Aquaporins and Leaf Water Relations

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Abstract Leaf water relations are a key factor of plant growth and productivity. Water is delivered to the leaf through its vasculature. It then exits xylem vessels by crossing living cells prior to vaporization and diffusion through stomatal apertures. The present chapter shows how the leaf aquaporin equipment contributes to the water transport capacity of inner leaf tissues (leaf hydraulic conductance, K_{leaf}) with a major role in the vascular bundles. Aquaporins provide optimal and locally adjusted water supply to the leaf during transpiration and leaf growth and movements. The respective roles of leaf vasculature and aquaporins in leaf hydraulic changes in response to endogenous or environmental stimuli are discussed. It is established that regulation of aquaporins at gene expression and protein phosphorylation levels mediates the effects of light, circadian rhythms and water and salt stress on K_{leaf}. However, the signaling mechanisms acting upstream are as yet unknown.

The water relations of leaves are at the crossroad of key plant physiological functions. The stomata present at the leaf surface mediate most of the gas exchange between the plant and atmosphere. Their regulated aperture allows a crucial tradeoff between carbon dioxide (CO_2) absorption and water loss by transpiration. Under high evaporative demand or low soil water availability, transpiration can markedly challenge the leaf water status, thereby impacting overall plant growth and

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productivity. In particular, photosynthetic carbon fixation requires a proper leaf hydration and can be dramatically reduced under drought. Expansive growth of leaves, which ultimately determines the ability of the plant to capture light, is also highly sensitive to the leaf water status.

The water transport capacity of inner leaf tissues (leaf hydraulic conductance, K_{leaf}) is a key player of leaf water relations. It allows a proper water import from the stem and optimized redistribution within the lamina. K_{leaf} can vary by up to 65-fold between plant species (Prado and Maurel 2013; Sack and Holbrook 2006). Differences in leaf anatomy and, in particular, in hydraulic design of their vasculature contribute to these large interspecific differences. However, nonvascular, living tissues can also determine key features of leaf hydraulics. For instance, K_{leaf} within a given plant species can show marked differences during development or under contrasting physiological conditions due to the expression and regulation of aquaporins (Prado and Maurel 2013; Sack and Holbrook 2006).

This present chapter discusses how aquaporins function in leaf tissues and allow a dynamic adjustment of leaf hydraulics in response to endogenous or environmental stimuli. Complementary information can be found in recent reviews (Chaumont and Tyerman 2014; Heinen et al. 2009; Maurel et al. 2015; Prado and Maurel 2013). The role of leaf aquaporins in CO_2 transport and carbon fixation will be presented in Chap. 10.

1 Principles of Leaf Hydraulics

1.1 Water Transport Pathways

After uptake by the root and transport through the stem xylem vessels, water (xylem sap) is delivered to the leaf through its vasculature. In brief, petiole xylem leads to the midrib that branches into progressively smaller veins embedded in the leaf mesophyll. Water then exits the vessels to cross the living cells forming the lamina, prior to vaporization in interstitial air spaces or substomatal chambers and diffusion through stomatal apertures. In this representation, liquid water transport is successively mediated through vascular and extravascular pathways, which thereby function in series. The respective hydraulic resistances of the two pathways are usually of the same order of magnitude (Sack and Holbrook 2006). While most intense water flows are observed under transpiring conditions during the day and under high evaporative demand, water is also delivered from vascular tissues to the leaf lamina at night or when expansive growth dominates. Conversely, a fraction of leaf water can be exported through phloem translocation.

Plant leaf vasculature shows a highly organized hierarchy of vein orders and species-specific branching or reticulation patterns. The significance of leaf venation with respect to hydraulics has been discussed previously (Sack and Scoffoni 2013). In all cases, vein distribution and density seem to be optimized for distributing water evenly across the leaf. The extravascular pathway first includes several cell types in the vascular bundle (xylem parenchyma cells, bundle sheath cells). Bundle sheath extensions provide, in addition, a direct delivery of water to the epidermis, whereas mesophyll cells mediate water transport from the veins to the substomatal chambers. Thus, leaf water transport can occur along multiple and composite paths. Nevertheless, bundle sheath cells, which are wrapped around the veins, appear as an obligatory passage for all these paths.

