Influence of saline stress on root hydraulic conductance and PIP expression in Arabidopsis

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Summary

Measurements of the root hydraulic conductance ($L_0$) of roots of Arabidopsis thaliana were carried out and the results were compared with the expression of aquaporins present in the plasma membrane of A. thaliana. $L_0$ of plants treated with different NaCl concentrations was progressively reduced as NaCl concentration was increased compared to control plants. Also, $L_0$ of plants treated with 60 mmol/L NaCl for different lengths of time was measured. Variations during the light period were seen, but only for the controls. A good correlation between mRNA expression and $L_0$ was observed in both experiments. Control plants and plants treated with 60 mmol/L NaCl were incubated with Hg and then with DTT. For these plants, $L_0$ and cell-to-cell pathway contributions to root water transport were determined. These results revealed that in control plants most water movement occurs via the cell-to-cell pathway, thus implying aquaporin involvement. But, in NaCl-stressed plants, the Hg-sensitive cell-to-cell pathway could be inhibited already by the effect of NaCl on water channels. Therefore, short periods of NaCl application to Arabidopsis plants are characterised by decreases in the $L_0$ of roots, and are related to down-regulation of the expression of the PIP aquaporins. This finding indicates that the well known effect of salinity on $L_0$ could involve regulation of aquaporin expression.

Key words: apoplastic pathway – aquaporins – Arabidopsis – Cell-to-cell pathway – oxygen consumption – root hydraulic conductance – mRNA expression

Introduction

Water channels or aquaporins, proteins that enhance the permeability of biological membranes to water, are widely distributed in living organisms. Several criteria have been used to infer the presence of water transporting channels in cell membranes. These include a high ratio of osmotic to diffusional water permeability ($P_o/P_d > 1$) (Zhang and Verkman 1991, Chrispeels and Agre 1994) and a low Arrhenius activation energy for water transport ($E_a < 6$ Kcal mol⁻¹) (Verkman et al. 1996). One of the most common characteristics of aquaporins is that they can be blocked by sulphydryl reagents, such as mercurials (e.g. HgCl₂), resulting in decreased water permeability of the membranes. These changes are reversed when the Hg²⁺ is removed from the membrane by reagents such as dithiothreitol (DTT) (Kammerloher et al. 1994). In addition, the...
hydraulic conductivity of the plasma membrane in the alga *Chara* was greatly reduced by brief exposure to mercury and was restored by treatment with DTT (Henzler and Steudle 1995). Similar results were obtained with the hydraulic conductance of wheat roots (Maggio and Joly 1995, Carvajal et al. 1996, Quintero et al. 1999), suggesting a relationship between hydraulic conductance and aquaporins.

In plants, aquaporins are likely to function in a variety of processes that require regulated water flow (Maurel 1997). The expression profile of several aquaporin isoforms suggests that these proteins also play a role in several processes such as seed germination, (Gao et al. 1999), leaf growth (Lu and Newmann 1999), cell elongation (Chaumont et al. 1998), and N2 fixing nodules (Serraj et al. 1998). Some water channels are not only selective for water, but also are capable of transporting low molecular weight solutes (Hertel and Steudle 1997). A new plasma membrane water channel from tobacco, NtAQP1, has been demonstrated to be permeable to water and glycerol (Biela et al. 1999) as well.

Aquaporins are 25 to 30 kDa membrane proteins with similar primary sequences belonging to the major intrinsic protein (MIP) family that forms water channels. These proteins exhibit a typical structure with six transmembrane spanning domains and some perfectly conserved residues, including a Asn-Pro-Ala motif, in both the first intra-cytoplasmic and third extracytoplasmic loops of the protein (Reizer et al. 1993). A cysteine residue (c-189) was first identified as the site of inhibition when binding to c-189, but Barone et al. (1997) observed an inhibitory effect of Hg2+ on water permeability in oocyte expression systems could be due in part to Hg2+ induced conformational change in the aquaporin structure.

