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Review Article

The role of water-transporting aquaporins of the PIP and TIP subfamilies in plant development and adaptation to stress factors

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ABSTRACT

The comparative analyses of current knowledge of the diversity of aquaporins in angiosperms are presented in the review. Their structure, coding, and diversity of regulatory pathways are considered. Special attention is paid to aquaporins responsible for water transport. Data on the participation of various aquaporins in plant adaptation to abiotic factors causing hydration and dehydration are presented. The participation of aquaporins in the processes of plant growth and development from germination to seed formation are considered in sufficient detail. The data presented in the review indicate the main directions of further research important for elucidation of the mechanisms involved in regulation of aquaporins, mainly responsive for transmembrane water transport. The special significance of the studies at the omics level — transcriptomic and proteomic is noted. They will allow identifying the specificity of aquaporin isoforms involved in the development of the adaptive response or at different stages of plant development.

Keywords: aquaporins; adaptation; stress; growth; development.

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Обзорная статья

Роль транспортирующих воду аквапоринов подсемейств PIP и TIP в онтогенезе растений и адаптации к стрессовым факторам

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АННОТАЦИЯ

В обзоре приведен анализ современных представлений о многообразии аквапоринов у покрытосеменных растений. Рассмотрено их строение, кодирование и разнообразие путей регуляции. Особое внимание уделено аквапоринам, ответственным за транспорт воды. Приведены данные об участии различных изоформ аквапоринов в адаптации растений к абиотическим факторам, вызывающим гидратацию и дегидратацию. Достаточно подробно рассмотрены данные об участии аквапоринов в процессах роста и развития растений от прорастания до формирования семян. Представленные в обзоре данные указывают на основные направления исследований по расшифровке механизмов регуляции работы аквапоринов, основная функция которых заключается в трансмембранном переносе воды. Отмечено особое значение уже начатых исследований на системном транскриптомном и протеомном уровнях. Они позволят выявить специфичность изоформ аквапоринов, участвующих в развитии адаптационного ответа или на различных этапах развития растений.

Ключевые слова: аквапорины; адаптация; стресс; рост; развитие.

Как цитировать

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INTRODUCTION

The ability to create and maintain gradients of ions and water-soluble bioactive compounds between the internal contents and the environment is the fundamental property of living cells. The implementation of this property is closely related to the selective permeability of many compounds, ions, and water, which is driven by the properties of biological membranes. It is very important to study water transport mechanisms, because the extra- and intracellular environments are aqueous. Biological membranes are lipid bilayers having intrinsic passive permeability to water. In various models, it has been demonstrated that the intensity of passive H_2O flux may vary within the range of 5–15 × 10^{-3} cm/s, depending on the lipid composition of the membrane, the asymmetry of the lipid bilayer, and other factors [1–3]. However, the vital activity of any cell is closely related to changes in the intensity of water fluxes passing through membranes (including a sharp increase), which are necessary for osmoregulation and cannot be fully explained by the passive permeability of the lipid bilayer.

Aquaporins are a large family of membrane transport proteins that function as selective channels for the transport of water and other molecules, including gases, through cell membranes along a concentration gradient in both directions [4]. Aquaporins are characterized by a high transport rate that exceeds that of many other transporters, including ion channels. In some cases, the transport rate may reach more than a billion water molecules per second [5]. Aquaporins belong to the family of highly conserved major intrinsic proteins (MIP). Representatives of this family have been identified in all living organisms, except for thermophilic archaea and several bacteria [6].

The greatest diversity of aquaporins is typical of the green plants (*Viridiplantae*), especially the higher plants (*Embryophyta*). *Embryophyta* are characterized by the highest number of aquaporin isoforms, which resulted from polyploidization that occurred during the evolution of this taxon [7]. The importance of this phenomenon is confirmed by the fact that at least 35% of existing flowering species are descendants of polyploid species [8, 9]. The subsequent conservation of many genes encoding these transporters is due to the need to effectively regulate water homeostasis under changing environmental conditions in an attached lifestyle [6, 10]. A total of 35 genes encoding aquaporins were identified in the genome of Arabidopsis, 33 in rice, 34 in orange, 41 each in maize and sorghum, 47 in tomato, 50 in banana, 55 in poplar, 66 in soybean, 71 in cotton, and 120 in rapeseed [6, 11, 12].

In recent years, a substantial body of research has been accumulated on the physiological significance of aquaporins during development and adaptation to stress factors [10, 13–16]. However, the mechanisms underlying these processes are not fully elucidated. This review aims to provide a comparative analysis of the primary mechanisms of aquaporin involvement in the development and adaptation to abiotic stress factors. A comparative analysis of adaptation to dehydration and growth underlying processes are of particular interest.

HISTORY OF DISCOVERY AND CLASSIFICATION OF AQUAPORINS

As early as 1953, the transport of water across biological membranes through specialized pores was hypothesized [17]. However, this assumption had not been experimentally confirmed until 1970, when the presence of such pores was observed in human erythrocytes [18]. In 1988, a protein with a molecular mass of 28 kDa was isolated from erythrocytes and renal tubules (CHIP28, AQP1), then purified, and partially characterized [19]. The genes of these proteins were cloned, and their transport function was demonstrated by heterologous expression of the corresponding genes in *Xenopus* oocytes [20, 21]. In plants, the first aquaporin was identified as Nodulin 26 (GmNOD26) in rhizobial tubercles of soybean [22]. Further studies of plant aquaporins have facilitated the detailed characterization of many membrane transporters and have resulted in a substantial expansion of our understanding of the water regime.

In plants, including algae and higher plants, such as mosses, lycopodium, dicotyledons and monocotyledons, there are up to eight subfamilies of aquaporins. These subfamilies include plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), nodulin26-like membrane proteins (NIPs), small basic intrinsic proteins (SIPs), uncharacterized X intrinsic proteins (XIPs), large integral proteins, GlpF-like intrinsic proteins (GIPs), and hybrid intrinsic proteins [10, 23]. Proteins belonging to the latter two groups are exclusively present in prokaryotes and certain lower plants, and they have been completely lost in seed plants. The number of isoforms in these groups is minimal (1–3). In green algae, homologs of the PIP and GIP families have been identified and classified into the MIP A-E subclasses [14]. The analysis of 82 plants (5200 aquaporin isoforms) indicates that the PIP subfamily (1807 isoforms) is the most abundant by the number of isoforms. The TIPs and NIPs subfamilies exhibit a high degree of similarity in terms of isoform diversity [24].

The general scheme of intracellular localization of aquaporins in plants is illustrated in Figure 1. It should be noted that members of different families can be identified or their localization in other cell membranes can be predicted, independent of their initial localization. Contrary to the prevailing view that mitochondrial membranes contain no aquaporins [14], a recent proteomic analysis

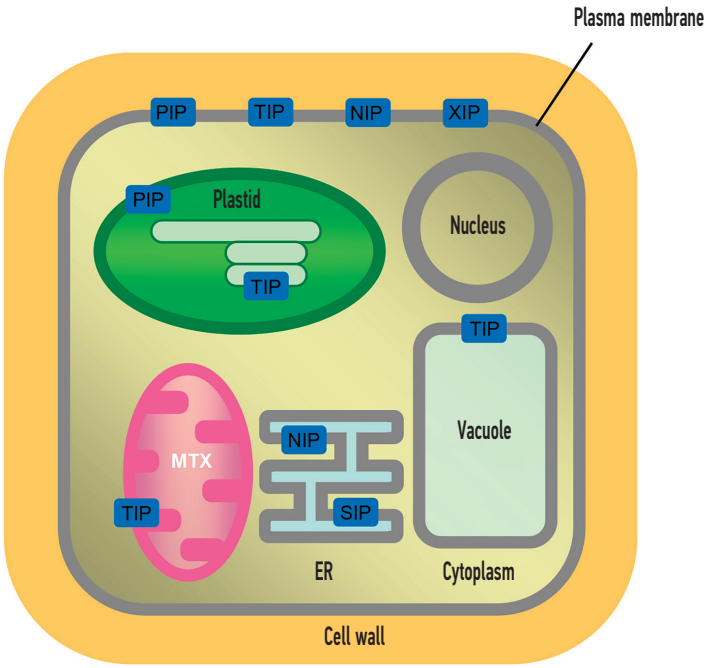

Fig. 1. Cellular localization of aquaporins. PIP, TIP, NIP, and XIP aquaporins are localized primarily in the plasma membrane and are present on the entire cell surface. SIP aquaporins and some NIP aquaporins were found in the endoplasmic reticulum (ЭПС) membrane. TIP aquaporins are localized in the tonoplast, the vacuole membrane. Some PIP and TIP aquaporins were predicted to be localized in the inner chloroplast membrane and the thylakoid membrane. A number of TIP aquaporins were found in mitochondrial (MTX) membranes

Рис. 1. Клеточная локализация аквапоринов. PIP-, TIP-, NIP- и XIP-аквапорины локализуются преимущественно в плазматической мембране и присутствуют на всей поверхности клетки. SIP-аквапорины и некоторые NIP-аквапорины были обнаружены в мембране эндоплазматической сети (ЭПС). TIP-аквапорины локализуются в тонопласте — мембране вакуоли. Было предсказано, что некоторые PIP- и TIP-аквапорины локализуются во внутренней мембране хлоропласта и мембране тилакоидов. Ряд представителей TIP-аквапоринов выявлен в мембранах митохондрий (MTX)

has identified these proteins, presumably belonging to the TIP subfamily [25, 26].

