

REVIEW PAPER

Regulation of root water uptake under abiotic stress conditions

Ricardo Aroca*, Rosa Porcel and Juan Manuel Ruiz-Lozano

Departamento de Microbiología del Suelo y Sistemas Simbióticos, Estación Experimental del Zaidín (CSIC), Profesor Albareda 1, 18008, Granada, Spain

* To whom correspondence should be addressed. E-mail: raroaca@eez.csic.es

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Abstract

A common effect of several abiotic stresses is to cause tissue dehydration. Such dehydration is caused by the imbalance between root water uptake and leaf transpiration. Under some specific stress conditions, regulation of root water uptake is more crucial to overcome stress injury than regulation of leaf transpiration. This review first describes present knowledge about how water is taken up by roots and then discusses how specific stress situations such as drought, salinity, low temperature, and flooding modify root water uptake. The rate of root water uptake of a given plant is the result of its root hydraulic characteristics, which are ultimately regulated by aquaporin activity and, to some extent, by suberin deposition. Present knowledge about the effects of different stresses on these features is also summarized. Finally, current findings regarding how molecular signals such as the plant hormones abscisic acid, ethylene, and salicylic acid, and how reactive oxygen species may modulate the final response of root water uptake under stress conditions are discussed.

Key words: Abiotic stresses, abscisic acid, aquaporins, ethylene, reactive oxygen species, root water uptake, salicylic acid, suberin.

Introduction

Plants are sessile organisms that cannot escape from environmental constraints and, as a result, they have evolved numerous adaptive responses to cope with environmental stresses. Most environmental stresses share common effects and responses such as a reduction in growth and photosynthesis, oxidative damage, hormonal changes, and the accumulation of numerous stress-related proteins. These changes are usually the result of tissue dehydration (Kacperska, 2004; Dobra *et al.*, 2010). Tissue dehydration occurs when there is an imbalance between root water uptake and leaf transpiration (Aroca *et al.*, 2001; Jackson *et al.*, 2003). When leaves begin to dehydrate plants generally start closing their stomata; however, under some environmental situations or in specific plant genotypes, modification of root water uptake capacity plays a more important role compared with stomatal closure in avoiding stress-induced growth reduction (Matsuo *et al.*, 2009). Water deficit occurs in tissues under drought, low temperature, heat, salt, or flooding

stress conditions (Zhang and Zhang, 1994; Aroca *et al.*, 2001, 2007; Wahid and Close, 2007). Under some environmental conditions, dehydration is the first signal that induces the plant to respond (Jia *et al.*, 2002; Christmann *et al.*, 2007), and the importance of the hydration state of tissues in the response of the plant to different stresses is well supported by experimental evidence (Aroca *et al.*, 2001; Bouchabke-Coussa *et al.*, 2008; Matsuo *et al.*, 2009).

The importance of root water uptake capacity in coping with several abiotic stress conditions is supported by the work of Aroca *et al.* (2001) who found that two maize genotypes differing in chilling sensitivity also differed in the response of their root water uptake rate to chilling stress. Hence, while the tolerant genotype kept its leaf transpiration and root water uptake rates unchanged during chilling periods, the sensitive genotype became dehydrated because it decreased first its root water uptake rate and then its leaf transpiration. Also, Matsuo *et al.* (2009), comparing three

rice genotypes, found a good correlation between root water uptake capacity (estimated as root hydraulic conductivity, *L*) and shoot dry weight under water-limited conditions. In the same way, Hattori *et al.* (2008) found that the ameliorative effect of silicon application in the response of sorghum plants to osmotic stress was mainly caused by an improvement of root water uptake capacity, avoiding water imbalance caused by the osmotic stress imposed. The studies cited above are examples that support the importance of root water uptake capacity to overcome abiotic stress-induced tissue dehydration.

The present review aims to highlight recent advances in our knowledge of how several abiotic stresses, namely drought, salt, low temperature, and flooding, modulate the root water uptake capacity of vascular plants. First a brief description of the basic concepts of root water uptake will be presented, followed by the specific effects of each particular stress on root water uptake properties. Finally, the possible involvement of some regulatory mechanisms common to all of these stresses will be postulated. It is intended that this review will open up new avenues in the research field of root water uptake properties.

Root water uptake concepts

Two main forces regulate the root water uptake rate, namely osmotic and hydrostatic forces. Hydrostatic force is generated by the transpiration stream, whereas osmotic force is generated by the root pressure (active transport of solutes or biosynthesis of new osmolytes). Root water transport is divided into radial and axial transport. The axial transport consists of the water moving along the xylem vessels to aerial parts, and it does not contribute in a major way to the resistance of water transport through the whole plant (Doussan *et al.*, 1998; Knipfer and Fricke, 2011). In woody plants, this axial transport can be an important determinant of resistance because of cavitation events (Dalla-Salda *et al.*, 2009). On the other hand, radial water flow from the soil solution to the root xylem vessels has high resistance to root water transport and involves three dynamically exchangeable paths (Steudle and Peterson, 1998). The apoplastic path comprises water moving through the pores between the fibrils of the cell wall and through the intercellular spaces. The symplastic path consists of water moving through the cytoplasm and through plasmodesmata between cells. Finally, the transmembrane path comprises water moving through the cytoplasm and the vacuoles crossing the plasma and vacuolar membranes. Since empirically the symplastic and transcellular paths cannot be discriminated, the sum of these two paths is called the cell-to-cell path (Steudle and Peterson, 1998).

It was assumed that under transpiring conditions the main route for radial water transport was the apoplastic path, and under conditions where transpiration is reduced, the main route would be the cell-to-cell path (Steudle and Peterson, 1998; Javot and Maurel, 2002). However, more recently, Knipfer and Fricke (2010, 2011) and Fritz and

Ehwald (2011) demonstrated that in some species and under some conditions water flowing by the cell-to-cell path could account for almost the whole radial root water transport even under transpiring conditions. However, it is possible that the above-mentioned findings only apply to barley (*Hordeum vulgare*) as previously found by Steudle and Jeschke (1983). Obviously, although more research is needed to clarify the predominant water movement path under various environmental conditions, these recent results highlight the importance of the cell-to-cell path in the overall radial root water transport. However, the role of root morphology and anatomy in the overall root water transport capacity cannot be underestimated (Bramley *et al.*, 2009).

