Interrelations of nutrient and water transporters in plants under abiotic stress

Gloria Barzana[†], Juan J. Rios[†], Alvaro Lopez-Zaplana, Juan Nicolas-Espinosa, Lucia Yepes-Molina, Paula Garcia-Ibañez and Micaela Carvajal*

Aquaporins Group. Centro de Edafologia y Biologia Aplicada del Segura. CEBAS-CSIC. Campus Universitario de Espinardo - 25. E-30100. Murcia. Spain

Correspondence

*Corresponding author,

e-mail: mcarvaja@cebas.csic.es

[†]These authors contributed equally to this work.

Environmental changes cause abiotic stress in plants, primarily through alterations in the uptake of the nutrients and water they require for their metabolism and growth and to maintain their cellular homeostasis. The plasma membranes of cells contain transporter proteins, encoded by their specific genes, responsible for the uptake of nutrients and water (aquaporins). However, their inter-regulation has rarely been taken into account. Therefore, in this review we identify how the plant genome responds to abiotic stresses such as nutrient deficiency, drought, salinity, and low temperature, in relation to both nutrient transporters and aquaporins. Some general responses or regulation mechanisms can be observed under each abiotic stress such as the induction of plasma membrane transporter expression during macronutrient deficiency, the induction of tonoplast transporters and reduction of aquaporins during micronutrients deficiency. However, drought, salinity and low temperatures generally cause an increase in expression of nutrient transporters and aquaporins in tolerant plants. We propose that both types of transporters (nutrients and water) should be considered jointly in order to better understand plant tolerance of stresses.

Introduction

As they are essential for plants, the maintenance of the optimal concentrations of certain mineral nutrients within the plant tissues is highly important for proper growth. Therefore, to complete the life

cycle, and for optimal development of morphology and anatomy, nutrient uptake should be rationalized according to the need of each plant (Barker and Pilbeam 2016). But, beside their involvement in primary metabolism, these mineral nutrients are the basis of the secondary metabolism, defense, signal transduction, hormone reception, and energy and molecular regulation of the plant (Maathuis and Diatloff 2013). Therefore, deficiencies in one or more of them produce a dramatic effect on plant physiology.

Root hydraulic conductivity is one of the main parameters that describe the capacity of the root to uptake water, conferring the ability to adapt to changes in environment (Armand et al. 2019). In this way, the plasticity of the changes of root hydraulic conductivity has been related to the presence and functionality of aquaporins, since they allow water to pass freely across cellular membranes, following osmotic or hydrostatic pressure gradients (Wang et al. 2019a).

There is a strong interaction between mineral uptake and water status in plants. Although both ions and water are taken up by specific membrane transporters (channels, antiporters, and specific transporters for ions, and aquaporins for water), the regulation of these transporters must be connected to ensure the cellular homeostasis. The apparently simple water transporters, aquaporins, are in fact highly complicated due to the wide number of families and isoforms. Therefore, the multiplicity of aquaporins isoforms, the interaction between isoforms and lipid bilayer and their response under different abiotic stress is still under study (Martínez-Ballesta and Carvajal 2016). Aquaporins can be classified into five families depending on their cellular membrane localization and amino acid sequence. Thus, they are classified as PIPs, if located in the plasma membrane; TIPs, in the tonoplast; NIPs, if they are nodulin-26-like; SIPs, if they are small and basic; and XIPs, if they are uncharacterized intrinsic proteins (for a review, see Martinez-Ballesta and Carvajal 2014). Reverse genetics and overexpression are effective tools for investigating the physiological functions of each aquaporin isoform in plants and for understanding their roles in water transport and abiotic stress responses. In this way, successful examples have been reviewed by Martinez-Ballesta and Carvajal (2014) as the expression of *Vicia faba* PIP1 in transgenic *Arabidopsis thaliana* and over-expression of PIP1 in *Oriza sativa* improved drought resistance by increasing root hydraulic conductivity.

In this sense, as vital regulators of plant short-distance cell to cell transport and homeostasis, the study of the response of aquaporins to abiotic stress has been implemented in recent years (reviewed by Afzal et al. 2016, Kapilan et al. 2018). Also, changes in nutrient transporters under different abiotic stresses have been studied, highlighting some relationship with tolerance (Hasanuzzaman et al. 2018).

In the context of the abiotic stresses that crops suffer, and with regard to climate change scenarios, attention has been focused on nutrient deficiency, salinity, drought, and sudden low temperatures. The impacts of these stresses on nutrient and water uptake have been studied, but rarely in an integrated way. In this review, we establish the relationship between nutrient transporters and aquaporins in abiotic stress situations, to reinforce the importance of studying their integrated regulation under environmental changes. Also, we will point out the need to complete our knowledge of nutrient transporters and aquaporins for a better interpretation of their key role under abiotic stress.

The influence of macronutrient deficiencies on the interaction of their transporters and aquaporins

The concentration of macronutrients required for plant optimal growth is above 0.1% on a dry matter in plant tissue (Karthika et al. 2018). Therefore, as macronutrients are required at high concentrations, it is not common to find macronutrient toxicity stress in field conditions. However, macronutrient deficiency is an important problem for crop productivity, affecting many plant physiological features (Pessarakli 2015) involving transporters and aquaporins (Fig. 1).

Nitrogen

Nitrogen (N) is taken up either as the nitrate ion (NO_3^-), the prevalent form of uptake, or as the ammonium ion (NH_4^+), depending on the plant species and the soil conditions regarding factors like pH and the redox state (Karthika et al. 2018). The principal transporters described for NO_3^- belong to the NRT family, a large protein family. They include high-affinity transporters such as NRT2 and low-affinity transporters such as NRT1 (Forde 2002). But, among the NRT1s, some transporters have been described that present a dual affinity for NO_3^-, such as AtNRT1;1 (or CHL1) (Gojon et al. 2011). Therefore, under low-NO_3^- conditions the NRT2 transporters (NRT2;1, NRT2;2, NRT2;4, and NRT2;5) take up approximately 95% of the total amount of this anion, NRT2;1 and NRT2;2 being the main contributors (Lezhneva et al. 2014). While it has been reported that *NRT2;5* is the only one up-regulated under NO_3^- starvation in wheat (*Triticum durum* L.) plants, in sorghum (*Sorghum vulgare* Pers, syn), N deficiency caused higher abundance of NRT2;2, NRT2;3, NRT2;5, and NRT2;6 transcripts (Gelli et al. 2014, Curci et al. 2017).

The root hydraulic conductivity (*Lp,* m^{-1} s^{-1} MPa^{-1}), which defines the intrinsic ability of roots to conduct water across a water potential gradient between the root surface and the xylem in the stem (Eissenstat

1997), is affected by N deficiency, showing a significant reduction in N-deficient plants. In this sense, the high contribution of aquaporins to the roots Lp value (Carvajal et al. 1996a, Gorska et al. 2008) suggests that N deficiency produces a reduction in aquaporins activity or expression (Clarkson et al. 2000). Ding et al (2018) showed, in rice (*Oryza sativa* L.) plants, that the expression of PIPs in roots was reduced under low-N conditions. Also, previous studies in *Arabidopsis thaliana* L. found a decrease in root plasma membrane aquaporins (*PIP2;1, PIP2;2, PIP2;4, PIP1;2*, and *PIP1;3*) expressions in response to N starvation for 6 days (Di Pietro et al. 2013). These results suggest that NRT2;1, that acts as a NO_3^- sensor, could trigger complex transcriptional and post-transcriptional regulations of aquaporins, leading to possible N-dependent root Lp regulation. Despite these results, the regulatory mechanism still remains unclear and further investigation is needed (Little et al. 2005, Tyerman et al. 2017).

Besides, NH_4^+ uptake by roots occurs mainly via NH_4^+ transporters (AMT) localized in the plasma membrane (Yuan et al. 2007). This ion is transported from the cytosol to the vacuole for N storage and to avoid its toxicity to the plant (Wang et al. 2008). It has been reported that this transport is probably facilitated by the tonoplast aquaporins AtTIP2;1 and AtTIP2;3 in *A. thaliana* cells (Loqué et al. 2005). Therefore, when N is needed, it could be remobilized by passive transport. In this way, the described low-affinity transport pathway may generally involve aquaporins of type TIP (Wang et al. 2016). In fact, several TIPs, such as ZmTIP1;1 and ZmTIP1;2, have been described as participating in NH_4^+ transport in corn plants (*Zea mays* L.*)* (Bárzana et al. 2014).

Members of the plasma membrane PIP and NIP and the tonoplast TIP subfamilies have been reported to facilitate urea transport through membranes (Liu et al. 2003). Accordingly, under N starvation, the expression of *ZmTIP4;4* has been observed to increase significantly in roots and expanded leaves, suggesting that ZmTIP4;4 is essential for urea efflux to the cytoplasm (Gu et al. 2012). This indicates that this aquaporin is a urea transporter involved in the mobilization of reserve pools in the vacuole under N deficiency (Figure 1).

Phosphorus

Normally, phosphorus (P) is taken up from soil mainly as its inorganic form (Pi), and its uptake by plants is an energy-consuming, co-transport process. In this sense, we can find high- and low-affinity Pi transporters whose activities mostly depend on the rhizosphere concentrations of P (Schachtman et al. 1998). Thereby, in *A. thaliana* and rice plants, five high-affinity Pi transporters (PHT1, PHT2, PHT3, PHT4, and PHT5) have been identified (Sun et al. 2017). In particular, members of the PHT1 group

have been shown to be predominant under Pi deficiency. This has been proven in in *A. thaliana* and wheat, were*AtPHT1;4* could become predominant, being up-regulated under Pi deficiency (Liu et al. 2013, Ayadi et al. 2015). However, in soybean (*Glycine max* L.) plants, most of the *PHT1* genes had elevated transcript levels under low-P conditions (Qin et al. 2012).

Also, P starvation could cause combined changes in root *Lp* and aquaporins gene expression together with the formation of endodermal apoplastic barriers in roots (Li et al. 2019a). In fact, recently, Li et al. (2019) showed a decrease in the gene expression of six PIPs aquaporins (*LcPIP1;1*, *LcPIP1;4*, *LcPIP2;1*, *LcPIP2;4*, *Put-LcPIP2;2*, and *Put-LcPIP2;5*) in *Leymus chinesis* L. under low P availability. Indeed, P starvation may also modulate aquaporins activity, due to changes in their phosphorylation status (Wang et al. 2016). A study in corn plants showed correlation between the expression patterns of the high-affinity Pi transporters *ZmPHT4;2* and *ZmPHT4;6* and that of the NIP-type aquaporin *ZmNIP2;1* (Yue et al. 2012), thus revealing the possible existence of a direct or indirect mechanism that regulates their expression under this mineral-deficiency stress.

Potassium

Most potassium ion (K^+) channels in plant cells can be considered as passive transporters. Although, other K^+ transporters usually behave as carriers, and function as co-transporters coupled with H^+ or sodium ion (Na^+) transport (Chen et al. 2008). In *A. thaliana*, a total of 71 K^+ transporters, channels and carrier proteins, have been identified. Also, they are divided into three channel families (the Shaker, TPK, and Kir-like families) and four transporter families (the KUP, KT/KUP/HAK-type, HKT, and CPA families) (Chen et al. 2008). Studies carried out with *A. thaliana* indicated that *AtHAK5*, *AtKEA5*, *AtKUP3*, *AtCHX13*, and *AtCHX17* were up-regulated and induced by potassium (K) starvation (Ahn et al. 2004, Cellier et al. 2004, Gierth et al. 2005, Zhao et al. 2008). In rice plants, Liu et al. (2006) found that K starvation induced the expression of *OsAKT1*, *OsHAK1*, and *OsPIP2;7*. The same authors also showed that the rice root *Lp* dramatically increased in response to K starvation, which could be the result of an increase in either the density or the activity of aquaporins. In addition, other authors reported that aquaporin genes were strongly up-regulated after K^+ resupply; in this sense, 12 aquaporins genes were identified in the shoots of *A. thaliana* plants and 15 in the roots (Armengaud et al. 2004). In contrast, Coffey et al. (2018) observed both increases, but mainly, decreases in gene transcript abundance in barley plants under low K conditions; in particular, the expression of *HvPIP2* in roots decreased. They also found a decrease in root *Lp*. These contradictory results could be due to the PIP isoforms-specific responses or the different experimental designs. While Coffey et al. (2018) grew the plants under K

starvation from the beginning, Liu et al. (2006) only grew the plants for a maximum time of 24 h in a K-deficient solution. Therefore, different plant responses might reflect, on the one hand, a long-term effect of K starvation and, on the other, a rapid response of the plant to changes in K availability. The results of Liu et al. (2006) suggest that aquaporins and K channels were functionally co-regulated during cell turgor regulation; this could reflect the co-regulation of both transporters in roots, leading to the possibility of discovering an unknown regulatory factor for both ion and water channels.

Calcium

Calcium (Ca) deficiency is rare in nature since Ca is usually abundant and available in soils. However, in cases of severe weathering and extreme leaching of soil, deficiency of Ca may occur (Karthika et al. 2018). Calcium ion (Ca^{2+}) channels - that could be Ca^{2+}-selective or non-selective ion channels - allow the entry of Ca into the roots. The influx of Ca^{2+} into the cytosol is carried out by three different types of channels classified on the basis of their voltage-dependence: depolarization-activated (DACC), hyperpolarization-activated (HACC), and voltage-independent (VICC) cation channels (White and Broadley 2003). Meanwhile, Ca^{2+} efflux from the cytosol, that requires energized active transport, is accomplished by either Ca^{2+}-ATPases, divided into two families (P-type ATPase IIA and IIB), or H^+/Ca^{2+}-antiporters (Sharma et al. 2017). Among the latter, the CAXs (Cation/H^+ exchangers) are a group of high-capacity, low-affinity transporters that export cations out of the cytosol to maintain ion homeostasis across biological membranes (Cheng et al. 2003). In particular, under Ca deficiency, amaranth (*Amaranthus hypochondriacus* L.) plants showed an up-regulation of the *AhCAX* and *calmodulin* (*CaM*, a protein that functions as a Ca sensor) genes, as described by Aguilar-Hernández et al. (2011).

On the other hand, Ca starvation generally produces down-regulation of aquaporin genes expression, despite the fact that Ca deprivation does not have a great impact on water relations at the whole plant level (Maathuis et al. 2003). Indeed, White (2001) described trans-root movement of Ca^{2+} as mainly apoplastic. For this reason, it was proposed that, when Ca is limiting, in order to ensure its adequate delivery, a shift to apoplastic water movement might be required through a decrease in symplastic water permeability, which relies on aquaporins activity (Maathuis et al. 2003). In fact, protoplasts extracted from pepper (*Capsicum annuum* L.) plants grown under Ca starvation showed no aquaporin functionality, while, when Ca^{2+} was added to the protoplasts, an increase in the aquaporin functionality of the plasma membrane was observed. In addition, when a Ca^{2+} channel blocker was added, no aquaporin functionality was observed (Cabañero et al. 2006).

Moreover, the gene of *ACA4* (calmodulin-regulated Ca^{2+} pump in endoplasmic reticulum) showed the same expression pattern as *NIP2;2* in corn (Yue et al. 2012). In addition, Kapilan et al. (2018) reported that aquaporins activity could be directly modulated by divalent cations like Ca^{2+}. Furthermore, Ca^{2+} seems to be involved in plasma membrane aquaporins regulation via a chain of processes within the cell but not by alteration of the stability of the plasma membrane (Carvajal et al. 2000, Cabañero et al. 2006). Although a relationship among the Ca^{2+} transporters and aquaporins has not been demonstrated, these findings could suggest an interrelation between aquaporins and Ca^{2+} transporters that needs to be investigated in further studies.

Magnesium

Although it is difficult to find magnesium (Mg) deficiency in soils, its bioavailability is decreased by acidic soils, high rainfall in tropical regions (Gransee and Führs 2013, Sun et al. 2013), aluminum toxicity (Chen and Ma 2013), heat stress (Mengutay et al. 2013), drought-affected soils, and high levels of competing elements (K, Ca, NH_4^+, and Na) (Guo et al. 2016). The homeostasis of Mg in *A. thaliana* cells is maintained by Mg transporters such as AtMHX (magnesium ion (Mg^{2+})/H^+ exchanger) (Berezin et al. 2008, Gaash et al. 2013). Another well-known family of Mg transporters is the CorA family; this superfamily groups together high-, low-, and dual-affinity types of transporters. They are considered the primary Mg^{2+}-transport system in plants and play major roles in Mg^{2+} uptake, distribution, and homeostasis in cells (Shaul 2002). In particular, under Mg-starvation conditions, BnMGT1;2 and BnMGT6;1 transporters, associated with Mg^{2+} translocation from root to shoot, were up-regulated in *Brassica napus* L. plants (Sun et al. 2019). There is some evidence that suggests a relationship between Mg deficiency and aquaporins activity since Yue et al. (2012) found that the CorA-like family protein (*MRS2-2*) has the same expression patterns as *ZmPIP1;5* in corn plants. However, there is no clear evidence of a direct relationship between Mg deficiency and aquaporins activity.

