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# Effect of water deficit and membrane destruction on water diffusion in the tissues of maize seedlings

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## Abstract

We investigated diffusion of water in maize seedlings (*Zea mays* L. cv. Dnepropetrovskaya) following addition of polyethylene glycol (PEG) 6000 (osmotic potential -0.1 and -0.3 MPa) to the root medium by NMR method with pulsed gradient of magnetic field. Diffusion coefficients of different water phases in plant tissues (water of apoplast and vacuoles, water transported through the membranes) have been estimated from multicomponent decays of echo amplitude. Different signs of changes of water diffusion coefficients of fast and slow components of diffusional echo decay in roots and leaves under the influence of PEG-induced water deficits were shown. It has been supposed that under water deficit a sharing of water flows takes places through the different pathways (apoplastic, symplastic and transmembrane). In roots, 1-h water deficit increased the rate of fast diffusing water (water of apoplasm, vacuoles and, perhaps, water contained in intercellular endoplasm system), and decreased the rate of slowly diffusing water (water passing across the membranes). A long-term water deficit increased to a small extent the rate of water transmembrane transfer in root tissue. Leaf response to water stress was in the intensification of rate of transmembrane water transport that could be connected with the expression of water channels, and in the decrease of apoplastic water flow and flow along endoplasm. The possibility of estimation of plant tissue (membrane) integrity on the basis of diffusional data has been demonstrated.

*Additional key words*: apoplastic water transport, symplastic water transport, water permeability, *Zea mays*.

## Introduction

For estimation of the physiological status of the plant under stress it is important to determine changes in metabolism underlying response to changed environmental conditions, and also to estimate quickly and certainly the level of organism injury. Great attention is paid to changes in cell membrane systems as the most sensitive to unfavourable environmental conditions (Navari-Izzo *et al.* 1993, Quartacci *et al.* 1995). It has been shown that osmotic stress induces rapid changes in cell wall conductivity (Nonami and Boyer 1990a,b, Chazen and Neumann 1994) and plasmalemma (Gennis 1997). The maintenance of membrane integrity plays a decisive role in the plant tolerance to osmotic stress (McKersie and Stinson 1980), freezing (Pearce 1985), and drying (Tetteroo *et al.* 1996). The permeability regulation can be accomplished by opening and closing of water channels formed by the membrane polypeptide complexes including aquaporins (Daniels *et al.* 1994, Robinson *et al.* 1996, Maurel 1997, Chrispeels *et al.* 1999), and also by phase transitions of the membrane lipids (Crowe *et al.* 1989, 1992).

It has been known that parallel apoplast, symplast and transcellular pathways play an important role during the passage of water across the different plant tissues and there is a rapid exchange of water between these pathways (Steudle 1997). Depending on the type of tissue, its developmental state and environmental conditions, a relative contribution of these pathways to overall water flow may differ. So, under conditions of water deficit, the apoplastic by-pass in the root is not effective and cell-to-cell component dominates (Steudle and Peterson 1998). Switching between water pathways

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*Abbreviations:* NMR - nuclear magnetic resonance, PEG - polyethylene glycol, $A(g^2)$ - diffusional decay of echo signal amplitude, $t_d$ - diffusion time, $D_{ef}$ - water diffusion coefficient.

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allows the plant to optimize the water relations under the unfavourable environmental conditions.

The use of NMR method for the study of water diffusion in plant tissues (Anisimov *et al.* 1983, 1998) gave the possibility of distinguishing the symplast water transport from the apoplast one (Anisimov and Ratkovic 1992). In recent investigations, the data confirming the presence of two transport channels of plasmodesmata-desmotubule and cytoplasmic ring (the known model of Robards), which connect correspondingly vacuoles and cytoplasm of the adjacent cells, were obtained by the method of confocal laser scanning microscopy (Knebel *et al.* 1990, Lassaro and Thomson 1996). This notion was used for interpretation of compound diffusional decays of echo signal amplitude of cellular water in the NMR experiment (Velikanov *et al.* 1999).

The aims of this study were *1*) to examine the influence of PEG-induced water deficit on the water diffusion in roots and leaves of maize seedlings with the attempt of subsequent assessment of contributions of different transport ways of water; *2*) to affect this transport by artificially induced changes of structural integrity of membranes. To achieve these aims we used the NMR method to determine the diffusion coefficients of water in intact, water stress exposed, and destroyed tissues of maize seedlings.

