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Robert T. Devane

Editor

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NEW PLANT PHYSIOLOGY RESEARCH

ROBERT T. DEVANE
EDITOR

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Chapter 3

ROOT WATER TRANSPORT UNDER ABIOTIC STRESS CONDITIONS

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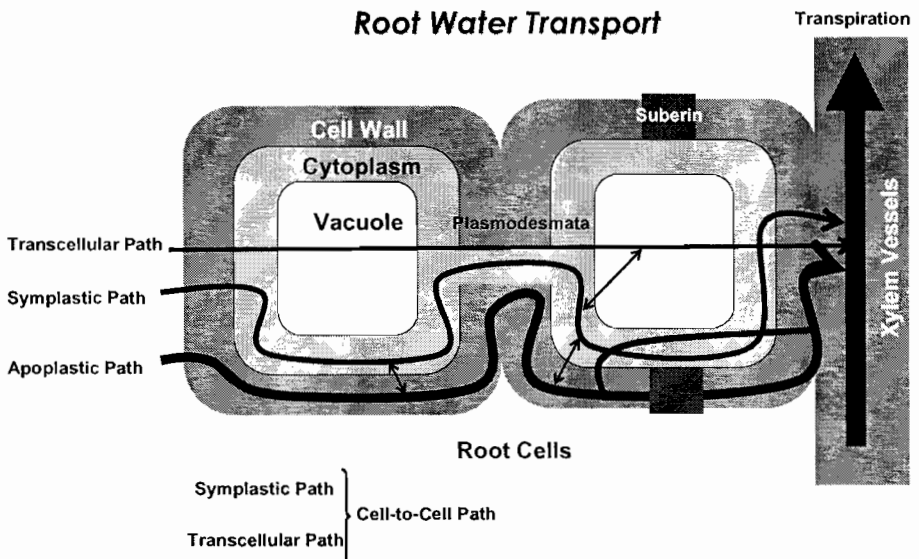
ABSTRACT

Plants in nature are constantly exposed to several environmental fluctuations, ranging from changes in light intensities to changes in soil water content. Alterations of almost all environmental factors may potentially cause a water deficit on plant tissues. Such water deficit is caused by the imbalance between leaf transpiration rate and root water uptake. In contrast with the amount of research done dealing with the regulation of leaf transpiration rate during abiotic stresses, studies about root water uptake under abiotic stresses are less abundant and controversy. There are two different water pathways inside the roots. Under normal conditions, the more important pathway is the apoplastic one. This pathway comprises the water flowing through the cell walls and it is governed by the transpiration rate. The second pathway includes the water flowing through the cells, crossing different cellular membranes and it is called "cell-to-cell" pathway. The "cell-to-cell" pathway is governed by the osmotic gradient between the soil solution and the root xylem sap, and it becomes predominant when the transpiration rate is restricted, for example under abiotic stress conditions. Both pathways are regulated to some extent by proteinaceous channels called aquaporins. Plant aquaporins were discovered fifteen years ago, and here we will summarize the most recent knowledge about their involvement in root water uptake under abiotic stress conditions. In general, under these conditions root water uptake diminishes. However, each kind of stress has its specific effects and we will detail herein how different abiotic stresses (drought, cold, salt or flooding) modify root water uptake. At the same time, we will describe how different stress-related plant hormones such as abscisic acid or methyl jasmonate, or molecular signals, i.e. calcium or hydrogen peroxide, also modify root water uptake. From the present data we highlight the importance of the knowledge of how root water uptake is governed under abiotic stress conditions in order to achieve plants more tolerant to such stresses.

INTRODUCTION

Since plants are sessile organisms, they need to develop several strategies to cope with environmental changes because they can not escape from them. Any environmental factor causing plant growth retardation or a modification in the normal plant physiology is called stress. Plant stresses can be divided in abiotic and biotic stresses; the latter refers to the stresses caused by living organism. Here we will only focus on abiotic stresses, i.e. when changes of the non living part of the environment cause a stress to the plant. For recent advances on plant biotic stresses readers are referred to Asselbergh et al. (2008) and Dreher and Callis (2007).

