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Plant aquaporins: Their roles beyond water transport

Qi Sun [a,d,1], Xin Liu [a,1], Yoshichika Kitagawa [b], Giuseppe Calamita [c], Xiaodong Ding [a,d,*]

[a] Key Laboratory of Agricultural Biological Functional Genes, Northeast Agricultural University, Harbin 150030, Heilongjiang, China
[b] Graduate School of Bioresource Sciences, Akita Prefectural University, Akita 010-0195, Japan
[c] Department of Biosciences, Biotechnologies and Biopharmaceuticals, University of Bari 'Aldo Moro', I-70125 Bari, Italy
[d] Key Laboratory of Soybean Biology of Chinese Education Ministry, Northeast Agricultural University, Harbin 150030, Heilongjiang, China

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ABSTRACT

Compared to other organisms, plants have evolved a greater number of aquaporins with diverse substrates and functions to adapt to ever-changing environmental and internal stimuli for growth and development. Although aquaporins were initially identified as channels that allow water molecules to cross biological membranes, progress has been made in identifying various novel permeable substrates. Many studies have characterized the versatile physiological and biophysical functions of plant aquaporins. Here, we review the recent reports that highlight aquaporin-facilitated regulation of major physiological processes and stress tolerance throughout plant life cycles as well as the potential prospects and possibilities of applying aquaporins to improve agricultural productivity, food quality, environmental protection, and ecological conservation.

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[*] Corresponding author.
E-mail address: xiaodong.ding@neau.edu.cn (X. Ding).
[1] These authors contributed equally to this work.

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1. Introduction

Plant growth and development depend on strict water transport and regulation in plants. Aquaporins (AQPs) (see Glossary), which mediate water transmembrane transport, are particularly important in plant water transport. Aquaporins were first discovered and studied in animals. In 1993, the first aquaporins, AtTIP1;1, γ-tonoplast intrinsic protein (γ-TIP) in plants was isolated from Arabidopsis by Maurel et al. [1] and its functional characterization laid the groundwork for elucidating the molecular mechanisms underlying water transport in plants [1,2]. Aquaporins belong to a superfamily of highly conserved membrane proteins called major intrinsic proteins (MIP) (see Glossary). Aquaporins in plants are more abundant than those in animals and microorganisms, and show greater diversity. For example, there are about 30–70 aquaporins homologues in Arabidopsis, soybean, corn, rice, tomato and other plants [3–7]. The discovery of these aquaporins provides evidence for studying the molecular basis of water transmembrane transport.

The rapid accumulation of genomic and transcriptomic data from previously unknown species contributes to a better understanding of the evolution of MIPs. Plant aquaporins are not only phylogenetically diverse but also functionally evolved, allowing them to transport more substrates with specific physiological functions than any other aquaporins [8]. Thus, based on structure and subcellular localization, the plant MIP superfamily proteins can be divided into various subfamilies that are not only permeable to water molecules but also to small molecules such as glycerol, boric acid, hydrogen peroxide, urea, and so on [1,9–12]. These accomplishments contribute to an overall improvement in the molecular characterization of plant membrane transport systems and introduce new paradigms to address the molecular basis of water utilization in plants. In this review, we summarize the recent advances in substrate transport of plant aquaporins, mainly including the role of substrate transport in plant growth and development and response to abiotic stress [13–19]. Finally, we focus on their practical applications of plant aquaporins in agriculture and environmental protection by absorbing beneficial and/or extruding harmful metalloids.

2. Plant aquaporin substrates and their functions

Recent reports have suggested that plants show a significantly higher diversity and abundance than those in animals [14]. The molecular basis for aquaporin substrate specificity is being widely investigated. Despite their highly conserved structures, key aquaporin motifs, such as NPA motifs, ar/R selectivity filters, and Froger's positions (Fig. 1A) are responsible for the differences in channel selectivity. In higher plant, aquaporins can be classified into five major subfamilies: PIP, TIP, NIP, SIP, and XIP based on their sequences, structures (Fig. 1B), and subcellular localization (Fig. 2). These aquaporins function in tandem to perform specific physiological functions throughout the plant life cycle [20]. The *Xenopus* oocyte system, yeast cells, and functional reconstitution of recombinant aquaporins in liposomes are the most common means of studying aquaporin permeability to water and other substrates. All expression systems have revealed that plant aquaporins are multifunctional channels with a wide range of selectivity profiles [2,8,12]. Here, we present the recently characterized plant aquaporins, as well as their permeable substrates and relevant physiological functions (Table 1).

2.1. Water (H_2O) and hydrogen peroxide (H_2O_2)

Most plant aquaporins, including the PIP, TIP, and NIP subfamily isoforms, can actively channel H_2O molecules across biological membranes [10,11,12,14,2,21,22]. Owing to the similarity in the chemical properties of H_2O and H_2O_2, some aquaporins can transport both H_2O_2 and H_2O [23]. These channels are known as peroxiporins (see Glossary) and are classified as a subclass of the aquaporin family [24]. As H_2O_2 is a relatively stable reactive oxygen species (ROS) (see Glossary) that acts as an extracellular and intracellular signal molecule that mediates pleiotropic effects in plants [25], its transport suggests that aquaporins may be involved in signal transduction in many pathways. Biotic and abiotic stresses induce rapid production of ROS in apoplasts·H_2O_2 can be easily transported into the cytoplasm via aquaporins [26,27].

Arabidopsis AtPIP2;1, AtPIP2;2, AtPIP2;4, AtPIP2;5, and AtPIP2;7 demonstrated H_2O and H_2O_2 transport in yeast. The H_2O_2 permeability of AtPIP2;4 was confirmed using proteoliposomes (see Glossary) [24]. A genome-wide association study (GWAS) discovered that the *AtNIP1;1* gene was correlated to the H_2O_2-sensitive phenotype, and AtNIP1;1 was verified as an H_2O_2 transporter [28]. ROS production is a consequence of many intracellular and extracellular signaling pathways in plants; therefore, it is of interest to investigate the physiological significance of aquaporin-mediated H_2O_2 transport. Stomatal movements play a key role in controlling plant water status and protecting plants against pathogens. Similar to abscisic acid (ABA), flg22, a pathogenic PAMP (see Glossary), requires AtPIP2;1 to induce stomatal closure [29]. The use of a generic probe for intracellular H_2O_2 revealed that both ABA and flg22 triggered the accumulation of H_2O_2 in wild-type guard cells but not in *atpip2;1* guard cells. When subjected to drought, excess light, and/or disease, ABA- and flg22-activated AtPIP2;1 is a key channel for reducing guard cell turgor and subsequently promoting stomatal closure (Fig. 3) [30]. However, a quadruple *atpip1;1/atpip1;2/atpip2;1/atpip2;2* mutant did not show a significant decrease in stomatal aperture and stomatal conductance (g_s) upon ABA treatment when compared to the wild-type line [31], suggesting that it requires further verification by other means.

Rice OsPIP2;2 transports pathogen-induced apoplastic H_2O_2 into the cytoplasm to intensify rice resistance to various pathogens. The OsPIP2;2-mediated transport of H_2O_2 is required for flg22 to activate the MAPK cascade and induce downstream defense responses [32]. A recent study demonstrated that wheat aquaporin TaPIP2;10 confers innate immunity against pathogens and aphid pests when phosphorylated at the S121 site to transport H_2O_2 from the apoplast into the cytoplasm [33]. *SlTIP1;1* knockout in tomatoes resulted in delayed organ abscission. Further analysis indicated that SlTIP1;1 mediated abscission via the gating of cytoplasmic H_2O_2 concentrations and cell turgor pressure, which in turn imposed a breaking force for abscission zone cell separation [34]. The accumulation of H_2O_2 in tobacco BY-2 cells expressing maize aquaporin *ZmPIP2;5* was detected using a fluorescence H_2O_2 sensor, indicating that ZmPIP2;5 can promote the transmembrane diffusion of H_2O_2. In contrast, the ZmPIP2W85A mutant protein lacks channel activity for transporting water or H_2O_2 [35]. A very recent study shows that an *AT1* (*Alkaline Tolerance 1*) locus was identified from natural high-alkaline-tolerant sorghum genome through GWAS analysis. AT1 encoding an atypical G protein γ subunit that affects the phosphorylation of aquaporins to modulate the distribution of hydrogen peroxide (H_2O_2). These processes appear to protect plants against oxidative stress by alkali [36].

2.2. Gases (CO_2, O_2, NO, NH_3)

The structural organization of aquaporins in tetramers results in the presence of a central or fifth pore located on the central symmetry axis of the four monomers. Structural biology studies suggest that these central pores and/or single pores can mediate the transport of gases (CO_2, O_2, NO, and NH_3) [37].