Various internal and external factors, such as plant development, stress, hormones and light, alter the expression of aquaporins. Previously, it has been suggested that N-deprived wheat roots could decrease PIP mRNA expression in parallel with lower root hydraulic conductivity of excised roots, Lp (Clarkson et al. 2000). A diurnal cycle of Lp, in the roots of *Lotus japonicus* has been observed independently of the rate of water flow across the root. The cycle was matched by fluctuations in the abundance of an mRNA that hybridizes with cDNA probes from *Arabidopsis thaliana* AthPIP1 a (Henzler et al. 1999). Furthermore, it has been reported that salinity alters water channel mRNA levels in *Mesembryanthemum crystallinum* and *Nicotiana excelsior* (Yamada et al. 1995, 1997). These results suggest that plants can modulate the abundance of water channel mRNAs in their tissues. Such modulation also could occur by phosphorylation (Maurel et al. 1995) and this may be the major mechanism by which plant cells alter their membrane permeability to water.

Plant material

Seeds of *Arabidopsis thaliana* (cv. Columbia) were maintained for 10 min at 4 °C, hydrated for 30 min with deionised water and then sterilised with 5% bleach solution. After rinsing twice with sterile water, seeds were germinated in the dark at 25 °C on trays containing vermiculite. After three days, trays were placed in a controlled environment chamber, with a 16-h photoperiod at 25 °C, 80% relative humidity (RH) and photosynthetically active radiation (PAR) of 400 µmol m⁻² s⁻¹, and 8 h in the dark at 22 °C and 60% RH. After two weeks, the seedlings were placed on 0.5 L containers filled with a continuously aerated nutrient solution based upon that of Gibeaut et al. (1997), but modified to give the following composition: KNO₃ (1.25 mmol/L), Ca(NO₃)₂ (1.50 mmol/L), NH₄H₂PO₄ (0.50 mmol/L), MgSO₄ (0.75 mmol/L), KCl (50 µmol/L), H₂BO₃ (25 µmol/L), MnSO₄ (2.0 µmol/L), ZnSO₄ (2.0 µmol/L), CuSO₄ (5.0 µmol/L). H₂MoO₄ (0.5 µmol/L), Fe-EDDHA (72 µmol/L).

Experimental design

In order to study the effect of NaCl on hydraulic conductance and the relationship with water channel AthPIP1;1 expression, different concentrations of NaCl were applied to the nutrient solution of the *Arabidopsis* plants. When the plants were 5 weeks old, concentrations of 20, 40, 60, 80, and 100 mmol/L NaCl were added and 24 h later the hydraulic conductance (Azaizeh and Steudle 1991, Carvajal et al. 1999, Martínez-Ballesta et al. 2000). Although the mechanism by which salinity reduces the hydraulic conductance in cells and roots is still unknown, we suggested that it could be due to changes either in the water channel function or in the mRNA levels present in the membrane (Carvajal et al. 1999, 2000, Martínez-Ballesta et al. 2000).

In this paper, we report on the relationship between PIP (plasma membrane intrinsic protein) gene expression and NaCl addition, taking into account different salt concentrations and different assay times after 60 mmol/L NaCl treatment. We also studied the correlation between Lp values and transcript levels. Based on the composite transport model (Steudle and Frensch 1996), water transport occurs via three parallel pathways: apoplastic, symplastic, and transcellular, including root aquaporins. However, because it is experimentally difficult to discriminate between symplastic and transcellular movement of water, they are collectively referred to as the cell-to-cell movement of water (Steudle and Peterson 1998). Dye solution was used to trace root water transport and to detect the effect of HgCl₂ on the cell-to-cell and apoplastic fluxes in control plants and plants treated with 60 mmol/L NaCl. Finally, we studied the HgCl₂ effect on control plants and on plants treated with 60 mmol/L NaCl, comparing the effects of Hg and NaCl on Lp. Also, the HgCl₂ effect on root respiration, measured as oxygen consumption, was studied in roots of control plants, before and after DTT addition, in order to discover the consequences of Hg addition on root respiration.
roots were treated with NaCl and the control roots were collected for RNA extraction and hydraulic conductance measurements. The NaCl treatments were applied to the nutrient solution in increments of 20 mmol/L each hour to give a final NaCl concentration of 20, 40, 60, 80, and 100 mmol/L NaCl. In the second experiment, a 60 mmol/L NaCl treatment was added to the nutrient solution, and the control roots and NaCl-treated roots were collected and root L₀ measured at different times after the addition of NaCl, which took place 2 h after the beginning of the light period. The NaCl treatment was applied to the nutrient solution in increments of 30 mmol/L each half an hour to give a final NaCl concentration of 60 mmol/L. Measurements were made 2, 6, 10, and 15 h after the beginning of the light period during the first day and 2 h after the beginning of the light period on the second and third days. Gene expression was determined also. Both gene expression experiments were repeated three times.