Abiotic stresses cause several alterations on plant physiology, being one of the most common the stomatal closure. Thus, when plants are exposed to environmental stressors such as cold, water limitation, high salts concentrations in the soil or flooding, they tend to close their stomata (Rood et al., 2003; Aroca et al., 2003a; Loreto and Centritto, 2008). This stomatal closure caused by abiotic stresses consequently diminishes the capacity of plants to take CO₂ up for photosynthesis. This diminution causes alterations on the leaf primary metabolism and enhances the production of toxic molecules such as reactive oxygen species. For recent reviews on this topic see Loreto and Centritto (2008) and Flexas et al. (2006).



Adapted from Steudle and Peterson (1998).

Figure 1. Scheme of the different paths involved on the radial root water transport. Little arrows indicate exchange of water among different water pathways.

Since root water uptake is mainly governed by leaf transpiration, when stomatal cells close their pore by abiotic stresses, water uptake is simultaneously reduced (Steudle and Peterson, 1998; Aroca et al., 2001). Water goes through roots from external solution to xylem vessels following three different paths (Figure 1). Under non stressful conditions, water goes mainly by the apoplastic path; that is crossing cell wall pores following a hydrostatic gradient caused by transpiration. However, when stomata are closed by a stressful agent, water goes

mainly by the “cell-to-cell” pathway comprising water circulating by the cytoplasm and plasmodesmata, and water crossing cell vacuoles. Hence, water goes by the “cell-to-cell” pathway thanks to the osmotic gradient between soil nutrient solution and xylem sap. These three paths are intercommunicated and there is an exchange of water among them as the plant environment changes. Since in developed roots suberin may diminished water permeability of apoplastic path, water molecules need to cross plant plasma membrane at least twice in order to reach xylem vessels. However, it is known that under non stressful conditions, apoplastic path has much less resistance to water flow than “cell-to-cell” path (Steudle and Peterson, 1998; Aroca et al., 2001). For more details on the root composite water transport model see Zhao et al. (2004) and Steudle (2000).



Protein sequences are taken from Johanson et al. (2001).

Figure 2. Phylogenetic tree including the four aquaporins groups of *Arabidopsis thaliana*.

Our understanding of how water molecules cross living membranes have changed in the last fifteen years since the discovery of aquaporins (Preston et al., 1992; Maurel et al., 1993; Kammerloher et al., 1994). Aquaporins are proteinaceous membrane channels that facilitate the transport of water across cell membranes following an osmotic gradient. Plant aquaporins are divided in four groups based on their sequence homology (Figure 2). The four groups are plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), nodulin like intrinsic proteins (NIPs), and small and basic intrinsic proteins (SIPs). Each subgroup is also subdivided, and for example there are PIP1 and PIP2 subgroups, having each subgroup several different proteins. In fact, in *Arabidopsis*, maize and rice there are around 30 different aquaporins genes (Chaumont et al., 2001; Johanson et al., 2001; Sakurai et al., 2005). At the same time, each aquaporin group differs in their capacity of transporting water and other small and neutral solutes and in their subcellular localization. For recent reviews see Kaldenhoff et al. (2008), Katsuhara et al. (2008), and Maurel et al. (2008).

From all the above information, it is known that the water deficit experienced by plants under abiotic stress conditions is caused by the imbalance between water lost by transpiration and by water uptake by roots, being root water uptake less studied comparing to leaf transpiration. Here, we focused on how root water uptake is as important as leaf transpiration in order to keep water status under abiotic stresses. At the same time, we describe how aquaporins regulate root water uptake under abiotic stress conditions and how several hormones and molecular signals regulate root water uptake. We divided the review in different sections, dealing each one with a different abiotic stress (drought, salinity, cold and flooding), or with different signals as hormones, oxygen radicals or calcium.

