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Review

Plant aquaporins: Roles in plant physiology ☆

Guowei Li, Véronique Santoni, Christophe Maurel *

Biochimie et Physiologie Moléculaire des Plantes, UMR 5004 CNRS/UMR 0386 INRA/Montpellier SupAgro/Université Montpellier 2, F-34060 Montpellier Cedex 2, France

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ABSTRACT

Background: Aquaporins are membrane channels that facilitate the transport of water and small neutral molecules across biological membranes of most living organisms.
Scope of review: Here, we present comprehensive insights made on plant aquaporins in recent years, pointing to their molecular and physiological specificities with respect to animal or microbial counterparts.
Major conclusions: In plants, aquaporins occur as multiple isoforms reflecting a high diversity of cellular localizations and various physiological substrates in addition to water. Of particular relevance for plants is the transport by aquaporins of dissolved gases such as carbon dioxide or metalloids such as boric or silicic acid. The mechanisms that determine the gating and subcellular localization of plant aquaporins are extensively studied. They allow aquaporin regulation in response to multiple environmental and hormonal stimuli. Thus, aquaporins play key roles in hydraulic regulation and nutrient transport in roots and leaves. They contribute to several plant growth and developmental processes such as seed germination or emergence of lateral roots.
General significance: Plants with genetically altered aquaporin functions are now tested for their ability to improve plant resistance to stresses. This article is part of a Special Issue entitled Aquaporins.

1. Introduction

Terrestrial plants establish a continuum between the soil and the atmosphere and contribute to water transfer between these two entities. In transpiring plants, the ascent of water is mediated through xylem vessels, capillaries made from dead cells. For a long time, water diffusion across the lipid phase of membranes was thought to be sufficient to support water exchanges in living plant cells and tissues [1]. In the very early 1990s, the existence of water channels in plants had not been clearly hypothesized, even though some aquaporins had been molecularly characterized due to their high abundance or remarkable expression properties. Thus, the functional characterization of plant aquaporins shortly after the pioneering work of Preston et al. [2] on human AQP1 opened unprecedented perspectives in the field of plant water relations. To date, the function and regulation of aquaporins is quite extensively integrated to explain the remarkable hydraulic properties of plants. However, additional surprises have come with the identification of other aquaporin substrates than water, some of them such as boron, silicon or carbon dioxide (CO_2) being of great physiological significance. Thus, the term "aquaporin" has been used in a broad sense and now refers to all plant Major Intrinsic Proteins (MIPs), whether or not their main role is in water transport.

In the present review, we present the comprehensive insights made on plant aquaporins in recent years, pointing to their molecular and physiological specificities with respect to animal or microbial counterparts. We discuss the diversity of plant aquaporin isoforms, of their substrates and cellular localizations. We emphasize their physiological functions with respect to whole plant hydraulics, plant development, nutrient acquisition, and plant responses to various environmental stresses.

2. The family of plant aquaporins and their substrates

2.1. High diversity of isoforms

Aquaporins belong to the large class of MIPs, with first member (Nodulin-26, *Gm*NOD26) identified in plants (soybean) as early as 1987 [3]. The water transport activity of plant aquaporins was first established for an *Arabidopsis* homolog (*At*TIP1;1) [4], and their function was thereafter described in numerous herbaceous or ligneous, wild or cultivated plant species. Aquaporins of higher plants exhibit a high diversity with 35, 36, 33 isoforms in *Arabidopsis*, maize and rice, respectively [5–7]. Plant aquaporin homologs can be classified according to their sequence into up to seven subfamilies [8,9], which may also correspond to distinct sub-cellular localizations. The so-called Plasma membrane Intrinsic Proteins (PIPs), which localize to the plasma membrane mostly, can be further divided into PIP1 and PIP2 subclasses. The Tonoplast Intrinsic Proteins (TIPs) are targeted to the vacuolar membrane (tonoplast). Although *Gm*NOD26 is exclusively expressed in the peribacteroid membrane of nitrogen-fixing symbiotic

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* Corresponding author at: Biochimie et Physiologie Moléculaire des Plantes, Bât. 7, Campus INRA/SupAgro, 2 place Viala, F-34060 Montpellier Cedex 2, France. Tel.: +33 499 612011; fax: +33 467 525737.
E-mail address: maurel@supagro.inra.fr (C. Maurel).

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nodules of legume roots, the NOD26-like Intrinsic Proteins (NIPs), which form the third subfamily, are also found in non-legume plant species, where they localize to the plasma membrane [10,11] or the endoplasmic reticulum (ER) [12]. The Small basic Intrinsic Proteins (SIPs) group comprises only a few isoforms (3 and 2 in *Arabidopsis* and rice, respectively). The uncategorized X Intrinsic Proteins (XIPs) were recently discovered in protozoa, fungi and plants and are of as yet unknown functions [13–15]. This subfamily is absent from plants such as *Arabidopsis*, maize, rice. Two additional subfamilies, the GlpF-like Intrinsic Proteins (GIPs) and the Hybrid Intrinsic Proteins (HIPs) are present exclusively in moss, not in vascular plants [8,9]. Whereas the first four subfamilies (PIPs, TIPs, NIPs and SIPs) are present in all terrestrial plants, from non-vascular plants to vascular plants, the PIPs are the only ones that are shared between algae and higher plants. Thus, the PIPs could represent the ancestor aquaporins that have been conserved throughout evolution of terrestrial plants. By contrast, the GIPs and HIPs may have been lost during this process.

