Biochimica et Biophysica Acta 1840 (2014) 1574–1582

Contents lists available at ScienceDirect

Biochimica et Biophysica Acta

journal homepage: www.elsevier.com/locate/bbagen

Review

Plant aquaporins: Roles in plant physiology ☆

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ARTICLE INFO

Article history:
Received 20 August 2013
Received in revised form 28 October 2013
Accepted 4 November 2013
Available online 15 November 2013

Keywords:
Aquaporin
Genetic diversity
Hydraulics
Nutrient acquisition
Plant signaling
Root
Stress
Water transport

ABSTRACT

Background: Aquaporins are membrane channels that facilitate the transport of water and small neutral molecules across biological membranes of most living organisms.
Scope of review: Here, we present comprehensive insights made on plant aquaporins in recent years, pointing to their molecular and physiological specificities with respect to animal or microbial counterparts.
Major conclusions: In plants, aquaporins occur as multiple isoforms reflecting a high diversity of cellular localizations and various physiological substrates in addition to water. Of particular relevance for plants is the transport by aquaporins of dissolved gases such as carbon dioxide or metalloids such as boric or silicic acid. The mechanisms that determine the gating and subcellular localization of plant aquaporins are extensively studied. They allow aquaporin regulation in response to multiple environmental and hormonal stimuli. Thus, aquaporins play key roles in hydraulic regulation and nutrient transport in roots and leaves. They contribute to several plant growth and developmental processes such as seed germination or emergence of lateral roots.
General significance: Plants with genetically altered aquaporin functions are now tested for their ability to improve plant resistance to stresses. This article is part of a Special Issue entitled Aquaporins.

1. Introduction

Terrestrial plants establish a continuum between the soil and the atmosphere and contribute to water transfer between these two entities. In transpiring plants, the ascent of water is mediated through xylem vessels, capillaries made from dead cells. For a long time, water diffusion across the lipid phase of membranes was thought to be sufficient to support water exchanges in living plant cells and tissues [1]. In the very early 1990s, the existence of water channels in plants had not been clearly hypothesized, even though some aquaporins had been molecularly characterized due to their high abundance or remarkable expression properties. Thus, the functional characterization of plant aquaporins shortly after the pioneering work of Preston et al. [2] on human AQP1 opened unprecedented perspectives in the field of plant water relations. To date, the function and regulation of aquaporins is quite extensively integrated to explain the remarkable hydraulic properties of plants. However, additional surprises have come with the identification of other aquaporin substrates than water, some of them such as boron, silicon or carbon dioxide (CO_2) being of great physiological significance. Thus, the term “aquaporin” has been used in a broad sense and now refers to all plant Major Intrinsic Proteins (MIPs), whether or not their main role is in water transport.

In the present review, we present the comprehensive insights made on plant aquaporins in recent years, pointing to their molecular and physiological specificities with respect to animal or microbial counterparts. We discuss the diversity of plant aquaporin isoforms, of their substrates and cellular localizations. We emphasize their physiological functions with respect to whole plant hydraulics, plant development, nutrient acquisition, and plant responses to various environmental stresses.

2. The family of plant aquaporins and their substrates

2.1. High diversity of isoforms

Aquaporins belong to the large class of MIPs, with first member (Nodulin-26, *Gm*NOD26) identified in plants (soybean) as early as 1987 [3]. The water transport activity of plant aquaporins was first established for an *Arabidopsis* homolog (*At*TIP1;1) [4], and their function was thereafter described in numerous herbaceous or ligneous, wild or cultivated plant species. Aquaporins of higher plants exhibit a high diversity with 35, 36, 33 isoforms in *Arabidopsis*, maize and rice, respectively [5–7]. Plant aquaporin homologs can be classified according to their sequence into up to seven subfamilies [8,9], which may also correspond to distinct sub-cellular localizations. The so-called Plasma membrane Intrinsic Proteins (PIPs), which localize to the plasma membrane mostly, can be further divided into PIP1 and PIP2 subclasses. The Tonoplast Intrinsic Proteins (TIPs) are targeted to the vacuolar membrane (tonoplast). Although *Gm*NOD26 is exclusively expressed in the peribacteroid membrane of nitrogen-fixing symbiotic