DROUGHT STRESS EFFECTS ON ROOT WATER UPTAKE

Soils too dry for crop production cover 28% of the dry land surface, so water limitation is one of the most common factors causing loss in crop production (Bray, 2004). When soil starts to become dry, plant roots detect a diminution of the soil water potential and synthesize chemical signals that are transported to the aerial part by the xylem stream in order to induce stomatal closure. Among these chemicals signals the most widely studied is the abscisic acid (ABA) (Hartung et al., 2005; Zhang et al., 2006). However, most recently, Christmann et al. (2007) has found some evidences supporting the idea that ABA is first synthesized in the leaves when plants experience a water deficit episode.

While stomatal closure occurs, root water uptake also decreases by means of several factors such as the drop in soil water potential, the lower hydrostatic gradient caused by transpiration, and the diminution of root hydraulic conductivity (L) (Aroca et al., 2006). A decrease of L upon exposure to soil water deficit has been extensively seen (Martre et al., 2001; Siemens and Zwiazek, 2003; Aroca et al., 2006, 2008; Mahdich et al., 2008), although in some cases a small stimulation has been observed (Lian et al., 2004; Siemens and Zwiazek, 2004). These discrepancies found in the literature are caused by different water deficit intensities, plant cultivation methods, and plant species used. However, it seems that under moderate drought stress or during the initial phases of drought, plants respond increasing L , and when drought is more severe or more prolonged L decreased (Table 1), although, this is

an assumption based in several independent studies, and comprehensive experiments to check this hypothesis are needed.

Table 1. Summary of some of the different effects of drought stress and recovery on root hydraulic conductivity (L). Data ordered chronologically

Drought treatment	Effect on L	Recovery	Plant specie	Reference
45d without watering	Down	Partially	<i>Opuntia acanthocarpa</i>	Martre et al. (2001)
16d without watering	Down	No	<i>Populus tremuloides</i>	Siemens and Zwiazek (2003)
10h 20% PEG ^a	UP	Not Checked	<i>Oryza sativa</i>	Lian et al. (2004)
Roots exposed to air during 17h	Partial increase	Not Checked	<i>Populus tremuloides</i>	Siemens and Zwiazek (2004).
4d without watering	Down	No	<i>Phaseolus vulgaris</i>	Aroca et al. (2006)
10d at 75% of field capacity	Down	Partially	<i>Lactuca sativa</i>	Aroca et al. (2008)
24h PEG ^a at -0.35 MPa	Down	Totally	<i>Nicotiana tabacum</i>	Mahdieh et al. (2008)

^a PEG: Polyethylenglycol.

Although general speaking L decreased under drought stress (see above), the proportion of water circulating by the apoplastic path increases with respect of water circulating by the “cell-to-cell” pathway under drought conditions (Ionenko et al., 2003; Siemens and Zwiazek 2003). At the same time, several researches have reported a diminution in the expression of root PIP aquaporin genes upon exposure to drought stress (Smart et al., 2001; Jang et al., 2004; Porcel et al., 2006; Aroca et al., 2008; Mahdieh et al., 2008), but the opposite has also been seen (Lian et al., 2004; Aroca et al., 2006), and eventually, the change in expression depends on the PIP gene analyzed (Jang et al., 2004; Aroca et al., 2007; Mahdieh et al., 2008). These results may indicate that each PIP gene has a specific function under drought stress since each gene respond differently to drought and also may regulate the expression of the other PIP gene family members (Jang et al., 2007). For a summary of the effect of drought on PIP gene expression see Table 2.

Upon recovery from drought stress, L not always recovers to pre-drought values (Siemens and Zwiazek, 2003; Aroca et al., 2006, 2008), even if in some cases transpiration is fully recovered (Aroca et al., 2006, 2008). These results indicate a possible increase on the water circulating by the apoplastic path. However, in other studies, L recovered totally (Mahdieh et al., 2008) or even showed highest values than pre-drought ones (Zhang et al., 1995). At the same time, PIP gene expression did not recover initial value in some studies (Aroca et al., 2006, 2008), but in others the recovery was total (Mahdieh et al., 2008). Therefore, as happen during drought, L and PIP responses to recovery from drought depend on the plant species studied or on stress intensity.