2.2. High diversity of sub-cellular localization

With respect to their animal counterparts, plant aquaporins show a broader array of sub-cellular localizations, in relation with the high degree of compartmentalization of plant cells. Aquaporins have been localized in nearly all of plant cell sub-cellular compartments, including plasma membrane, tonoplast, ER, Golgi apparatus and chloroplast. Localization of aquaporins in the chloroplast, which quasi exclusively relies on proteomic studies, is still debated [16]. Interestingly, some aquaporins exhibit multiple sub-cellular localizations. For instance, *Nt*AQP1, a tobacco PIP1 homolog, was observed in both the plasma membrane and chloroplast inner envelope membrane of tobacco leaf cells [17]. Seed-specific TIPs of *Arabidopsis* (*At*TIP3;1, *At*TIP3;2), which predominantly sit in the protein storage vacuoles, are also transiently expressed at the plasma membrane during the early stages of seed germination and maturation [18]. In these two cases, however, it will be important that these observations can be extended to other plant species. Several mechanisms that determine the trafficking of newly synthesized PIPs or TIPs to their destination membranes have recently been discovered. In PIP2s, diacidic motifs and C-terminal phosphorylation were found to favor export from the ER [19–21]. In contrast, homologs of the PIP1 sub-class showed trafficking defects, unless they were co-expressed with PIP2s and formed heterotetramers [21–23]. These molecular interactions seem to be necessary for PIP1s to reach the plasma membrane (see 4.3). In addition, a role for Soluble NSF Attachment Protein REceptors (SNAREs) in PIP trafficking to the plasma membrane was recently uncovered [24,25]. However, the mechanisms that determine the multiple localizations of some aquaporins are as yet unknown.

2.3. High diversity of substrates

Functional expression of plant aquaporins in heterologous systems such as *Xenopus* oocytes or yeast cells revealed a great diversity of substrates. They include water and the related molecule H_2O_2, solutes transported by animal and bacterial homologs (urea, glycerol), metalloid species [boric acid: $B(OH)_3$; silicic acid: $Si(OH)_4$, arsenious acid: $As(OH)_3$], lactic acid, or dissolved gas molecules (CO_2, ammonia: NH_3) [26,27]. With respect to this large array of substrates, plant aquaporins can exhibit complex yet specific selectivity profiles. For instance, *At*TIP1;1 facilitates the transport of H_2O, H_2O_2 and urea [4,28,29] whereas *Os*NIP2;1 from rice functions as a transporter of H_2O, methylated arsenic species, silicic acid and antimonite [10,30–32]. Atomic structures of microbial, animal, and plant homologs have shown that highly conserved structural features can confer on aquaporins their transport selectivity for water and/or solutes [33]. Accordingly, homology modeling approaches based on the aromatic/arginine selectivity filter have been developed to predict plant aquaporin selectivity [34,35]. However, further investigations are still required. For instance, mammalian AQP1 and AQP4 facilitate the transport of nitric oxide (NO) [36,37]. NO plays a role in plant signaling and may well be transported by plant aquaporins.

3. Aquaporins and water transport in plant roots and leaves

3.1. Root hydraulic conductivity (Lp_r)

Water uptake by roots occurs through successive transport along the radial and axial paths. Axial water transport is mediated by xylem vessels, which do not present significant membrane barriers. The radial path allows water transport from the soil to the vessels and involves three concurrent pathways: apoplastic (across cell walls), symplastic (through plasmodesmata and cytoplasmic continuities) or transcellular (across membranes) [38]. The latter pathway is contributed in part by aquaporins but is difficult to distinguish experimentally from the symplastic pathway. They together form the cell-to-cell pathway. Many aquaporins are known to be highly expressed in roots [7,39–41], supporting a role of aquaporins in root water transport. Mercury ions (Hg^{2+}), which act as common aquaporin blockers by binding to Cys residues within or in the vicinity of the pore [42], were first used in tomato roots [43] and later on in various other species [44,45] to show that aquaporins can contribute to >70% of Lp_r. This figure was confirmed using other types of aquaporin inhibitors (azide, weak acids) which showed a very similar inhibition profile as mercury among natural accessions of Arabidopsis [45]. First genetic evidence for the contribution of a specific aquaporin to overall Lp_r was reported by Javot et al. [46]. These authors showed that *Arabidopsis* *At*PIP2;2 is highly expressed in several root cell types including endodermis, and that, by comparison to wild-type plants, the Lp_r of corresponding knock-out mutants (*pip2*;*2*) was reduced by 14%. More recently, Sutka et al. [45] reported that the transcript abundance of several PIPs (*AtPIP1*;*1*, *AtPIP1*;*2*, *AtPIP1*;*4*, *AtPIP2*;*1*, *AtPIP2*;*3*, *AtPIP2*;*4* and *AtPIP2*;*5*) in *Arabidopsis* roots is positively correlated with Lp_r, in good agreement with published genetic data. For instance, the Lp_r of *pip1*;*2* mutants and *pip2*;*1 pip2*;*2* double mutants was decreased by 20% and 40%, respectively, compared to that of wild type [47,48].