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http://dx.doi.org/10.1016/j.bbagen.2013.11.004

nodules of legume roots, the NOD26-like Intrinsic Proteins (NIPs), which form the third subfamily, are also found in non-legume plant species, where they localize to the plasma membrane [10,11] or the endoplasmic reticulum (ER) [12]. The Small basic Intrinsic Proteins (SIPs) group comprises only a few isoforms (3 and 2 in *Arabidopsis* and rice, respectively). The uncategorized X Intrinsic Proteins (XIPs) were recently discovered in protozoa, fungi and plants and are of as yet unknown functions [13–15]. This subfamily is absent from plants such as *Arabidopsis*, maize, rice. Two additional subfamilies, the GlpF-like Intrinsic Proteins (GIPs) and the Hybrid Intrinsic Proteins (HIPs) are present exclusively in moss, not in vascular plants [8,9]. Whereas the first four subfamilies (PIPs, TIPs, NIPs and SIPs) are present in all terrestrial plants, from non-vascular plants to vascular plants, the PIPs are the only ones that are shared between algae and higher plants. Thus, the PIPs could represent the ancestor aquaporins that have been conserved throughout evolution of terrestrial plants. By contrast, the GIPs and HIPs may have been lost during this process.

2.2. High diversity of sub-cellular localization

With respect to their animal counterparts, plant aquaporins show a broader array of sub-cellular localizations, in relation with the high degree of compartmentalization of plant cells. Aquaporins have been localized in nearly all of plant cell sub-cellular compartments, including plasma membrane, tonoplast, ER, Golgi apparatus and chloroplast. Localization of aquaporins in the chloroplast, which quasi exclusively relies on proteomic studies, is still debated [16]. Interestingly, some aquaporins exhibit multiple sub-cellular localizations. For instance, *Nt*AQP1, a tobacco PIP1 homolog, was observed in both the plasma membrane and chloroplast inner envelope membrane of tobacco leaf cells [17]. Seed-specific TIPs of *Arabidopsis* (*At*TIP3;1, *At*TIP3;2), which predominantly sit in the protein storage vacuoles, are also transiently expressed at the plasma membrane during the early stages of seed germination and maturation [18]. In these two cases, however, it will be important that these observations can be extended to other plant species. Several mechanisms that determine the trafficking of newly synthesized PIPs or TIPs to their destination membranes have recently been discovered. In PIP2s, diacidic motifs and C-terminal phosphorylation were found to favor export from the ER [19–21]. In contrast, homologs of the PIP1 sub-class showed trafficking defects, unless they were co-expressed with PIP2s and formed heterotetramers [21–23]. These molecular interactions seem to be necessary for PIP1s to reach the plasma membrane (see 4.3). In addition, a role for Soluble NSF Attachment Protein REceptors (SNAREs) in PIP trafficking to the plasma membrane was recently uncovered [24,25]. However, the mechanisms that determine the multiple localizations of some aquaporins are as yet unknown.

2.3. High diversity of substrates

Functional expression of plant aquaporins in heterologous systems such as *Xenopus* oocytes or yeast cells revealed a great diversity of substrates. They include water and the related molecule H_2O_2, solutes transported by animal and bacterial homologs (urea, glycerol), metalloid species [boric acid: $B(OH)_3$; silicic acid: $Si(OH)_4$, arsenious acid: $As(OH)_3$], lactic acid, or dissolved gas molecules (CO_2, ammonia: NH_3) [26,27]. With respect to this large array of substrates, plant aquaporins can exhibit complex yet specific selectivity profiles. For instance, *At*TIP1;1 facilitates the transport of H_2O, H_2O_2 and urea [4,28,29] whereas *Os*NIP2;1 from rice functions as a transporter of H_2O, methylated arsenic species, silicic acid and antimonite [10,30–32]. Atomic structures of microbial, animal, and plant homologs have shown that highly conserved structural features can confer on aquaporins their transport selectivity for water and/or solutes [33]. Accordingly, homology modeling approaches based on the aromatic/arginine selectivity filter have been developed to predict plant aquaporin selectivity [34,35]. However, further investigations are still required. For instance, mammalian AQP1 and AQP4 facilitate the transport of nitric oxide (NO) [36,37]. NO plays a role in plant signaling and may well be transported by plant aquaporins.

