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A plant aquaporin (SoPIP2; 1): Regulatory protein channel in plants under stress

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ABSTRACT

Aquaporins (AQPs), are the highly regulated trans-membrane water channel protein', having the great potential to develop resistance in crop plant under the stress conditions. 30 genes of different subfamily of aquaporins play an important role in plant tolerance against the abiotic stress. On the basis of conserved NPA motifs and amino acid residues (aromatic/or arginine regions), AQPs under stress classified into three main subfamilies: (i) subfamily-1 'AQPs involved in water and ion transport'; (ii) subfamily-2 'GLPs permeable to glycerol and neutral molecules; and (iii) subfamily-3 'GLAs (aqua-glyceroporins)' permeable to both water and glycerol. In plants SoPIP2; 1 is the only plant aquaporin whose atomic structure is available. It has Leu197, residues-His99, Val104 and Leu108 residues of amino acids, which form a hydrophobic barrier, that narrows the pore diameter and regulate water transport in stress.

INTRODUCTION

Plant cell membrane water channel protein 'Aquaporins'

Plant cell membrane having ubiquitous 'trans-membrane water channel protein' called as aquaporins (AQPs), which facilitate the movement of water across membrane of the plants. Aquaporins act as highly regulated and controlling channels in plant under stress conditions. The first aquaporin member, Nodulin-26, GmNOD26 was identified in soybeans (Zhang et al. 2013). Aquaporins belong to a highly conserved super family of membrane proteins and recognized as the most intrinsic plasma membrane trans-protein (MIP). The N and C terminal ends always faces toward the cytosol (fig. 1). It having six trans-membrane helices (TM-helices 1-6), five inter-helical loops (La-Le), and two highly conserved NPA-box (Asp-Pro-Ala).

Aquaporin (AQP1) membrane topology was study by the functional epitope scanning mutants and vectorial proteolysis methods (Preston et al., 1994; Karkouri et al, 2005). Sequence analysis shows that N and C terminal ends of AQP1 were related with gene duplication. Each tandem repeat contains three trans-membrane helices (the two repeats are oriented 180x to each other). Each AQP1 repeat contains the highly conserved asparagine–proline–alanine (N-terminal asparagine-proline-alanine, [NPA]) motif. The NPA motifs are located in the cytoplasmic B-loop and the extracellular E loop, and they are hydrophyllic in nature. Presently, more than 800 MIPs have been identified in bacteria, yeast, protozoa, archaea, and plants. Unicellular organisms such as bacteria, yeast showed the least diversity in MIPs. They possess only one or two aquaporin encoding genes (Maurel et al., 2002; 2015).

A plant aquaporin (SoPIP2; 1): Terrestrial plants evolved to cope with rapid changes in the availability of water by regulating AQPs in their plasma membrane. The structure of SoPIP2;1 were determined by X-ray crystallography (fig. 2). According to Johansson et al. (2001) plasma membrane AQPs closed via the dephosphorylation of highly conserved two serine residues (Ser247 and Ser115) presented towards cytosolic loop B and the C-terminal region, under the conditions of drought stress or through the protonation of a conserved histidine residue in loop D following a drop in cytoplasmic pH due to anoxia during flooding. The most striking difference between the structure of SoPIP2;1 and that of other AQPs is the conformation of the cytoplasmic loop D connecting trans membrane helices 4 and 5 and it should be responsible for the gating mechanism of opening and closing of the water pore (Vera-Estrella et al., 2004; Tornroth-Horsefield et al. 2006) (Table 1). In plants SoPIP2; 1 aquaporin Leu197, residues-His99, Val104 and Leu108 form a hydrophobic barrier that narrows the pore diameter. Besides their function as water transporters, MIPs have been reported to transport typical substrates, including ammonia, arsenite, boron, carbon dioxide, formamide, glycerol, hydrogen peroxide (H_2O_2), lactic acid, silicon, and urea (i.e. making aquaporins multi-functional channels). Conserved NPA motifs and amino acid residues (including the aromatic/or arginine regions) are considered as the two foremost characteristic factors for the identification of substrate selectivity. Based on substrate specificity and protein sequence similarities, different 800 MIPs have been classified into three main subfamilies: (i) subfamily-1 'AQPs involved in water and ion transport'; (ii) subfamily-2 'GLPs (glycerol-facilitators)' permeable to glycerol and neutral molecules; and (iii) subfamily-3 'GLAs (aqua-glyceroporins)' permeable to both water and glycerol (Table 1).

