Chapter 10
The Anatomical Determinants of Leaf Hydraulic Function

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1 Introduction

Leaves are enormously diverse in size and shape, and especially in their internal anatomy, including their venation architecture (Figs. 10.1, 10.2, and 10.3) (Esau 1977; Ellis et al. 2009). Across species, venation systems vary in the branching and arrangements of leaf major veins, i.e., the first-order vein(s) entering the leaf from the petiole, and the second- and third-order veins branching off—and the minor veins, i.e., the 3–5 additional orders of smaller veins embedded within the lamina and forming a continuous mesh with the major veins (Figs. 10.1 and 10.2). Additionally, leaf veins vary strongly in their internal anatomy—i.e., that of the parenchyma, xylem, and phloem inside—and in their external anatomy—including the parenchymatous and sometimes sclerenchymous bundle sheath (Fig. 10.3). Leaves are additionally enormously variable in the anatomy of the lamina outside the veins—i.e., the arrangement and sizes of the spongy and palisade mesophyll tissues, and sometimes water storage and accessory transport tissues (Fig. 10.3). Of all the plant lineages, angiosperms evolved the most exceptional diversity across species in all of these vein and outside-vein anatomical traits, as for the rest of their

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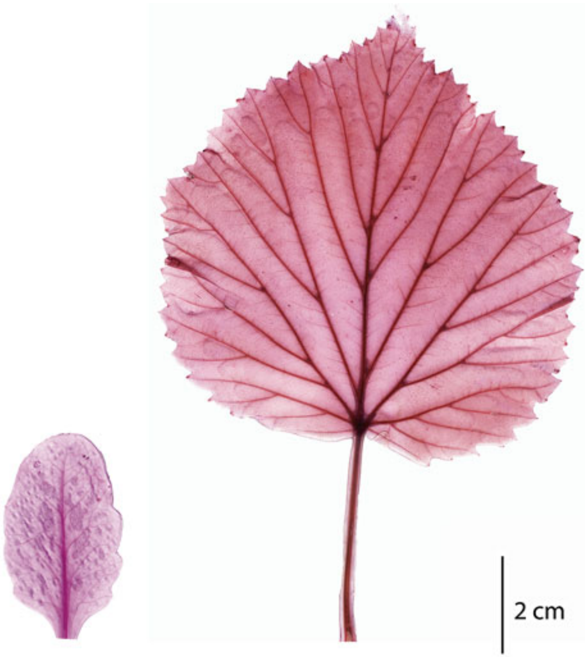

Fig. 10.1 Diversity of leaf major venation. Chemically cleared and stained whole leaves of *Arabidopsis thaliana* Col-0 (Brassicaceae, *left*) and *Viburnum molle* (Adoxaceae, *right*). Photo credit: *A. thaliana* (M. Caringella)

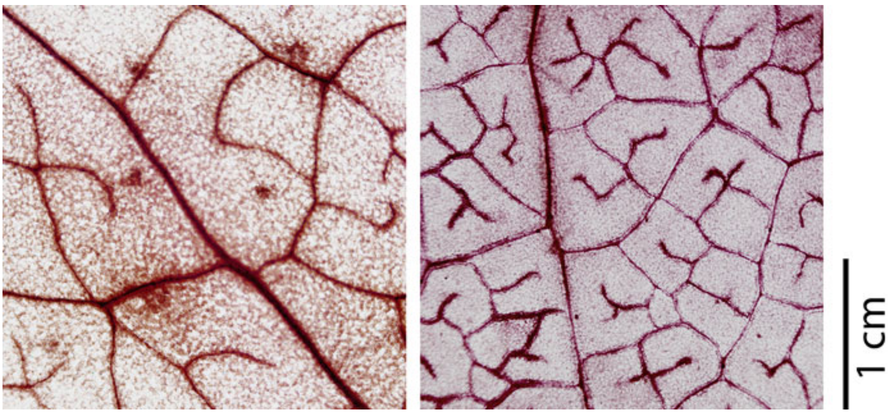

Fig. 10.2 Diversity of leaf minor venation. Chemically cleared and stained micrographs of *Arabidopsis thaliana* Col-0 (Brassicaceae, *left*) and *Viburnum molle* (Adoxaceae, *right*). Photo credit: *A. thaliana* (M. Caringella)

morphology and physiology (Augusto et al. 2014). The variation across species in vein and lamina anatomy carries extensive information about the physiological function, development, evolution, ecology, and paleohistory of leaves (Haberlandt 1914; Roth-Nebelsick et al. 2001; Brodribb et al. 2010; Sack and Scoffoni 2013). Further, much of the functional importance of the leaf's anatomy relates to its role