Table 2. Summary of some of the effects of drought stress on root PIP expression. Data ordered chronologically

Drought treatment	Effect on PIP Expression	Plant specie	Reference
3 to 4d without watering	Decrease	<i>Nicotiana glauca</i>	Smart et al. (2001)
4 to 48h 250 mM Mannitol	9 PIPs decrease, 4 PIPs increase	<i>Arabidopsis thaliana</i>	Jang et al. (2004)
2 to 10h with 20% PEG	Increase	<i>Oryza sativa</i>	Lian et al. (2004)
4d without watering	Increase	<i>Phaseolus vulgaris</i>	Aroca et al. (2006)
10d at 70% of field capacity	Decrease	<i>Glycine max</i> and <i>Lactuca sativa</i>	Porcel et al. (2006)
4d without watering	2 PIPs increase, 1 PIP decrease, 1 PIP not change	<i>Phaseolus vulgaris</i>	Aroca et al. (2007)
24h PEG at -0.35 MPa	2 PIPs decrease, 1 PIP increase	<i>Nicotiana tabacum</i>	Mahdieh et al. (2008)

SALT STRESS EFFECTS ON ROOT WATER UPTAKE

Plants under high salt concentration in the soil solution have to solve two main problems. The first problem is the toxicity of solutes. This toxicity is higher when Na^+ and Cl^- ions are involved. For a review on the toxic effects of salt ions on plants see Ferguson and Grattan (2005). Here we will focus on the second effect that salt stress cause on plant physiology: the osmotic effect, which decrease soil water potential.

Similarly to drought stress, salt stress causes a diminution of root water uptake, although when plants are exposed to salt for a long time they retain some capacity to recover their water uptake rate. Under salt conditions toxic ions like Cl^- or Na^+ are absorbed as well and thus plants need to find equilibrium between the necessity to take up water and the importance to avoid absorption of toxic ions.

Salt stress, as well as drought, causes a reduction on the transpiration rate of plants (Gama et al., 2007; Neocleous and Vasilakakis, 2007). However, in some studies, no effect on transpiration rate has been observed (Aroca et al. 2007; Sawas et al., 2007). On the contrary, L decreases in almost all studies due to the high osmotic gradient between soil solution and the inner part of the roots (Martínez-Ballesta et al., 2006). Under salt stress, it has been usually observed a decrease in the expression and abundance of PIP aquaporins genes and proteins (Boursiac et al., 2005; Martínez-Ballesta et al., 2006). Also, Boursiac et al. (2005) found an internalization of plasma membranes containing PIP proteins in *Arabidopsis* root cells upon exposure to salt. These results could explain the diminution of L under salt stress. However, the above cited experiments were undertaken during a short period of time, no more that 24 h. On the contrary, when salt exposure is prolonged for a week, an enhancement of some PIP gene expression has been observed (Kawasaki et al. 2001; Aroca et al., 2007). In fact, Aroca et al. (2007) found an increase on the root exudation rate in bean

plants subjected to 50 mM NaCl during one week, when these plants were inoculated with a mycorrhizal fungus. The different response of PIP genes under salt stress depending on the time scale could be explained as follows. Since PIP proteins facilitate the pass of water following an osmotic gradient, it could be beneficial for the plants to reduce their expression in plasma membrane to avoid loss of water under salt stress. However, plants have the capacity to reduce their cell osmotic potential by accumulating different compatible solutes by a process known as osmotic adjustment (Ashraf, 2004). When the osmotic adjustment takes place, it is possible that roots recover the ability to take up water and so they need again aquaporins in the plasma membranes of their cells (Figure 3).