## Materials and methods

The experiments were conducted with 7- to 10-d-old seedlings of maize (*Zea mays* L. cv. Dnepropetrovskaya). After germinating in darkness on moistened filter paper for 3 d, the seedlings were mounted in drilled holes in special plastic holders and transferred to containers (5 $dm^3$ capacity, 25 plants per container) with continuously aerated, ¼ strength Hoagland-Arnon nutrient solution. Plants were grown under controlled conditions: 14-h photoperiod, irradiance of 15 W $m^{-2}$, day/night temperature of 25/18 °C and relative humidity of 60 %. To study the effect of PEG-induced water deficits intact seedlings were transferred to nutrient solutions containing polyethylene glycol 6000 (PEG) of various concentrations (osmotic potential -0.1 and -0.3 MPa) for 1 h and for 24 h. Then the seedlings were taken from solution, the roots were rinsed in distilled water, leaves and roots were cut and taken for the diffusion measurements. To study the effect of factors causing the membrane destruction, the excised roots were affected by the vapour of liquid nitrogen or diethyl ether, or boiling water vapour for 5 min, or by long-term low temperature (-10 °C for 24 h).

Diffusion of water was measured in the excised roots (in radial direction) and leaves (in transversal direction) by the spin echo NMR method with pulsed magnetic field gradient on a frequency of 19.2 MHz. Registration of diffusional decays of echo signal amplitude $A(g^2)$ in the range of 3 orders of magnitude affords the most complete estimation of the translational diffusion of different water phases. Multicomponent diffusional decay typical of plant tissue was divided into components by consecutive subtraction of exponents. Water diffusion coefficients ($D_{ef}$) were calculated for each component. Achievement of the plateau in dependence of $D_{ef}$ on diffusion time ($t_d$) (see Fig. 2*A*) allows us to determine the range of effective averaging of water diffusion between cells due to membrane permeability effect.

## Results and discussion

The dependence of diffusional decays $A(g^2)$ for water of excised roots of maize seedlings at different diffusion times ($t_d$) is of a nonexponential character at all $t_d$ (Fig. 1). Therefore the key moment is the division of $A(g^2)$ in components and then the attribution of these components to the concrete water fractions of the studying system. At least two components can be distinguished in this dependence: fast and slow decaying components. The fast decaying component, characterized by high diffusion rate, is attributed to water of apoplast and vacuoles; the slow component to intracellular water motion-limited both by the effect of cell membrane permeability and the interactions with non-water cell components (Anisimov and Ratkovic 1992). Also water diffusion along vacuole symplasm (or intercellular endoplasm) can contribute to fast component of diffusional decay (Velikanov *et al.* 1999). Intercellular endoplasm is a continuous transport system including vacuoles, connected by endoplasmic reticulum, which forms the endoplasmic channel in plasmodesmata - desmotubule (van Bel 1996, Gamaleï 1998). Intercellular continuity and fluidity of endoplasm have been confirmed by the investigations with labeled lipids (Grabski *et al.* 1993).

The dependence of $D_{ef}$ of slow and fast components of diffusional decay on $t_d$ for control and PEG exposed maize roots in region of $t_d < 300$ ms, the so-called region of restricted diffusion, mainly characterizes the intracellular water transport depending on water interactions with nonwater cell components. Diffusion coefficient values in region of $t_d > 300$ ms, the so-called region of hindered diffusion, are defined by intercellular water transport and depend on plasmalemma permeability (Fig. 2).

Characteristic restricting dimensions estimated from the equation of Einstein-Smolukhovsky ($a^2 = 6\ D_{rest} \times t_d$, at $t_d$ = 300 ms and $D_{rest}$ =2.5 × $10^{-6}$ $cm^2\ s^{-1}$) is 21 µm, corresponding to the average dimensions of root cells. The coefficient of membrane water permeability $P_d$ of maize seedling roots, calculated from the equation of Crick (1970):

$$1/D_{ef} = 1/D_o + 1/P_d \times r$$

where $D_{ef}$ is the effective coefficient of water diffusion in the region of hindered diffusion (2.5 × $10^{-6}$ $cm^2\ s^{-1}$), $D_o$ is the self diffusion coefficient of water at min $t_d$ (2.5 × $10^{-5}$ $cm^2\ s^{-1}$), r is the distance between membranes (in this case it is equal to average cell diameter, *i.e.* 21µm), amounts to 1.3 × $10^{-3}$ cm $s^{-1}$, that is comparable with the plasmalemma permeability. Pd of maize roots affected by PEG for 1 h amounts to 0.8 × $10^{-3}$ cm $s^{-1}$ ($D_{ef}$ = 1.7 × $10^{-6}$ $cm^2\ s^{-1}$). According to Nobel (1991) the coefficient of water permeability for plasmalemma of maize root is 1 × $10^{-2}$ cm $s^{-1}$.

