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PLANT AQUAPORINS

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Abstract: This mini-review briefly presents the main types of plant aquaporins, highlighting their importance for different plant species and for plant cellular functions. Aquaporins (AQPs), families of water channel proteins (WCPs) are transmembrane proteins that are present in prokaryotes, animals, plants, and humans. The plant aquaporins are part of the Major Intrinsic Proteins (MIPs) family which resides in the following plant organs: roots, stems, leaves, flowers, fruits, and seeds. According to the sub-cellular localization, to their sequence homologies and to their phylogenetic distribution, plant aquaporins have been divided in five subgroups: (a) plasma membrane intrinsic proteins (PIPs); (b) tonoplast intrinsic proteins (TIPs); (c) Nodulin26-like intrinsic membrane proteins (NIPs); (d) small basic intrinsic proteins (SIPs) and (e) uncharacterized intrinsic proteins (XIPs). Different subclasses of the plant aquaporins allow several types of transport using: water, glycerol, urea, hydrogen peroxide, organic acids, ethanol, methanol, arsenite, lactic acid, and gaseous compounds. Plant aquaporins have a significant role in cell response to cold stress, photosynthesis, plant growth, cell elongation, reproduction, and seed germination.

Keywords: plant aquaporins, water transport, plasma membrane proteins, tonoplast membrane proteins, nodulin26-like membrane proteins, small basic proteins, uncharacterized proteins.

1. Introduction

Aquaporins (AQPs), families of water channel proteins (WCPs) are transmembrane proteins that form a membrane pore and allows water to rapidly pass through biological membranes by osmosis (Agre et al., 1993; Agre, 2004; Benga, 2012). The first WCP, discovered in the red blood cell membrane by Benga's research group (Benga et al., 1986 a,b), was purified by Agree's group scientists and was named aquaporin 1 (AQP1) (Agre et al., 1993; Agre, 2004).

AQPs are present in prokaryotes (Tanghe et al., 2006), in various animals (Benga, 2013), plants (Maurel et al., 1993; Maurel et al., 2008; Sutka et al, 2017) and humans (Benga and Huber, 2012; Papadopoulos and Verkman, 2012; Verkman, 2013).

Some studies have shown that tomato, soybean, corn and spinach leaf aquaporins have a certain homology with human aquaporin-4 (Lambert et al., 2019).

The first plant WCP was discovered by Maurel et al. (1993) in the vacuolar membrane of *Arabidopsis thaliana*, named AQP (γTIP or *At*TIP1;1) (Maurel et al., 1993; Wudick et al., 2009). Comparatively to the animals/humans,

plants contain a much higher number of AQPs (between 30 and 70) (Wudick et al., 2009; Deshmukh et al., 2016; Kapilan et al., 2018).

The plant aquaporins (AQPs) are part of the Major Intrinsic Proteins (MIPs) family that are integral α-helical proteins and allow passive water and neutral solute bidirectional transport across biological membranes and, also have a significant role in cell response to cold stress (Rouge and Barre, 2008; Hernandez-Sanchez et al., 2019) and to osmotic stress (Balarynová et al., 2018), also are important during leaf and petal movements, cell elongation, reproduction, and seed germination (Maurel, 2007).

The plant aquaporins have typical structural particularities: the six transmembrane core as α-helical domains with N- and C-terminal ends towards on the cytoplasmic side of the membrane, linked by five loops (A-E), that define an aqueous transmembrane pore; the pore stability and specificity is given by two hydrophobic motifs Asp-Pro-Ala (NPA) of the B and E loops that are embedded in center of the membrane. The high specificity for substrate is determined by an aromatic/Arg (ar/R) motif. AQPs monomers function as water channel within membrane and four AQPs monomers tend to form homotetramers by hydrogen bonds among the monomer loops; tetrameric structure of the holoproteins gives protein stability and functionality (Shapiguzov, 2004; Wudick et al, 2009; Kaldenhoff et al., 2014; Kapilan et al., 2018).

Aquaporin`s permeability depends on water structure. However, aquaporin permeability is the same for both distilled water and original tap water (Kozumi and Kitagawa, 2016).

The plant aquaporins are present in the following plant organs: roots, stems, leaves, flowers, fruits and seeds (Kapilan et al., 2018). The phosphorylation level of the AQPs subunits determines their sub-cellular localization (Kapilan et al., 2018). AQPs are located in different intracellular places: plasma membrane, vacuoles (tonoplast), plastids, endoplasmic reticulum, and, in some species, interact with symbiotic organisms (Maurel et al., 2015).

