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► **To cite this version:**

Christophe Maurel, Colette Tournaire-Roux, Lionel Verdoucq, Véronique Santoni-Kervella. Hormonal and environmental signaling pathways target membrane water transport. *Plant Physiology*, 2021, 10.1093/plphys/kiab373 . hal-03440937

HAL Id: hal-03440937

<https://hal.science/hal-03440937>

Submitted on 28 Nov 2022

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1 *Special issue on Transport and signaling*

2 **Short title: Signaling pathways target membrane water transport**

3 **Corresponding author:** Christophe Maurel: christophe.maurel@cnrs.fr

4 **Hormonal and environmental signaling pathways target membrane**
5 **water transport**

6 **Christophe Maurel, Colette Tournaire-Roux, Lionel Verdoucq, and Véronique Santoni**

7 BPMP, Univ Montpellier, CNRS, INRAE, Institut Agro, Montpellier, France.

8 **ORCID IDs:** 0000-0002-4255-6440 (CM); 0000-0002-2966-5597 (C. T.-R); 0000-0001-8238-3700 (L.V.);

9 0000-0002-1437-0921 (V.S.);

10 **Materials distribution statement:**

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12 accordance with the policy described in the Instructions for Authors

13 (<https://academic.oup.com/plphys/pages/General-Instructions>) is: _

14 Christophe Maurel (christophe.maurel@cnrs.fr).

15 **One-sentence summary:** This paper describes the multiple signaling pathways targeting cell
16 and tissue hydraulics to maintain the plant water status, and it reveals the commonalities of these
17 pathways.

18 **Author contributions:** All authors contributed to the literature survey. CM wrote the article
19 which was revised by all other authors. C. T.-R., L.V. and V.S. designed the figures and table.

20 **Funding information:** This work was supported in part by the Agence Nationale de la
21 Recherche (ANR- 18-CE92-0055)

22 **Introduction**

23 As elaborate terrestrial living organisms, vascular plants have to maintain their water status as tightly
24 as possible and throughout their life cycle (Davies and Bennett 2015; Steudle 1992). Particularly
25 challenging processes include the expansion/growth of underground and aerial parts and the
26 desiccation, imbibition and germination of seeds and pollen. Most often, these processes occur
27 under variable environmental conditions, including changes to water availability and temperature in
28 the soil and atmosphere, which have marked impacts on the plant water status. The latter is
29 primarily maintained through tight stomatal regulation controlling transpirational water flow
30 (Tardieu et al. 2015). Osmotic adjustment and regulation of water permeability (hydraulics), which
31 both contribute to water potential gradients and water movement intensity, provide a
32 complementary and finely-tuned regulation of plant water relations at the cell and tissue levels. In
33 support for these general principles, a large body of studies has shown that plant water transport
34 and its molecular components are responsive, across diverse time scales, to an extremely wide array
35 of environmental and hormonal signals (Maathuis et al. 2003; Maurel et al. 2015; Chaumont et al.
36 1998; Aroca et al. 2012). Thus, plant water relations are under constant adjustment in virtually any
37 physiological context.

38 Plant aquaporins, which are present in the plasma and intracellular membranes of most plant
39 cells, play a central role in these processes by ensuring cell-to-cell water transport and to a lesser
40 extent, single cell osmotic regulation (Maurel et al. 2015; Chaumont and Tyerman 2014; Tyerman et
41 al. 1999). More generally, aquaporins have emerged as central membrane targets of environmental
42 and hormonal signalling pathways acting on plant water relations. In addition, aquaporins are highly
43 abundant proteins amenable to biochemical (proteomic) and cell biological approaches. Besides
44 studies in the plant, their function and regulation can be easily studied after functional reconstitution
45 (proteoliposomes) or heterologous expression (yeast, *Xenopus* oocytes). Thus, aquaporins are
46 particularly relevant and convenient entry points for bottom up dissections of plant signalling
47 cascades.

48 Due to the central position of aquaporins in multiple hormonal and environmental responses
49 determining the plant water status, the first aim of the present review was to inventory
50 corresponding signalling pathways. Beyond the diversity of these pathways, a knowledge network
51 with common or converging paths is now emerging. Conversely, the dedicated study of signalling
52 pathways per se seems to reveal regulation states/contexts that escaped classical physiological
53 analyses of plant water relations. A particularly challenging question is to understand how plants are
54 able to perceive and respond to combined stresses.

55 **1) Water deficit, abscisic acid (ABA) and related signals**

56 **1.1 Drought.**

57 **ABA-dependent pathways.**

58 Whereas physiological links between drought stress, ABA and plant water transport have been
59 identified for some time, it is only recently that the signalling mechanisms involved have started to
60 be elucidated. Studies on epidermal peels from wild-type and aquaporin knock-out Arabidopsis
61 (*Arabidopsis thaliana*) plants have revealed that the plasma membrane aquaporin Plasma Membrane
62 Intrinsic Protein 2;1 (*AtPIP2;1*) is required for ABA-induced stomatal closure, but dispensable during

63 light- and CO₂-induced stomatal movements (Grondin et al. 2015). Consistent with this, isolated
64 guard cell protoplasts responded to exogenous ABA by a two-fold increase in osmotic water
65 permeability that was strictly dependent on the functionality of *AtPIP2;1*. This aquaporin, which is
66 known to be permeable to H₂O₂ (Dynowski et al. 2008), was also required for ABA-induced
67 accumulation of H₂O₂ in the guard cell interior (Rodrigues et al. 2017). These studies establish a dual
68 water- and H₂O₂-transport function for guard cell plasma membrane aquaporins as players and
69 targets of signalling processes triggering stomatal closure (Grondin et al. 2015; Rodrigues et al. 2017).
70 More specifically, *in vitro* phosphorylation assays and transgenic plant analysis led to a model
71 whereby Snf1-related protein kinase 2.6 (SnRK2.6)/Open stomata 1 (OST1), a protein kinase that
72 plays a pivotal role in ABA signalling, is able to phosphorylate *AtPIP2;1* at a specific cytosolic Ser
73 residue (Ser121), with this phosphorylation being necessary for proper ABA-induced stomatal
74 closure. SnRK2.6/OST1 also activates plasma membrane NADPH oxidases, which feed superoxide
75 dismutases for production of apoplastic H₂O₂ (Maurel et al. 2016) (Figure 1A). While the above
76 mentioned studies were performed on epidermal peels of wild-type and *pip2;1* plants, we are
77 concerned that intact leaves of a quadruple *pip1;1 pip1;2 pip2;1 pip2;2* mutant showed normal
78 responses to ABA (Ceciliato et al. 2019). We hypothesize that integration of guard cells within whole
79 leaf physiology can compensate for the defects captured in isolated guard cells or protoplasts. We
80 also note that, in contrast to stomata, ABA can down-regulate aquaporin activity in bundle-sheaths
81 (Shatil-Cohen et al. 2011) and roots (Rosales et al. 2019). Whereas the canonical ABA signaling
82 machinery formed by RCAR/PYR/PYL receptors, Protein Phosphatase 2C (PP2C) co-receptors acting
83 on Class 2 Sucrose-Non-Fermenting Protein kinases (SnRK2s) is likely to be involved, in roots in
84 particular (Rosales et al. 2019), the exact components providing these hydraulic regulations remain
85 as yet unknown. Aquaporins and water transport can also be under ABA control through more
86 indirect pathways. In Arabidopsis, ABA induced the expression of the membrane protein Tryptophan-
87 rich sensory protein/translocator (TPSO), which physically interacts with *AtPIP2;7* in the early
88 secretory pathway, to trigger its degradation through the autophagic pathway, thereby reducing its

89 water transport activity at the plasma membrane (Hachez et al. 2014b). In rice (*Oryza sativa*), the
90 gene encoding a leucine-rich repeat (LRR) receptor like kinase (RLK) named Leaf Panicle 2 (LP2) is
91 down-regulated by drought and ABA, and acts a negative regulator of drought response (Wu et al.
92 2015). Its action involves a molecular interaction at the plasma membrane with the drought-
93 responsive aquaporins *OsPIP1;1*, *OsPIP1;3*, and *OsPIP2;3*.

94 **ABA-independent pathways**

95 Drought can also exert ABA-independent effects on aquaporin expression and function. For instance,
96 several aquaporin gene promoters harbour Drought Responsive Elements (DRE) that promote the
97 binding of DREB transcription factors (Rae et al. 2011). Other classes of transcription factors (*e.g.*
98 AP2/EREBP, ASR1) also confer drought-dependent expression on aquaporin genes (Zhu et al. 2014;
99 Ricardi et al. 2014). Furthermore, induction under severe drought of ubiquitin-conjugating (E2)
100 enzyme UBC32 and RING-type E3 ligase, which both interact with *AtPIP2;1* and *AtPIP2;2*, leads to
101 ubiquitination and degradation of these aquaporins, thereby preventing their negative impact on
102 drought tolerance (Chen et al. 2021).