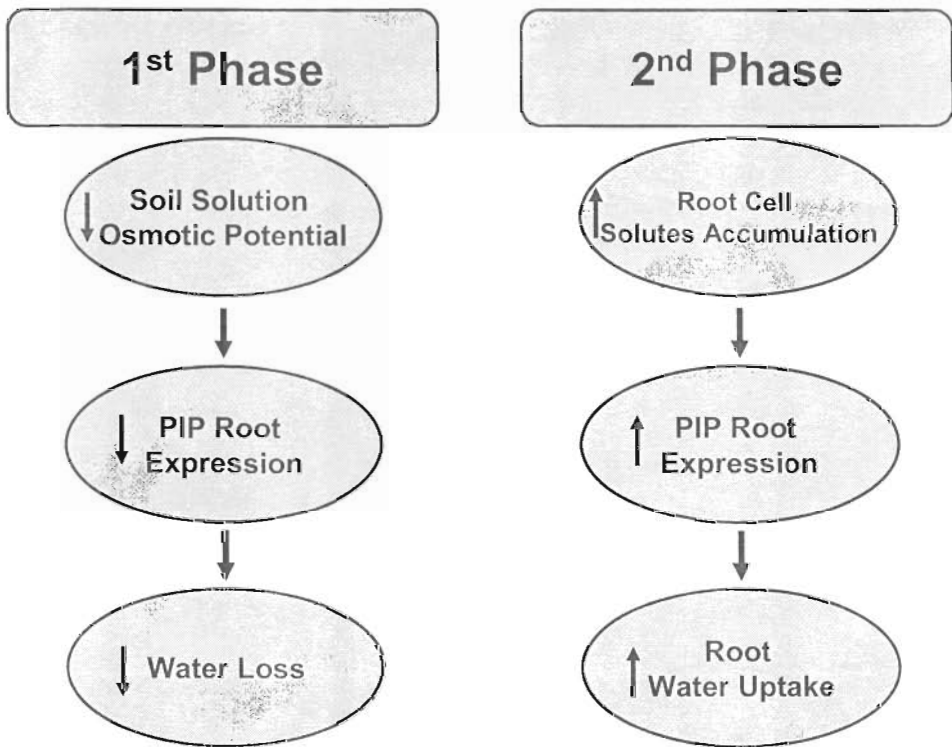


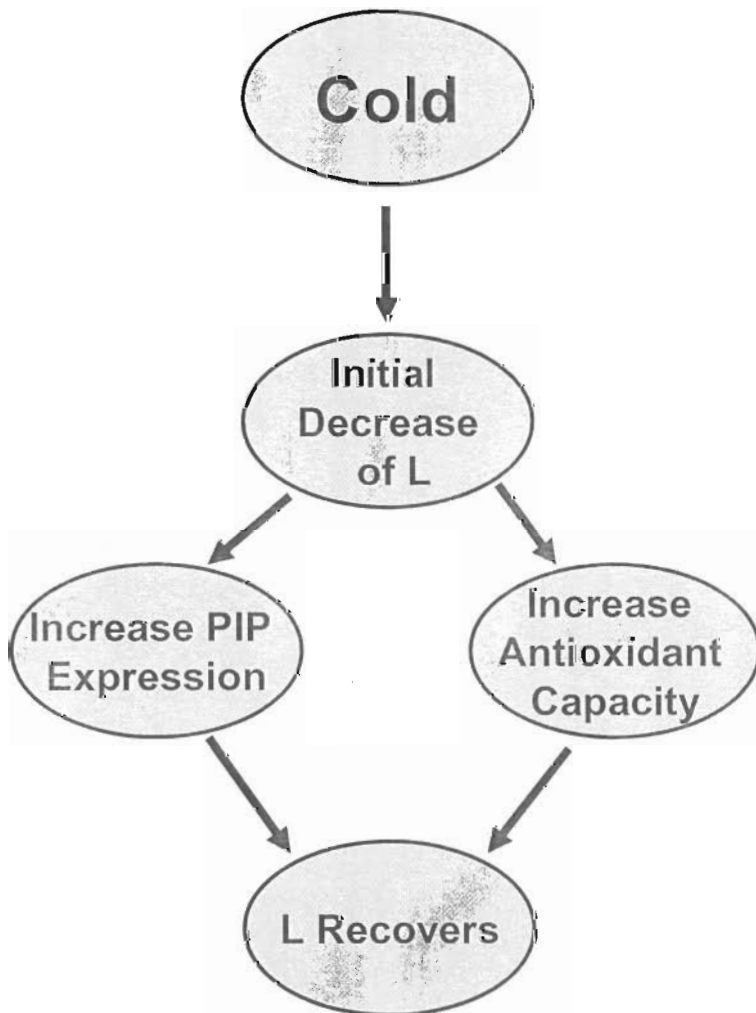
Figure 3. Scheme summarizing the possible behaviour of root hydraulic properties and PIP aquaporins under salt stress.

