ORIGINAL ARTICLE

Growth function and intercellular water transfer in excised roots

A. V. Anisimov[1] · N. R. Dautova[1] · Maksim A. Suslov[1]

Abstract
On the example of maize seedling roots, it was shown that segments of the root suction zone excised from intact mother seedlings maintain the function of elongation growth and are able to regulate water transfer. Using the gradient NMR method, the effective intercellular permeability of root suction zone segments was shown to reduce with respect to intact seedling roots. The segment fragmentation into smaller pieces 3 mm long resulted in the permeability decrease by 60%. The reduction is associated with the cell defensive response to water loss through cuts and blocking of the additive water transfer along the segment length, resulting from segment cutting.

Keywords Water transfer · Excised root segments · Effective intercellular permeability · Growth

Abbreviations

NMR	Nuclear magnetic resonance
D_{ef}	Effective diffusion coefficient of water
P_{d_eff}	Effective permeability coefficient of water
DD	Diffusional decay
t_d	Diffusion time

Introduction

Roots are common objects to study various sides of plant metabolism, including water exchange. The possibility to choose root zones with respect to their functionality (meristem, suction zone, elongation zone) permits to study various processes in roots which present a lower water flow driving force. For example, the suction zone, which allows the fast transfer of water solutions from the external medium into root apoplast and symplast compartments, is often used by biophysicists and plant physiologists to study plant water relationships. Steudle had proposed a composite model for root functioning (composite transport model—CTM) (Steudle

✉ Maksim A. Suslov
makscom87@mail.ru

1 FRC Kazan Scientific Center, Russian Academy of Sciences, Kazan Institute of Biochemistry and Biophysics, Lobachevskogo 2/31 st, P.O. Box 30, Kazan 420111, Russia

1994; Steudle and Peterson 1998). According to the model, three parallel pathways are involved in water and solute transport in roots: apoplast, symplast, and transcellular pathway. The apoplastic path provides the water transfer along the tissue intercellular space. The symplastic transfer from cell to cell occurs via plasmodesmata when molecules do not exit into the intercellular space. And finally, the transcellular pathway involves water transport across plasma membrane bilayers and through aquaporins into the intercellular space and entering adjacent cells (Steudle and Peterson 1998).

Different driving forces, such as hydrostatic/bulk and osmotic ones, are used by these pathways. The hydrostatic pressure gradient is caused by the tension due to transpiration from a shoot and transferred into a root xylem (Steudle 2000). In the absence of transpiration, the active pumping of ions into the xylem causes the osmotic water flow and the development of root pressure (Steudle 2000). A number of experiments on water and solute transport in roots were carried out since the CTM was proposed, and the results were explained from the point of view of CTM (Suku et al. 2014; Vandeleur et al. 2014).

Experimental data of the last decade showed the necessity to update the classical CTM by adding the connected in series resistances of root epidermis, exodermis, middle cortex, and endodermis (Gambetta et al. 2013; Ranathunge et al. 2017). Within the updated model, the special attention was paid to the aquaporin (AQPs) role in the transmembrane transfer (Maurel et al. 2015; Hachez et al. 2012). For example, Knipfer and coauthors (2011) showed that the conductivity of a primary root (L_{pr}), secondary root, and the whole root system of barley

can be reduced by applying the AQP inhibitor $HgCl_2$ by 40–74%, the effect on the cell level being even larger—83–95%. The AQP contribution into water transport in roots is proved to vary depending on plant species, driving forces (hydrostatic or osmotic), root age, and the degree of the apoplast barrier development. The latter are presented mainly by Casparian strips which appear permeable for water, but can stop the apoplast ion transfer (Ranathunge et al. 2017). Root segments along with the intact roots are widely used in the studies. One of the reasons of using root segments is caused by technical potentials when the experiments on intact roots are inconvenient or impossible. On the other hand, root excision causes a stress and it is used for studying the accumulation of the excessive amount of reactive oxygen species (ROS) (Ross et al. 2006), ROS effect on water transfer (Boursiac et al. 2008; Ehlert et al. 2009), dynamics of excised root aging (Gordon et al. 1991), and kinetics of transient processes (Velikanov et al. 2015).

The use of root segments in the studies of water exchange has a number of specific features caused, first of all, by the disruption of xylem and phlem pathways of water transfer and the pressure release in the plant hydro system. Consequently, the study of water exchange in root segments reduces mainly to the near water transport, and many results are obtained using the NMR spin-echo method (Anisimov et al. 1991, 2004; Ionenko et al. 2003; Velikanov et al. 2015). The method allows the registration of the rate of the transmembrane water exchange. The latter together with the magnetic field pulsed gradient technique allows the measurements of water translational diffusion coefficients (Stejskal and Tanner 1965; Tanner and Stejskal 1968; Anisimov et al. 1991; Cho et al. 2003), selective studies of water transfer along different pathways in plant tissues (Anisimov et al. 2004),

When root segments are excised from the mother plant, among the reasons of water transfer changes in segments, one can expect (1) changes in the total resistance to the water transfer due to the exclusion of the resistance of removed plant parts, (2) changes in the gradient of intercellular water potential caused by the breakdown of water out flux all on the xylem and phloem, (3) the pressure change in the root hydro system, the sign of which depends on the transpiration level: the low transpiration results in the pressure drop, and the high transpiration results in the increase from the negative tension pressure to the positive one.