Sulfur

Sulfur (S) is taken up and transported as the sulfate ion (SO_4^{2-}), by a family of high-affinity transmembrane SO_4^{2-} transporters that includes SULTR1;1, SULTR1;3, SULTR1;2, SULTR3;1, SULTR3;2, SULTR3;4, SULTR3;5, SULTR4;1, and SULTR4;2 (Yue et al. 2012). Under S deprivation, the expression of the SO_4^{2-} transporter genes *AtSultr1;1*, *AtSultr1;2*, and *AtSultr4;1* is up-regulated in *A. thaliana*, showing the importance of these high-affinity transporters under S deficiency (Buchner et al. 2004). Although there is no evidence of a direct relationship between PIP aquaporins activity or

expression and S transporters, Yue et al. (2012) found that *ZmSULTR2;1* exhibited the same expression patterns as *ZmTIP2;2*, while *ZmSULTR3;4* exhibited the same expression patterns as *ZmTIP3;2*. This suggests the involvement of aquaporins in S transfer from the S pool in the vacuole to the cytoplasm. This could be the starting point for future studies focused on the cooperation of S transporters and aquaporins in stressed plants.

The influence of deficiencies of micronutrients on the interaction of their transporters and aquaporins

Micronutrient deficiencies are extensive in crop soils. Although the total concentration of micronutrients in soil may be optimal, their bioavailability is determined by soil factors such as pH, microorganisms, and water status (Mikula et al. 2020). However, as pointed out below, the interrelation of transporters and aquaporins need investigation (Fig. 1).

The micronutrients are transported by big transporters families as ZRT-IRT-like Protein (ZIP), CAX, natural resistance-associated macrophage protein (NRAMP), heavy metal transporters (HMA) and yellow stripe like (YSL). ZIP, NRAMP and YSL are mainly influx transporters while CAX and HMA are mainly efflux ones, but their specific function depend on nutrient concentration and cellular localization (Dalcorso et al. 2014). Although, all families have members that could transport several micronutrient, the isoforms are highly specific (Haydon and Cobbett 2007). However, under deficient conditions, some overexpressed transporters can transport other similar cations, increasing their concentration (Williams et al. 2000).

Iron

Although iron (Fe) is an abundant element in soil, most of it is present as non-available (insoluble) forms (Ricachenevsky et al. 2013). Plants possess different strategies of Fe uptake from soil, involving reduction of insoluble Fe^{3+} to soluble Fe^{2+} (Strategy I) or direct chelation in the rhizosphere (Strategy II) (Briat et al. 2015).

Thus far, the relationship between Fe and water flow has not been directly studied. Under Fe deficiency, plants seem to produce a signal that could influence the water movement through the plant. Lei et al. (2014) concluded that in Fe-deficient *A. thaliana* plants the contents of some hormones, such as abscisic acid (ABA) increase, as well as the expression of tonoplast *AtNRAMP3*, leading to the removal of Fe from vacuolar pools. Also, the expression of plasma membrane transporters localized mainly in pericycle and vascular cells - namely, *AtFRD3*, *AtYSL2*, and *AtNAS1* - was increased to

enhance long-distance transport of Fe. In addition, a study performed by Hopff et al. (2013), in maize roots, showed a decrease in PIP2.2 abundance under Fe deficiency, but no relationship has been found between the two types of transporter (Fe-transporters and aquaporins). Now, Fe uptake and transport have been studied in depth, but the roles of aquaporins as plasma membrane proteins could be a starting point for future investigation of Fe movement.

Manganese

Deficiencies of manganese (Mn) often appear in plants growing in alkaline soils or in soils with a high concentration of other minerals, such as Fe, Mg, Ca, or P, which decreases Mn bioavailability (Marschner 2011). Manganese could be a substrate of many membrane transporters that have been reported to contribute to the influx and efflux of this element. In this regard, the transporter families can be separated according to their participation in Mn efflux or influx. Then, NRAMP, ZIP, and YSL are considered Mn influx transporters. NRAMP is a big family of transporters localized in the plasma membrane, NRAMP1 being the main member that contributes to Mn uptake. Also, other members, such as NRAMP3 and 4, have been found in the tonoplast, where they regulate the Mn homeostasis in cells (Thomine et al. 2003). Besides, members of the ZIP family are known to transport metals in plants; they are localized mainly in the plasma membrane and are composed of eight transmembrane domains (Rogers et al. 2000). Studies in *A. thaliana* have demonstrated that many members - such as AtZIP1, AtZIP2, AtZIP5, AtZIP6, AtZIP7, and AtZIP9 - are involved in Mn uptake, mainly under Mn deficiency (Milner et al. 2013); AtZIP1 is localized in the tonoplast, suggesting that it is involved in Mn movement from vacuole to cytoplasm. In addition, some YSL transporters, which are proteins involved in the long-distance and intracellular transport of metals, have been shown to be involved in Mn influx. In *A. thaliana*, YSL 4 and 6 have been localized in the membranes of the vacuole and chloroplast, moving Mn from these organelles to the cytosol. Also, in rice plants, these transporters were found in the plasma membrane, involved in Mn uptake from the apoplast (Socha and Guerinot 2014).

Also, there are many protein families involved in Mn efflux - such as the cation exchanger (CAX), Ca cation exchanger (CCX), and vacuolar Fe transporter (VIT) families - together with Ca-permeable channels (Gollhofer et al. 2011, Zhang et al. 2012). Thus, CAX and CCX have been localized in the tonoplast and they are involved in Mn movement from cytosol to vacuole in *A. thaliana*. Also, VITs were found in the tonoplast of rice and *A. thaliana*. Under Mn deficiency, Mn can pass through the plasma membrane via Ca-permeable channels, from apoplast to cytoplasm (White et al. 2002).

Although there has been no investigation that relates water flow, aquaporins, and Mn nutrition status, the fact that there is a relationship with other micronutrients supports some unknown interrelations.

Copper

Copper (Cu) is moved by membrane transporters of several families, such as COPT, ZIP, HMA, and YSL. Under Cu deficiency, there is up-regulation of *COPT 1 and 2* and *ZIP 2* and *4*, which encode proteins localized in the plasma membrane, mainly in root tips and the zone of differentiation. Also, COPT5, localized in the tonoplast, mediates influx transport to increase the Cu concentration in the cytosol. In addition, under Cu deficiency, the abundance of YSL 2 increases since it is involved in long-distance transport of Cu, from the xylem to sink cells. However, there are other important transporters, like HMA5, that have a contrary role depending on the plant. So, in rice, HMA5 is up-regulated to facilitate long-distance Cu transport since it mediates Cu efflux across the plasma membrane. While, in *A. thaliana*, HMA5 is localized in the tonoplast, mediating Cu efflux to the vacuole; under Cu deficiency its expression is down-regulated (Bernal et al. 2012, Aguirre and Pilon 2016, Printz et al. 2016).

Few studies have demonstrated the relationship of Cu stress with water uptake and transport. It has been reported that in the leaves of Cu-deficient plants of safflower (*Carthamus tinctorius* L.) and cotton *(Gossypium hirsutum* L.) the water flow was decreased, since these plants had low stomatal conductivity (Sharma 2006). However, an excess of Cu could affect aquaporins functioning in the plasma membrane, inhibiting their water transport. In this way, the blue copper-binding protein（GhBCP2) has been reported to inhibit the cotton GhPIP2;6 activity, suggesting that Cu levels could regulate the function of this aquaporin decreasing the water flow across it (Li et al. 2013). Recently, Landa et al. (2017) reported that excess Cu provoked the down-regulation of genes involved in metal homeostasis and aquaporins synthesis in *A. thaliana* plants. A high Cu concentration provoked a decrease in the transcription of aquaporins genes, such as *PIP1C*, *DELTATIP*, *TIP2*, and *PIP2;4*, reducing water uptake. Also, these authors indicated that the reduction of water flow was due to damage to the membrane structure caused by the low content and expression of aquaporins under this condition.

In addition, Noronha et al. (2016) described a XIP in grapevine (*Vitis vinifera* L.), VvXIP1, that transports Cu and Ni, but an excess of Cu provoked a down-expression of this aquaporin. The mechanism by which cations cross the aquaporins pore is unknown at this time. But, these authors suggested similarities with the results found in human aquaporins. They pointed out that PIP1 is formed by four subunits having one pore each, and water should be transported by each individual pore, but the central pore could facilitate the diffusion of charged solutes in response to cyclic nucleotide binding.

Previously, Yool and Weinstein (2002) found similarities between the carboxy tail domains of cyclic nucleotide gated (CNG) channels and PIP1. This could open the way to future studies that help us to understand the possible role of aquaporins in the transport of cations.

Molybdenum

Molydenum (Mo) uptake is mediated by a plasma membrane transporter known as MOT1, described in *A. thaliana*; due to its analogy with S transport it was known previously as SULTR5;2 (Mendel and Kruse 2012). Also, there is another Mo transporter localized in the vacuolar membrane, known as MOT2; normally, it accumulates and its activity increases in senescing leaves, suggesting that MOT2 could transport Mo from vacuole to cytosol (Vatansever et al. 2017).

In relation to Mo and water status, there are no studies that found a direct relationship between them. However, under Mo deficiency, nitrate reductase is inactive and the NO_3^- concentration increases in cells and tissues. This could enhance TIPs activity since these aquaporins are involved in NO_3^- efflux to the vacuole (Little et al. 2005), which would avoid NO_3^- toxicity as the first step under Mo deficiency. Therefore, although there are no studies relating transporters of Mo and aquaporins, the indirect evidence for such a relationship supports the need for mutual regulation.

Zinc

Zinc (Zn) uptake by plants is carried out by six families of transporters that include: ZIP, cation diffusion facilitator proteins (CDF), P-type ATPase, NRAMP, ATPase, HMA, and CAX (Kobae et al. 2004). Members of the ZIP family move Zn from apoplast to cytosol, so they are considered the main transporters involved in Zn uptake from soil (Lin et al. 2009). However, Zn movement at the vacuolar level is controlled by CDF (efflux) and NRAMP (influx) (Oomen et al. 2009), so that the cytosolic Zn concentration is highly controlled. Under Zn deficiency, many ZIP transporters are strongly induced, mainly ZIP4, which is localized in the plasma membrane of root tip and epidermal cells (Assunção et al. 2010). Also, it seems that there is a general response to Zn deficiency in higher plants, since the transcription factors involved in the increase in these ZIP transporters are found in several species (Assunção et al. 2010; Kabir et al. 2014). In addition, NRAMP transporters in the tonoplast are up-regulated while CDF are down-regulated, to transfer vacuolar Zn to the cytosol (Kabir et al. 2014). Furthermore, HMA transporters, mainly HMA2, are found in the plasma membrane of root vascular cells and affect the loading of Zn into the xylem for transport to the shoot in times of deficiency. Also,

these transporters permit Zn to cross the plasma membrane of root cells, reaching the xylem and finally the shoots (Hussain et al. 2004).

Zinc deficiency has been shown to provoke changes in water relations in plants similar to those observed under drought stress, but aquaporins have not been studied in this regard. However, Jain et al. (2008) showed that excess Zn acted as an inhibitor of PIPs functions in seeds of tomato (*Solanum lycopersicum* L.). Also, Devi et al. (2016) studied the effect of excess Zn in soybean plants, observing no increase in aquaporins transcription, but there was inhibition of aquaporins function, with reduced water flow across cells. In this way, Gitto and Fricke (2018) showed decreased plant water flow together with a decrease in aquaporins functionality (14-80%), mainly for PIP1;3, PIP2;4, and PIP2;5 that are involved in water flux. But, a recent work in poplar (*Populus trichocarpa* L.) reported that excess Zn not only down-regulated *PIP1*, but also provoked post-translational changes - since it was observed that PIP1 was co-localized in the vacuolar membrane together with TIP1, in *A. thaliana* protoplasts (Ariani et al. 2019) - which could be involved in the control of water fluxes to maintain the cell homeostasis under excess Zn. Future investigations are needed to understand the Zn-water flux relationship, but reports on the relationship between Zn deficiency and aquaporins are scarce.

Boron

Boron (B) deficiency is one of the most widespread micronutrient deficiencies in crops. Boron can be taken up by plants in different ways. For a long time, passive diffusion was considered the only way of entry of B into roots and cells. This probably is the main mechanism under optimal or high B conditions (Miwa and Fujiwara 2010). But, at low external B concentrations, this element can be taken up by an active process mediated by the specific efflux transporter BOR1 localized in the inner domain of root cells (Dannel et al. 2000). In addition, some aquaporins - such as NIP5;1 - are able to transport B (Kato et al. 2009). Takano et al. (2006) reported that, under B deficiency, damage to the xylem could reduce water transport to leaves, affecting the distribution of other elements: in this situation, aquaporin NP5;1 was highly expressed in *A. thaliana* plants, with an increase of almost 15-fold. Also, the expression of *NIP6;1*, which is expressed mainly in the phloem of stems, doubled under B-deficient conditions (Tanaka et al. 2008). Such increases in expression have also been observed for other NIPs, such as *NIP3,1* in rice and *NIP2,1* in barley (*Hordeum vulgare* L.); the latter was described as participating in B transport, indicating the important roles of this channel protein in B uptake and transport (Hanaoka and Fujiwara 2007, Schnurbusch et al. 2010). In addition, other B transporters, like BOR1, should be activated under these conditions to increase the B movement across root cells to the stele, due to the

opposite localizations of NIP and BOR in the plasma membrane that facilitates B movement. Another transporter, known as BOR2, is involved in the efflux of B from symplast to apoplast, to maintain the formation in root cells of the cell wall, due to the importance of this structure to plant cells.

Although, under B toxicity, normally BOR1 is quickly degraded to avoid excessive transport of B to the shoot (Poschenrieder et al. 2019), in rice an enhancement of other aquaporins, such as OsPIP2,4 and OsPIP2,7 (Kumar et al. 2014), to augment B movement to the leaves, was observed. Sutton et al. (2007), in barley plants, demonstrated an enhanced expression of efflux transporters in cells of leaves and roots; the key to tolerance lies in an increase in B efflux from the sensitive symplast to the apoplast, with later efflux of this B from hydathodes to the leaf surface, mediated by BOR1 (Reid and Fitzpatrick 2009). In addition, a member of the TIP aquaporins family localized in the tonoplast, AtTIP5,1 has been described as participating in B transport, effluxing it to the vacuole and thereby increasing the tolerance of B toxicity in *A. thaliana* plants (Pang et al. 2010). Finally, due to the importance of B to plants, a large number of aquaporins, of distinct types, participate in its homeostasis, mediating both influx and efflux processes. Thus, its movement is highly regulated, to maintain optimal B concentrations in cells and tissues.

Effect of drought on the interaction of nutrient transporters and aquaporins

The main effect of drought stress is the reduction of crop growth and yield, which ranges from 10 to 90% depending on the severity and the phenological stage of the plant when subjected to water deficit. The reduced water availability leads to a reduction in cell turgor, inhibiting cell elongation and promoting stomatal closure. The latter inhibits CO_2 absorption and photosynthetic efficiency, but also reduces water and nutrients uptake (Akinci and Lösel 2012).