3.2. Leaf hydraulics

Aquaporins are also highly expressed in plant leaves, where they contribute to the hydraulic conductance of inner tissues [49–51]. First evidence for aquaporin function was obtained in sunflower leaves by inhibition experiments using $HgCl_2$ [52]. More recently, combined physiological and genetic approaches have indicated that, in *Arabidopsis* at least, the function of PIP aquaporins in leaf veins (xylem parenchyma and bundle sheath) critically determines leaf hydraulics [47,53,54]. However, the contribution of aquaporins to leaf hydraulic conductance (~25%) was much less than that in the roots (>70%) [45,47,55]. This indicates that vessels represent an important hydraulic limitation in leaves. The interplay between vascular and extra-vascular (mediated by aquaporins mostly) transport of water will deserve more physiological studies in the future.

3.3. Regulation of root and leaf hydraulics by aquaporins

Plants have the remarkable ability to sense various signals from the surrounding environment and accordingly adjust their water transport properties. For instance, many abiotic stresses imposed by soil, such as salinity, oxygen deprivation or nutrient starvation, markedly reduce Lp_r in various plant species [56]. Irradiance and the stress hormone abscisic acid (ABA) both act as potent regulators of stomata-mediated transpiration and also regulate aquaporin-dependent leaf hydraulic conductance. Recent studies in *Arabidopsis* have established the involvement in light-dependent leaf hydraulic conductance of a single

aquaporin isoform (*At*PIP2;1) expressed in veins [54]. Moreover, root hydraulic conductance was found to be positively correlated with the size of the shoots among *Arabidopsis* natural accessions [57], and recent evidence indicated that in poplar, root conductance can be regulated according to the transpiration demand from shoots [58]. Thus, complex aquaporin regulation mechanisms are at work in both roots and shoots. The following section addresses the molecular and cellular mechanisms involved.

4. Modes of aquaporin regulation

4.1. Cotranslational and posttranslational modifications

Application over the last 10 years of well-developed proteomics and mass spectrometry techniques have led to a comprehensive description of cotranslational and posttranslational modifications of plant aquaporins in their native membranes [54,59–61]. Combined with *in vivo* and *in vitro* labeling studies, these approaches have indicated that PIP1s and PIP2s from various species can be phosphorylated at multiple sites on the N-terminal or C-terminal tail, respectively. In addition, various environmental conditions such as drought, salinity or oxidative stresses induce quantitative changes in PIP, TIP or NIP phosphorylation [20,59,61–63]. However, knowledge of the protein kinases and protein phosphatases determining reversible aquaporin phosphorylation is still scarce [64,65]. Whereas aquaporin phosphorylation is very common, glycosylation was identified in only a few homologs such as soybean *Gm*NOD26 and a TIP from *Mesembryanthemum crystallinum* (ice plant) [66,67]. First evidence for methylation in aquaporins, and even plant membrane proteins, was obtained with *Arabidopsis* *At*PIP2;1, Lys3 and Glu6 of which were di- and monomethylated, respectively [68]. Altogether, these studies suggest that intricate co- and post-translational regulation mechanisms regulate plant aquaporins (Fig. 1). However, we are far from having a comprehensive view of how the numerous environmental or hormonal signals that intervene during plant growth and development target, in time and space, the multiple aquaporin isoforms expressed throughout the plant.