Some studies have described several types of transport using different subclasses of the plant aquaporins: water, glycerol, urea, hydrogen peroxide (H_2O_2), organic acids, ethanol, methanol, arsenite, lactic acid and gaseous compounds (oxygen – O_2, ammonia – NH_3, carbon dioxide – CO_2 (Shapiguzov, 2004; Wudick et al., 2009; Kapilan et al., 2018). Some AQPs are sensitive to inhibitors that contain mercury, which induces conformational changes in AQPs and block water passage through the channel (Shapiguzov, 2004).

According to the substance type transported, plant aquaporins have been classified in three subgroups: (a) aquaporins specific for water transport (AQPs); (b) aquaporins GlpFs specific for small carbohydrates (glycerol) transport and (c) aquaglyceroporins (AQP3s) specific for both water and small non-ionic dissolved molecules transport (Rouge and Barre, 2008). According to the sub-cellular localization, to their sequence homologies and to their phylogenetic distribution, plant aquaporins have been divided in five subgroups: (a) plasma membrane intrinsic proteins (PIPs); (b) tonoplast intrinsic proteins (TIPs); (c) Nodulin26-like intrinsic membrane proteins (NIPs); (d) small basic intrinsic proteins (SIPs), and (e) uncharacterized intrinsic proteins (XIPs) (Rouge and Barre, 2008; Deshmukh et al., 2016; Hernandez-Sanchez et al., 2019). The phylogenetic classification takes into account the characteristics and functions of each AQPs (Deshmukh et al., 2016).

2. Plasma membrane intrinsic proteins (PIPs)

The plants PIPs are the largest proteins subgroup with high variability of terminal domains and are located in the plasma membrane, but also into other structures as vascular tissues, guard cells, and flowers. There are 13 isoforms in *Arabidopsis*, which have been subdivided into two phylogenetic subgroups: PIP1 and PIP2, containing similar amino acid sequences, but with different water transport ability. N-terminal tails of PIP1 are longer compared to PIP2 and PIP1 C-terminal tails are shorter (Shapiguzov, 2004; Wudick et al., 2009; Kapilan et al., 2018).

PIPs are important proteins in regulating the water transport, photosynthesis, plant growth, development and restriction of root water uptake, regulated by low pH values (Agre, 2004; Wudick et al., 2009; Zhu and Ming, 2019). PIPs own an important role in the regulation of water transport under abiotic stress (Ding et al., 2019).

The PIP1 subgroup consists of five members: PIP1;1 to PIP1;5. All the PIP1 proteins have low water permeability because some of them cannot act one with another and they must form heterotetramers with PIP2 monomers (Kapilan et al., 2018). PIP1 trafficking to the plasma membrane depends on PIP2 interaction. These facts suggest a functional interaction between PIP1 and PIP2 and, also support roles for PIP1 in water transport. When expressed alone, some PIP1 do not localize to the plasma membrane. PIP1-PIP2 interactions represent post-translational regulatory mechanisms that influence intrinsic permeability of PIPs (Yaneff et al., 2015). It is also considered that PIPs phosphorylation has an important role in the gating mechanisms and sub-cellular dynamics (Verdoucq et al., 2014; Pawłowicz and Masajada, 2019) and in redox-dependent modulation of osmotic water permeability in plasmalemma from roots (Piotrovskii et al., 2019). An example is phosphorylation of Ser or Thr residues of the cytoplasmic C-terminal tail of the *Arabidopsis* root PIP2s (Maurel et al., 2009). Within *Arabidopsis*, the tetramer structure of the AtPIP2;1 is essential for water permeability. In the plasma membrane, inter-transmembrane interactions between monomers played an important role in tetramer formation of the AtPIP2;1 (Yoo et al., 2016).

The PIP2 subgroup consists of eight members: PIP2;1 to PIP2;8 than, are more efficiently compared to PIP1 group members (Kapilan et al., 2018; Nada and Abogadallah, 2019). PIP2s are organized in homotetramers that translocate to the plasma membrane by interacting with SNARE proteins (Yaneff et al., 2015).