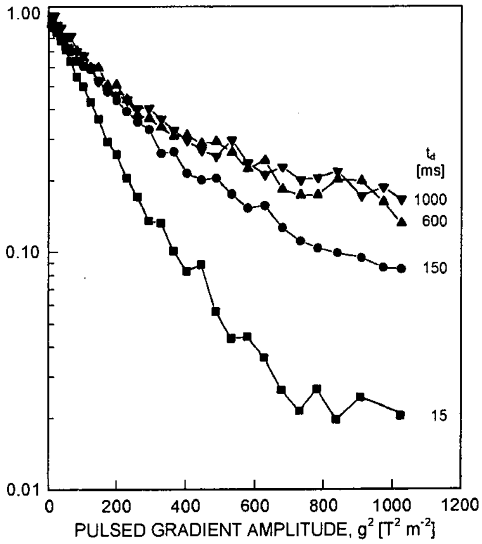

Fig. 1. Diffusional decays of relative echo signal amplitude, A, *vs.* pulsed gradient amplitude, $g^2$, for maize seedling roots at various diffusion times, $t_d$.

The 1-h treatment with PEG (-0.1 and -0.3 MPa) on roots of intact seedlings led to $D_{ef}$ decrease of slow component and $D_{ef}$ increase of fast component (Fig. 2). Taking into account the above mentioned arguments for possible contribution of diffusion of the different water fractions to measurable components of diffusional decay, one can assume that PEG-induced water deficits resulted in the decrease of the water transfer rate across the membranes (transmembrane transfer) and increase of water diffusion along root apoplasm and vacuoles, united into the system of intercellular endoplasm. Decrease of transmembrane transfer can be connected with the reduced activity of water channels and the decreased permeability of membrane lipid bilayer under water shortage. The reduced permeability to water of both root cells and whole maize roots was observed under high salinity (Azaizeh and Steudle 1991, Azaizeh *et al.* 1992). Intensification of water flow along "vacuolar continuum" of symplasm (endoplasm) after water stress can promote the fast recovery of pressure potential along all tissue. A number of studies have shown that replacing the nutrient solution with test solutions of higher osmotic pressure caused biphasic response in root cells: fast decline in pressure potential accompanied by tissue shrinkage and subsequent recovery of pressure potential and growth (Kuzmanoff and Evans 1981, Frensch and Hsiao 1994, 1995).

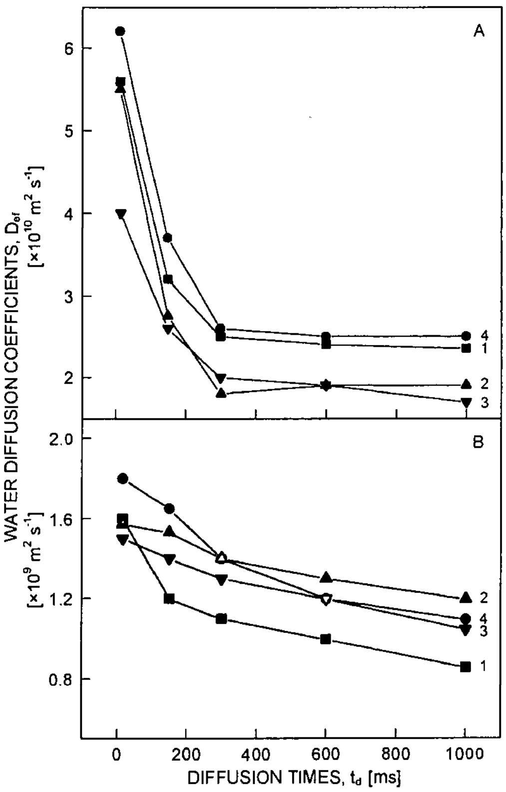

Fig. 2. Dependence of water diffusion coefficients, $D_{ef}$, of slow (*A*) and fast (*B*) components on diffusion times, $t_d$, for maize seedling roots: *1* - control; *2* - PEG -0.1 MPa (1 h); *3* - PEG -0.3 MPa (1 h); *4* - PEG -0.1 MPa (24 h). Each data point is the mean of four measurements obtained from separate samples (SE ± 5 %).