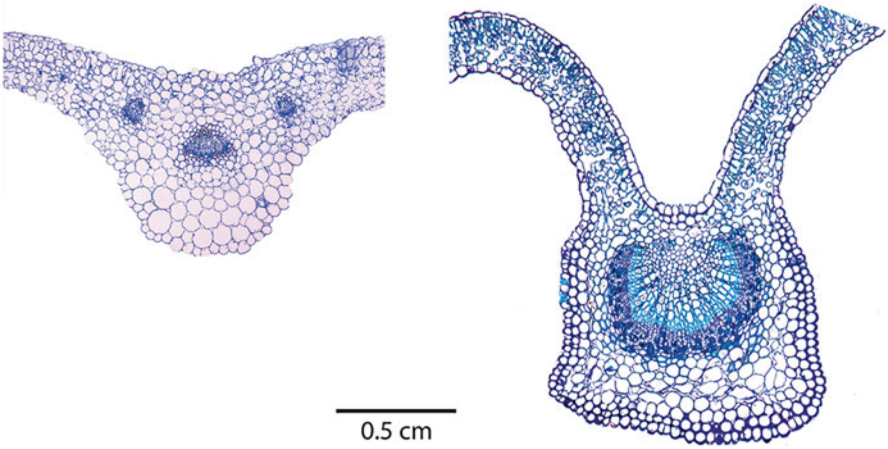

Fig. 10.3 Diversity of leaf midrib and lamina anatomy. Transverse cross-sections of *Arabidopsis thaliana* Col-0 (Brassicaceae, *left*) and *Viburnum molle* (Adoxaceae, *right*). Photo credit: *A. thaliana* (M. Caringella)

within the plant water transport system. This review focuses on the contribution of both the vein system and the outside-vein system to the leaf hydraulic conductance (K_{leaf}) and to K_{leaf} dynamics with leaf water status.

We focus on hydraulic function because it is a backbone of whole plant physiological performance (Tyree and Zimmermann 2002; Brodribb 2009). When the stomata open for CO_2 assimilation, the leaf's moist internal airspaces are exposed to the dry outside air, resulting in transpirational water loss. Consequently, if the hydraulic system did not replace sufficient water, the mesophyll would desiccate and stomata would close (Sack and Holbrook 2006). The plant hydraulic system thus imposes a major constraint on the ability of the stomata to remain open to allow photosynthesis. Indeed, leaves generally evolve and develop with hydraulic and stomatal traits matched such that transpiration and photosynthesis can proceed with sufficient water supply (Sack et al. 2003; Dunbar-Co et al. 2009; Brodribb and Jordan 2011; Carins Murphy et al. 2012). The hydraulic system can be analyzed using concepts from electronics or plumbing: the plant is considered as a series of resistors in series or parallel (also including capacitors in fully elaborated models), where the efficiency of the system can be summarized with a single ratio: the flow rate divided by the pressure driving force. Thus, the plant hydraulic conductance (K_{plant}) is determined as the transpiration rate divided by the water potential gradient from soil to leaf, and K_{leaf} as the transpiration rate divided by the water potential gradient from petiole to evaporation sites within the leaf; in these calculations, the water potential of the evaporating sites is often approximated for practical purposes as the bulk leaf water potential. Studies of plant communities around the world have revealed strong correlations of the hydraulic conductances of organs or whole plants with gas exchange and photosynthetic rates, and with species' ecological specializations. Indeed, a number of studies have shown close correlations of K_{leaf} with stomatal conductance, transpiration rate, and maximum photosynthetic rates across diverse species, consistent with the leaf being a major bottleneck in the whole plant hydraulic system with consequent influence on photosynthetic gas exchange (Sack et al. 2003; Franks 2006; Sack and Holbrook 2006; Brodribb et al. 2007).