103 A functional interaction between an aquaporin (*RhPIP2;1*) and a membrane tethered MYB
104 protein named *RhPTM* was recently described in rose (Zhang et al. 2019b). In brief, dehydration
105 stress induced C-terminal phosphorylation of *RhPIP2;1* at Ser273, which in turn led to membrane
106 release and nuclear activation of *RhPTM*. *RhPTM* itself acts as a transcription factor with general
107 growth inhibitory effects. This landmark work establishes an unexpected link between hydraulics and
108 a transcriptionally determined metabolic control of growth that promotes water deficiency
109 tolerance. Yet, the protein kinases/phosphatases that act on Ser273 of *RhPIP2;1* and their drought-
110 dependent activation/inhibition mechanisms remain to be identified. Similarly, some PIP aquaporins
111 of *Arabidopsis* (*e.g. AtPIP2;4*) show enhanced phosphorylation as early as 5 min after exposure to a
112 hypertonic stress (0.3 M mannitol) (Stecker et al. 2014).

113 Cell biological approaches are now developed to address associated regulatory mechanisms.
114 An improved super-resolution microscopic technique called single particle tracking Photo-Activated

115 Localization Microscopy (sptPALM) was used to monitor the lateral mobility of proteins at the plasma
116 membrane (LTi6a, AtPIP2;1) and tonoplast (AtTIP1;1) (Hosy et al. 2015). In contrast to the other
117 membrane proteins, AtPIP2;1 showed a low lateral mobility, was confined to membrane
118 nanodomains and its mobility was enhanced upon a hyperosmotic stress. sptPALM further showed
119 how reactive oxygen species (ROS) control specific diffusion and nano-organization of membrane
120 cargo proteins (Martiniere et al. 2019). In particular, ROS initiated clustering of AtPIP2;1 and its
121 removal from the plasma membrane. This process is achieved in part by clathrin-mediated
122 endocytosis. It is linked to further aquaporin internalization and transfer into the endocytic pathways
123 (Zwiewka et al. 2015). In the longer term, the same aquaporins are subjected to ubiquitination and
124 further degraded (Lee et al. 2009) in a phosphorylation-dependent manner (Chen et al. 2021). In
125 addition, a role of autophagic pathways was recently uncovered in *Medicago truncatula* under water
126 deficit (Li et al. 2020b). A dehydrin (*MtCAS31*) was shown to act as a cargo receptor for the *MtPIP2;7*
127 aquaporin. *MtCAS31* further promoted complex formation with the autophagy-related protein
128 ATG8a to facilitate *MtPIP2;7* degradation. This, in turn, reduced water loss under water deficit and
129 improved drought tolerance (Li et al. 2020b). The possible relation of this mechanism with the ABA-
130 dependent TPSO pathway (Hachez et al. 2014b) mentioned above is not yet clear.

131 Finally, a bottom-up approach was used to further explore the signaling mechanisms acting
132 upstream of aquaporins in the Arabidopsis root under hyperosmotic stress. A RESPIRATORY BURST
133 OXIDASE HOMOLOG (RBOH) pathway defined by two NADPH oxidases and an additional pathway
134 involving apoplastic ascorbate and iron were found to mediate osmotic stress-induced ROS
135 production (Martiniere et al. 2019). Furthermore, osmotic stress was shown to trigger interaction of
136 a Rho GTPase, Rho-of-Plant 6 (ROP6) with the two NADPH oxidases (Smokvarska et al. 2020). This
137 interaction occurs in specific plasma membrane nanodomains that are necessary and sufficient to
138 transduce production of ROS and several plant adaptive responses to osmotic constraints (Figure 1B).

139 **1.2 Salinity**

140 Under salt stress, PIP aquaporins are subjected to cellular regulations that are reminiscent of those
141 seen under a purely osmotic stress. In Arabidopsis roots for instance, a 100 mM NaCl treatment
142 decreased C-terminal phosphorylation at Ser283 of *AtPIP2;1* after 2-4 h (Prak et al. 2008). On a
143 shorter timescale (30 min), a salt treatment also enhanced the lateral diffusion of *AtPIP2;1* at the
144 plasma membrane (Li et al. 2011) and its constitutive cycling (Luu et al. 2012). These movements lead
145 to internalization of *AtPIP2;1* from the plasma membrane, and its transfer to the pre-vacuolar and
146 vacuolar compartments, a process that is mediated by ROS (Boursiac et al. 2008) (Figure 1B) and is
147 dependent on clathrin, phosphatidylinositol 3-kinase (PI3K) and phosphatidylinositol 4-kinase
148 (PI4K)(Ueda et al. 2016). These mechanisms may well be generalized: *AtPIP2;7*, another major
149 aquaporin isoform in the Arabidopsis root, showed a combined transcriptional down-regulation and
150 protein internalization that resulted in a dramatic decrease in cell and tissue hydraulics (Pou et al.
151 2016). As in the case of osmotic stress, the primary signalling events triggering salt-dependent
152 aquaporin regulation are not elucidated. Yet, salt-dependent expression of *AtPIP2;3* and *AtPIP2;5* is
153 in part mediated by SnRK2s of subclass 1 (Kawa et al. 2020). Some of these protein kinases (SnRK2.4,
154 SnRK2.10) interact with and phosphorylate VARICOSE (VCS) and VARICOSE RELATED (VCR) (Kawa et
155 al. 2020; Soma et al. 2017), two components of the mRNA decapping complex that catalyzes the first
156 step of mRNA decay.

157 A role of PIP aquaporins in ion transport, tentatively associated to the so-called Non Selective
158 Cation Channels described by patch clamp in many cell types, was recently proposed in Arabidopsis
159 and barley (Tran et al. 2020; Byrt et al. 2017). As thoughtfully discussed by (Tyerman et al. 2021), this
160 activity may well be central during plant response to salinity stress. The ionic conductance of
161 *AtPIP2;1* is repressed by calcium and strongly enhanced upon C-terminal phosphorylation (Qiu et al.
162 2020). In barley, *HvPIP2;8* shows similar regulation, and, in addition, its gene is induced in shoots of
163 salt stressed plants, specifically in a tolerant cultivar (Tran et al. 2020). The connections of these
164 regulatory processes to upstream salt stress signaling events and, possibly, to water transport
165 regulation remain to be investigated.

166 **2) Other abiotic constraints and stimuli**

167 **2.1 Oxygen availability**

168 Flooding stress, whether due to water logging or submergence, deeply impacts plant water relations
169 by favoring a massive inflow of water through roots while transpiration is directly or indirectly
170 impaired (Tan et al. 2018). Two pathways leading to aquaporin regulation have been uncovered in
171 this context (Maurel and Nacry 2020). On the short term, a pronounced cytosolic acidosis can be
172 observed under oxygen (O₂) deprivation due to the metabolic production of organic acids while a
173 drop in cellular respiration and ATP production hampers efficient proton (H⁺) extrusion by H⁺-
174 ATPases. This in turn induces protonation of a His residue located on the second cytosolic loop of
175 PIPs, triggering channel gating. It is remarkable that this His residue is perfectly conserved in PIPs of
176 all species, supporting the generality of the H⁺-dependent gating mechanism (Tournaire-Roux et al.
177 2003). We note that certain plant species do not show any effect of hypoxia on root hydraulic
178 conductivity (*L_{p,r}*). In the case of two lupin species (*Lupinus angustifolius*, *Lupinus luteus*), hypoxia
179 induced a marked inhibition of cortical cell hydraulic conductivity but had no substantial effect at the
180 whole root level, suggesting the predominance of an apoplastic pathway during water uptake
181 (Bramley et al. 2010).

182 The second pathway was recently uncovered through quantitative genetic analysis of
183 Arabidopsis root hydraulics. It is under the control of *Hydraulic Conductivity of Root 1 (HCR1)*
184 (Shahzad et al. 2016). HCR1 mediates root responses to hypoxia in relation to potassium (K⁺)
185 availability, thereby acting as a negative regulator of *L_{p,r}* and root aquaporins. HCR1 encodes a RAF-
186 type MAP3K protein kinase that specifically accumulates in the presence of K⁺ and absence of O₂.
187 HCR1 enhances the abundance of RAP2.12, a key Ethylene Response Factor (ERF) VII transcription
188 factor that is stabilized under O₂ starvation and triggers the core anaerobic transcriptional response.
189 We have proposed that HCR1 phosphorylates RAP2.12 or one of its direct regulators in planta and

190 thereby potentiates the most early plant responses to O₂ starvation (Shahzad et al. 2016). However,
191 the mode of aquaporin down-regulation through this pathway has not been elucidated.