The aforementioned scheme appears to be inconclusive due to the potential variability in the distribution of aquaporins within cell membranes across diverse shoot and root tissues. This variability may also depend on the developmental stage of the plant organism and the impact of stress factors on the plant [24, 27]. This phenomenon is exemplified by the localization and intracellular redistribution of representatives of the PIP and TIP aquaporin subfamilies.

STRUCTURE AND TRANSPORT PROPERTIES OF AQUAPORINS

Like all members of the MIP superfamily, aquaporins possess the following structural characteristics (Fig. 2):

- Six transmembrane alpha-helical domains [6];
- Localization of N- and C-termini in the cytosol; and
- Five loops connecting transmembrane domains (A–E: A, C, and E face outward, whereas B and D face into the cytosol).

The classical structure of aquaporins (six transmembrane domains) is thought to have arisen from a tandem intragenic duplication of the coding sequence for a protein with three transmembrane domains, which may have functioned as a homodimer [10].

The assembly of four monomers of aquaporins results in the formation of homo- or heterotetrameric complexes [4]. Each monomer of the complex functions as an independent water channel having an activity determined by its amino acid composition, interaction with neighboring monomers, post-translational modification, and the action of various signaling molecules [10, 27]. Two conserved loops (cytoplasmic loop B and outer loop E) contain the NPA-motif (Asn-Pro-Ala), which is critical for aquaporin functionality. This motif regulates the permeability of the transporter to substrates, including water [4]. Loops B and E form half-helices that are directed inside the membrane and converge in the middle to form a pore. At the point of convergence, there are two NPA motifs that, together with four amino acid (AA) residues located on the apoplastic side of the second (Phe81) and fifth (His210) transmembrane helices and within the E loop (Thr, Arg; known as the aromatic/arginine [ar/R] filter), contribute to the determination of the substrate specificity of the pore [10]. Another distinguishing trait of aquaporins is the presence of AEF (Ala-Glu-Phe) or AEFXXT (Ala-Glu-Phe — any AK — any AA-Thr) motifs in the N-terminal domain [6].

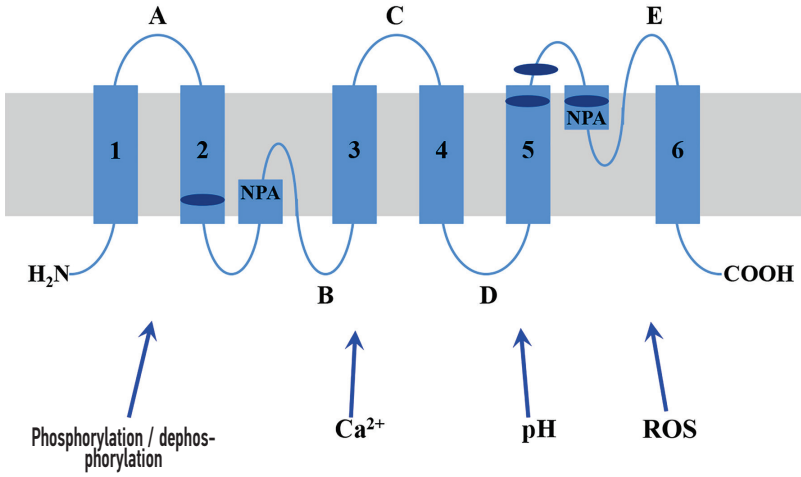

Fig. 2. The structure of plant aquaporin. Transmembrane domains (1–6), loops (A–E), NPA (Asn-Pro-Ala) motifs are located in loops B and E. Posttranslational modification is possible as a result of changes in phosphorylation, depends on pH, Ca^{2+} ions, and the presence of reactive oxygen species (ROS). Dark ellipse — aromatic/arginine filter — ar/R filter (from [4], with alterations)
Рис. 2. Структура аквапорина растений. Трансмембранные домены (1–6), петли (A–E), мотивы NPA (Asn-Pro-Ala) находятся в петлях B и E. Посттрансляционная модификация возможна в результате изменения фосфорилирования, зависит от pH, ионов Ca^{2+}, а также присутствия активных форм кислорода (ROS). Темный элипс — ароматический/аргининовый фильтр — ar/R filter (по: [4], с изменениями)

Table 1. Transport functions of aquaporin subfamilies in angiosperms
Таблица 1. Транспортные функции подсемейств аквапоринов покрытосеменных растений

Aquaporin subfamily	Transport specificity according to [10]
PIP (plasma membrane intrinsic proteins)	Transport of water, hydrogen peroxide, and carbon dioxide (different functions in different members of the subfamily)
TIP (tonoplast intrinsic proteins)	Transport of water, hydrogen peroxide, ammonium, and urea
NIP (Nodulin26-like intrinsic proteins)	Permeable to a wide range of substrates, including both beneficial and toxic metalloids, but poorly permeable to water (different functions in different members of the subfamily)
SIP (small basic intrinsic proteins)	Low water permeability
XIPs (uncharacterized/X intrinsic proteins)	Low water permeability

The above data indicate the complex structure of the channel, which determines its permeability. Although aquaporins were originally characterized as water transporters, this property is not exhibited by all groups of plant aquaporins. Furthermore, variations in substrate permeability can be observed within the same subfamily. This phenomenon has been demonstrated for PIP [10], TIP, and NIP aquaporins [28], as well as SIP [29] and XIP aquaporins [30]. The peculiarities of the transport function of angiospermous aquaporins are presented in Table 1.

The following model systems are used to determine the transport properties of aquaporins with respect to specific substrates: (1) isolated tissues (e.g., leaf discs); (2) protoplasts; (3) membrane vesicular fractions isolated from cells of wild-type or transgenic plants with recombinant aquaporins; (4) *Xenopus* clawed frog oocytes; (5) yeast cells; (6) liposomes with purified and embedded aquaporin proteins (proteoliposomes) or flat lipid bilayers [10, 31]. However, data obtained for the same protein in different model systems may differ [32]. Therefore, caution should be exercised when transferring results obtained on proteoliposomes, oocytes, or yeast to *in planta* conditions.

AQUAPORIN ENCODING IN DIFFERENT PLANT SPECIES

As previously mentioned, *Viridiplantae* are distinguished by a substantial number of genes that encode aquaporins. Table 2 presents examples of aquaporin encoding from five primary subfamilies across diverse species of higher plants. It is evident that the number of aquaporin genes may vary considerably even among closely related species. The presence of 120 genes in rapeseed, in contrast to the 35 genes observed in

Arabidopsis, is particularly noteworthy. This increase in the number of aquaporin genes may be attributed to genome-wide duplication during evolution [11, 33].

It is hypothesized that PIP-aquaporins diverged into two highly conserved groups (PIP1 and PIP2) prior to the emergence of land plants. Although the number of groups did not increase further, a significant increase in the number of isoforms of PIP1 and PIP2 aquaporins was observed [10]. A separate subfamily of TIP aquaporins was exclusively formed in land plants, with TIP2, TIP3, and TIP4 representing the predominant groups. Conversely, TIP1 and TIP5 appear as sister groups to TIP3 and TIP2, respectively, in flowering plants. Furthermore, the NIP subfamily is distinguished by its high degree of variability among different species. Another noteworthy phenomenon pertains to the encoding of the XIP subfamily. The loss of the entire XIP subfamily is a distinctive feature of monocotyledons and certain dicotyledons, as evidenced by many species within the *Brassicaceae* family.