Independently of the radial water pathway that predominates under specific environmental conditions, the role of aquaporins in root water uptake has been abundantly documented (Kaldenhoff *et al.*, 1998; Javot *et al.*, 2003; Postaire *et al.*, 2010). Aquaporins first described in plants by Maurel *et al.* (1993) are membrane intrinsic proteins found in all living organisms (Agre *et al.*, 1993) that facilitate the passage of water by forming a proteinaceous pore in the membrane. Osmotic gradients drive water transport through aquaporins. In plants, aquaporins are divided into five families: PIPs, plasma membrane intrinsic proteins; TIPs, tonoplast intrinsic proteins; NIPs, nodulin-26-like intrinsic proteins; SIPs, small and basic intrinsic proteins; and XIPs, uncharacterized intrinsic proteins. The number of aquaporin genes present in a plant species is very high, ranging from 30 to >70 (Maurel *et al.*, 2008; Park *et al.*, 2010). At the same time, although aquaporins were first characterized as water channels, it has now been demonstrated that some specific plant aquaporins also transport other small neutral solutes such as glycerol or ammonia, nutrients such as boron or silicon, gases such as CO₂, or metalloids such as arsenic (Bienert *et al.*, 2008; Tanaka *et al.*, 2008; Maurel *et al.*, 2009). Moreover, the localization of each aquaporin protein inside the plant cells varies among cell membranes. At the same time, the membrane aquaporin location in the cell is dynamic since some transport of them from internal membranes to the plasma membrane has been found (Zelazny *et al.*, 2007; Wudick *et al.*, 2009). For recent reviews about cellular functionality and localization of plant aquaporins, see Katsuhara *et al.* (2008), Maurel *et al.* (2008, 2009), and Wudick *et al.* (2009).

To estimate the root water uptake capacity of a single root or of the whole root system, *L* measurements are undertaken, and a direct correlation between *L* values and root water uptake rates has been observed (Nobel and Alm, 1993; Gallardo *et al.*, 1996; Nardini and Pitt, 1999; Li *et al.*, 2005). In this sense, the contribution of aquaporins to *L* values has been tested by several approaches. In the 1990s, the involvement of aquaporins in *L* regulation was assayed by the inhibition of *L* by mercurial reagents (Maggio and Joly, 1995; Carvajal *et al.*, 1996), since several plant aquaporins have a cysteine residue sensitive to Hg (Daniels *et al.*, 1996). However, not all plant aquaporins are sensitive to Hg (Daniels *et al.*, 1994), and Hg could have other

secondary effects as well (Gaspar *et al.*, 2001). More conclusive approaches involved the use of transgenic plants in which the expression of some aquaporins was inhibited. Siefritz *et al.* (2002) and Postaire *et al.* (2010) found that a specific plasma membrane aquaporin (PIP) of tobacco and *Arabidopsis*, respectively, regulated L under hydrostatic forces. On the other hand, again Siefritz *et al.* (2002) and Javot *et al.* (2003) found that a specific PIP of tobacco and *Arabidopsis*, respectively, regulated L under osmotic forces. These findings clearly support the involvement of PIP aquaporins in the regulation of L under both osmotic and hydrostatic forces and, therefore, their involvement in the whole root water uptake rate.

Root water uptake under drought conditions

Plants experience drought stress when a fixed percentage of volumetric soil water content is not replenished by natural rainfall or irrigation (Bréda *et al.*, 1995; Chen *et al.*, 2010). From this point onward, transpiration and root water uptake start to decline (Bréda *et al.*, 1995; Duursma *et al.*, 2008). Thus, overall root water uptake under drought conditions depends on soil, soil–root air gaps, and L. L limits overall root water uptake in the initial phases of drought periods, and soil conductivity and the lack of contact between root and soil are limiting to water movement when drought becomes more pronounced (Nobel and Cui, 1992; North and Nobel, 1997). Researchers consistently report a decline of L under drought conditions (Nobel and Cui, 1992; Rieger, 1995; North *et al.*, 2004; Trifilo *et al.*, 2004; Aroca *et al.*, 2006, 2008b; YX Gao *et al.*, 2010).

The initial decrease of L under drought conditions could be a mechanism to avoid water flow from root to soil while soil water potential is decreasing progressively. However, soil drying does not occur at the same rate at different depths, and the drying rate is more pronounced in the superficial soil layers than in the deeper ones. Thus, plants able to develop a deeper root system usually are more tolerant to drought than plants with a more superficial root system (Pinheiro *et al.*, 2005; Alsina *et al.*, 2011). In fact, some plant species are able to transport water from wetter deeper soil to superficial drier soils, a mechanism known as hydraulic lift; this ability could be crucial in some circumstances to tolerate drought stress (Wan *et al.*, 2000).

Although L decreases upon root exposure to drought, under some specific drought circumstances an increase in L has been reported. Singh and Sale (2000) found that white clover plants well supplied with phosphorus increased their L (estimated by the Hagen–Poiseuille equation which takes into account the vessels' diameters) after drought treatment (soil moisture depletion down to -1.5 MPa). Also, Siemens and Zwiazek (2004) found that *Populus tremuloides* trees subjected to mild drought stress (exposing roots to a high humidity air chamber for 17 h) showed an up-regulation of L measured under hydrostatic forces. This up-regulation of L could be a mechanism to absorb water from soil when soil water

potential does not fall below the water potential of roots. Anyway, the signals (hydraulics or chemicals) that regulate L behaviour under drought conditions are still unknown.

