Aquaporins in Plant-Pathogen Interaction

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It is well known that plant aquaporins are channel proteins facilitating passive diffusion of water and small molecules across membrane. In addition to this function, aquaporins also have important functions in mediating host-pathogen interaction, which have appealed general interests. In turns, phytopathogens also employ aquaporins to modulate their growth, development, and pathogenicity. This review focuses on the latest progress in deciphering the functions of aquaporins in host-pathogen interaction. Understanding of the sophisticated functions of aquaporins may not only broaden our insights into the machinery underlying host-pathogen interaction, but also provide references for developing new strategies for controlling diseases.

Keywords: aquaporins ; plant immunity ; pathogenicity ; plant-pathogen interaction

1. Introduction

Aquaporins (AQPs) are membrane channel proteins that are primarily associated with water transport across cell membranes [1]. Water transportation is extremely important for all living cells to maintain cellular functions and normal vital activities under various conditions. Less than 30 years after the discovery in human red blood cell membranes, AQPs are now known to exist in nearly all living organisms, suggesting their essential role in physiological functions [1][2][3]. In addition to water, some AQPs can also transport small solutes (including urea, ammonium, arsenite, lactic acid, boric acid, and glycerol), micronutrients (including silicon and boron), other small molecules (reactive oxygen species, ROS), and even gas molecules (including CO_2, O_2 and NO), some of which may function as crucial signaling molecules during various cellular responses under stress conditions [4][5][6][7][8][9][10]. In contrast, non-transporting functions of some AQPs include cell-cell adhesion, membrane polarization, and regulation of interacting proteins, such as ion channels [1]. Compared to the functions of AQPs in symbiotic plant-microbe interaction, it has become increasingly clear that AQPs also play an important role in host-pathogen interaction. The present review focuses on the roles of AQPs in plant immunity, pathogen pathogenicity, and communications during pathogenic plant-microbe interaction.

The numbers of *AQP* genes vary significantly among different species [11]. Recent genomic sequencing projects have shown that AQPs are more abundant in eukaryotes as compared to prokaryotes [12]. To date, at least 35, 36, 33, 70, 47 aquaporin genes of higher plants have been identified in *Arabidopsis*, maize, rice, cotton, and tomato, respectively [13][14][15][16][17]. The first reported AQP in the plant was AtTIP1;1, a tonoplast intrinsic protein from *Arabidopsis*. Its functions have been further analyzed through expression studies in *Xenopus* oocytes and cell-swelling experiments in hypoosmotic media [18]. Since their discovery in the 1990′s, numerous AQPs have been identified and investigated in plants. Based on their sequence similarity and specific subcellular localization, AQPs in the plant are divided into five major subgroups, including the plasma membrane (PM) intrinsic proteins (PIPs), X intrinsic proteins (XIPs), and nodulin 26 like intrinsic proteins (NIPs) in the PM, tonoplast intrinsic proteins (TIPs) in tonoplast, and small basic intrinsic proteins (SIPs) in the endoplasmic reticulum [19][20]. Each subfamily can be further divided into different subgroups according to their specific locations and functions. For example, PIPs have been classified into two subgroups, namely, the PIP1 subfamily composed of PIP1;1 to PIP1;5 and the PIP2 subfamily composed of PIP2;1 to PIP2;8 [21]. PIPs are mainly in charge of substrate transport between the exterior and interior of cells, whereas the others function in transport between organelles [22][23]. Gene knockout studies have revealed that AQPs participate in regulating the many physiological processes in plants, including water uptake, gas exchange, nutritional elements and heavy metal acquisition, seed formation and germination, calcium, and ROS-mediated signaling and biotic and abiotic stresses responses [19][21]. Some microbes, such as bacteria, show less aquaporin diversity, typically possessing only one or two *AQP* genes, and the absence of such genes has not revealed any definite phenotype [1]. Moreover, AQP-deletion mutants have also been studied in *Botrytis cinerea* and *Fusarium graminearum*, respectively, suggesting that AQPs also have important roles in growth, development, secondary metabolism, and pathogenicity of fungal pathogens [5][24].

AQPs are tightly controlled through multiple mechanisms, mostly including transcriptional control of their expression and post-translational modifications to control their abundance and transport activity [25][26]]. Many reports suggest that AQPs are upregulated or downregulated in plants in response to environmental cues [27][28][29]. Nevertheless, the post-translational regulation (such as phosphorylation, methylation, deamidation, and acetylation) that regulates PM delivery and the activity of PIPs is still unexplored [19][30]. These regulation mechanisms can influence the conformation of AQP monomers, their stability in PMs, and their trafficking or subcellular localization [26][31]. Phosphorylation is a common mode of post-translational modification that acts as a molecular 'switch' to regulate protein activity in response to various stresses. It has been proven that phosphorylation of AtPIP2;1 at multiple sites in the C-terminal occurs under salt stress conditions, leading to the switch of AtPIP2;1 from PMs to intracellular regions, reducing the hydraulic conductivity of *Arabidopsis* [32].

2. The Function of Aquaporins in Plant-Pathogen Interaction

Plants are constantly under attack by pathogens, including viruses, bacteria, and fungi, which leads to various diseases in economically important plants and significant economic losses [33][34]. Plant pathogens have developed efficient strategies to attack the hosts, whereas plants also employ functional innate immune systems for defenses against pathogens [35]. The PM is one of the first compartments where plant-pathogen interaction occurs, which mainly depends on the functions of membrane proteins and other biomacromolecules. Increasing evidence suggests that AQPs play key roles in plant-pathogen interaction involved in plant immunity and pathogen pathogenicity.

3. Prospects for Future Research

AQPs are membrane channel proteins that primarily transport water and small solutes across membranes in nearly all living organisms [1]. Recent studies have shown that AQPs play pivotal roles both in plant immunity and pathogen pathogenicity during plant-pathogen interaction. Although diverse classes of AQPs in plants are differentially regulated upon pathogen attack, their roles, especially the intracellular AQPs (such as TIPs, NIPs, and SIPs), in plant-pathogen interaction, are largely unknown. Apart from expression analysis, abundance, activity, gating, trafficking, and subcellular relocalization of AQPs should be further evaluated by integrating physiological, biochemical, and molecular genetic methods. Notably, plants may employ tissue- or cell type-specific *AQP* genes in different biological contexts, thus responding to diversified environmental conditions [36]. Further studies are still required to go into details to decipher the assembly of protein complexes and underlying mechanisms.

AQPs are tightly regulated at multiple levels in their expression, abundance, and transport activity, but the molecular mechanisms involving transcriptional, post-translational regulatory mechanisms, and molecular interactions need to be further deciphered. It may appeal to great interests to determine how AQPs are involved in endocytic activities and how effectors are simultaneously internalized with PM protein via membrane trafficking. Answers to these questions may provoke new ideas for efficiently protecting crops and controlling pathogens. Moreover, further characterization of upstream signaling events and their cross-talks also represents significant challenges for future research. Although accumulating evidence has shown that AQPs are indispensable for growth, development, and pathogenicity of pathogens, a more comprehensive understanding of the interacting partners and regulations on cellular redox homeostasis of AQPs still requires further investigation.

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