AQUAPORIN REGULATION

In the last two decades, a lot of studies have been conducted to evaluate changes in the activity of plant aquaporins at the level of gene expression and protein accumulation as an adaptation to stress factors causing changes in water regime [15]. The most common subjects of analysis are factors leading to dehydration,

Table 2. Coding of aquaporins in some species of angiosperms

Таблица 2. Кодирование аквапоринов у некоторых видов цветковых растений

Plant species	Total AQP genes	*PIP1*	*PIP2*	Total *PIP*	*TIP1*	*TIP2*	*TIP3*	*TIP4*	*TIP5*	Total *TIP*	*NIP1*	*NIP2*	*NIP3*	*NIP4*	*NIP5*	*NIP6*	*NIP7*	Total *NIP*	*SIP1*	*SIP2*	Total *SIP*	*XIP1*	*XIP2*	*XIP3*	Total *XIP*	Reference*
Thale cress *Arabidopsis thaliana* (L.) Heynh.	**35**	5	8	**13**	3	3	2	1	1	**10**	2	1	1	2	1	1	1	**9**	2	1	3	0	0	0	**0**	[34]
Rapeseed *Brassica napus* L. (canola)**	**120**	19	24	**43**	9	13	10	1	2	**35**	4	4	6	6	5	4	2	**31**	6	5	11	0	0	0	**0**	[11]
Brassica oleracea L. var. *italica* broccoli	**65**	8	15	**23**	6	7	5	1	1	**20**	2	2	3	5	3	2	1	**18**	2	2	4	0	0	0	**0**	[35]
Gossypium hirsutum L. upland cotton**	**71**	15	13	**28**	14	7	0	2	0	**22**	3	1	0	0	2	6	0	**12**	7	0	7	1	0	0	**1**	[36]
Populus trichocarpa black cottonwood Torr.& A.Gray ex Hook.	**55**	5	10	**15**	8	4	2	1	2	**17**	5	1	5	0	0	0	0	**11**	4	2	6	5	1	0	**6**	[37]
Glycine max (L.) Merr. soy bean	**66**	8	14	**22**	9	7	4	2	1	**23**	5	2	0	1	1	2	2	**13**	6	0	6	2	0	0	**2**	[38]
Cucumis melo L. melon	**31**	2	10	**12**	3	2	1	1	1	**8**	1	2	0	1	2	1	1	**8**	1	1	2	1	0	0	**1**	[25]
Daucus carota subsp. *sativus* (Hoffm.) Arcang garden carrot	**47**	6	8	**14**	4	5	2	1	2	**14**	6	1	1	2	2	1	0	**13**	2	2	4	2	0	0	**2**	[39]
Oryza sativa L. rice	**33**	3	8	**11**	2	2	2	3	1	**10**	4	2	3	1	0	0	0	**10**	1	1	2	0	0	0	**0**	[40]
Hordeum vulgare L. barley	**40**	5	14	**19**	2	3	2	3	1	**11**	2	3	2	1	0	0	0	**8**	1	1	2	0	0	0	**0**	[41]
Sorghum bicolor (L.) Moench sorghum	**41**	4	10	**14**	2	3	3	3	2	**13**	5	2	3	1	0	0	0	**11**	2	1	3	0	0	0	**0**	[42]
Zea mays L. maize	**41**	4	9	**13**	2	4	4	4	1	**15**	3	4	2	1	0	0	0	**10**	2	1	3	0	0	0	**0**	[12]

Note. The total number of genes encoding aquaporins or their subfamilies is shown in bold. *The authors of references cited here used not only the amino acid sequences of proteins, but also information about the genomes and transcriptomes of the plants studied, so the table specifically refers to genes encoding full-length proteins. **Evolutionarily young polyploids.

Примечание. Полужирным шрифтом выделено общее количество генов, кодирующих аквапорины или их подсемейства. *Авторы приведенных здесь статей использовали не только аминокислотные последовательности белков, но и информацию о геномах и транскриптомах изучаемых растений, поэтому в таблице речь идет именно о генах, кодирующих полноразмерные белки. **Эволюционно молодые полиплоиды.

such as drought, salinity, or high and low temperatures. However, the factors leading to excessive environmental moisture for land plants, including short-term stress conditions such as flooding and long-term stress conditions for higher plants that have evolved to live in an aquatic environment, remains underexplored with regard to the involvement of aquaporins in the response formation.

The above processes are accompanied by changes in water fluxes, both through the plasmalemma and across intracellular membranes. This assumption is consistent with the data on changes in the expression patterns of genes encoding various aquaporins, the accumulation spectra of the corresponding proteins, and the modification of their functional activity. A large body of evidence points to the formation of a complex regulatory system at the transcriptional and post-translational levels. The mechanisms implemented at the protein level include phosphorylation and dephosphorylation, changes in protein reconstitution (Fig. 2), functional tetramerization of aquaporin monomers, and the intensity of incorporation/replacement of different aquaporin isoforms within cell membranes [4].

The current understanding of these mechanisms, which allow for the regulation of water transport intensity through various membranes of the plant cell, will be discussed in more detail.

Transcriptional regulation under dehydration conditions

Several studies have shown that the expression of genes encoding aquaporins is tissue specific and strongly influenced by environmental factors such as drought, salinity, and high/low temperatures. The data summarized in Table 3 clearly show that the studied genes encoding aquaporins of the PIP and TIP subfamilies, which are specialized in water transport, significantly change their expression profile. In addition, the level of transcript accumulation of PIP family genes is the most variable.

The data on stress-induced change in expression presented in Table 3 demonstrate three key findings: (1) not all aquaporin genes within the same subfamily undergo unidirectional changes in expression intensity in response to stress; (2) the effects of transcriptional exposure to the same stressor may vary in its impact on the accumulation of expression products, depending on the studied organ (e.g., roots or leaves) and/or its age; (3) a change in gene expression in several tested aquaporins exhibit complex changes over time. These data support the existence of regulation at the transcriptional level, although the mechanisms underlying these phenomena are far from understanding. In the foreseeable future, a renewed interest in this regulatory form is likely to accompany the deciphering of promoter regions of genes and the identification of transcription factors.

Table 3. Regulation of aquaporins at the transcriptional level under dessication stress

Таблица 3. Регуляция аквапоринов на транскрипционном уровне в условиях обезвоживания

Analyzed gene, species and tissue specificity	Acting factor	Changes in transcript abundance	Reference
FaPIP1;2, FaPIP2;1 and *FaTIP1;1* in the leaves of *Festuca arundinacea* Vill.	Drought	*FaPIP1;2* and *FaTIP1;1* expression decreased in both analyzed genotypes (with high and low drought tolerance); *FaPIP2;1* expression decreased only in the genotype with high drought tolerance	[43]
	Salinization	*FaPIP1;2* expression decreased in the high salt tolerance genotype; *FaTIP1;1* expression increased in both genotypes	
FpPIP1;2, *FpPIP2;1* and *FpTIP1;2* in the leaves of *F. pratensis* Huds.	Low positive temperatures	Reduced expression in both genotypes (high and low cold tolerance)	
TaPIP1-1, *TaPIP1-4*, *TaPIP2-26* in the elongation zone of the third true leaf of *Triticum aestivum* L.; *TaPIP1-2*, *PutTaPIP2-2*, *TaPIP2-2C3*, *TaPIP2-3C1*, *TaPIP2-4C1*, *TaAQP2* in the mature zone of the second true leaf	Salinization	*TaPIP2-26*: an increase compared to the control at night. *TaPIP1-2*: a decrease compared to the control during both day and at night. *PutTaPIP2-2*: a decrease compared to the control during the day. *TaPIP2-3C1*: a decrease compared to the control at night. *TaPIP2-4C1*: an increase compared to the control during the day. *TaAQP2*: a decrease compared to the control both during the day and at night	[44]