As previously indicated, L behaviour is regulated partially by aquaporin function, specifically by PIPs (Javot *et al.*, 2003; Postaire *et al.*, 2010). However, looking at many studies, it is hard to find a common response of root PIP aquaporin expression and PIP protein abundance under drought conditions. The results of nine representative studies where PIP expression under drought conditions was measured in roots were analysed (Table 1). Among the 37 PIP genes studied, 15 were down-regulated, 13 up-regulated, and nine unaltered. Even in the same experiment some PIP genes were down-regulated, others up-regulated, and others unaltered (Aroca *et al.*, 2007; Ruiz-Lozano *et al.*, 2009). So, based on expression studies it is difficult to assign a role for PIP genes in regulating L during drought stress. In fact, there is evidence that each PIP gene could have a specific function under specific stress circumstances. For example, Jang *et al.* (2007a, b) found that the overexpression of a certain PIP aquaporin gene induced tolerance to some environmental stresses but sensitivity to others. Similarly, Aharon *et al.* (2003) found that the overexpression of a foreign PIP aquaporin gene in transgenic tobacco improved plant vigour under favourable growth conditions but not under drought or salt stress conditions.

Different regulation of PIP protein abundance in root tissues under drought conditions has also been observed (Table 1). Commonly a decrease in abundance of PIP2 proteins has been recorded (Aroca *et al.*, 2006, 2007; Ruiz-Lozano *et al.*, 2009), but an accumulation of PIP1 proteins under drought conditions has also been found (Lian *et al.*, 2004; Aroca *et al.*, 2007). Anyway, a correlation between PIP protein abundance and L behaviour has not always been observed. Zhang *et al.* (2007) found an accumulation of PIP2 protein in root membranes of *Jatropha curcas* upon exposure to osmotic stress simulated by polyethylene glycol, but at the same time these authors found a decrease in L values. This discrepancy could be caused by a different subcellular localization of PIP proteins (invaginations of the plasma membrane; Boursiac *et al.*, 2005, 2008) or by different PIP protein localization along the root axis (Benabdellah *et al.*, 2009).

Vandeleur *et al.* (2009) found that the anisohydric (plants that vary their leaf water potential during the day) grapevine cultivar Chardonnay increased the expression of a PIP1 gene in its roots upon exposure to drought, correlating with an increase in the cortical cell L. However, the same authors also found a diminution in the whole root system hydrostatic L. These results confirmed the hypothesis of Steudle and Peterson (1998) that when the transpiration is restricted (such as during drought), the cell-to-cell path should dominate. At the same time, the diminution of overall L observed by Vandeleur *et al.* (2009) could be caused by suberin and lignin depositions restricting the apoplastic water flow which was not compensated by the cell-to-cell path water flow. However, other authors have found that under drought conditions, the diminution of

Table 1. Summary of drought stress effects on PIP gene expression, protein abundance, and L in different experimental set-ups and plant species

Species	Treatment	PIP expresión	Protein regulation	L	Source
<i>Arabidopsis thaliana</i>	(4–48 h) 250 mM mannitol	AtPIP1;3, 1;2, 2;1, 2;5 UP AtPIP1;1, 1;2, 1;5, 2;2, 2;3, 2;4, 2;6, 2;7, 2;8 DOWN	?	?	Jang et al. (2004)
<i>Lactuca sativa</i>	10 d at 75% of field water capacity	LsPIP2 DOWN	?	DOWN	Aroca et al. (2008b)
<i>Vitis berlandieri</i> × <i>Vitis rupestris</i>	7 d with stomatal conductance down to 55–18% of control plants	VvPIP1;1, 1;2, 2;1 EQUAL	?	?	Galmés et al. (2007)
<i>Nicotiana tabacum</i>	24 h at –0.35 MPa by applying PEG6000	VvPIP1;3, 2;2 UP NtPIP1;1, 2;1 DOWN	?	DOWN	Mahdieh et al. (2008)
<i>Phaseolus vulgaris</i>	4 d without watering	PvPIP1;1 EQUAL PvPIP1;3, 2;1 UP PvPIP1;2 DOWN	PIP1s UP PIP2s DOWN	DOWN	Aroca et al. (2007)
<i>Vitis vinifera</i>	8–10 d without watering	VvPIP2;2 EQUAL VvPIP1;1 UP	?	Whole root system L DOWN Cell L UP	Vandeleur et al. (2009)
<i>Oryza sativa</i>	10 h with 20% PEG6000	OsPIP1;3 UP	UP	?	Lian et al. (2004)
<i>Zea mays</i>	4 d without watering	ZmPIP1;1 UP ZmPIP2;5, 2;6 DOWN ZmPIP1;2, 1;5, 2;1, 2;2 EQUAL	ZmPIP1;2 EQUAL ZmPIP2;1, 2;5 DOWN	EQUAL	Ruiz-Lozano et al. (2009)
<i>Gossypium hirsutum</i>	Different PEG treatments	GhPIP1;1, 2;1 UP GhPIP2;2 EQUAL	?	?	Li et al. (2009)

whole root system L is correlated with an increase in the proportion of water moving by the apoplastic path (Siemens and Zwiazek, 2003, 2004). These discrepancies could be caused by the different strategies to overcome drought stress by the different plants species or cultivars. In fact, Vandeleur et al. (2009) found an opposite behaviour in the isohydric grapevine cultivar Grenache. It is clear that more research is needed in order to ascertain which signals (hydraulics or chemicals) are responsible for L and PIP aquaporin regulation during drought stress. At the end of this review a section is devoted to this topic.

On the other hand, the overexpression of TIP aquaporins in plants also produces plants with different tolerance to drought stress. This has been attributed to a bigger root system capable of exploring more soil to capture water, since cell elongation requires a vacuolar membrane with high water permeability capacity (Peng et al., 2007), or to a stimulation of anisohydric plant behaviour (Sade et al., 2009). However, Wang et al. (2011) found that *Arabidopsis* plants overexpressing a TIP aquaporin from soybean were more susceptible to dehydration stress. Thus, TIPs and possibly other kinds of aquaporins besides PIPs could be involved in the response of plants to drought stress. However, at present, not very much information about these topics is available.