The K_{leaf} varies by over 65-fold across species (Sack and Holbrook 2006). This variation is consistent with the nature of K_{leaf} as a single value summarizing a complex micro-hydrological system, influenced by both the leaf xylem and outside-xylem compartments. The xylem compartment relates to the leaf venation, and the outside-xylem compartment to the flow of water across the xylem parenchyma and bundle sheath, and then through and/or around mesophyll cells to the site of water evaporation within the leaf (Sack and Scoffoni 2013). Early work had assumed that K_{leaf} would be mainly limited by the outside-xylem compartment, because it involves flow across membranes, whereas flow through the venation is via xylem conduits that are dead and hollow at maturity. However, this understanding has changed. There is now general recognition of the role of aquaporins in membrane flow, increasing the permeability of membranes by orders of magnitude relative to that of a simple phospholipid bilayer, and appreciation that water flows through the leaf xylem in very narrow vessels and tracheids. Most importantly, measurements have been made of the low hydraulic conductance in vein xylem (K_x), which is typically of the same order as that outside the xylem, i.e., across the bundle sheath and mesophyll (K_{ox}) (Zwieniecki et al. 2002; Sack et al. 2004). Current understanding is that there is substantial hydraulic resistance both inside and outside the xylem and thus the anatomy of both the vein system and the outside-vein lamina can influence K_{leaf}, and scale up to influencing leaf gas exchange and whole plant performance (Sack and Holbrook 2006).

Hydraulic conductance is not a constant. Indeed, declines of hydraulic conductance may occur throughout the plant during strong transpiration or especially during soil and atmospheric drought. Hydraulic decline is often stronger in leaves than stems due to more negative water potentials, lower resistance to embolism, and/or the collapse of mesophyll tissues (Hao et al. 2008; Brodribb 2009; Johnson et al. 2011, 2012a).

Our aim is to review the correlations in the literature of K_{leaf} and K_{leaf} vulnerability to dehydration with cell, tissue, and whole leaf structure and composition (Tables 10.1, 10.2, and 10.3). Our overall thesis is that K_{leaf} and its vulnerability depend on multiple traits in concert, at different levels of tissue and organ construction.

2 Venation Traits

A number of vein traits are causal drivers or correlates across species of K_{leaf} for hydrated leaves (Table 10.1). The best supported anatomical correlate of K_{leaf} is the minor vein length per leaf area (minor VLA), or the total vein length per area (VLA, also known as "vein density"), which are themselves tightly correlated because

Table 10.1 Vein traits that contribute to leaf hydraulic conductance in hydrated leaves at full irradiance (K_{max}) and/or influence leaf hydraulic vulnerability

	K_{max}	K_{leaf} vulnerability
Greater xylem conduit numbers or sizes	Contributes to higher vein conductivity within and across species (Sack and Frole 2006; Maherali et al. 2008; Dunbar-Co et al. 2009; Taneda and Terashima 2012). In turn higher vein conductivity, especially in lower-order veins, can contribute to higher K_{leaf} as shown in computer modeling (McKown et al. 2010), and across diverse angiosperm species, and within species (Nardini et al. 2005; Sack and Frole 2006)	Narrow xylem conduits in midribs and greater xylem conduit cell wall thickness/lumen breadth ratios in minor veins may contribute to resistance to hydraulic decline within crowns, or across species within a genus or across diverse species adapted to a gradient of moisture (Cochard et al. 2004; Johnson et al. 2009; Blackman et al. 2010; Nardini et al. 2012; Jordan et al. 2013)
Major vein length per area	High major VLA contributes to higher K_{leaf} as shown in computer modeling and across closely related species, and varieties of a given species (McKown et al. 2010; Sommerville et al. 2012; Nardini et al. 2014)	High major VLA provides tolerance of disruption to the hydraulic system caused by damage or drought as shown in computer modeling and across diverse angiosperm species, and within angiosperm genera (Sack et al. 2008; McKown et al. 2010; Scoffoni et al. 2011; Nardini et al. 2012, 2014)
Minor vein length per area	High minor VLA can contribute to higher K_{leaf} as shown in computer modeling (McKown et al. 2010), across tropical tree species (Sack and Frole 2006) and species of diverse lineages (Brodribb et al. 2007), and correlates with higher stomatal conductance (Boyce et al. 2009; Feild et al. 2011), and higher light-saturated photosynthetic rates per leaf area and mass across diverse species (Brodribb et al. 2010; Feild et al. 2011; Walls 2011; Sack et al. 2013)	
Free ending veins per unit area	Numerous FEVs per unit area can correlate with higher K_{leaf} across diverse species (Scoffoni et al. 2011)	
Vein topology		Increased looping provides optimal transport given fluctuating flow or damage according to mathematical and computer models (Corson 2010; Katifori et al. 2010)

Table 10.2 Bundle sheath and bundle sheath extension traits that contribute to leaf hydraulic conductance in hydrated leaves at full irradiance (K_{max}) and/or influence leaf hydraulic vulnerability