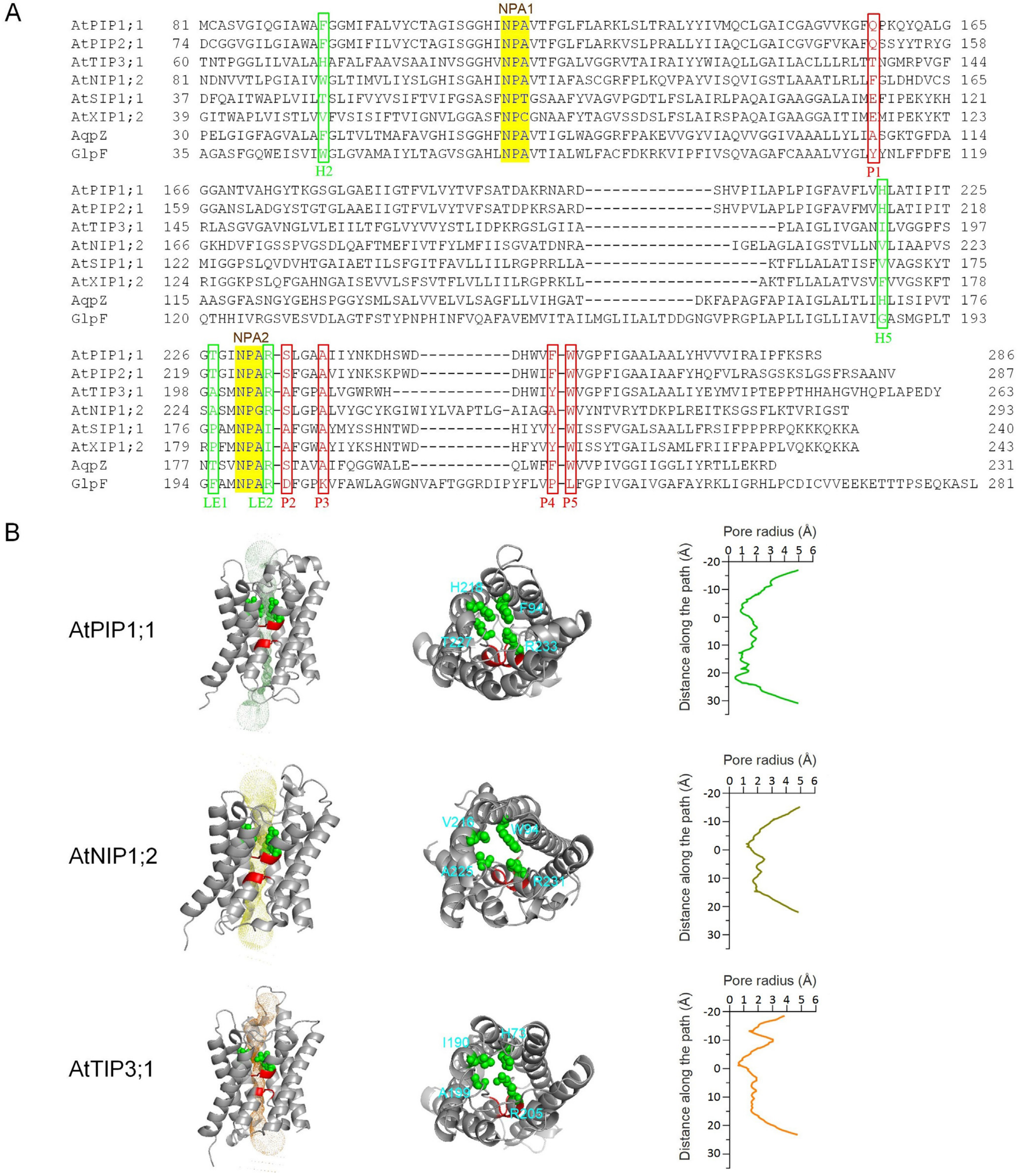

Fig. 1. Sequence alignment and channel structures of the representative aquaporins. (A) Comparison of NPA motifs (yellow highlighted), ar/R selectivity filters (in green), and Froger's positions (in red) of representative Arabidopsis and bacterial aquaporins from different subfamilies. (B) 3D channel structures, pathways, and pore sizes. The NPA motifs folded as half membrane-spanning helices that create dipole movement and stop proton (H^+) entry into the cell. The ar/R selectivity filters act as size exclusion filters for water and small molecules. Replacement of the hydrophilic H218 in AtPIP1;1 by the hydrophobic V216 and I190 in AtNIP1;2 and AtTIP3;1, and their different pore sizes and distances along the pathways that allow the permeation of multiple molecules besides water, and subsequently endow plant aquaporins with more physiological functions [61,85,89].

CO_2 is a substrate for plant photosynthesis and an end product of catabolism. The plasmalemma and chloroplast envelope membranes impose significant barriers to CO_2 diffusion in pathways from the substomatal cavity to the chloroplast stroma, limiting photosynthetic efficiency. Mounting evidence shows that CO_2-permeable aquaporins function in leaf mesophyll and stomatal

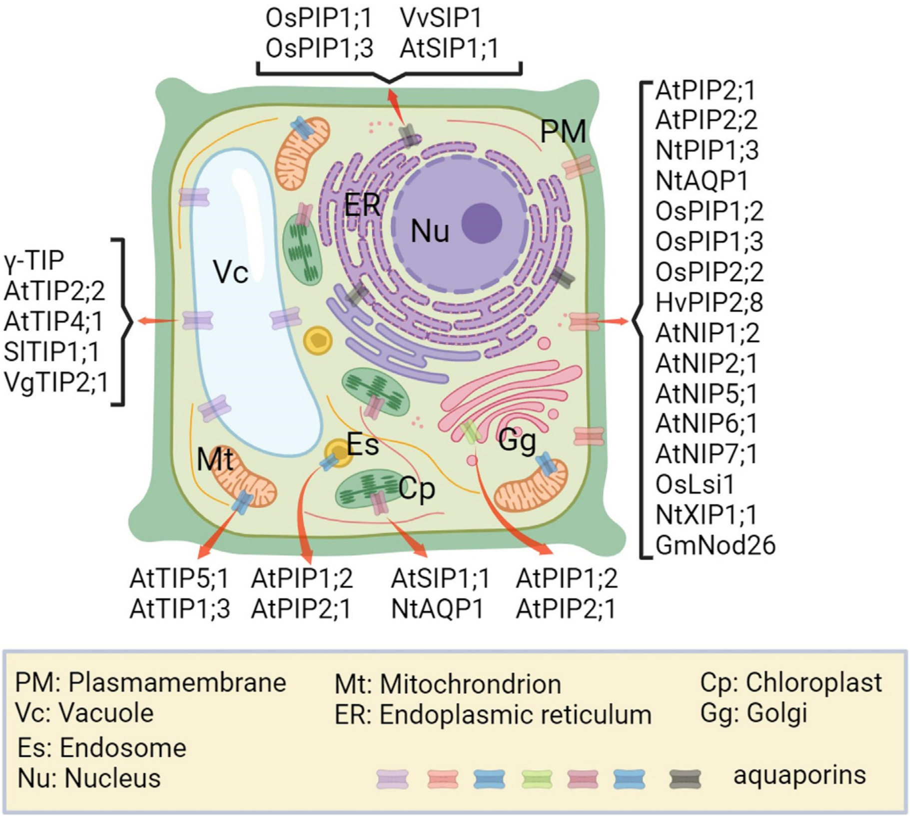

Fig. 2. Subcellular localization of the representative plant aquaporins and their permeable substrates and physiological functions. PM-localized aquaporins: AtPIP2;1: H_2O, H_2O_2, and ions for stomatal movement, resistance to disease and salt stresses [135,136]; AtPIP2;2: H_2O, H_2O_2, As, and ions for pollen dehydration and resistance to salt stress [97,135,136]; NtPIP1;3: O_2 for photosynthesis [44]; NtAQP1: H_2O and CO_2 for photosynthesis [39]; OsPIP1;2: H_2O and CO_2 for plant growth and yield [40,41]; OsPIP1;3: H_2O, CO_2, and NO_3^- for plant growth and resistance to disease and drought [20,22,50]; OsPIP2;2: H_2O and H_2O_2 for resistance to drought and disease [33,137]; HvPIP2;8: Na^+ and K^+ for plant resistance to salt stress [110]; AtNIP1;1: H_2O_2, glycerol, As and Sb for tolerance to abiotic and biotic stresses [29,69,104]; AtNIP2;1: lactic acid and As for resistance to hypoxia and metalloid stresses [66,67,69]; AtNIP5;1: urea, B and As for flower development and vegetative growth [53,64,103]; AtNIP6;1: urea, B and As for plant growth [53,64,89,103]; AtNIP7;1: Sb and B for resistance to metalloids and pollen development [53,70,74,103]; OsLsi1: B, Si, As, and Se for plant growth and tolerance to metalloids [69,79.80,81,88,90,99,133]; NtXIP1;1: B for plant development [77]; GmNod26: H_2O, NH_3, and glycerol for plant growth, nitrogen fixation, symbiosis, and resistance to salt stress [54,60,109]. ER-localized aquaporins: AtSIP1;1: H_2O and H_2O_2 for pollen germination [138]; VvSIP1: H_2O for stress tolerance [139]; OsPIP1;1: H_2O for seed germination, plant growth and salt resistance [41]; OsPIP1;3: H_2O, CO_2, and NO_3^- for plant growth and drought stress [22,50]. Es-localized aquaporins: AtPIP1;2 and AtPIP2;1: H_2O and ions for plant growth and resistance to salt stress [140]. Gg-localized aquaporins: AtPIP1;2 and AtPIP2;1: H_2O and ions for plant growth and resistance to salt stress [140]. Mt-localized aquaporins: AtTIP5;1: H_2O and urea for hypocotyl elongation and pollen development [141–143]; AtTIP1;3: H_2O and urea for pollen development [142,144]. Cp-localized aquaporins: AtSIP1;1: H_2O for pollen germination and pollination [138]; NtAQP1: H_2O and CO_2 for photosynthesis [39]. Vc-localized aquaporins: γ-TIP: H_2O [1,2]; AtTIP2;2: Zn^{2+} for resistance to heavy metal stress [113]; AtTIP4;1: H_2O and urea for seed germination [63]; SlTIP1;1: H_2O and H_2O_2 for organ abscission [35]; VgTIP2;1: H_2O and urea for plant growth [65]. This figure was designed with Biorender (https://biorender.com).