In general, most of the genes encoding nitrate transporters and the enzymes responsible for NO_3^- assimilation and remobilization are down-regulated under drought stress (Goel and Singh 2015). However, in *Brassica juncea* L. plants, the expression of *BjNRT1;1* and *BjNRT1;5* was found to be up-regulated after 1 h of exposure to different abiotic stresses, indicating an early reaction of N accumulation upon detection of the onset of stress, but down-regulation occurred after 24 h, affecting most of the N transporters, including BjNRT2;1 (Goel and Singh 2015). However, there are differences in the regulation of NRTs among different species and varieties of the same plant species. As an example, Duan et al. (2016) showed that a N-inefficient variety of winter wheat (*Triticum aestivum* L.) up-regulated *NRT1;1*, *NRT1;2*, and *NRT2;2* in the reproductive stage and had strong down-regulation

of *NRT2;1*, *2;2*, and *2;3* (high-affinity transporters) in vegetative tissues after 30 days of drought stress (long-term stress). Meanwhile, a N-efficient variety maintained the expression of almost all the NO_3^- transporters, including the fundamental sensor *NRT1;1* and the *NRT2;1* and *NRT2;2*, at the same levels (Duan et al. 2016), demonstrating a better NO_3^- uptake capacity. Curiously, the N-efficient variety also showed an up-regulation of *AMT1;2* (NH_4^+ transporter), that points to a fine sensing of changes in the availability of N forms in the soil and to better resource utilization under such long periods of drought stress.

Under drought conditions, Pi uptake in plants is likely associated with alterations in the expression of the PHT family of transporters, and reflects the degree of drought tolerance in plants. In poplar *PtPHO9* and *PtPHT1;2* were up-regulated under drought (Zhang et al. 2016a); in apple (*Malus domestica* L.) *MdPHT1;5*, *MdPHT1;7*, and *MdPHT4;7* were up-regulated in roots, and *MdPHT3;7* and *MdPHT4;3* in leaves (Sun et al. 2017); and in *B. napus* only three genes, *BnaPT11*, *BnaPT3*4, and *BnaPT3*8 (BnPHT1 family), were up-regulated in roots while 18 genes of the BnPHT1 family were up-regulated in the leaves under drought stress, and, in addition, no genes were down-regulated (Li et al. 2019c).

Regarding the K^+ transporters, it has been reported that the grapevine K^+ transporter VvK1.1, the counterpart of the *A. thaliana* AKT1 channel, has a major role in K^+ uptake from the soil solution and its expression is strongly sensitive to drought stress. Nevertheless, the highest expression of *VvK1;1* has been shown in berries, where it is localized in the phloem vasculature, pointing to a major role in K^+ loading into berry tissues, especially upon drought stress (Cuéllar et al. 2010). Also, in chickpea (*Cicer arietinum* L.), the *CarAKT1,2* influx K^+ transporter and *CarGORK* (putatively involved in the K^+ efflux directly related to stomatal closure (Osakabe et al. 2013)) were both up-regulated in response to drought stress (Azeem et al. 2018). However, decreased expression of *CarKAT1,1* in chickpea and of *HvAKT1* in barley indicates that the change in the transcript level of some members of the AKT1 family might not be related to drought tolerance (Azeem et al. 2018, Cai et al. 2019). The results demonstrate that a fine regulation of K^+ transporters is essential to develop a strategy to cope with drought stress, although the response seems to be time- and genotype-dependent (Cai et al. 2019).

Calcium plays a key role as signaling molecule. When plants are exposed to abiotic stress, transient peaks of Ca^{2+} in cytoplasm regulate the response of different genes and proteins activity depending on the intensity and duration of the stress (Choi et al. 2014, Jing et al. 2019). For this reason, there is high variability in the regulation of calcium transporters under drought stress depending on tissues and specific functions. Plant Ca^{2+} pumps are involved in Ca^{2+} efflux from the cytosol. The

transcript level of P-IIB Ca-ATPase PCA1 rose in *Physcomitrella patens*, B&S. were up-regulated in response to dehydration and abscisic acid (Qudeimat et al. 2008), and some auto-inhibited calcium ATPases (ACAs) and ER-type ATPases (ECAs) pumps have shown to be regulated by short-term dehydration stress in rice, *ACA5* and *ACA7* being strongly up-regulated in roots and seedlings, while *ECA1* and *ACA4* were strongly down-regulated and *ACA3*, *ACA5*, and *ACA7* were up-regulated in mature leaves (Singh et al. 2014). In *Brassica oleracea* L., the *BoACA4* and *BoACA11* levels remained high for 24 h in leaves under dehydration stress (Lee et al. 2013). For *A. thaliana* and rice CAX (exchangers of Ca^{2+}), transcripts levels increased or decreased in abundance in response to water deficit (Bickerton and Pittman 2015). A wide-ranging analysis in rice showed differences in the patterns of regulation between tissues, almost all the CAX exchangers being down-regulated in roots but not in leaf tissues (Singh et al. 2014). Also, in *B. oleracea* the expression level of *BoCAX1* in leaf tissues gradually increased with the drought stress imposed (Lee et al. 2013), probably indicating a link to drought tolerance.

Under drought stress, differences in the response of aquaporins have been shown between different aquaporin homologs in diverse plant species (Gambetta et al. 2017), cultivars of the same plant species with differing drought tolerance strategies (Vandeleur et al. 2009), and between tissues (Martins et al. 2015) or even between portions of the same tissue (Knipfer et al. 2011). Indeed, root transcriptome analysis showed both up and down-regulation of different PIPs, TIPs, and NIPs homologs under drought stress (Molina et al. 2008, Aroca et al. 2012, Afzal et al. 2016) and different homologs responded differently depending on the intensity and nature of the stress applied (Aroca et al. 2012, Bárzana et al. 2014). Among the aquaporin groups, PIPs are the most responsive to drought stress, undergoing a general transcriptional down-regulation, particularly in roots (Jang et al. 2004, Alexandersson et al. 2005, Mahdieh et al. 2008, Ruiz-Lozano et al. 2009, Šurbanovski et al. 2013, Bárzana et al. 2014). Only a few PIP genes (mostly from the PIP1 subgroup) were found to be up-regulated - in specific tissues and drought conditions, especially in leaves (Jang et al. 2004, Lian et al. 2004, Aroca et al. 2007, Mahdieh et al. 2008, Li et al. 2009, Ruiz-Lozano et al. 2009, Vandeleur et al. 2009, Bárzana et al. 2014, Martins et al. 2015). This up-regulation of specific isoforms of the PIP1 subgroup in leaves implies their involvement in gas and water exchange and stomatal behavior under stress conditions (Flexas et al. 2006, Cui et al. 2008, Uehlein et al. 2012, Wang et al. 2016, Zwiazek et al. 2017).

Studies with transgenic plants overexpressing PIP aquaporin genes have also yielded complex outcomes, sometimes with increased plant resistance (Lian et al. 2004, Cui et al. 2008, Ayadi et al. 2011, Sreedharan et al. 2013, Xu et al. 2014, Zhuang et al. 2015), but not in other cases (Aharon et al. 2003,

Katsuhara et al. 2003, Jang et al. 2007), while silencing of PIP genes commonly increases the susceptibility of the plants to drought stress (Martre et al. 2002, Siefritz et al. 2002, Yu et al. 2005).

Besides PIPs, also TIPs and NIPs could be involved in the response of plants to drought stress. However, studies involving the overexpression of TIP and NIP homologs in different plants are scarce and also provide contradictory results. The constitutive expression of *SlTIP2;2* converted tomato plants from isohydric to anisohydric drought-tolerance behavior (Sade et al. 2009). Overexpression of *Panax ginseng,* C.A.Mey. *PgTIP1* in *A. thaliana* plants was detrimental to drought resistance under limited water supply due to rapid drying of the rooting medium and faster water loss through leaves by enhanced transpiration, but may be beneficial under slight drought stress and favorable growing conditions (Peng et al. 2007). Transgenic *A. thaliana* plants expressing *TaNIP* showed much longer roots and higher salt tolerance (Gao et al. 2010), while the tolerance of drought was not directly tested.

The regulation of aquaporins by different N forms provides an effective mechanism to increase plant water stress tolerance and water use efficiency. Aquaporins are tightly linked with N metabolism in higher plants, and members of the PIP, NIP, and TIP subfamilies have been shown to transport NH_3 and urea, and are directly involved in maintenance of the cytoplasm-vacuole balance (Gaspar et al. 2003, Liu et al. 2003, Jahn et al. 2004, Loqué et al. 2005, Wallace and Roberts 2005, Bertl and Kaldenhoff 2007, Gu et al. 2012, Bárzana et al. 2014, Yang et al. 2015, Zhang et al. 2016b). Moreover, NO_3^- and NH_4^+ are critical signaling factors for radial water fluxes in the roots (Gorska et al. 2008, Ding et al. 2015). PIP expression has been shown to be controlled by both exogenous and internal NO_3^- concentrations and the increased root hydraulic conductivity stimulated by NO_3^- correlated with up-regulation of PIP expression (Li et al. 2016). Under water stress, NH_4^+ increased the drought tolerance of rice plants by inducing aquaporin expression and activity, which corresponded with increased root water uptake (Ding et al. 2015). In relation to urea, while DUR3 was identified as a high-affinity urea transporter, members of the PIP, NIP, and TIP sub-groups of aquaporins were identified as low-affinity transporters (Liu et al. 2003, Gu et al. 2012, Yang et al. 2015, Zhang et al. 2016b). The uptake or reutilization of urea as a N source could be extremely useful to the plant under drought conditions, when the NO_3^- availability in soil decreases considerably. In *Cucumis sativus* L., CsNIP2;1 has a function in root urea uptake (Zhang et al. 2016b), and both CsNIP2;1 and DUR3 are up-regulated under conditions of N limitation such as under drought stress (Wang et al. 2016). Indeed, an up-regulation of maize ZmTIP1.1 and ZmTIP1.2 with a direct link to water, NH_4^+, and urea transport, and a possible role in the remobilization of N under severe drought stress, has been described (Bárzana et al. 2014), while

ZmTIP4;4 has been related to vacuolar unloading under N-deprivation (Gu et al. 2012). We cannot rule out, therefore, that DUR3 and AMT1 are equally involved in such redistribution under drought stress.

There are several studies that relate Pi uptake with water flow. The fact that Pi accumulation was reduced under drought conditions indicates that aquaporins expression was also reduced (Carvajal et al. 1996b, Lovelock et al. 2006, Wang et al. 2016). Similarly, it has been reported that augmented Pi uptake is related to increased aquaporins expression and/or activity during the recovery of plant water status after drought stress (Shangguan et al. 2005).

There is also a close relationship between water and K under drought stress. Both are transported throughout the plant by channels/transporters which share regulatory mechanisms under drought stress. Transmembrane channels for water and K^+ channels/transporters are co-regulated and function in a coordinated manner to maintain the cytosolic osmolality. The first evidence of this coordination was obtained with K^+-channel inhibitors that produce a diminution in the hydraulic conductivity of the roots (Tazawa et al. 2001) and down-regulation of both water channels (*PIP1;2*, *PIP2;2*, and *TIP1;2*) and the K transporter *HAK5* (Sahr et al. 2005). Similar co-regulation has been observed under drought stress in rice plants, where water deficiency strongly affects PIPs aquaporins and the OsAKT1, OsHAK1, and OsHKT1 K^+ channel and transporters in a coordinated manner that directly affects hydraulic conductance (Liu et al. 2006). These authors suggested that a common factor should exist for ion and water channels regulation in plants, ABA being the suggested candidate.

The interaction between Ca^{2+} and water channels/transporters under drought stress has not been directly measured, but it is well known that Ca^{2+} can indirectly and directly regulate the water transport in plants. The first clues of an indirect regulation of the closure of aquaporin channels by phosphorylation mediated by Ca^{2+} were provided in the 1990s for PIPs, TIPs, and NIPs isoforms, and the relationship of this aquaporin gating with a diminished water conductance of membranes mediated by Ca^{2+} and, to a lesser degree, by Mg^{2+} is well established (Johnson and Chrispeels 1992, Weaver and Roberts 1992, Johansson et al. 1996, Gerbeau et al. 2002). In roots, *AtPIP2;1*, *AtPIP2;2*, and *AtPIP2;7* are important for the regulation of water flow through plants, and *AtPIP2;1* is also implicated in signaling for stomatal closure; these aquaporins are Ca^{2+}-regulated, by direct interaction (Byrt et al. 2017, Kourghi et al. 2017).

Effect of salinity on the interaction of nutrient transporters and aquaporins

Salinity is one of the most widespread plant abiotic stresses around the world. Around 6% of the total land area is affected by salinity, which corresponds to 800 million hectares (Munns and Tester 2008). Soil is considered saline when the EC is greater than 4 dS m^{-1} and the osmotic pressure is ~ 0.2 MPa (USDA-ARS 2008). This stress entails large losses in agriculture, since moderate levels of environmental salt cause important decreases in the yield of crops because the most important crops are glycophytes (sensitive to saline stress) (Cheeseman 2015). This problem has arisen firstly due to natural causes and secondly through human-induced changes, and soil salinization is expected to increase further owing to climate change (Munns and Tester 2008, Zaman et al. 2018). Therefore, there has been an increase in the scientific research with the objective of understanding mechanisms of salt tolerance in plants. Different ways to solve the salinity problem have been proposed, such as the establishment of halophytic plants (resistant to saline stress) as new crops or the improvement of the tolerance of the main crop species by crossing or transferring genes from halophytes (Cheeseman 2015).

The accumulation of salt in the soil results in a plant stress that can be divided in two phases: (1) a rapid osmotic and water stress, caused by a decrease in water uptake (Sharma et al. 2012) and (2) a slower ionic and nutritional stress, due to the competition among saline ions (Na$^+$, Cl$^-$) and ionic forms of nutrients and/or the toxicity of saline ions (Munns and Tester 2008). Therefore, primary C and N metabolism in plant cells is altered (Ashraf et al. 2018) especially, NO$_3^-$ uptake and transport through roots is disrupted (Gallegos-Cedillo et al. 2016), the levels of many signalling molecules are modified (Zhang et al. 2016c), protein synthesis is reduced (and the transmembrane movement of water is altered (Patankar et al. 2019). Regarding tolerance mechanisms to deal with this stress, there are three types of plant response or tolerance (Munns and Tester 2008): (1) tolerance of osmotic stress with a primary response, namely the inhibition of root water uptake and a decrease in Lp (Boursiac et al. 2005), (2) Na$^+$ exclusion from leaf blades, to ensure that Na does not reach a toxic concentration, and (3) intracellular compartmentalization of Na, to avoid a toxic accumulation within the cytoplasm. These tolerance mechanisms vary or are more or less efficient depending on whether the plant is a halophyte or glycophyte (Munns 2002, Himabindu et al. 2016).

Therefore, saline stress is associated with nutritional stress caused by a deficit in the uptake of essential nutrients from the soil, because excessive concentrations of Na$^+$ and Cl$^-$ impair the uptake of beneficial ions (K$^+$ and Ca^{2+}) (Acosta-Motos et al. 2017). Furthermore, a balanced K$^+$/Na$^+$ ratio inside metabolically-active tissue and an adequate Ca^{2+} status, which is part of the signalling mechanism of Na$^+$ exclusion (Chakraborty et al. 2018), are important factors for salt tolerance. Hence, nutrient transporters have a key role in the response and tolerance mechanisms employed against saline stress.

The most studied transporters in this regard are K^+ (HAK, AKT, KT, and KUP families) and Na^+ (SOS, NHX, and HKT families) specific transporters, which control the cellular ion homeostasis and salt tolerance (Chakraborty et al. 2018). As a response to salt stress, the genes of these transporters are up- (Wang et al. 2017) or down-regulated (Chen et al. 2017a) depending on plant type or in relation to the degree of tolerance.

Apart from these elements, saline stress also affects the homeostasis of other ions, such as Ca^{2+}, Mg^{2+}, or NO_3^-, and the plant response in this sense is also important to confer salt tolerance. Hence, different studies, mainly in *A. thaliana*, have shown that CAX transporters (H^+/Ca^{2+} antiporters located in the tonoplast) are precisely modulated under salt stress - with CAX expression being higher or lower in response to salinity, depending on the isoform - to provide tolerance (reviewed in Bickerton and Pittman 2015). Regarding Mg^{2+}, Chen et al. (2017b) reported that a Mg transporter (OsMGT1) was involved in enhancing the activity of OsHKT1;5 in the stelar tissues of the root mature zone; specifically, the Mg^{2+} transported by OsMGT1 was the enhancer of this activity. In the tolerance of this stress, OsHKT1;5 plays an essential role, restricting Na^+ accumulation in the shoots by excluding Na^+ from the xylem (Cotsaftis et al. 2012). The exact mechanism of its activation is unknown but Mg^{2+} could be required for the stereo-structure of the OsHKT1;5 protein (Chen et al. 2017b). As for NO_3^-, there is a family of specific transporters (NRT). As indicated above, NO_3^- uptake is altered under saline stress; this will involve these transporters, specifically NRT2, whose genes are mainly expressed in the roots (Wang et al. 2003). For example, *NRT2;1* genes are down-regulated under high salinity in different plants, such as *Solanum pennelli* L., *S. esculentum* L., *B. juncea*, and *A. thaliana* (Yao et al. 2008, Goel and Singh 2015, Taochy et al. 2015, Abouelsaad et al. 2016). Also, as NRT2.1 is involved in promoting lateral root (Remans et al. 2006), a reduction in the mRNA content of NRT2.1 could subsequently reduce nitrate uptake under salt stress.