	K_{max}	K_{leaf} vulnerability
Bundle sheath cell size	Correlates with K_{leaf} across ontogenetically different leaves of *Ginkgo biloba* (Leigh et al. 2011)	Hypothesized to act in cavitation repair in the xylem in C_3 and C_4 grasses (Griffiths et al. 2013)
Bundle sheath extensions length and volume per area	Correlates with K_{leaf} across ontogenetically different leaves of *Ginkgo biloba* (Leigh et al. 2011) and across *Acacia* species (Sommerville et al. 2012)	
	A tomato mutant with reduced BSEs had lower K_{leaf} (Zsögön et al. 2015)	
	Correlates with the response of K_{leaf} to irradiance across diverse species (Scoffoni et al. 2008)	
	Correlates with the water delivery to the epidermis which can damp responses of K_{leaf} and gas exchange to vapor pressure deficit (Buckley et al. 2011)	
Bundle sheath permeability	ABA signaling and aquaporin activation/deactivation in the bundle sheath control K_{leaf} (Lee et al. 2008, 2009; Ache et al. 2010; Shatil-Cohen et al. 2011; Flexas et al. 2013; Griffiths et al. 2013; Pantin et al. 2013; Prado et al. 2013; Prado and Maurel 2013; Sack and Scoffoni 2013; Secchi and Zwieniecki 2013; Chaumont and Tyerman 2014)	Aquaporins in BS and xylem parenchyma may play a role in xylem refilling in leaves and stems (Laur and Hacke 2014a, b)

minor veins make up the bulk of leaf veins length (Sack and Frole 2006; Brodribb et al. 2007). Across vascular plants, early branching clades such as ferns exhibit low VLA and K_{leaf} compared with later groups such as angiosperms (Boyce et al. 2009). Even among angiosperms there has been a tendency for VLA and K_{leaf} to increase over time (Brodribb and Feild 2010). These strong trends found across large clades are often weaker among specific groups such as the eudicots, suggesting that other factors are also important in determining K_{leaf} (McKown et al. 2010; Scoffoni et al. 2011; Sack et al. 2013; Sack and Scoffoni 2013). Notably, many traits influence K_{leaf}, as explored throughout this chapter, and thus in certain species sets K_{leaf} may be weakly related or uncorrelated with any given trait in certain lineages or species sets due to a greater variation in other key traits. Additional vein traits that influence the maximum value of K_{leaf} (K_{max}, which occurs at high water potential and high irradiance) include larger xylem conduit numbers and sizes, higher major vein length per area, vein topology with greater reticulation, and a greater number of free ending veins per area (Table 10.1).

Leaf hydraulic vulnerability also depends on vein traits (Table 10.1). Leaf dehydration may lead to embolism in the vein xylem, leading to decline of K_x in combination with declines in K_{ox} that could arise due to tissue shrinkage (see following section). The question of whether embolism occurs in all orders of leaf veins

Table 10.3 Leaf lamina mesophyll anatomy traits that contribute to leaf hydraulic conductance in hydrated leaves at full irradiance (K_{max}) and/or influence leaf hydraulic vulnerability

	K_{max}	K_{leaf} vulnerability
Spongy mesophyll: palisade mesophyll thickness ratio (or spongy mesophyll + epidermis: palisade mesophyll thickness ratio)	Hypothesized to contribute to K_{leaf}; negatively correlated with vein length per area and positively correlated with K_{leaf} across diverse angiosperms (Wylie 1946; Sack and Frole 2006)	Tissue shrinkage may contribute to K_{leaf} decline, and thus leaves with higher elastic modulus might be more resistant to hydraulic decline (Charra-Vaskou et al. 2012; Scoffoni et al. 2014)
Leaf mesophyll thickness	Correlated with K_{leaf} across species (Aasamaa et al. 2001; Sack et al. 2003; Sack and Frole 2006) and for sun vs. shade leaves within canopies (Sack et al. 2003; Brodribb and Jordan 2011)	
Accessory transport elements	Accessory transport elements may contribute to K_{leaf} in cycads, conifers, and angiosperms (Esau 1977; Brodribb et al. 2007, 2010; Sack and Scoffoni 2013)	Accessory transport elements might act as water storage to buffer cell water potentials from transiently high transpiration rates (Takeda 1913)
		Collapse of transfusion tracheids in conifers is associated with K_{leaf} decline in dehydrating leaves (Brodribb and Holbrook 2005; Zhang et al. 2014)