The differences in effects of PEG of various osmotic potentials (-0.1 and -0.3 MPa) are revealed in the region of short times of diffusion $t_d$ (Fig. 2*A*). A considerable decrease of $D_{ef}$ following the influence of PEG (-0.3 MPa) in the region of restricted diffusion can be caused by the viscosity increase of cytoplasm. The seedlings exposed in PEG solution of -0.1 MPa for 24 h showed $D_{ef}$ increase of slow component at all $t_d$ relative to control level. It is perhaps due to the plant adaptive response, connected with switching between water pathways under the influence of long water stress: decrease of apoplastic component and activation of water channels. It has been found that water shortage increases the expression of water channels in maize roots (Guerrero *et al.* 1990).

To determine whether the $D_{ef}$ increase is connected with the membrane injuries, we measured water diffusion under the influence of factors, which cause the membrane destruction (Fig. 4). A considerable increase of $D_{ef}$ and the lack of $D_{ef}$ response to $t_d$, the absence of restriction region at $t_d$ < 200 ms, testifies to the integrity breaking and loss of barrier properties of membranes under the influence of 5 min effect of vapour of liquid nitrogen and diethyl ether and boiling water vapour (Fig. 4). Root freezing at temperature -10 °C in cool camera for 24 h has led to diffusion increase, but the restriction effect has remained apparently at the expense of incomplete cell destruction. Thus the diffusion data allow quickly and safely enough to estimate the structural integrity of membranes after the effect of various destructive factors. Taking into account the data of Fig. 4, we conclude that the $D_{ef}$ increase of maize roots subjected to osmotic stress within 24 h can not be the consequence of some injuries of the membrane structures.

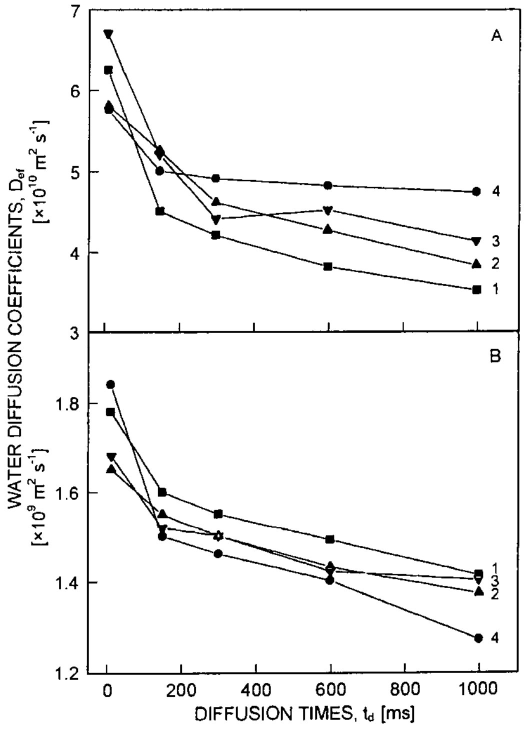

Fig. 3. Dependence of water diffusion coefficients, $D_{ef}$, of slow (*A*) and fast (*B*) components on diffusion times, $t_d$, for maize seedling leaves. Numeric designations are the same as in Fig. 2. Each data point is the mean of four measurements obtained from separate samples (SE ± 5 %).

In the seedling leaves the PEG-induced water deficit caused qualitatively different $D_{ef}$ response: $D_{ef}$ increased in slow and decreased in fast components of echo attenuation (Fig. 3). The lowering of water content in leaf cells under the water stress conditions results in endoplasm breaking, *i.e.* rupture of intercellular contacts (plasmodesmata) or their conformational changes (Gamaleï 1994, 1998) and as consequence in the rate decrease of the intercellular water transfer through plasmodesmata. It is known that plasmodesmata are the most vulnerable part of the transport net (Gamaleï 1996). Another cause of decrease of the rate of fast diffusing water can be the conductivity reduction of cell wall for water under the osmotic influence. Nonami and Boyer (1990b) and Wu *et al.* (1996) observed the decrease in hydraulic conductivity of cell wall at low water potentials. Thus lowering of conductivity of plasmodesmata (desmotubule) and cell wall can be the cause of $D_{ef}$ decrease of fast component.

