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Review

Toward understanding of the high number of plant aquaporin isoforms and multiple regulation mechanisms

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ABSTRACT

Since the discovery of the first plant aquaporin (AQP) in 1993, our conception of the way plants control cell water homeostasis as well as their global water balance has been revisited. Plant AQPs constitute a large family of evolutionarily related channels that, in addition to water, can also facilitate the membrane diffusion of a number of small solutes, such as urea, CO_2, H_2O_2, ammonia, metalloids, and even ions, indicating a wide range of cellular functions. At the cellular level, AQPs are subject to various regulation mechanisms leading to active/inactive channels in their target membranes. In this review, we discuss several specific questions that need to be addressed in future research. Why are so many different AQPs simultaneously expressed in specific cellular types? How is their selectivity to different solutes controlled (in particular in the case of multiple permeation properties)? What does the molecular interaction between AQPs and other molecules tell us about their regulation and their involvement in specific cellular and physiological processes? Resolving these questions will definitely help us better understand the physiological advantages that plants have to express and regulate so many AQP isoforms.

1. Introduction

Plant growth and development occur under ever-fluctuating environmental conditions, and their ability to continuously sense and respond to these changes guarantees their survival and reproduction. During their lifespan, plants have to adjust the abundance of different transporters and channels in their membranes depending on their own developmental requirements and on the environmental availability of water and nutrients. Aquaporins (AQPs) are proteinaceous channels, first described in the early 1990's as water transporters [1]. Since then, huge progress has been made in the characterization of this family, allowing insights to be gained into their role in the control of plant-water relations [2].

The plant AQP family is a large family of evolutionarily related channels with a generally conserved hourglass pore structure, and includes not only water channels, but also channels that allow the membrane diffusion of other solutes, in addition or instead of water. Therefore, the physiological roles of AQPs expand to more than water channels, being involved in a diversity of functions such as the transport of micronutrients (boron, silicon…), signaling molecules (H_2O_2…) or photosynthetic substrates (CO_2) [3].

Based on sequence identity, five AQP subfamilies have been identified in vascular plants: the plasma membrane intrinsic proteins (PIPs), the tonoplast intrinsic proteins (TIPs), the nodulin-26 like intrinsic proteins (NIPs) (found in the symbiotic membranes of legumes but also in the plasma membrane and endoplasmic reticulum (ER)), the small basic intrinsic proteins (SIPs) (located in the ER and the plasma membrane) and, finally, the X-intrinsic proteins (XIPs) found in the plasma membrane [4–8]. Whereas PIPs, TIPs, NIPs, and SIPs have been described for most land plant lineages, XIPs have not been found in Brassicaceae and monocots [6]. The expansion of these subfamilies by gene duplications and horizontal gene transfer events during the course of the evolution of higher plants has resulted in AQP families, including between 30 and 70 AQPs isoforms [9].

Many excellent reviews on plant AQP regulation have been published [2,3,10–12]. Here, we will discuss several specific questions that would need to be addressed in future research. Why are so many different AQPs simultaneously expressed in specific cellular types? How is the selectivity to different solutes controlled, particularly those that appear to have multiple permeation properties? What does the molecular interaction between AQPs and other proteins and lipids tell us about their regulation and their involvement in specific cellular and

Abbreviations: AQP, aquaporin; PIP, plasma membrane intrinsic protein; TIP, tonoplast intrinsic protein; NIP, nodulin-26 intrinsic protein; SIP, small basic intrinsic protein; XIP, X-intrinsic protein; ER, endoplasmic reticulum; PTM, post-translational modification; TM, transmembrane domain

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physiological processes?

2. Why are so many different AQPs simultaneously expressed in specific cellular types?

2.1. Evolution and diversity of membrane intrinsic proteins

Since the discovery of the first AQPs in the early 90s, a vast number of AQP sequences have been identified in the three kingdoms of life, potentiated mainly by genome and transcriptome sequencing initiatives. This collection of data prompted different studies intending to understand the coexistence of a great diversity of membrane intrinsic proteins on an evolutionary framework. In this regard, phylogenetic analyses depicted scenarios of evolution where an early gene duplication event gave origin to water channels and glycerol channel families [13–15]. Whereas water channels are present in all eukaryotes sequenced so far, glycerol channels (also named aquaglyceroporins) are present in most eukaryotes including green algae and mosses, but not in vascular plants. Interestingly, in vascular plants, the AQP family present a great expansion, even in terms of AQP subfamilies (*i.e.* PIPs, TIPs, NIPs, XIPs, and SIPs) as well as members within each subfamily [9]. This multiplicity of AQP isoforms raises the following questions: does such gene redundancy imply a diversification of functions, or is there only a high functional overlap between duplicated genes? Closely related plant AQPs evolved under purifying selective pressure which means that, between them, a limited functional divergence occurred in the coding region [16,17]. In this regard, the study of the impact of *Glycine max* whole-genome duplication on gene expression revealed that, generally, paralogs evolve under purifying selection and 50% of them undergo tissue expression sub-functionalization [18]. Accordingly, in *Populus trichocarpa*, most of the pairs of duplicated AQP genes show divergent patterns of expression, even if there are cases where the functional redundancy cannot be excluded [16]. In addition to that, a certain degree of redundancy between paralogs is supported by the absence of the obvious phenotype of different single AQP mutants [2,19,20]. Besides the spatio-temporal sub-functionalization, neo-functionalization may have evolved, particularly in the case of intracellular AQPs [9], as the ancestral membrane intrinsic protein was only exposed to the extracellular medium. Neo-functionalization can originate from the acquisition or loss of different solute selectivity, as water transport is the only ancestral feature shared by the PIP, TIP, and SIP subfamilies [14]. The acquisition by horizontal gene transfer of the NIP subfamily from bacteria also contributes to the diversification of land plant AQPs (reviewed in [21]).