The pressure effect on water transfer is poorly studied compared to other environmental effects and therefore demands a special attention. According to Franks et al. (2001) and Pritchard et al. (1990), the xylem pressure can amount to 5–6 bar. Comparatively large, up to 4 MPa, external pressure might cause changes in the water transfer along the symplast (Anisimov et al. 2014). Oparka and Prior (1992) showed the irreversible plasmodesmata blocking at the pressure gradient between cells of 200 kPa on the example of *Nicotiana*

clevelandii leaf trachoma using dyes. Suku et al. (2014) pointed out that L_{pr} of the excised root system might differ from L_{pr} of intact transpiring plants with the feedback from shoots to roots. A number of experiments showed that both transpiration and its cease caused by topping affected the root AQP activity (Almeida-Rodriguez et al. 2011; Sakurai-Ishikawa et al. 2011; Laur and Hacke 2013; Vandeleur et al. 2014) showed on the example of grapevine (*Vitisvinifera* L.), soybean (*Glycinemax* L.), and maize (*Zea mays* L.) that topping results in the reduction of the root hydraulic conductance. This can be connected with xylem-dependent hydraulic signals and gating of some AQPs (Wan et al. 2004; Kim et al. 2018).

Finally, Ortega (2010) in his theoretical paper predicted the time-dependent response of the intercellular transfer to the external pressure changes, which was connected to the pressure variation in the apoplast (Pessoa and Calbo 2004). Besides, because of the air-filled intercellular spaces, the pressure changes resulted in changes in the equilibrium level of concentration of air gases dissolved in the apoplast and symplast water (Henry's law). Changes in the dissolved oxygen concentration in segments during the changes in the external air pressure were shown in NMR experiments (Anisimov and Suslov 2016). Even common meteorological changes in the atmosphere pressure appeared to affect the times of plant tissue water magnetic relaxation (Anisimov and Suslov 2016). Presumably, the ROS level correlates with the level of dissolved oxygen. The data on changes in the root hydraulic conductance during ROS accumulation are presented in literature (Boursiac et al. 2008; Ehlert et al. 2009). The processes of lipid peroxidation and/or aquaporin activity modulation are among the mechanisms of ROS effect on the hydraulic conductance (Clarkson et al. 2000; Lee et al. 2004; Boursiac et al. 2008; Chaumont and Tyerman 2014; Velikanov et al. 2015). Finally, the pressure changes can result in mechanical deformations in the plant tissue architecture due to the presence of air-filled intercellular space and, consequently, activation of mechanosensors involved into the regulation of various metabolism processes, including water transfer (Peyronnet et al. 2014; Christmann et al. 2013).

As a result, the root excision, having a dramatic impact on plants, extends the field of study. In particular, there are questions whether the segments remain viable, and to what extent and for how long they preserve growth functions, and whether the blocking of the intercellular water transfer in root segments, as a defensive response to the opportunity of the water loss through the excision zone, takes place.

The aim of the present paper is to study whether the root segments preserve growth functions and if yes, then to what extent, and what changes occur in the intercellular water transfer in a segment after its excision from the mother plant.

Materials and methods

Plant growth conditions and preparation of samples

Intact roots and segments of the root absorption zone of 7-day-old maize seedlings (*Zea mays* L., var. Kuban) were studied. The seedlings were grown hydroponically in the 0.25 mM $CaCl_2$ solution (pH 6.3) for 7 days at 22 °C under the 16-h photoperiod (irradiance of 15 W/m^{-2}) and relative humidity of 60%. In NMR diffusional experiments, simultaneously 20–25 intact plants, placed into the Teflon sample tube, were used.

Estimation of growth function

The estimation of the root growth function is based on the control of root segment length changes using the computer program of size analysis MacBiophotonics ImageJ. The segment and intact root growth function in the norm and under the pressure of 2 MPa and pressure release were estimated. A pressure chamber with a window-viewport (Suslov and Anisimov 2017) was used to measure the growth rate.

The pressure was created by a pressure gas generator (Anisimov et al. 2012). Root segments in the amount of 10 pieces were arranged on the glass surface of the window-viewport in a thin water layer. The chamber was placed so that the window-viewport was on the recording surface of the computer scanner. The growth estimation was carried out by repeated recording of root segment images by the scanner. The obtained images were processed by MacBiophotonics ImageJ.

NMR measurements

The analysis of the characteristic features of the intercellular translational water transfer in intact roots and root segments was based on the NMR spin-echo diffusion measurements. The dependence of water molecule diffusion coefficients on the diffusion time, t_d, in porous systems, including water in biological systems, is known to be S-shaped (Fig. 1). The upper plateau (1) of the S-shaped curve characterizes the region of free unrestricted diffusion of the most part of water molecules. In this region, the selfdiffusion coefficient D_0 is constant and close to the bulk waterselfdiffusion coefficient. The descending part of the curve (2) corresponds the region of restricted diffusion where the averaging of local water transtlational movements over the large volume of cell community does not take place. Finally, the lower plateau of the curve (3) describes the region of hindered diffusion, which characterizes the intercellular permeability. The latter results in the diffusion averaging at distances larger than the cell size. In this region water self-diffusion coefficient D_∞ is independent of t_d. For the quantitative estimation of the intercellulat permeability coefficient P_d for water moleculeas, the Crick
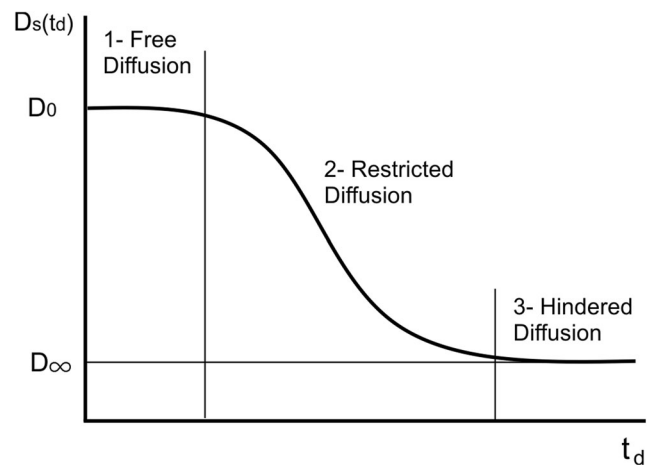
Fig. 1 Idealized dependence of water self-diffusion coefficient D_s on diffusion time in plant cell compartments with permeable walls (Valiullin and Skirda 2001)