An important aspect regarding the PIPs response to various environmental conditions is transcriptional and post-transcriptional regulation mechanisms. In the secretory pathways, PIPs are synthesized within the rough endoplasmic reticulum (RER). Then, PIP2 proteins are associated with PIP1 proteins and form PIP oligomers that transit Golgi apparatus and then, are loaded into secretory vesicles, being transported to the plasma membrane, where it merges through SNARE proteins. PIPs internalization it depends on environmental factors or signaling molecules and is achieved in constitutive pathway through clathrin-coated vesicles (Hachez et al., 2013).

AQPs, in particular PIPs, support more post-translational modifications: deamination, phosphorylation, methylation, acetylation, that influence their activity and trafficking. So, PIP and NIP residues phosphorylation plays a key role in the gating of the pore and regulation of the protein sub-cellular localization (Fox et al., 2017). The plant aquaporins gating (opening and closing of the water channel pore) may be regulated by phosphorylation, protons and divalent cations. Phosphorylation was first

proposed for spinach SoPIP2;1 and pea PvTIP3;1 (Li et al., 2014). In addition, it is considered that PIPs gating is regulated by cytosolic pH and the intracellular Ca^{2+} concentration (Tan et al., 2018).

Some studies showed that heterotetramerization, cytosolic acidification and loop B serine phosphorylation affect aquaporin gating. Loop B serine phosphorylation affects pH gating of FaPIP2;1 but not of FaPIP1;1 from *Fragaria* x *ananassa* (Yaneff et al., 2016).

Based on the expression level, it is considered that for rice, the ability of PIP1 to allow water diffusion was relatively low or absent, compared to a PIP2, that was high. Within rice, three PIP1s (PIP1;1-PIP1;3) were highly expressed in roots (Ding et al., 2019) and the expression of PIP2;1 was the highest among the six PIP2s (Ding et al., 2019). Also, enhancing AQPs activity, increased the ability of root water uptake and drought tolerance of rice supplied with NH_4^+ (Ding et al., 2015).

Regarding the effect of high root temperature on the water uptake capability of broccoli was observed increase in osmotic water permeability at higher temperature. This process was not due to changes in the PIPs abundance, but was probably due to increase of permeability through lipid bilayer and changes in plasma membrane fluidity (Iglesias-Acosta et al., 2010).

A recent study showed that during flooding a rapid decrease of cytosolic pH it takes place, due to anoxia. This process leads to a simultaneous aquaporin closure in the plasma membrane, mechanism where it is involved a conserved histine on cytosolic loop D of the aquaporin (Frick et al., 2013).

Aquaporins have been used as target proteins in genetic manipulation, to improve plant water relations under environmental stress. For example, *Vicia faba* PIP1 (VfPIP1) expression in transgenic *Arabidopsis thaliana* improved drought resistance by reducing water loss through transpiration (Martinez-Ballesta and Carvajal, 2014).

For *Nicotiana tabacum*, a member of PIP1 subgroup (NtAQP1) decreased plant resistance to water stress. Some members of PIPs (NtAQP1) are involved in water transport and can participate in carbon dioxide transport, thus contributing to photosynthesis (Pawłowicz and Masajada, 2019).

In *Pisum sativum*, PIP1 has an important role in water absorption during seed water uptake. (Kapilan et al., 2018).

The plant protection against dehydration stress depends on the interaction between specific proteins such dehydrins and aquaporins, that protect other proteins from damage during dehydration. Dehydrins are intrinsically disordered proteins that accumulate during abiotic stress conditions. It is considered that two classes of proteins behave simultaneously for AQPs denaturation and inactivation (Hernandez-Sanchez et al., 2019).

In *Saccharum ssp.*, three aquaporins (ShPIP2;1, ShPIP2;5 and ShPIP2) replied to water deficit conditions and their expressions were depending on genotype, experimental conditions and duration of drought stress (Mara de Andrade et al., 2016).

The relevance of aquaporin root water transport at low temperatures has been demonstrated by over-expressing of PtdPIP2;5 (PtdPIP2;5ox) at transgenic *Populus tremula* x *alba*. Over-expression of PtdPIP2;5 was efficient in attenuation of the effect at low root temperature, on hydraulic conductivities and gas exchange (Ranganathan et al., 2016).

Some members of the PIP1 subgroup had a relevant role in glycerol and CO_2 transport (Kapilan et al., 2018). High rates of photosynthesis are provided by PIP1 aquaporins, using CO_2 channels that are

important for the mesophyll and stomatal CO_2 conductance in leaves (Yaneff et al., 2015).