As indicated above, salinity stress is directly related to the water status of plants; specifically, water transport rates are quickly reduced. Therefore, aquaporins play an important role in the response to this stress (Chaumont et al. 2005, Kapilan et al. 2018) and in the tolerance mechanisms (Afzal et al. 2016). Salinity affects the expression of aquaporins genes and produces biochemical changes in these proteins (Martínez-Ballesta et al. 2006); the changes occur to regulate water transport and to try to maintain the water homeostasis. It is difficult to establish a general pattern for the behaviour of aquaporins under saline stress. In some reports, general conclusions appear, such as that in *A. thaliana* there is a 60 to 75% decrease in the abundance of *PIP* and *TIP* transcripts in the medium-to-long term after salt treatment (100 mM NaCl) (Boursiac et al. 2005, Sutka et al. 2011, Afzal et al. 2016). However,

this effect varies according to the type of aquaporin, the duration and intensity of the stress, and the tolerance of the plant and tissue (Kapilan et al. 2018). In *A. thaliana* seedlings, clear differences in the response to salt stress, regarding aquaporins expression in aerial parts and roots, were revealed (Jang et al. 2004): for example, in aerial parts, after a short exposure to NaCl, *PIP2;2* and *PIP2;3* were up-regulated and *PIP2;6* down-regulated, and in roots *PIP1;1*, *PIP1;2*, *PIP1;3*, and *PIP2;7* were up-regulated and *PIP1;5* down-regulated. Nevertheless, in other work, Pou et al. (2016) showed that *PIP2;7* expression was repressed in *A. thaliana* seedlings under salt stress; the main difference with respect to the previous work mentioned was the age of the plants, which in the first work was 2 weeks and in the second only 8 days. In the same way, Muries et al. (2011) showed that PIP1 and PIP2 were down-regulated in roots of broccoli plants after NaCl treatment for 15 days, although the amount of PIP1 and PIP2 in PM increased. Nonetheless, the water transport capacity of the roots decreased after 15 days of saline stress.

Overexpression of different aquaporins genes is widespread as a way to elucidate the role of these proteins in the response to salinity. In this sense, different works have shown that transgenic plants overexpressing certain aquaporins genes possessed higher salinity tolerance: for example, *MaPIP2;7* and *MaPIP1;2* in banana plants (*Musa acuminata* L.) (Sreedharan et al. 2013, Xu et al. 2020), *PdPIP1;2* in date palm (*Phoenix dactylifera* L.) (Patankar et al. 2019), or *ScPIP1;1* from jojoba (*Simmondsia chinensis* L.) and *MsPIP2;2* from alfalfa (*Medicago sativa* L.) in *A. thaliana* (Li et al. 2019b, Wang et al. 2019).

In addition to these subfamilies of aquaporins, others - such as the NIP subfamily - have been reported to have a role in salt tolerance. For instance, Gao et al. (2010) showed that the expression of *TaNIP* in winter wheat was up-regulated under salinity, while transgenic *A. thaliana* plants over-expressing *TaNIP* had higher salt tolerance. The greater tolerance of these transgenic plants is due to the role of the overexpressed aquaporins in (1) the accumulation of compatible solutes to improve osmotic adjustment, since previous works have shown the role of certain aquaporins in the permeability of the vacuole membrane to small solutes; for example, NtTIPa in tobacco (Gerbeau et al. 1999), (2) the improvement of the antioxidant defence system, to reduce membrane damage, and the activation of immunity signalling pathways, since some aquaporins transport H_2O_2 into the cytoplasm (Boursiac et al. 2008, Tian et al. 2016), and (3) the decline in Na^+ and K^+ contents and the maintenance of a balanced K^+/Na^+ ratio, which is in consonance with the evidence that certain aquaporins are involved in Na^+ uptake by roots (Byrt et al. 2017).

Regardless of the effect of salinity on aquaporins in terms of gene expression, this stress causes changes at the protein level and in the function and status of aquaporins. For example, changes in the cytosolic levels of pH and Ca^{2+} trigger modification in the aquaporins. It has been reported that in salt-sensitive plants the cytosolic pH decreases (Kader et al. 2007), causing aquaporin closure due to a pH-sensitive His residue that helps to maintain the aquaporin in a closed state (Törnroth-Horsefield et al. 2006). Also, the reduction in cytosolic Ca^{2+} caused by salt stress seems to be associated with an inhibition of aquaporins (Martínez-Ballesta et al. 2008).

The importance of nutrient and water transport under saline stress for the correct development of plants suggests that there could be a key relationship between some nutrient transporters and aquaporins in the maintenance of the cell homeostasis and in the improvement of salt tolerance in plants. In *A. thaliana* plants that over-expressed a *NIP* aquaporin, produced more salt-tolerant when the expression of *SOS2* (a Na^+-specific transporter) was suppressed (Gao et al. 2010). Cheng et al. (2004) found that SOS2 could regulate CAX1 (a H^+/Ca^{2+} antiporter) negatively, so it is possible that NIP is involved in Ca^{2+} homeostasis, which is a salt stress response regulating the cytosolic pH (Pittman and Hirschi 2016). Another example of interaction is that of NRT2;1 (a NO_3^- transporter) and PIP aquaporins in *A. thaliana*. Li et al. (2016) revealed modification of Lp mediated by NO_3^- and NRT2;1, there being a positive correlation between Lp and NO_3^-. The modification of Lp is through regulation of PIP aquaporins, which are mainly responsible for Lp and thus there is a direct relationship between PIPs and water transport. As we have indicated above, a reduction in *NRT2;1* abundance in roots under salinity has been reported, which could cause a decrease in the content or functionality of PIP aquaporins, since *NRT2;1* triggers a regulation of aquaporins at the transcriptional and post-transcriptional levels (Li et al. 2016). A lower activity of PIP aquaporins would lead to a decrease in Lp, which is a plant response to salt stress (Boursiac et al. 2005). The work cited and the existing knowledge about saline stress and the response of plants to it allow us to conclude that the regulation of Lp as a response to salinity could depend on the external and internal NO_3^- concentrations and the NRT2;1 activity, through regulation of PIP aquaporins. This last aspect would be in accordance with previous knowledge on the correlation between nitrogen and water uptake into plant roots (Clarkson 2000).

Effect of low temperature on the interaction of nutrient transporters and aquaporins

Extreme temperature is a major abiotic stress for plants and one of the main environmental factors that hinder plant growth and development and vegetation distribution (Jeon and Kim 2013). Due to climate

changes, weather punctuated by extreme temperature events will affect future agricultural production. In crop production areas, sudden low temperatures nowadays very often produce yield reduction (Lohani et al. 2019). Therefore, it is vital to understand how temperature can affect the transport of nutrients and water by plants, to optimize the production (Fig. 2).

One of the most important nutrients whose transport is affected by low temperatures is nitrogen, for several reasons. Firstly, low temperatures modify the form (NH_4^+ or NO_3^-) in which nitrogen is found in soil. At low temperatures, nitrifying bacteria become inactivated, increasing the NH_4^+/NO_3^- ratio, NH_4^+ being less mobile (Laanbroek 1990, Warren 2009). Also, NH_4^+ uptake via the high-affinity transport system (HATS) has been reported to be reduced by low temperatures (Wang et al. 1993). Also, a study in *B. juncea* reported that low temperatures decrease the expression of the main transporters of NO_3^- *(NRT1;1, NRT1;2, NRT1;4, NRT1;5, NRT1;8, NRT2;1)* and of an NH_4^+ transporter *(AMT2)* (Goel and Singh 2015). A decrease in the temperature can also modify intracellular transport; for example, through the overexpression of the vacuolar transporter *CAX1*, via abscisic acid, which was found to raise the cytosolic free Ca^{2+} concentration (Catalá et al. 2003).

Low temperatures have been reported to affect the uptake of micronutrients via a reduction in the expression of their transporters, as was the case of Mn in *A. thaliana* with the *AtNRAMP1* transporter (Ihnatowicz et al. 2014). However, although there are many studies on micronutrients concentrations in plants grown under low-temperature stress (e.g., a recent study with sweet pepper that showed a decrease in Fe and Zn due to low temperatures; Ropokis et al. 2019), there are no studies about their transporters. Another important aspect affected by low temperatures is the root and leaf hydraulic conductivity, which is directly regulated by aquaporins (Aroca et al. 2005, Ahamed et al. 2012). Thus, many studies revealed a direct correlation among PIP1s and PIP2s abundance, high hydraulic conductance, and low-temperature tolerance (Matsumoto et al. 2009, Lee et al. 2012, Ranganathan et al. 2016). In studies of isoforms, similarities between plants were observed. Thus, when low temperatures were applied to *A. thaliana*, there was down-regulation of root *PIP1;1, PIP 1;2, PIP1;5, PIP2;2, PIP2;3, PIP2;4*, and *PIP2;7* expression, but *PIP2;5* was up-regulated, while in the aerial part *PIP1;1, PIP 1;2, PIP1;4, PIP1;5, PIP2;1, PIP2;2, PIP2;3*, and *PIP2;4* were down-regulated but *PIP2;5* was up-regulated (Jang et al. 2004). Also, in roots of rice plants, the protein levels of the aquaporins PIP1;1, PIP1;2, PIP1;3, PIP2;1, PIP2;2, PIP2;3, PIP2;4, PIP2;5, PIP2;6, TIP1;1, TIP2;1, and TIP2;2 decreased and only PIP2;5 had an increase in its protein level (Ahamed et al. 2012), indicating an important role of PIP2;5 in cold-stress acclimation (Ahamed et al. 2012, Lee et al. 2012, Ranganathan et al. 2016).

There are a number of recent studies about the overexpression of aquaporins to increase the tolerance of low temperatures, such as the over-expression of *TaAQP7*, a PIP2 gene of wheat, in tobacco plants (Huang et al. 2014). Other recent studies have shown how the overexpression of PIP2;7 from *Medicago falcata* L. and banana increased cold tolerance in transgenic tobacco (Zhuo et al. 2016) and banana (Xu et al. 2020), respectively, evincing also the involvement of this aquaporin in the response to cold stress. Finally, studies with rice plants indicate that inhibition of water uptake at low temperatures is not associated directly with the abundance of aquaporins in the root membrane, but with the inhibition of their activity (Murai-Hatano et al. 2008), coming into play not only the decrease/increase in transcription or translation levels, but also a posttranslational regulation of aquaporins (Chaumont and Tyerman 2014).

Nonetheless, the relationship among aquaporins, other nutrient transporters, and abiotic stresses like extreme temperature is poorly understood, notwithstanding the capacity of aquaporins to transport some elements like N (as urea or NH_4^+), B (boric acid), Si (silicic acid), As (arsenite), or H_2O_2 (Bienert et al. 2008; Bienert and Chaumont 2011). Also, a decrease in nutrient transport and the generation of reactive oxygen species (ROS), like H_2O_2, is a typical response of plants to extreme temperatures (Giri et al. 2017; Hsu and Hsu 2019). There are some recent, pioneering studies of the relationships of aquaporins with other nutrient transporters under low-temperature stress. One of them shows a possible regulation of aquaporins PIP2;1 and PIP2;6 in the response to cold stress, through a calcium-dependent protein kinase, *OsCPK17* (Almadanim et al. 2017); so, an increase in the vacuolar expression of a Ca^{2+} transporter like CAX1 could be related to aquaporins (Catalá et al. 2003). In another example, the tissue B concentration did not change in spite of the decrease in the protein level of BOR1 (a B transporter), while the levels of NIP5;1 remained stable (Giri et al. 2017) - suggesting that the B levels were maintained despite the stress due to the stability of the aquaporin. In a work performed with tomato, it was demonstrated that the P deficit (common in low-temperature situations) can be compensated by a greater concentration of Si (Zhang et al. 2019), which can be transported by some aquaporins in the form of silicic acid (Jian et al. 2006). Other studies related the transport of Si, in the form of silicic acid (Pandey et al. 2016), and Se nutrition (Pandey et al. 2015) to a decrease in the uptake of As through competitive inhibition; Si and Se mitigated its toxicity, because they share the transporter *Lsi1*, an aquaporin (Ma et al. 2007).

Conclusions

The expression of both nutrient transporters and aquaporins genes should be regulated in the response of plants to environmental stress - such as nutrient deficiency, drought, salt stress, and low temperatures - so that they can cope with the stress. Therefore, although the interactions of both type of transporters deserve more investigation, attention should be paid to that the first signal which triggers the rest of the responses must be hydric. In this way, the involvement of aquaporins to the initial stress sensing needs to be taken into account to understand the integrated physiological responses.

The results summarized in this review highlight some general responses. For instance, a deficiency of each macronutrient induces its own transporters expression but reduces the expression of plasma membrane aquaporins. In other way, deficiencies of micronutrients induce their tonoplast transporters for remobilization from the vacuole and also reduce aquaporins presence. Also, the fact that some aquaporins have been reported to transport mineral nutrients - such as NH_4^+, B, and urea - to ensure nutrient availability under abiotic stress, should be taken into account.

While the response of plants to drought and salinity depends on the specific mechanism and degree of tolerance of each species, for drought we can generalize that higher expression of transporters and aquaporins is observed in tolerant plants (Fig. 3). However, the complexity of salinity in all facets of the stress suggests several transport processes as key to the tolerance, decreasing Na uptake but increasing K and N uptake. Also, under saline stress, some aquaporins have been demonstrated to be important in water transport, for the correct development of plants (Fig. 4). Therefore, the link between nutrient transporters and aquaporins in the maintenance of the cell homeostasis should be studied in each particular case. Under low-temperature stress, a general decrease in the expression of aquaporins has been found but the fact that *PIP2;5* or *PIP2;7* was increased in all the studies assigns them a key role in the response.

Understanding the interactions between aquaporins and mineral nutrients under environmental stress conditions will enable us to modulate the water and mineral nutrient uptake and assimilation to improve the water and nutrient use efficiency in plants. Therefore, much more research is needed to clarify the signaling and regulation of aquaporins and nutrient transport in tandem since only the modification of their joint response will improve tolerance.