PEG treatment of plant roots is considered to cause the leaf changes *via* hydraulic (Kramer 1988, Nonami and Boyer 1990a) or hormonal (Saab and Sharp 1989, Davies and Zhang 1991) signals. It is known that water stress causes a sharp increase in ABA concentration in maize seedling leaves (Beardsell and Cohen 1975, Saab *et al.* 1990) that greatly increases the hydraulic conductance of membranes (Glinka 1980, Van Stevenink *et al.* 1988). According to our data (Ionenko and Zyalalov 1999) exogenous ABA increases also the water permeability of membranes of maize root cells. Thus one of the causes of

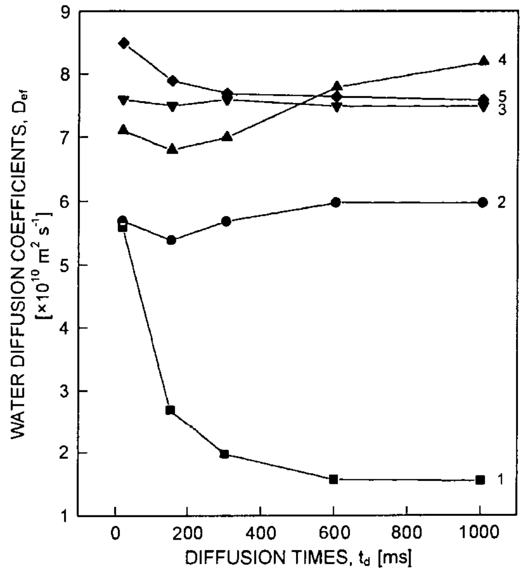

Fig. 4. Diffusional transfer of water in maize seedling roots following the influence of the destruction factors: *1* - control; *2* - the vapour of liquid nitrogen; *3* - the boiling water vapour; *4* - the vapour of diethyl ether; *5* - low temperature -10 °C. Each data point is the mean of four measurements obtained from separate samples (SE ± 7 %).

$D_{ef}$ increase of slow component in leaves after the influence of PEG-induced water deficits can be the intensification of transmembrane water exchange due to the increase of the membrane permeability.

The different signs of $D_{ef}$ changes of slow and fast components of diffusional decay in roots and leaves of maize seedlings points, in our opinion, to the different mechanisms of adaptation of these organs to PEG-induced water deficits. Under water deficit a sharing of water flows apparently takes place through the different pathways: through apoplast and intercellular endoplast, on the one hand, and through the membranes (plasmalemma), on the other hand. In the first place (at least for 1 h) root response is in the intensification of apoplastic transport and water transport through intercellular endoplast (vacuole symplast). This response is important because may promote the fast recovery of pressure potential in root cells bordering with osmotic solution and the maintenance of water balance of all tissue. A long water deficit does not reduce the rate of transmembrane transfer, but increases it to a small extent. Response to water stress in the leaves is also in the intensification of transmembrane component of water transfer. Perhaps it is connected with the expression of water channels. In this connection the study of the osmotic stress influence on conductivity of the membrane protein pores (aquaporins) would be of interest.

## References

Anisimov, A.V., Evarestov, A.S., Ionenko, I.F., Gusev, N.A.: [Pulsed NMR method for estimation of intercellular water transport on symplasm.] - Dokl. Akad. Nauk SSSR **271**: 1246-1249, 1983. [In Russ.]

Anisimov, A.V., Ratkovic S.: Transport Vody v Rasteniyach. Issledovanie Impul'snym Metodom YaMR. [Water Tranport in Plants. Determination by pulsed NMR.] - Nauka, Moskva 1992. [In Russ.]

Anisimov, A.V., Sorokina, N.Yu., Dautova, N.R.: Water diffusion in biological porous systems: a NMR approach. - Magnetic Resonance Imaging **16**: 565-568, 1998.