3. Aquaporins and water transport in plant roots and leaves

3.1. Root hydraulic conductivity (Lp_r)

Water uptake by roots occurs through successive transport along the radial and axial paths. Axial water transport is mediated by xylem vessels, which do not present significant membrane barriers. The radial path allows water transport from the soil to the vessels and involves three concurrent pathways: apoplastic (across cell walls), symplastic (through plasmodesmata and cytoplasmic continuities) or transcellular (across membranes) [38]. The latter pathway is contributed in part by aquaporins but is difficult to distinguish experimentally from the symplastic pathway. They together form the cell-to-cell pathway. Many aquaporins are known to be highly expressed in roots [7,39–41], supporting a role of aquaporins in root water transport. Mercury ions (Hg^{2+}), which act as common aquaporin blockers by binding to Cys residues within or in the vicinity of the pore [42], were first used in tomato roots [43] and later on in various other species [44,45] to show that aquaporins can contribute to >70% of Lp_r. This figure was confirmed using other types of aquaporin inhibitors (azide, weak acids) which showed a very similar inhibition profile as mercury among natural accessions of Arabidopsis [45]. First genetic evidence for the contribution of a specific aquaporin to overall Lp_r was reported by Javot et al. [46]. These authors showed that *Arabidopsis* *At*PIP2;2 is highly expressed in several root cell types including endodermis, and that, by comparison to wild-type plants, the Lp_r of corresponding knock-out mutants (*pip2*;*2*) was reduced by 14%. More recently, Sutka et al. [45] reported that the transcript abundance of several PIPs (*AtPIP1*;*1*, *AtPIP1*;*2*, *AtPIP1*;*4*, *AtPIP2*;*1*, *AtPIP2*;*3*, *AtPIP2*;*4* and *AtPIP2*;*5*) in *Arabidopsis* roots is positively correlated with Lp_r, in good agreement with published genetic data. For instance, the Lp_r of *pip1*;*2* mutants and *pip2*;*1 pip2*;*2* double mutants was decreased by 20% and 40%, respectively, compared to that of wild type [47,48].

3.2. Leaf hydraulics

Aquaporins are also highly expressed in plant leaves, where they contribute to the hydraulic conductance of inner tissues [49–51]. First evidence for aquaporin function was obtained in sunflower leaves by inhibition experiments using $HgCl_2$ [52]. More recently, combined physiological and genetic approaches have indicated that, in *Arabidopsis* at least, the function of PIP aquaporins in leaf veins (xylem parenchyma and bundle sheath) critically determines leaf hydraulics [47,53,54]. However, the contribution of aquaporins to leaf hydraulic conductance (~25%) was much less than that in the roots (>70%) [45,47,55]. This indicates that vessels represent an important hydraulic limitation in leaves. The interplay between vascular and extra-vascular (mediated by aquaporins mostly) transport of water will deserve more physiological studies in the future.

3.3. Regulation of root and leaf hydraulics by aquaporins

Plants have the remarkable ability to sense various signals from the surrounding environment and accordingly adjust their water transport properties. For instance, many abiotic stresses imposed by soil, such as salinity, oxygen deprivation or nutrient starvation, markedly reduce Lp_r in various plant species [56]. Irradiance and the stress hormone abscisic acid (ABA) both act as potent regulators of stomata-mediated transpiration and also regulate aquaporin-dependent leaf hydraulic conductance. Recent studies in *Arabidopsis* have established the involvement in light-dependent leaf hydraulic conductance of a single