192 **2.2 Nitrogen (N)**

193 Nitrate (NO₃⁻) is the major inorganic N source absorbed by non-wetland plants and its uptake and
194 metabolism are tightly associated with water utilization. Whereas ammonium has a rather negative
195 effect on water absorption, NO₃⁻ was shown to enhance L_{pr} in multiple plant species. Although post-
196 translational regulation may also be involved, the increase in L_{pr} induced by NO₃⁻ was shown to
197 correspond to up-regulation of aquaporin expression (Gorska et al. 2008; Gloser et al. 2007). It has
198 also been disputed whether NO₃⁻ acts directly or through its assimilation products. In Arabidopsis,
199 the conserved L_{pr} response of a nitrate reductase mutant (*nia*) supports the first hypothesis (Li et al.
200 2016). Furthermore, characterization of various Arabidopsis genotypes, altered in NO₃⁻ transport,
201 assimilation, or signaling and growing under various N supply conditions revealed a strong positive
202 relationship between L_{pr} and NO₃⁻ accumulation, but in shoots rather than in roots (Li et al. 2016).
203 This suggests a control of L_{pr} by putative long-distance signals generated in the shoots. Such systemic
204 regulation of aquaporins was also observed in split-root experiments with rice plants subjected to
205 heterogeneous NO₃⁻ treatments (Ishikawa-Sakurai et al. 2014). We also note that L_{pr} regulation by
206 transpiration or wounding (Laur and Hacke 2013; Ishikawa-Sakurai et al. 2014; Liu et al. 2014;
207 Vandeleur et al. 2014) may also be mediated by shoot-borne signals acting on root hydraulics.

208 Although NRT1.1 is considered as the major NO₃⁻ sensor, the high-affinity nitrate transporter
209 NRT2.1 is also thought to have a signaling role. In contrast with *nrt1.1* plants, *nrt2.1* plants showed a
210 pronounced reduction in L_{pr} , by up to 30% (Li et al. 2016). Surprisingly, this regulation was
211 independent of NO₃⁻ and hence, of *NRT2.1* expression level. Thus, the signalling mechanisms involved
212 in this newly discovered pathway remain fairly mysterious.

213 **2.3 Cold**

214 Both moderate cold and freezing challenge the plant water status. For instance, low temperature,
215 which reduces L_p , due to a higher viscosity of water and aquaporin down-regulation, causes water
216 deficit and growth arrest in leaves (Lee et al. 2012). In maize, aquaporins seems to play a key role in
217 the recovery of L_p that is specifically observed in chilling tolerant genotypes (Aroca et al. 2005).
218 Similarly, cold acclimation of Arabidopsis seedlings is accompanied by upregulation of two specific
219 PIP genes (*AtPIP1;4*; *AtPIP2;5*) (Rahman et al. 2020), which also show mRNA accumulation in leaves
220 under water deficit (Alexandersson et al. 2005). In rice, proper expression and function of Calcium-
221 dependent Protein Kinase (CDPK) *OsCPK17* appears to be key for plant adaptation to low
222 temperature stress (Almadanim et al. 2017). A comparative phosphoproteomic approach further
223 identified *OsPIP2;1* and *OsPIP2;6* as putative targets of *OsCPK17*. A direct activation by *OsCPK17* is
224 further supported by *in vitro* assays showing that the two aquaporins can be phosphorylated by the
225 protein kinase in a calcium-dependent manner. Since *OsCPK17* also targets sugar metabolism, it was
226 proposed that cold stress-activated *OsCPK17* phosphorylates *OsPIP2;1* and *OsPIP2;6* to coordinate
227 membrane water transport with cell osmotic regulation (Almadanim et al. 2017).

228 **2.4 Circadian control.**

229 The circadian clock allows the fine tuning and synchronization of key physiological, metabolic and
230 signaling pathways, in phase with daily variations of environmental parameters. While circadian
231 regulation of tissue hydraulics has been largely documented (Henzler et al. 1999), it is only recently
232 that the corresponding modes of aquaporin regulation have been investigated. In roots of
233 Arabidopsis and maize, the control of aquaporin expression seems to be largely transcriptional and
234 depends on well-identified clock components such as ELF3 (Takase et al. 2011; Caldeira et al. 2014).
235 In maize, the oscillation amplitude of aquaporin expression and plant hydraulic conductance was
236 strongly enhanced under water deficit, while oscillating expression of the core circadian clock genes
237 was not altered (Caldeira et al. 2014). Interestingly, this specific potentiation of the hydraulic
238 outputs, which possibly depends on ABA, appears to be beneficial for cumulated plant growth under

239 water deficit whereas steady tissue hydraulic properties are more appropriate under water replete
240 conditions. These data show how adaptive responses of plant hydraulics to specific environmental
241 variations rely on exquisite coupling to endogenous signalling mechanisms.

242 In contrast with roots, the circadian control of leaf hydraulics seems to be mediated through
243 post-translational modifications of proteins (Prado et al. 2019; Choudhary et al. 2015). In particular,
244 the rosette hydraulic conductivity (K_{ros}) of *Arabidopsis* shows circadian oscillations with a peak at
245 midday, in phase with quantitative variations of PIP2 aquaporin phosphorylation (Prado et al. 2019).
246 Remarkably, this modification is necessary but not sufficient for circadian control of K_{ros} , which
247 requires the additional contribution of 14-3-3 proteins (Prado et al. 2013; Prado et al. 2019). Two of
248 these (GRF4, GRF10) can physically interact with *AtPIP2;1* and modulate its function in *Xenopus*
249 oocytes depending on the phosphorylation status of the aquaporin C-terminal tail, with more
250 pronounced effects on phosphomimetic than on phosphodeficient forms (Prado et al. 2019). Much
251 remains to be learned about the protein kinase/protein phosphatase machinery that ensures
252 oscillations in aquaporin phosphorylation and, possibly, a synchronized activation of 14-3-3 proteins.

253 **3) A multiplicity of endogenous signals**

254 **3.1 Auxin.**

255 Transcriptomic analyses in *Arabidopsis* have revealed a dramatic down-regulation of aquaporin
256 expression during lateral root formation (Péret et al. 2012). This effect is mediated in part by auxin
257 which, more generally, down-regulates most aquaporin expression in roots within 5-10 hours, and,
258 consequently, *Lp.* Auxin also induces, after 24h, a drop in turgor of cortical cells. Interestingly,
259 mutant analyses have shown that all these molecular and physiological responses are mediated
260 through Auxin Response Factor 7 (ARF7), a transcription factor that serves as a master regulator of
261 lateral root formation and emergence. Yet, the down-stream targets of ARF7 in these responses
262 remain to be identified. Our current understanding is that a finely tuned spatial and temporal control
263 of *PIP* expression favours water entry into the lateral root primordium. This inflow is made at this

264 expense of overlaying cells, thereby reducing their mechanical resistance and facilitating lateral root
265 emergence.

266 **3.2 Methyl jasmonate (MeJa)**

267 Contrasting effects of MeJa on root water transport have been reported by different groups.
268 (Sanchez-Romera et al. 2014) observed that exogenously supplied MeJA increases L_p in bean,
269 tomato and Arabidopsis. These effects are associated with an increased phosphorylation of PIP2s and
270 partly depend on ABA, which accumulates in response to MeJa. In bean, the fluoridone inhibitor
271 counteracted the effects of MeJA on both ABA accumulation and L_p . By contrast, exogenous MeJa
272 induced a decrease in cell hydraulic conductivity in the cortex of Arabidopsis roots (Lee and Zwiazek
273 2019). Surprisingly, *fad3-2* and *fad7-2* plants, which are defective in MeJa endogenous biosynthesis,
274 were insensitive to this external treatment. These contrasting results suggest that effects of MeJa on
275 root hydraulics are cell-type specific, somewhat indirect and involve important hormonal cross-talks
276 that remain to be uncovered.