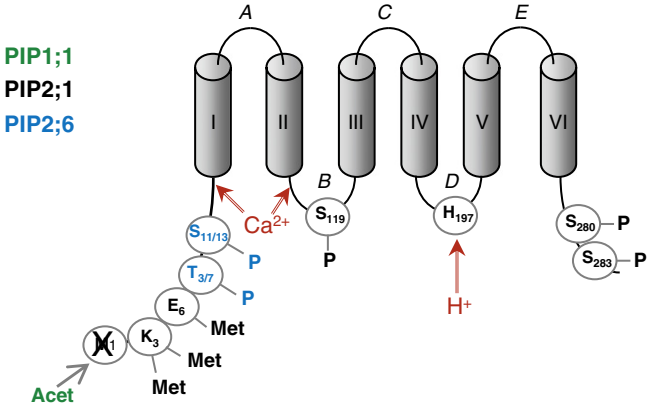

Fig. 1. Multiple post-translational regulations of PIP aquaporins in *Arabidopsis*. The figure shows a schematic representation of a PIP aquaporin with its 6 transmembrane domains (I to VI), five connecting loops (*A*–*E*), and N- and C-terminal tails bathing in the cytosol. Covalent modifications indicated in green, black and blue concern *At*PIP1;1, *At*PIP2;1 and *At*PIP2;6, respectively. The modification profiles of *Arabidopsis* PIPs were mostly determined by mass spectrometry: in *At*PIP2;1, the initiating Met residue is co-translationally cleaved (cross) whereas in *At*PIP1;1 this residue is N-α-acetylated (Acet). Di-methylation (Met Met) of Lys3 (K_3), mono-methylation (Met) of Glu6 (E_6), and phosphorylation (P) of Ser280 (S_{280}) and Ser283 (S_{283}) have been established experimentally. By contrast, the phosphorylation of loop *B* at Ser119 (S_{119}) was inferred from studies on spinach *So*PIP2;1 [33,63]. According to PhosPhAt database (http://phosphat.mpimp-golm.mpg.de/), the N-terminal tail of *At*PIP2;6 is phosphorylated at Thr3 (T_3) and/or Thr7 (T_7) as well as at Ser11 (S_{11}) and/or Ser13 (S_{13}). Because each of the indicated phosphorylation and methylation site can be found in its unmodified or modified form, a great variety of modified forms can be anticipated for PIPs. In addition to covalent modifications, PIPs are post-translationally regulated (gated) by calcium (Ca^{2+}) and protons (H^+) [55,70,71]. Their sites of action (binding) are shown.

4.2. Gating

The gating of plant aquaporins, that is, the opening and closing of the water channel pore, can be regulated by multiple effectors, such as phosphorylation, protons (H^+), and divalent cations. An activating role for phosphorylation was first proposed for pea *Pv*TIP3;1, *Gm*Nod26 and spinach *So*PIP2;1, based on functional expression in oocytes of wild-type and phosphorylation mutant forms, together with alterations of oocyte protein phosphatase and/or kinase activities [59,63,69]. Water transport assays in purified plasma membranes from *Arabidopsis* and sugar beet (*Beta vulgaris*) also indicated that H^+ and divalent cations, with calcium (Ca^{2+}) being the most efficient, can regulate the activity of PIPs [70,71]. These effects were further established after reconstitution of purified *At*PIP2;1 in proteoliposomes [72]. Furthermore, the sidedness and molecular bases of H^+-dependent gating were dissected using *Xenopus* oocyte expression and the central role as pH sensor of a His residue, perfectly conserved in the second cytosolic loop (loop *D*) of PIPs, was established [55] (Fig. 1).

The X-ray structures of SoPIP2;1 in an open and closed conformation [33] were crucial in determining a conserved molecular mechanism for PIP gating. In brief, the model showed how a hydrophobic (Leu) residue of loop *D* can protrude in the cytosolic pore vestibule, to prevent any passage of water. The conformation of loop *D* itself is determined by ionic and H-bond interactions between residues of loops *D* (His193) and *B* (Ser115) and the N-terminal tail (Asp28, Glu31). Divalent cations binding to Asp28 and Glu31 or protonation of loop *D* at His193 can tighten this interaction, locking the water channel in a closed state. By contrast, phosphorylation of Ser115 in loop *B* or Ser274 in the C-terminus favors the unfolding of loop *D* to open the water channel.

4.3. Cellular trafficking

Regulated trafficking also plays a key role in plant aquaporin expression and regulation. PIP1s have been described since long as having no or a weak water transport activity when individually expressed in *Xenopus* oocytes. This can be explained by a failure to traffic properly to the oocyte plasma membrane [22], this defect being overcome after co-expression with PIP2 homologs. Direct evidence for a physical interaction between PIP1s and PIP2s was obtained in oocytes or plants by affinity copurification, coimmunopurification and fluorescence resonance energy transfer (FRET) methods [22,23]. Thus, formation of heterotetramers comprising various PIP1 and PIP2 combinations may be crucial for proper localization of PIPs at the surface of plant cells.

Stimulus-induced subcellular trafficking of plant aquaporins was first characterized in ice plant *Mc*TIP1;2. This aquaporin was found to be redistributed from tonoplast to intracellular vesicles during osmotic stress by a glycosylation-dependent mechanism [67]. Regulated trafficking of PIPs and TIPs was also proposed to play an important role during root response to salt and oxidative stresses [24,25]. Following treatment of *Arabidopsis* roots with 100 mM NaCl for 4 h or with 2 mM H_2O_2 for 15 min, Lp_r was inhibited by >70% and an intracellular relocalization of several highly expressed plasma membrane and tonoplast aquaporins was observed [39]. Further studies showed that the salt-induced relocalization of PIPs is mediated by reactive oxygen species (ROS)-activated cell signaling cascades. In addition, the role of *At*PIP2;1 phosphorylation at Ser283 in directing the protein to a specific endosomal (prevacuolar) compartment was demonstrated [20,73]. Advanced fluorescence microscopic approaches have recently brought deeper insights into the effects of salt on the membrane dynamics of PIPs in root epidermal cells. Variable-angle

evanescent wave microscopy indicated that the diffusion rate of a PIP2;1-GFP fusion at the cell surface was increased by 2-fold by salt stress, whereas fluorescence correlation spectroscopy revealed that PIP2;1-GFP density in the plasma membrane was decreased by 46% [74]. Moreover, a novel Fluorescence Recovery After Photobleaching (FRAP) approach indicated that salt stress enhances PIP cycling between the cell surface and endosomes, by acting on both endocytosis and exocytosis [75,76]. The cellular mechanisms that govern the surface diffusion and cycling of PIPs are still undetermined.