For maize, the pairs ZmPIP1;5-ZmPIP2;5 and ZmPIP1;1-ZmPIP2;1 are functional units whitin roots, important in salt stress cell response and during root development (Yaneff et al., 2015). For *Saccharomyces cerevisiae*, some PIP2 transport H_2O_2, while in maize, ZmPIP1;2 does not allow peroxide transport (Yaneff et al., 2015). For stability and increase of water permeability, maize ZmPIP1s and ZmPIP2s interact; similar results were observed for *Nicotiana tabacum*, *Beta vulgaris*, *Mimosa pudica*, *Vitis vinifera*, *Hordeum vulgare*, *Triticum turgidum* (Bienert et al., 2014). Using a yeast system, it was observed that ZmPIP1;2 is not permeable to hydrogen peroxide, comparatively to wild type ZmPIP2;5 (Bienert et al., 2014). Differences in H_2O_2 permeability between various AQP isoforms are due to differences in open mechanism of channels and to miss targeting to cellular membranes other than plasma membrane (Bienert and Chaumont, 2014). The oxidative stress responses were investigated in the *Arabidopsis* roots, through redistribution of PIPs from plasma membrane to intracellular membranes. AtPIP2;1 analyses with endomembrane markers showed that H_2O_2 determined AtPIP2;1 accumulation in the late endosomal compartments. The high stability of PIPs was maintained under oxidative stress conditions due to the intracellular redistribution of PIPs without degradation (Wudick et al., 2015).

In case of *Chrysanthemum morifolium*, CmPIP1 and CmPIP2 differ in their response expression to salt, presenting higher expression in the leaves and lower in stems and flowers. Their role is very important: stomatal opening and closing, transpiration and photosynthesis (Zhang et al., 2019).

3. Tonoplast intrinsic proteins (TIPs)

The The tonoplast intrinsic proteins (TIPs) are the most abundant aquaporins in the vacuolar membrane (tonoplast). Some TIPs isoforms are found in small vacuoles and in the membrane surrounding the protein storage vacuoles (PSV), having a storage function for protein and play a role in protein degradation (Wudick et al., 2009; Kapilan et al., 2018). TIPs are the first water transporting proteins that have been identified in tonoplast of *Arabidopsis thaliana* (AtTIP1;1) (Maurel et al., 1993; Wudick et al., 2009; Kapilan et al., 2018). According to their sequence homologies, in maize, rice, and *Arabidopsis*, TIP group consists of five subgroups: TIP1-TIP5. For example, ten tonoplast intrinsic protein (TIP) homologues are present in *Arabidopsis* (Wudick et al., 2009) and 17 TIPs are present in *Populus trichocarpa* (Kapilan et al., 2018).

The tonoplast TIPs play a key role in transporting small solutes (diffusion of water, urea, ammonia, H_2O_2) and gases, in maintenance of cell turgor pressure, and TIPs genes become under-expressed after drought stress (Abascal et al., 2014; Fox et al., 2017; Kapilan et al., 2018). Water permeability of the tonoplast is higher than that of the plasma membrane, due to the abundance of the aquaporines in the tonoplast (Kapilan et al., 2018).

TIPs isoforms can have different physiological functions. For example, in *Mesembryanthemum crystallinum*, TIPs may play an important role in stress responses, therefore when the plant was exposed to salt stress, the abundance of TIP1;2 decreased to 75% (Kaldenhoff and Fischer, 2006; Wudick et al., 2009; Kapilan et al., 2018).

TIPs proteins are aquaporin synthesized during seed maturation and found in vacuolar membranes of cotyledons. TIPs that function in seed drying, cytoplasmic osmoregulation, seed

rehydration can be regulated by phosphorylation (Daniels et al., 1999; Li et al., 2014).

TIPs may play a role in equilibrating urea concentrations between the vacuole and the cytoplasm (Kaldenhoff and Fischer, 2006).

An implication of TIPs in urea transport was first described in tobacco suspension cells, where, in accordance with NtTIPa expression, vesicles showed higher permeability to urea. In *Arabidopsis*, almost all TIP subclasses (AtTIP1;1, AtTIP1;2, AtTIP1;3, AtTIP2;1, AtTIP4;1, AtTIP5;1) transport urea. In plants, TIPs may allow a non-saturable and pH-independent transport of urea during nitrogen metabolism or nutrition (Wudick et al., 2009).