277 **3.3 Ethylene**

278 The effects of ethylene on aquaporin function in various plant species and organs have revealed the
279 contribution of multiple signalling pathways. In rose, ethylene acts as a repressor of flower opening.
280 It negatively controls petal cell expansion through down-regulation of *RhPIP2;1* (Ma et al. 2008) and
281 *RhPIP1;1* (Chen et al. 2013), which functionally interacts with the former. Consistent with these
282 negative hormonal effects, silencing of ethylene receptors (*RhETRs*) which, in the absence of the
283 hormone function as repressors of ethylene effects, resulted in an ethylene-independent decrease in
284 *RhPIP1;1* expression (Chen et al. 2013). In Arabidopsis leaves, ethylene exerts positive effects on
285 water transport through enhanced C-terminal phosphorylation of *AtPIP2;1* (Qing et al. 2016). These
286 post-translational effects require the ETR-1 receptor and its interacting partner Constitutive Triple-
287 Response 1 (CTR1). They are independent of the major transcriptional pathway involving Ethylene-
288 Insensitive 1 (EIN1) and Ethylene-Insensitive 3-like (EIL3), which would in turn mediate the

289 transcriptional down-regulation of PIPs, as mentioned above. Tentative regulatory networks acting
290 on aquaporin phosphorylation, under the control of ethylene and through balanced effects on
291 protein kinases and phosphatases, were inferred in part from a differential phosphoproteomics
292 approach in Col-0 and *ctr1* plants (Yang et al. 2013). Since ethylene enhances auxin accumulation,
293 hormonal interactions will also have to be taken into account to comprehend the multiple pathways
294 leading to ethylene-dependent aquaporin regulation (Yang et al. 2013; Qing et al. 2016)

295 **3.4 Sugars**

296 Sugars act as metabolites but also signalling molecules to regulate various whole plant and cellular
297 processes such as photosynthesis and stomatal movements. With respect to tissue water transport,
298 sucrose was shown to enhance Arabidopsis L_p , specifically in the dark, whereas it inhibited L_p in the
299 light, as did other osmotica (Di Pietro et al. 2013). Sucrose also induced changes in AtPIP2;6
300 phosphorylation (Niittylä et al. 2007), thereby providing a tentative link between light, sugars and
301 aquaporins. This link was corroborated by the high negative correlation existing between the
302 expression of aquaporins and either exogenous glucose or the expression of Hexokinase 1 (*AtHXK1*)
303 in over-expressing or knock-out transgenic Arabidopsis (Kelly et al. 2017). Protein kinases that are
304 involved in sucrose-induced phosphorylation responses, among which RLKs (*e.g.* SIRK1) and receptor-
305 like cytoplasmic kinases (RLCKs *e.g.* Brassinosteroid Signaling Kinase 8 (BSK8)) have been identified
306 through typical changes in their phosphorylation status within the few minutes following sucrose
307 resupply. Some aquaporins were subsequently identified as downstream targets of these protein
308 kinases (Wu et al. 2019; Wu et al. 2013; Wu et al. 2014). For instance, molecular interactions of SIRK1
309 with AtPIP2;6 were established through pull down experiments and phosphorylation assays using an
310 AtPIP2;6-specific peptide. The mesophyll protoplast water permeability of Arabidopsis lines showing
311 different expression levels of active SIRK1 revealed that the RLK directly regulates aquaporins via
312 phosphorylation in a sucrose dependent manner (Wu et al. 2013). In addition, SIRK1 forms a complex
313 with its co-receptor QSK1. SIRK1 shows autophosphorylation, subsequently trans-phosphorylates

314 QSK1, which in turn enhances and stabilizes the interaction of aquaporins with the receptor kinase
315 complex (Wu et al. 2019). Our understanding of BSK8 action on aquaporins is not as precise, but the
316 RLCK possibly acts on another isoform, AtPIP2;7, that shows reduced phosphorylation in a *bsk8*
317 mutant. Although still incomplete, the whole set of data suggests intricate osmotic, metabolic and
318 signalling effects of sugars acting on aquaporins through multiple receptor pathways and time frames
319 (Wu et al. 2014). At the whole plant level, the somewhat opposite effects of sugar on hydraulics
320 depending on organs, timing, or environmental conditions surely reflect contrasting contexts where
321 maintenance of growth or of water content dominate one another.

322 **3.5 Peptidic hormones and other unknown ligands**

323 The endodermis functions as a major barrier within the root, determining fundamental features of
324 water and nutrient absorption from the soil (Doblas et al. 2017). These properties follow from the
325 typical differentiation of endodermal cells, with an initial formation of Casparian strips made out of
326 lignin and further deposition of suberin lamellas that wrap the whole cell. Casparian strips mostly
327 block apoplastic solute movements and favor xylem loading by preventing solute backflow from the
328 stele to the cortex. Suberin lamellas, rather, limit transcellular transport of nutrients and possibly
329 water at the endodermis. These barriers, which are at the cross-roads of mineral nutrient and water
330 uptake, are therefore under tight control by endogenous and environmental factors (Barberon et al.
331 2016). For instance, the loss of Casparian strip integrity is detected by diffusible vasculature-derived
332 peptides CASPARIAN STRIP INTEGRITY FACTORS 1 & 2 (CIF1 & 2) which act through the SCHENGEN3
333 receptor-like kinase (Pfister et al. 2014, Doblas et al. 2017, Nakayama et al. 2017) to rebalance water
334 and mineral nutrient uptake. More specifically, CIF1 and CIF2 induce a reduction in L_p , driven by the
335 deactivation of aquaporins (Wang et al. 2019). They also limit ion leakage through deposition of
336 suberin in endodermal cell walls. Inhibition of aquaporins seems to be a primary effect of CIFs, which
337 in turn may promote suberin deposition. Interestingly, CIF1 and CIF2 act independently of ABA
338 signaling, which can also be a potent regulator of aquaporins in endodermal cells.

339 Casparian strip deposition is guided by the local expression of a family of Casparian Strip
340 domain Proteins (CASPs). Related proteins named CASP-like are expressed throughout the plant.
341 Four of these (CASPL1B1, CASPL1B2, CASPL1D1, and CASPL1D2) were identified as interacting with
342 AtPIP2;1 (Bellati et al. 2016). Although the physiological relevance of these molecular interactions is
343 not known, CASPL1B1 was shown to specifically activate phosphorylated AtPIP2;1 (Champeyroux et
344 al. 2019), pointing to a putative composite regulatory pathway.

345 **4) Biotic interactions**

346 **4.1 Plant immunity**

347 In recent years, several landmark works have reported a crucial role of aquaporins in plant defense
348 (Zhang et al. 2019a; Li et al. 2020a; Wang et al. 2018; Tian et al. 2016; Ai et al. 2021). AtPIP1;4 was
349 identified as one of the PIPs, the expression of which is induced by infection with *Pseudomonas*
350 *syringae* pv. *Tomato* (Tian et al. 2016). The use of intracellular and extracellular ROS dyes in yeast
351 and transgenic Arabidopsis further revealed the capacity of AtPIP1;4 to mediate the diffusion of
352 apoplastic H₂O₂ into the cytoplasm. This process represents a major step in the signaling response of
353 plants to pathogen-associated molecular patterns (PAMPs), which activate RBOH NADPH oxidases
354 present on the plasma membrane. More generally, analysis of knock-out mutants and overexpressing
355 plants revealed that AtPIP1;4 is necessary for PAMP-triggered immunity (Tian et al. 2016) and
356 mediates systemic acquired resistance (SAR) through a parallel pathway involving activation of
357 NONINDUCER OF PR GENES1 (NPR1). These findings establish a major signaling role of PIPs in plant
358 defense (Figure 1C). Interestingly, a mechanism allowing bacterial effectors to counteract this
359 aquaporin signalling function was recently uncovered (Ai et al. 2021). In brief, a Crinkler effector
360 (CRN78) from *Phytophthora* displaying a protein kinase activity was shown to phosphorylate the C-
361 terminal tail of several H₂O₂-transporting PIPs of soybean or *Nicotiana benthamiana*, thereby
362 triggering their degradation through a proteasome-dependent pathway. This led to inhibition of

363 H₂O₂-accumulation and reduced immunity of these plants when infected by *Phytophthora* oomycetes
364 (Ai et al. 2021).

365 A signalling role for aquaporins during plant defense was also uncovered for AtPIP2;1 in
366 guard cells, with this aquaporin being necessary for flg22-induced stomatal closure. In this case, a
367 pathway was proposed, whereby the bacterial PAMP flg22 binds to its receptor FLS2 leading to the
368 successive activation of the BAK1 co-receptor and SnRK2.6 protein kinase. This in turn
369 phosphorylates AtPIP2;1 at Ser121 to promote both water and H₂O₂ transport as shown in the
370 context of ABA-induced stomatal closure (Rodrigues et al. 2017) (Figure 1A). Flagellin (flg22) also
371 enhanced lateral diffusion of AtPIP2;1 at the guard cell plasma membrane through effects on
372 microtubules, resulting in its internalization to the cell (Cui et al. 2021). It is not yet clear whether
373 these effects contribute to the primary role of AtPIP2;1 in stomatal closure or reflect a feedback
374 inhibition of its function due to flg22-induced ROS accumulation. Interestingly, AtPIP2;1 dynamics at
375 the plasma membrane of adjacent (subsidiary) cells showed a distinct dependency on the
376 cytoskeleton and were somewhat insensitive to flg22 (Cui et al. 2021). Thus, cell-specific regulation
377 of aquaporins probably contributes to an integrated control of water exchange between cell types
378 during stomatal movements.