Subfamily-1 of aquaporins includes seven subfamilies, which are categorized according to their intracellular locations and sequence similarities (fig. 3). They are: the plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), NOD26-like intrinsic proteins (NIPs) and small, basic intrinsic proteins (SIPs), the GlpF-like intrinsic proteins (GIPs), hybrid intrinsic protein (HIP), and the uncategorized-X-intrinsic protein (XIP). PIPs, NIPs, and XIPs are generally restricted to the plasma membrane and articulated on the entire cell surface, while TIPs are localized to the tonoplast or vacuolar membrane. In plant PIPs and TIPs are highly conserved. They have highly conserved NPA motifs, which only contribute to the selectivity for water molecules. Such PIP Aquaporins act as signaling molecule in abiotic stress condition in plant. Studies have shown that TIPs are involved in glycerol, urea, and ammonia transport, controlling of water exchange between cytosolic and vacuolar compartments via regulating the cell turgor under the abiotic stress conditions in plants (Fetter et al., 2004; Bienert et al., 2011, 13).

Roles of Aquaporins in Plant–Water Relations under abiotic stress

The injurious effects of different types of abiotic stress on plant growth involve: (1) the low osmotic potential of the soil solution (water stress), (2) nutritional imbalance, (3) specific ion effects (salt stress), or (4) a combination of these factors. Hence maintenance of the cell's osmotic potential under stress conditions is a major challenge for plant growth and development (Lian et al., 2004; Alexandersson et al., 2005). Plants are often exposed to challenging environments such as drought, salinity, and cold shock (i.e. abiotic stress). The majority of abiotic stress conditions directly impact on the plant water relations and stimulate an array of complicated cellular and physiological responses, that lead to turning on plant water-saving strategies such as closing of stomatal (to cut off water loss during transpiration). It finally decreases the photosynthetic activity due to the unavailability of CO_2 (fig. 4). Hence all such circumstances require balanced water uptake and transport against adverse osmotic potential for survival. As a result, a dreadful need exists to understand the fundamental system which control plant–water relations in terms of photosynthesis under biotic and abiotic stresses (Park et al., 2015; Afzal et al., 2016). Aquaporins, as vital regulators of plant–water relations, are potential targets in developing stress resistant crop plants. Three different pathways of water transport through plant tissues have been described: the apoplastic path around the protoplasts, the symplastic path through the plasmodesmata, and the trans-cellular path across the cell membranes, which are tightly controlled by the activity of aqua channel proteins (Peng et al., 2007).

Water movement: Aquaporins-channels between root and shoots

Regulation of aquaporin-mediated water flow, through indirect or direct means, appears to be a mechanism by which plants can control cellular and tissue water movement. One manner of plant water channel

regulation appears to be at the level of gene expression. The growth-inducing signals of light and the hormones like: abscisic acid and gibberellic acid causes the transcription of aquaporin (Estrada-Melo et al., 2015; Kim, 2014). In root-to-shoot signaling under water stress, classic ABA signaling pathway is involved. Under this signaling pathway, hydraulic/ pressure-signals releases ABA in the shoot. All this lowered the transpiration rate, which leads to down regulation of aquaporin activity in plant leaves. In the aquaporin family of plants more than 30 genes of different subfamilies are present which play an important role in plant tolerance against the abiotic stress. In order to save the loss of water through transpiration, stomatal closing is the vital water saving strategy used by the plants, which result in a reduced rate of photosynthesis due to the unavailability of CO2. Under this condition some PIPs and TIPs are effectively involve in plant. Many PIP genes, including PIP1;1, PIP1;2, and PIP2;3, were up-regulated, whereas PIP1;5 and PIP2;6 were down-regulated (Table 2). Down-regulation of the PIP genes is thought to reduce water loss and to help prevent backflow of water to drying soil (fig. 5). The down regulation and up regulation of aquaporin gene expressions under stress can be monitored via using microarray approach (Surbanovski et al., 2013; Zhuang et al., 2015). Further it has been observed that water stress response of aquaporins is highly variable depending on stress levels, aquaporin isoform, tissue/ species, presence of symbionts, and the nature of stimuli causing dehydration. Comparative transcriptome studies revealed differential expression of multiple aquaporin homologs in response to drought stress suggesting definite roles in stress responses. Induced expression of AtPIP2;3 under drought stress conditions is one of the earliest evidence of a drought responsive aquaporin (Yamaguchi-Shinozaki et al., 1992). Alexandersson et al. (2005) monitored the expression of all 35 aquaporin homologs in Arabidopsis in response to drought stress alone and found that most PIP and some TIP genes have high levels of expression, while NIP genes have very low expression. Recent research on transcriptomics, reveals that transcriptome data, is not sufficient to identify and explain the concerted pattern of aquaporin expression under the stress condition. Reverse genetics approaches based on one or a few genes may provide better prints than the whole transcriptome studies.