**Measurement of L₀**

A Scholander pressure chamber was used to measure hydraulic conductance (L₀). The method was based on volume flow through a detached root system. The aerial parts of the plant were removed leaving a stem cylinder, which was sealed with silicone grease into a tapered glass tube. Detached roots were placed into the chamber and a gradual increase of pressure (from 0.1 to 0.5 MPa) was applied to the solution surrounding the roots. The solution had the same composition as the one used during the growth of the plants. The xylem sap exuded for 4 min at each pressure was collected in Eppendorf tubes and weighed. Finally, the roots were weighed as well. The slope of the linear part of the calculated xylem flow, Jᵥ, plotted versus pressure gave the L₀ value (Else et al. 1995). Saturation of roots was not compromised.

**Measurement of apoplastic pathway**

Light green dye (Light Green SF Yellowish; Aldrich Chemical Co. Ltd., Gillingham, Dorset, UK) moves through healthy plant tissue apoplastically, but not symplastically (Epel and Bandurski 1990). Dye solution (253.3 µmol/L) was added 15 min prior to sap collection for control plants and plants treated with 60 mmol/L NaCl. Xylem sap was collected from de-topped roots pressurised from 0.2 to 0.5 MPa, as described above. The concentration of the dye was determined immediately in samples of xylem sap, using a Beckman DU-40 UV spectrophotometer, at 630 nm. Percentage of apoplastic pathway was calculated from the concentration of dye in xylem sap. 100% was considered the concentration of the dye in the nutrient solution.

**Effect of Hg on L₀ and on oxygen consumption**

The effect of HgCl₂ on L₀ and water transport (cell-to-cell and apoplastic) was determined. Control plants and plants treated with 60 mmol/L NaCl were incubated with 50 µmol/L HgCl₂ for 10 min. After this time, the plants were transferred into a new container with fresh nutrient solution to avoid Hg toxicity. Then L₀ was measured. Subsequently, the Hg was scavenged by 2 mmol/L DTT (for 15 min) and L₀ was measured again.

**RNA extraction**

Root tissue from 10 plants (1.5 g fw) was ground in a mortar with liquid nitrogen and total RNA was isolated by a modified protocol of Verwoed et al. (1989) using 6 mL of extraction buffer and 6 mL of phenol/chloroform/isooamylic alcohol (25:24:1). After centrifugation, the supernatants were washed with phenol/chloroform/isooamylic alcohol. Finally, total RNAs were resuspended in 50 mL of DEPC-treated water and the concentrations were estimated spectrophotometrically by absorbance at 260 nm. In order to visualise the quality of extractions, total RNAs were run in 1% agarose TAE gels and stained with ethidium bromide.

**Probe synthesis**

A specific clone containing the gene AthPIP1;1 (927 bp), kindly provided by D.T. Clarkson, was used to obtain a DIGoxigenin-labeled DNA probe. Enzymatic digestion was carried out and the gene fragment obtained was purified from gel using the Quiaagen kit. 1 µg of this fragment was used to synthesise the DIG DNA probe, the subsequent quantification was as described by the manufacturer (Roche).

**Northern analysis**

For Northern analysis, total RNA (20 µg) was fractionated in a denaturating formaldehyde agarose (1%) gel and transferred overnight onto nylon membranes (Roche) by capillarity using 10×SSC buffer, pH 7.0 (Sambrook et al. 1989). Membranes were air-dried and the nucleic acids were bound (fixed) by using UV irradiation from a transilluminator for 3 min. Northern blots were pre-hybridised for 2 h at 58°C with high SDS concentration hybridisation solution (Roche; 7% SDS, 50% deionised formamide, 0.1% sodium-laurylsarcosine, 2% blocking reagent). Hybridisations were carried out overnight in the same solution at 58°C with the addition of 25 ng of DIGoxigenin-labelled DNA probe. After hybridisations, the membranes were washed as previously described by Pallás et al. (1998), but with two additional washes at 58°C for 15 min with 0.5×SSC plus 1% (w/v) SDS, which were incorporated after the two washes at room temperature. Chemical luminescence detection, using CSPD (Disodium 3-[4-methoxyphenyl]-1,2-dioxo-tane-3,2′-chloro tricyclo[3.3.1.1^{3,7}] decan]-4-yl)phosphosphate) reagent as substrate, was carried out as recommended by the manufacturer (Roche). Films were exposed for 30–60 min before development.
Signal density of northern stains

Signal density of Northern stains was measured using a densitometer (Shimazdu CS-9000). The area of the peaks provided by the densitometer was used for signal intensity calculations. Control plant area was 100% of signal intensity and other percentages were calculated from that (Data not shown).