5. Aquaporins and plant nutrient acquisition

5.1. Mineral nutrient uptake

Boron is an essential element for plant growth, which, however, can be toxic when present at high concentrations. A role of aquaporins in boric acid transport was first proposed by Dordas et al. [77]. These authors showed that plasma membrane vesicles purified from squash roots had boric acid permeability, which was 6-fold higher than that of microsomal vesicles, and was partly inhibited by $HgCl_2$. *At*NIP5;1 represents the first aquaporin shown to play a significant contribution to boron uptake in plants. Its gene is strikingly induced in response to boron deficiency and boric acid transport activity of the protein was demonstrated after oocyte expression or using *nip5;1* knock-out plants [11]. Later on, *At*NIP6;1 and *At*NIP7;1, which are selectively expressed in leaf nodes and floral anthers, respectively [78,79], were also identified as boric acid channels. Takano et al. [79] proposed a cooperative boron transport mechanism whereby *At*NIP5;1 absorbs boric acid [$B(OH)_3$] from the soil, whereas *At*BOR1 serves a secondary active efflux transporter of borate [$B(OH)_4^-$] [80], to load boron into the xylem. In accordance with this model, *Arabidopsis* plants were conferred with enhanced tolerance to low boron concentrations by functional activation of both *At*NIP5;1 and *At*BOR1. Conversely, tolerance of a barley cultivar to high boron toxicity was associated to low expression of a NIP homolog [81].

Silicon is another major mineral component for certain plants including cereals (it can account for 10% of shoot dry weight in rice), where it enhances resistance to abiotic and biotic stresses [82,83]. A forward genetic approach in rice identified *Lsi1* (*Os*NIP2;1) as the first silicon transport protein of plants [10]. *Os*NIP2;1 and its maize homolog (*Zm*NIP2;1) are both localized on the distal sides of exodermal and endodermal root cells. *Os*NIP2;1 functions as an influx channel for silicic acid and works in concert with the efflux transporter Lsi2, to facilitate silicon uptake from the soil into the root stele and vascular tissues [10,84]. Another silicic acid-transporting NIP homolog (Lsi6 or *Os*NIP2;2) exhibits a polar localization in xylem transfer cells of rice nodes and may play a role in xylem unloading of silicon to enhance transfer into panicles [85]. In *Arabidopsis*, silicon also plays a role in resistance to fungal pathogen [86]. However, phylogenetic or structural analyses did not reveal any clear functional homologs of cereal silicic acid channels (*Os*NIP2;1, *Zm*NIP2;1, *Zm*NIP2;2) among *Arabidopsis* NIPs [35,87]. Thus, it will be interesting to investigate whether NIPs can similarly function as silicic acid transporters in dicot plants.

5.2. Ammonia transport

Ammonium/ammonia (NH_4^+/NH_3) is an important nitrogen fertilizer for crops. Whereas NH_4^+ transporters have been identified in plants since long, NH_3 was initially suggested to cross membrane by free diffusion [88]. Yet, several TIP2 homologs of *Arabidopsis* and wheat were found to have a remarkable permeability to NH_3, and may therefore participate in NH_3 compartmentalization in vacuoles [88–90]. This idea remains to be assessed at the whole plant level and, for instance, overexpression of *At*TIP2;1 or *At*TIP2;3 in *Arabidopsis* failed to enhance whole plant NH_4^+/NH_3 accumulation [90].

The symbiotic interaction of plants with soil microorganisms may provide an interesting context to understand the role of aquaporins in plant NH_4^+/NH_3 acquisition. Firstly, mycorrhizal symbiosis causes significant changes in aquaporin expression in host plants [91–93] and specific aquaporins of legumes, such as *Gm*NOD26, are expressed in the peribacteroid membrane of N_2-fixing root nodules [3]. Secondly, recent work has demonstrated that *Gm*NOD26 is a NH_3-transporting aquaporin that binds cytosolic glutamine synthase to create a metabolite funnel and possibly enhance ammonia assimilation efficiency [94,95]. Thirdly, some of fungal aquaporins expressed in ectomycorrhiza showed a high NH_3 permeability [96], and could contribute to NH_3 export from the fungal cytoplasm into the plant apoplasm. Interestingly, a high-affinity NH_4^+ transporter was found to be specifically expressed in arbuscular mycorrhizal (AM) roots of *Lotus japonicus* [97]. The interplay between these two types of NH_4^+ or NH_3 transport proteins may provide a basis to explain the fungus-based nitrogen nutrition of plants in symbiotic roots.