CONCLUSION

Aquaporins may well consider as osmotic-turgor sensors and potential regulators for the study of plant cell water relations under stress condition. They reflect key roles in plant cell osmoregulation, root hydraulic conductivity (Lpr), leaf hydraulic conductivity, transpiration, and cell elongation. Despite that there is the limitation of tools to measure accurate movement across trans-membrane aquaporin channels. Still, more information is untouched in respect to their structure, sub-cellular localization and their roles in various metabolic/ physiological processes in plant growth and development (Chevalier and Chaumont, 2015; Tornroth-Horsefield et al., 2006; Maurel 2007). Rapid changes in the expression levels of aquaporins, in response to diverse stresses, have been documented repeatedly, but the molecular and cellular mechanisms underlying these responses are still unknown. More detailed studies are needed to map different pathways of aquaporin activities in plant physiology and stress responses. Differential responses of aquaporin homologs to stress induced hormones need thorough investigation to uncover their mechanistic involvement in plant stress responses. Though, forward and reverse genetic approaches have also been used comprehensively to define their roles in plant defense mechanisms against the different type of stresses but a clear cut mechanistic pathway of aquaporin homology in response to a particular environmental stress has not yet been established.

Table 1: Chronological overview over AQP structures

Type of aquaporin	Medium
AQP1	the red blood cell water pore
GlpF	the E. coli glycerol facilitator
AQPZ	the E. coli water pore
AQP0	the lens-specific aquaporin
AQP4	the main aquaporin in brain
SoPIP2 ;1	a plant aquaporin
AQPM	an Archaea bacteria- aquaporin

Table 2: A list of subfamilies of aquaporins involved in stress response

Gene	Stress	Reference
PpPIP2;1/PpPIP2;2	Water-deficit	(Lienard et al., 2008)
AtPIP1a/b	Hypotonic	(Kaldenhoff et al., 1998)
AtPIP2;2	Hypotonic	(Javot et al., 2003)
AtNIP3-1	As tolerance	(Xu et al., 2015)
AtTIP1;3/AtTIP5;1	N deficiency	(Soto et al., 2010)
NtAQP1	Drought	(Siefritz et al., 2002)
PIP1	Drought	(Secchi and Zwieniecki, 2013)
Lsi1	Leaf blight	(Ma et al., 2006)
NIP3;1 (tls1)	Boron deficiency	(Durbak et al., 2014)
NIP5;1	Boron deficiency	(Takano et al., 2006)
AtPIP1;2	Low CO2	(Uehlein et al., 2012)

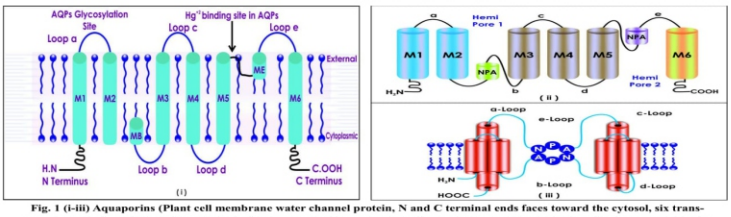

Fig. 1 (i-iii) Aquaporins (Plant cell membrane water channel protein, N and C terminal ends faces toward the cytosol, six trans-membrane helices (TM-Helices M1-M6), five inter-helical loops (La-Le), Glycosylation and Hg+2 binding sites in and two highly conserved NPA-Box (Asp-Pro-Ala)