guard cells. Low concentrations of CO_2 induce stomatal opening, whereas high concentrations induce stomatal closure (Fig. 3) [38]. The functional dissection of an aquaporin (SsAqpZ) in the cyanobacterium *Synechococcus* sp. PCC7942 revealed the significant role of aquaporins in CO_2 gas diffusion. In yeast cells, SsAqpZ demonstrated CO_2 permeability. The *ssaqpz* mutant cyanobacterial lines exhibited lower CO_2 uptake, photosynthesis rate, and growth than the wild-type line in the air at different CO_2 concentrations [32]. Tobacco NtAQP1 is localized in the plasma membrane and the inner envelope of the chloroplast where it can substantially increase cellular CO_2 uptake rates (Fig. 2) [39]. In rice, the expression of *OsPIP1;2* in the leaves increased five-fold through high-CO_2 treatment. *OsPIP1;2* overexpression promotes mesophyll CO_2 conductance and photosynthetic efficiency. In field experiments, transgenic rice lines generated more effective tillers and spikelets per panicle and yielded 25% more grains than the wild-type line [40]. A similar report indicated that overexpression of *OsPIP1;3* in rice enhanced the photosynthesis rate and grain yield by 30% and 11%–34%, respectively [20]. Additional evidence suggests that the rice *ospip1;1* and *ospip1;2* mutant lines showed significantly lower mesophyll CO_2 conductance, photosynthetic rate, tiller number, and plant height than the wild-type line [41]. TaPIP2;10 can transport CO_2 to promote wheat photosynthesis and grain yield when phosphorylated at S280 [34]. However, the role of aquaporins as CO_2 permeable channels remains debatable [42]. Some studies have shown that simple manipulation of these aquaporins did not result in changes in mesophyll conductance or photosynthetic efficiency. In Arabidopsis, the mesophyll CO_2 conductance values of *atpip1;2*, *atpip1;3,* and *atpip2;6* mutants were not significantly different from those of the wild-type Arabidopsis line [43]. In addition, the ectopic expression of *AtPIP1;2* or *AtPIP1;4* in tobacco did not further increase mesophyll conductivity, nor the assimilation rate of CO2. Knockout of a PIP2 aquaporin (AtPIP2;3), which had no effect on CO_2-related processes.

O_2 is required for respiration in plants, and it is released as a byproduct of photosynthesis. Both direct and indirect evidence indicate the involvement of plant aquaporins in the transport of O_2 [44,45]. Plant response to hypoxia (see Glossary) involves the downregulation of aquaporin activity and function by pH-dependent gating and phosphorylation [46–48]. In trembling aspen (*Populus tremuloides*) seedlings, hypoxia inhibits the expression of aquaporin genes and root hydraulic conductance. Exoge-

Table 1
The permeable substrates and physiological functions of the representative plant and plant-related aquaporins.

Sub-family	Species	Aquaporin isoform	Substrate specificity	Physiological relevance	Reference
PIP1	*Arabidopsis thaliana*	AtPIP1;2	H_2O, CO_2	Growth, pollen dehydration, photosynthesis and resistance to salt stress	Luu et al. [140]; Kromdijk et al. [43]; Windari et al. [138]
		AtPIP1;3	H_2O, CO_2	Photosynthesis	Clarke et al. [38]
		AtPIP1;4	H_2O	Cold acclimation and freezing tolerance	Rahman et al. [158]
	Nicotiana tabacum	NtAQP1	H_2O, CO_2	Growth and photosynthesis	Fernández-San Millán et al. [39]
		NtPIP1;3	H_2O, O_2	Hypoxia	Zwiazek et al. [44]
	Oryza sativa	OsPIP1;1	H_2O, Na^+, K^+	Seed germination, growth and resistance to salt stress	Huang et al. [41]; Tao et al. [159]
		OsPIP1;2	H_2O, CO_2	Grain yield	Xu et al. [40]
		OsPIP1;3	H_2O, CO2, NO_3^-	Growth and stress resistance	Liu et al. [50]; Liu et al. [22]; Chen et al. [20]
	Citrus limonia	ClPIP1;1 ClPIP1;2	H_2O, Al^{3+}	Resistance to Al^{3+} stress	Cavalheiro et al. [160]
	Zygophyllum xanthoxylum	ZxPIP1;3	H_2O, H_2O_2	Growth and resistance to salt stress	Li et al. [147]
	Solanum nigrum	SnPIP1;5	H_2O, NH_4^+	Resistance to Cd stress	Zhang et al. [112]
	Helianthemum almeriense	HaPIP1;1	H_2O, CO_2, NH_3	Tolerance to drought stress	Navarro-Ródenas et al. [161]
PIP2	*Arabidopsis thaliana*	AtPIP2;1	H_2O, Na^+, K^+, CO_2, H_2O_2	Seed germination, root growth, stomatal movement and tolerance to salt and drought stresses	Luu et al. [140]; Byrt et al. [136]; Kourghi et al. [162]; Rodrigues et al. [10]; Ding et al. [146]; Qiu et al. [47]; Cui et al. [29]; Rodrigues et al. [30]; Hoai et al. [163]
		AtPIP2;2	H_2O, H_2O_2, Na^+, As	Growth and resistance to As and salt stresses	Hooijmaijers et al. [135]; Byrt et al. [136]; Kourghi et al. [162]; Modareszadeh et al. [97]
		AtPIP2;4	H_2O, H_2O_2	Growth	Hooijmaijers et al. [135]
		AtPIP2;5	H_2O, H_2O_2	Growth and cold acclimation	Hooijmaijers et al. [135]; Rahman et al. [158]
		AtPIP2;7	H_2O, H_2O_2	Growth	Hooijmaijers et al. [135]
	Zea mays	ZmPIP2;1	H_2O	AM symbiosis and resistance to drought stress	Quiroga et al. [151]
		ZmPIP2;4	H_2O, NH_4^+, urea	AM symbiosis and resistance to drought stress	Quiroga et al. [58]
		ZmPIP2;5	H_2O, H_2O_2, Li^+	Stomatal closure and redox signaling	Ahmed et al. [35]; He et al. [118]
	Oryza sativa	OsPIP2;2	H_2O, H_2O_2	Defense, drought tolerance	Bai et al. [137]; Zhang et al. [32]
		OsPIP2;4 OsPIP2;6 OsPIP2;7	H_2O, As	Growth	Mosa et al. [100]
		OsPIP2;8	H_2O	Seed germination	Liu et al. [50]
	Gentiana scabra	GsPIP2;2	H_2O	Corolla movement, flower development	Nemoto et al. [164]
	Beta vulgaris	BvPIP2;2	H_2O	pH gating and sensing and resistance to hypoxia stress	Scochera et al. [48]
	Hordeum vulgare	HvPIP2;8	H_2O, Na^+, K^+	Salt stress resistance	Tran et al. [110]
	Populus tremuloides	PtPIP2;4 PtPIP2;5	H_2O	Resistance to hypoxia stress	Tan et al. [49]
	Prunus dulcis	PdPIP2;2	H_2O	Growth	Rios et al. [126]
	Triticum aestivum	TaPIP2;10	H_2O, H_2O_2, CO_2	Growth and defense	Lu et al. [33]
	Nicotiana benthamiana	NbPIP2;2	H_2O, H_2O_2	Disease resistance	Ai et al. [153]
	Kandelia obovata	KoPIP2;1	H_2O	Cold tolerance	Fei et al. [165]
	Solanum nigrum	SnPIP2;7	H_2O, NH_4^+	Resistance to Cd stress	Zhang et al. [112]
	Gossypium hirsutum	GhPIP2;7	H_2O, urea	Resistance to drought	Guo et al. [154]
	Helianthemum almeriense	HaPIP2;1	H_2O, CO_2, NH_3	Tolerance to drought stress	Navarro-Ródenas et al. [161]
TIP	*Arabidopsis thaliana*	AtTIP1;1	H_2O, urea	Growth and resistance to nematode	Liu et al. [63]; Baranowski et al. [152]
		AtTIP1;2	H_2O, urea	Growth and resistance to nematode	Liu et al. [63]; Baranowski et al. [152]
		AtTIP1;3	H_2O, urea	Pollen development	Soto et al. [144]; Wudick et al. [142]
	Zea mays	ZmTIP1;1	H_2O, NH_4^+, urea	AM symbiosis and resistance to drought stress	Quiroga et al. [58]
	Solanum lycopersicum	SlTIP1;1	H_2O, H_2O_2	Pedicel abscission	Wang et al. [34]
	Helianthemum almeriense	HaTIP1;1	H_2O, CO_2, NH_3	Tolerance to drought stress	Navarro-Ródenas et al. [161]
	Prunus dulcis	PdTIP1;1	H_2O	Growth	Rios et al. [126]