remains open, but both cavitation and collapse appear to be greater in conduits with larger lumens, and thus the major vein xylem may be more likely to embolize than collapse because it contains the widest vessels in the leaf, and because it is more mechanically reinforced (Blackman et al. 2010; Sack and Scoffoni 2013). Studies reporting embolism-induced reductions in K_{leaf} have found support for cavitation events occurring in leaf petioles or midribs using a range of hydraulic measurements and visualization approaches, and for collapse of tracheids in some pine species (Nardini et al. 2001; Bucci et al. 2003; Cochard et al. 2004; Johnson et al. 2009, 2012b; Charra-Vaskou et al. 2012). Similarly, K_{leaf} vulnerability may be lower for species with narrower xylem conduits in the midrib and/or minor veins, if these embolize or collapse at a lower leaf water status. Two studies of angiosperms found that species having smaller leaf midrib conduits were more resistant to embolism (Johnson et al. 2009; Nardini et al. 2012). Further, across four species of pines, the two species with smaller diameter leaf vein tracheids had much more negative conduit collapse pressures than did the two species with larger tracheid diameters (Cochard et al. 2004). Additionally, along a height gradient in Douglas fir, the hydraulic vulnerability of leafy shoots was lower for shoots with needles with narrower xylem conduits, fewer tracheids per cross-sectional leaf area, and fewer pits per tracheid (Woodruff et al. 2008). In dicotyledons, narrower conduits in minor veins may be protected during collapse under strong xylem tensions arising during drought. Thus, leaf minor vein conduit cell wall thickness to lumen breadth ratio ($[t/b]^3$) was positively related to leaf hydraulic vulnerability for 20 angiosperm species (Blackman et al. 2010), and positively correlated with moisture availability in 67 species from the Proteaceae (Jordan et al. 2013).

Higher leaf major vein length per area may also confer resistance to hydraulic dysfunction. Indeed, small leaves from drier habitats tend to have higher leaf major VLA, which would provide a greater level of drought tolerance. Thus, in studies of ten species from diverse angiosperm families (Scoffoni et al. 2011), and six angiosperm species (three *Acer* sand three *Quercus* species) (Nardini et al. 2012) and four *Coffea arabica* varieties, a greater resistance to leaf hydraulic dysfunction correlated with higher major VLA (Nardini et al. 2014).

Additionally, the topology of the vein system (i.e., arrangement of veins) may confer resistance to hydraulic decline. Greater vein connectivity should render the system relatively tolerant to the effects of embolism if it can route water around blockages through highly conductive veins (Sack et al. 2008; Corson 2010; Katifori et al. 2010; Scoffoni et al. 2011).

3 Bundle Sheath and Bundle Sheath Extension Traits

The tissues immediately surrounding the veins provide a hydraulic interface with the mesophyll and can strongly influence K_{leaf} (Table 10.2). The bundle sheath (BS) is a cylinder of parenchyma cells that surround the vascular tissues in the leaf vein (Esau 1977) and as such is the tissue that water must move through between xylem and the mesophyll. Classically, researchers expected the BS and bundle sheath extensions (BSE), a tissue composed of parenchyma and sometimes sclerenchyma that in many species extends between the veins and epidermis, to influence water transport in the leaf (Wylie 1952; Canny 1990a). Indeed, recent research shows that these features influence K_{leaf} and its dynamics in relation to light and water supply (Scoffoni et al. 2008; Buckley et al. 2011). In some species, the BS has suberized layers in its anticlinal walls, analogous to the Casparian strip in root endodermis, which could greatly reduce the conductivity of the BS by preventing extracellular water transport (Lersten 1997). A Casparian strip in the BS is consistent with accumulation of tracers at the proximal margins of BS cells (Canny 1990b), and with genes being expressed during development of the leaf BS in common with the root endodermis (Slewinski et al. 2012), but the distribution of a BS Casparian strip across species is largely unknown. Indeed, BS cells might act on controlling the import and export of water just as they are used for loading phloem cells (Ache et al. 2010; Nardini et al. 2010), and thus prevent water loss and solute leakage from the veins (O'Brien and Carr 1970; Canny 1990a; Mertz and Brutnell 2014). This is consistent with growing evidence that the BS is a central "control point" for integrating whole leaf function (Flexas et al. 2013; Griffiths et al. 2013; Sack and Scoffoni 2013).