At the subcellular level, the paths used for liquid water transport, from cell to cell (transcellular and symplastic paths) or through the cell walls (apoplastic path), are similar to those operating in other organs and, as in the root, are still disputed. Low cell packing and the presence of air spaces in the mesophyll suggested that the apoplastic path may predominate in this tissue. In contrast, transcellular water transport may be crucial in vascular bundles, due to a tighter organization and differentiation of apoplastic barriers (Ache et al. 2010).

1.2 Leaf Hydraulic Measurements

K_{leaf} links, at the organ level, the flow of liquid water across inner leaf tissues to the driving force, i.e., the difference in water potential between the petiole and substomatal chambers. Three main methods have been developed for measuring K_{leaf}: the evaporative flux method, the high-pressure flow method, and the vacuum pump method. A critical comparison of these techniques has been published elsewhere (Prado and Maurel 2013; Sack et al. 2002). Although each method has specific pitfalls, their careful manipulation can yield very similar K_{leaf} values.

2 The Leaf Aquaporin Equipment

2.1 Expression Patterns

In agreement with the high isoform multiplicity of plant aquaporins, transcriptomic and proteomic studies have revealed the complex aquaporin equipment of plant leaves (Alexandersson et al. 2005; Hachez et al. 2008; Monneuse et al. 2011). In maize leaves, for instance, transcripts for 12 out 13 PIP isoforms were present, with the two most abundant ones (*ZmPIP1;1*, *ZmPIP2;1*) accounting for 60 % of *PIP* transcripts. While some PIPs, such as tobacco *Nt*AQP1, show strong expression in the spongy mesophyll parenchyma (Otto and Kaldenhoff 2000), a preferential expression of aquaporins was observed in the vascular bundles of most plant species investigated (Frangne et al. 2001; Hachez et al. 2008; Kirch et al. 2000; Prado et al. 2013). Aquaporins can also be found in phloem companion cells and epidermal and guard cells (Hachez et al. 2008).

Genome-wide co-expression analyses in developing maize leaves have revealed strong links between aquaporins and nutrient homeostasis and transport (Yue et al. 2012). Thus, the various expression patterns of aquaporins in leaves are indicative of isoform-specific roles of aquaporins in transcellular water transport or cell osmoregulation (Hachez et al. 2008; Heinen et al. 2009). Aquaporins can transport physiologically relevant molecules other than water, such as CO_2, ammonia (NH_3), and hydrogen peroxide (H_2O_2). An upregulation of PIP1;3 expression by H_2O_2 has been observed in *Arabidopsis* leaves (Hooijmaijers et al. 2012).

2.2 *Overall Contribution of Aquaporins to* $\mathbf{K}_{leaf}$

Whereas axial transport of water in xylem vessels does not involve living cell structures, aquaporins possibly account for a large part of downstream extravascular pathways. Aquaporin gene silencing using microRNA constructs in transgenic *Arabidopsis* has revealed the overall contribution of aquaporins to ~35 % and ~50 % of hydraulic conductivity of whole rosettes (K_{ros}) or individual leaves (K_{leaf}), respectively (Sade et al. 2014). Surprisingly, earlier experiments using antisense inhibition of *PIP1* or *PIP2* genes had failed to reveal a role for these aquaporins in leaf water transport in control conditions, whereas a marked impact of aquaporin inhibition on K_{leaf} was observed under water stress (Martre et al. 2002). Aquaporin research in plants and animals critically lacks specific chemical blockers. Although they are potentially toxic, mercury and azide block plant aquaporins through distinct modes of action. Consistent with the genetic studies above, their use indicated a contribution by 25–50 % of aquaporins to K_{leaf} in sunflower, grapevine, various deciduous trees, or *Arabidopsis* (Aasamaa and Sober 2005; Nardini and Salleo 2005; Postaire et al. 2010; Pou et al. 2013).