(continued on next page)

Table 1 (*continued*)

Sub-family	Species	Aquaporin isoform	Substrate specificity	Physiological relevance	Reference
	Arabidopsis thaliana	AtTIP2;1	H_2O, urea, NH_3	Growth	Liu et al. [63]; Loqué et al. [55]; Kirscht et al. [56]
		AtTIP2;2	H_2O, Zn^{2+}	Resistance to heavy metal	Wang et al. [24]
		AtTIP2;3	H_2O, urea, NH_3	Growth	Loqué et al. [55]
	Gossypium hirsutum	GhTIP2;1	H_2O, urea	Resistance to drought	Guo et al. [154]
	Citrus sinensis	CsTIP2;1	H_2O, H_2O_2	Growth, redox	Martins et al. [166]
	Zea mays	ZmTIP2;1	H_2O, Co^{2+}	Resistance to heavy metal	Ozfidan-Konakci et al. [167]
	Vriesea gigantea	VgTIP2;1	H_2O, urea	Growth	Matiz et al. [65]
	Prunus persica	PpTIP2	H_2O	Temperature sensitivity, flower type and size	Lian et al. [168]
	Vitis heyneana	VhTIP2;1	H_2O	Drought tolerance	Zhang et al. [169]
	Solanum nigrum	SnTIP2;1	H_2O, NH_4^+	Resistance to Cd stress	Zhang et al. [112]
	Zea mays	ZmTIP3;1	H_2O	Seed germination and seedling development	Su et al. [170]
	Arabidopsis thaliana	AtTIP4;1	H_2O, urea	Growth	Liu et al. [63]
	Pteris vittata	PvTIP4;1	H_2O, As	Stress resistance	He et al. [130]
	Arabidopsis thaliana	AtTIP5;1	H_2O, urea	Pollen development	Soto et al. [144]
	Populus alba	Aqua1	H_2O, Zn^{2+}	Resistance to heavy metal	Neri et al. [129]
NIP	*Arabidopsis thaliana*	AtNIP1;1	H_2O, H_2O_2, As, Sb	Cell death, hypoxia stress	Bienert et al. [69]; Kamiya et al. [104]; Sadhukhan et al. [28]
		AtNIP1;2	H_2O, As, Al^{3+}	Resistance to Al^{3+} stress	Kamiya et al. [104]; Wang et al. [115]
	Prunus avium	PaNIP1;1	H_2O, lactic acid	Hypoxia stress	Mateluna et al. [171]
	Oryza sativa	OsNIP1;1	H_2O, As	Resistance to metalloids	Sun et al. [101]
	Vitis vinifera	VvTnNIP1.1	H_2O, gly, Co^{2+}, Se	Not determined	Sabir et al. [61]
	Arabidopsis thaliana	AtNIP2;1	H_2O, lactic acid, As	Hypoxia stress	Choi et al. [66]; Bienert et al. [69]; Beamer et al. [67]
	Oryza sativa	OsNIP2;1 (Lsi1)	H_2O, Si, Se, As, B, Sb	Growth, seed development, and tolerance to various biotic and abiotic stresses	Ma et al. [79]; Bienert et al. [69]; Ma et al. [99]; Zhao et al. [90]; Fang et al. [80]; Li et al. [81]; Kiany et al. [133]; Mukarram et al. [88]
		OsNIP2;2 (Lsi6)	H_2O, As, Sb, Si	Growth	Bienert et al. [69]; Ma et al. [99]; Kiany et al. [133]
	Hordeum vulgare	HvNIP2;1	H_2O, Ge, B, As, KCl, $MgSO_4$, sucrose, and lactose	Resistance to metalloids	Venkataraghavan et al. [111]
	Cajanus cajan	CcNIP2-1	H_2O, As, Sb, Ge	Resistance to metalloids	Mandlik et al. [105]
	Lagenaria siceraria	LsiNIP2-1	H_2O, Si	Leaf development	Kumawat et al. [172]
	Vitis vinifera	VvNIP2;1	H_2O, Si, As	Fruit development	Noronha et al. [87]
	Vigna radiata	VrNIP2-1	H_2O, As, GeO_2, Si	Uptake of metalloids	Thakral et al. [173]
	Oryza sativa	OsNIP3;2	H_2O, As, Sb	As absorption and transport	Bienert et al. [69]; Chen et al. [148]
		OsNIP3;3	H_2O, As	Resistance to metalloids	Sun et al. [101]
	Brassica napus	BnNIP4;1	H_2O, B	Growth and pollen development	Diehn et al. [174]
	Arabidopsis thaliana	AtNIP5;1	H_2O, As, B, urea, Sb	Flower development and vegetative growth	Takano et al. [68]; Bhattacharjee et al. [103]; Kamiya et al. [104]; Yang et al. [64]; Pommerrenig et al. [89]; Kolbert et al. [53]
	Vitis vinifera	VvTnNIP5;1	H_2O	Not determined	Sabir et al. [61]
	Medicago truncatula	MtNIP5;1	H_2O, B	Rhizobial symbiosis	Granado- Rodríguez et al. [149]
	Physcomitrella patens	PpNIP5;2	H_2O, B, As, Ge	Growth	Pommerrenig et al. [89]
	Brassica napus	BnNIP5;1	H_2O, B	Growth and pollen development	Diehn et al. [174]
	Arabidopsis thaliana	AtNIP6;1	H_2O, As, B, urea, Sb	Growth	Bhattacharjee et al. [103]; Yang et al. [64]; Pommerrenig et al. [89]; Kolbert et al. [53]
	Vitis vinifera	VvTnNIP6;1	gly	Not determined	Sabir et al. [61]
	Brassica napus	BnNIP6;1	H_2O, B	Growth and pollen development	Diehn et al. [174]
	Arabidopsis thaliana	AtNIP7;1	H_2O, Sb, B, As	Growth and pollen development	Bhattacharjee et al. [103]; Isayenkov et al. [70]; Routray et al. [74]; Kolbert et al. [53]
	Brassica napus	BnNIP7;1	H_2O, B	Growth and pollen development	Diehn et al. [174]
	Glycine max	GmNOD26	H_2O, gly, NH_3, formamide, malate	Growth, nitrogen fixation, nodule symbiosis and resistance to salt stress	Dean et al. [60]; Hwang et al. [54]; Tyerman et al. [109]
SIP	*Arabidopsis thaliana*	AtSIP1;1	H_2O	Pollen dehydration	Windari et al. [138]
	Vitis vinifera	VvSIP1	H_2O	Not determined	Noronha et al. [139]
XIP	*Nicotiana tabacum*	NtXIP1;1	H_2O, B, gly, H_2O_2, urea	Flower development	Bienert et al. [175]; Bienert et al. [77]
	Vitis vinifera	VvXIP1	H_2O, gly, H_2O_2, B, Cu^{2+}, As, Ni^{2+}	Resistance to abiotic stresses	Noronha et al. [176]

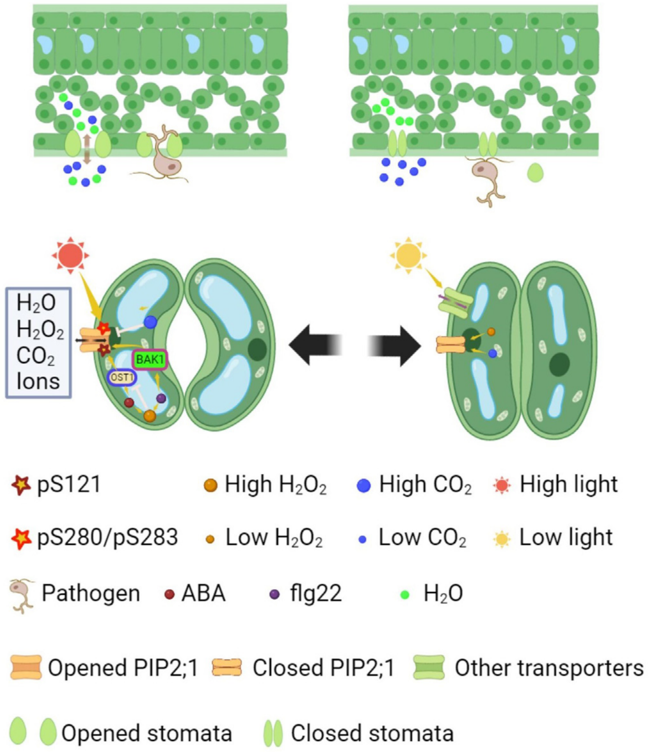

Fig. 3. Participation of aquaporins in the regulation of stomatal movement. AtPIP2;1 can transport H_2O, H_2O_2, CO_2, and ions across the plasma membrane of guard cells [30]. ABA and pathogen PAMP flg22 can activate OST1 and BAK1 kinases to phosphorylate Ser121 of AtPIP2;1 and close the stomata to block pathogen and drought stress [10]. The excess light triggers phosphorylation of the S280/S283 sites to close stomata via the induction of high levels of H_2O_2. The low levels of H_2O_2 and CO_2 may directly activate AtPIP2;1 to induce stomatal opening, and the low light may activate the other channels or transporters to induce stomatal opening [31,145]. The appropriate regulation of stomatal movement is critical for plant transpiration, photosynthesis, and prevention from pathogen attack and drought stress. This figure was designed with Biorender (https://biorender.com).

nous ethylene treatment enhances the transcript abundance of *PtPIP2;4* and *PtPIP2;5* in hypoxic roots. The increased number of aquaporins could potentially facilitate root water transport, which could in turn enhance gas exchange in hypoxic plant leaves and roots [49].