Azaizeh, H., Gunse, B., Steudle, E.: Effects of NaCl and $CaCl_2$ on water transport across root cells of maize (*Zea mays L.*) seedlings. - Plant Physiol. **99**: 886-894, 1992.

Azaizeh, H., Steudle, E.: Effects of salinity on water transport of excised maize (*Zea mays* L.) roots. - Plant Physiol. **97**: 1136-1145, 1991.

Beardsell, M.F., Cohen, D.: Relationships between leaf water status, abscisic acid levels, and stomatal resistance in maize and sorghum. - Plant Physiol. **56**: 207-212, 1975.

Chazen, O., Neumann, P.M.: Hydraulic signals from the roots and rapid cell-wall hardening in growing maize (*Zea mays* L.) leaves are primary responses to polyethylene glycol-induced water deficits. - Plant Physiol. **104**: 1385-1392, 1994.

Chrispeels, M.J., Crawford, N.M., Schroeder, J.I.: Proteins for transport of water and mineral nutrients across the membranes of plant cells. - Plant Cell **11**: 661-676, 1999.

Crick, F.: Diffusion in embryogenesis. - Nature **225**: 420-422, 1970

Crowe, J.H., Hoekstra, F.A., Crowe, L.M.: Membrane phase transitions are responsible for imbibitional damage in dry pollen. - Proc. nat. Acad. Sci. USA **86**: 520-523, 1989.

Crowe, J.H., Hoekstra, F.A., Crowe, L.M.: Anhydrobiosis. - Annu. Rev. Plant Physiol. Plant mol. Biol. **54**: 570-599, 1992.

Daniels, M., Mirkov, T.E., Chrispeels, M.: The plasma membrane of *Arabidopsis thaliana* contains a mercury-insensitive aquaporin that is homolog of the tonoplast water channel protein TIP. - Plant Physiol. **106**: 1325-1333, 1994.

Davies, W.J., Zhang, J.: Root signals and the regulation of growth and development of plants in drying soil. - Annu. Rev. Plant Physiol. Plant mol. Biol. **42**: 55-76, 1991.

Frensch, J., Hsiao, T.C.: Transient responses of cell turgor and growth of maize roots as affected by changes in water potential. - Plant Physiol. **104**: 247-254, 1994.

Frensch, J., Hsiao, T.C.: Rapid response of the yield threshold and turgor regulation during adjustment of root growth to water stress in *Zea mays*. - Plant Physiol. **108**: 303-312, 1995.

Gamaleï, Yu.V., Van Bel, A.J.E., Pakhomova, M.V., Sjutkina, A.V.: Effect of temperature on the conformation of the endoplasmic reticulum and on starch accumulation in leaves with the symplasmic minor-vein configuration. - Planta **194**: 443-453, 1994.

Gamaleï, Yu.V.: [Efflux of photoassimilates under natural and experimental conditions.] - Fiziol. Rast. **43**: 328-343, 1996. [In Russ.]

Gamaleï, Yu.V.: [Photosynthesis and photosynthates export. Development of transport system and donor-acceptor relations.] - Fiziol. Rast. **45**: 614-631, 1998. [In Russ.]

Gennis, R.B.: Biomembrany. Molekulyarnaya Struktura i Funktsii. [Biomembranes. Molecular Structure and Functions.] - Mir, Moskva 1997. [In Russ.]

Glinka, Z.: Abscisic acid promotes both volume flow and ion release to the xylem in sunflower roots. - Plant Physiol. **65**: 537-540, 1980.

Grabski, S., de Feijter, A.V., Schindler, M.: Endoplasmic reticulum forms a dynamic continuum for lipid diffusion between contiguous soybean root cells. - Plant Cell **5**: 25-38, 1993.

Guerrero, F.D., Jones, J.T., Mullet, J.E.: Turgor-responsive gene transcription and RNA levels increase rapidly when pea shoots are wilted. Sequence and expression of three inducible genes. - Plant mol. Biol. **15**: 11-26, 1990.

Ionenko, I.F., Zyalalov, A.A.: Effect of potassium, and abscisic and indole-3-acetic acids, on maize root xylem exudation and potassium efflux. - Biol. Plant. **42**: 137-141, 1999.

Knebel, W., Quader, H., Schnepf, E.: Mobile and immobile endoplasmic reticulum in onion bulb epidermis cells: short- and long-term observations with a confocal laser scanning microscope. - Eur. J. Cell Biol. **52**: 328-340, 1990.