2.3 *Tissue-Specific Functions of Leaf Aquaporins*

Several recent studies have investigated which cell layers are hydraulically limiting during extravascular transport, the underlying idea being that these cells should be a preferential site for aquaporin expression and regulation. One first approach was to search for correlations between K_{leaf} and the water permeability of tissue-specific protoplasts. *Arabidopsis* leaves subjected to exogenous ABA or changes in irradiance revealed parallel changes in K_{leaf} and osmotic water permeability of bundle sheath protoplasts (Prado et al. 2013; Shatil-Cohen et al. 2011). Xylem parenchyma protoplasts also showed a consistent response to irradiance, whereas water permeability in isolated mesophyll protoplasts was not correlated to K_{leaf} under various ABA or light treatments. These data support the idea that vascular bundles, rather than the mesophyll, represent a hydraulically limiting structure in the extravascular pathway. Recent genetic approaches have brought more direct evidence for tissue-specific function of leaf aquaporins. Single PIP knockout mutants of *Arabidopsis* have revealed that, in this species, three aquaporin isoforms (*At*PIP1;2, *At*PIP2;1, *At*PIP2;6) can individually contribute to ~20 % of K_{ros} (Postaire et al. 2010; Prado et al. 2013). Their common expression in the veins was interpreted to mean that the living cells of these tissues can be hydraulically limiting. Another strategy was to express microRNAs in bundle sheath cells using a SCR promoter (Sade et al. 2014). Although a marked decreased in K_{leaf} (−65 %) was induced in the transgenic plants, it was associated with a concomitant inhibition of bundle sheath and mesophyll protoplast water permeability. Thus, it could not be concluded which tissue water permeability was the rate-limiting step. Another strategy was to genetically complement aquaporin-deficient plants by using aquaporin constructs under the control of vein- or bundle sheath-specific promoters. The partial or full recovery of K_{leaf} or K_{ros} in these plants provides supportive evidence for the importance of PIP functions in veins (Prado et al. 2013; Sade et al. 2015).

These findings do not exclude, however, a minor contribution of the mesophyll to whole leaf water transport. Aquaporin may also contribute to osmoregulation of mesophyll cells, in relation to their high metabolic activity (Morillon and Chrispeels 2001; Prado and Maurel 2013).

3 Key Physiological Roles of Leaf Aquaporins

3.1 Transpiration

The function of aquaporins during plant transpiration represents a key question in plant water relations. Overall, K_{leaf} and stomatal conductance show a tight coupling by diverse and most often unknown mechanisms. For instance, the regulation of aquaporins by light and circadian mechanisms may favor a constant adjustment of K_{leaf} to the transpiration demand. Consistent with this, low air humidity enhanced the K_{leaf} of *Arabidopsis*, by up to threefold and in <1 h (Levin et al. 2007). Interestingly, Pou et al. (2013) observed a strong correlation across control and water stress conditions between the expression level of a TIP2 homolog and stomatal conductance in grapevine. It is not clear whether this tonoplast aquaporin truly contributes to transcellular water transport during transpiration or whether it plays an osmoregulatory role in cells challenged by a high rate of water transport through the leaf. A paradoxical observation was made in mesophyll protoplasts of *Arabidopsis*, where water permeability was strongly but negatively correlated to the plant transpiration regime: thus, protoplast water permeability was maximal at reduced transpiration (Morillon and Chrispeels 2001).

A high evaporative demand can also lead to coordinated hydraulic responses throughout the whole plant body. Transpiration was shown to enhance the expression and function of aquaporins in rice and poplar roots, by signaling mechanisms that remain to be discovered (Laur and Hacke 2013; Sakurai-Ishikawa et al. 2011).

3.2 Leaf Growth

Expansive growth is primarily driven by cell turgor and thereby highly sensitive to the cell and tissue water status (Pantin et al. 2011) (see also chapter "Plant Aquaporins and Cell Elongation"). The idea that expansive growth of the leaf can be limited by water transfer from vascular to peripheral tissues was initially raised by the detection of local growth-induced water potential gradients (Tang and Boyer 2002). This idea is now well formalized, using hydraulic modeling of whole plants under varying water availability in the soil or the atmosphere (Caldeira et al. 2014). At the molecular and cellular levels, it is supported by the finding that, in barley and maize, the leaf growth zone shows enhanced expression of specific leaf aquaporins isoforms together with a high cell hydraulic conductivity (Hachez et al. 2008; Volkov et al. 2007). We note that the expression and function of aquaporins in roots can also impact leaf expansive growth (Caldeira et al. 2014; Ehlert et al. 2009), through effects on leaf xylem water potential.

3.3 Leaf Movements

Plants show diurnal leaf movements for optimizing exposure to incident light. In *Samanea saman*, these movements are mediated through circadian regulation of *PIP* expression and osmotic water permeability in leaf motor cells (Moshelion et al. 2002). Tobacco plants expressing an antisense copy of NtAQP1 revealed a role for this aquaporin in the differential elongation of the upper and lower sides of the petiole thereby contributing to leaf unfolding (Siefritz et al. 2004). In *Rhododendron* leaves, extracellular freezing under subfreezing temperature results in leaf water redistribution and thermonasty (curling). This response was shown to be associated to downregulation of *PIP2* genes (Chen et al. 2013).