relation (Crick 1970) can be used. This relation is obtained from the resistance to water transfer across a series of parallel permeable barriers separated by a distance a:

$$\frac{1}{D_\infty} = \frac{1}{D_0} + \frac{1}{P_d a} \qquad (1)$$

where D_∞ and D_0 are the self-diffusion coefficient in the region of hindered diffusion and the bulk water self-diffusion coefficient, respectively. The relation (1) is independent on the mechanisms of intercellular transfer. It permits to apply the relation for the total permeability of the complex membrane + plasmodesmata estimation. Since the cell-to-cell pathway consists of the symplastic one via plasmodesmata (Robards and Clarkin 1976) and the transcellular one through membrane bilayers and aquaporins, then one can measure experimentally the integral permeability coefficient of both pathways denoted as the effective permeability coefficient P_{d_ef} ($P_d = P_{d\_ef}$). It is important to note that, as a rule, the routine methods of permeability (conductance) measurements apply an external excitation in the form of pressure (osmotic, hydrostatic, hydrodynamic). The diffusional NMR is a unique method allowing the non-invasive detection of diffusional translational motion of water molecules across membranes under the equilibrium conditions without external excitation.

The necessary for calculations characteristic parameter a which is related, as a rule, to the cell size, can be determined from the Einstein relation:

$$D_s(t_d) = \frac{a^2}{6t_d} \qquad (2)$$

using the diffusion coefficient measured under the conditions of the diffusion complete restriction. The measured diffusion coefficient measured under the conditions of the completely confined within the restricting compartment molecule movement is known to become the linear function of the inverse

diffusion time $(t_d{}^{-1})$ (Tanner and Stejskal 1968). However, when the compartment walls are permeable, this dependence is distorted due to the molecule transfer through the restricting barriers (Fig. 1) (Valiullin and Skirda 2001) The scaling approach when the dependence D_s (t_d) is renormalized into the dependence $D_{ef2}(t_d)$ versus $t_d{}^{-1}$ (Maklakov et al. 1990; Valiullin and Skirda 2001) allows to avoid the effect of permeability on D_s. For long t_d, the renormalization is given by the relation (Maklakov et al. 1990):

$$D_{ef2}(t_d) = \frac{D_0 D_{ef1}}{D_0 - D_{ef1}} \qquad (3)$$

where $D_{ef1}(t_d) = D_0 \frac{D_s(t_d) - D_\infty}{D_0 - D_\infty}$.

The modified relation (Sibgatullin et al. 2010) should be used for the whole range of diffusion times:

$$D_s(t_d) = D_{ef2} \frac{(D_0 - D_\infty)}{(D_{ef2} + D_0)} + D_\infty \qquad (4)$$

where $D_{ef2}(t_d) = \frac{d^2}{2t_d}$.

Since t_d is restricted by the relaxation time, D_∞ often cannot be determined directly from experiments, and then after renormalization, D_∞ is considered to be an adjustable parameter, changing the experimental dependence D_s (t_d) into the dependence $D_{ef2}(t_d{}^{-1})$.

In the present work, the three-pulse sequence of stimulated echo (Fig. 2) was used to monitor the summarized transcellular and symplast transport in the radial root direction. Diffusional decays (DD) of water magnetization were registered as the dependences of relative stimulated echo signal amplitudes (R) on the magnetic field gradient pulses (g^2), with the interval between pulses–the diffusion time (t_d), and pulse duration (δ) being variable parameters. For the diffusional transfer assessment, the formalism of the average effective diffusional coefficient D_{ef} was used (Anisimov et al. 1991; Anisimov et al. 2004; Valiullin and Skirda 2001). The value of D_{ef} was determined from the relation $R = \exp(-\gamma^2 \delta^2 g^2 t_d D_{ef})$ according to the condition $D_{ef}(t_d) = -\lim_{q \to 0} \frac{\partial \log[A(q, t_d)]}{\partial q^2}$ (Stejskal and Tanner 1965), from the DD initial slope (Valiullin and Skirda 2001), where R is the relative echo amplitude, which equals the ratio of echo amplitudes in the presence and absence of the magnetic field gradient, $R = A(g)/A(0)$; γ is the proton gyromagnetic ratio (the constant is equal to $2.67 \times \cdot 10^8$ T^{-1} s^{-1}); D_{ef} is the effective self-diffusion coefficient. The generalized argument $b = (-\gamma^2 \delta^2 g^2 (t_d - \delta/3))$ is used for figure captions.