5.3. CO_2 transport

Several lines of evidence suggest that aquaporins may contribute to CO_2 diffusion within leaf tissues, to favor its transfer from the atmosphere to the sites of photosynthetic carboxylation in the mesophyll cell chloroplasts. The first evidence was that CO_2-dependent photosynthesis and deduced mesophyll conductance to CO_2 in *Vicia faba* and *Phaseolus vulgaris* (French bean) leaves were reversibly inhibited by a $HgCl_2$ treatment [98]. In addition, *Nt*AQP1 and *At*PIP1;2 were shown to facilitate CO_2 transmembrane transport after heterologous expression in *Xenopus* oocytes or yeast cells [99,100]. Genetic alteration of their function in tobacco or *Arabidopsis* plants revealed a positive correlation between their expression and mesophyll conductance to CO_2 [99,101]. There have been concerns, however, that with respect to cell walls and carbonic anhydrases, the contribution of membranes to mesophyll conductance to CO_2 may not be predominant [102]. We also note that both *Nt*AQP1 and *At*PIP1;2 significantly contribute to whole plant water transport [47,103]. This suggests a fine interplay between CO_2 and H_2O transport in inner leaf tissues. Also, it cannot be excluded that hydraulic alterations in plant aquaporin mutants exerts indirect effects on mesophyll conductance to CO_2.

6. Aquaporins and plant development

Seeds play a crucial role in the reproductive cycle and dissemination of higher plants. Most seeds are highly desiccated organs, and extensive and well-defined water exchanges are associated with seed maturation and germination, the latter process including seed imbibition and subsequent embryo growth [104]. A fine regulation of aquaporin expression during these processes has been described in many species, including ice plant and *Brassica napus* [105,106]. In particular, TIP3s of all plant species examined show seed-specific expression and their abundance markedly decreased during germination [107–110]. TIP3 expression may accompany the massive deposition of storage proteins, oligosaccharides and phytins in protein storage vacuoles during late seed development [111]. In *Arabidopsis* and pea, mercury derivatives reduced the rate of seed germination and seed imbibition, respectively [110,112], suggesting a role of aquaporins in these processes. To date, clear genetic evidence for a role of aquaporins in seed germination has only been provided in rice using transgenic plants with loss- and gain-of-function of *Os*PIP1;3. Gene expression studies further indicated that this aquaporin may mediate the effects of NO on seed germination [113].

A strong link between aquaporin expression, cell expansion and plant growth has emerged in recent years. For instance, the expression pattern of the *AtTIP1;1* promoter in *Arabidopsis* is correlated with cell enlargement in roots, hypocotyls, leaves and flower stems [114], and *AtTIP1;1* expression was induced by the growth-promoting

phytohormone gibberellic acid (GA_3) [115]. *At*TIP1;1 may be involved in the exchange of water and solutes across the tonoplast, during the formation of the large central vacuoles of mature cells. Numerous studies using transgenic plants also point to a positive role of aquaporins in plant growth. For instance, over-expression of *Arabidopsis At*PIP1;2 in tobacco and of *Panax ginseng Pg*TIP1 in *Arabidopsis* significantly increased plant growth [116,117]. Whereas these results may suggest that growth was hydraulically limited in these materials, we cannot exclude that altered aquaporin expression resulted in stomatal deregulation or enhanced mesophyll conductance to CO_2, thereby promoting carbon fixation and plant growth. In line with the former hypothesis, the transgenic tobacco plants overexpressing *At*PIP1;2 showed enhanced leaf dehydration under drought stress conditions [117].

A recent work on the role of PIPs during lateral root emergence [48] provides a more complete dissection of the role of aquaporins in plant tissue growth. The hormone auxin, which orchestrates root growth and development, was found to dramatically down-regulate the transcription of nearly all of *PIP* and *TIP* genes in the *Arabidopsis* root, thereby providing a fine control of aquaporin expression at the sites of lateral root emergence. The hormone also inhibited water transport at the cell and whole root levels. Aquaporin mutant analysis allowed demonstrating the role of several aquaporin isoforms in facilitating root emergence. A mathematical model was elaborated showing how aquaporin regulation favors water influx into the root primordium, which thereby forces its way through the surrounding layers of cells in the main root [48]. Thus, plant roots appear to use auxin to regulate aquaporins and therefore fine-tune water flow to speed up lateral root emergence.

7. Aquaporins and response to abiotic stresses

7.1. Plants under multiple environmental stresses

Maintaining their water balance under adverse conditions is a formidable challenge for land plants. Under dry air, windy and/or high temperature conditions, for instance, the evaporative demand is markedly increased. Depending on plant species and physiological contexts (*e.g.* availability or deficit of water in the soil), transpiration can either be restricted through stomatal closure or maintained to favor CO_2 uptake and lower leaf temperature. In the latter case, the hydraulics of roots and leaves should not be non-limiting to prevent plant dehydration. This example illustrates how plant water transport has to constantly adapt to a variable environment and various kinds of abiotic stresses. Thus, one major objective of current research is to identify the signaling mechanisms that govern the regulation of aquaporin expression and activity in plants under stresses. Several types of signaling molecules involved are shown in Fig. 2 and discussed below.