Root water uptake under salt conditions

Soil salinity is one of the most important factors that restrict agricultural production in the world. The negative

effect of salinity is most intense in arid and semi-arid climatic areas because the amount of salt increases as a result of irrigation and in soils used for intensive agriculture because the use water reservoirs already having high amounts of salts (Mostafazadeh-Fard et al., 2009). Commonly, root water uptake decreases upon exposure to salt stress. This decrease can be caused by both osmotic and toxic effects, depending on the salt concentration present. Silva et al. (2008) found that pepper plants treated with a low concentration (30 mM) of NaCl, or with a nutrient solution with the same osmotic value, decreased their root water uptake rate and L values to the same extent. However, when the NaCl concentration was further increased to 60 mM and the osmotic pressure of the nutrient solution rose to the same value (–0.290 MPa), only plants treated with NaCl decreased their root water uptake rate and L values further. So, the decrease in the root water uptake rate and L under higher concentrations of NaCl was caused by specific toxic effects due to the accumulation of Na⁺ and Cl[–] ions in root tissues, or by the imbalance in the acquisition of other nutrients.

A decrease of L under saline conditions has been observed frequently (Azaizeh et al., 1992; Navarro et al., 2003; Boursiac et al., 2005; Silva et al., 2008; Nedjimi, 2009; Wan, 2010; Muries et al., 2011; Sutka et al., 2011). The initial L decrease upon salt exposure may be caused by an osmotic shock as a result of an aquaporin conformational change caused by negative pressures (Wan et al., 2004). Moreover, applying a final NaCl concentration of 50 mM to maize roots in two steps (25 mM each) reduced the L

value of cortical cells to a lesser extent than when 50 mM NaCl was applied all at once. The 50 mM application would produce a higher osmotic shock (Wan, 2010). At the same time, L could decrease as the result of a direct effect of Na⁺ ions in aquaporin functioning (Carvajal *et al.*, 1999). The decrease of L under salt stress conditions could be a strategy to diminish water flow from roots to soil while the soil osmotic potential is lower than that of the roots. A similar response also operates under drought conditions (see above). The initial diminution of L was correlated with a down-regulation of PIP aquaporin genes (Martínez-Ballesta *et al.*, 2003a; Boursiac *et al.*, 2005). Most interesting were the results of Boursiac *et al.* (2005) who observed internalization of plasma membrane vesicles containing PIP proteins; this resulted in a decrease in L. The decrease in L in the initial phase of salt stress was correlated with an increment in the percentage of water moving via the apoplastic path (Martínez-Ballesta *et al.*, 2003a). Thus, in the initial phase (a few hours) of salt stress a decrease in L is caused mainly by an osmotic shock, which correlates with a decrease in cortical cell L. The low rate of water uptake that remains after salt application is responsible for the low transpiration rate (Martínez-Ballesta *et al.*, 2003a, b), and it follows the apoplastic path.

At later stages of salt stress (after few days), a partial or total recovery of L has been described in some species (Martínez-Ballesta *et al.*, 2003a; Wan, 2010). Thus, maize root cortical cells recovered their L values after 6 d of exposure to 50 mM NaCl (Wan, 2010). Also, *Arabidopsis* plants partially recovered their L values after 3 d of exposure to 60 mM NaCl (Martínez-Ballesta *et al.*, 2003). This recovery of L after a long exposure to salt conditions observed in some species is accompanied by an increase in suberin contents in endodermal and/or exodermal root cells (Schreiber *et al.*, 2005), potentially diminishing apoplastic water flow and Na⁺ and Cl⁻ entrance into xylem vessels (Zimmermann *et al.*, 2000; Ranathunge and Schreiber, 2011). Thus, this partial L recovery observed after a long exposure to salt could be caused by an enhancement of the cell-to-cell pathway, since water flowing by the apoplastic pathway is restricted. In fact, accumulation of PIP proteins in roots of salt-treated plants for long periods (from 3 d to 15 d) has been found (Marulanda *et al.*, 2010; Muries *et al.*, 2011), which could favour the cell-to-cell pathway. Also, López-Pérez *et al.* (2009) found that plasma membranes of broccoli roots subjected for 15 d to 80 mM NaCl increased their unsaturated fatty acid ratio: the membranes became more fluid, which also could have an additive effect to the function of PIP aquaporins.

The increase in L due to the cell-to-cell path should be accompanied by an osmotic adjustment of the root cells (accumulation of compatible solutes) in order to avoid cell dehydration (Wan, 2010). However, although under salt conditions an osmotic adjustment has been seen eventually in root tissues (Rodríguez *et al.*, 1997; An *et al.*, 2002), in these studies no L measurements were undertaken. Thus, which chemical signals are behind this L acclimation under salt stress remains to be explored. Nevertheless, a picture of how L responds to salinity can be drawn (Fig. 1). In any

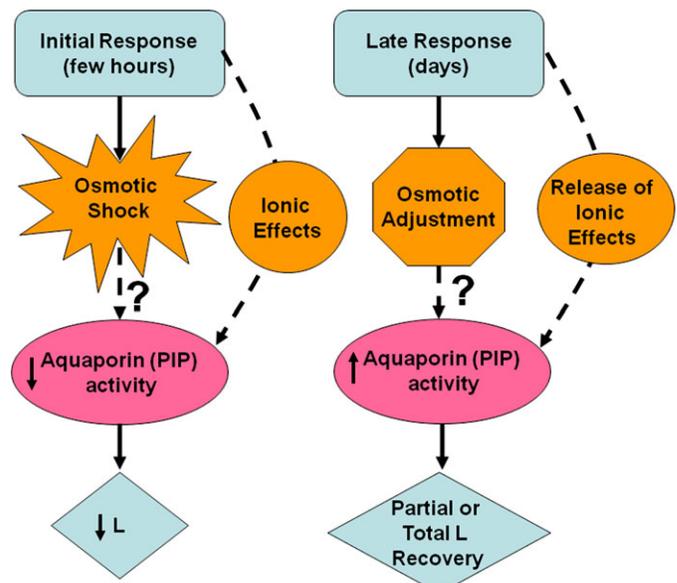


Fig. 1. Diagram representing root hydraulic conductance (L) responses to salt. At the initial stages (within hours), L decreases, possibly caused by lower aquaporin (PIP) activity, initially resulting from an osmotic shock or ionic effects. At later stages (within days), L could recover by the sum of the osmotic adjustment, release of ionic effects, and the increase in the activity of PIP aquaporins. '?' and dashed arrows indicate as yet unidentified signals.

case, the recovery of L after some days of salt application can only take place if the root cells also overcome other toxic effects of salt stress such as the production of reactive oxygen species (ROS; Boursiac *et al.*, 2008).