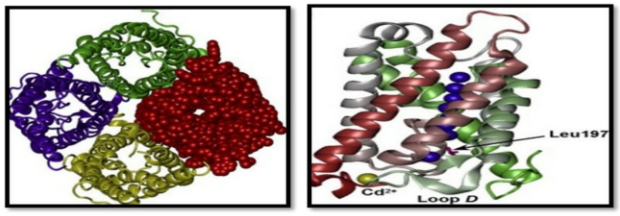

Fig. 2 X-ray crystallographic-3D structure of SoPIP2;1 (only plant aquaporin for which an atomic structure is available). (i) open conformation structure showing conserved tetrameric arrangement; (ii) closed conformation structure, Cd2+ ion binds on the N-terminal end anchored with the loop D; hydrophobic gate channel represented by Leu 197 (suspended the continuity of water molecules) [Horsefield et. al. (2006)]

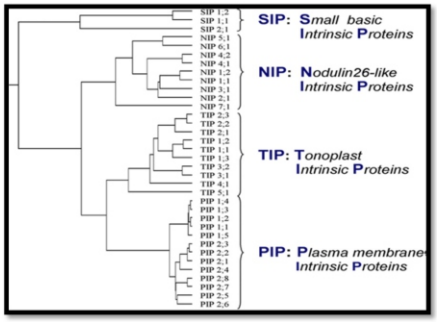

Fig. 3 Phylogenetic tree showing homology between the 35 AQPs of four subfamilies SIP, NIP, TIP, PIP [Maurel (2007)]

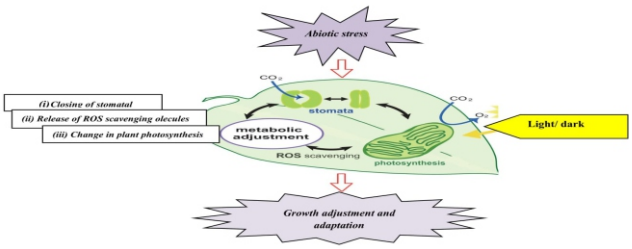

Fig. 4 Growth adjustment and adaptation of plant under abiotic stress condition

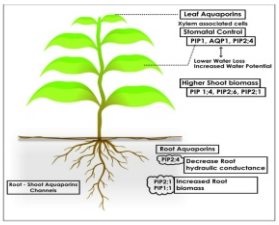

Fig. 5 Regulatory channels of aquaporin proteins between root and shoot under abiotic stress condition