References

Abouelsaad I, Weihrauch D, Renault S (2016) Effects of salt stress on the expression of key genes related to nitrogen assimilation and transport in the roots of the cultivated tomato and its wild salt-tolerant relative. Sci Hortic (Amsterdam) 211:70–78

Acosta-Motos JR, Ortuño MF, Bernal-Vicente A, Diaz-Vivancos P, Sanchez-Blanco MJ, Hernandez JA (2017) Plant responses to salt stress: Adaptive mechanisms. Agronomy 7:18

Afzal Z, Howton TC, Sun Y, Mukhtar MS (2016) The roles of aquaporins in plant stress responses. J Dev Biol 4:1–22

Aguilar-Hernández HS, Santos L, León-Galván F, Barrera-Pacheco A, Espitia-Rangel E, De León-Rodríguez A, Guevara-González RG, Barba de la Rosa AP (2011) Identification of calcium stress induced genes in amaranth leaves through suppression subtractive hybridization. J Plant Physiol 168:2102–2109

Aguirre G, Pilon M (2016) Copper delivery to chloroplast proteins and its regulation. Front Plant Sci 6:1250

Ahamed A, Murai-Hatano M, Ishikawa-Sakurai J, Hayashi H, Kawamura Y, Uemura M (2012) Cold stress-induced acclimation in rice is mediated by root-specific aquaporins. Plant Cell Physiol 53:1445–1456

Aharon R, Shahak Y, Wininger S, Bendov R, Kapulnik Y, Galili G (2003) Overexpression of a plasma membrane aquaporin in transgenic tobacco improves plant vigor under favorable growth conditions but not under drought or salt stress. Plant Cell 15:439–447

Ahn SJ, Shin R, Schachtman DP (2004) Expression of KT/KUP genes in Arabidopsis and the role of root hairs in K+ uptake. Plant Physiol 134:1135–1145

Akinci S, Lösel DM (2012) Plant water-stress response mechanisms. In: Rahman IMM (ed) Water Stress. IntechOpen, pp 15–42

Alexandersson E, Fraysse L, Sjövall-Larsen S, Gustavsson S, Fellert M, Karlsson M, Johanson U, Kjellbom P (2005) Whole gene family expression and drought stress regulation of aquaporins. Plant Mol Biol 59:469–484

Almadanim MC, Alexandre BM, Rosa MTG, Sapeta H, Leitão AE, Ramalho JC, Lam TKT, Negrão S, Abreu IA, Oliveira MM (2017) Rice calcium-dependent protein kinase OsCPK17 targets plasma membrane intrinsic protein and sucrose-phosphate synthase and is required for a proper cold stress response. Plant Cell Environ 40:1197–1213

Ariani A, Barozzi F, Sebastiani L, di Toppi LS, di Sansebastiano G Pietro, Andreucci A (2019) AQUA1 is a mercury sensitive poplar aquaporin regulated at transcriptional and post-translational levels by

Zn stress. Plant Physiol Biochem 135:588–600

Armand T, Cullen M, Boiziot F, Li L, Fricke W (2019) Cortex cell hydraulic conductivity, endodermal apoplastic barriers and root hydraulics change in barley (Hordeum vulgare L.) in response to a low supply of N and P. Ann Bot 124:1091–1107

Armengaud P, Breitling R, Amtmann A (2004) The potassium-dependent transcriptome of arabidopsis reveals a prominent role of jasmonic acid in nutrient signaling. Plant Physiol 136:2556–2576

Aroca R, Amodeo G, Fernández-Illescas S, Herman EM, Chaumont F, Chrispeels MJ (2005) The role of aquaporins and membrane damage in chilling and hydrogen peroxide induced changes in the hydraulic conductance of maize roots. Plant Physiol 137:341–353

Aroca R, Porcel R, Ruiz-Lozano JM (2012) Regulation of root water uptake under abiotic stress conditions. J Exp Bot 63:43–57

Aroca R, Porcel R, Ruiz-Lozano JM (2007) How does arbuscular mycorrhizal symbiosis regulate root hydraulic properties and plasma membrane aquaporins in Phaseolus vulgaris under drought, cold or salinity stresses? New Phytol 173:808–816

Ashraf M, Shahzad SM, Imtiaz M, Rizwan MS (2018) Salinity effects on nitrogen metabolism in plants– focusing on the activities of nitrogen metabolizing enzymes: A review. J Plant Nutr 41:1065–1081

Assunção AGL, Schat H, Aarts MGM (2010) Regulation of the adaptation to zinc deficiency in plants. Plant Signal Behav 5:1553–1555

Ayadi A, David P, Arrighi JF, Chiarenza S, Thibaud MC, Nussaume L, Marin E (2015) Reducing the genetic redundancy of arabidopsis phosphate transporter1 transporters to study phosphate uptake and signaling. Plant Physiol 167:1511–1526

Ayadi M, Cavez D, Miled N, Chaumont F, Masmoudi K (2011) Identification and characterization of two plasma membrane aquaporins in durum wheat (Triticum turgidum L. subsp. durum) and their role in abiotic stress tolerance. Plant Physiol Biochem 49:1029e1039

Azeem F, Ahmad B, Atif RM, Ali MA, Nadeem H, Hussain S, Manzoor H, Azeem M, Afzal M (2018) Genome-Wide Analysis of Potassium Transport-Related Genes in Chickpea (Cicer arietinum L.) and Their Role in Abiotic Stress Responses. Plant Mol Biol Report 36:451–468

Barker A V., Pilbeam DJ (2016) Handbook of plant nutrition

Bárzana G, Aroca R, Bienert GP, Chaumont F, Ruiz-Lozano JM (2014) New Insights into the Regulation of Aquaporins by the Arbuscular Mycorrhizal Symbiosis in Maize Plants Under Drought Stress and Possible Implications for Plant Performance. Mol Plant-Microbe Interact MPMI 27:349–363

Berezin I, Brook E, Mizrahi K, Mizrachy-Dagry T, Elazar M, Zhou S, Shaul O (2008) Overexpression of the vacuolar metal/proton exchanger AtMHX in tomato causes decreased cell expansion and modifications in the mineral content. Funct Plant Biol 35:15–25

Bernal M, Casero D, Singh V, Wilson GT, Grande A, Yang H, Dodani SC, Pellegrini M, Huijser P, Connolly EL, Merchant SS, Krämer U (2012) Transcriptome sequencing identifies SPL7-regulated copper acquisition genes FRO4/FRO5 and the copper dependence of iron homeostasis in Arabidopsis. Plant Cell 24:738–761

Bertl A, Kaldenhoff R (2007) Function of a separate NH3-pore in Aquaporin TIP2;2 from wheat. FEBS Lett 581:5413–5417

Bickerton PD, Pittman JK (2015) Role of cation/proton exchangers in abiotic stress signaling and stress tolerance in plants. Springer, New York, NY, USA

Bienert GP, Chaumont F (2011) Plant Aquaporins: Roles in Water Homeostasis, Nutrition, and Signaling Processes. In: Transporters and pumps in plant signaling. Springer, Berlin, Heidelberg. pp 3–36

Bienert GP, Schüssler MD, Jahn TP (2008) Metalloids: essential, beneficial or toxic? Major intrinsic proteins sort it out. Trends Biochem Sci 33:20–26

Boursiac Y, Chen S, Luu DT, Sorieul M, Van Den Dries N, Maurel C (2005) Early effects of salinity on water transport in Arabidopsis roots. Molecular and cellular features of aquaporin expression. Plant Physiol 139:790–805

Boursiac Y, Prak S, Boudet J, Postaire O, Luu DT, Tournaire-Roux C, Santoni V, Maurel C (2008) The response of Arabidopsis root water transport to a challenging environment implicates reactive oxygen species- and phosphorylation-dependent internalization of aquaporins. Plant Signal Behav 3:1096–1098

Briat JF, Dubos C, Gaymard F (2015) Iron nutrition, biomass production, and plant product quality. Trends Plant Sci 20:33–40

Buchner P, Takahashi H, Hawkesford MJ (2004) Plant sulphate transporters: Co-ordination of uptake, intracellular and long-distance transport. In: Journal of Experimental Botany. pp 1765–1773

Byrt CS, Zhao M, Kourghi M, Bose J, Henderson SW, Qiu J, Gilliham M, Schultz C, Schwarz M, Ramesh SA, Yool A, Tyerman S (2017) Non-selective cation channel activity of aquaporin AtPIP2;1 regulated by Ca2+ and pH. Plant Cell Environ 40:802–815

Cabañero FJ, Martínez-Ballesta MC, Teruel JA, Carvajal M (2006) New evidence about the relationship between water channel activity and calcium in salinity-stressed pepper plants. Plant Cell Physiol. https://doi.org/10.1093/pcp/pci239

Cai K, Gao H, Wu X, Zhang S, Han Z, Chen X, Zhang G, Zeng F (2019) The ability to regulate transmembrane potassium transport in root is critical for drought tolerance in barley. Int J Mol Sci 20:4111

Carvajal M, Cerdá A, Martínez V (2000) Does calcium ameliorate the negative effect of NaCl on melon root water transport by regulating aquaporin activity? New Phytol 145:439–447

Carvajal M, Cooke DT, Clarkson DT (1996a) Plasma membrane fluidity and hydraulic conductance in

wheat roots: Interactions between root temperature and nitrate or phosphate deprivation. Plant, Cell Environ 19:1110–1114

Carvajal M, Cooke DT, Clarkson DT (1996b) Responses of wheat plants to nutrient deprivation may involve the regulation of water-channel function. Planta 199:372–381

Catalá R, Santos E, Alonso JM, Ecker JR, Martínez-Zapater JM, Salinas J (2003) Mutations in the Ca2+/H+ Transporter CAX1 Increase CBF/DREB1 Expression and the Cold-Acclimation Response in Arabidopsis. Plant Cell 15:2940–2951

Cellier F, Conéjéro G, Ricaud L, Doan TL, Lepetit M, Gosti F, Casse F (2004) Characterization of AtCHX17, a member of the cation/H+ exchangers, CHX family, from Arabidopsis thaliana suggests a role in K + homeostasis. Plant J 39:834–846

Chakraborty K, Basak N, Bhaduri D, Ray S, Vijayan J, Chattopadhyay K, Sarkar RK (2018) Ionic Basis of Salt Tolerance in Plants: Nutrient Homeostasis and Oxidative Stress Tolerance. In: Hasanuzzaman M, Fujita M, Oku H, et al. (eds) Plant Nutrients and Abiotic Stress Tolerance. Springer Singapore, Singapore, pp 325–362

Chaumont F, Moshelion M, Daniels MJ (2005) Regulation of plant aquaporin activity. Biol Cell 97:749–764

Chaumont F, Tyerman SD (2014) Aquaporins: Highly regulated channels controlling plant water relations. Plant Physiol 164:1600–1618

Cheeseman JM (2015) The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions. New Phytol 206:557–570

Chen J, Zhang H, Zhang X, Tang M (2017a) Arbuscular mycorrhizal symbiosis alleviates salt stress in black locust through improved photosynthesis, water status, and K+/Na+homeostasis. Front Plant Sci 8:1739

Chen YF, Wang Y, Wu WH (2008) Membrane transporters for nitrogen, phosphate and potassium uptake in Plants. J Integr Plant Biol 50:835–848

Chen ZC, Ma JF (2013) Magnesium transporters and their role in Al tolerance in plants. Plant Soil 368:51–56

Chen ZC, Yamaji N, Horie T, Che J, Li J, An G, Ma JF (2017b) A magnesium transporter OsMGT1 plays a critical role in salt tolerance in rice. Plant Physiol 174:1837–1849

Cheng NH, Pittman JK, Barkla BJ, Shigaki T, Hirschi KD (2003) The Arabidopsis cax1 mutant exhibits impaired ion homeostasis, development, and hormonal responses and reveals interplay among vacuolar transporters. Plant Cell 15:347–364

Cheng NH, Pittman JK, Zhu JK, Hirschi KD (2004) The Protein Kinase SOS2 Activates the Arabidopsis H+/Ca 2+ Antiporter CAX1 to Integrate Calcium Transport and Salt Tolerance. J Biol Chem 279:2922–2926

Choi WG, Toyota M, Kim SH, Hilleary R, Gilroy S (2014) Salt stress-induced Ca2+ waves are associated with rapid, long-distance root-to-shoot signaling in plants. Proc Natl Acad Sci U S A 111:6497–6502

Clarkson DT (2000) Root hydraulic conductance: diurnal aquaporin expression and the effects of nutrient stress. J Exp Bot 51:61–70

Clarkson DT, Carvajal M, Henzler T, Waterhouse RN, Smyth AJ, Cooke DT, Steudle E (2000) Root hydraulic conductance: diurnal aquaporin expression and the effects of nutrient stress. J Exp Bot 51:61–70

Coffey O, Bonfield R, Corre F, Sirigiri JA, Meng D, Fricke W (2018) Root and cell hydraulic conductivity, apoplastic barriers and aquaporin gene expression in barley (Hordeum vulgare L.) grown with low supply of potassium. Ann Bot 122:1131–1141

Cotsaftis O, Plett D, Shirley N, Tester M, Hrmova M (2012) A two-staged model of Na+ exclusion in rice explained by 3d modeling of HKT transporters and alternative splicing. PLoS One 7:e39865

Cuéllar T, Pascaud F, Verdeil JL, Torregrosa L, Adam-Blondon AF, Thibaud JB, Sentenac H, Gaillard I (2010) A grapevine Shaker inward K+ channel activated by the calcineurin B-like calcium sensor 1-protein kinase CIPK23 network is expressed in grape berries under drought stress conditions. Plant J 61:58–69

Cui XH, Hao FS, Chen H, Chen J, Wang XC (2008) Expression of the Vicia faba VfPIP1 gene in Arabidopsis thaliana plants improves their drought resistance. J Plant Res 121:207–214

Curci PL, Aiese Cigliano R, Zuluaga DL, Janni M, Sanseverino W, Sonnante G (2017) Transcriptomic response of durum wheat to nitrogen starvation. Sci Rep 7:1–14

Dalcorso G, Manara A, Piasentin S, Furini A (2014) Nutrient metal elements in plants. Metallomics 6:1770–1778

Dannel F, Pfeffer H, Römheld V (2000) Characterization of root boron pools, boron uptake and boron translocation in sunflower using the stable isotopes 10B and 11B. Aust J Plant Physiol 27:397–405

Devi MJ, Sinclair TR, Taliercio E (2016) Silver and zinc inhibitors influence transpiration rate and aquaporin transcript abundance in intact soybean plants. Environ Exp Bot 122:168–175

Di Pietro M, Vialaret J, Hem S, Prado K, Rossignol M, Maurel C, Santoni V (2013) Coordinated post-translational responses of aquaporins to abiotic and nutritional stimuli in arabidopsis roots. Mol Cell Proteomics 12:3886–3897

Ding L, Gao C, Li Y, Li Y, Zhu Y, Xu G, Shen Q, Kaldenhoff R, Kai L, Guo S (2015) The enhanced drought tolerance of rice plants under ammonium is related to aquaporin (AQP). Plant Sci 234:14–21

Ding L, Li Y, Gao L, Lu Z, Wang M, Ling N, Shen Q, Guo S (2018) Aquaporin expression and water transport pathways inside leaves are affected by nitrogen supply through transpiration in rice

plants. Int J Mol Sci 19:256

Duan J, Tian H, Gao Y (2016) Expression of nitrogen transporter genes in roots of winter wheat (Triticum aestivum L.) in response to soil drought with contrasting nitrogen supplies. Crop Pasture Sci 67:128–136

Eissenstat DM (1997) Trade-offs in root form and function. In: Ecology in agriculture. Academic Press, pp 173–199

Flexas J, Ribas-Carbó M, Hanson DT, Bota J, Otto B, Cifre J, McDowell N, Medrano H, Kaldenhoff R (2006) Tobacco aquaporin NtAQP1 is involved in mesophyll conductance to CO 2 in vivo. Plant J. https://doi.org/10.1111/j.1365-313X.2006.02879.x

Forde BG (2002) Local and long-range signaling pathways regulating plant responses to nitrate. Annu Rev Plant Biol 53:203–224

Gaash R, Elazar M, Mizrahi K, Avramov-Mor M, Berezin I, Shaul O (2013) Phylogeny and a structural model of plant MHX transporters. BMC Plant Biol 13:75

Gallegos-Cedillo VM, Urrestarazu M, Álvaro JE (2016) Influence of salinity on transport of nitrates and potassium by means of the xylem sap content between roots and shoots in young tomato plants. J Soil Sci Plant Nutr 16:991–998

Gambetta GA, Knipfer T, Fricke W, McElrone AJ (2017) Aquaporins and Root Water Uptake. In: Book Plant Aquaporins, From Transport to Signaling. Springer, pp 133–153

Gao Z, He X, Zhao B, Zhou C, Liang Y, Ge R, Shen Y, Huang Z (2010) Overexpressing a putative aquaporin gene from wheat, TaNIP, enhances salt tolerance in transgenic arabidopsis. Plant Cell Physiol 51:767–775

Gaspar M, Bousser A, Sissoëff I, Roche O, Hoarau J, Mahé A (2003) Cloning and characterization of ZmPIP1-5b, an aquaporin transporting water and urea. Plant Sci 165:21–31

Gelli M, Duo Y, Konda AR, Zhang C, Holding D, Dweikat I (2014) Identification of differentially expressed genes between sorghum genotypes with contrasting nitrogen stress tolerance by genome-wide transcriptional profiling. BMC Genomics 15:

Gerbeau P, Amodeo G, Henzler T, Santoni V, Ripoche P, Maurel C (2002) The water permeability of Arabidopsis plasma membrane is regulated by divalent cations and pH. Plant J 30:71–81

Gerbeau P, Güçlü J, Ripoche P, Maurel C (1999) Aquaporin Nt-TIPa can account for the high permeability of tobacco cell vacuolar membrane to small neutral solutes. Plant J 18:577–587

Gierth M, Mäser P, Schroeder JI (2005) The potassium transporter AtHAK5 functions in K+ deprivation-induced high-afinity K+ Uptake and AKT1 K + channel contribution to K + uptake kinetics in Arabidopsis roots. Am Soc Plant Biol 137:1105–1114

Giri A, Heckathorn S, Mishra S, Krause C (2017) Heat stress decreases levels of nutrient-uptake and - assimilation proteins in tomato roots. Plants 6:6