COLD STRESS EFFECTS ON ROOT WATER UPTAKE

Most crop plants original from tropical regions like maize or tomato are cultivated in temperate regions. Since these plant species belong to warmer regions they suffer several disorders when they are growing in cold areas. One of the effects of cold in plant sensitive species is dehydration of leaf tissues (Pardossi et al., 1992; Aroca et al., 2001). Under low temperature conditions, plant sensitive species keep their stomata open, and are unable to maintain their leaf water status unchanged (Pardossi et al., 1992; Aroca et al., 2001). However, the way the root takes water up under cold conditions is also crucial in keeping leaf water status unchanged. Hence, when two maize genotypes differing in their cold sensitivity

were subjected to 5 °C, both of them presented the same transpiration rate, but the tolerant genotype had greater root exudation rate and L than the sensitive one (Aroca et al., 2003b). In fact, recovery from the water deficit caused by cold is associated to the recovery of the capacity of the roots to take water up again in bean plants (Vernieri et al., 2001).

Aroca et al. (2005) carried out the first approach at a molecular level dealing with the role of PIP aquaporins on the recovery of root water uptake upon cold treatment in two maize genotypes differing in cold sensitivity. In this research it was found that cold treatment increased the amount of PIP proteins in the roots of both genotypes, but only the tolerant one also increased L. The same behaviour of PIP proteins and L was found when both genotypes were subjected to hydrogen peroxide treatment. Therefore, authors concluded that PIP aquaporins are necessary to recover root water uptake upon cold exposure, but not sufficient. Plants also need to cope with the oxidative damage coupled to cold stress (Figure 4).



Adapted from Aroca et al. (2005).

Figure 4. Scheme summarizing the possible response of L and PIP aquaporins to cold stress in cold tolerant species.

FLOODING STRESS EFFECTS ON ROOT WATER UPTAKE

Plant flooding stress occurs in soils close to riparian zones or in regions with transitory heavy rains and poor soil drainage (Nicolás et al., 2005; Herrera et al., 2008). Under flooding conditions oxygen molecules are depleted quickly by root and microbial respiration. Hence, root metabolism is altered changing from aerobic respiration to fermentation causing a drop in the cytoplasmic pH (Kulichikhin et al. 2007). This acidification plus other chemical signals from the roots induce stomatal closure and decrease transpiration rate (Ahmed et al., 2006; Else et al., 2006). At the same time root exuded sap flow diminishes together with L (Jackson et al., 2003). However, under certain circumstances, a recovery of L upon flooding has been observed (Herrera et al., 2008). This recovery is due to the transpiration recovery and to the aeration of the roots, caused by changes in its anatomy (Herrera et al., 2008).

In an elegant study, Tournaire-Roux et al. (2003) found a close relationship between a decrease of cytosolic pH and a decrease of L in *Arabidopsis* plants. At the same time, these authors found that a drop of cytosolic pH caused the protonation of a histidine residue of PIP genes, and that this protonation caused, at the same time, a decrease of PIP water transport activity. Although Tournaire-Roux et al. (2003) were focused on flooding stress, a drop of cytosolic pH have been also observed in other abiotic stresses like salt in sensitive species (Kader et al., 2007). Therefore, this regulation mechanism of PIP activity could be involved in the reduction of L by other stresses, but it needs to be checked empirically.