It is worth noting that some plant species/ecotypes do not decrease their L values upon exposure to salt. Sutka *et al.* (2011) found that a particular ecotype of *Arabidopsis* (Monte-Tosso-0, Mr-0) did not change its L value after exposure of roots to 100 mM NaCl for 4 h. The authors stated that this particular ecotype is more tolerant to drought stress, but no data supporting this fact were shown in their report. Therefore, whether such behaviour is linked to salt tolerance is at the moment unknown.

Also, apart from the role of PIP aquaporins in the regulation of water uptake under salt stress, the role of other aquaporin subfamilies in the tolerance of plants to salinity has been observed. Hence, Peng *et al.* (2007) found that *Arabidopsis* plants overexpressing a TIP aquaporin from seeds from the ginger plant were capable of germinating and the seedlings grew even at 150 mM NaCl. In contrast, Wang *et al.* (2011) found that *Arabidopsis* plants overexpressing a TIP aquaporin from soybean were more sensitive to salt stress. This apparently contradictory result could possibly be explained as follows: Peng *et al.* (2007) used a TIP1 aquaporin isoform and Wang *et al.* (2011) a TIP2 isoform for their work. Perhaps the two types of TIPs are localized in different kind of vacuoles (lytic for TIP1 and protein storage for TIP2), or differ in their tissue localization along the root axis (Gattolin *et al.*, 2010). At the same time, it is known that the overexpression of one

foreign aquaporin in a plant alters the pattern of expression of the endogenous aquaporins (Jang *et al.*, 2007b).

The role of TIP aquaporins under salt stress conditions could be to equilibrate the osmotic potential of the cytoplasm by the exchange of water with the vacuole (Kjellbom *et al.*, 1999). Z Gao *et al.* (2010) found that *Arabidopsis* plants overexpressing a NIP aquaporin from wheat were more tolerant to salt stress than untransformed plants. The transformed plants had better root growth under salt conditions, as well as higher accumulation of Ca^{2+} and lower levels of Na^+ . The precise mechanism of this tolerance enhancement is unknown. Obviously, more research is needed to understand completely the role of other plant aquaporins (beside PIPs) in the responses of plants to salt stress.

Root water uptake under low temperature conditions

In this section low temperature refers to temperatures between 0 °C and 15 °C, and studies dealing with temperatures below 0 °C, known as freezing temperatures, are not included. Thus, it is well established that low temperature conditions cause leaf dehydration in sensitive plants (Pardossi *et al.*, 1992; Janowiak and Markowski, 1994; Aroca *et al.*, 2001; Nagasuga *et al.*, 2011). As for other stresses, this leaf dehydration is caused by the imbalance between water lost by leaf transpiration and water uptake by roots (Pardossi *et al.*, 1992; Aroca *et al.*, 2001; Vernieri *et al.*, 2001). Hence, although the transpiration rate decreases under low temperature conditions because of a decrease in the vapour pressure difference (VPD) between the leaf surface and the atmosphere (Aroca *et al.*, 2003), stomata of the sensitive plants remain open, while those of the tolerant plants close more rapidly (Aroca *et al.*, 2001, 2003; Bloom *et al.*, 2004). At the same time, root water uptake also decreases drastically when the temperature goes down, because of the decrease in the VPD (Aroca *et al.*, 2003) and the increase in the viscosity of water (Bloom *et al.*, 2004). However, the increase in water viscosity cannot fully explain the decrease in the root water uptake rate (Wan *et al.*, 2001; Bloom *et al.*, 2004). Also, L decreases faster than stomatal conductance when only the roots were subjected to low temperature stress (Wan *et al.*, 2001). So, the reduction of L under low temperature conditions not only has a physical explanation, but also has biological–metabolic causes. Thus, based on Arrhenius plot studies (plotting the logarithmic values of L against the inverse of temperature in Kelvin degrees), it has been suggested that the decrease in L upon exposure to low temperatures could be caused by an inhibition of aquaporin activity (Wan *et al.*, 2001; Murai-Hatano *et al.*, 2008; Ionenko *et al.*, 2010). These studies were performed with excised roots subjected to low temperature conditions. In fact, under high irradiance conditions that induced higher transpiration rates, the decrease in L of root cells caused by low root temperature was higher, and an increase in the water flowing by the apoplastic path was also observed (Lee *et al.*, 2008).

In some species or in plants grown under particular conditions before the low temperature treatment is applied,

a break point in the Arrhenius plot experiments was observed (see table 1 of Murai-Hatano *et al.*, 2008). These break points are attributed to membrane injury, most probably caused by a phase transition of membrane lipids (Nishida and Murata, 1996).

Hence, as for salt stress, it seems that the decline in L at the initial phase (within a few hours) of low temperature stress is also caused by a diminution of aquaporin activity. However, Murai-Hatano *et al.* (2008) did not find any significant changes in the amount of several PIP and TIP proteins in root tissues of rice during the first 5 h of low temperature treatment, whereas they observed an abrupt decline of L. Therefore, they hypothesized that the decrease in L observed could be caused by closure of aquaporin pores rather than by a decrease in protein amounts. One possibility could be a closure of aquaporins due to acidification of the cytosol during low temperature periods (Kawamura 2008), as this response has been demonstrated under hypoxia conditions (Tournaire-Roux *et al.*, 2003).