3.4 Leaf Water Uptake and Secretion

Whereas roots usually account for most if not all of water uptake, leaf water uptake can be crucial in certain plant species for response to extreme environmental conditions. In epiphytes, for instance, leaf trichomes allow capturing air moisture under drought conditions (Ohrui et al. 2007), whereas in conifers, absorption of melting snow favors embolism refilling after winter (Laur and Hacke 2014a). These processes are associated with enhanced expression of aquaporins at the sites of water absorption. In halophytes such as the tropical mangrove tree *Avicennia officinalis*, excess salt can be secreted by specialized salt glands forming in the leaf epidermis. Salt-induced expression of aquaporins in these glands together with mercury inhibition experiments have suggested that these aquaporins may contribute to both secretion and water reabsorption (Tan et al. 2013; Tyerman 2013).

4 Regulation of Leaf Hydraulics

4.1 *Light and Circadian Rhythms*

The daily variations of light regime represent the most common regulators of K_{leaf} studied across plant species. In most cases, diurnal rhythms of leaf hydraulics were studied on a 24-h time window (Cochard et al. 2007; Lo Gullo et al. 2005), and K_{leaf} was the highest at high irradiance, consistent with a peak in evaporative demand and transpiration at midday. A few studies showed that leaf hydraulic conductivity was also regulated by the circadian clock. In particular, experiments with sunflower plants under constant darkness revealed that, at least in this species, K_{leaf} is under control of the circadian clock and peaks at the subjective midday (Nardini et al. 2005).

The mode of leaf aquaporin regulation by irradiance may vary depending on species. In walnut, for instance, light-dependent variations in K_{leaf} were tightly associated with parallel changes in transcript abundance of several *PIP1* and *PIP2* genes (Baaziz et al. 2012; Cochard et al. 2007). In maize, most *PIP* genes showed diurnal regulation with a peak in expression during the first hours of the light period (Hachez et al. 2008). The aquaporin mRNA levels of *Samanea saman* leaves were regulated diurnally in phase with leaflet movements, and *SsAQP2* transcription was under circadian control (Moshelion et al. 2002). NtAQP1 abundance was also under circadian regulation in tobacco leaves (Siefritz et al. 2004). In contrast, phosphorylation of a single aquaporin, *At*PIP2;1, was shown to mediate light-dependent regulation of K_{ros} in *Arabidopsis* (Prado et al. 2013). Quantitative proteomics revealed that phosphorylation at two adjacent C-terminal sites (Ser280, Ser283) was enhanced, together with K_{ros}, in response to a dark treatment. Transformation of a *pip2;1* mutant with *At*PIP2;1 forms carrying phosphomimetic mutations of these residues was sufficient to restore the responsiveness of K_{ros} to light whereas *At*PIP2;1 forms carrying phosphorylation-deficient mutations did not.

4.2 *Water and Salt Stress*

Soil water deficit (drought) results in a decrease in K_{leaf} in many species including *Arabidopsis* (Shatil-Cohen et al. 2011) and poplar (*Populus trichocarpa*) (Laur and Hacke 2014b). Under severe conditions, this decrease is mediated through both xylem embolism in leaf veins (see chapter "Role of Aquaporins in the Maintenance of Xylem Hydraulic Capacity") and downregulation of the aquaporin pathway. These two actions may result in a drop in leaf water potential thereby promoting stomatal closure (Pantin et al. 2013). Regulation of K_{leaf} in *Arabidopsis* under drought is mediated by ABA (Pantin et al. 2013; Shatil-Cohen et al. 2011), and a possible role of aquaporin dephosphorylation has been invoked (Kline et al. 2010; Prado et al. 2013).

Genetic and aquaporin expression analyses have shown that leaf aquaporins of both the PIP and TIP subfamilies support the recovery of droughted plants upon rewatering (Laur and Hacke 2014b; Martre et al. 2002). In particular, aquaporins expressed in the xylem parenchyma may contribute to embolism refilling and smooth delivery of water to the whole leaf blade.

4.3 Other Signals

Leaves are exposed to numerous types of biotic aggressions, by herbivories or microbial pathogens. The associated hydraulic responses have been barely investigated and will deserve more attention in the future. For instance, partial defoliation of poplar seedlings resulted in a five to tenfold increase in expression of a specific PIP isoform, which paralleled an increase in transpiration and lamina hydraulic conductivity (Liu et al. 2014).