2.2. Plant AQP expression

Nowadays, RNA-seq technology produces high coverage of transcriptomes and allows a more complete profiling of AQP expression previously circumscribed by the high sequence similarity between *AQP* genes from the same subfamily. While the mRNA level of a gene is not necessarily strictly related to the abundance and activity of a protein in a cell or tissue, changes in the mRNA expression level often reflect the protein abundance. Developmental transcriptome profiles of different angiosperms, such as Arabidopsis and maize have been obtained in recent years [22,23]. The RNA-seq databases constitute interesting tools to analyze how the different AQP subfamilies/isoforms are regulated, and to deduce their putative physiological role in cell water or solute homeostasis. We organized the RNA-seq developmental data of maize [23] to better depict the complex expression profile of AQPs (Fig. 1). As expected from previous qPCR or protein expression studies performed on maize *PIP* genes [24–26], AQP isoforms have different patterns of expression according to the organs and the developmental stages. *PIP* genes are generally highly expressed (absolute values – circle size), especially in roots, and show a large amplitude of variation in expression (relative values – circle color). TIPs are also highly expressed in roots, especially TIP1s and TIP2s, whereas TIP3s are mostly expressed in seeds. SIPs show quite a constant and low expression level. Similarly, a globally low expression is observed for NIPs, that however display a larger amplitude of variation than SIPs. This dynamic is very similar to the one reported for Arabidopsis [27], highlighting the existence of similar patterns across monocot and dicot species estimated to diverge 150–300 million years ago [28]. This suggests that the physiological diversification of AQPs is likely conserved between distant plant species.

Transcriptomic studies also have an immense potential to help understand the functional contribution of AQPs in response to different stresses. Changes in the expression pattern of closely related AQPs in plants exposed to stress point to differential roles of AQP paralogs under stress conditions (reviewed in [12,29]). Transcriptomic studies now offer the possibility to assess a potential correlation between the expression of specific AQPs and other cellular transporters, a topic that has been poorly studied in the past. However, the disadvantage of these high throughput studies performed from different tissues is the loss of information about individual cell types. The application of recent advances in single-cell type isolation protocols and single cell profiling in plants [30,31] provide a unique opportunity for detailed studies of AQP paralogs. For instance, laser micro-dissection of maize stomatal complexes allowed us to identify the PIPs specifically expressed in these cells during the day or during the night [32]. Surprisingly, in these stomatal complexes like in all other cell types or tissues analyzed so far, members of the PIP1 and PIP2 subfamilies are always co-expressed. Interestingly, the ratio between the PIP1 and PIP2 isoforms can differ significantly between the cell types/tissues, but we wonder why a single cell needs to express several paralogs at the same time. A more complete understanding of the *in vivo* transport activity of these AQPs is definitely required to discern between diversification and redundancy among paralogs, and to obtain a deeper understanding of the adaptive advantage conferred by the expression of several AQPs in a specific cell type.

2.3. Substrates

Plant AQPs, first discovered as water channels, also facilitate the membrane diffusion of an increasing number of small solutes, such as urea, CO_2, H_2O_2, ammonia, metalloids and, as recently reported, ions, O_2, and Al-Malate [33–35]. This large list of solutes suggests a wide range of putative physiological roles that have been recently reviewed (for metalloids transport [36], H_2O_2 [37], CO_2 [38], or more general reviews [3,39,40]). Currently, the solute transport description of AQPs is far from exhaustive, even for model species that have been extensively studied. Nevertheless, the channel substrate specificity is generally conserved within a given family, even if exceptions are reported (Figs. 1 and 2). For instance, most of the characterized PIPs facilitate water diffusion; the TIPs facilitate the diffusion of water, urea, ammonia, and H_2O_2, and the NIPs the diffusion of metalloids (boric acid and arsenite) in addition to glycerol and water. In addition, some AQPs exhibit specific channel activities, such as, for instance, the ability to transport CO_2, which is restricted to some PIP isoforms [41]. However, it has to be mentioned that the transport specificity of AQPs is generally tested after heterologous expression in Xenopus oocytes or in the yeast *Saccharomyces cerevisae*. While the water channel activity of AQPs in the plant cell membrane can be deduced from protoplast swelling assays or the use of a cell pressure probe and treatments with AQP inhibitors (such as mercury, silver, or cytoplasmic acidification), demonstrating the facilitated diffusion of other solutes through AQPs in a plant cell is more complex. In heterologous expression systems, the functional assays may detect a substrate specificity that might not be relevant in plant cells due to specific regulation events or to the absence of substrate. To overcome this issue, several studies analyzed the physiological effects resulting from the deregulation of AQP expression (knockout, down- or over-expression). For example, knockout mutants

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