NH_3 transport was first described for TIP2 members from wheat (TaTIP2;1) and *Arabidopsis* (AtTIP1;2, AtTIP2;1, AtTIP2;3). TIPs play a function in sub-cellular partitioning of NH_3 and contribute to the detoxification of NH_3 excess amounts in the cytosol (Wudick et al., 2009). Expression of AtTIP2;1 in roots was up regulated in response to nitrogen starvation (Jahn et al., 2004).

For tomato, the over-expression of SlTIP2;2 attenuated the reduction of plant transpiration under stress, ensuring an adequate balance between CO_2 uptake and water and nutrient supply (Martinez-Ballesta and Carvajal, 2014).

A key role of the tonoplast is to maintain turgor pressure against the cell wall. Recent studies have shown that in grapevine tonoplast, TIP2;1 activity is regulated by turgor induced membrane tension, changing from an opened to a closed state. Membrane tension may induce water channels closure, preventing fast water loss. This turgor that depends on TIP2;1 gating may be a mechanism to regulate vacuolar size and shape in grapevine (Leitao et al., 2014).

Furthermore, a specific role for PIPs and TIPs in primary root elongation and development of lateral roots was showed that may contribute to improving drought resistance (Zargar et al., 2017).

In drought conditions, the expression of PIPs and TIPs from tea plant remained relatively high after leaf rehydration, but they were repressed in the roots. CsPIP and CsTIP genes play an essential role in stress response, as well as in flower development and opening process. More, some CsNIPs, CsSIPs and CsXIPs can regulate flower development and opening process (Yue et al., 2014).

4. Nodulin26-like intrinsic membrane proteins (NIPs)

Nodulin26-like intrinsic membrane proteins (NIPs), aquaporins that have been initially localized in peribacteroid membrane of nitrogen-fixing root nodules of leguminous plants, are present in plasma membrane of the non-symbiotic plants too (Wudick et al., 2009; Kapilan et al., 2018). Aquaporins identified as nodulin26 proteins were first characterized in soybean and then in other rhizobia-symbiotic vegetables (Rouge and Barre, 2008).

Nodule formation is a result of symbiotic relationship between plant and nitrogen fixing bacteria. During the process of nodule formation, nodulin proteins are expressed by plants and transferred to the membranes. Nodulin 26 proteins are expressed at the symbiosome membrane and have similar sequences to NIP proteins (Kapilan et al., 2018).

NIPs have been classified in five phylogenetic groups (NIP1-NIP5) and in three functional groups (NIP I, NIP II, NIP III), based on similarity of the aromatic/arginine constriction (Mateluna et al., 2018).

Comparatively with other aquaporins, NIPs play a similar role as transporters of water, but in contrast with PIPs and TIPs, NIPs have lower water transport activity (Maurel et al., 2015; Kapilan et al., 2018). However, besides glycerol and water (Kruse et al., 2006),

NIPs are permeable to small organic solutes and mineral nutrients and mediate diffusion of metalloids (boric acid, silicon and selenium) and toxic elements (arsenic) (Martinez-Ballesta and Carvajal, 2014; Maurel et al., 2015; Fox et al., 2017). NIPs transport functions have been established by direct mutagenesis and by expression in oocytes (Martinez-Ballesta and Carvajal, 2014). NIP I proteins are permeable to water, glycerol and ammonia, NIP II proteins transport urea and metalloid nutrients (boron), but have lower water permeability and NIP III proteins transport larger molecules (silicic acid, urea) (Mateluna et al., 2018).

Some structural particularities in NPA motif (alanine is replaced with serine, glycine or valine) might render NIPs capable of transporting substrates other than water (Wudick et al., 2009). NIP2 proteins have a wider pore than those of NIP1 and are permeable to large solutes (urea). Also, AtNIP2;1 is expressed in the endoplasmic reticulum of roots, whereas AtNIP5;1 is expressed in plasma membrane of roots elongation zones. The AtNIP2;1 mediates lactic acid transport, being very important to the adaptation to lactic fermentation under anaerobic stress (Gomes et al., 2009). When NIPs phosphorylation is increased, NIPs have an important role in maintaining plant water balance and in drought and salt stress responses (Martinez-Ballesta and Carvajal, 2014; Kapilan et al., 2018).

NIPs proteins have multifunctional transport properties of water and/or uncharged solutes as glycerol. NIP gene transcripts were found in seed coat, shoot and roots (Kaldenhoff and Fischer, 2006).