Table 3 (continued) / Окончание таблицы 3

Analyzed gene, species and tissue specificity	Acting factor	Changes in transcript abundance	Reference
13 *AtPIP* genes (5 *PIP1* genes, 8 *PIP2* genes) in roots and aerial parts of *Arabidopsis thaliana* (L.) Heynh.	Drought (mannitol 250 mM)	Aerial parts: There was a strong decrease in the expression of *PIP1;5*, *PIP2;2*, *PIP2;3*, and *PIP2;6*. The expression of PIP1;1 first increased and then gradually decreased. The expression level of *PIP1;2*, *PIP2;7* and *PIP2;8* initially remained at the same level, followed by a gradual decrease. The expression of *PIP1;3*, *PIP1;4*, *PIP2;1*, and *PIP2;5* increased strongly in both roots and aerial parts, whereas the expression of *PIP1;5*, *PIP2;2*, and *PIP2;3* decreased in both roots and aerial parts. The expression level of *PIP2;4* decreased much more in roots than in the aerial parts. The expression level of *PIP2;6* decreased less in roots than in the aerial parts	[45]
	Salinization (150 mM NaCl)	Aerial parts: *PIP1;2* and *PIP1;5* expression levels exhibited an initial increase, followed by a subsequent decline; *PIP2;6* expression levels demonstrated a decline; the remaining genes exhibited an increase in expression. Roots: *PIP1;5* expression demonstrated a decrease, whereas the expression of other genes exhibited an increase	
	Low positive temperatures (4 °C)	Aerial parts: There was an increased expression of *PIP2;5* and *PIP2;6*, and a decreased expression of all other genes. Roots: there was an increased expression of *PIP1;4*, *PIP2;1*, *PIP2;5*, and *PIP2;6*; the expression of *PIP2;8* first increased, then decreased (in total, no changes); there was a decreased expression of all other genes	
12 *CmPIP* genes (2 *PIP1* genes, 10 *PIP2* genes) in roots and leaves of *Cucumis melo* L.	Salinization (50 mM NaCl in Hoagland solution)	Roots: *PIP2.1*, *PIP2.5*, and *PIP2.6* showed a significant decrease in expression. Leaves: *PIP1.1* showed a significant increase	[46]
	Exposure to high temperatures (40 °C)	Roots: *PIP1.1*, *PIP1.2*, and *PIP2.2* showed a significant increase, whereas *PIP2.1*, *PIP2.5*, *PIP2.6*, *PIP2.9*, and *PIP2.10* showed a significant decrease. Leaves: *PIP2.6* showed a marked increase	
8 *CmTIP* genes (3 *TIP1* genes, 3 *TIP2* genes, *TIP3.1*, *TIP4.1*, and *TIP5.1*) in roots and leaves of *C. melo*	Salinization (50 mM NaCl in Hoagland solution)	Roots: *TIP1.1* showed a weak increase in expression, whereas *TIP2.2*, *TIP4.1* showed no significant differences	
	Exposure to high temperatures (40 °C)	Roots: *TIP1.1* showed a significant increase in expression; other genes showed a decrease. Leaves: *TIP1.1* showed a significant decrease, *TIP1.3* showed a significant increase, and *TIP2.1* showed an increase	
AcAQP2 (from the *PIP1* group) in roots, bulbs, and leaves of *Allium cepa* L.	Salinization (25, 50, 75, and 100 mM NaCl)	In roots, a decrease was observed for all concentrations except for 75 mM NaCl	[47]
AcAQP1 (from the *PIP2* group) in roots, bulbs, and leaves of *A. cepa*		In roots, a statistically significant decrease in expression was detected at 100 mM NaCl, whereas in bulbs, a statis-tically significant decrease was detected at all concentra-tions except for 75 mM NaCl.	
AcAQP3 from the *TIP2* group in roots, bulbs, and leaves of *A. cepa*		Leaves showed a decrease in expression for concentra-tions of 50 and 100 mM NaCl; roots showed a decrease for all concentrations but most pronounced for 50 mM NaCl; bulbs showed a decrease for concentrations of 50, 75, and 100 mM NaCl	
ZmPIP2;2 and *ZmPIP2;6* in roots of *Zea mays* L.	Drought	No changes compared with control	[48]
10 *PIP* genes (4 *PIP1* genes, 6 *PIP2* genes) in leaves of *Brassica oleracea* L. var. *italica*	Salinization	*PIP1–2* showed an almost threefold increase in expression compared with control leaves	[49]

Therefore, it is currently impossible to characterize the regularities of the observed differences and to assess the extent to which the change in transcription of different aquaporins is due to a non-specific or, conversely, a specific response to stress factor exposure.

Post-translational regulation during dehydration

The findings from the aforementioned studies indicate the possibility of regulating the aquaporin activity at both the gene and protein levels. An evident mechanism of the latter involves the alteration in the spectrum of aquaporin isoforms, which is consistent with the previously characterized change in the transcription of aquaporin-encoding genes. Nevertheless, there may be mechanisms that result in changes in the activity of existing aquaporins within specific membranes. The mechanisms underlying the regulation of aquaporins at the post-translational level are described below. Membrane transporters, including aquaporins, are characterized by conformational changes, which is one of the mechanisms of permeability control. An analysis of the three-dimensional structure of several aquaporins has led to the conclusion that the gate mechanism is in a constant dynamic equilibrium that shifts in response to changes in external conditions. Phosphorylation, protonation, and binding of bivalent cations are critical factors in this regulatory response. The process of phosphorylation and dephosphorylation of serine and threonine residues within aquaporins is subject to the regulation of protein kinases, leading to alterations in the tertiary structure and, consequently, the pore size [50–53]. A key aspect of water transport across the plasma membrane is the phosphorylation of Ser256 compared with the phosphorylation of Ser264 and Ser269 [54]. Another mechanism that may lead to a decrease in aquaporin activity is the destruction of disulfide bridges, a process that involves the participation of heavy metals such as mercury and silver [55, 56]. The effect of reactive oxygen species (ROS) on aquaporin activity is similar [57]. However, high levels of ROS inhibit the activity of aquaporins, whereas low levels have a stimulating effect [58].

Some alternative regulatory mechanisms at the protein level have been identified for aquaporins. One such mechanism involves a change in the rate of aquaporin transport from the synthesis site in the endoplasmic reticulum (ER) to the corresponding membranes [59, 60]. This mechanism may offer a potential explanation for the discrepancy between the stress-induced change in the accumulation of transcription products and the pool of encoded proteins detected in studies [61]. The mechanisms underlying this process are still unclear. One hypothesis proposes the involvement of two-acid motifs in the amino acid sequences of PIP aquaporins, which are likely involved in the mechanism of ER exit. An alternative mechanism involves the regulation of SNARE (soluble N-ethylmaleimide-sensitive factor adaptor protein receptors) proteins of the syntaxin family, which are involved in membrane fusion during vesicular transport. Together, these mechanisms may account for the observed constant "recycling" between membranes detected for aquaporins, although the rate of this recycling may vary. In addition to redistribution between cell membranes, aquaporins may be rapidly removed from their respective membranes under osmotic and salt stress, which subsequently reduces membrane permeability to water. The rapid response is believed to be partially determined by the degree of phosphorylation of the C-terminal domain [4, 10]. Consequently, a complex system of changes in the aquaporin pool within membranes, encompassing the plasmalemma and tonoplast, serves to regulate the dynamic equilibrium of aquaporin permeability to water under both normal conditions and stressors [27].

The examples evaluated in this section unmistakably demonstrate the heterogeneity of mechanisms that regulate the involvement of aquaporins in the development of adaptation mechanisms in plants. These mechanisms are manifested at the level of both transcripts and proteins. Furthermore, the identified changes vary by their orientation and velocity, depending on both the stressor type and the studied aquaporin. Currently, the PIP family of aquaporins is the most extensively studied, which can be attributed to the deep interest of researchers in this group, considering the critical role of plasmalemma permeability to water. Moreover, these data indicate the need to continue and expand studies aimed at further identification of multiple pathways regulating the aquaporin activity at different levels of organization and during dehydration. Further improvements in the accurate identification of closely related aquaporin-encoding genes and isoforms of these transporters are essential. A comparison of the rate and direction of aquaporin transport in the cell with the rate of their synthesis/degradation may be important.

Aquaporins in flooding and in aquatic higher plants

A large body of data indicates that the spectrum of aquaporins and their activity change when exposed to the risk of dehydration (salinity, drought, and high and low temperatures). However, the mechanisms for aquaporin contribution to the adaptive response to factors that are expected to increase the water flux into cells are not clearly understood. These factors include flooding (short-term response) and the growth of secondary aquatic higher plants in an aquatic environment (long-term adaptation).

The role of aquaporins in flooding has been studied for several decades. However, most of this research has focused on elucidating the effect of oxygen deficiency that develops during flooding on water transport. A decrease in hydraulic conductivity has been identified as

one of the earliest effects observed during flooding [62]. This phenomenon may be attributed to a rapid decrease in aquaporin permeability. The regulatory mechanisms include a rapid decrease in pH induced by hypoxia, as well as the subsequent protonation of histidine residues [63]. Another potential mechanism may involve the accumulation of ROS, which have been identified as regulators of aquaporin activity [57]. However, the existing data do not allow for a clear distinction between the effects of oxygen deficiency and excess water. This challenge may be partially addressed by studying the changes in aquaporin activity under conditions of well-aerated hydroponics. Unfortunately, no studies have been found that directly address this question, although some insights can be obtained from papers on control plants cultivated in hydroponics. The following examples provide illustrative cases.

As demonstrated in previous studies, a decline in the expression of genes encoding aquaporins HvPIP2;1, HvPIP2;2, and HvPIP2;5 is accompanied by a reduction in water absorption by barley roots [64]. However, a comparative analysis of aquaporins belonging to the PIP subfamily in root hairs of wild-type barley seedlings and *brb* mutants, characterized by a complete absence of hairs, which were cultivated in hydroponics, revealed no significant differences [65]. Consequently, it was concluded that aquaporin isoforms specifically expressed in root hairs are not involved in water absorption.

As a second example, we can mention another study that compared the roots of soybean seedlings grown in hydroponic systems (aerated and hypoxic). It was shown that the expression of four tested genes encoding PIP2 aquaporins varied significantly in control, but according to the authors, it this variation corresponded to the diurnal rhythm [66]. Thus, it is currently impossible to assess the effect of flooding on aquaporin activity in the absence of oxygen deficiency during short-term exposure.