379 PAMPs such as chitin are produced during plant attack by fungi and insects. Aquaporin-
380 mediated water transport in leaf tissues such as the mesophyll and bundle sheath was shown to be
381 down-regulated by chitin (Attia et al. 2020). This inhibition could contribute to plant defense by
382 hampering vascular pathogen propagation in xylem vessels and by promoting stomatal closure
383 through long-distance hydraulic signalling. Although the mode of aquaporin regulation by chitin
384 remains as yet unknown, the contribution of two chitin receptor-like kinases, chitin elicitor receptor
385 kinase 1 (CERK1) and lysine motif receptor kinase 5 (LYK5), could be established (Attia et al. 2020)

386 Recent work also points to another molecular role of aquaporin during bacterial infection.
387 For instance, rice *OsPIP1;3* and Arabidopsis *AtPIP1;4* molecularly interact with the bacterial protein
388 harpin (Hpa1) which is secreted by Gram-negative pathogenic bacteria. Thus, PIPs serve as receptors

389 for harpins at the plant plasma, which in turn mediate the delivery of effector proteins (such as
390 PthXo1) into the plant cell cytoplasm (Li et al. 2019; Li et al. 2015b). Along the same lines, AtPIP2;7
391 was recently shown to form a molecular complex with the protease domain of the tobacco etch
392 potyvirus NIa protein (Martinez et al. 2016). Due to its numerous additional connections to stress
393 responses, the aquaporin seems to be a preferential target during viral infection.

394 The overall data show that aquaporins are at the heart of the arms race between plants and
395 their aggressors. On the one hand, aquaporins help plants resist pathogens by contributing to
396 defense signaling pathways and by preventing their ingress through promotion of stomatal closure
397 (Zhang et al. 2019a; Li et al. 2020a). On the other hand, some aquaporins can be hijacked by bacterial
398 or viral pathogenic machineries, thereby promoting pathogen propagation.

399 **4.2 Mycorrhizae**

400 Aquaporins also contribute to positive plant–microbe interactions whereby they play important roles
401 in nutrient transport and abiotic stress responses. In particular, arbuscular mycorrhizal symbiosis can
402 notably improve the plant water status. A fine dialog exists between the fungus and the host plants,
403 leading to precise transcriptional and post-translational regulation of plant aquaporins, particularly
404 under drought (Quiroga et al. 2019). Similarly, the sub-cellular expression of specific tonoplast
405 aquaporins seems to be subtly targeted in N-fixing symbiotic nodules (Gavrin et al. 2014). Although
406 strong hormonal interplays are suspected, the signaling pathways leading to these regulations are as
407 yet unknown.

408 **5) Commonalities of signalling pathways**

409 The survey above provides a broad but scattered knowledge of signalling processes targeting cell and
410 tissue hydraulics in plants (Table 1). Yet, a few main principles do emerge from this information.

411 Whereas transcriptional control is definitely key for long-term adjustment of plant hydraulics
412 in response to environmental or developmental cues, post-translational mechanisms seem to
413 dominate short term (min and hours) regulations, as these are more tailored for fast and reversible

414 responses to the multiple factors (including water availability) acting on the plant water status. Here,
415 we discuss a few common players of the latter regulatory mechanisms.

416 Firstly, ROS play a central signalling role in such regulation of plant water transport (Figure 1).
417 They are produced in response to numerous stimuli including osmotic, salt and cold stress, nutrient
418 deprivation and hormones (salicylic acid, ABA). Although several ROS generating systems may
419 operate at the plasma membrane (Martiniere et al. 2019), RBOH NADPH oxidases seem to occupy a
420 central position in this device (Li et al. 2011; Martiniere et al. 2019). By enhancing constitutive cycling
421 of aquaporins at the plasma membrane and shifting the equilibrium towards endocytosis, ROS
422 promote aquaporin internalization, thereby reducing their density at the cell surface and, as a
423 consequence, cell hydraulic conductivity (Boursiac et al. 2008; Wudick et al. 2015). As suggested by
424 recent work in guard cells (Cui et al. 2021), this mechanism could provide a feedback regulation in
425 contexts where aquaporins contribute to the initial steps of ROS signalling.

426 The sub-cellular trafficking and regulated degradation of aquaporins also appears to be a
427 main component of plant responses to environmental stimuli. Syntaxins and other traffic proteins,
428 such as adaptor proteins (AP), play well-established roles in these processes (Besserer et al. 2012;
429 Hachez et al. 2014a; Pertl-Obermeyer et al. 2016). While some internalized aquaporins accumulate in
430 pre-vacuolar compartments (Luu et al. 2012), a stress-response pathway under the control of
431 Tryptophan-rich sensory protein/translocator (TPSO) (Hachez et al. 2014b) can relay the above
432 mentioned trafficking to promote aquaporin degradation. The autophagic pathways described in
433 *Medicago truncatula* under water deficit (Li et al. 2020b) may also operate under other stressing
434 conditions. In addition, two recent works have pointed to a control by phosphorylation of ubiquitin-
435 dependent degradation of aquaporins in plants under abiotic or biotic stress (Ai et al. 2021; Chen et
436 al. 2021). This mechanism, which allows control of aquaporin abundance, further expands the
437 multiple, and possibly opposite, roles of phosphorylation in controlling aquaporin function.

438 In relation to the central role of phosphorylation, aquaporins are known to be targeted by
439 multiple classes of protein kinases. This feature holds promises to further decipher aquaporin

440 signalling pathways in bottom-up approaches (Figure 2). CDPKs have long been proposed as major
441 players of aquaporin regulation (Johnson and Chrispeels 1992; Johansson et al. 1996). Yet, there are
442 very few cases where their role was formally established (Ji et al. 2017; Almadanim et al. 2017). We
443 also note that CDPKs can be involved in upstream steps and therefore indirectly act on aquaporin
444 regulation (Li et al. 2015a). Due to their key role during stomatal movements (Yip Delormel and
445 Boudsocq 2019), it will be worth exploring the action of CDPKs on guard cell aquaporins in closer
446 detail.

447 SnRK2s represent another potentially important class of protein kinases acting on plant
448 aquaporins. Besides SnRK2.6 (OST1), which mediates ABA- and flg22-dependent activation of
449 AtPIP2;1 in guard cells (Grondin et al. 2015; Rodrigues et al. 2017), other SnRK2s may delineate
450 additional ABA- or osmotic-stress dependent pathways acting on aquaporins. In support for this,
451 functional expression of plant signalling pathways in yeast using a transcriptional readout indicated
452 that four SnRK2s initially thought to be specific for osmotic responses can also contribute to ABA
453 signalling (Ruschhaupt et al. 2019). Thus, the model of ABA-dependent regulation of AtPIP2;1 may be
454 extended to additional pairs of SnRK2s and PIPs.

455 RLKs constitute another major a class of serine/threonine kinases that perceive
456 environmental and extracellular developmental signals and transduce them via their intracellular
457 kinase domain. While their role in aquaporin regulation in the endodermis (SGN3) and during sugar
458 response (SIRK1, BSK8) can serve as models, we anticipate a role for RLKs in many other cellular
459 contexts including water stress (see Outstanding questions). For instance, a RLK (LP2) and a
460 Cytoplasmic Receptor-like Kinase (OsRLCK311), both from rice, were shown to interact with PIPs *in*
461 *vivo* (Wu et al. 2015; Sade et al. 2020), but the functional role of these interactions was not
462 definitively elucidated. Moreover, Arabidopsis RKL1, the activating signals of which remain to be
463 identified, was shown to molecularly interact with AtPIP2;1 (Bellati et al. 2016). Co-expression of
464 AtPIP2;1 with RKL1 in *Xenopus* oocytes resulted in enhanced AtPIP2;1 water transport activity by an
465 as yet unknown mechanism (Bellati et al. 2016). RLKs may also regulate aquaporins by non-canonical

466 mechanisms. For instance, co-expression of FERONIA and AtPIP2;1 in *Xenopus* oocytes leads to
467 inactivation of the latter (Bellati et al. 2016). This inactivation seems to require the protein kinase
468 activity of FERONIA and is favored by two C-terminal phosphorylation sites of AtPIP2;1 that, in
469 contrast, have been described as activating sites. Thus, these phosphorylated residues may favor the
470 FERONIA-AtPIP2;1 interaction, which in turn would lead to aquaporin inhibition.

471 Finally, CBL-interacting protein kinases (CIPKs) represent major regulators of plant nutrition
472 and response to abiotic stresses (Dong et al. 2020). It is rather surprising that, despite efforts from
473 several laboratories including ours, no aquaporin has ever been identified as one of their numerous
474 substrates. In addition, protein phosphatases, which surely play a key role in phosphorylation-
475 dependent regulation of aquaporins, will deserve specific attention in future studies.