5 Conclusions

The hydraulics of leaves has been rather difficult to comprehend, both biophysically and physiologically, due to entangled contributions of the vasculature and living structures (aquaporins), the former showing a complex reticulate organization. The vascular system of leaves mediates crucial hydraulic changes during development and, through localized embolisms, in leaf response to extreme drought or low temperatures. Aquaporins play complementary roles and appear to be at work in multiple physiological conditions. In particular, their capacity to mediate diurnal and spatially restricted adjustments of leaf water transport may be a key factor of plant performance and productivity.

Despite recent progress, we are still far from a clear understanding of leaf hydraulics. Mathematical models have addressed the impact of venation pattern (including vein hierarchy and conductivities) on leaf hydraulics in relation to leaf construction costs (McKown et al. 2010). Models that go beyond a classical Ohm's law analogy are also under development (Rockwell et al. 2014). However, we still lack a leaf hydraulic model that would include a comprehensive description of aquaporin function and regulation.

Although much remains to be learned about aquaporin functions in leaves, two directions should deserve a specific attention in future research. One is water transport in tree leaves, due to its high agronomical and ecological importance. Molecular studies are emerging, and the recent development of genetic tools in poplar (Secchi and Zwieniecki 2013) opens interesting perspectives to understand the role of aquaporins in tree leaf response to extreme drought episodes. Focus should also be put onto the signaling mechanisms that mediate the regulation of aquaporins by endogenous or environmental signals. In particular, the coupling of leaf aquaporins to stomatal functions (see chapter "Roles of Aquaporins in Stomata") and their dual role in water and CO_2 transport (see chapter "Plant Aquaporins and CO_2") represent central questions for future studies.

References

Aasamaa K, Sober A (2005) Seasonal courses of maximum hydraulic conductance in shoots of six temperate deciduous tree species. Funct Plant Biol 32:1077–1087

Ache P, Bauer H, Kollist H, Al-Rasheid KA, Lautner S, Hartung W, Hedrich R (2010) Stomatal action directly feeds back on leaf turgor: new insights into the regulation of the plant water status from non-invasive pressure probe measurements. Plant J 62:1072–1082

Alexandersson E, Fraysse L, Sjovall-Larsen S, Gustavsson S, Fellert M, Karlsson M, Johanson U, Kjellbom P (2005) Whole gene family expression and drought stress regulation of aquaporins. Plant Mol Biol 59:469–484

Baaziz KB, Lopez D, Rabot A, Combes D, Gousset A, Bouzid S, Cochard H, Sakr S, Venisse JS (2012) Light-mediated K_{leaf} induction and contribution of both the PIP1s and PIP2s aquaporins in five tree species: walnut (*Juglans regia*) case study. Tree Physiol 32:423–434

Caldeira CF, Bosio M, Parent B, Jeanguenin L, Chaumont F, Tardieu F (2014) A hydraulic model is compatible with rapid changes in leaf elongation under fluctuating evaporative demand and soil water status. Plant Physiol 164:1718–1730

Chaumont F, Tyerman SD (2014) Aquaporins: highly regulated channels controlling plant water relations. Plant Physiol 164:1600–1618

Chen K, Wang X, Fessehaie A, Yin Y, Arora R (2013) Is expression of aquaporins (plasma membrane intrinsic protein 2s, PIP2s) associated with thermonasty (leaf-curling) in Rhododendron? J Plant Physiol 170:1447–1454

Cochard H, Venisse JS, Barigah TS, Brunel N, Herbette S, Guilliot A, Tyree MT, Sakr S (2007) New insights into the understanding of variable hydraulic conductances in leaves. Evidence for a possible implication of plasma membrane aquaporins. Plant Physiol 143:122–133

Ehlert C, Maurel C, Tardieu F, Simonneau T (2009) Aquaporin-mediated reduction in maize root hydraulic conductivity impacts cell turgor and leaf elongation even without changing transpiration. Plant Physiol 150:1093–1104

Frangne N, Maeshima M, Schaffner AR, Mandel T, Martinoia E, Bonnemain JL (2001) Expression and distribution of a vaculoar aquaporin in young and mature leaf tissues of *Brassica napus* in relation to water fluxes. Planta 212:270–278