Nitric oxide (NO) is an important gas signaling molecule that is involved in several pathways. An early study in rice showed that exogenous NO stimulates the expression of *OsPIP1;1*, *OsPIP1;2*, *OsPIP1;3*, and *OsPIP2;8* in germinating seeds, suggesting that aquaporins play a critical role in seed germination in response to NO signaling [50]. NO is a key regulator of plant-rhizobium symbioses (see Glossary). The fungus *Laccaria bicolor* has an ectomycorrhizal association with its host plant, trembling aspen. The expression of fungal *LbAQP1* and *LbAQP6* in yeast revealed that LbAQP1, but not LbAQP6, had NO permeability, suggesting that the aquaporin LbAQP1 acts as a molecular signaling channel, which is essential in the development of ectomycorrhizal symbiosis in *P. tremuloides* roots [51]. NO also participates in the regulation of plant responses to salt and metalloid stress. Salt treatment enhances the protein levels of aquaporins HaPIPs and HaTIPs in sunflower (*Helianthus annuus*) roots, whereas exogenous application of NO downregulates the abundance of these aquaporins, suggesting a correlation between AQPs and ion homeostasis in response to salt stress and NO [52]. The primary role of NO in metalloid stress response is to alleviate oxidative stress by activating antioxidant defense at the level of protein activity and gene expression. Since metalloid transporters are proteins and NO signaling is achieved mainly by posttranslational modifications, NO may regulate proteins via S-nitrosation, increasing or decreasing their metalloid transport activity. This hypothesis has been validated in silico. NO intensified the stress-mitigating effect of silicon (Si) but enhanced the toxic effects of arsenic (As) and antimony (Sb), whereas NO promoted the beneficial effect of Se at low concentrations and alleviated the damage caused by boron (B) deficiency [53].

NH_3 is a gaseous nitrogen nutrient for plants and a product of nitrogen fixation by rhizobia during symbiosis·NH_3 must be transported to specific locations to be converted into non-toxic products and exported out of the cells·NH_3 transport across membranes has received new attention in light of a subgroup of animal and plant aquaporins named ammoniaporins (see Glossary). The presence of isoleucine or valine in the constriction region of NIPs and TIPs makes the channels more hydrophobic and allows NH_3 transport (Fig. 1B) [12]. Soybean GmNod26 is the most abundant aquaporin protein in the symbiosome (see Glossary) membrane (SM). The isolated SM vesicles demonstrated NH_3 permeability, which could be inhibited by Hg^{2+}, suggesting that this activity was mediated by aquaporins [54]. Arabidopsis AtTIP2;1 and AtTIP2;3 facilitate NH_3 transport into vacuoles [55,56]. In the model pennate diatom *Phaeodactylum tricornutum*, both *PtAQP1* and *PtAQP2* were highly induced by ammonia and high CO_2 (1%). Constitutive overexpression of *PtAQP1* and *PtAQP2* significantly increased CO_2 and NH_3 permeability in *P. tricornutum*, indicating that these algal aquaporins mediated CO_2/NH_3 conductance [57]. Arbuscular mycorrhizae (AM) (see Glossary) symbioses are usually beneficial to host plants. In maize, *ZmTIP1;1* and *ZmPIP2;4* genes were upregulated by ammonia and AM symbiosis, suggesting the importance of their roles in AM-mediated N homeostasis in maize [58].

2.3. Neutral organic compounds (glycerol, urea, lactic acid)

The MIP superfamily can be divided into aquaporin and aquaglyceroporin (see Glossary) families based on evolutionary pathways, structure, and substrate selectivity. Aquaglyceroporin families contain subfamilies with multiple functions including the transport of H_2O and some neutral organic compounds [59].

Similar to the well-known glycerol transporter GlpF in *E. coli*, the soybean GmNod26 could transport glycerol 43-fold higher than the control in the SM vesicles, which was further confirmed in *Xenopus* oocytes showing that GmNod26 facilitated glycerol flux in a manner indistinguishable from the GlpF glycerol facilitator [60]. Several Nod26-like intrinsic proteins have since been functionally characterized. When grape (*Vitis vinifera*) *VvTnNIP1;1*, *VvTnNIP5;1*, and *VvTnNIP6;1* were heterogeneously expressed in a yeast *aqy*-null mutant, VvTnNIP5;1 exhibited only water permeability and VvTnNIP1;1 demonstrated high water and glycerol permeability, whereas VvTnNIP6;1 was impermeable to water but presented high glycerol permeability. Phylogenetic analysis of NIPs from various plant sources demonstrated the unambiguous clustering of VvTnNIP1;1 with the archetype GmNod26 [61]. The physiological importance of glycerol in plants is still unclear because no apparent role in osmoregulation has been found in opposition to the aquaglyceroporin (Fps1) channel in yeast. However, glycerol has been proposed as a carbon source in plants, and exogenous glycerol has been shown to affect plant and root growth [62].

Urea is a plant nutrient that is rapidly degraded by soil microorganisms to ammonia and nitrate; it is also directly acquired and utilized by plants. Similar to glycerol, urea needs larger pores to pass through than water molecules (Fig. 1B). Using heterologous complementation of a urea uptake-defective yeast mutant, AtTIP1;1, AtTIP1;2, AtTIP2;1, and AtTIP4;1 were found to transport urea from an Arabidopsis cDNA library. Uptake studies using ^{14}C-labeled urea in *AtTIP2;1*-expressing *Xenopus* oocytes demonstrated that AtTIP2;1 facilitated urea transport in a

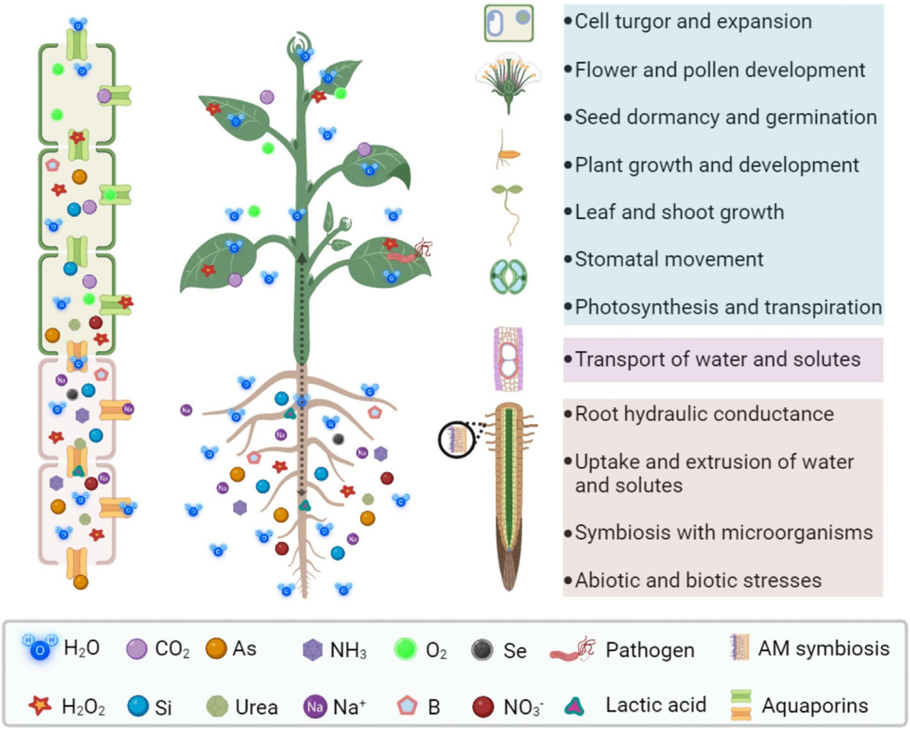

Fig. 4. Schematic diagram of uptake of different molecules by aquaporins and the resulting physiological phenomena in plants. Plant aquaporins can take up and transport several molecules besides water to exert many physiological functions. Water flux via aquaporins directly determines cell turgor, expansion, and division [22,41]; flower opening, seed germination, and seedling growth [8,12,74]; CO_2 uptake, O_2 release, photosynthesis, and transpiration [20,37,38,42–44]; leaf and root growth and development [12,41,146,147]; Uptake and extrusion of beneficial and harmful elements besides water by roots from soil [69,71,94,99,120,121,132,136,148,149]; plant-rhizobium symbioses [58,150,151]; Abiotic and biotic stresses [84,123,137,152–155]. This figure was designed with Biorender (https://biorender.com).