476 Lipid signalling represents another emerging component targeting aquaporins (see
477 Outstanding questions). For instance, genetic alteration of phosphoinositides (phosphatidyl inositol
478 [4,5] bisphosphate: PtdInsP2) in tobacco (*Nicotiana tabacum*) increased the osmotic water
479 permeability and aquaporin activity of protoplasts isolated from suspension cells (Ma et al. 2015).
480 The lipid effects may operate through direct interaction with aquaporins or through indirect cellular
481 effects of PtdInsP2. For instance, interaction of PtdInsP2 with TPO is required for interaction with
482 AtPIP2;7 and its subsequent degradation (Jurkiewicz et al. 2020). A role for lipid signaling in PIP
483 regulation is also suggested by the physical interaction between AtPIP2;1 and two phospholipases D
484 (PLD δ and PLD γ 1) (Bellati et al. 2016). In plants, PLDs and their enzymatic product phosphatidic acid
485 (PA) play key roles in cellular responses to hormonal and abiotic stimuli. Along these lines, AtPIP2;1
486 and AtPIP2;2 were identified as PA-binding proteins (McLoughlin et al. 2013) but the functional
487 effects of these interactions remain to be elucidated.

488 In complement to these targeted studies, we believe that systems biology approaches will
489 help uncover previously unidentified signalling pathways targeting aquaporins. For instance, protein
490 interaction networks involving aquaporins have pointed to links with clusters associated with
491 brassinosteroid signaling (Bellati et al. 2016). A genome-wide search for membrane-protein

492 complexes has revealed other clusters that are enriched in aquaporins and have potential roles in
493 stimulus-dependent regulation of water transport (Jones et al. 2014). Finally, a close inspection of
494 aquaporin gene position in gene regulation networks will for sure reveal other modes of
495 developmental or environmental regulation of aquaporins (Alexandersson et al. 2010).

496 **6) Perspectives**

497 Whereas this overview principally deals with chemical signals, whether abiotic or hormonal, there is
498 still much to be learned about how physical cues lead to aquaporin regulation (see Outstanding
499 questions). Particularly challenging seems the direct link between tissue hydraulics and transpiration
500 that may well be mediated through hydraulic signals, or in other words, pressure-dependent
501 regulation of aquaporins (Pou et al. 2013; Laur and Hacke 2013). Such dependency may also be at the
502 basis of wound-induced alterations in root or leaf hydraulic conductivity (Vandeleur et al. 2014; Liu et
503 al. 2014). Plant defence is another emerging context in which aquaporin regulation will have to be
504 investigated. While the plant water status is crucial for resilience of plants under attacks, it is also a
505 key target for pathogens to facilitate their proliferation within the plant (Xin et al. 2016). We now
506 have some ideas on how aquaporins serve as both signalling components and targets during innate
507 immunity (Zhang et al. 2019a). In contrast, the action of effectors on aquaporins and possible
508 resistance mechanisms associated to these are just emerging (Ai et al. 2021).

509 Beyond regulation of water transport in a strict sense, we realize that mechanisms targeting
510 other aquaporin transport functions may have some relevance for plant water relations or share
511 similarities with mechanisms targeting the latter. For instance, aquaporin-mediated CO₂ transport is
512 regulated through interaction with β CA4 carbonic anhydrase (Wang et al. 2016), indicating that the
513 various molecular functions of aquaporin interactants and their ability to associate aquaporin
514 regulation to upstream signalling cascades still represent a gold mine of information. Also, the ion
515 transport of *AtPIP2;1*, which is strongly dependent on divalent cations and pH (Byrt et al. 2017),
516 confirms that both Ca²⁺ and H⁺ are definitely crucial second messengers acting on aquaporin activity.

517 Because plants are continuously exposed to combinations of environmental constraints, we
518 realize that our analytic representation of single signalling pathways remains largely inappropriate.
519 Although we emphasized how conserved pathways and their cross talks ultimately act on aquaporins,
520 our knowledge of these processes remains very poor. More generally, basic information on how
521 plant water transport is adjusted in response to combined stresses is still lacking. This large field of
522 investigation, combining fundamental plant physiology and systems biology, is now necessary to
523 properly comprehend the amazing capacity of plants to acclimate to a large array of stressful
524 environments.
525

526 **Advances.**

- 527 • ABA-dependent and independent signalling pathways act on aquaporins in plants under
528 water deficit.
- 529 • Aquaporin-mediated water transport is targeted by multiple abiotic, biotic, or endogenous
530 stimuli; recently identified stimuli include peptide hormones and PAMPs.
- 531 • ROS play a central signalling role in regulating water transport in plants by acting on
532 aquaporin subcellular dynamics, localization and/or phosphorylation.
- 533 • Plasma membrane aquaporins exhibit a dual water- and H₂O₂-transport function, acting as
534 players in and targets of signalling processes.
- 535 • Phosphorylation of aquaporins, which interferes with their gating, trafficking, and stability, is
536 a major target of plant signalling cascades, and multiple classes of protein kinases that act on distinct
537 phosphorylation sites have been identified.

538

539 **Outstanding questions.**

- 540 • Is aquaporin-mediated H₂O₂ transport a common process in plant cell signaling?
- 541 • Which cellular signals trigger RLK-dependent aquaporin regulation?
- 542 • What is the role of lipid signaling in water transport regulation?
- 543 • What are the mechanisms for coupling physical stimuli to aquaporin regulation?
- 544 • How do aquaporins contribute to plant defense? What are their active roles in plant
545 immunity, and how can they be hijacked by pathogens?
- 546 • What are the effects of combined stresses on plant water transport, and which signaling
547 pathways are involved?

548

549 **Acknowledgments.** The authors thank their colleagues of the Aqua team for fruitful discussions. This
550 work was supported in part by the Agence Nationale de la Recherche (ANR- 18-CE92-0055).

551 **TABLE****Table 1:** Molecular signaling mechanisms involved in aquaporin regulation under abiotic and biotic stresses and by endogenous signals

Type of signal	Stimulus	Signalling intermedia te	Molecular mechanism on aquaporins	Aquaporin regulation	Reference
ABIOTIC	drought (ABA-dependent)	SnRK2.6	AtPIP2;1 loop phosphorylation	B up-regulated activity	Grondin et al., 2015; Rodrigues et al., 2017
		LP2	interaction with OsPIP1;1, OsPIP1;3 and OsPIP2;3	down-regulated activity	Wu et al., 2015
	drought (ABA-independent)	RhPTM	interaction with RhPIP2;1	nd	Zhang et al., 2019
		TSPO	nd	AtPIP2;7 protein degradation	Hachez et al., 2014b
		MtCas31/MtATG8	MtCas31 as a cargo receptor for MtPIP2;7	protein degradation by autophagy	Li et al., 2020b
		nd	increased phosphorylation of AtPIP2;4	C-ter nd	Stecker et al., 2014
	osmotic	RBOHs and ROP6 clathrin	membrane lateral mobility	clustering in nano-domains	Hosy et al., 2015; Martiniere et al., 2019; Smokvarska et al., 2020
		Rma1H1	AtPIP2;1 ubiquitination	protein degradation	Zwiewka et al., 2015
		UBC32	AtPIP2;1 ubiquitination	protein degradation	Lee et al., 2009
		UBC32	AtPIP2;1 ubiquitination	protein degradation	Chen et al., 2021
	salinity	clathrin, PI3K, PI4K, SnRK2.4, SnRK2.10	C-ter phosphorylation of PIPs; enhanced mRNA decay	protein internalization and down-regulated activity	Prak et al., 2008; Boursiac et al., 2008; Ueda et al., 2016; Pou et al., 2016; Kawa et al., 2020
	oxygen	cytosolic protons	His protonation of PIPs	down-regulated activity	Tournaire-Roux et al., 2003
	availability	HCR1	nd	down-regulated activity	Shahzad et al., 2016
	Nitrogen	NRT2;1	nd	enhanced gene expression, protein accumulation and up-regulated activity	Li et al., 2016; Ishikawa-Sakurai et al., 2014
	cold	nd	AtPIP1;4 and AtPIP2;5 gene expression	up-regulation of gene expression	Rahman et al., 2020
	OsCPK17	OsPIP2;1 and OsPIP2;6 C-ter phosphorylation	up-regulated activity	Almadanin et al., 2017	
circadian clock	14-3-3	AtPIP2;1 phosphorylation	C-ter up-regulated activity	Prado et al., 2019	
	ELF3	AtPIP1;2 and AtPIP2;1 gene expression	oscilating activity	Caldeira et al., 2014; Takase et al., 2011	
flg22	BAK1 and SnRK2.6	increased phosphorylation	AtPIP2;1 loop B up-regulated activity	Rodrigues et al., 2017	