To register the effect of root cutting without distortion of sample arrangement in the NMR probe, the Teflon sample tube with transverse slots was fabricated. The Fig. 3 shows the scheme of the Teflon sample tube for intact maize plants
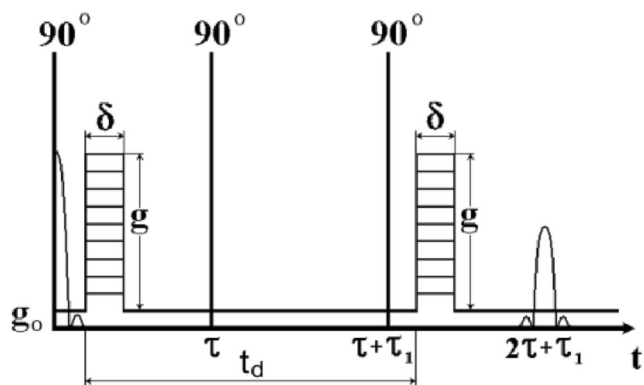

Fig. 2 The stimulated spin echo sequence with the pulsed magnetic field gradient (Tanner 1970)

with transverse slots. Along the slots, the consecutive dissection of intact roots was carried out till the level of the absorption zone and the roots at the absorption zone were cut into 3-mm-long segments. Intact maize seedlings in the amount of 20–25 pieces were placed into the Teflon sample tube so that only root suction zone was in the NMR probe measuring circuit. Then right in the sample tube, the plants part above measurement zone, including leaf zone (step 1), meristem, and elongation zone (step 2) were cut off and only root suction
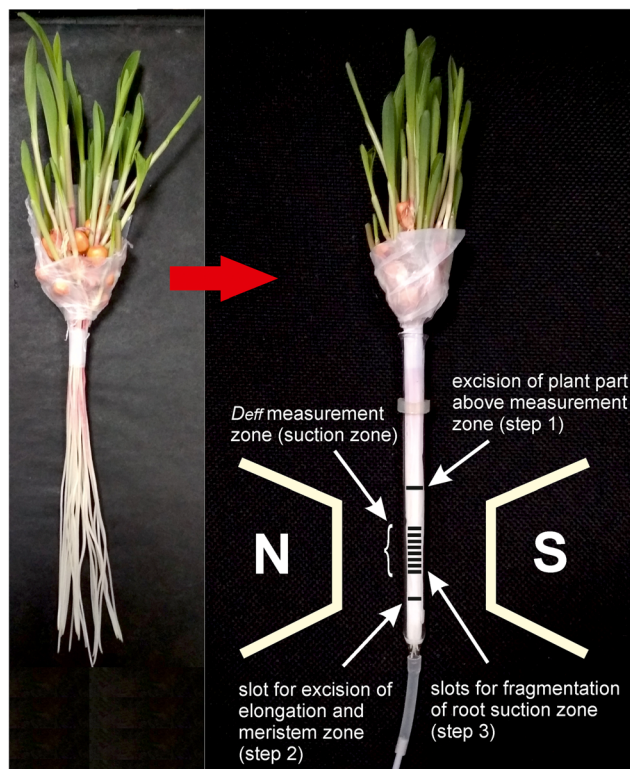

Fig. 3 Intact maize plants in the Teflon sample tube with slots. Then right in the sample tube, the plant part above NMR measurement zone, including leaf zone (step 1), meristem and elongation zone (step 2) were cut off and only root suction zone segment was left in the measurement zone. The last step 3 was fragmentation of the root suction zone segment into 3-mm-long sections

zone segment was left in the measurement zone. The last step 3 was fragmentation of the root suction zone segment into 3-mm-long sections (Fig. 3). Each step of cutting was followed by the registration of effective water diffusion coefficients of the root suction zone. It is important to note that the idea of a sample tube with transverse slots for the consecutive dissection of intact roots without extracting them from the sample tube was a methodically lucky find. Plenty preliminary experiments with extracting samples from a tube for cutting them and then packing them back resulted is a large scatter of data (up to 20%) mainly resulting from inevitable seedling damaging. When using the sample tube with slots, the data scatter reduced to 5% obviously because of less damage to the seedlings. It is also important that control-test results could be compared for one and the same sample. To control the maintenance of the dynamic range of the intercellular water transfer regulation in segments after cutting from the mother plant, changes in echo signal diffusional decays after the blocking of water transfer by sodium azide within the concentration range of 10^{-3}–10^{-2} M were registered.

Statistics

NMR diffusional and growth rate measurement experiments were performed in three recordings. The statistical analysis was carried out using the OriginPro 8.5 (OriginLab Corp., Northampton, MA, USA) software. In the figures, bars show SE.

Results and discussion

Growth function as an indicator of root segment viability

The control of the segment length using the computer method of size analysis indicates the increase in segment length by 2–2.5% after the cutting from the mother plant under the normal atmosphere pressure and temperature of 23 °C (Fig. 4). The increase in the segment length continued for 5–6 h and is irreversible. The elongation cease under the effect of cell respiration blocking agents, sodium azide (NaN_3, 10^{-2} M) and mercuric chloride(10^{-3} M), indicate that the increase in the length appears to just cell growth by elongation. For intact roots, the growth rate is much larger—12–15% for 4.5 h versus 2–2.5% for root segments (Fig. 5, Fig. 4). Does the pressure loss in the root hydrosystem after its excision from the intact mother plant affect the growth rate? The segment growth rate happened to increase (up to 5%) under the pressure of 2 MPa (Fig. 4) while the intact root growth rate, on the contrary, slows down, but tends to return to the norm after the pressure release (Fig. 5). Obviously, the normal atmosphere pressure provides evolutionally polished optimal growth
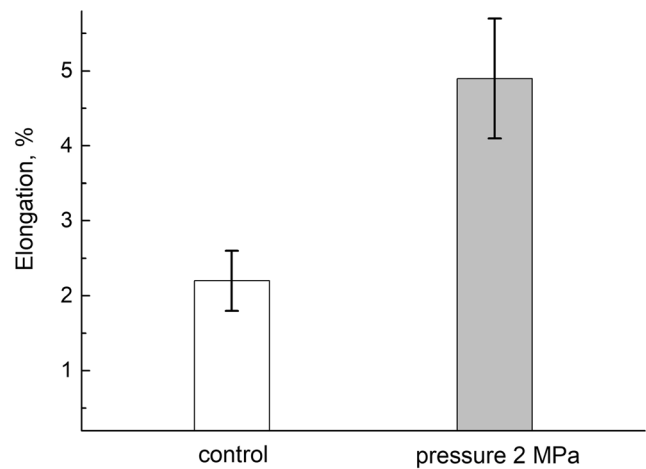