If flow across the BS is predominantly across the plasma membrane, then aquaporin function probably determines its contribution to K_{leaf} (Shatil-Cohen et al. 2011; Moshelion et al. 2015). Consequently, recent work has implied that the BS is a major influence on the outside component of K_{leaf}, i.e., K_{ox}, and thus on K_{leaf} itself (Buckley et al., unpublished data). Indeed, *Arabidopsis* and *Populus* mutants in which aquaporins are disrupted in the BS and vein parenchyma show diminished K_{leaf} (Prado et al. 2013; Prado and Maurel 2013; Secchi and Zwieniecki 2013; Chaumont and Tyerman 2014). Aquaporins present in BS cells, phloem cells, and transfusion parenchyma may facilitate radial water flow in *Picea glauca* needles (Laur and Hacke 2014a). Additionally, in *Arabidopsis*, abscisic acid (ABA) influences K_{leaf} via the BS (Shatil-Cohen et al. 2011; Pantin et al. 2013). In maize, a reduction of turgor in the midrib BS reduced K_{leaf} (Kim and Steudle 2007). The BS may also influence the distribution of water from veins across the lamina; BS cell permeability was higher in minor than major veins in tobacco (Lee et al. 2009).

The BS and vein internal parenchyma may also control K_{leaf} dynamics in response to the leaf's external environment and internal water status (Table 10.2). Thus, in *Arabidopsis*, whole rosette hydraulic conductance declined under high irradiance, and was correlated with the permeability of BS and vein parenchyma cells, but not with that of mesophyll cells (Prado et al. 2013). Notably, however, the BS cell permeability would have a complex relationship with K_{leaf} for given species, given that it may increase with aquaporin activity but decline with reduced turgor. Thus, K_{leaf} increased under higher irradiance for fig leaf gourd and tobacco, though BS cell permeability declined, as the cells lost turgor with the higher transpiration, due to potassium efflux and reduced aquaporin activity (Lee et al. 2008, 2009).

Bundle sheath cells and vein parenchyma cells have been hypothesized to play a major role in xylem cavitation repair, through the same process as root exudation (Nardini et al. 2008; Laur and Hacke 2014b). A correlation of BS size with low precipitation and aridity index across both C_3 and C_4 grasses supported the inference of a possible role for cavitation repair, and indeed, that selection on BS cell size could enable C_4 Kranz anatomy evolution (Griffiths et al. 2013). Foliar uptake and aquaporins in BS might even play a role in stem xylem refilling in *Picea glauca* (Laur and Hacke 2014a).

BSEs are more frequent in sun-adapted species, and in exposed leaves within canopies (Kenzo et al. 2007; Sack and Scoffoni 2013), consistent with a role in facilitating greater transpiration and photosynthetic rates under high irradiance. Indeed, BSEs apparently enhance K_{leaf}, by providing a larger surface area for water movement between xylem and the epidermis or mesophyll and/or for water to evaporate into the intercellular spaces (Sheriff and Meidner 1974; Zwieniecki et al. 2007; Ye et al. 2008). After the water is delivered to the epidermis via the BSEs, conduction may be more efficient from the epidermis to the mesophyll than through the mesophyll (Wylie 1943; Sheriff and Meidner 1974). Thus, dye experiments with lead showed water is transported to the epidermis via the apoplast of BSEs in *Tradescantia virginiana* (Byott and Sheriff 1976). *Acacia* phyllodes with more BSEs had higher K_{leaf} (Sommerville et al. 2012), and in *Ginkgo biloba*, long shoot leaves have higher K_{leaf} than short shoot leaves, corresponding with their having larger BSEs

(Leigh et al. 2011). Further, a tomato mutant with reduced BSEs had lower K_{leaf} (Zsögön et al. 2015). Additionally, BS and/or BSEs may influence the dynamics of K_{leaf} to light and VPD. Thus, species with BSEs tend to more frequently show K_{leaf} responses to irradiance (Scoffoni et al. 2008). Species with BSEs may maintain an especially close hydraulic connection between epidermis and vascular tissues. In these species, stomatal closure may be more closely connected with bulk leaf water potential, whereas, in leaves without BSEs where epidermis is thus isolated from the veins, stomatal dynamics may be expected to be less influenced by bulk leaf turgor loss. Consequently, species with BSEs also tend to have faster responses of stomatal conductance to changes in water supply and demand, but more so for supply (Buckley et al. 2011), which is consistent with enhancement of K_{leaf} by BSEs.