Hachez C, Heinen RB, Draye X, Chaumont F (2008) The expression pattern of plasma membrane aquaporins in maize leaf highlights their role in hydraulic regulation. Plant Mol Biol 68:337–353

Heinen RB, Ye Q, Chaumont F (2009) Role of aquaporins in leaf physiology. J Exp Bot 60: 2971–2985

Hooijmaijers C, Rhee JY, Kwak KJ, Chung GC, Horie T, Katsuhara M, Kang H (2012) Hydrogen peroxide permeability of plasma membrane aquaporins of *Arabidopsis thaliana*. J Plant Res 125:147–153

Kirch H-H, Vera-Estrella R, Golldack D, Quigley F, Michalowski CB, Barkla BJ, Bohnert HJ (2000) Expression of water channel proteins in *Mesembryanthemum crystallinum*. Plant Physiol 123:111–124

Kline KG, Barrett-Wilt GA, Sussman MR (2010) *In planta* changes in protein phosphorylation induced by the plant hormone abscisic acid. Proc Natl Acad Sci U S A 107:15986–15991

Laur J, Hacke UG (2013) Transpirational demand affects aquaporin expression in poplar roots. J Exp Bot 64:2283–2293

Laur J, Hacke UG (2014a) Exploring *Picea glauca* aquaporins in the context of needle water uptake and xylem refilling. New Phytol 203:388–400

Laur J, Hacke UG (2014b) The role of water channel proteins in facilitating recovery of leaf hydraulic conductance from water stress in *Populus trichocarpa*. PLoS One 9:e111751

Levin M, Lemcoff JH, Cohen S, Kapulnik Y (2007) Low air humidity increases leaf-specific hydraulic conductance of *Arabidopsis thaliana* (L.) Heynh (Brassicaceae). J Exp Bot 58:3711–3718

Liu J, Equiza MA, Navarro-Rodenas A, Lee SH, Zwiazek JJ (2014) Hydraulic adjustments in aspen (*Populus tremuloides*) seedlings following defoliation involve root and leaf aquaporins. Planta 240:553–564

Lo Gullo MA, Nardini A, Trifilo P, Salleo S (2005) Diurnal and seasonal variations in leaf hydraulic conductance in evergreen and deciduous trees. Tree Physiol 25:505–512

Martre P, Morillon R, Barrieu F, North GB, Nobel PS, Chrispeels MJ (2002) Plasma membrane aquaporins play a significant role during recovery from water deficit. Plant Physiol 130: 2101–2110

Maurel C, Boursiac Y, Luu DT, Santoni V, Shahzad Z, Verdoucq L (2015) Aquaporins in plants. Physiol Rev 95:1321–1358

McKown AD, Cochard H, Sack L (2010) Decoding leaf hydraulics with a spatially explicit model: principles of venation architecture and implications for its evolution. Am Nat 175:447–460

Monneuse JM, Sugano M, Becue T, Santoni V, Hem S, Rossignol M (2011) Towards the profiling of the *Arabidopsis thaliana* plasma membrane transportome by targeted proteomics. Proteomics 11:1789–1797

Morillon R, Chrispeels MJ (2001) The role of ABA and the transpiration stream in the regulation of the osmotic water permeability of leaf cells. Proc Natl Acad Sci U S A 98:14138–14143

Moshelion M, Becker D, Biela A, Uehlein N, Hedrich R, Otto B, Levi H, Moran N, Kaldenhoff R (2002) Plasma membrane aquaporins in the motor cells of *Samanea saman*: diurnal and circadian regulation. Plant Cell 14:727–739

Nardini A, Salleo S (2005) Water stress-induced modifications of leaf hydraulic architecture in sunflower: co-ordination with gas exchange. J Exp Bot 56:3093–3101

Nardini A, Salleo S, Andri S (2005) Circadian regulation of leaf hydraulic conductance in sunflower (*Helianthus annuus* L. cv Margot). Plant Cell Environ 28:750–759

Ohrui T, Nobira H, Sakata Y, Taji T, Yamamoto C, Nishida K, Yamakawa T, Sasuga Y, Yaguchi Y, Takenaga H, Tanaka S (2007) Foliar trichome- and aquaporin-aided water uptake in a drought-resistant epiphyte *Tillandsia ionantha* Planchon. Planta 227:47–56

Otto B, Kaldenhoff R (2000) Cell-specific expression of the mercury-insensitive plasma-membrane aquaporin NtAQP1 from *Nicotiana tabacum*. Planta 211:167–172