Fig. 4 The increase (in per cent) in root segment length 4.5 h after cutting off at 23 °C and the atmosphere pressure (control) and under the treatment with the air pressure of 2 MPa

conditions in the intact root hydro system. After root excision, the root hydro system experiences the pressure fall, which results in the growth suppression. The applying of the external air pressure to the segments compensates the pressure loss, and, as a result, the segment growth accelerates.

Thus, the excised roots preserve the function of growth by elongation. The growth by elongation necessarily assumes the water uptake by cells, i.e., maintenance of the conditions for water transfer. The direct quantitative data on the transmembrane water transfer can be obtained from diffusional NMR experiments.
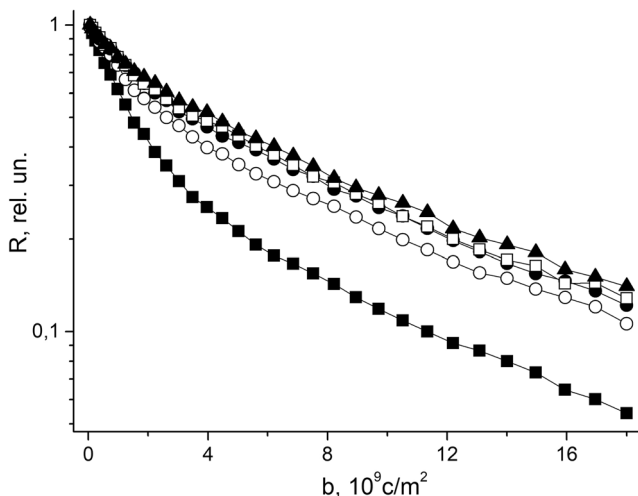
Diffusion results

Classification of the transfer pathways in diffusional NMR experiments correlates with the composite transport model (CTM) proposed by Steudle and coauthors (Steudle and Peterson 1998). Water transfer takes place in tissue compartments and canals that differ in form and size, and due to restrictions to water diffusion exerted by cell components (membranes, cell walls, etc.) water transfer mobility along different pathways differ, and it is displayed in the slope steepness of the diffusional decays of echo signals in NMR experiments (Tanner and Stejskal 1968). Diffusional decays (DDs) of echo signals for roots in the norm are characterized by two regions which differ in steepness and can be attributed to different water fractions, i.e., they have a two-phase behavior (Fig. 6). The paramagnetic doping method (Anisimov and Ratkovic (1992) allows one to determine whether these regions of the decay curve refer to intercellular or intracellular water fractions. The principle of the method is that a paramagnetic compound which does not penetrate into cells is inserted into the intercellular space. The intercellular (apoplastic) water molecules experience fast magnetic relaxation due to the contact with paramagnetic ions (within 1–2 msec depending on the
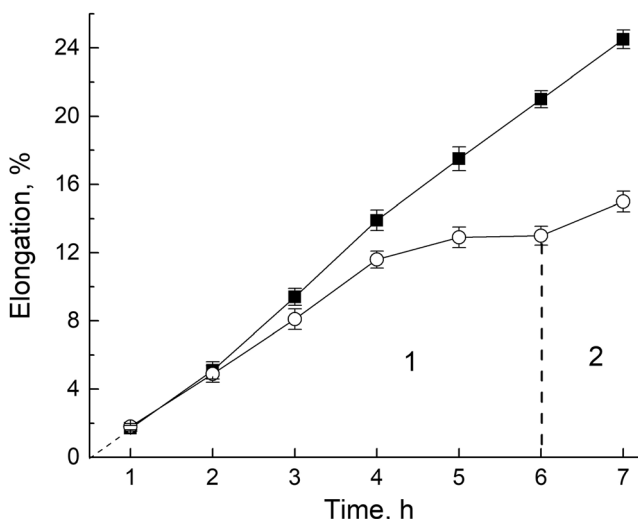
Fig. 5 Time course of elongation (in per cent) of the intact roots at 23 °C under the atmosphere pressure (solid squares) and under impact of external air pressure of 2 MPa (open circles). After 6 h of 2 MPa pressure impact (region 1), the pressure was released to level of atmosphere (region 2)

paramagnetic compound concentration). As a result, the inter-cellular water molecules become invisible in the DDs while the intracellular water molecules, moving along the symplast and still having longer relaxation time due to their isolation from the paramagnetic ions, remain visible in DDs. Paramagnetic compound Gd-DTPA (diethylenetriaminepentaacetic acid salt—gadopentetate), used as a contrasting agent for MRI (Carr et al. 1984), was applied.
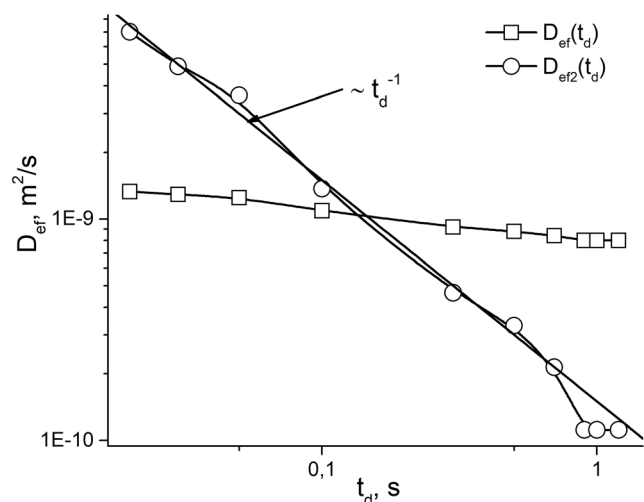
In the experiments with roots, the significant decrease in the portion of fast-decaying part of DDs under the effect of the paramagnetic compound is observed and consequently this fast-decaying part can be attributed to the intercellular water.