pH-independent manner [63]. Although AtNIP5;1 and AtNIP6;1 demonstrated urea permeability in *Xenopus* oocytes, they exhibited distinct expression patterns in response to exogenous urea in Arabidopsis. *AtNIP5;1* was induced but *AtNIP6;1* was strongly repressed by urea [64]. In maize roots, urea-induced *ZmTIP1;1*, and the use of ^{15}N-labelled urea showed that ZmTIP1;1 is involved in urea transport in yeast and *in planta* [58]. Tropical plant epiphytic bromeliads (*Vriesea gigantea*) can obtain nitrogen by decomposing debris and excreta of associated organisms. $HgCl_2$ treatment reduced urea absorption by 78%, indicating the role of aquaporins in urea uptake. Functional characterization of *VgPIP1;1*, *VgPIP1;2*, and *VgTIP2;1* in yeast and *Xenopus* oocytes suggests that VgTIP2;1 is capable of transporting urea and H_2O [65].

The first aquaporin to transport lactic acid was identified in *Lactobacillus plantarum* [66]. Similar to animals, when plants experience O_2 depletion, the energy crisis triggers anaerobic fermentation to produce lactic acid and induces the expression of *NIP* aquaporin genes to overcome hypoxic stress by mediating lactic acid transport [45]. Arabidopsis *AtNIP2;1* is predominantly expressed in root vascular tissues and is significantly upregulated by hypoxic stress. Functional characterization in *Xenopus* oocytes indicated that AtNIP2;1 mediates lactic acid permeability in a pH-dependent manner [67]. In response to a hypoxic challenge, the Arabidopsis *atnip2;1* mutant lines accumulate lactic acid within root tissues and compromise acidification of the external medium due to reduced efflux of lactic acid. The *atnip2;1* mutant lines also exhibit poor survival during hypoxic stress with a high incidence of chlorosis and seedling death [67].

2.4. Metalloids (B, Si, Se, As, Sb, Ge)

Metalloids (see Glossary) are present in polluted soil and water as either negatively charged ions or uncharged molecules, depending on the environmental pH and redox potential. Metalloids play a variety of roles in biological processes, ranging from essential to toxic. Metalloid homeostasis in plants is primarily regulated by aquaporins [68–72].

B is essential for the growth of most plant species and must be finely regulated to an optimal range. Plant NIP aquaporins play critical roles in plant growth and development by facilitating the efficient transport of B across biological membranes [73]. Arabidopsis AtNIP7;1 is involved in pollen cell wall formation and exhibits boron permease activity without water permeability. The *atnip7;1* mutant produces defective pollen with low germination rates and causes deformative siliques with the abortion of seed development [74]. Rapeseed (*Brassica napus*) is an oil crop that requires plenty of B for growth and reproduction. In rapeseed QY10 variety, *BnaA3.NIP5;1*, *BnaA2.NIP5;1,* and *BnaA3.NIP5;1* were identified as B-efficient candidate genes. Genetic modification of these gene expression levels significantly alters B uptake. Notably, elevated expression of a *BnaA3.NIP5;1*^{Q} allele caused by the presence of a CTTTC tandem repeat in its 5′ UTR made a significant contribution to high rapeseed yields in natural populations and near-isogenic lines (NILs) [75,76]. In addition to the NIP subfamily, the XIP subfamily may facilitate B transport. Some monocots and dicots, including *A. thaliana* are assumed to have lost XIPs. B deprivation induced the tobacco *NtXIP1;1* transcript, and the encoded protein transported B in *Xenopus* oocytes. Overexpression of *NtXIP1;1* in plants caused abnormal growth and infertility, but exogenous boric acid effectively alleviated these symptoms [77].

Si has beneficial effects on plants. Staple food crops such as rice, wheat, barley, and maize accumulate high levels of Si, resulting in improved plant growth and crop yields. In the past decade, silicon-transporting proteins have been identified in several monocot and dicot species [78]. The discovery of the first silicon transport channel protein, OsLsi1 (OsNIP2;1) in rice prompted the search for silicon transport mechanisms in other plant species. *OsLsi1* mutation resulted in reduced Si uptake and accumulation. The *oslsi1* mutant rice yielded only one-tenth of the grains of wild-type rice and was susceptible to pests and diseases [79]. *OsLsi1*-OE rice plants deposited significant amounts of Si, displaying a high tolerance to various biotic and abiotic stresses [80,81]. Silicon can upregulate *OsLsi1* expression and can subsequently stimulate the *Salt-Overly Sensitive* (SOS) pathway to enhance salinity stress tolerance and yield in rice [82]. The o*slsi1* mutant plants displayed higher susceptibility to leaffolder (*Cnaphalocrocis medinalis*) and blast fungus (*Magnaporthe grisea*) [83,84]. The crystal structure of the rice OsLsi1 protein shows that the hydrophilic selectivity filter comprising five residues (T65, G88, S207, G216, and R222) is critical for its activity [85]. The tobacco (*Nicotiana sylvestris*) NsLsi1 protein is a rare exception with these molecular signatures and has been reported to be a low-Si accumulator. In *Xenopus* oocytes, NsLsi1 exhibited approximately 10% Si permeability of OsLsi1 but the NsLsi1(P125F) mutant displayed significantly enhanced Si transportability [86]. Recently, several novel Si transporters from woody plants have been functionally characterized [61,87,88].

The trace mineral Se is essential to human and animal health. Although the importance of Se in higher plants has not been recognized, plants are the main sources of dietary Se. However, the mechanisms by which plants absorb Se from the environment are poorly understood [89]. Se can also be transported by the rice silicon transporter OsNIP2;1. When the *oslsi1* rice mutant and wild-type rice lines were exposed to Se solutions for a certain period, the accumulated Se levels in shoots and xylem saps of the wild-type line were significantly higher than those in the *oslsi1* mutant lines. Moreover, the expression of *OsNIP2;1* in yeast enhances selenite uptake in a pH-dependent manner [90]. Plants can absorb both inorganic and organic Se through aquaporins. Radish, rice, and wheat can uptake organic Se when fed with selenomethionine (SeMet), methylselenocysteine (MeSeCys), and selenomethionine-oxide (SeOMet), which could be inhibited to different degrees by aquaporin inhibitors ($AgNO_3$ and carbonyl cyanide 3-chlorophenylhydrazone (CCCP)), suggesting that Se may be transported through aquaporins [91–93]. Recently, the tea (*Camellia sinensis*) aquaporin (*CsNIP2;1*) gene was found to be upregulated by exogenous Se, providing evidence that aquaporins are involved in Se transport in woody plants [94].

Arsenic (As) is a non-essential toxic metalloid found in all living organisms. Aquaporins are critical for As uptake and efflux. Owing to the structural similarity between arsenite and glycerol, *E. coli*, yeast, and mammalian aquaglyceroporins GlpF, FPS1, AQP7, and AQP9 have been found to transport As in addition to glycerol [95]. Several plant NIP aquaporins, such as Arabidopsis AtNIP1;1, AtNIP1;2, AtPIP2;2, AtNIP3;1, AtNIP5;1, AtNIP6;1, and AtNIP7;1, have been shown to transport arsenite and arsenate *in planta* and in heterologous systems [72,96–98]. Rice is a hyperaccumulator of As. In *Xenopus* oocytes and yeast, OsLsi1 (OsNIP2;1) showed As influx permeability. The *oslsi1* rice mutant accumulated less As than the wild-type rice. As and Si are efficiently accumulated in rice as they have a common highly efficient pathway in grains [99–101]. In addition, OsNIP1;1, OsNIP2;2, OsPIP2;4, OsPIP2;6, OsPIP2;7, OsNIP3;1, OsNIP3;2, and OsNIP3;3 showed arsenite permeability *in vitro* and *in planta* [99–101]. OsNIP1;1 and OsNIP3;3 were also found to be highly permeable to arsenite in *Xenopus* oocytes. The overexpression of *OsNIP1;1* or *OsNIP3;3* inhibited root-to-shoot translocation of arsenite and markedly decreased the shoot arsenic concentration [101]. Expression of wheat *TaNIP2;1* in yeast *Δfps1* and *Δacr3* mutants altered yeast sensitivity to As stress, and ectopic expression of *TaNIP2;1* in Arabidopsis increased As levels in transgenic plants [102].