Gitto A, Fricke W (2018) Zinc treatment of hydroponically grown barley plants causes a reduction in root and cell hydraulic conductivity and isoform-dependent decrease in aquaporin gene expression. Physiol Plant 164:176–190

Goel P, Singh AK (2015) Abiotic stresses downregulate key genes involved in nitrogen uptake and assimilation in brassica juncea l. PLoS One 10:e0143645

Gojon A, Krouk G, Perrine-Walker F, Laugier E (2011) Nitrate transceptor(s) in plants. J Exp Bot 62:2299–2308

Gollhofer J, Schläwicke C, Jungnick N, Schmidt W, Buckhout TJ (2011) Members of a small family of nodulin-like genes are regulated under iron deficiency in roots of Arabidopsis thaliana. Plant Physiol Biochem 49:557–564

Gorska A, Zwieniecka A, Michele Holbrook N, Zwieniecki MA (2008) Nitrate induction of root hydraulic conductivity in maize is not correlated with aquaporin expression. Planta 228:989–998

Gransee A, Führs H (2013) Magnesium mobility in soils as a challenge for soil and plant analysis, magnesium fertilization and root uptake under adverse growth conditions. Plant Soil 368:5–21

Gu R, Chen X, Zhou Y, Yuan L (2012) Isolation and characterization of three maize aquaporin genes, ZmNIP2;1, ZmNIP2;4 and ZmTIP4;4 involved in urea transport. BMB Rep 45:96–101

Guo W, Nazim H, Liang Z, Yang D (2016) Magnesium deficiency in plants: An urgent problem. Crop J 4:83–91

Hanaoka H, Fujiwara T (2007) Channel-mediated boron transport in rice. Plant Cell Physiol 48:S227

Hasanuzzaman M, Bhuyan MHMB, Mahmud JA, Nahar K, Mohsin SM, Parvin K, Fujita M (2018) Interaction of sulfur with phytohormones and signaling molecules in conferring abiotic stress tolerance to plants. Plant Signal Behav 13:e1477905

Haydon MJ, Cobbett CS (2007) Transporters of ligands for essential metal ions in plants: Research review. New Phytol 174:499–506

Himabindu Y, Chakradhar T, Reddy MC, Kanygin A, Redding KE, Chandrasekhar T (2016) Salt-tolerant genes from halophytes are potential key players of salt tolerance in glycophytes. Environ Exp Bot 124:39–63

Hopff D, Wienkoop S, Lüthje S (2013) The plasma membrane proteome of maize roots grown under low and high iron conditions. J Proteomics 91:605–618

Hsu CH, Hsu YT (2019) Biochemical responses of rice roots to cold stress. Bot Stud 60:1–12

Huang C, Zhou S, Hu W, Deng X, Wei S, Yang G, He G (2014) The wheat aquaporin gene TaAQP7 confers tolerance to cold stress in transgenic tobacco. Zeitschrift fur Naturforsch - Sect C J Biosci 69:142–148

Humayan Kabir A, Swaraz AM, Stangoulis J (2014) Zinc-deficiency resistance and biofortification in

plants. J Plant Nutr Soil Sci 177:311–319

Hussain D, Haydon MJ, Wang Y, Wong E, Sherson SM, Young J, Camakaris J, Harper JF, Cobbett CS (2004) P-type ATPase heavy metal transporters with roles in essential zinc homeostasis in arabidopsis. Plant Cell 16:1327–1339

Ihnatowicz A, Siwinska J, Meharg AA, Carey M, Koornneef M, Reymond M (2014) Conserved histidine of metal transporter AtNRAMP1 is crucial for optimal plant growth under manganese deficiency at chilling temperatures. New Phytol 202:1173–1183

Jahn TP, Møller ALB, Zeuthen T, Holm LM, Klærke DA, Mohsin B, Kühlbrandt W, Schjoerring JK (2004) Aquaporin homologues in plants and mammals transport ammonia. FEBS Lett 574:31–36

Jain N, Ascough GD, Van Staden J (2008) A smoke-derived butenolide alleviates HgCl2 and ZnCl2 inhibition of water uptake during germination and subsequent growth of tomato - Possible involvement of aquaporins. J Plant Physiol 165:1422–1427

Jang JY, Kim DG, Kim YO, Kim JS, Kang H (2004) An expression analysis of a gene family encoding plasma membrane aquaporins in response to abiotic stresses in Arabidopsis thaliana. Plant Mol Biol 54:713–725

Jang JY, Lee SH, Rhee JY, Chung GC, Ahn SJ, Kang H (2007) Transgenic Arabidopsis and tobacco plants overexpressing an aquaporin respond differently to various abiotic stresses. Plant Mol Biol 64:621–632

Jeon J, Kim J (2013) Cold stress signaling networks in Arabidopsis. J Plant Biol 56:69–76

Jian FM, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M (2006) A silicon transporter in rice. Nature 440:688–691

Jing X, Cai C, Fan S, Wang L, Zeng X (2019) Spatial and temporal calcium signaling and its physiological effects in Moso Bamboo under drought stress. Forests 10:224

Johansson I, Larsson C, Ek B, Kjellbom P (1996) The major integral proteins of spinach leaf plasma membranes are putative aquaporins and are phosphorylated in response to Ca2+ and apoplastic water potential. Plant Cell 8:1181–1191

Johnson KD, Chrispeels MJ (1992) Tonoplast-bound protein kinase phosphorylates tonoplast intrinsic protein. Plant Physiol 100:1787–1795

Kader MA, Lindberg S, Seidel T, Golldack D, Yemelyanov V (2007) Sodium sensing induces different changes in free cytosolic calcium concentration and pH in salt-tolerant and -sensitive rice (Oryza sativa) cultivars. Physiol Plant 130:99–111

Kapilan R, Vaziri M, Zwiazek JJ (2018) Regulation of aquaporins in plants under stress. Biol Res 51:1–11

Karthika KS, Rashmi I, Parvathi MS (2018) Biological functions, uptake and transport of essential nutrients in relation to plant growth. In: Plant Nutrients and Abiotic Stress Tolerance. Springer

Singapore, pp 1–49

Kato Y, Miwa K, Takano J, Wada M, Fujiwara T (2009) Highly boron deficiency-tolerant plants generated by enhanced expression of NIP5;1, a boric acid channel. Plant Cell Physiol 50:58–66

Katsuhara M, Koshio K, Shibasaka M, Hayashi Y, Hayakawa T, Kasamo K (2003) Over-expression of a Barley Aquaporin Increased the Shoot/Root Ratio and Raised Salt Sensitivity in Transgenic Rice Plants. Plant Cell Physiol 44:1378–1383

Knipfer T, Besse M, Verdeil JL, Fricke W (2011) Aquaporin-facilitated water uptake in barley (Hordeum vulgare L.) roots. J Exp Bot 62:4115–4126

Kobae Y, Uemura T, Sato MH, Ohnishi M, Mimura T, Nakagawa T, Maeshima M (2004) Zinc transporter of Arabidopsis thaliana AtMTP1 is localized to vacuolar membranes and implicated in zinc homeostasis. Plant Cell Physiol 45:1749–1758

Kourghi M, Nourmohammadi S, Pei J V., Qiu J, McGaughey S, Tyerman SD, Byrt CS, Yool AJ (2017) Divalent cations regulate the ion conductance properties of diverse classes of aquaporins. Int J Mol Sci 18:2323

Kumar K, Mosa KA, Chhikara S, Musante C, White JC, Dhankher OP (2014) Two rice plasma membrane intrinsic proteins, OsPIP2;4 and OsPIP2;7, are involved in transport and providing tolerance to boron toxicity. Planta 239:187–198

Laanbroek HJ (1990) Bacterial cycling of minerals that affect plant growth in waterlogged soils: a review. Aquat Bot 38:109–125

Landa P, Dytrych P, Prerostova S, Petrova S, Vankova R, Vanek T (2017) Transcriptomic Response of Arabidopsis thaliana Exposed to CuO Nanoparticles, Bulk Material, and Ionic Copper. Environ Sci Technol 51:10814–10824

Lee J, Park I, Lee ZW, Kim SW, Baek N, Park HS, Park SU, Kwon S, Kim H (2013) Regulation of the major vacuolar Ca2+ transporter genes, by intercellular Ca2+ concentration and abiotic stresses, in tip-burn resistant Brassica oleracea. Mol Biol Rep 40:177–188

Lee SH, Chung GC, Jang JY, Ahn SJ, Zwiazek JJ (2012) Overexpression of PIP2;5 aquaporin alleviates effects of low root temperature on cell hydraulic conductivity and growth in Arabidopsis. Plant Physiol 159:479–488

Lei GJ, Zhu XF, Wang ZW, Dong F, Dong NY, Zheng SJ (2014) Abscisic acid alleviates iron deficiency by promoting root iron reutilization and transport from root to shoot in Arabidopsis. Plant, Cell Environ 37:852–863

Lezhneva L, Kiba T, Feria-Bourrellier AB, Lafouge F, Boutet-Mercey S, Zoufan P, Sakakibara H, Daniel-Vedele F, Krapp A (2014) The Arabidopsis nitrate transporter NRT2.5 plays a role in nitrate acquisition and remobilization in nitrogen-starved plants. Plant J 80:230–241

Li D Di, Ruan XM, Zhang J, Wu YJ, Wang XL, Li XB (2013) Cotton plasma membrane intrinsic protein 2s (PIP2s) selectively interact to regulate their water channel activities and are required for fibre

development. New Phytol 199:695–707

Li D Di, Wu YJ, Ruan XM, Li B, Zhu L, Wang H, Li XB (2009) Expressions of three cotton genes encoding the PIP proteins are regulated in root development and in response to stresses. Plant Cell Rep 28:291–300

Li G, Tillard P, Gojon A, Maurel C (2016) Dual regulation of root hydraulic conductivity and plasma membrane aquaporins by plant nitrate accumulation and high-affinity nitrate transporter NRT2.1. Plant Cell Physiol. https://doi.org/10.1093/pcp/pcw022

Li L, Pan S, Melzer R, Fricke W (2019a) Apoplastic barriers, aquaporin gene expression and root and cell hydraulic conductivity in phosphate-limited sheepgrass plants. Physiol Plant 118–132

Li S, Liu J, An Y, Cao Y, Liu Y, Zhang J, Geng J, Hu T, Yang P (2019b) MsPIP2;2, a novel aquaporin gene from Medicago sativa, confers salt tolerance in transgenic Arabidopsis. Environ Exp Bot 165:39–52

Li Y, Wang X, Zhang H, Wang S, Ye X, Shi L, Xu F, Ding G (2019c) Molecular identification of the phosphate transporter family 1 (PHT1) genes and their expression profiles in response to phosphorus deprivation and other abiotic stresses in Brassica napus. PLoS One 14:e0220374

Lian HL, Yu X, Ye Q, Ding XS, Kitagawa Y, Kwak SS, Su WA, Tang ZC (2004) The role of aquaporin RWC3 in drought avoidance in rice. Plant Cell Physiol 45:481–489

Lin YF, Liang HM, Yang SY, Boch A, Clemens S, Chen CC, Wu JF, Huang JL, Yeh KC (2009) Arabidopsis IRT3 is a zinc-regulated and plasma membrane localized zinc/iron transporter. New Phytol 182:392–404

Little DY, Rao H, Oliva S, Daniel-Vedele F, Krapp A, Malamy JE (2005) The putative high-affinity nitrate transporter NRT2.1 represses lateral root initiation in response to nutritional cues. Proc Natl Acad Sci U S A 102:13693–13698

Liu HY, Sun WN, Su WA, Tang ZC (2006) Co-regulation of water channels and potassium channels in rice. Physiol Plant 128:58–69

Liu LH, Ludewig U, Gassert B, Frommer WB, Von Wirén N (2003) Urea Transport by Nitrogen-Regulated Tonoplast Intrinsic Proteins in Arabidopsis. Plant Physiol 133:1220–1228

Liu X, Zhao X, Zhang L, Lu W, Li X, Xiao K (2013) TaPht1;4, a high-affinity phosphate transporter gene in wheat (Triticum aestivum), plays an important role in plant phosphate acquisition under phosphorus deprivation. Funct Plant Biol 40:329–341

Lohani N, Singh MB, Bhalla PL (2019) High Temperature Susceptibility of Sexual Reproduction in Crop Plants. J Exp Bot 71:555–568

Loqué D, Ludewig U, Yuan L, Von Wirén N (2005) Tonoplast intrinsic proteins AtTIP2;1 and AtTIP2;3 facilitate NH 3 transport into the vacuole. Plant Physiol. https://doi.org/10.1104/pp.104.051268

Lovelock CE, Ball MC, Choat B, Engelbrecht BMJ, Holbrook NM, Feller IC (2006) Linking

physiological processes with mangrove forest structure: Phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf Rhizophora mangle. Plant, Cell Environ 29:793–802

Ma JF, Yamaji N, Mitani N, Tamai K, Konishi S, Fujiwara T, Katsuhara M, Yano M (2007) An efflux transporter of silicon in rice. Nature 448:209–212

Maathuis FJM, Diatloff E (2013) Roles and functions of plant mineral nutrients. Methods Mol Biol 953:1–21

Maathuis FJM, Filatov V, Herzyk P, Krijger GC, Axelsen KB, Chen S, Green BJ, Li Y, Madagan KL, Sánchez-Fernández R, Forde BG, Palmgren MG, Rea PA, Williams LE, Sanders D, Amtmann A (2003) Transcriptome analysis of root transporters reveals participation of multiple gene families in the response to cation stress. Plant J 35:675–692

Mahdieh M, Mostajeran A, Horie T, Katsuhara M (2008) Drought stress alters water relations and expression of PIP-type aquaporin genes in Nicotiana tabacum plants. Plant Cell Physiol 49:801–813

Marschner P (2011) Marschner's Mineral Nutrition of Higher Plants: Third Edition

Martinez-Ballesta M del C, Carvajal M (2014) New challenges in plant aquaporin biotechnology. Plant Sci 217–218:71–77

Martínez-Ballesta M del C, Carvajal M (2016) Mutual interactions between aquaporins and membrane components. Front Plant Sci 7:1322

Martínez-Ballesta MC, Cabañero FJ, Maurel C, Olmos E, Carvajal M (2008) Nutritional Calcium as the regulator of the aquaporin activity in plants grown under salinity. Planta 228:15–25

Martínez-Ballesta MDC, Silva C, López-Berenguer C, Cabañero FJ, Carvajal M (2006) Plant aquaporins: New perspectives on water and nutrient uptake in saline environment. Plant Biol. 8:535–546

Martins CDPS, Pedrosa AM, Du D, Gonçalves LP, Yu Q, Gmitter FG, Costa MGC (2015) Genome-wide characterization and expression analysis of major intrinsic proteins during abiotic and biotic stresses in sweet orange (Citrus sinensis L. Osb.). PLoS One 10:e0138786

Martre P, Morillon R, Barrieu F, North GB, Nobel PS, Chrispeels MJ (2002) Plasma membrane aquaporins play a significant role during recovery from water deficit. Plant Physiol 130:2010–2110

Matsumoto T, Lian HL, Su WA, Tanaka D, Liu CW, Iwasaki I, Kitagawa Y (2009) Role of the aquaporin PIP1 subfamily in the chilling tolerance of rice. Plant Cell Physiol 50:216–229

Mendel RR, Kruse T (2012) Cell biology of molybdenum in plants and humans. Biochim Biophys Acta - Mol Cell Res 30:1787–1797

Mengutay M, Ceylan Y, Kutman UB, Cakmak I (2013) Adequate magnesium nutrition mitigates

adverse effects of heat stress on maize and wheat. Plant Soil 368:57–72

Mikula K, Izydorczyk G, Skrzypczak D, Mironiuk M, Moustakas K, Witek-Krowiak A, Chojnacka K (2020) Controlled release micronutrient fertilizers for precision agriculture – A review. Sci Total Environ 712:e136365

Milner MJ, Seamon J, Craft E, Kochian L V. (2013) Transport properties of members of the ZIP family in plants and their role in Zn and Mn homeostasis. J Exp Bot 97:12356–12360

Miwa K, Fujiwara T (2010) Boron transport in plants: Co-ordinated regulation of transporters. Ann Bot 135:588–600

Molina C, Rotter B, Horres R, Udupa SM, Besser B, Bellarmino L, Baum M, Matsumura H, Terauchi R, Kahl G, Winter P (2008) SuperSAGE: The drought stress-responsive transcriptome of chickpea roots. BMC Genomics 9:553