Several low temperature-tolerant plant species (or genotypes of a particular plant species) are able to recover their L after a prolonged time (a few days) of exposure to low temperature (Bigot and Boucaud, 1996; Fennell and Markhart, 1998; Aroca *et al.*, 2001, 2003, 2005; Vernieri *et al.*, 2001; Nagasuga *et al.*, 2011). Based on HgCl_2 experiments, it was hypothesized that this recovery could be caused by an enhancement of aquaporin activity (Aroca *et al.*, 2001). Aroca *et al.* (2005) found that a maize low temperature-tolerant genotype accumulated PIP proteins in its roots after 3 d of exposure to 5 °C, concomitantly with an increase in the phosphorylation state of the PIP2 proteins. This PIP accumulation was correlated with even higher L values of the low temperature-treated maize plants. Aquaporin phosphorylation has been shown to enhance aquaporin activity (Maurel *et al.*, 1995) by keeping aquaporin pores in the open state (Daniels and Yeager, 2005; Tornroth-Horsefield *et al.*, 2006). Aroca *et al.* (2005) also found the same PIP aquaporin response in a low temperature-sensitive maize genotype, which kept its L at very low levels during low temperature stress. So, the response of PIP aquaporins to low temperature stress was not the only explanation for the different L behaviour between the sensitive and the tolerant maize genotypes. Aroca *et al.* (2005) also found that the root membranes of the sensitive genotype were injured by the low temperature treatment. Hence, to tolerate low temperature stress it was not sufficient to accumulate more PIP proteins in the root membranes. The tolerant genotype also possessed robust mechanisms against membrane injury caused by low temperature conditions.

In agreement with the accumulation of PIP proteins in roots during low temperature periods, other researchers also found that some plants grown at low temperatures had higher L than plants grown at higher temperatures, when L was measured at the higher temperatures (Bigot and Boucaud, 1994; Wan *et al.*, 1999; Lee *et al.*, 2005b). Also, Matsumoto *et al.* (2009) found that rice plants overexpressing one PIP1 aquaporin were more tolerant to low temperature stress than untransformed plants. So, it seems

that accumulation of PIP proteins is crucial to tolerate low temperature stress.

However, other factors besides PIP aquaporin expression or abundance may govern L during low temperature periods. Indeed, Lee *et al.* (2005b) found that a low temperature-sensitive plant species (*Cucumis sativus*) accumulated more suberin in both root exo- and endodermis than a tolerant species (*Cucurbita ficifolia*). This higher suberin accumulation was correlated with lower L values under low temperature conditions of the sensitive species. Moreover, Lee *et al.* (2005a) also observed a more pronounced and constant increase in the double bond index of the root plasma membrane in *C. ficifolia* plants than in that of *C. sativus* under low temperature conditions. Such an increase was caused by raising the amount of linolenic acid and by diminishing the amount of stearic acid. The increase in the double bond index could be correlated with the higher L observed in *C. ficifolia* than in *C. sativus* under low temperature conditions (Lee *et al.*, 2005b; López-Pérez *et al.*, 2009).

In summary, although the involvement of PIP aquaporins seems to be crucial to maintain root water uptake under low temperature conditions and avoiding leaf dehydration, other aspects contributing to the regulation of root water uptake are also involved, including maintenance of membrane integrity, degree of fatty acid saturation, suberin content, or cytoplasmic acidosis. Therefore, more research is needed to elucidate how these factors contribute to the regulation of root water uptake properties during low temperature periods.

Root water uptake under flooding conditions

It is well documented that flooding paradoxically can cause leaf dehydration (Ruiz-Sánchez *et al.*, 1996; Domingo *et al.*, 2002; Nicolás *et al.*, 2005). However, this symptom of flooding does not always appear, and depends on the soil O₂ and CO₂ partial pressures and on the plant species (Blanke and Cooke, 2004; Araki, 2006). In fact, one of the problems with summarizing the effects of flooding on plants and their water relations is the wide diversity of treatments employed, different soil O₂ partial pressures, and no record of the soil CO₂ concentration in most of the studies (Araki, 2006; Table 2). The most common effect of flooding stress is a reduction in leaf transpiration; that is, an increase in stomatal closure (Blanke and Cooke, 2004; Yetisir *et al.*, 2006; Atkinson *et al.*, 2008), most probably mediated by chemical signals (Jackson *et al.*, 2003; Araki, 2006; Else *et al.*, 2006). However the exact nature of the possible chemical signals is still unknown. In contrast, initial stomatal closure could be attributed to leaf dehydration in some species (Else *et al.*, 2001).

At the same time that stomatal conductance is restricted by flooding conditions, L is also changed—usually decreased—upon exposure to flooding. In several cases no changes or even an overshoot have been observed (Table 2). As noted above, these different results could be caused by

different experimental set-ups. Araki (2006) found that soybean plants only decreased their L values when, besides low O₂ partial pressure in the soil, it was accompanied by an elevated CO₂ partial pressure. However, CO₂ partial pressure is usually not recorded in flooding experiments (Table 2). Thus, CO₂ accumulated during flooding conditions by soil root respiration could be transformed to its acid form (H₂CO₃), transported to the cytoplasm of root cells, and inhibit aquaporin activity. In fact, cytosolic acidification is one of the main causes of the inhibition of L caused by anaerobiosis resulting from flooding conditions (Tournaire-Roux *et al.*, 2003), as a result of the protonation of a histidine residue in loop D of PIP proteins. However, the exact mechanism of L inhibition by CO₂ is still unknown.

The inhibition of aerobic respiration by flooding may also cause the inhibition of L (Kamaluddin and Zwiazek, 2001; Tournaire-Roux *et al.*, 2003). However, how the accumulation of several toxic compounds in the root cells, such as ethanol, acetaldehyde, or lactic acid, under flooding conditions (Mustroph *et al.*, 2006; Zaidi *et al.*, 2007) may affect L has not been explored yet. Plants adapted to withstand flooding conditions are able to develop suberin depositions in the exo- and/or endodermis to avoid radial O₂ loss from the root surface (De Simone *et al.*, 2003; Enstone and Peterson, 2005). This suberin deposition could also potentially decrease L values under flooding conditions (Ranathunge and Schreiber, 2011). Ranathunge *et al.* (2011) recently found that these suberin depositions in rice roots do not alter L values but decrease solute transport to the xylem. Moreover, the response of the overall L to flooding conditions depends on the main radial water transport pathway used by each plant species. Namely, in species such as lupins in which radial water transport is dominated by the apoplastic path, flooding stress did not change L. In contrast, in wheat plants, in which the cell-to-cell path dominates radial water transport, flooding stress decreases L (Bramley *et al.*, 2010).