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REFERENCES

1. Afzal Z., Howton T.C., Sun Y., Mukhtar M.S. (2016), The roles of aquaporins in plant stress responses. J. Dev. Biol. 9: 1–22
Alexandersson
2. E., Fraysse L., Gustavsson S., Fellert M., Karlsson M., Johanson U., Kjellbom P. (2005), Whole gene family expression and drought stress regulation of aquaporins. Plant Mol. Biol. 59(3): 469-484
3. Bienert G.P. and Chaumont F. (2013), Aquaporin facilitated transmembrane diffusion of hydrogen peroxide. Biochem. Biophys. Acta. 1840: 1596- 1604
4. Bienert G.P., Bienert M.D., John T.P., Boutry M., Chaumont F. (2011), Solanaceae XIPs are plasma membrane aquaporins that facilitate the transport of many uncharged substrates. Plant J. 66: 306–317
5. Chevalier A.S. and Chaumont F.O. (2015), Trafficking of plant plasma membrane aquaporins: Multiple regulation levels and complex sorting signals. Plant Cell Physiol. 56: 819–829
6. Estrada-Melo A.C., Ma C., Reid M.S., Jiang Z. (2015), Over expression of an ABA biosynthesis gene using a stress inducible promoter enhances drought resistance in petunia. Hort. Res. 2: 11–13
7. Fetter K., Van Wilder V., Moshelion M., Chaumont F. (2004), Interactions between plasma membrane aquaporins modulate their water channel activity. Plant Cell 16: 215–22
8. Horsefield T., Wang S., Hedfalk Y., Johanson K., Karlsson U., Tajkhorshid M., Neutze E., Kjellbom P. (2006), Structural mechanism of plant aquaporin gating. Nature 439: 688–694
9. Johanson U., Karlsson M., Johansson I., Gustavsson S., Sjovall S., Fraysse L., Weig A.R., Kjellbom P. (2001), The complete set of genes encoding major intrinsic proteins in Arabidopsis provides a framework for a new nomenclature for major intrinsic proteins in plants. Plant Physiol. 126: 1358–1369
10. Karkouri K., Gueune G., Delamarche C. (2005), MIPDB: A relational database dedicated to MIP family proteins. Biol. Cell 97: 535–543
11. Kim T. H. (2014), Mechanism of ABA signal transduction: agricultural highlights for improving drought tolerance. J. Plant Biol. 57: 1–8
12. Lian H. L., Yu X., Ye Q., Ding X.S., Kitagawa Y., Kwak S.S., Su W.A., Tang Z.C. (2004), The role of aquaporin RWC3 in drought avoidance in rice. Plant and Cell Physiol. 45: 481-489
13. Maurel C. (2007), Plant aquaporins: Novel functions and regulation properties. FEBS Letters 581: 2227–2236
14. Maurel C., Boursiac Y., Luu D.T., Santoni V.R., Shahzad Z., Verdoucq L. (2015), Aquaporins in plants. Physiol. Rev. 95: 1321–1358
15. Maurel C., Javot H., Lauvergeat V., Gerbeau P., Tournaire C., Santoni V., Heyes J. (2002), Molecular physiology of aquaporins in plants. Int. Rev. Cytol. 215: 105–148
16. Park W.J. and Campbell B.T. (2015), Aquaporins as targets for stress tolerance in plants: Genomic complexity and perspectives. Turk. J. Bot. 39: 879–886
17. Peng Y., Lin W., Cai W., Aroca R. (2007), Over expression of a Panax ginseng tonoplast aquaporin alters salt tolerance, drought tolerance and cold acclimation ability in transgenic Arabidopsis plants. Planta 226: 729-740
18. Preston G.M., Jung J.S., Guggino W.B., Agre P. (1994), Membrane topology of aquaporin CHIP: Analysis of functional epitope-scanning mutants by vectorial proteolysis. J. Biol. Chem. 269: 1668–1673
19. Surbanovski N., Sargent D.J., Else M.A., Simpson D.W., Zhang H., Grant O.M. (2013), Expression of fragaria vesca PIP aquaporins in response to drought stress: PIP down-regulation correlates with the decline in substrate moisture content. PLoS ONE 8: e74945
20. Tornroth-Horsefield S., Wang Y., Hedfalk K., Johanson U., Karlsson M., Tajkhorshid E., Kjellbom P. (2006), Structural mechanism of plant aquaporin gating. Nature 439: 688–694
21. Vera-Estrella R., Barkla B.J., Bohnert H.J., Pantoja O.L. (2004), Novel regulation of aquaporins during osmotic stress. Plant Physiol. 13: 2318–2329
22. Yamaguchi-Shinozaki K., Koizumi M., Urao S., Shinozaki K. (1992), Molecular cloning and characterization of 9 cDNAs for genes that are responsive to desiccation in Arabidopsis thaliana: Sequence analysis of one cDNA clone that encodes a putative trans membrane channel protein. Plant Cell Physiol. 33: 217–224
23. Zhang Y., Ali Z., Wang C.B., Xu L., Yi J.X., Xu Z.L., Liu X.Q., He X.L., Huang Y.H., Khan I.A. (2013), Genome-wide sequence characterization and expression analysis of major intrinsic proteins in soybean (Glycine max L). PLoS ONE 8: e56312
24. Zhuang L., Liu M., Yuan X., Yang Z., Huang B. (2015), Physiological effects of aquaporin in regulating drought tolerance through over expressing of festuca arundinacea aquaporin gene FaPIP2;1. J. Am. Soc. Hortic. Sci. 140: 404–412