Munns R (2002) Comparative physiology of salt and water stress. Plant, Cell Environ 25:239–250

Munns R, Tester M (2008) Mechanisms of Salinity Tolerance. Annu Rev Plant Biol 59:651–681

Murai-Hatano M, Kuwagata T, Sakurai J, Nonami H, Ahamed A, Nagasuga K, Matsunami T, Fukushi K, Maeshima M, Okada M (2008) Effect of low root temperature on hydraulic conductivity of rice plants and the possible role of aquaporins. Plant Cell Physiol 49:1294–1305

Muries B, Faize M, Carvajal M, Martínez-Ballesta MDC (2011) Identification and differential induction of the expression of aquaporins by salinity in broccoli plants. Mol Biosyst. https://doi.org/10.1039/c0mb00285b

Noronha H, Araújo D, Conde C, Martins AP, Soveral G, Chaumont F, Delrot S, Gerós H (2016) The grapevine uncharacterized intrinsic protein 1 (VvXIP1) is regulated by drought stress and transports glycerol, hydrogen peroxide, heavy metals but not water. PLoS One 11:e0160976

Oomen RJFJ, Wu J, Lelièvre F, Blanchet S, Richaud P, Barbier-Brygoo H, Aarts MGM, Thomine S (2009) Functional characterization of NRAMP3 and NRAMP4 from the metal hyperaccumulator Thlaspi caerulescens. New Phytol 181:637–650

Osakabe Y, Arinaga N, Umezawa T, Katsura S, Nagamachi K, Tanaka H, Ohiraki H, Yamada K, Seo SU, Abo M, Yoshimura E, Shinozaki K, Yamaguchi-Shinozaki K (2013) Osmotic stress responses and plant growth controlled by potassium transporters in Arabidopsis. Plant Cell 25:609–624

Pandey C, Khan E, Panthri M, Tripathi RD, Gupta M (2016) Impact of silicon on Indian mustard (Brassica juncea L.) root traits by regulating growth parameters, cellular antioxidants and stress modulators under arsenic stress. Plant Physiol Biochem 104:216–225

Pandey C, Raghuram B, Sinha AK, Gupta M (2015) MiRNA plays a role in the antagonistic effect of selenium on arsenic stress in rice seedlings. Metallomics 7:857–866

Pang Y, Li L, Ren F, Lu P, Wei P, Cai J, Xin L, Zhang J, Chen J, Wang X (2010) Overexpression of the tonoplast aquaporin AtTIP5;1 conferred tolerance to boron toxicity in Arabidopsis. J Genet

Genomics 37:389–397

Patankar H V., Al-Harrasi I, Al-Yahyai R, Yaish MW (2019) Functional characterization of date palm aquaporin gene pdpip1;2 confers drought and salinity tolerance to yeast and arabidopsis. Genes (Basel) 10:390

Peng Y, Lin W, Cai W, Arora R (2007) Overexpression of a Panax ginseng tonoplast aquaporin alters salt tolerance, drought tolerance and cold acclimation ability in transgenic Arabidopsis plants. Planta 226:729–740

Pessarakli M (2015) Plant Responses under Environmental Stress Conditions. Adv Plants Agric Res 2:

Pittman JK, Hirschi KD (2016) CAX-ing a wide net: Cation/H(+) transporters in metal remediation and abiotic stress signalling. Plant Biol (Stuttg) 18:741–749

Poschenrieder C, Busoms S, Barceló J (2019) How plants handle trivalent (+3) elements. Int J Mol Sci 20:3984

Pou A, Jeanguenin L, Milhiet T, Batoko H, Chaumont F, Hachez C (2016) Salinity-mediated transcriptional and post-translational regulation of the Arabidopsis aquaporin PIP2;7. Plant Mol Biol 92:731–744

Printz B, Lutts S, Hausman JF, Sergeant K (2016) Copper trafficking in plants and its implication on cell wall dynamics. Front Plant Sci 7:601

Qin L, Guo Y, Chen L, Liang R, Gu M, Xu G, Zhao J, Walk T, Liao H (2012) Functional Characterization of 14 Pht1 Family Genes in Yeast and Their Expressions in Response to Nutrient Starvation in Soybean. PLoS One 7:

Qudeimat E, Faltusz AMC, Wheeler G, Lang D, Holtorf H, Brownlee C, Reski R, Frank W (2011) Erratum: A P IIB-type Ca 2+-ATPase is essential for stress adaptation in Physcomitrella patens (Proceedings of the National Academy of Sciences of the United States of America (2008) 105, 49 (19555-19560) DOI: 10.1073/pnas.0800864105). Proc Natl Acad Sci U S A 108:18566

Ranganathan K, El Kayal W, Cooke JEK, Zwiazek JJ (2016) Responses of hybrid aspen over-expressing a PIP2;5 aquaporin to low root temperature. J Plant Physiol 192:98–104

Reid R, Fitzpatrick K (2009) Influence of leaf tolerance mechanisms and rain on boron toxicity in barley and wheat. Plant Physiol 151:413–420

Remans T, Nacry P, Pervent M, Girin T, Tillard P, Lepetit M, Gojon A (2006) A central role for the nitrate transporter NRT2.1 in the integrated morphological and physiological responses of the root system to nitrogen limitation in Arabidopsis. Plant Physiol 140:909–921

Ricachenevsky FK, Menguer PK, Sperotto RA, Williams LE, Fett JP (2013) Roles of plant metal tolerance proteins (MTP) in metal storage and potential use in biofortification strategies. Front Plant Sci 4:144

Rogers EE, Eide DJ, Guerinot M Lou (2000) Altered selectivity in an Arabidopsis metal transporter.

Proc Natl Acad Sci U S A 97:12356–12360

Ropokis A, Ntatsi G, Kittas C, Katsoulas N, Savvas D (2019) Effects of temperature and grafting on yield, nutrient uptake, and water use efficiency of a hydroponic sweet pepper crop. Agronomy 9:110

Ruiz-Lozano JM, Del Mar Alguacil M, Bárzana G, Vernieri P, Aroca R (2009) Exogenous ABA accentuates the differences in root hydraulic properties between mycorrhizal and non mycorrhizal maize plants through regulation of PIP aquaporins. Plant Mol Biol. https://doi.org/10.1007/s11103-009-9492-z

Sade N, Vinocur BJ, Diber A, Shatil A, Ronen G, Nissan H, Wallach R, Karchi H, Moshelion M (2009) Improving plant stress tolerance and yield production: Is the tonoplast aquaporin SlTIP2;2 a key to isohydric to anisohydric conversion? New Phytol 181:651–661

Sahr T, Voigt G, Paretzke HG, Schramel P, Ernst D (2005) Caesium-affected gene expression in Arabidopsis thaliana. New Phytol 165:747–754

Schachtman DP, Reid RJ, Ayling SM (1998) Phosphorus Uptake by Plants: From Soil to Cell. Plant Physiol. 116:447–453

Schnurbusch T, Hayes J, Hrmova M, Baumann U, Ramesh SA, Tyerman SD, Langridge P, Sutton T (2010) Boron toxicity tolerance in barley through reduced expression of the multifunctional aquaporin HvNIP2;1. Plant Physiol 153:1706–1715

Shangguan ZP, Lei TW, Shao MA, Xue QW (2005) Effects of phosphorus nutrient on the hydraulic conductivity of sorghum (Sorghum vulgare Pers.) seedling roots under water deficiency. J Integr Plant Biol 47:421–427

Sharma A, Shankhdhar D, Shankhdhar SC (2017) The role of calcium in plant signal transduction under macronutrient deficiency stress. In: Plant Macronutrient Use Efficiency: Molecular and Genomic Perspectives in Crop Plants. Elsevier Inc., pp 181–196

Sharma C (2006) Plant Micronutrients. Science Publishers

Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive Oxygen Species, Oxidative Damage, and Antioxidative Defense Mechanism in Plants under Stressful Conditions. J Bot 2012:

Shaul O (2002) Magnesium transport and function in plants: The tip of the iceberg. BioMetals 15:309–323

Siefritz F, Tyree MT, Lovisolo C, Schubert A, Kaldenhoff R (2002) PIP1 plasma membrane aquaporins in tobacco: From cellular effects to function in plants. Plant Cell 14:869–876

Singh A, Kanwar P, Yadav AK, Mishra M, Jha SK, Baranwal V, Pandey A, Kapoor S, Tyagi AK, Pandey GK (2014) Genome-wide expressional and functional analysis of calcium transport elements during abiotic stress and development in rice. FEBS J 281:894–915

Socha AL, Guerinot M Lou (2014) Mn-euvering manganese: The role of transporter gene family

members in manganese uptake and mobilization in plants. Front Plant Sci 5:106

Sreedharan S, Shekhawat UKS, Ganapathi TR (2013) Transgenic banana plants overexpressing a native plasma membrane aquaporin MusaPIP1;2 display high tolerance levels to different abiotic stresses. Plant Biotechnol J 11:942–952

Sun J, Li S, Wang S, Xiao Z, Zhang Z, Li J, Luo F, Li N (2019) Characterization of the main magnesium transporters mediating different Mg translocation from root to shoot between Mg-tolerant and Mg-sensitive Brassica napus cultivars under magnesium deficiency stress. Plant Soil 445:453–468

Sun T, Li M, Shao Y, Yu L, Ma F (2017) Comprehensive genomic identification and expression analysis of the phosphate transporter (PHT) gene family in apple. Front Plant Sci 8:426

Sun X, Kay AD, Kang H, Small GE, Liu G, Zhou X, Yin S, Liu C (2013) Correlated Biogeographic Variation of Magnesium across Trophic Levels in a Terrestrial Food Chain. PLoS One 8:e78444

Šurbanovski N, Sargent DJ, Else MA, Simpson DW, Zhang H, Grant OM (2013) Expression of Fragaria vesca PIP Aquaporins in Response to Drought Stress: PIP Down-Regulation Correlates with the Decline in Substrate Moisture Content. PLoS One 8:e74945

Sutka M, Li G, Boudet J, Boursiac Y, Doumas P, Maurel C (2011) Natural variation of root hydraulics in Arabidopsis grown in normal and salt-stressed conditions. Plant Physiol 155:1264–1276

Sutton T, Baumann U, Hayes J, Collins NC, Shi BJ, Schnurbusch T, Hay A, Mayo G, Pallotta M, Tester M, Langridge P (2007) Boron-toxicity tolerance in barley arising from efflux transporter amplification. Science (80-) 318:1446–1449

Takano J, Wada M, Ludewig U, Schaaf G, Von Wirén N, Fujiwara T (2006) The Arabidopsis major intrinsic protein NIP5;1 is essential for efficient boron uptake and plant development under boron limitation. Plant Cell 18:1498–1509

Tanaka M, Wallace IS, Takano J, Roberts DM, Fujiwara T (2008) NIP6;1 is a boric acid channel for preferential transport of boron to growing shoot tissues in Arabidopsis. Plant Cell 20:2860–2875

Taochy C, Gaillard I, Ipotesi E, Oomen R, Leonhardt N, Zimmermann S, Peltier JB, Szponarski W, Simonneau T, Sentenac H, Gibrat R, Boyer JC (2015) The Arabidopsis root stele transporter NPF2.3 contributes to nitrate translocation to shoots under salt stress. Plant J 83:466–479

Tazawa M, Sutou E, Shibasaka M (2001) Onion root water transport sensitive to water channel and K+ channel inhibitors. Plant Cell Physiol 42:28–36

Thomine S, Lelièvre F, Debarbieux E, Schroeder JI, Barbier-Brygoo H (2003) AtNRAMP3, a multispecific vacuolar metal transporter involved in plant responses to iron deficiency. Plant J 34:685–695

Tian S, Wang X, Li P, Wang H, Ji H, Xie J, Qiu Q, Shen D, Dong H (2016) Plant aquaporin AtPIP1;4 links apoplastic H2O2 induction to disease immunity pathways. Plant Physiol 171:1635–1650

Törnroth-Horsefield S, Wang Y, Hedfalk K, Johanson U, Karlsson M, Tajkhorshid E, Neutze R,

Kjellbom P (2006) Structural mechanism of plant aquaporin gating. Nature 587:989–993

Tyerman SD, Wignes JA, Kaiser BN (2017) Root hydraulic and aquaporin responses to N availability. In: Plant Aquaporins. Signaling and Communication in Plants. Springer, Cham, pp 207–236

Uehlein N, Sperling H, Heckwolf M, Kaldenhoff R (2012) The Arabidopsis aquaporin PIP1;2 rules cellular CO 2 uptake. Plant, Cell Environ 35:1077–1083

USDA-ARS (2008) Research Databases. Bibliography on Salt Tolerance. Georg E Brown, Jr Salin Lab US Dep Agric, Agric Res Serv Riverside, CA

Vandeleur RK, Mayo G, Shelden MC, Gilliham M, Kaiser BN, Tyerman SD (2009) The role of plasma membrane intrinsic protein aquaporins in water transport through roots: Diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. Plant Physiol 149:445–460

Vatansever R, Ozyigit II, Filiz E (2017) Essential and Beneficial Trace Elements in Plants, and Their Transport in Roots: a Review. Appl Biochem Biotechnol 181:464–482

Wallace IS, Roberts DM (2005) Distinct transport selectivity of two structural subclasses of the nodulin-like intrinsic protein family of plant aquaglyceroporin channel. Biochemistry 44:16826–16834

Wang M, Ding L, Gao L, Li Y, Shen Q, Guo S (2016) The interactions of aquaporins and mineral nutrients in higher plants. Int J Mol Sci 17:

Wang MY, Siddiqi MY, Ruth TJ, Glass ADM (1993) Ammonium uptake by rice roots: II. Kinetics of 13NH4+ influx across the plasmalemma. Plant Physiol 103:1259–1267

Wang N, Qi H, Qiao W, Shi J, Xu Q, Zhou H, Yan G, Huang Q (2017) Cotton (Gossypium hirsutum L.) genotypes with contrasting K+/Na+ ion homeostasis: implications for salinity tolerance. Acta Physiol Plant 39:77

Wang P, Calvo-Polanco M, Reyt G, Barberon M, Champeyroux C, Santoni V, Maurel C, Franke RB, Ljung K, Novak O, Geldner N, Boursiac Y, Salt DE (2019a) Surveillance of cell wall diffusion barrier integrity modulates water and solute transport in plants. Sci Rep 9:4227

Wang R, Okamoto M, Xing X, Crawford NM (2003) Microarray analysis of the nitrate response in Arabidopsis roots and shoots reveals over 1,000 rapidly responding genes and new linkages to glucose, trehalose-6-phosphate, iron, and sulfate metabolism. Plant Physiol 132:556–567

Wang WH, Köhler B, Cao FQ, Liu LH (2008) Molecular and physiological aspects of urea transport in higher plants. Plant Sci. 175:467–477

Wang X, Gao F, Bing J, Sun W, Feng X, Ma X, Zhou Y, Zhang G (2019b) Overexpression of the Jojoba aquaporin gene, ScPIP1, enhances drought and salt tolerance in transgenic Arabidopsis. Int J Mol Sci 20:153

Warren CR (2009) Why does temperature affect relative uptake rates of nitrate, ammonium and glycine: A test with Eucalyptus pauciflora. Soil Biol Biochem 41:778–784

Weaver CD, Roberts DM (1992) Determination of the Site of Phosphorylation of Nodulin 26 by the Calcium-Dependent Protein Kinase from Soybean Nodules. Biochemistry 31:8954–8959

White PJ (2001) The pathways of calcium movement to the xylem. J Exp Bot 52:891–899

White PJ, Bowen HC, Demidchik V, Nichols C, Davies JM (2002) Genes for calcium-permeable channels in the plasma membrane of plant root cells. Biochim Biophys Acta - Biomembr 1564:299–309

White PJ, Broadley MR (2003) Calcium in plants. Ann Bot 92:487–511

Williams LE, Pittman JK, Hall JL (2000) Emerging mechanisms for heavy metal transport in plants. Biochim. Biophys. Acta - Biomembr.