As shown in Table 2, in some special circumstances an up-regulation of L after the initial decrease was observed (Else *et al.*, 1995; Gibbs *et al.*, 1998). At the same time, some flooding-tolerant species exposed for several days to flooding conditions are able to develop new adventitious roots with high L values (Islam and MacDonald, 2004). The recovery of L values or the high L observed in adventitious roots of tamarack trees (Islam and MacDonald, 2004) could be caused by the accumulation of aquaporins in their cell membranes. Thus, although stomatal conductance would remain low and consequently apoplastic water flow would be restricted, cell-to-cell water flow could be favoured by the accumulation of aquaporins. However, only the report of Zou *et al.* (2010) found an up-regulation of the expression of one PIP1 gene after prolonged flooding conditions in roots of maize plants. Most recently, Rodríguez-Gamir *et al.* (2011) found a down-regulation of two PIP aquaporin genes of *Carrizo citrange* plants after 35 d of flooding, correlating with a large decrease in L. As far as is known, no other data about flooding regulation of root aquaporins at the gene or protein levels are available.

Table 2. Summary of how different flooding treatments modify L in different plant species
 pO₂ and pCO₂ indicate partial pressures of O₂ and CO₂, respectively.

Species	L	[O ₂] or pO ₂	[CO ₂] or pCO ₂	Source
<i>Triticum aestivum</i>	Root and cell L DOWN	50 μM	Not determined	Bramley <i>et al.</i> (2010)
<i>Lupinus luteus</i> and <i>Lupinus angustifolia</i>	Root L UNCHANGED, Cell L DOWN	50 μM	Not determined	Bramley <i>et al.</i> (2010)
<i>Glycine max</i>	Root L UNCHANGED	2 kPa	0.4 kPa	Araki (2006)
<i>Glycine max</i>	Root L DOWN	2 kPa	2 kPa	Araki (2006)
<i>Picea mariana</i>	Root L DOWN	Not determined	Not determined	Islam and MacDonald (2004)
<i>Larix laricina</i>	Root L UNCHANGED	Not determined	Not determined	Islam and MacDonald (2004)
<i>Arabidopsis thaliana</i>	Root L DOWN	Not determined	Not determined	Tournaire-Roux <i>et al.</i> (2003)
<i>Ricinus communis</i>	Root L DOWN	2–12 kPa	Not determined	Else <i>et al.</i> (2001)
<i>Gerbera jamesonii</i>	Root L DOWN	190 μM	Not determined	Olivella <i>et al.</i> (2000)
<i>Zea mays</i>	Root L DOWN TRANSIENTLY	50 μM	Not determined	Gibbs <i>et al.</i> (1998)
<i>Solanum lycopersicum</i>	Root L UNCHANGED	Not determined	Not determined	Jackson <i>et al.</i> (1996)
<i>Solanum lycopersicum</i>	Root L, initial DOWN, later UP	0–8 kPa	9–12 kPa	Else <i>et al.</i> (1995)
<i>Zea mays</i>	Root L DOWN	0–13 μM	Not determined	Birner and Steudle (1993)
<i>Vaccinium corymbosum</i>	Root L DOWN	Not determined	Not determined	Davies and Flore (1986)

In summary, although the most common effect of flooding in root water transport properties is the inhibition of L, and the molecular features of such inhibition have been elucidated (Tournaire-Roux *et al.*, 2003), several aspects of the regulation of L during flooding conditions are still unresolved. These open questions would include, among others, which chemical compounds really inhibit L during flooding and what are the molecular aspects of the recovery of L observed in some species at late stages of flooding stress.

Signals regulating root water uptake under stress conditions

The concentration of a number of molecules increases in root cells upon exposure to environmental stresses. Among them, the focus here is on some plant hormones [abscisic acid (ABA), ethylene (ET), and salicylic acid (SA)] and on ROS.

It is well known that ABA modifies root hydraulic properties. The most common effect is an increase in L when ABA is added to the root medium (Zhang *et al.*, 1995; Aroca, 2006; Mahdih and Mostajeran, 2009; Ruiz-Lozano *et al.*, 2009). Nevertheless, in some cases no effect (Wan and Zwiazek, 2001) or even a decrease in L (Aroca *et al.*, 2003) was observed. The most robust evidence about the role of ABA in regulating L comes from studies of ABA-deficient plants or ABA-overproducing plants. Thus, ABA-deficient tomato plants have lower whole-plant hydraulic conductance, as well as a lower root exudation rate (Nagel *et al.*, 1994). Also, Thompson *et al.* (2007) found that tomato plants overproducing ABA had higher L values than wild-type plants. ABA is known to accumulate in root cells exposed to abiotic stresses such as drought (Simonneau *et al.*, 1998), salt (Jia *et al.*, 2002), low temperature (Aroca *et al.*, 2003), or flooding (Olivella *et al.*, 2000). In the case of flooding stress, a decrease of root ABA contents has also

been observed (Rodríguez-Gamir *et al.*, 2011). Hence, it is possible that ABA may regulate, at least in part, L changes under stress conditions. However, ABA addition and drought stress usually have opposite effects on L. Thus, while ABA usually increases L, drought inhibits it (Aroca *et al.*, 2006). This apparent contradiction could possibly be explained by assuming that exogenous application of ABA to the roots causes an excess of ABA or a different cellular location of the ABA (Aroca *et al.*, 2003). Nevertheless, under some specific drought conditions, an increase in L values has been observed (Singh and Sale, 2000; Siemens and Zwiazek, 2004), although in these studies ABA levels were not determined.

Most recently, Wan (2010) found that external application of ABA inhibited the negative effect of NaCl on cell L, and explained this by suggesting that ABA promoted cell osmotic adjustment. However, no direct measurements supporting that osmotic adjustment were presented. Exogenous ABA also modulates root PIP aquaporin expression and protein abundance (Jang *et al.*, 2004; Aroca *et al.*, 2006, 2008b; Mahdih and Mostajeran, 2009; Ruiz-Lozano *et al.*, 2009). When expression of four PIP genes was studied in ABA-deficient tomato plants, it was found that under well-watered conditions, two PIP genes remained unchanged and two other PIP genes were up-regulated by ABA depletion. In contrast, under drought conditions, three PIP genes were down-regulated and only one gene was up-regulated (Aroca *et al.*, 2008a). However, no protein data are available from this study. Hence, it is clear that ABA is involved in the response of L and PIP aquaporins to different abiotic stresses, although the mechanism behind such regulation is still far from being understood.