Kramer, P.J.: Changing concepts regarding plant water relations. - Plant Cell Environ. **11**: 565-568, 1988.

Kuzmanoff, K.M., Evans, M.L.: Kinetics of adaptation to osmotic stress in lentil (*Lens culinaris* Med.) roots. - Plant Physiol. **68**: 244-247, 1981.

Lassaro, M.D., Thomson, W.W.: The vacuolar-tubular continuum in living trichomes of chickpea (*Cicer arietinum*) provides a rapid means of solute delivery from base to tip. - Protoplasma **193**: 181-190, 1996.

Maurel, C.: Aquaporins and water permeability of plant membranes. - Annu. Rev. Plant Physiol. Plant mol. Biol. **48**: 399-429, 1997.

McKersie, B.D., Stinson, R.H.: Effect of dehydration on leakage and membrane structure in *Lotus corniculatus* L. seeds. - Plant Physiol. **66**: 316-320, 1980.

Navari-Izzo, F., Quartacci, M.F., Melfi, D., Izzo, R.: Lipid composition of plasma membranes isolated from sunflower seedlings grown under water stress. - Physiol. Plant. **87**: 508-514, 1993.

Nobel, P.S.: Physicochemical and Environmental Plant Physiology. - Academic Press, San Diego 1991.

Nonami, H., Boyer, J.S.: Primary events regulating stem growth at low water potentials. - Plant Physiol. **93**: 1601-1609, 1990a.

Nonami, H., Boyer, J.S.: Wall extensibility and cell hydraulic conductivity decrease in enlarging stem tissues at low water potentials. - Plant Physiol. **93**: 1610-1619, 1990b.

Pearce, R.C.: A freeze-fracture study of membranes of rapidly drought stressed leaf bases of wheat. - J. exp. Bot. **36**: 1209-1221, 1985.

Quartacci, M.F., Pinzino, C., Sgherri, C.L.M., Navari-Izzo, F.: Lipid composition and protein dynamics in thylakoids of two wheat cultivars differently sensitive to drought. - Plant Physiol. **108**: 191-197, 1995.

Robinson, D.G., Sieber, H., Kammerloher, W., Schaffner, A.R.: PIP 1 Aquaporins are concentrated in plasmalemmasomes of *Arabidopsis thaliana* mesophyll. - Plant Physiol. **111**: 645-649, 1996.

Saab, I.N., Sharp, R.E.: Non hydraulic signals from maize roots in drying soil: inhibition of leaf elongation but not stomatal conductance. - Planta **179**: 466-474, 1989.

Saab, I.N., Sharp, R.E., Pritchard J., Voetberg, G.S.: Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. - Plant Physiol. **93**: 1329-1336, 1990.

Steudle, E.: Water transport across plant tissue: role of water channels. - Biol. Cell **89**: 259-273, 1997.

Steudle, E., Peterson, C.A.: How does water get through roots? - J. exp. Bot. **49**: 775-788, 1998.

Tetteroo, F.A.A., De Bruijn, A.V., Henselmans, R.N.M., Wolkers, W.F., Van Aelst, A.C., Hoekstra, F.A.: Characterization of membrane properties in desiccation-tolerant and -intolerant carrot somatic embryos. - Plant Physiol. **111**: 403-412, 1996.

Van Bel, A.J.E.: Carbohydrate processing in the mesophyll trajectory in symplasmic and apoplasmic phloem loading. - Progr. Bot. **57**: 140-167, 1996.

Van Stevenink, R.F.M., Van Stevenink, M.E., Läuchli, A. The effect of abscisic acid and K on xylem exudation from excised roots of *Lupinus luteus*. - Physiol. Plant. **72**: 1-7, 1988.

Velikanov, G.A., Volobueva, O.V., Khokhlova, L.P.: [Water selfdiffusion inside vacuolar and cytoplasmic symplasms.] - Dokl. Russ. Akad. Nauk **368**: 420-422, 1999. [In Russ.]

Wu, Y., Sharp, R.E., Durachko, D.M., Cosgrove, D.J.: Growth maintenance of the maize primary root at low water potentials involves increases in cell-wall extension properties, expansin activity, and wall susceptibility to expansins. - Plant Physiol. **111**: 765-772, 1996.