In contrast to higher land plants, higher secondary aquatic plants absorb soluble substances mainly through leaves rather than roots [67]. The data indicate that only 25 aquaporin genes have been identified in the genome of *Zostera marina* L., including only 4 *PIP* genes, which is much fewer than in land angiosperms. This phenomenon may be related to a reduced need for proteins responsible for water absorption and mineral elements in plants growing in the aquatic habitat [67].

The study of tissue localization and aquaporin activity in such plants is still at its early stages. The interpretation of data obtained from monocotyledonous angiosperms of the genera *Zostera* and *Posidonia* is complicated by the fact that these plants grow in the sea, and the need to avoid excessive watering of tissues in these plants is combined with the need to cope with salinity (in contrast to glycophytic angiosperms). Nonetheless, Table 4 demonstrates a substantial accumulation of transcripts of genes encoding representatives of PIP aquaporins in shoot cells of apical meristems and epidermis. Conversely, transcripts of TIP protein genes were observed when the effect of salinization and vacuole size increased. The data in Table 4 underscores the need for further research on potential changes in the function of aquaporins and the mechanisms of their regulation in aquatic plants.

AQUAPORINS IN PLANT DEVELOPMENT

The ability of organisms to adapt to adverse environmental factors is predicated on genetic programs that ensure individual development under normal conditions. In the ontogenesis of flowering plants, there are stages that are similar to the periods of dehydration or increased hydration. One example is the well-known process of dehydration during seed formation, which increases the dormant period. It is also known that intensive hydration processes result in a significant increase in cell volume. Such processes include seed germination, elongation

Table 4. PIP and TIP aquaporins in marine angiosperms

Таблица 4. Аквапорины PIP и TIP у морских покрытосеменных растений

Plant species	Expressed gene, accumulated protein	Reference
Zostera marina L.	In contrast to land plants, *PIP* gene expression was higher in shoots than in roots. Specific expression of *TIP1* and *TIP5* genes was observed in male flowers.	[67]
	The role of PIP proteins in the regulation of water content during growth, seed germination, and the tidal cycle has been demonstrated	[68]
Posidonia oceanica (L.) Delile	*PoPIP1;1* transcripts were detected in meristematic regions of shoot and root apical meristems, epidermal and subepidermal cells of leaves, and vascular tissues. *PoTIP1;1* transcripts were detected in tissues whose cells had a well-defined vacuole. Upon exposure to elevated salinity, *PoTIP1;1* expression was greatly increased compared with *PoPIP1;1* expression.	[69]
	The immunolocalization of *PoPIP1;1* protein on leaf transversal sections re-vealed its presence in the epidermis and, to a lesser extent, in vascular bun-dles and the mesophyll; the accumulation of this protein increased when ex-posed to increased salinity	[70]

(unique to plant cells), apical growth of the pollen tube and root hair, and isodiametric cell growth (observed, for example, during leaf development). These processes involve enhanced transport of water and dissolved compounds through the plasmalemma and tonoplast. Nonetheless, the data on the role of PIP and TIP proteins in the aforementioned processes, as presented in the literature, remain rather fragmentary. The following examples illustrate their involvement at different stages of development, as evidenced by changes in the transcriptional and protein profiles of aquaporins.

Aquaporins in seed germination

Seed swelling, which involves hydration of the endosperm and embryo, accompanied by metabolic activation, including the formation of lytic vacuoles, appears to be the primary stage in the development of angiosperms [16]. Using Arabidopsis seeds as an example, the water content has been shown to increase from 11% in dry seeds to 82% 24 h after the onset of germination [71]. During the germination process, an increase in water flux is observed, accompanied by elongation of seedling cells and vacuolization [72, 73].

The example of Arabidopsis seeds shows that active expression of aquaporin genes belonging to the PIP1 (*PIP1;1*, *PIP1;2*, and *PIP1;4*) and PIP2 (*PIP2;1*, *PIP2;2*, *PIP2;6*, and *PIP2;7*) subfamilies as well as tonoplast aquaporin genes (*TIP1;1*, *TIP1;2*, and *TIP2;1*) starts after germination. A similar increase in the accumulation of PIP and TIP aquaporin gene transcripts was found in rice, bean, and horse chestnut. The involvement of aquaporins in the enhancement of water absorption is confirmed by inhibitor analysis (mercury ions) as well as by the studies of transgenic and mutant plants of rice, Arabidopsis, and tobacco. For example, knockout mutants in the *OsPIP1;3* gene were characterized by a strong decrease in germination rate, whereas an increase in the expression of this gene enhanced the germination process [74]. The role of these proteins in the regulation of germination and longevity of Arabidopsis seeds has been demonstrated using *TIP3* aquaporin gene mutants [75]. Therefore, the enhancement of water transport through both the plasmalemma and the tonoplast is evident.

The sprouting stage is followed by the development of seedlings and their juvenile organs, whose cells undergo significant elongation, thereby establishing the polarity of the emerging plant organism. This initial developmental stage passes into the vegetative growth phase, accompanied by a shift in the function of aquaporins.

Aquaporins and axial organ growth

Root aquaporins

Primary roots are formed from embryonic roots in seeds. There is evidence that PIP and TIP aquaporins are important for the growth of primary root cells [72]. Whereas PIP aquaporins determine the intensity of water entry from the outside, TIP1 and TIP2 proteins are involved in the biogenesis of provacuoles and the development of lytic vacuoles, providing water transport within vacuoles during root cell growth. This hypothesis is supported by the increased expression of *VfTIP2;1* and *VfTIP2;2* genes during root growth after germination in horse beans [76].

The data on the role of PIP and TIP aquaporins during root development are presented in Table 5. They have been characterized in detail in maize seedlings [77]. The transcriptional spectrum of the *ZmPIP1;1, ZmPIP1;5, ZmPIP2;1*, and *ZmPIP2;5* genes and the expression of the encoded isoforms showed a certain zonality when moving from the tip of the primary root to the zone of lateral root emergence. Using *in situ* hybridization and immunocytochemical approaches, aquaporin isoforms were localized to different zones (e.g., cortex, epidermis) depending on the stage of root development. The most comprehensive studies are presented for rice, grape (*Vitis vinifera* L.), maize, Arabidopsis, and barley. In the maize root, a change in the expression of *ZmPIP1;1, ZmPIP1;5, ZmPIP2;1*, and *ZmPIP2;5* genes was observed when moving from the tip of the primary root to the zone of lateral root emergence (Table 5) [77]. The specificity of aquaporin isoform distribution has also been shown for the root zones of rice seedlings [78]. The authors suggested that the specificity of the distribution of different representatives of aquaporins is associated with differences in the mechanisms of intercellular water transport, as well as with the development of aerenchyma that is typical of hydrophytes. In grape roots, the gene expression and protein levels of VvPIP1s and VvPIP2s were shown to be equally distributed in the cortex and vascular tissue at the root tip. However, their levels are reduced in cortical cells of mature root zones [79].

A comparison of the zonality of expression of genes encoding aquaporin isoforms in grape roots with their homologs in Arabidopsis demonstrated that most aquaporin isoforms were distributed similarly in these two species. The expression of PIP aquaporin genes was found to be significantly higher in the root tip compared to more mature regions along the primary root axis [79].

The tissue localization of transcripts of six aquaporin isoforms (*HvPIP2;2*, *HvPIP2;5*, *HvPIP2;7*, *HvPIP1;2*, *HvTIP1;1*, and *HvTIP2;3*) has been examined in barley [81]. The results demonstrated an intensive accumulation of aquaporin gene expression products in the epidermis and protoxylem. Expression in the endodermis and stem was primarily observed in less mature secondary roots, suggesting a potential role of aquaporins in regulating radial water transport. Among all aquaporin genes examined in barley, *HvTIP1;1* exhibited ubiquitous expression, whereas *HvPIP2;5* was predominantly expressed in the bark.