4 Mesophyll Traits

The tissues outside the vein xylem are an important component of the leaf hydraulic system and thus can strongly influence K_{leaf} (Table 10.3). Once water passes the BS, it flows as a liquid and/or as vapor through or around mesophyll and epidermal cells to the terminal evaporation sites. While the terminal sites are still not known, classical observations and recent modeling shows that water may evaporate deep within the leaf or near the stomata and travel as vapor through the leaf, and this may depend on the leaf anatomy and also on the leaf's environment (Sheriff 1977; Boyer 1985; Rockwell et al. 2014; Buckley 2015; Scoffoni 2015). Modeling suggests that the bulk of water transport in leaves is in the liquid phase, but that leaves with low tissue density may have significant vapor phase transport of water under conditions of high irradiance when heat is absorbed by chlorophyllous mesophyll layers (Rockwell et al. 2014; Buckley 2015). The degree that mesophyll anatomy will influence K_{ox} depends on its resistance relative to that of the BS and in fact the sites of evaporation may be dictated by the resistances of different pathways through the tissues (Buckley 2015).

Whether the anatomy of the mesophyll is a large influence on K_{ox}, and therefore K_{leaf} is a subject for current debate. The thickness of the mesophyll layer between the veins and the stomata ("vein–epidermal distance"; VED) has been proposed to negatively influence K_{leaf} (Brodribb et al. 2007), as a potential determinant of the flow path between veins and the sites of evaporation (referred to as the "mesophyll-distance" for flow outside the xylem, D_m). A physical model supported that idea, and the corollary that VLA and VED should be negatively correlated across species, as expected if they were colimiting to K_{leaf} (Noblin et al. 2008; Zwieniecki and Boyce 2014). However, that idea presumes that the bulk of water outside the xylem is transported across the mesophyll to the substomatal cavity before evaporation, but others have suggested that much water may evaporate near the BS. Which scenario is most accurate may vary with species' leaf anatomy, leaf water status, and ambient environment (Sack et al. 2013). Indeed, several studies have reported positive rather than negative correlations of K_{leaf} with leaf thickness and/or with spongy/palisade ratio (Aasamaa et al. 2001; Sack et al. 2003; Sack and Frole 2006), and leaves adapted or acclimated to high irradiance generally tend to be thicker and yet tend to have a higher K_{leaf} than accounted for by simply a higher VLA (Brodribb and Jordan 2011). These facts would suggest that the VED might impose little constraint on K_{leaf} per se, or indeed, that outside xylem flow efficiency may in some cases be increased by parallel horizontal layers. Indeed, the classical expectation was that water transport through the spongy mesophyll and epidermis is effective (Wylie 1939, 1946). There is a general trend across species for low VLA to correlate with a high ratio of the thickness of spongy mesophyll (and/or the thickness of spongy-mesophyll-plus-epidermis) to the thickness of palisade mesophyll, and this was interpreted as showing that a greater K_{ox} would be conferred by a thicker spongy mesophyll to compensate for larger flow distances outside the vein in leaves with lower VLA (Wylie 1946). A recent theoretical analysis also found that mesophyll cell porosity and connectivity were key parameters influencing K_{leaf} (Buckley 2015). Under high irradiance, when vapor phase transport driven by vertical temperature gradients is important, the greater tissue porosity of spongy mesophyll may contribute even more strongly to a high K_{leaf}. Because temperature is predicted to peak within the palisade mesophyll, temperature gradients are probably greater across the lower half of the leaf, thus increasing the spongy mesophyll's potential to contribute to the vapor phase component of K_{leaf}. The role of outside-xylem anatomy in determining K_{leaf} remains an important focus for future modeling and experimental work.

Mesophyll anatomy may also have an influence on K_{ox} vulnerability (Table 10.3). The degree of mesophyll shrinkage during leaf dehydration correlates with hydraulic declines (Charra-Vaskou et al. 2012; Scoffoni et al. 2014). The resulting declines in K_{ox} could be due to reduced cell surface area for evaporation, severed cell–cell connections and thus fewer water flow pathways, and/or to lower aquaporin activity. Potentially, a higher modulus of elasticity, conferred by a thicker or denser cell wall relative to the size of the cell lumens, may thus confer tolerance to hydraulic decline by reducing cell volumetric shrinkage (Scoffoni et al. 2014).