Data analysis

Data were analysed using analysis of variance (ANOVA) procedures and means separated by Duncan’s multiple range test.

Results

Effect of salinity on root hydraulic conductance

Measurements of the root hydraulic conductance were performed with control plants and plants treated for 24 h with different NaCl concentrations (20, 40, 60, 80 and 100 mmol/L) using the Scholander pressure chamber (Fig. 1). There were no significant differences between \( L_0 \) of control plants and \( L_0 \) of plants treated with 20 mmol/L NaCl. However, with 40, 60, 80, and 100 mmol/L NaCl treatments, \( L_0 \) decreased progressively with respect to control plants. There were no significant

Figure 1. Root hydraulic conductance (\( L_0 \)) (measured with the Scholander pressure chamber) of Arabidopsis control plants and plants treated with different NaCl concentrations (20, 40, 60, 80, and 100 mmol/L) for 24 h. Number of plants = 5. Error bars = SE. For each column, values with the same letter are not significantly different at 5%.

Figure 2. Variation of root hydraulic conductance (\( L_0 \)) (measured with the Scholander pressure chamber) for Arabidopsis control plants and plants treated with 60 mmol/L NaCl during the light period of the first day and after 1 and 2 days. Salt was applied the first day, 2 h after light started. Number of plants = 5. Error bars = SE.
differences between the $L_0$ values of roots of plants treated with 80 mmol/L and 100 mmol/L NaCl, showing reductions of 72% with respect to control.

The variation with time during the light period of the root hydraulic conductance in controls and in plants treated with 60 mmol/L NaCl was determined (Fig. 2). In control plants, a change during light period in $L_0$ was observed. A significant increase in $L_0$, which reached a maximum 6–7h after the light came on, was observed. A decrease then occurred 4 h later, with the minimum value being just before the dark period started. In plants treated with 60 mmol/L NaCl, $L_0$ decreased significantly after 4 h of NaCl application, but a slight and progressive increase was observed after the first and second day of treatment. The diurnal cycle did not significantly affect $L_0$ values of NaCl treated plants, which were similar for different time intervals during the light period.

Sensitivity to mercury

The effect of HgCl$_2$ was examined for control plants and plants treated with 60 mmol/L NaCl (Fig. 3). $L_0$ of control plants declined rapidly after 5 min of treatment with 50 µmol/L HgCl$_2$ (prior to measurement of $L_0$) to values similar to those obtained for 60 mmol/L NaCl treated plants; the reduction was 51%. Addition of DTT (2 mmol/L) restored $L_0$ to values similar to initial (pre-HgCl$_2$) values. In 60 mmol/L NaCl treated plants $L_0$ values were only slightly affected when HgCl$_2$ or DTT was added, showing a reduction of 9%.

The effect of HgCl$_2$ on total root respiration was measured in control plants (Fig. 4). There were no significant differences in oxygen uptake between control plants and plants treated with 50 µmol/L HgCl$_2$, or plants treated with 2 mmol/L DTT after Hg addition.
Measurement of apoplastic and cell-to-cell pathway

Control and 60 mmol/L NaCl treated plants were incubated for 30 min with a dye that was transported only by the apoplastic pathway (Fig. 5). In control plants, we observed that 87% of water was transported by the cell-to-cell pathway, whereas in plants treated with NaCl the percentage was 70%. When HgCl₂ was added to control plants, the percentage of water transported by cell-to-cell pathway decreased to 56%, but in plants treated with 60 mmol/L NaCl there was no significant change after Hg addition. When DTT was added, water transport via the cell-to-cell route increased to the initial percentage observed in control plants. However, in plants treated with 60 mmol/L NaCl, the cell-to-cell pathway percentage remained unchanged.