Table 5. Root aquaporins

Таблица 5. Аквапорины в корнях

Object	Expressed gene, accumulated protein	Plant	Reference
Root of 7–8-day old seedlings (0–5 mm from the tip)	*ZmPIP1;1*, *ZmPIP2;1* and *ZmPIP2;6* contribute most to expression, with the ZmPIP2;6 protein exhibiting a consist-ently low expression level across all root zones, yet being the most abundantly detected protein	*Zea mays* L.	[77]
Root of 7–8-day old seedlings (5–10 mm from the tip)	Predominant expression of *ZmPIP1;1*, *ZmPIP2;1*, and *ZmPIP2;5*, whereas *ZmPIP1;5* expression is increased compared with the tip. Of the proteins, ZmPIP2;1/2;2 and small amounts of ZmPIP1;2 and ZmPIP2;6 are detected	*Z. mays*	[77]
Root of 7–8-day old seedlings (10–20 mm from the tip)	Predominant expression of *ZmPIP1;1*, *ZmPIP1;2* and *ZmPIP2;5*, with a slightly smaller contribution of *ZmPIP1;5*. The accumulation of ZmPIP1;2 protein reaches the first maximum, and ZmPIP2;1/2;2, ZmPIP2;5, and ZmPIP2;6 proteins are also detected	*Z. mays*	[77]
Root of 7–8-day old seedlings (30–40 mm from the tip)	Predominant expression of *ZmPIP1;5*, *ZmPIP2;1* and *ZmPIP2;5* and accumulation of ZmPIP2;5 protein; lower levels of ZmPIP1;2 protein compared with the previous zone	*Z. mays*	[77]
Root of 7–8-day old seedlings (50–60 mm from the tip)	Predominant expression of *ZmPIP1;5* and *ZmPIP2;5* and the accumulation of ZmPIP1;2 (second maximum), ZmPIP2;1/2;2, ZmPIP2;5 and ZmPIP2;6 proteins	*Z. mays*	[77]
Root of 7–8-day old seedlings (100–110 mm from the tip)	Predominant expression of *ZmPIP1;5* and *ZmPIP2;5* and the accumulation of ZmPIP1;2 (second maximum), ZmPIP2;1/2;2 and ZmPIP2;5 proteins	*Z. mays*	[77]
Root of 38-day-old plants, 4 mm zone from root tip	OsPIP1s, OsPIP2;1, OsPIP2;3, OsPIP2;5 and OsTIP2;1 were predominantly localized in the endoderm of the root tip	*Oryza sativa* L.	[78]
Root of 38-day-old plants, 35 mm zone from root tip	The distribution of proteins among the tissues was found to be relatively uniform; however, their prevalence was found to be minimal	*O. sativa*	[78]
Root of a 5-day-old seedling (above the growth zones)	Active expression of *RsPIP1*, *RsPIP2*, and *RsTIP* in vessels and endoderm, with weaker expression in pericycle and xylem parenchyma; *RsTIP* is expressed in the epidermis	*Raphanus sativus* L.	[80]
Grape root tip	The distribution of VvPIP1s and VvPIP2s is uniform; however, their expression levels are 100- to 1000-fold greater in the meristem and elongation zone	*Vitis vinifera* L.	[79]
Mature root zones	The expression of *VvPIP1-1* was predominantly observed in the periderm, whereas *VvPIP2* accumulation was relatively uniform in different root tissues	*V. vinifera*	[79]
Growing root zones	Intensive accumulation of *HvPIP1;2*, *HvPIP2;2*, *HvPIP2;5*, *HvTIP1;1*, and *HvTIP2;3*	*Hordeum vulgare* L.	[81]
Sprout roots	Almost all the PIP aquaporins studied showed the highest level of expression in zones of rapid root elongation in 4-day-old seedlings, as opposed to 7-day-old seedlings	*Z. mays*	[12]
Root hairs (in aqueous solution)	*PIP2;2* expression not detected	*Arabidopsis thaliana* (L.) Heynh.	[82]
Root hairs of hydro-ponic plants	No differences in expression (transcripts of *HvPIP1;1-4*, *HvPIP2;1-2*, *HvPIP2;4-5*, *HvTIP1;1-2*, and *HvTIP2;3* genes were tested) between wild-type plants and mutants lacking root hairs in the root epidermis; no aquaporin genes specifically expressed in root hairs were identified	*H. vulgare*	[65]

Thus, the activity of aquaporin protein expression and accumulation was repeatedly demonstrated in the youngest zones of the root, often adjacent to meristems. In these zones, the cells are characterized by elongation, leading to a dramatic increase in cell length along the vertical axis. Interestingly, no such direct dependence on the presence of aquaporins was found for another type of cell growth, the apical type, observed during root hair formation (Table 5).

As the plant undergoes further development, including the root, the need to augment the absorption of water and aqueous solutions, in addition to their transportation to the aerial organs, becomes increasingly evident. The inhibitor analysis data indicate that the contribution of aquaporins to the hydraulic conductivity of roots ranges from 64% in Arabidopsis to 70%–80% in wheat, 60%–70% in maize, 57% in tomato, and over 90% in barley [16]. Furthermore, mutants exhibiting impaired coding of the *PIP1* and *PIP2* genes demonstrated a 20%–30% decrease in permeability. However, the role of aquaporins in determining permeability is hypothesized to undergo changes during the development. For example, the permeability levels in the meristematic zone and the zone of extension in grape roots were demonstrated to be approximately 1000-fold higher compared with the zone of the formed root.

The findings suggest that the function of aquaporins belonging to the PIP1 and PIP2 subfamilies undergoes substantial changes during the root development. Among these proteins, the highest degree of diversity is observed in the youngest growing zones. However, it remains a challenge to identify the precise factors that determine the observed tissue and species specificity of the aquaporin transcriptional and protein profiles.

Shoot aquaporins

Shoot development is characterized by intensive growth processes. These processes start during the formation of seedling structures (i.e., juvenile organs such as hypocotyl/epicotyl and coleoptile) and persist throughout stem and leaf development. The process of stem growth and development, similar to that of root development, involves changes in the intensity of water transport at both the cellular level and the level of the entire shoot. Unfortunately, there is much less data on the changes in aquaporin isoform abundance during stem development compared with that in the root.

Hypocotyl and stem aquaporins

The hypocotyl, an embryo component, assumes an intermediate anatomical position between the embryonic root and stem during germination. This juvenile organ serves as a model organ in the study of various physiological processes, including the regulation of growth involving aquaporins. Already in the late 1990s, data on the involvement of aquaporins in water absorption during the growth of sunflower hypocotyl cells were obtained using an inhibitor assay [83]. Furthermore, in non-growing tissues of hypocotyls, the effect of inhibitors was considerably weaker, suggesting a modification in the contribution of aquaporins. Subsequent studies of hypocotyl growth in plants such as Arabidopsis, common radish, and castor bean, among others, revealed the participation of various representatives of the PIP and TIP subfamilies of aquaporins. The primary outcomes of these studies are summarized in Table 6.

The differential accumulation of various isoforms of aquaporins belonging to the PIP and TIP families has been demonstrated in radish [84, 85]. In hypocotyls, *RsPIP1-2* mRNA and the corresponding protein exhibited the highest accumulation. For the majority of the genes and encoded proteins of RsPIP1, RsPIP2, and RsTIP2 groups, the accumulation was much weaker. The accumulation of transcripts and TIP2 protein was also observed in the hypocotyls of Arabidopsis [86, 87].

A detailed study was conducted on growing hypocotyls of castor bean [88]. In etiolated development at 6–8 days, the accumulation of the RcPIP2-1 aquaporin corresponded to the intensity of hypocotyl elongation. Conversely, growth inhibition, induced by illumination, resulted in suppressed accumulation of this particular isoform. This relationship was not observed in the other aquaporins (RcTIP1-1 and RcPIP1-1).

Aquaporins belonging to these families regulate stem growth at later stages of plant development. For example, studies on pea seedlings have demonstrated that the expression of aquaporin genes, specifically PIP1, PIP2, and TIP2, is initiated in hypocotyls and subsequently continues in young stems [89]. This effect is also evident at later stages of plant development, where stems maintain/exhibit the capacity for substantial growth. In particular, the accumulation of *PsPIP2;1* transcripts gradually increased with stem elongation. Expression of genes encoding different isoforms of aquaporins of the PIP1, PIP2, and TIP2 subfamilies was detected in the stems of two cereal species (bristle grass and deep-water rice) and flax, which are characterized by internode growth (Table 6).

The data from various plant species have demonstrated that changes (increase/decrease) in the expression of aquaporin genes belonging to the PIP1, PIP2, and TIP2 subfamilies result in corresponding changes in the growth intensity of hypocotyls and stems, as well as in the stem/root ratio [16].

Consequently, the involvement of aquaporins belonging to the PIP1, PIP2, and TIP2 subfamilies in shoot growth at both the juvenile development stage and the vegetative growth stage was demonstrated at the transcriptional and protein levels.