BIOTIC	<i>Phytophthora sojae</i>	CRN78	<i>GmPIP2;13</i> and phosphorylation	<i>NbPIP2;2</i>	protein degradation		Ai et al., 2021	
	chitin	CERK1 and LYK5	nd			up-regulated activity	Attia et al., 2020	
	<i>Xanthomonas oryzae</i>	Harpin	interaction with and <i>AtPIP1;4</i>	<i>OsPIP1;3</i>	nd		Li et al., 2015b; Li et al., 2019	
ENDOGENOUS	auxin	ARF7	<i>PIP</i> gene expression			down-regulated activity	Péret et al., 2012	
	MeJa	nd	<i>PIP2</i> C-ter phosphorylation			up-regulated activity	Lee and Zwiazek, 2019	
	ethylene	<i>RhETRs</i>	<i>RhPIP1;1</i> and <i>RhPIP2;1</i> gene expression			down-regulated gene expression		Ma et al., 2008 ; Chen et al., 2013
		ETR1 and CTR1	<i>AtPIP2;1</i> phosphorylation		C-ter		up-regulated activity	Qing et al., 2016; Yang et al., 2013
	sucrose	SIRK1, QSK1	<i>AtPIP2;6</i> phosphorylation		C-ter		up-regulated activity	Niittyla et al., 2007; Wu et al., 2014; Wu et al., 2019; Wu et al., 2013
		BSK8	<i>AtPIP2;7</i> phosphorylation		C-ter	nd		Wu et al., 2014
	CIF peptide	SGN3	nd				down-regulated activity	Wang et al., 2019
Other	CASPL1B1	physical interaction with <i>AtPIP2;1</i>				up-regulated activity	Champeyroux et al., 2019	

552

553 Figure legends

554 **Figure 1.** Cellular responses to biotic or abiotic stimuli involving hydrogen peroxide (H_2O_2) and
555 aquaporins. **A,** In guard cells (right), the Snf1-Related protein Kinase 2.6 (SnRK2.6) is a key
556 component of abscisic acid (ABA)- and flagellin (flg22)-induced stomatal closure. Flg22 is a Pathogen-
557 Associated Molecular Pattern (PAMP) recognized by the plasma membrane Flagellin-Sensitive 2
558 (FLS2) receptor, which acts in concert with BRI1-Associated Kinase 1 (BAK1). Upon activation,
559 SnRK2.6 phosphorylates two NADPH oxidases, Respiratory Burst Oxidase Homolog protein D
560 (RBOHD) and RBOHF, and the AtPIP2;1 aquaporin. The latter facilitates the influx of H_2O_2 and the
561 efflux of water, thereby promoting stomatal closure (Grondin et al. 2015; Rodrigues et al. 2017).
562 Flg22 also enhances the lateral mobility of AtPIP2;1 at the guard cell plasma membrane (left),
563 thereby promoting its internalization (Cui et al. 2021). **B,** The root hydraulic conductivity (L_p) is
564 strongly decreased in response to abiotic stresses such as osmotic and salt stress, or hormones such
565 as salicylic acid (SA). All these stimuli act through accumulation of H_2O_2 which lowers AtPIP2;1
566 phosphorylation (P), alters its plasma membrane mobility and promotes its internalization (Boursiac
567 et al. 2008; Wudick et al. 2015). In contrast, PIP phosphorylation promotes its trafficking to the
568 plasma membrane. The increased apoplastic H_2O_2 production observed in response to an osmotic
569 stress is mediated through the clustering in nanodomains of the Rho-related GTPase of plants 6
570 (Rop6) together with the RBOHD and F NADPH oxidases (Smokvarska et al. 2020; Martiniere et al.
571 2019). **C,** In mesophyll cells, PAMPs are perceived by plasma membrane receptors, which trigger, in
572 combination with BAK1 co-receptor and other non-represented cellular components, the activation
573 of RBOHB NADPH oxidase and, as a consequence, apoplastic accumulation of H_2O_2 . The AtPIP1;4
574 aquaporin plays a key role in facilitating the diffusion of apoplastic H_2O_2 into the cytoplasm (Tian et
575 al. 2016). The increase in cytoplasmic H_2O_2 concentration ultimately leads to activation of key
576 proteins (Pathogenesis-Related protein 1: PR1; Pathogenesis-Related protein 2: PR2; Plant Defensin
577 1.2: PDF1.2; Noninducer of PR genes 1 : NPR1; Mitogen-Activated Protein Kinase 3 : MAPK3; Glucan
578 Synthase-like 5: GSL5) involved in Systemic Acquired Resistance (SAR) or Pathogen Triggered
579 Immunity (PTI), as indicated. The figure also shows how the Crinkler 78 (CRN78) effector of
580 *Phytophthora* can penetrate the plant cell where it interacts with phosphorylated NbPIP2;2, to
581 induce its internalization and further degradation, thereby preventing its role in PAMP signaling (Ai et
582 al., 2021). Thick blue arrows and thick red arrows indicate initial effects of stimuli and their output
583 responses, respectively; thin dotted blue line arrows refer to diffusion of the indicated molecules; red
584 dotted line arrows represent protein phosphorylation by indicated protein kinases; red dashed-
585 dotted line arrows and red dashed-dotted line blunt arrows describe indirect activation and

586 inactivation pathways, respectively; brown line arrows indicate movements of proteins or membrane
587 compartments.

588

589 **Figure 2.** Signaling pathways converging on PIP phosphorylation. The figure represents a prototypal
590 PIP aquaporin with its transmembrane domains (1-6) and extracellular (A, C, E) or cytosolic (B, D)
591 loops. The indicated stimuli lead to enhanced (arrows) or reduced (blunt arrow) phosphorylation of
592 Ser residues in loop B or C-terminal tail. The inset shows three pathways acting on unknown PIP
593 phosphorylation sites (white question marks). Signaling intermediates are indicated with the
594 following color code: Snf1-related protein kinase 2 (SnRK2): blue; Calcium-Dependent Protein Kinase
595 (CDPK), green; Receptor-Like Kinase (RLK), red; others, black. Note that the indicated protein kinases
596 do not necessarily act directly on the indicated sites. Other abbreviations: Brassinosteroid Signaling
597 Kinase 8 (BSK8); Chitin Elicitor Receptor Kinase 1 (CERK1); Calcium-dependent Protein Kinase 17
598 (CPK17); Constitutive Triple-Response 1 (CTR1); Leaf Panicle 2 (LP2); Lysine motif receptor Kinase 5
599 (LYK5); phosphatidylinositol 3-kinase (PI3K); phosphatidylinositol 4-kinase (PI4K); Qian Shou Kinase 1
600 (QSK1); Receptor-like Kinase 1 (RKL1), Sucrose Induced Receptor Kinase 1 (SIRK1); 14-3-3 protein (14-
601 3-3). For more details and references see text and Table 1.

602

603

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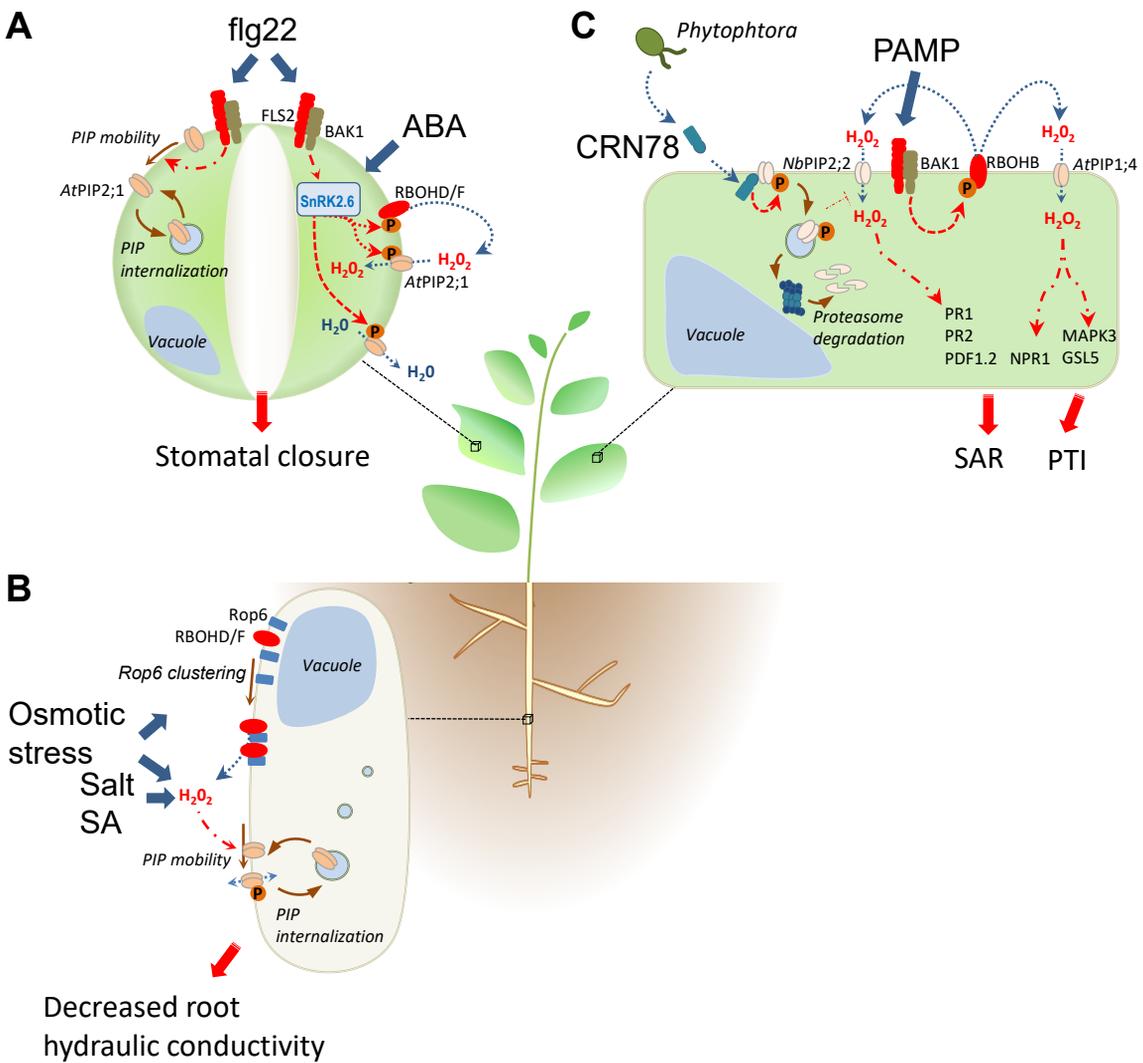