Effect of salinity on gene expression

Total RNA from the control roots and those treated with different concentrations of NaCl (20, 40, 60, 80 and 100 mmol/L) for 24 h was extracted. Transcripts hybridising to an AthPIP1;1 cDNA probe were abundant (Fig. 6) and the amount of mRNA decreased as the concentration of NaCl increased. Thus, the abundance of the hybridising transcript was much lower for plants treated with 100 mmol/L NaCl as compared with the control plants. There is a great deal of sequence homology between members of the large aquaporin gene family. It is probable that the aquaporin probe hybridises to several homologues in the mRNA pool. Hybridisation cannot be taken, therefore, as evidence for the specific existence of the PIP1;1 member of the gene family.

Roots from plants grown in a controlled environment with a 16-h photoperiod were harvested at intervals and their total RNA was extracted as described in the Material and Methods section. In control plants, transcripts varied in abundance during the diurnal cycle; a distinct maximum was evident 6–7 h into the photoperiod, followed by a marked decline to a minimum value at, or shortly after, the beginning of the dark period. There was an indication that the abundance of the hybridising transcripts increased with a new photoperiod (at 26 h and 50 h). In plants treated with 60 mmol/L NaCl, the amount of hybridising mRNAs was lower than in control plants and a diurnal rhythm was observed with respect to the abundance of transcripts, but the time of day effect was not strong enough to explain the difference from control plants (Fig. 7).

Discussion

The reductions in root hydraulic conductivity (Lₚ) of salinised plants have been suggested as being due to the hyperosmo-
the PIPs mRNA expression of *A. thaliana* induced by desiccation (Fray et al. 1994, Guerrero et al. 1999). Therefore, the responses to stresses in plants have been related to aquaporins. For example, in *glycophytes*, expression of water channel PIPs genes was induced by desiccation (Fray et al. 1994, Guerrero et al. 1990). In rice, an initial decline of aquaporin expression after water stress, followed by up-regulation after one day, has been observed (Malz and Sauter 1999). For *M. cristalinum* and *N. excelsior*, expression of aquaporin genes was down-regulated for the first 30 h after salt stress (Yamada et al. 1995, 1997).

The results shown by Henzl et al. (1999) with *L. japonicus* suggested that there may be a *de novo* synthesis and/or degradation of aquaporins during the diurnal cycle that affects water flow by changing the root L₀. The second experiment of the current work took that factor into account. We studied the time course effect of 60 mmol/L NaCl addition, with respect to a control. The results presented in this paper show a diurnal variation in root hydraulic conductance (L₀) of *A. thaliana*. L₀ reached its maximum value 6–7 h after the start of the light period. This variation was coincident with a diurnal rhythm of the expression of mRNA encoding PIP aquaporins in the plasma membrane of roots. These results were similar to those obtained in *L. japonicus* (Henzl et al. 1999, Clarkson et al. 2000). We also observed that L₀ values in plants treated with 60 mmol/L NaCl were lower than in control plants, coinciding with the lesser abundance of hybridising transcripts. This fact suggested that NaCl decreased the amount of mRNA that encoded the aquaporin proteins. The diurnal cycle variation was not significant in plants treated with 60 mmol/L NaCl, for either L₀ or mRNA expression, indicating that stress repressed the diurnal rhythm.

Heavy metal ions, such as Hg²⁺, are known to inhibit the water transport activity of some mammalian aquaporins (Zhang et al. 1993), some tonoplast water channels (Maurel et al. 1993) and some plant plasma membrane aquaporins (Kammerloher et al. 1994), although some plasma membrane aquaporins are mercury-insensitive (Daniels et al. 1994). Using site-directed mutagenesis, it has been shown that Hg²⁺ binds to cysteine residues in or near the aqueous pore of the aquaporins, thereby inhibiting water transport (Agre et al. 1998, Daniels et al. 1996). The assumption that the addition of a heavy metal solution specifically blocks aquaporins was supported by the fact that the swelling of water channel-expressing oocytes could be reduced greatly by a specific concentration of mercury chloride (Preston et al. 1992). To account for these results, we conclude that heavy metal ions specifically block aquaporins and, consequently, which could indicate the significance of these proteins in whole plant or cellular water transport. Although this conclusion seems to be reasonable, it is necessary to bear in mind that the pharmacology of mercurials includes numerous secondary effects (Schütz and Tyerman 1997). In any case, some of the aquaporins are known to be characteristically Hg-sensitive, either by a direct blockade of the channel or by a secondary effect. Respiration experiments showed that 0.1 mmol/L HgCl₂ did not significantly reduce root respiration during the initial hour of treatment in aspen seedlings (Wan and Zwiazek 1999).