7.2. Plant hormones

Plant hormones are important signaling molecules that play numerous vital roles in controlling plant hydraulics and growth under both favorable and stressful conditions. The drought-induced hormone ABA not only induces stomatal closure, but also regulates plant aquaporin function in the whole plant. Treatment of plants with exogenous ABA [118–121], and the characterization of ABA-deficient and overproducing plants [122,123] have revealed positive effects of ABA on Lp_r. By contrast, ABA reduced the leaf hydraulic conductance in *Arabidopsis*, by down-regulating aquaporins in bundle sheath cells [47], with consistent reducing effects on phosphorylation of several PIP2s in *Arabidopsis* plantlets [124]. Hose et al. [125] were among the first to report that auxin (IAA) reduces the hydraulic conductivity of root cortical cells. Recent studies in *Arabidopsis* indicated that IAA acts through an Auxin Response Factor 7 (ARF7)-dependent path to inhibit the expression of most PIPs at both transcriptional and translational levels [48]. ARF7 was previously identified as one of the major transcription factors involved in auxin-regulated hypocotyls growth and lateral root development. Salicylic acid, a hormone induced by pathogen attack and abiotic stresses, acts similar to salt and down-regulates PIP aquaporins and Lp_r by a ROS-mediated mechanism [73,126]. Other growth-promoting hormones such as GA3 and brassinolides also regulate aquaporin expression [127,128], but by as yet unknown mechanisms.

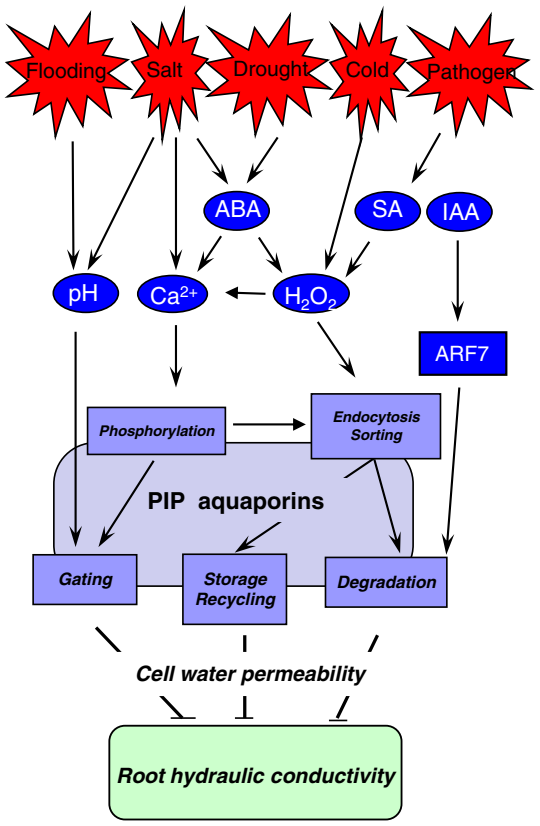

Fig. 2. Signaling diagram of root hydraulic conductivity (Lp_r) regulation under various stress conditions. Lp_r is repressed by various stresses (*e.g.* flooding, salt, drought, cold or pathogen attack), which effects are mediated by phytohormones (ABA, SA) [56,126] or signaling intermediates (cytosolic pH, Ca^{2+} and H_2O_2) [55,70,71,73]. These signals can alter the modification status (for instance, phosphorylation) and/or the sub-cellular dynamics (endocytosis and intracellular sorting) of PIP aquaporins. These mechanisms determine the gating, storage and recycling, or degradation of PIPs, and ultimately root cell hydraulic conductivity. Recently, it was reported that auxin (IAA) down-regulates Lp_r, through a pathway involving the auxin response factor-7 (ARF7) [48]. For the sake of simplicity, the transcriptional up- or down-regulation of specific PIP isoforms by several of the indicated stresses or hormones is not shown.

7.3. Ca^{2+} and pH

Cytosolic Ca^{2+} and pH, which function as potent regulators of plant aquaporins, are crucial signaling intermediates in plant responses to stresses and hormones. For instance, soil flooding results in an oxygen deprivation in roots, which traps cells in a deep cytosolic acidosis, and thereby inhibits Lp_r by proton-dependent gating of PIPs [55]. The effects of Ca^{2+} seem to be more diverse and contribute to multiple signaling cascades. For instance, an exogenous supply of Ca^{2+} enhanced the stimulation of sunflower Lp_r by ABA [129], and counteracted its inhibition by salt stress in maize and melon [130,131]. Whereas structure–function analyses have elucidated the mode of Ca^{2+} and proton-dependent gating of PIPs [33,55,70], the numerous Ca^{2+}-dependent protein kinases that exist in plant certainly provide additional regulation mechanisms that need to be elucidated.

7.4. H_2O_2

This ROS is a by-product of plant metabolism which can be toxic at high (mM) concentrations. At lower concentrations, it can serve as a signal molecule during plant response to various stresses, including salt, drought and cold. In addition to being a putative substrate of certain aquaporins [26], H_2O_2 is a potent inhibitor of aquaporins and root water transport. For instance, exogenous H_2O_2 reduced cell and/or root water conductivity in cucumber, maize, and *Arabidopsis* [73,132,133]. Whereas H_2O_2 was proposed to gate algal aquaporins by a direct oxidation mechanism [134], this compound was not able to inhibit *Arabidopsis* aquaporins after expression in *Xenopus* oocytes. In *Arabidopsis* roots, H_2O_2 rather acts through signaling pathways involving a Ca^{2+} influx, phosphorylation events, and leading to relocalization of PIPs in intracellular vesicles [73]. However, this response seems to vary according to species and for instance, no effect of exogenous H_2O_2 on L_{p_r} was observed in maize or figleaf gourd (*Cucurbita ficifolia*) [132,135] whereas a low exogenous H_2O_2 concentration increased L_{p_r} in French bean [136].