The transport of Sb and Ge by aquaporins has seldom been reported. Since antimonite Sb(III), germanite Ge(III), and arsenite As(III) have similar structures and chemical properties as glycerol, they can all be absorbed by *E. coli* via the glycerol channel GlpF. In plants, these metalloids may be taken up in similar ways. Arabidopsis can take up Sb through AtNIP5;1, AtNIP6;1, and AtNIP7;1, with different affinities [103]. Expression of *AtNIP5;1* and *AtNIP6;1* in yeast lowers sensitivity to Sb, but *AtNIP7;1* elevates yeast sensitivity to Sb [104]. Pigeonpea (*Cajanus cajan*) is a silicon accumulator, mainly through CjNIP2;1. Exogenous Si application induces the expression of *CjNIP2;1* and alleviates Sb toxicity, implying that Si may competitively antagonize Sb to pass through CjNIP2;1 [105]. Barley (*Hordeum vulgare*) is highly sensitive to Ge toxicity. Two barley QTLs associated with Ge toxicity symptoms were located on chromosomes 6H and 2H. The 6H locus includes *HvNIP2;1*. In yeasts, functional expression of *HvNIP2;1* in yeast enhances sensitivity to Ge stress. Expression of *HvNIP2;1*(G88A) and *HvNIP2;1* (G88C) alleviated yeast sensitivity to B and Ge, but enhanced yeast sensitivity to As, suggesting that HvNIP2;1 may transport Ge, B, and As [106]. The grape *VvNIP2;1* gene is predominantly expressed in roots. VvNIP2;1 showed Ge, Si, and As permeability in *Xenopus* oocytes [87]. Overall, the mechanisms underlying Sb and Ge transport remain elusive, and further investigation is required in the future.

2.5. Charged ions

Most aquaporins transport water and/or uncharged inorganic or organic molecules. A subset of aquaporins, however, can transport charged cations or anions and act as ion-conducting aquaporins [107,108]. Although the concept of ion channel function in aquaporins remains controversial, researchers are beginning to define not only the ion channel function but also the detailed molecular mechanisms that govern and mediate multifunctional aquaporin capabilities [109].

Since the first ion-conducting aquaporin, soybean GmNod26, was characterized, several plant ion-conducting aquaporins have been reported. AtPIP2;1 is implicated in stomatal closure (Fig. 3). In *Xenopus* oocytes and yeast, AtPIP2;1 increased water permeability and induced non-selective cation conductance, mainly associated with Na^+. The phosphorylation states of S280 and/or S283 promoted AtPIP2;1-facilitated water and cation (Na^+ and K^+) transport [47]. In *Xenopus* oocytes, the expression of barley *HvPIP2;8* showed ion conductance of Na^+ and K^+, implying that HvPIP2;8 may be involved in barley salt-stress responses [110]. Unlike barely PIP family members, the solute selectivity analysis of NIP family member HvNIP2;1 showed that HvNIP2;1 permeated disaccharide sucrose and hydrated ion pairs KCl and $MgSO_4$ at a high rate, while CH_3COONa and $NaNO_3$ ion pairs transported at a lower rate [111]. Novel ion-conducting aquaporins have also been reported. Cd^{2+} can upregulate the expression levels of *SnPIP1;5*, *SnPIP2;7*, and *SnTIP2;1* to enhance NH_4^+ but inhibit NO_3^- absorption in *Solanum nigrum*, implying that the ions may be taken up through these channels [112]. A very recent study shows that a novel fluorescent photo-switchable Li^+ sensor was used to determine the cation channel activity of ZmPIP2;5 in BY-2 cells [35]. AtTIP2;2 is localized to the tonoplasts in the root cells, it presumably facilitates Zn sequestration from the cytosol to the vacuole of the root cell [113]. The cellular GSH could function as an AtTIP2;2 activator, or it may be part of the transport substrate of AtTIP2;2 in the form of a GSH-Zn complex. When expressed in yeast, AtTIP2;2 facilitates the across tonoplast transport of GSH-Zn complexes. *Hydrangea macrophylla* regulates flower color by transporting Al^{3+} through aquaporins HmVALT and HmPALT1, the overexpression of *VALT* and *PALT1* in Arabidopsis conferred Al-tolerance and Al-sensitivity, respectively [114]. Arabidopsis AtNIP1;2 can transport malate and AtNIP2;1 can conduct lactate [67,115]. We used an electrophysiological approach to demonstrate that rice OsPIP1;3

showed permeability to nitrate (NO_3^-). Overexpression of OsPIP1; 3 in tobacco promotes plant growth and resistance to drought stress [22].

With the development of new techniques, an increasing number of novel substrates for known and unknown aquaporins can be identified, which can help us understand how aquaporins play critical functions in plant biology and physiology (Fig. 4).

3. Potential biotechnology applications of plant aquaporins

With the rapid development of biotechnology and bioengineering, many promising aquaporin genes have been genetically manipulated in certain plants to generate expected phenotypes and performances for practical applications. These applications include genetic modification and the use of nanomaterials such as nanoparticles (see Glossary), quantum dots (see Glossary), graphene oxide (GO) (see Glossary), and chemicals to regulate aquaporin activities [116,117]. A very recent report shows that coronatine (COR), a jasmonic acid analog, can enhance the expression level of *ZmPIP2;5* gene and the hydraulic conductivity in maize roots by binding to the N241 residue in loop E of ZmPIP2;5 [118]. These technologies advance our understanding of how a given AQP isoform contributes to the homeostasis of water and other components, particularly under adverse conditions. Several functional genomics studies have shown that aquaporin modulation can increase plant tolerance to stress conditions and crop yield [13,59,116]. For example, the treatment of broccoli protoplasts with 10 μg mL^{-1} nanotubes significantly increased *BoPIP1* and *BoPIP2* expression levels and osmotic permeability under normal conditions but not under salt stress conditions [119]. Here, we focus on the recent progress in the uptake of beneficial and/or extrusion of harmful metalloids by the regulation of plant aquaporins, and the potential value of these technologies in agriculture, horticulture, and environmental protection.

3.1. Enrichment of beneficial elements and application in agriculture

Some plant aquaporins transport selenium and silicon. Se is an essential trace nutrient for animals. People who are Se-deficient suffer from many health problems (e.g., cancers and cardiovascular diseases); therefore, it is important to acquire sufficient Se nutrients from food sources. Plants, especially cereals and their products, are the principal sources of dietary selenium, but their selenium content is usually too low to meet human nutritional requirements. Genetic manipulation of specific aquaporins may enhance Se content in plants. For example, the aquaporin OsLsi1 (OsNIP2;1) transports Se in rice. *OsLsi1* knockout resulted in a significant decrease in Se concentration in the shoots, xylem sap fluids, and rice grains [90]. Therefore, the proper modification of *OsLsi1* expression should efficiently increase Se uptake in rice grains. Another method for increasing plant Se content is to apply Se fertilizer to the plants. Red Se nanoparticles (SeNPs) are highly bioactive in plants. Under the SeNPs treatment, Se was primarily accumulated in roots of rice rather than in shoots, whereas the addition of aquaporin inhibitors reduced the absorption of SeNPs by rice [120]. Similar results were observed for the SeNP-treated wheat seedlings [121]. These findings suggest that SeNPs are mainly taken up via the aquaporin pathways. A recent report indicated that SeNPs elevated the expression levels of *BnPIP1;1* and *BnPIP2;1* in rapeseed (*Brassica napus*) and increased plant resistance to salt stress [122].

Si is a beneficial macronutrient for plants. The application of Si fertilizer is known to be an ecologically compatible and environmentally friendly technique for stimulating plant growth and enhancing plant resistance to multiple stresses [123]. Silicon nanoparticles (SiNPs) and silicon quantum dots (SiQDs) have been used in agriculture and postharvest preservation of horticultural products. Treating ginger (*Zingiber officinale*) rhizomes with 50–100 μg mL^{-1} SiNPs increased the firmness and disease resistance and decreased decay severity. SiNPs likely decreased water loss by altering the expression of aquaporin genes in the ginger rhizomes [124]. In cucumber (*Cucumis sativus*) seedlings, treatments with a wide range of concentrations of SiQD significantly promoted the expression levels of aquaporin genes and plant growth [125]. Many horticultural crops require adequate amounts of boron for vegetative and reproductive growth. Foliar application of nanoencapsulated boron in almond (*Prunus dulcis*) trees allows B movement within trees and induces water uptake and transport by upregulating the expression levels of *PdPIP2.2* and *PdTIP1;1* aquaporin genes [126]. Treatment of sweet cherry (*Prunus avium*) with 0.5% $CaCl_2$ upregulated the expression level of *PaPIP1;4* which is dominantly expressed in the fruit peduncle to prevent fruit cracking [127].

3.2. Detoxification of harmful heavy metal(loid)s and application in agriculture

With the rapid development of worldwide industrialization, economic prosperity is being accompanied by severe environmental pollution. Pollutants include, but are not limited to, heavy metals and metalloids such as Cd and As. Pollutants in soil and water can be absorbed and accumulated in plants, which directly affects crop yield and quality. Contaminated plants can adversely affect animals and humans via the food chain [128]. Thus, pollution control and treatment via phytoremediation and phytoextraction are currently of high priority.