Table 6. Aquaporins in hypocotyls and stems

Таблица 6. Аквапорины в гипокотилях и стеблях

Object	Expressed gene, accumulated protein	Plant	Reference
Hypocotyls of 6-day-old castor bean seed-lings	The presence of RcPIP2-1 correlated with growth intensity. The levels of RcPIP1-1 and RcTIP1-1 did not change	*Ricinus communis* L.	[88]
Hypocotyls of 4-day-old seedlings	Intense accumulation of transcription products and syn-thesis of aquaporin-encoded proteins of RsPIP1;2, RsPIP1;1, RsPIP1;3, and RsTIP1;1, whereas RsPIP2;1, RsPIP2;3, and RsTIP2;1 were weaker	*Raphanus sativus* L.	[84, 85]
Hypocotyls of 6-day-old seedlings	TIP2 (δ-TIP) accumulates intensively	*Arabidopsis thaliana* (L.) Heynh.	[87]
Hypocotyls of 2-day-old seedlings	Active expression of *AtTIP1* (γ-TIP) in the growth zone, disappearing after 24 hours	*A. thaliana*	[86]
Hypocotyls and stems of etiolated seedlings (0–7 days old)	The expression of *PsPIP1;1*, *PsPIP2;1*, and *PsTIP1;1* was observed for all 7 days; *PsPIP2;1* expression gradually in-creased	*Pisum sativum* L.	[89]
Young stems	*SvPIP2;1* expression	*Setaria viridis* (L.) P. Beauv.	[90]
Fast growing inter-nodes	Enhanced expression of *OsTIP1;1*, *OsTIP2;2*, *OsPIP1;1*, *OsPIP2;1*, and *OsPIP2;2*	*Oryza sativa* L. var. *indica* (deepwater rice)	[91]
Stems	Expression of genes encoding PIP1-3, PIP1-4, PIP1-5, PIP2-1 and PIP2-2, PIP2-4, PIP2-5 and PIP2-11 aquaporins	*Linum usitatissimum* L.	[92]
Young stems	Expression of genes encoding PIP1-1, PIP1-3, PIP1-6, PIP2-1, and PIP2-9, as well as TIP1-8, TIP1-11, and TIP2-3	*Gossypium hirsutum* L.	[36]

Coleoptile and leaf aquaporins

Leaves are an integral part of the shoot. The physiological development of these organs can be divided into two processes: (1) growth and formation of the lamina and (2) provision of photosynthesis. Both processes depend on the availability of water and other compounds that can be transported by aquaporins. We mostly focus on growth processes.

At the earliest stages of development of a flowering plant seedling, the cotyledon (first embryonic leaf) forms the first embryonic leaves, which are then replaced by true leaves. Their functions include both the nutrition during photosynthesis, and protective function when germinating through the soil layer. This function is especially expressed in coleoptiles as embryonic organs of monocotyledons, modified from the second leaf. Cotyledon cells are characterized by their rapid and intensive growth, which may be associated with aquaporins, as indicated by limited data. For example, the expression of the *AtTIP1* gene (γ-TIP; Table 7) has been observed during the development of petioles and in the cotyledons of Arabidopsis plants [86].

Intensive growth is also typical of a juvenile organ such as the coleoptile. The parenchyma cells of the coleoptile, a modified leaf of cereals with a specialized defense function, are characterized by elongation. Studies on maize coleoptiles undoubtedly point to the role of aquaporins of the PIP family (Table 7) [12]. The accumulation of mRNA of the *PIP1-1, PIP1-2, PIP1-3, PIP1-5, PIP2-1, PIP2-2, PIP2-3, PIP2-5, PIP2-6, TIP1-1*, and *TIP1-2* genes was shown. However, the intensity of accumulation of most transcription products was much weaker than in mesocotyls and other juvenile organs, such as parts of the germinal stem (Table 7) [12]. The exceptions include *PIP2-3, PIP2-6, TIP1-1*, and *TIP1-2*.

The study sought to elucidate the role of aquaporins from these two subfamilies in the subsequent development of the lamina (Table 7). Previous studies have conducted a detailed investigation of aquaporin gene expression during leaf development. One of the studies involved growing barley leaves [93]. Of the 23 genes analyzed, 17 exhibited differences in the accumulation of transcription products in young growing tissues and in well-developed photosynthetic zones. Notably, the study identified tissue and age specialization. Seven of the tested genes were predominantly expressed in growth zones (Table 7). *HvPIP2;5* was found to be expressed in the mesophyll, whereas *HvPIP1;1* and *HvPIP2;2* were expressed in the epidermis. In the elongation zone of barley leaves, *HvPIP1;1* and *HvPIP2;5* transcripts constituted 90% of the total number of transcripts of the *PIP1* and *PIP2* genes. The analysis further revealed that the *ZmPIP1;1*

Table 7. Aquaporins in leaves and coleoptiles

Таблица 7. Аквапорины в листьях и колеоптилях

Object	Expressed gene, accumulated protein	Plant	Reference
Growing cotyledons of 3–5-day old seedlings	*AtTIP1* (γ-TIP) is expressed in the petioles of the cotyledons and in the cotyledons themselves; expression is observed in the vascular bundles and, to a lesser extent, in the mesophyll; by Day 5, expression is ceased in the vascular bundles first	*Arabidopsis thaliana* (L.) Heynh.	[86]
Coleoptiles of seed-lings (96 h after seed swelling)	Expression: *PIP1-1, PIP1-2, PIP1-3, PIP1-5, PIP2-1, PIP2-2, PIP2-3, PIP2-4, PIP2-5, PIP2-6, TIP1-1,* and *TIP1-2*	*Zes mays* L.	[12]
Leaf petiole of a 5-day-old seedling	The expression of *RsPIP1*, *RsPIP2*, and *RsTIP* is observed in all tissues, with particularly pronounced intensity in vascular bundle tissues	*Raphanus sativus* L.	[80]
Primary leaf of a 5-day-old seedling	*HvTIP1* is highly expressed in the elongation zone; however, it is not expressed in fully elongated cells (in both the wild type and the mutant)	*Hordeum vulgare* L.	[95]
Leaves of seedlings at the 3rd leaf stage	The expression of *HvPIP1;6* in the growing zone of the leaf accounts for up to 85% of the total *PIP1*, which is consistent with protein accumulation	*H. vulgare*	[96]
Young leaf of a 6-day-old seedling	*AtTIP2* is intensively expressed in cotyledons and young leaves	*A. thaliana*	[87]
Young leaves of 14–16-day-old seedlings	The expression of *HvPIP1;1*, *HvPIP1;5*, *HvPIP2;2*, *HvPIP2;5*, *HvTIP1;1*, and *HvTIP2;3* genes is observed in various growth zones; *HvPIP2;5* is expressed in the mesophyll, whereas *HvPIP1;1* and *HvPIP2;2* are expressed in the epidermis	*H. vulgare*	[93]
Leaf (near the leaf sheath)	*ZmTIP1* expression is notably pronounced in the vascular bundle, which is located between the xylem and phloem in the parenchyma	*Z. mays*	[97]
Young leaves of 2-week-old plants	The expression of *BnTIP1* and *BnPIP1* in the mesophyll and bundle sheath, exhibiting a weak tendency to differentiate in bundle cells	*Brassica napus* L.	[98]
Rosette plant	*AtTIP1* is expressed in growing bracts and vascular bundles of petioles and in young leaves; there was no expression in stem apex and leaf buds	*A. thaliana*	[86]
Mature leaves	Expression of genes encoding aquaporins PIP1-1, PIP1-6, PIP2-1 and PIP2-9, and TIP2-3 is observed; accumulation of transcripts is increased compared with young leaves	*Gossypium hirsutum* L.	[36]

and *ZmPIP2;1* homologs in maize also contributed significantly to the total transcripts of *PIP1* and *PIP2* genes in the maize leaf elongation zone, along with *ZmPIP2;2* [94]. The findings on the role of PIP aquaporins do not exclude the importance of TIP subfamily representatives. The results obtained from the analysis of Arabidopsis, barley, maize, and rapeseed are summarized in Table 7. The increased expression of TIP aquaporin genes indicates their critical role in the vacuolization of leaf cells.

Furthermore, an accumulation of transcripts from the *PIP1-1, PIP1-6*, *PIP2-1*, *PIP2-9*, and *TIP2-3* genes, was observed in mature cotton leaves, with this accumulation increasing with leaf age [36]. The proteins encoded by these genes are thought to be involved in the supply of water and nutrients needed for metabolic processes.

The significance of aquaporins belonging to the PIP1, PIP2, and TIP1, TIP2 subfamilies was shown through the use of transgenic plants. The increase in the accumulation of transcripts for genes belonging to the aforementioned aquaporin subfamilies, including heterologous ones, has been observed in these models, resulting in the intensification of leaf growth [16]. Consequently, a substantial body of evidence has emerged regarding the enhanced transcription of aquaporin genes belonging to the PIP1, PIP2, and TIP subfamilies during the leaf development. However, there is a lack of research on the specificity of transcript accumulation of these genes depending on age (i.e., juvenile developmental stage and mature leaf stage) and tissue specificity.

Aquaporins in the development of reproductive organs

The reproductive process in angiosperms comprises several stages, including flower bud formation, flower development, fertilization, embryo formation, and seed and fruit development. Obviously, each stage depends on the availability of water and nutrients. Therefore,

it may be assumed that aquaporins play their role in these processes. However, studies addressing this subject are limited, because most of them investigate on the role of aquaporins in fruit and seed formation. This particular aspect was the primary focus in preparation for the present review.