As mentioned above, the detection of the average effective diffusion coefficient dependence on the diffusion time D_s (t_d) (Fig. 1) is required to estimate the effective permeability coefficient P_{d_ef}. The experimental dependence of the average effective diffusion coefficient on the diffusion time for intact seedling roots (control) after renormalization of $D_{ef}(t_d)$ into $D_{ef2}(t_d)$ as a function of t_d^{-1} (Fig. 7) gives the characteristic size of restrictions of 25 μm, and this in its turn determines the effective water permeability coefficient P_{d_ef}. The similar experimental DD dependences after the successive cutting off the plants part above measurement zone, including leaf zone, meristem and elongation zone, and fragmentation of the root suction zone into 3-mm-long sections show the decrease in effective permeability coefficient of the root suction zone segment followed by maximum decrease after the fragmentation of the root suction segment into 3-mm-long sections (Table 1).

Cutting off of the plants part above measurement zone (step 1) reduces the permeability coefficient on the average by 10% from the control value for the intact seedling root permeability. The following cutting off the meristem and elongation zone (step 2) reduces this value by 20%. The fragmentation of the root suction zone segment into 3-mm-long sections (step 3) results in the permeability decrease by 60%. Since by the time of fragmentation, the root (step 3) is deprived of the upper water flow driving force, the data obtained after fragmentation favor the transfer blocking on the cutting frontiers. The arising pressure gradient on the cutting frontiers, taking into account the data of Oparka and Prior (1992), obviously, causes the defensive prevention of the water loss through the cutting frontiers. The question is whether the dynamic range of permeability regulation remains unchanged. The answer is obtained from the DD behavior during the water transfer blocking in suction zone of root segments by increasing

Fig. 6 Echo signal DD versus the magnitude of magnetic field gradients for roots in the norm (solid squares) and after different time of incubation intact maize seedlings in 0.025 M GdDTPA solution: 1-h incubation (open circles), 2-h incubation (solid circles), 3-h incubation (open squares), 4-h incubation (solid triangles)


Fig. 7 The dependence of the average effective diffusion coefficient on the diffusion time for intact seedling roots (solid squares) and the result of the renormalization of $D_{ef}(t_d)$ into the dependence $D_{ef2}(t_d)$ as a function of t_d^{-1}. Arrow point to linear approximation of $D_{ef2}(t_d)$

Table 1 Effective water permeability coefficient P_{d_ef} in suction zone of maize roots for control (intact plants) and after successive excision of plant part above NMR measurement zone, including leaf zone (step 1), meristem and elongation zone (step 2), and after fragmentation of segments in suction zone into 3-mm-long sections (step 3). Bars show SE ($n = 3$)

Sample treatment	P_{d_ef}, m/s
Control (intact plants)	$(6.3 \pm 0.3) \times 10^{-5}$
Excision of plants part above NMR measurement zone (step 1)	$(5.7 \pm 0.3) \times 10^{-5}$
Excision of meristem and elongation zone (step 2)	$(4.9 \pm 0.3) \times 10^{-5}$
Fragmentation of segments into 3-mm-long sections (step 3)	$(2.7 \pm 0.2) \times 10^{-5}$

concentrations of sodium azide up to 10^{-2} M (Fig. 8). As concentration increased, azide happened to reduce successively water transfer in segments, and it is observed in the decrease in the DD initial slope steepness. In other words, segment cells "properly" respond to the azide treatment. The cell destruction under the azide treatment does not occur. Otherwise, DD in Fig. 8 would become straight lines with the slope close to that of bulk water.

The considered constituents of water transport in plants mechanisms, such as osmosis, tension of water continuity under the effect of transpiration, capillary forces, cell contractile activity, etc., during the active vegetation period can explain almost all experimentally observed water transfer processes, but each of these mechanisms has its own weak point, and it is not easy to adjust these mechanisms to interseasonal environmental changes. The recent article on the modification of the composite water transport model in roots (Kim et al. 2018; Couvreur et al. 2018) shows the necessity of the further development of the water transport in plants model. As a further
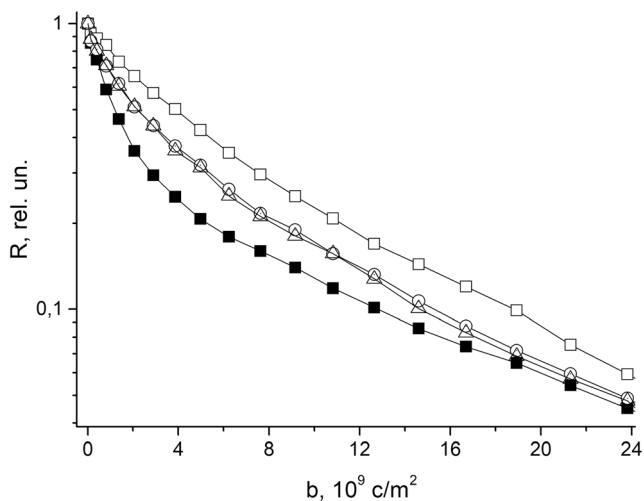
Fig. 8 DD dependence for suction zone in root segments: control (solid square), 20-min treatment with sodium azide of different concentration: 10^{-2} M (open square), 10^{-3} M (open circle), 5×10^{-4} M (open triangle)

development of this model, one can imagine a cell-distributed water flow driving force in plants, mentioned by Bos (1964) and Zholkevich et al. (1979). The fact that, even after a very severe stress with the transpiration shutdown and the meristem and elongation zone cutting-off, the segments retain growth functions and the intercellular water transfer can indirectly point to the existence of the distributed driving force.