Populus alba is highly tolerant to heavy metals, such as Cd^{2+} and Zn^{2+}. Overexpression or knocking out its aquaporin gene, *AQUA1*, greatly altered the response to heavy metal stress [129]. Fern *Pteris vittata* is an As hyperaccumulator. Heterologous expression of the *PvTIP4;1* gene in yeast demonstrated that PvTIP4;1 facilitates As diffusion. Thus, hyperaccumulator plants like *Pteris vittate* can function as pioneer and indicator plants to control arsenic pollution [130]. In rice roots, overexpression of *OsNIP1;1* and *OsNIP3;3* disrupts arsenite radial transport [101].

Another potential strategy is to use plant-associated microbes to remediate the contaminated soils. Endophytic microbes isolated from plants growing in contaminated habitats possess specialized properties that help their hosts detoxify contaminants. The endophytes from the As-tolerant plant *Lantana camara* could enhance As resistance of the As-sensitive plant *Solanum nigrum* whose aquaporin *SnTIP2-2* and *SnPIP1* gene expression was upregulated upon endophyte inoculation. Therefore, the As-tolerant endophytic consortium could regulate aquaporins to improve the As-phytoremediation efficiency of other crops [131]. The medicinal plant *Dittrichia viscosa* is an As hyperaccumulator. The expression ratio of *DvNIP1;1* in roots and shoots is a promising selection marker to predict As content in soils and can be used as an As-indicator plant [132]. In rice, the application of thiourea (a non-physiological ROS scavenger) at millimolar concentrations can efficiently mitigate As toxicity and reduce grain As accumulation by downregulating the expression levels of *OsNIP2;1* (*OsLsi1*) but upregulating the expression levels of *OsPIP1;1*, *OsPIP2;1*, and *OsTIP4;1* [117].

Application of silicon nanoparticles (SiNPs) could modulate *OsLsi1*, *OsLsi2*, and *OsLsi6* expression patterns by increasing Si but decreasing As uptake in metal(loid)-exposed rice plants [133]. SiNPs can also activate aquaporin OsLsi1 in rice to take up more Si and antagonize Cd and As [88]. Graphene oxide (GO) is another promising nanomaterial for pollution control. GO application in wheat and tomato could upregulate *TaPIP1;1*, *TaNIP4;2*, *SlPIP1;1*,

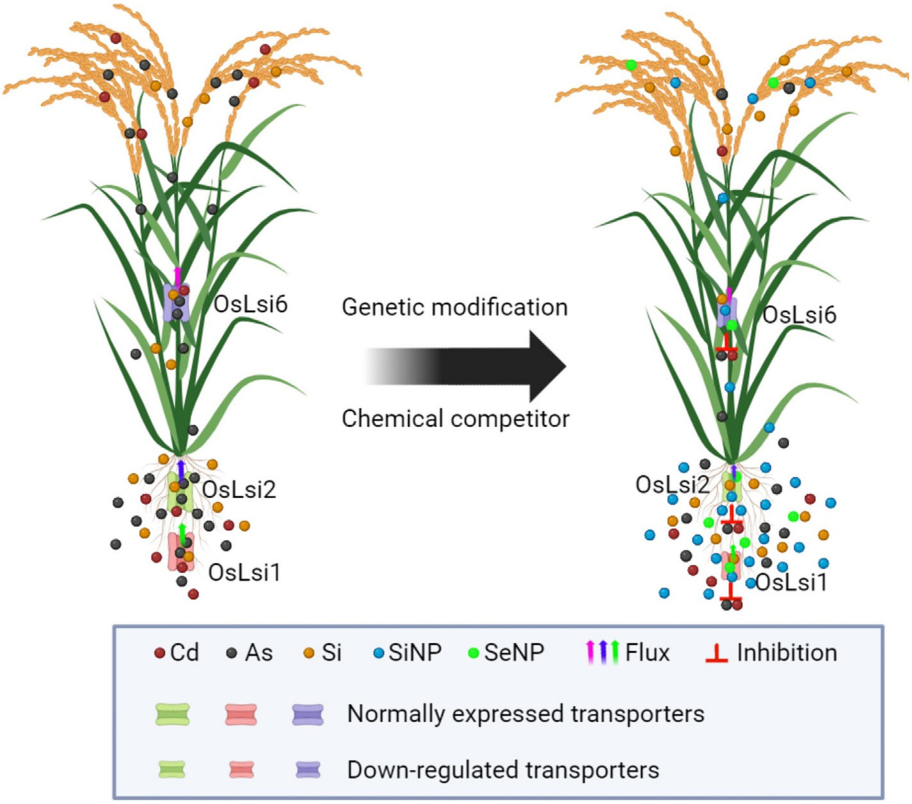

Fig. 5. Genetic and chemical regulation of the expression levels and channel activities of aquaporins inhibit the uptake of harmful elements and promote the uptake of beneficial elements into rice grains.

SlTIP1;2, and *SlNIP1;2* expression levels and alleviate As toxicity in plants [134].

Overall, plant aquaporins are important genetic and/or chemical targets for efficiently regulating the uptake of beneficial and harmful elements into food crops (Fig. 5) [98,111].

OsLsi1, OsLsi2, and OsLsi6 are the major Si, Se, and As transporters in rice. Appropriate downregulation of the expression levels and activities of these aquaporins can alleviate As uptake [101,102,128]. Alternatively, the application of silicon nanoparticles (SiNPs), selenium nanoparticles (SeNP), and other compounds can alter the transporter functions to competitively inhibit As uptake by up-regulating Si and Se transport into rice grains [95,120,133,156,157]. Figure was designed using Biorender (https://biorender.com).

4. Conclusion and perspectives

Significant progress has been made in recent years in understanding the uptake, extrusion, and speciation of water, hydrogen peroxide, gases, neutral molecules, ions, and metal(loid)s in plants [12]. However, substantial knowledge gaps exist, particularly regarding the mechanisms and physiological functions of aquaporin-permeating substrate(s) in specific spatiotemporal patterns. Hence, using genetic and pharmacological approaches, we can efficiently regulate the expression levels and/or channel activities of aquaporins to maintain the homeostasis of water and other substances necessary for plant growth, development, metabolism, and adaptation to environmental stresses [14,84]. The drastic physiological relevance of the characterized aquaporin isoforms leads us to suspect that the importance of these aquaporins for plant physiology is more far-reaching than currently known. Future research on aquaporins at molecular, genetic, and physiological levels is essential to fully unravel the regulation of substance transport processes to improve agriculture, environmental protection, and other industries, as our current knowledge about plant aquaporins is still limited.

Glossary

1. Aquaporin (AQP): A class of membrane proteins with six transmembrane domains to form channels to permeate water, and some members can also permeate small neutral molecules and ions through the channels.
2. Major intrinsic protein (MIP): A protein superfamily consisting of six transmembrane domains to form a channel to permeate water and other small molecules.
3. Peroxiporin: Aquaporin proteins which can transport H_2O_2.
4. Reactive oxygen species (ROS): Highly reactive molecules which are produced from the incomplete reduction reaction of oxygen. These include superoxide (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (OH^-) and so on.
5. Proteoliposome: The unilamellar lipid bilayer vesicles reconstituted with proteins embedded in the membrane for functional assay
6. Pathogen-associated molecular pattern (PAMP): The specific pathogenic molecule or compound which can stimulate the immunological reaction of the host organism. e.g. the bacterial flg22 can cause hypersensitive reaction (HR) in Arabidopsis.
7. Hypoxia: The oxygen-deprivation or low-oxygen condition which induce anaerobic respiration in the cells.
8. Symbiosis: A specific microorganism lives in a large multicellular organism to benefits to each other. e.g. the relationship of nitrogen-fixation rhizobium and soybean.

9. Symbiosome: Within the infected nodule cells, the rhizobia are enclosed in a plant-derived membrane to form an organelle-like compartment called the symbiosome.

10. Arbuscular mycorrhizae (AM): A symbiosis between plants and members of an ancient phylum of fungi, the Glomeromycota, improves the supply of water and nutrients, such as phosphate and nitrogen, to the host plant.

11. Ammoniaporin: Protein channel transporting ammonia.

12. Aquaglyceroporin: Protein channel transporting glycerol.

13. Metalloid: Elements between metal and nonmetal. e.g. arsenic (As), antimony (Sb), boron (B), germanium (Ge), silicon (Si) and tellurium (Te).

14. Nanoparticle (NP): The various materials with nanometer sizes potential applications in diagnostics, imaging, gene and drug delivery and other types of therapy.

15. Graphene oxide (GO): A distinct 2D carbon-based nanomaterial composed of a number of functional oxygen groups and graphene layer.

16. Quantum dot (QD): a special type of engineered nanomaterials with outstanding optoelectronic properties that make them as a very promising alternative to conventional luminescent dyes in biomedical applications, including biomolecule (BM) targeting, luminescence imaging and drug delivery.

CRediT authorship contribution statement

Qi Sun: Writing – original draft. **Xin Liu:** Investigation. **Yoshichika Kitagawa:** Conceptualization. **Giuseppe Calamita:** Conceptualization. **Xiaodong Ding:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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