ABSCISIC ACID AND OTHER SIGNALS EFFECTS ON ROOT WATER TRANSPORT

Plant response to abiotic stresses is mediated by several molecular signals including different hormones and chemicals. Abscisic acid (ABA) is the most studied plant hormone involved on plant response to abiotic stresses (Hirayama and Shinozaki, 2007; Kim, 2007). At leaf level, it is well known how ABA induces stomatal closure (Wang and Song, 2008). Thus, ABA induces the production of reactive oxygen species and reactive nitrogen species, which stimulate the release of calcium, the activation on anion channels and eventually the efflux of potassium that causes the stomatal closure (Munemasa et al., 2007). However, the signals involved in ABA modification of root hydraulic properties are poorly explored (Aroca, 2006).

When ABA is applied exogenously to plants via foliar spraying (Aroca et al. 2006) or dilution into nutrient solution (Aroca et al., 2003; Aroca, 2006), ABA induces (Aroca, 2006; Aroca et al., 2006), has no effect (Wan and Zwiazek, 2001), or reduces (Aroca et al., 2003) L. These discrepancies could be caused by the different plant species used, differences in ABA concentrations applied, or the different environmental conditions. However, the most common effect of ABA is increasing L. Aroca (2006) found that, at certain ABA concentrations (between 1 and 5 μM), exogenous application of catalase (an enzyme that removes H_2O_2) or ascorbate (a broad range antioxidant) diminished the increase of L mediated by ABA. However, at higher concentrations of ABA, exogenous catalase had the opposite effect. Hence, although a clear conclusion was not possible to establish, it seemed obvious that reactive oxygen species were involved in the effect of ABA on L.

In apparently opposite studies to that of Aroca (2006), several authors have found that exogenous H_2O_2 induced a reduction of L (Ktitorova et al., 2002; Rhee et al., 2007). However, in other studies the effect of H_2O_2 on L depended on the plant tolerance to an oxidative stress (Aroca et al., 2005). Therefore, as it has been pointed out (Miller et al., 2008), H_2O_2 can have a dual function acting either as a molecular signal or as a damaging agent, depending on its concentration in the plant cells.

Other hormone involved in the regulation of plant water relations under abiotic stress conditions is methyl jasmonate (MeJ). In fact, MeJ acts similarly to ABA in closing stomata during abiotic stresses (Munemasa et al., 2007). However, little is known about the effect of MeJ on root water transport properties. Only a study by Lee et al. (1996) deals marginally with the effect of MeJ on root exudation rate in rice, reporting a positive effect.

The well known second messenger Ca^{2+} has also a role on regulating root hydraulic properties under abiotic stress conditions, especially under salt stress. In fact, although under *in vitro* conditions, Ca^{2+} ions inhibit aquaporin activity (Gerbeau et al., 2002), it is well known that Ca^{2+} also alleviates the inhibition of L caused by salt stress (Martínez-Ballesta et al., 2006). Again deeper studies are needed to understand the role of Ca^{2+} on the regulation of root hydraulic properties under abiotic stress conditions.

CONCLUSION

In the last decade a big effort has been taken to understand how root water transport responded to abiotic stresses, especially to drought and salinity, being other abiotic stresses less studied. It is well established that root water transport is as important as stomata regulation in order to keep plant water status in normal values under abiotic stress conditions. Nevertheless, it still remains unknown how this response is achieved at a molecular level. In fact, although it seems clear that aquaporins should be involved in that response, it is difficult to set a scenary integrating aquaporins and L, most probably due to the size and diversity of plant aquaporins gene family and to the different role of each plant aquaporin in response to each type of abiotic stress. At the same time, we need also to integrate the several molecular signals involved in the response of root hydraulic properties to different abiotic stresses.

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