Xu Y, Hu W, Liu J, Zhang J, Jia C, Miao H, Xu B, Jin Z (2014) A banana aquaporin gene, MaPIP1;1, is involved in tolerance to drought and salt stresses. BMC Plant Biol 14:59

Xu Y, Hu W, Liu J, Song S, Hou X, Jia C, Li J, Miao H, Wang Z, Tie W, Xu B, Jin Z (2020) An aquaporin gene MaPIP2-7 is involved in tolerance to drought, cold and salt stresses in transgenic banana (Musa acuminata L.). Plant Physiol Biochem 147:66–76

Yang H, Menz J, Haüssermann I, Benz M, Fujiwara T, Ludewig U (2015) High and Low Affinity Urea Root Uptake: Involvement of NIP5;1. Plant Cell Physiol 56:1588–1597

Yao J, Shi WM, Xu WF (2008) Effects of salt stress on expression of nitrate transporter and assimilation-related genes in tomato roots. Russ J Plant Physiol 55:232–240

Yool AJ, Weinstein AM (2002) New roles for old holes: Ion channel function in aquaporin-1. News Physiol Sci 17:68–72

Yu Q, Hu Y, Li J, Wu Q, Lin Z (2005) Sense and antisense expression of plasma membrane aquaporin BnPIP1 from Brassica napus in tobacco and its effects on plant drought resistance. Plant Sci 169:647e656

Yuan L, Loqué D, Kojima S, Rauch S, Ishiyama K, Inoue E, Takahashi H, Von Wiréna N (2007) The organization of high-affinity ammonium uptake in Arabidopsis roots depends on the spatial arrangement and biochemical properties of AMT1-type transporters. Plant Cell 19:2636–2652

Yue X, Zhao X, Fei Y, Zhang X (2012) Correlation of aquaporins and transmembrane solute transporters revealed by genome-wide analysis in developing maize leaf. Comp Funct Genomics 2012:

Zaman M, Shahid SA, Heng L, Shahid SA, Zaman M, Heng L (2018) Soil Salinity: Historical Perspectives and a World Overview of the Problem. In: Guideline for Salinity Assessment, Mitigation and Adaptation Using Nuclear and Related Techniques. pp 43–53

Zhang C, Meng S, Li M, Zhao Z (2016a) Genomic identification and expression analysis of the phosphate transporter gene family in poplar. Front Plant Sci 7:1398

Zhang L, Yan J, Vatamaniuk OK, Du X (2016b) CsNIP2;1 is a plasma membrane transporter from

cucumis sativus that facilitates urea uptake when expressed in saccharomyces cerevisiae and arabidopsis thaliana. Plant Cell Physiol 57:616–629

Zhang M, Smith JAC, Harberd NP, Jiang C (2016c) The regulatory roles of ethylene and reactive oxygen species (ROS) in plant salt stress responses. Plant Mol Biol 91:651–659

Zhang Y, Liang Y, Zhao X, Jin X, Hou L, Shi Y, Ahammed GJ (2019) Silicon compensates phosphorus deficit-induced growth inhibition by improving photosynthetic capacity, antioxidant potential, and nutrient homeostasis in tomato. Agronomy 9:733

Zhang Y, Xu YH, Yi HY, Gong JM (2012) Vacuolar membrane transporters OsVIT1 and OsVIT2 modulate iron translocation between flag leaves and seeds in rice. Plant J 72:400–410

Zhao J, Cheng NH, Motes CM, Blancaflor EB, Moore M, Gonzales N, Padmanaban S, Sze H, Ward JM, Hirschi KD (2008) AtCHX13 is a plasma membrane K+ transporter. Plant Physiol 148:796–807

Zhuang L, Liu M, Yuan X, Yang Z, Huang B (2015) Physiological effects of aquaporin in regulating drought tolerance through overexpressing of festuca arundinacea aquaporin gene FaPIP2;1. J Am Soc Hortic Sci 140:404–412

Zhuo C, Wang T, Guo Z, Lu S (2016) Overexpression of MfPIP2-7 from Medicago falcata promotes cold tolerance and growth under NO3- deficiency in transgenic tobacco plants. BMC Plant Biol 16:138

Zwiazek JJ, Xu H, Tan X, Navarro-Ródenas A, Morte A (2017) Significance of oxygen transport through aquaporins. Sci Rep 12:40411
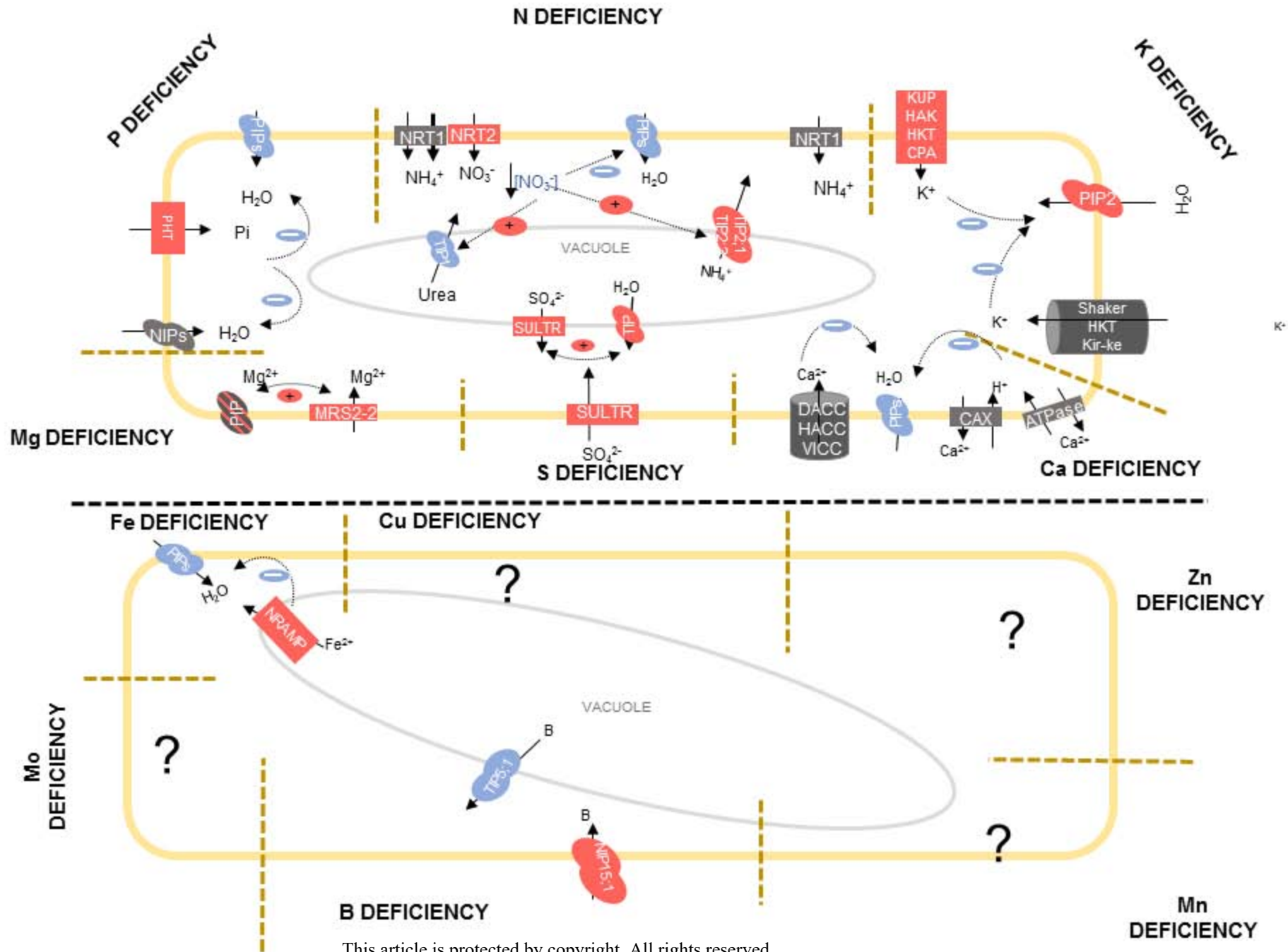
Figure legends

Fig. 1. Scheme of the interregulation of aquaporins and nutrient transporters under nutrients deficiency. Plasma membrane aquaporins PIPs reduced the expressions in response to N deprivation in coordination to NRT transporters. Several TIPs, participate in NH_4^+ an urea transport under N deficiency. Low-K conditions reduced expression of PIP2. A coordinated response to Ca deficiency reducing aquaporin and Ca^{2+} transporters gene expression is observed. Under S starvation some SULTR transporters exhibited the same expression patterns as some TIPs. Under Mg deficiency, some MRS transporter has the same expression patterns as some PIPs. Low P availability showed a decrease in the gene expression of PHT, PIPs and NIPs. Under under Fe deficiency, the inhibition of NRAMP transporters showed is related to some PIPs abundance. Under B deficiency some NIPs and TIPs participate in B transport. The interregulation of Cu, Zn, Mn and Mo transporters and aquaporins under Cu, Zn, Mn and Mo deficiency is unknown.

Fig. 2. Scheme of the interregulation of aquaporins and nutrient transporters under cold stress in order
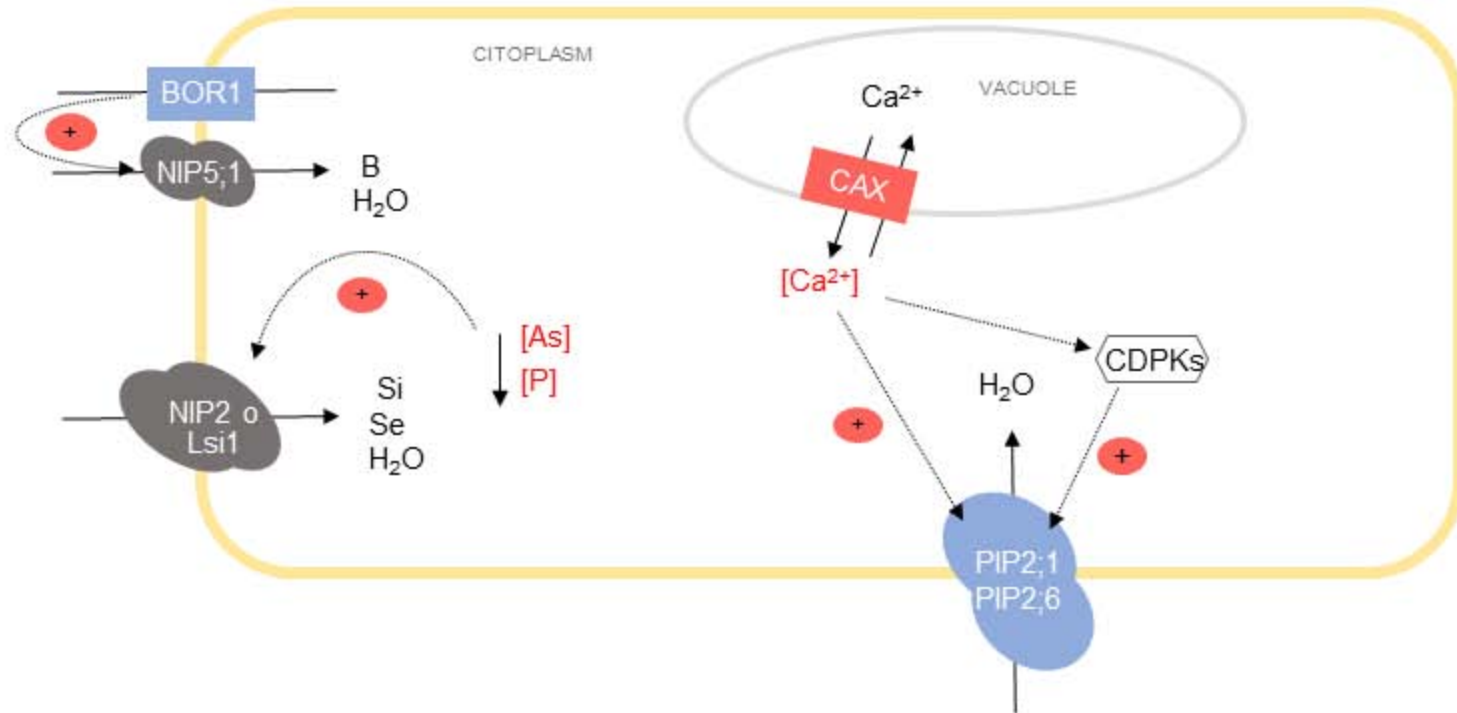
to provide higher tolerance. The regulation of aquaporins PIP2;1 and PIP2;6 in the response to cold stress, through a calcium-dependent protein kinase, OsCPK17 is related to the vacuolar expression of a Ca^{2+} transporter like CAX1. The decrease in the protein level of BOR1 (a B transporter) is replaced by the aquaporin NIP5;1 for maintaining the B levels. The P deficit and low As concentrations that appeared under cold stress can be compensated by higher concentrations of Si and Se transported through the aquaporin NIP2 or Lsi1.

Fig. 3. Scheme of the interregulation of aquaporins and nutrient transporters under drough stress in order to provide higher tolerance. NO_3^- and NH_4^+ are signaling factors for PIP expression. DUR3, high-affinity urea transporter, and PIP, NIP, and TIP identified as low-affinity transporters, up-regulate TIP. Pi transporter is related positively with PIP. Transmembrane channels for K^+ and PIPs are coordinately regulated. Ca^{2+} transporters regulate positively PIPs, TIPs, and NIPs isoforms.
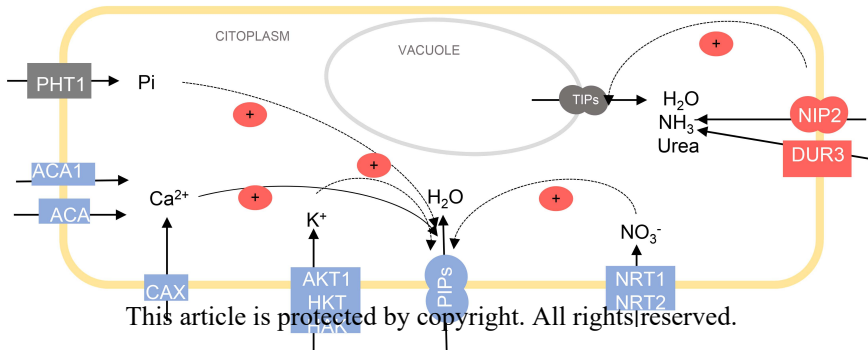
Fig. 4. Scheme of the interregulation of aquaporins and nutrient transporters under salinity stress in order to provide higher tolerance. Over-expressed a *NIP* aquaporin, and suppression of *SOS2* provide higher tolerance. SOS2 regulate negatively CAX1 reducing cytosolic Ca^{2+} and regulating negatively PIPs aquaporins. But NIPs could reduce cytosolic regulating positively PIPs. Interaction of NRT2;1 and PIP aquaporins is positively correlated.
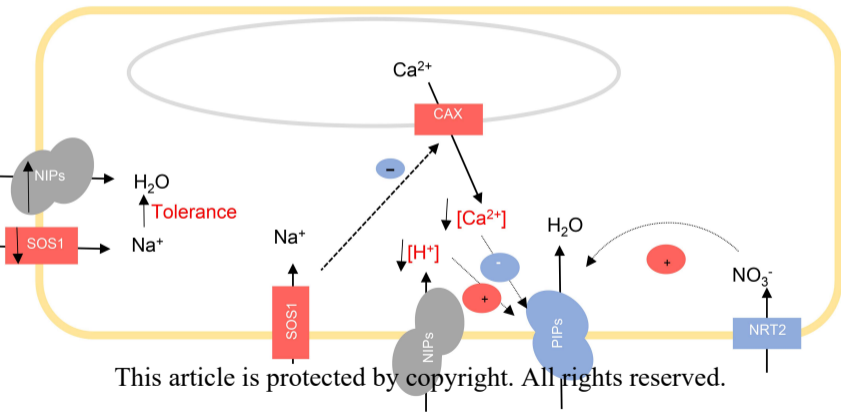
N DEFICIENCY

P DEFICIENCY

K DEFICIENCY

Mg DEFICIENCY

S DEFICIENCY

Ca DEFICIENCY

Fe DEFICIENCY

Cu DEFICIENCY

Zn DEFICIENCY

Mo DEFICIENCY

B DEFICIENCY

Mn DEFICIENCY

COLD STRESS

DROUGHT STRESS

CITOPLASM

VACUOLE

PHT1 → Pi

ACA1 →

ACA →

Ca²⁺

CAX

K⁺

AKT1
HKT

PIPs

H₂O

NO₃⁻

NRT1
NRT2

TIPs → H₂O
NH₃
Urea

NIP2

DUR3

SALINITY STRESS