7.5. Aquaporins and plant resistance to abiotic stresses

As discussed above, exposure of plants to abiotic constraints as diverse as soil water deficit or dry air, heat or cold stress, ionic stress or nutrient deprivation, or changes in irradiance challenge the plant water status and trigger highly specific hydraulic responses [27,56]. Molecular analyses on regulation of the whole aquaporin family in these contexts have often revealed complex transcriptional and post-translational response patterns, with sometimes opposite profiles between isoforms. Genetic approaches have been developed, as a complement of these expression studies. However, they also led to somewhat contrasting results, depending on the plant species or stress conditions investigated. For instance, antisense inhibition of PIP1s in transgenic tobacco plants reduced L_{p_r} and leaf water potential, and enhanced plant sensitivity to drought stress [137]. In contrast, inhibition of PIP1s and/or PIP2s using a similar antisense approach in *Arabidopsis* did not modify leaf water potential and hydraulic conductivity in plants under normal or water deficit conditions. After rewatering, however, the recovery of leaf water potential and plant hydraulic conductivity was significantly delayed in antisense as compared to wild-type plants [138]. These data indicate that PIPs can play an important role during the early phase of water stress, by acting on root water transport (a transient ABA-mediated increase in L_{p_r} can be observed before a longer term inhibition), or during recovery from water stress, by favoring water mobilization in dehydrated leaves.

Overexpression of aquaporin genes has become a widely used strategy to understand and possibly engineer plant water relations under stress. Numerous studies have shown that enhancing aquaporin expression can confer on transgenic plants either a higher resistance [116,139–143], or a higher sensitivity [117,144,145] to stresses. Remarkably, negative effects on stress resistance were rather seen when an aquaporin of interest was over-expressed in a heterologous plant species [117,144,145]. We speculate that the foreign aquaporin may not be properly recognized by the endogenous stress response machinery. Among the few success stories, we may cite the case of *Os*PIP1;3, which is induced by water-deficit in a drought-resistant rice cultivar. Its expression in a lowland drought-sensitive rice cultivar, using a stress-induced promoter, significantly enhanced plant water stress resistance [142]. Spectacular results were also obtained with *Sl*TIP2;2, a stress-induced aquaporin of tomato [146]. Its over-expression in the same species dramatically altered plant water relations, enhancing transpiration and modifying leaf water potential maintenance under drought. Nevertheless, the transgene had beneficial effects on plant growth and fruit yield under both control and water stress conditions.

Despite these punctual successes, aquaporin manipulation will not be sufficient for developing optimal stress-resistant genotypes. Whereas beneficial effects may be observed in certain conditions, it will be difficult to optimize plant growth in a wide range of climatic scenarios. In addition, targeting other genes and functions that may be needed to avoid or repair the damage caused by the stresses has been proposed [132,147]. The most relevant genes are those involved in antioxidant metabolism, or encoding heat-shock proteins and stress-responsive transcription factors.

8. Conclusions

During the last twenty years, tremendous progresses have been achieved in understanding the structure and function of plant aquaporins. The realization that plant aquaporins transport water but also many other physiological substrates has contributed to the great expansion of this research field. As a result, specific aquaporin isoforms were identified for their contribution to physiological and developmental processes as diverse as seed germination, regulation of leaf and root hydraulics, lateral root emergence but also carbon fixation or nutrient absorption. Yet, we are still far from a fully integrated view. Aquaporins show a particularly high molecular diversity in plants and the function of many isoforms, even in the most studied model species (*Arabidopsis*, rice), is as yet undetermined. In addition, each aquaporin often contributes, in concert with other isoforms, to several physiological functions. Thus, thorough cell-specific expression analyses of the whole plant aquaporin family, in plants under optimal or stress conditions, are still needed. Reverse genetic analyses of aquaporins in plants require sharp phenotyping procedures and careful examination of possible genetic redundancies. However, they provide a necessary functional dimension to these integrative studies.

Understanding the multiple molecular and cellular mechanisms that govern aquaporin regulation will also require more research efforts. At present, we know that numerous co- and post-translational modifications, and molecular interactions involving distinct aquaporin isoforms and regulatory proteins act, together with signaling intermediates such as cytosolic H^+ and Ca^{2+}, to regulate aquaporin gating and subcellular trafficking. However, these mechanisms often need to be placed in their genuine cellular context. The upstream signaling events and their cross-talks during plant cell response to hormone or environmental stimulations are also largely unknown.

Another important avenue for future studies is the role of aquaporins in plant growth. Understanding how aquaporins can hydraulically control tissue expansion, as recently discovered in lateral roots, will deserve a specific attention. Also, many reports indicate that some aquaporin genes can to some extent improve the resistance of transgenic plants to adverse environmental conditions, whereas others have opposite effects. Further analyses of the mechanisms behind may improve our knowledge on the role of aquaporins in plant stress responses.

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