Conclusion

Thus, the excised roots keep the function of elongation growth. The latter necessarily assumes the water uptake by cells, i.e., the preservation of conditions for water transfer. Simultaneously, the excision of the root suction zone from the mother plant results in the reduction of the effective intercellular permeability on the average by 20%, i.e., the dramatic changes in water transfer do not occur. The fragmentation of a segment into small sections results in the permeability decrease by about 60%. The reduction is associated with the cell defensive response to water loss through cuts and blocking of the additive water transfer along the segment length, resulting from segment cutting.

References

Almeida-Rodriguez AM, Hacke UG, Laur J (2011) Influence of evaporative demand on aquaporin expression and root hydraulics of hybrid poplar. Plant Cell Environ 34:1318–1331. https://doi.org/10.1111/j.1365-3040.2011.02331

Anisimov AV, Ratkovic S (1992) Water transport in plants. Study by pulsed NMR method. Nauka, Moscow (in Russian)

Anisimov AV, Suslov MA (2016) The effect of external gas pressure on the magnetic relaxation of water in plant cells. Biofizika 61(1):67–72 (in Russian)

Anisimov AV, Evarestov AS, Dautova NR, Ratkovic S (1991) The effect of osmotics on plant cells: a study using 1H NMR relaxation and self-diffusion of water. Gen Physiol Biophys 10(b):569–576

Anisimov AV, Ionenko IF, Romanov AV (2004) Spin-echo NMR study of the translational water diffusion selectively along the apoplast and the cytoplasmic and vacuolar symplasts of plants. Biophysics 49:816–821

Anisimov AV, Suslov MA, Zuikov VA (2012) Equipment to studies of mass transfer under the effect of ststic and dynamic pressure directly in the probe of the gradient NMR. Datchiki i Sistemy 7:64–67 (in Russian)

Anisimov AV, Suslov MA, Alyab'ev AY (2014) Symplasmic transport of water along the root depends on pressure. J Plant Physiol 61(4):512

Bos DCH (1964) Plant autographs and their content. In: Selected papers on plant irritability, vol v2, Nauka, pp 171–340 in Russian

Boursiac Y, Boudet J, Postaire O, Luu DT, Tournaire-Roux C, Maurel C (2008) Stimulus-induced down-regulation of root water transport involves reactive oxygen species-activated cell signaling and plasma membrane intrinsic protein internalization. Plant J 56:207–218

Carr DH, Brown J, Bydder GM et al (1984) Gadolinium-DTPA as a contrast agent in MPI: initial clinical experience in 20 patients. Am J Radiol 143(2):215–224

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

Cho C-H, Young-ShickHong KK, Volkov VI, Skirda V (2003) Water self-diffusion in Chlorella sp. studied by pulse field gradient NMR. Magn Reson Imaging 21:1009–1017

Christmann A, Grill E, Huang J (2013) Hydraulic signals in long-distance signaling. Curr Opin Plant Biol 16:293–300

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

Couvreur V, Faget M, Lobet G, Javaux M, Chaumont F, Draye X (2018) Going with the flow: multiscale insights into the composite nature of water transport in roots. Plant Physiol Preview. https://doi.org/10.1104/pp.18.01006

Crick F (1970) Diffusion in embryogenesis. Nature 225:420–422

Ehlert C, Maurel C, Tardieu F, Simonneau T (2009) Aquaporin-mediated reduction in maize root hydraulic conductivity impacts cell turgor and leaf elongation even without changing transpiration. Plant Physiol 150:1093–1104

Franks PJ, Buckley TN, Shope JC, Mott KA (2001) Guard cell volume and pressure measured concurrently by confocal microscopy and the cell pressure probe. Plant Physiol 125:1577–1584. https://doi.org/10.1104/pp.125.4.1577

Gambetta GA, Fei J, Rost TL, Knipfer T, Matthews MA, Shackel KA et al (2013) Water uptake along the length of grapevine fine roots: developmental anatomy, tissue-specific aquaporin expression, and pathways of water transport. Plant Physiol 163:1254–1265. https://doi.org/10.1104/pp.113.221283

Gordon LK, VYa A, Minibaeva FV et al (1991) Transient processes during excised root adaptive aging. Citologia 5:88–94 (in Russian)

Hachez C, DYe V, Reinhardt H, Knipfer T, Fricke W et al (2012) Short-term control of maize cell and root water permeability through plasma membrane aquaporin isoforms. Plant Cell Environ 35:185–198. https://doi.org/10.1111/j.1365-3040.2011.02429

Ionenko IF, Anisimov AV, Romanov AV (2003) Effect of water stress and mercuric chloride on the translational diffusion of water in maize seedling roots. Russ J Plant Physiol 50:79–83

Kim YX, Kosala R, Seulbi L, Yejin L, Deogbae L, Jwakyung S (2018) Composite transport model and water and solute transport across plant roots: an update. Frontiers in Plant Science 9(193):1–9