Pantin F, Simonneau T, Rolland G, Dauzat M, Muller B (2011) Control of leaf expansion: a developmental switch from metabolics to hydraulics. Plant Physiol 156:803–815

Pantin F, Monnet F, Jannaud D, Costa JM, Renaud J, Muller B, Simonneau T, Genty B (2013) The dual effect of abscisic acid on stomata. New Phytol 197:65–72

Postaire O, Tournaire-Roux C, Grondin A, Boursiac Y, Morillon R, Schäffner T, Maurel C (2010) A PIP1 aquaporin contributes to hydrostatic pressure-induced water transport in both the root and rosette of Arabidopsis. Plant Physiol 152:1418–1430

Pou A, Medrano H, Flexas J, Tyerman SD (2013) A putative role for TIP and PIP aquaporins in dynamics of leaf hydraulic and stomatal conductances in grapevine under water stress and re-watering. Plant Cell Environ 36:828–843

Prado K, Maurel C (2013) Regulation of leaf hydraulics: from molecular to whole plant levels. Front Plant Sci 4:255

Prado K, Boursiac Y, Tournaire-Roux C, Monneuse J-M, Postaire O, Ines O, Schäffner AR, Hem S, Santoni V, Maurel C (2013) Regulation of *Arabidopsis* leaf hydraulics involves light-dependent phosphorylation of aquaporins in veins. Plant Cell 25:1029–1039

Rockwell FE, Holbrook NM, Stroock AD (2014) Leaf hydraulics II: vascularized tissues. J Theor Biol 340:267–284

Sack L, Holbrook NM (2006) Leaf hydraulics. Annu Rev Plant Biol 57:361–381

Sack L, Scoffoni C (2013) Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. New Phytol 198:983–1000

Sack L, Melcher PJ, Zwieniecki MA, Holbrook NM (2002) The hydraulic conductance of the angiosperm leaf lamina: a comparison of three measurement methods. J Exp Bot 53: 2177–2184

Sade N, Shatil-Cohen A, Attia Z, Maurel C, Boursiac Y, Kelly G, Granot D, Yaaran A, Lerner S, Moshelion M (2014) The role of plasma membrane aquaporins in regulating the bundle sheath-mesophyll continuum and leaf hydraulics. Plant Physiol 166:1609–1620

Sade N, Shatil-Cohen A, Moshelion M (2015) Bundle-sheath aquaporins play a role in controlling Arabidopsis leaf hydraulic conductivity. Plant Signal Behav 10:e1017177

Sakurai-Ishikawa J, Murai-Hatano M, Hayashi H, Ahamed A, Fukushi K, Matsumoto T, Kitagawa Y (2011) Transpiration from shoots triggers diurnal changes in root aquaporin expression. Plant Cell Environ 34:1150–1163

Secchi F, Zwieniecki MA (2013) The physiological response of *Populus tremula* x *alba* leaves to the down-regulation of PIP1 aquaporin gene expression under no water stress. Front Plant Sci 4:507

Shatil-Cohen A, Attia Z, Moshelion M (2011) Bundle-sheath cell regulation of xylem-mesophyll water transport via aquaporins under drought stress: a target of xylem-borne ABA? Plant J 67: 72–80

Siefritz F, Otto B, Bienert GP, Krol A, Kaldenhoff R (2004) The plasma membrane aquaporin NtAQP1 is a key component of the leaf unfolding mechanism in tobacco. Plant J 37:147–155

Tan WK, Lin Q, Lim TM, Kumar P, Loh CS (2013) Dynamic secretion changes in the salt glands of the mangrove tree species *Avicennia officinalis* in response to a changing saline environment. Plant Cell Environ 36:1410–1422

Tang AC, Boyer JS (2002) Growth-induced water potentials and the growth of maize leaves. J Exp Bot 53:489–503

Tyerman SD (2013) The devil in the detail of secretions. Plant Cell Environ 36:1407–1409

Volkov V, Hachez C, Moshelion M, Draye X, Chaumont F, Fricke W (2007) Water permeability differs between growing and non-growing barley leaf tissues. J Exp Bot 58:377–390

Yue X, Zhao X, Fei Y, Zhang X (2012) Correlation of aquaporins and transmembrane solute transporters revealed by genome-wide analysis in developing maize leaf. Comp Funct Genom 2012:546930