}}^{\text{max}}$ varies at least 65-fold across species, and scales with $K_{\text{plant}}$; the leaf is a substantial resistance in the plant pathway, 30% and upward of whole-plant resistance.

2. The partitioning of resistances within the leaf among petiole, major veins, minor veins, and pathways outside the xylem is variable across species. Substantial hydraulic resistances occur both in the leaf xylem as well as in the flow paths across the mesophyll to evaporation sites. These components respond differently to ambient conditions, including irradiance and temperature, indicating an involvement of aquaporins.

3. $K_{\text{leaf}}^{\text{max}}$ is coordinated with maximum gas exchange rates for species of a particular life form and habitat. This coordination arises from convergence in water relations parameters, especially $\Psi_{\text{leaf}}$ at peak transpiration. $K_{\text{leaf}}^{\text{max}}$ is also coordinated with a framework of other traits related to leaf water flux, including stomatal pore area, midrib xylem conduit diameters, and palisade richness. However, $K_{\text{leaf}}^{\text{max}}$ is independent of the complex of traits linked with leaf mass per area, and traits relating to leaf drought tolerance.

4. $K_{\text{leaf}}$ is highly dynamic—varying diurnally, as leaves age, and in response to changes in leaf hydration, irradiance, temperature, and nutrient supply. The decline in $K_{\text{leaf}}$ in response to lower $\Psi_{\text{leaf}}$ arises from reductions in xylem conductivity due to cavitation or collapse, and/or from changes in the conductivity of the pathways outside the xylem. Some short-term declines in $K_{\text{leaf}}$ can be rapidly reversed. Dynamic changes in $K_{\text{leaf}}$ impact gas exchange via stomatal regulation of $\Psi_{\text{leaf}}$ and could play a role in leaf senescence.

### FUTURE ISSUES

1. Still needed is a fully quantitative understanding of how $K_{\text{leaf}}^{\text{max}}$ is determined by the vein architecture and the extraxylem pathways, including the identity and behavior of aquaporins in these pathways.
2. The precise correlations that link $K_{\text{leaf}}$ with gas exchange and leaf structure among species of particular life forms and habitats need to be determined, as well as the shifts of this coordination across life forms and habitats. The patterns of general coordination will enable predictions of water relations behavior for whole sets of species from simply measured hydraulic parameters.

3. The mechanisms for the diurnal and developmental dynamics of $K_{\text{leaf}}$, and for the reversible $K_{\text{leaf}}$ responses to irradiance and to dehydration need to be elucidated in detail. Understanding the mechanisms behind these changes will enhance the ability to model the influence of these dynamics on gas exchange over short and long time scales.

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