Knipfer T, Fricke W (2011) Water uptake by seminal and adventitious roots in relation to whole-plant water flow in barley (Hordeum vulgare L.). J Exp Bot 62:717–733

Laur J, Hacke UG (2013) Transpirational demand affects aquaporin expression in poplar roots. J Exp Bot 64:2283–2293. https://doi.org/10.1093/jxb/ert096

Lee SH, Singh AP, Chung GC, Ahn SJ, Noh EK, Steudle E (2004) Exposure of roots of cucumber (cucumber sativus) to low temperature severely reduces root pressure, hydraulic conductivity and active transport of nutrients. Physiol Plant 120:413–420

Maklakov AI, Skirda VD, Fatkullin NF (1990) Self-Diffusion in Polymer Systems. In: Encyclopedia of Fluid Mechanics. Gulf-Publishing Co, Houston, Chap. 22, pp 705–745

Maurel C, Boursiac Y, Luu DT, Santoni V, Shahzad Z, Verdoucq L (2015) Aquaporins in plants. Physiol Rev 95:1321–1358. https://doi.org/10.1152/physrev.00008

Oparka A, Prior M (1992) Direct evidence for pressure-generated closure of plasmodesmata. Plant J 2(5):741–750

Ortega J (2010) Plant cell growth in tissue. Plant Physiol 154:1244–1253

Pessoa J, Calbo A (2004) Apoplasm hydrostatic pressure on growth of cylindrical cells. Braz J Plant Physiol 16(1):17–24

Peyronnet R, Tran D, Girault T, Frachisse J-M (2014) Mechanosensitive channels: feeling tension in a world under pressure. Front Plant Sci (Plant Physiol) 5:558. https://doi.org/10.3389/fpls.2014.00558

Pritchard J, Barlow PW, Adam JS, Tomos AD (1990) Biophysics of the inhibition of the growth of maize roots by lowered temperature. Plant Physiol 93:222–230

Ranathunge K, Kim YX, Wassmann F, Kreszies T, Zeisler V, Schreiber L (2017) The composite water and solute transport of barley (Hordeumvulgare) roots: effect of suberized barriers. Ann Bot 119:629–643. https://doi.org/10.1093/aob/mcw25226

Robards A, Clarkin D (1976) The role of plasmadesmata in the transport of water and nutrients across roots. In: Gunning BES, Robards AW (eds) Intercellular communication in plants: studies on Plasmadesmata. Springer-Verlag, Berlin, pp 181–199

Ross C, Küpper FC, Jacobs RS (2006) Involvement of reactive oxygen species and reactive nitrogen species in the wound response of Dasycladus vermicularis. Chem Biol 13:353–364

Sakurai-Ishikawa J, Murai-Hatano M, Hayashi H, Ahamed A, Fukushi K, Matsumoto T et al (2011) Transpiration from shoots triggers diurnal changes in root aquaporin expression. Plant Cell Environ 34:1150–1163. https://doi.org/10.1111/j.1365-3040.2011.02313.x

Sibgatullin TA, Vergeldt FJ, Gerkema E, Van As H (2010) Quantitative permeability imaging of plant tissues. Eur Biophys J 39:699–710

Stejskal EO, Tanner JE (1965) Spin diffusion measurements: spin echoes in the presence of a time-dependent field gradient. J Chem Phys 42:288–292

Steudle E (1994) Water transport across roots. Plant Soil 167:79–90. https://doi.org/10.1007/BF01587602

Steudle E (2000) Water uptake by plant roots: an integration of views. Plant Soil 226:45–56. https://doi.org/10.1023/A:1026439226716

Steudle E, Peterson CA (1998) How does water get through roots? J Exp Bot 49:775–788. https://doi.org/10.1093/jxb/49.322.775

Suku S, Knipfer T, Fricke W (2014) Do root hydraulic properties change during the early vegetative stage of plant development in barley (Hordeum vulgare)? Ann Bot 113:385–402. https://doi.org/10.1093/aob/mct270

Suslov MA, Anisimov AV (2017) Pressure chamber with a viewport and magnet manipulators to study biological samples. Instrum Sci Technol. https://doi.org/10.1080/10739149.2017.1395743

Tanner JE (1970) Use of the stimulated echo in NMR diffusion studies. J Chem Phys 2:2523–2526

Tanner JE, Stejskal EO (1968) Restricted self-diffusion of protons in colloidal systems by the pulse-gradient spin-echo method. J Chem Phys 49:1768–1777

Valiullin R, Skirda V (2001) Time dependent self-diffusion coefficient of molecules in porous media. J Chem Phys 114(1):452–458

Vandeleur RK, Sullivan W, Athman A, Jordans J, Gilliham M, Kaiser BN et al (2014) Rapid shoot-to-root signalling regulates root hydraulic conductance via aquaporins. Plant Cell Environ 37:520–538. https://doi.org/10.1111/pce.12175

Velikanov GA, Sibgatullin TA, Belova LP, Ionenko IF (2015) Membrane water permeability of maize root cells under two levels of oxidative stress. Protoplasma 252:1263–1273. https://doi.org/10.1007/s00709-015-0758-9

Wan XC, Steudle E, Hartung W (2004) Gating of water channels (aquaporins) in cortical cells of young corn roots by mechanical stimuli (pressure pulses): effects of ABA and of HgCl2. J Exp Bot 55:411–422

Zholkevich VN, Sinitsina ZA, Peisakhzon BI et al (1979) On the nature of root pressure. Physiologia rastenii 26(5):978–993 in Russian