Nevertheless, the involvement of aquaporins in other steps will be described below. For example, an increase in transcription of *PpTIP1* and *PpPIP2* has been shown during flower bud development in peach trees [99]. It has been demonstrated that PIP2;2 aquaporins play a regulatory role in the process of reversible petal opening in tulips and rough gentian [100, 101]. Furthermore, the studies have revealed that *NtPIP2;1*, but not *NtPIP1;1*, is expressed in tobacco plants during pollen germination on the pistil stigma [102]. In addition, the expression of *AtTIP1;3* and *AtTIP5;1* genes has been detected in Arabidopsis pollen during pollen formation and subsequent germination [103, 104].

Fruit aquaporins

Fruit growth and development are driven by two primary processes: cell division and cell elongation. Cell elongation, in particular, depends on aquaporin-mediated water transport through the plasmalemma and tonoplast, resulting in subsequent accumulation in the vacuole. The driving force of this water flux is the high osmotic pressure generated by the accumulated metabolites, primarily sugars. Table 8 presents data on changes in the expression level of aquaporin-encoding genes during the development and ripening of fruits of different plant species.

One of the earliest documented examples of the correlation between the fruit development and the expression of tonoplast aquaporin genes was observed in Arabidopsis fruits. In addition, the accumulation of transcription products has been observed in the early stages of fetal development, although this has not been detected in the embryo [86]. Subsequent research demonstrated the expression of aquaporin TIP1 genes in pea, with maximal expression occurring at the onset of seed formation [106]. In addition, the role of TIP1 in grape berry development has been demonstrated, with increasing expression levels during the ripening process [108]. Specific expression of the *CsTIP1;1 and CsTIP2;1* genes has been detected during the formation of cucumber fruits [114].

Further evidence supporting the involvement of PIP aquaporins in fruit development is provided in the studies of various plant species, including beans, grapes, tomatoes, and apples (Table 8). These studies revealed an accumulation of PIP transcription products, particularly those belonging to the *PIP1* group. This accumulation was found to be phase-dependent, with a peak during the ripening stage and a subsequent decline at the end of the ripening period [109, 113, 114]. However, the profile of genes encoding different isoforms of PIP1 aquaporins differed considerably. The expression of genes belonging to the *PIP2* group has been demonstrated in some plants studied during fruit formation and ripening [108, 110].

Consequently, the role of aquaporins belonging to the PIP and TIP families was demonstrated through the observation of fruit formation. The most frequent specific expression of PIP1 and TIP1 aquaporin genes, which depended on the ripening phase and the intensity of fruit vacuolization, was observed in the studies.

Role of aquaporins in seed formation

The formation of seeds may be regarded as the culminating stage in the life cycle of higher plants. During the early stages of seed development, there was an intensive expression of genes encoding aquaporins of the PIP1 and PIP2 groups in various tissues. Several publications from the early 2000s have reported the accumulation of transcripts of the aquaporins PIP1;1, PIP1;2 PIP2;1, and PIP2;2, as well as TIP2;1 and TIP2;2, for various plants, including Arabidopsis, soybean, tomato, and rice [115]. The increase in the number of expressed aquaporin genes and in the intensity of their transcription are associated with the provision of photosynthesis and the transport of aqueous sucrose solution, which promotes seed development. Another aquaporin, TIP3, has been identified as a marker of mature seeds [12]. It has been identified in the membranes of protein bodies derived from the vacuolar system in maturing bean seed cells [116, 117]. Later, this aquaporin was identified in seeds of several plants, including Arabidopsis, pea, maize, and horse chestnut [115]. However, the process of TIP3 accumulation in the membranes of protein bodies is typical of desiccated orthodox seeds, whereas in recalcitrant seeds (which are unstable to dehydration, such as in oak and horse chestnut), it was preserved in the tonoplast [13]. In addition, TIP3 was shown to be localized in the plasmalemma. It has been hypothesized that TIP3 functions as a partial compensatory mechanism for transport processes within the plasmalemma, since the abundance of aquaporins PIP1 and PIP2 decreases significantly during maturation [118].

At later stages of seed maturation, especially in orthodox seeds, aquaporins participate in the rapid outflow of water during seed desiccation [71, 75]. Eleven isoforms of PIP aquaporins were found in dry seeds of Arabidopsis, with almost no accumulation of transcripts of the corresponding genes. In dry rice seeds, active expression of only the *PIP2;7* gene was observed, whereas the expression of the *PIP1;1*, *PIP1;2*, and *PIP2;1* genes was very low [74].

The obtained data demonstrate that the distinct aquaporin isoforms present at varying stages of seed development induce an initial increase in seed size and an accumulation of nutrients within the seed. This

Table 8. Fruit aquaporins

Таблица 8. Аквапорины плодов

Object	Expressed gene, accumulated protein	Plant	Reference
Growing pod	*AtTIP1* (γ-TIP) expression is observed during ovary-to-fruit development and later in pod flaps; no expression in seed embryos	*Arabidopsis thaliana* (L.) Heynh.	[86]
Seed coat of growing beans	*PvPIP2;3* in the phloem unloading zone involved in phloem water entry	*Phaseolus vulgaris* L.	[105]
Pericarp of growing beans (up to 5 days after flowering)	Maximum expression of *PsTIP1* (γ-TIP) in fruits is observed on Day 4	*Pisum sativum* L.	[106]
Pericarp of growing berries	Expression of the aquaporin genes AQ1 and AQ2 corre-sponded to periods of rapid growth	*Vitis vinifera* L.	[107]
Berry ripening	Expression of *VvTIP1;2*, *VvTIP1;3*, *VvPIP2;3*, and *VvPIP2;5* genes increased during maturation	*V. vinifera*	[108]
Growing tomato fruits	Expression of *LePIP1;1*, *LePIP1;4*, and *LePIP1;5*	*Lycopersicon esculentum* Mill.	[109]
Growing fruits (15 days after flowering)	Very strong expression of *ScPIP2a*	*Solanum chacoense* Bitter	[110]
Mature fruits (40 days after flowering)	Almost no expression of *ScPIP2a*	*S. chacoense*	[110]
Cotton fibers	TIP aquaporin genes are expressed during the period of maximal fiber elongation	*Gossypium hirsutum* L.	[111]
Growing apple fruits	Expression of *MdPIP1a* and *MdPIP1b* genes	*Malus domestica* Baumg.	[112]
Peel and pulp of ripening apples	*MdAQP* gene expression varied at the climacteric stage depending on tissue identity and apple cultivar	*M. domestica*	[113]
Cucumber fruits	Expression of *CsTIP1;1*, *CsTIP2;1*, and *CsPIP1;3* was fruit specific	*Cucumis sativus* L.	[114]

is subsequently followed by desiccation and a dormant state. Consequently, multidirectional water fluxes are initiated through different cell membranes. The precise mechanism of such initiation is still unclear.

CONCLUSION

A comprehensive literature review reveals that aquaporins constitute a substantial group of membrane proteins that facilitate the permeability of the plasmalemma and intracellular membranes to water and a variety of other compounds. An extensive experimental database has been amassed, enabling to assess the diversity of mechanisms that regulate their activity (from transcriptional to post-translational). Of particular interest are the data on the physiological role of aquaporins, particularly their involvement in the growth and development of plants. One of the fundamental processes underlying these phenomena is elongation. There is compelling evidence that H^+-ATPases localized on the plasmalemma and tonoplast participate in this process [119, 120]. The data presented in this review indicate the active involvement of aquaporins belonging to the PIP and TIP subfamilies, localized on the plasmalemma and tonoplast, in this type of growth. These aquaporins are the most conservative in the course of evolution [23]. They are predominantly involved in the regulation of the growth intensity of a wide variety of plant organs, starting from juvenile parts (Tables 5–8). It is hypothesized that the intensity of water transport by TIP is significantly superior to that of PIP, a finding that aligns with the established role of plasmalemma and tonoplast aquaporins. The former are responsible for the entry of water into the cell from the outside, whereas the latter facilitate the rapid transportation of water into the vacuole to prevent cell damage. This balance of functions plays a critical role in the successful execution of growth processes during development. Interestingly, aquaporins of the same subfamilies are involved in the reverse process, the dehydration that occurs during seed formation. Furthermore, the intensity of this process determines the longevity of seed formation.

The selected mechanism is probably further used by plants in adapting to unfavorable conditions, primarily those associated with water deficiency, including salinity, drought, and low temperatures. Table 3 summarizes the data on the role of aquaporins PIP1 and PIP2 in the regulation of water fluxes through the plasmalemma under these conditions. The reverse stress factor, characterized by flooding leading to excess water, also appears to necessitate the active involvement of TIP aquaporins; however, the available data are limited. Most of the data presented in this review were obtained at the transcriptional level. In some cases, changes in expression were confirmed at the protein level. A detailed analysis of the protein profiles of plasmalemma and tonoplast is required, because the diversity of aquaporin isoforms and multiple mechanisms of post-translational regulation are not always considered. In general, the data collected so far are still too fragmentary to characterize the role of these aquaporins in normal and stress-stimulated states. These factors can either stimulate or inhibit growth, as well as to determine the intensity of adaptation processes.

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