ET, another stress-related plant hormone, could also play a role in the regulation of root water uptake under several abiotic stress conditions. It is known that ET levels vary under different abiotic stress conditions such as drought (Liang, 2003), salt (Quinet *et al.*, 2010), or flooding (Huang *et al.*, 1997). For example, Kamaluddin and Zwiazek (2002)

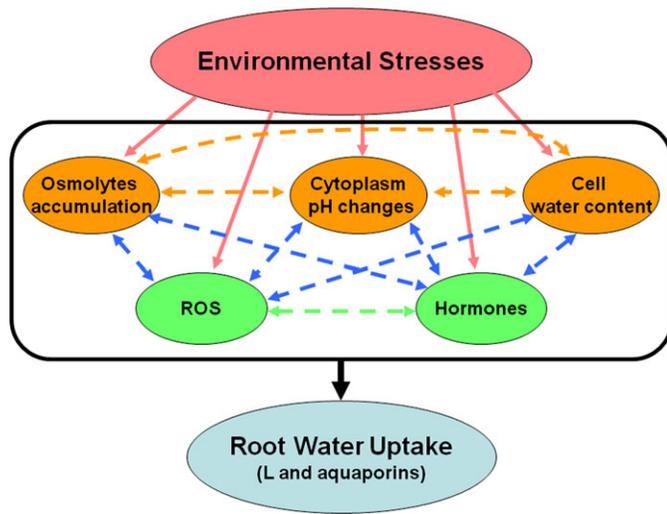


Fig. 2. Diagram showing which cell components are modulated by environmental stresses, and how the interaction among these components may modulate the root water uptake rate under such stresses. Other components such as respiration or protein phosphorylation which do not appear in the figure may also influence root water uptake rate.

and Islam *et al.* (2003) found an enhancement of L values by an exogenous application of ET in several tree species. In contrast, YS Li *et al.* (2009) found a negative effect of ET application on L values in *Medicago falcata* plants. No other data are available about L regulation by exogenous ET. Therefore, the contrasting results described above could be caused by different concentration, time of exposure, or, simply, the different plant species used. Qaderi *et al.* (2007) found that canola plants with low levels of ET production have lower L values under non-stressed conditions. However, no data about the effect of ET on PIP aquaporin expression at the root level are available. Another stress-related plant hormone that regulates L is SA. Boursiac *et al.* (2008) found that exogenous SA inhibited L in *Arabidopsis* plants by causing invaginations of plasma membranes containing PIP proteins, as occurs under salt stress conditions. Moreover, Volobueva *et al.* (2004) found that SA treatment inhibited symplastic water transport in maize roots. Apart from the above results, no more information is available about how other plant hormones could regulate root water uptake under abiotic stress conditions.

Other groups of molecules that may govern root water uptake under abiotic stress conditions are the ROS. ROS are generated in root tissues under different abiotic stress conditions (Blokhina *et al.*, 2001; Aroca *et al.*, 2005; Katsuhara *et al.*, 2005; Bian and Jiang, 2009). Among ROS, hydrogen peroxide (H_2O_2) is the most studied molecule in relation to root water uptake properties (Lee *et al.*, 2004; Aroca *et al.*, 2005; Ye and Steudle, 2006; Rhee *et al.*, 2007; Boursiac *et al.*, 2008; Benabdellah *et al.*, 2009). In the earlier studies of Lee *et al.* (2004) and Aroca *et al.* (2005), it was shown that exogenous application of H_2O_2 inhibited cell and root L, respectively. Several mechanisms including membrane damage (Aroca *et al.*, 2005), closure of

aquaporin pores (Ye and Steudle, 2006), or formation of plasma membrane vesicles containing PIP aquaporins (Boursiac *et al.*, 2008) have been postulated. However, in specific plant species or genotypes (more precisely, plants tolerant to low temperature conditions), no effect of exogenous H_2O_2 on L was observed (Aroca *et al.*, 2005; Rhee *et al.*, 2007). In addition, Benabdellah *et al.* (2009) found that low concentrations of exogenous H_2O_2 increased L in *Phaseolus vulgaris* plants. Consequently, ROS may serve as signals in controlling L behaviour under abiotic stress conditions, stimulating or inhibiting L depending on their cellular concentration. This hypothesis is also supported by the fact that the L response to ABA is modified by the addition of antioxidants (Aroca, 2006). Obviously, more research is needed in order to ascertain how ROS may be involved in L regulation under several stress conditions.

Concluding remarks

It is clear that root water uptake is crucial to overcoming abiotic stress conditions and that the expression of PIP aquaporins is an important factor that regulates L under stress conditions. However, it is also clear that there are many unknown processes that affect root water uptake rate during and after environmental stresses. How aquaporins besides PIPs may regulate L and stress tolerance is almost unexplored. Completely unresolved is the nature of the cellular signals that mediate the final response of L, although there is some information on how aquaporin genes are regulated under stress conditions and how aquaporin activity is modulated. Nevertheless, as shown in Fig. 2, environmental stresses may modify a number of cellular properties such as osmolytes (quantity and quality), cytoplasmic pH, or water content, which may also modify the concentration of other compounds such as ROS or hormones. The interaction among these cell changes and other as yet unknown biochemical changes may modify suberin deposition and aquaporin activity leading to the observed L regulation. Obviously, the possible contribution of each of the potential mechanisms behind regulation of root water uptake under abiotic stress conditions should be the focus of future investigations.

To bring clarity to this field it will be necessary to make more extensive use of mutants in which the expression of specific aquaporins is down-regulated. It is also necessary to know which aquaporins are expressed in which cell types so that the results obtained with those mutants can be interpreted. To create the tools necessary to make progress, researchers will need to make transgenic plants with cell type- or tissue-specific promoters.

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