Figure 1. Cellular responses to biotic or abiotic stimuli involving hydrogen peroxide (H₂O₂) and aquaporins. **A**, In guard cells (right), the Snf1-Related protein Kinase 2.6 (SnRK2.6) is a key component of abscisic acid (ABA)- and flagellin (flg22)-induced stomatal closure. Flg22 is a Pathogen-Associated Molecular Pattern (PAMP) recognized by the plasma membrane Flagellin-Sensitive 2 (FLS2) receptor, which acts in concert with BRI1-Associated Kinase 1 (BAK1). Upon activation, SnRK2.6 phosphorylates two NADPH oxidases, Respiratory Burst Oxidase Homolog protein D (RBOHD) and RBOHF, and the AtPIP2;1 aquaporin. The latter facilitates the influx of H₂O₂ and the efflux of water, thereby promoting stomatal closure (Grondin et al. 2015; Rodrigues et al. 2017). Flg22 also enhances the lateral mobility of AtPIP2;1 at the guard cell plasma membrane (left), thereby promoting its internalization (Cui et al. 2021). **B**, The root hydraulic conductivity (L_p) is strongly decreased in response to abiotic stresses such as osmotic and salt stress, or hormones such as salicylic acid (SA). All these stimuli act through accumulation of H₂O₂ which lowers AtPIP2;1 phosphorylation (P), alters its plasma membrane mobility and promotes its internalization (Boursiac et al. 2008; Wudick et al. 2015). In contrast, PIP phosphorylation promotes its trafficking to the plasma membrane. The increased apoplastic H₂O₂ production observed in response to an osmotic stress is mediated through the clustering in nanodomains of the Rho-related GTPase of plants 6 (Rop6) together with the RBOHD and F NADPH oxidases (Smokvarska et al. 2020; Martiniere et al. 2019). **C**, In mesophyll cells, PAMPs are perceived by plasma membrane receptors, which trigger, in combination with BAK1 co-receptor and other non-represented cellular components, the activation of RBOHB NADPH oxidase and, as a consequence, apoplastic accumulation of H₂O₂. The AtPIP1;4 aquaporin plays a key role in facilitating the diffusion of apoplastic H₂O₂ into the cytoplasm (Tian et al. 2016). The increase in cytoplasmic H₂O₂ concentration ultimately leads to activation of key proteins (Pathogenesis-Related protein 1: PR1; Pathogenesis-Related protein 2: PR2; Plant Defensin 1.2: PDF1.2; Noninducer of PR genes 1: NPR1; Mitogen-Activated Protein Kinase 3: MAPK3; Glucan Synthase-like 5: GSL5) involved in Systemic Acquired Resistance (SAR) and Pathogen Triggered Immunity (PTI), as indicated. The figure also shows how the Crinkler 78 (CRN78) effector of *Phytophthora* can penetrate the plant cell where it interacts with phosphorylated NbPIP2;2, to induce its internalization and further degradation, thereby preventing its role in PAMP signaling (Ai et al., 2021). Thick blue arrows and thick red arrows indicate initial effects of stimuli and their output responses, respectively; thin dotted blue line arrows refer to diffusion of the indicated molecules; red dotted line arrows represent protein phosphorylation by indicated protein kinases; red dashed-dotted line arrows and red dashed-dotted line blunt arrows describe indirect activation and inactivation pathways, respectively; brown line arrows indicate movements of proteins or membrane compartments.

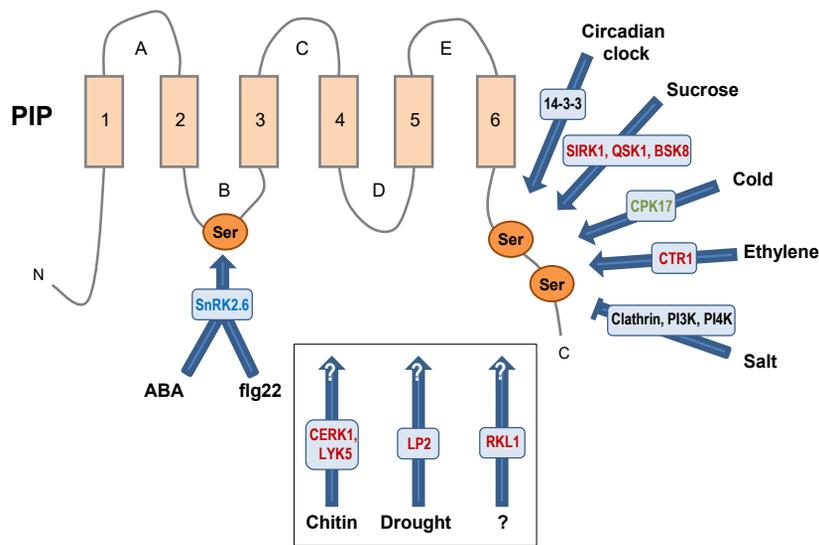


Figure 2. Signaling pathways converging on PIP phosphorylation. The figure represents a prototypal PIP aquaporin with its transmembrane domains (1-6) and extracellular (A, C, E) or cytosolic (B, D) loops. The indicated stimuli lead to enhanced (arrows) or reduced (blunt arrow) phosphorylation of Ser residues in loop B or C-terminal tail. The inset shows three pathways acting on unknown PIP phosphorylation sites (white question marks). Signaling intermediates are indicated with the following color code: Snf1-related protein kinase 2 (SnRK2): blue; Calcium-Dependent Protein Kinase (CDPK), green; Receptor-Like Kinase (RLK), red; others, black. Note that the indicated protein kinases do not necessarily act directly on the indicated sites. Other abbreviations: Brassinosteroid Signaling Kinase 8 (BSK8); Chitin Elicitor Receptor Kinase 1 (CERK1); Calcium-dependent Protein Kinase 17 (CPK17); Constitutive Triple-Response 1 (CTR1); Leaf Panicle 2 (LP2); Lysine motif receptor Kinase 5 (LYK5); phosphatidylinositol 3-kinase (PI3K); phosphatidylinositol 4-kinase (PI4K); Qian Shou Kinase 1 (QSK1); Receptor-like Kinase 1 (RKL1), Sucrose Induced Receptor Kinase 1 (SIRK1); 14-3-3 protein (14-3-3). For more details and references see text and Table 1.

ADVANCES

- ABA-dependent and independent signalling pathways act on aquaporins in plants under water deficit.
- Aquaporin-mediated water transport is targeted by multiple abiotic, biotic, or endogenous stimuli; recently identified stimuli include peptide hormones and PAMPs.
- ROS play a central signalling role in regulating water transport in plants by acting on aquaporin subcellular dynamics, localization and/or phosphorylation.
- Plasma membrane aquaporins exhibit a dual water- and H₂O₂-transport function, acting as players in and targets of signalling processes.
- Phosphorylation of aquaporins, which interferes with their gating, trafficking, and stability, is a major target of plant signalling cascades, and multiple classes of protein kinases that act on distinct phosphorylation sites have been identified.

OUTSTANDING QUESTIONS

- Is aquaporin-mediated H_2O_2 transport a common process in plant cell signaling?
- Which cellular signals trigger RLK-dependent aquaporin regulation?
- What is the role of lipid signaling in water transport regulation?
- What are the mechanisms for coupling physical stimuli to aquaporin regulation?
- How do aquaporins contribute to plant defense? What are their active roles in plant immunity, and how can they be hijacked by pathogens?
- What are the effects of combined stresses on plant water transport, and which signaling pathways are involved?

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