This suggested that the mercuric inhibition of root water flow was probably not due to metabolic inhibition. Only higher

**Figure 7.** (A) Northern blot of total RNA extracted from roots of Arabidopsis control plants and plants treated with 60 mmol/L NaCl applied 2 h after beginning of the light period. Samples were taken at different times during the photoperiod (2 h after starting), 2 h, 6 h, 10 h, 15 h, 26 h, 48 h. Total RNA was hybridised with a specific probe for the water channel PIP1a present in the plasma membrane from *A. thaliana*. (B) As a reference for differences in loading total RNA in the same concentration for the different treatments, was stained with ethidium bromide.

Aquaporins allow water to pass freely across cellular membranes following osmotic or hydrostatic pressure gradients (Chrispeels and Maurel 1994). These proteins provide an organism with the possibility to accelerate water movement across membranes, but diffusion will still occur in parallel. Furthermore, the ability to increase or decrease the water permeability of a cell seems to justify the enormous effort involved in expressing large amounts of these proteins (Schäffner 1998). Therefore, the responses to stresses in plants have been related to aquaporins. For example, in *glycophytes*, expression of water channel PIPs genes was induced by desiccation (Fray et al. 1994, Guerrero et al. 1999).
concentrations of HgCl₂ and longer treatments reduced root oxygen consumption. In A. thaliana we observed that there were no significant differences in oxygen consumption during the period of Hg treatment (10 min). These results suggested that, although it is known that Hg has an effect on general metabolism, the short exposure time and the low concentration of Hg used did not affect root respiration. It has been reported also that the Hg⁺ concentration (50 µmol/L) and duration of exposure (10 min) used only seemed to affect water transport through roots, demonstrated by the fact that the flux of K⁺ into the xylem was not altered (Maggio and Joly 1995, Carvajal et al. 1999). The effect of Hg⁺ is important in light of a report that suggested that the regulation of sulfhydryl groups by a plasma membrane reductase system can alter the transport of osmotically important cations, especially K⁺, across the root cell plasma membrane (Welch et al. 1993).

The apoplastic dye was used to trace root water transport and to detect the cell-to-cell and apoplastic flux, revealing that in control plants the percentage of water through the apoplastic pathway was lower than in plants treated with 60 mmol/L NaCl. When Hg was added this percentage increased for control plants, whereas in plants treated with NaCl the HgCl₂ effect was not significant. These results, and the fact that the apoplastic route was restored to initial values in control plants after DTT addition, showed that most water movement occurred via the cell-to-cell pathway, implying the involvement of aquaporins. But in NaCl-stressed plants the cell-to-cell Hg-sensitive pathway already could be inhibited by an effect on aquaporins.

The hypothesis suggested previously, that the very weak response of the Lₒ of salt-stressed roots to Hg-treatment could be because water channels were greatly reduced in numbers, or, if present, were non-functional, is supported by the results of this paper. Although we reported previously that the inhibition of water channel activity in NaCl-treated melon plants or protoplasts was probably due to a direct action on the proteins that regulate water channel opening and closing (Martínez-Ballesta et al. 2000), the results of this paper reveal that gene regulation is also involved in the response of plants to salt stress. Therefore, it could be possible that both types of regulation act depending on factors like NaCl concentration, duration of stress application or plant genotype. Short periods of NaCl application to Arabidopsis plants are characterised by marked changes in the Lₒ of roots and are related to the down-regulation of the expression of aquaporins. This finding indicates that the well known effect of salinity on Lₒ, involves regulation of aquaporins expression. Therefore, differences in the regulation of aquaporin function may reflect stress tolerance in plants. Consequently, if aquaporins dominate trans-membrane water movement and can be regulated like other channels, then this introduces the possibility of control of water movement under salt stress conditions. However, the implication of each PIP water channel of Arabidopsis should be investigated.

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Root hydraulic conductance, salinity and aquaporins


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