Many species have "accessory transport or storage" tissues within their BS or lamina mesophyll tissues (Brodribb et al. 2010). Such additional transport cells in leaves can be observed as sclerified cells that can be isolated in the mesophyll or connect to the leaf veins branching out into areoles. Indeed, transfusion tracheids are present in all gymnosperm leaves (Hu and Yao 1981) and have long been thought to serve as either sites for water storage (Takeda 1913) or for transport of water and solutes between the mesophyll and the vascular tissue inside leaf veins (Esau 1977). Species with such tissues appear to have higher K_{leaf} than would be expected simply from their VLA (Brodribb et al. 2007), indicating a potential shortening of flow pathways, or additional evaporative surface (Tomlinson and Fisher 2005; Brodribb et al. 2007, 2010; Sack and Scoffoni 2013; Zhang et al. 2014). Transfusion tracheids collapse during leaf dehydration in *Podocarpus* (Brodribb and Holbrook 2005) and in *Taxus* (Zhang et al. 2014), associated with dehydration-induced declines in K_{leaf}, and may recover with rehydration (Zhang et al. 2014). However, a study of two *Pinus* species (Johnson et al. 2009) found that transfusion tracheids did not collapse during dehydration but did empty at water potentials less negative than would cause loss of K_{leaf}. The role of transfusion tracheids in leaf hydraulic vulnerability is still unclear.

5 Relationship with Photosynthetic Anatomy and Coordinated Development

Anatomical traits may be correlated with K_{leaf} across species for several distinct reasons (Sack et al. 2013; Sack and Scoffoni 2013). Correlations may arise due to a mechanistic causality, to a common developmental mechanism, to coselection during evolution across environments, and/or to a common plastic trajectory during growth in given environments (Brodribb et al. 2013; John et al. 2013; Sack et al. 2013). The specific type of correlation among traits may vary across species sets, and elucidating the basis for these correlations is essential both to understand their functional significance and also their generality and predictiveness.

Many of the correlations described above and in Tables 10.1, 10.2, and 10.3 are mechanistic, i.e., they arise because given traits contribute directly to the flow efficiency through the leaf. However, coselection of traits that are not directly linked in hydraulic function, for overall optimality in adaptation to environment is equally common. The leaf hydraulic conductance is not an isolated system, but rather fully integrated within the leaf gas exchange system. Thus, additional correlations are frequently observed between hydraulic traits and traits related to gas exchange at the leaf and plant scales. Thus, for example, stomatal density and pore area are also often correlated across species with maximum K_{leaf}, which arises at least in part due to coordination between VLA and stomatal density (Aasamaa et al. 2001; Sack et al. 2003, 2005; Dunbar-Co et al. 2009; Feild et al. 2011; Carins Murphy et al. 2012, 2014; Zhang et al. 2012). While stomatal density does not directly influence VLA or K_{leaf}, selection for rapid gas exchange should act to increase all three traits. Further, much of the anatomy relevant to K_{leaf} also influences mesophyll control of CO_2 assimilation. For example, the conductance between the sites of evaporation and the sites of carboxylation, or "mesophyll conductance" (g_m) correlates across species with K_{leaf} (Flexas et al. 2013). This link may arise due to shared dependence of K_{ox} and/or g_m on mesophyll surface area, and on a shared role of aquaporins in both H_2O and CO_2 transport.

Indeed, many anatomical traits show coordinated development, which provides a direct and effective route for selection to optimize a species' function. In particular, some anatomical features that are important for hydraulic function and gas exchange depend on cell or leaf size, and thus they develop in a coordinated way (Brodribb et al. 2013; John et al. 2013). For example, smaller leaves have higher major VLA, which will tend to confer lower K_{leaf} vulnerability, and if the smaller leaves under consideration are formed from smaller cells, as is true in certain cases, then they will also tend to have higher minor VLA and higher stomatal density, which will confer higher K_{leaf} and higher potential gas exchange rates. In such cases, development is a means to coordinate all traits to match function.

6 Conclusions

Many traits within and outside the xylem contribute to leaf hydraulic conductance and its dynamics in response to water stress. For over 100 years, these questions have been recognized as essential for understanding the limits of plant performance. Computer modeling, focused experiments, and new visualization technologies will continue to reveal the anatomical underpinnings of K_{leaf} at higher resolution. However, fundamental biophysical questions that impact strongly on K_{leaf} still remain unanswered by experiment, including the hydraulic conductivity of cell walls to long distance transport and the osmotic water permeabilities of mesophyll and epidermal cells. Models are especially needed that allow the effects of individual anatomical traits on K_{leaf} to be examined both in isolation from one another and in concert. Experiments that "tweak" individual features are needed on model plants such as Arabidopsis and poplar. Additionally, further comparisions are needed within and among lineages with strong variation in anatomical features. Using all these approaches in combination will result in a full appreciation of the functional consequences of the great variation in leaf hydraulic anatomy, with certain benefits for predictive ecology and for optimal crop design.

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