5. Small basic intrinsic proteins (SIPs)

As the TIPs proteins, SIPs proteins are small, but very basic, and can be found in seed plants and mosses (Abascal et al., 2014; Kapilan et al., 2018). Their small sizes are due to the very short cytosolic N-terminal region (Kapilan et al., 2018). SIPs proteins are associated with intracellular membranes, particularly with endoplasmic reticulum, having a key role for facilitating the intracellular water movement. Also, SIPs participate in the passage of water through the endoplasmic reticulum membranes and regulate the morphology of the organelle (Gomes et al., 2009).

SIPs proteins comprises four classes, of which in *Arabidopsis* there are three members of the SIPs (Wudick et al., 2009). In case of cotton, based on NPA sequence, SIPs include SIP1 subgroup that is divided into SIP1;1 and SIP1;2 (Gomes et al., 2009; Kapilan et al., 2018). Different SIP isoforms have different solute permeability, due to different sites of characteristic residues. So, in SIPs of cotton, alanine residues present in the first NPA motif was converted to tyrosine (Kapilan et al., 2018). From a functional point of view, although SIPs have an original pore conformation, it ensures only a moderate water transport (Maurel et al., 2015).

Three SIPs were identified in potato and were included in the SIP1 subgroup. Some of the potato aquaporins (PIP1;4, PIP2;1, TIP2;4, SIP1;1a, SIP1;1b and NIP5;1) were abundant in stolons, swollen stolons and tubers, suggesting that these aquaporins may play a potential role in the tuberization process (Venkatesh et al., 2013).

6. Uncharacterized intrinsic proteins (X intrinsic proteins - XIPs)

XIPs have been characterized in protozoa, fungi, mosses and dicots. There have been 19 XIP members: five XIPs in *Populus trichocarpa*, ten in dicots other than *Populus*, three from moss and one from protozoa (Kapilan et al., 2018). XIPs are absent in Brassicaceae, monocots and in certain dicots such as *Arabidopsis* (Li et al., 2014; Mara de

Andrade et al., 2016; Kapilan et al., 2018). XIP homologues have also been found in flowering plants (dicot species), in Solanaceae species (*Solanum lycopersicum*), *Glycine max* and *Jatropha curcas* (Wudick et al., 2009; Pawłowicz and Masajada, 2019). The potato contains more XIPs comparatively with other dicot species (cotton, *Vitis*). Except XIP1, which was less expressed in root tissues, but higher expressed in leaves, XIP2, XIP3;1 and XIP4;1 were highly expressed in potato root. The rapid transport of inorganic solutes and metabolites can make possible a higher expression of aquaporins in roots (Venkatesh et al., 2013).

The same as PIPs and NIPs, XIPs are localized in the plasma membrane (Yaneff et al., 2015; Pawłowicz and Masajada, 2019). It is considered that XIPs are multifunctional channels permeable to water and metalloids (Maurel et al., 2015). In grapevine, VvXIP1 play a key role in osmotic regulation in addition to H_2O_2 transport and metal homeostasis (Kapilan et al., 2018).

Another two sub-families were discovered in moss (*Physcomitrella patens*), and not in vascular plants: GIPs (GlpF-like intrinsic protein) and HIPs (hybrid intrinsic proteins) (Wudick et al., 2009; Abascal et al., 2014; Li et al., 2014; Yaneff et al., 2015; Pawłowicz and Masajada, 2019).

Conclusions

In plants, aquaporins are very abundant and are important for whole plant, for water transport to and from the vascular tissues. At the cellular level, plant aquaporins have key roles in control of the osmotic fluctuations. Due to the regulated abundance and activity of aquaporins, plants have the ability to control water transport. Plasma membrane proteins are important in regulating water transport, photosynthesis, transpiration, plant growth, development and restriction of roots water uptake regulated by low pH values. Tonoplast membrane proteins play key roles in transporting small solutes and gases, maintaining cell turgor pressure. Nodulin26-like membrane proteins are permeable to small organic solutes and mineral nutrients and mediate diffusion of metalloids and toxic elements. Small basic proteins participate in the passage of water through the endoplasmic reticulum membranes and regulate the morphology of the organelle. Uncharacterized proteins play key roles in osmotic regulation besides H_2O_2 transport and metal homeostasis.

A better understanding of the AQPs in plants and evaluation of various distribution models of aquaporins, depending on the degree of cell compartmentation, can lead to a better knowledge of cellular functions and to the development and management of plants better adapted to changing environmental conditions.

Conflict of Interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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