=== **COMPLEX SYSTEMS BIOPHYSICS** ===

Mathematical Modeling of Measuring the Hydraulic Conductivity of Roots by the Relaxation Method

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Abstract—The continuum model of radial mass transfer in plant roots developed previously has been used for processing the nonstationary experiments on determining the root hydraulic conductivity. In contrast to compartmental models, our model allows describing the shape of the relaxation curve, in particular, separating segments with different relaxation times. It is shown that to correctly determine the hydraulic conductivity, the method of data processing should be modified. A method for estimating the extracellular to intracellular conductivity ratio is proposed.

Keywords: hydraulic conductivity of roots, root pressure relaxation, multiphase continuum, mathematical modeling

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INTRODUCTION

Water and solutes absorbed by plant roots are transported to remote parts of the plant via a specialized conduction system formed by xylem vessels. Xylem vessels are formed in mature parts of the root and extend to the sites of water evaporation in leaves; in transverse root sections they occupy the central part. Comparison of axial and radial flow resistance in e.g. maize roots [1, 2] has shown that the radial resistance is the main factor limiting water movement in roots and thereby the water supply in the whole plant.

Liquid transfer through the root is usually described with a linear relationship linking the flux across a unit area of the root lateral surface J_w with the applied action: $J_w = L_p(\Delta p - \sigma\Delta\pi)$. Here L_p is a coefficient of hydraulic conductivity integral for the root, reflecting its ability to move water from the surrounding medium into the xylem vessels, Δp is the hydrostatic pressure difference, $\Delta\pi$ is osmotic pressure difference between the surrounding medium and the xylem vessels, σ is integral reflection coefficient.

One of the methods of experimentally determining the integral hydraulic conductivity coefficient L_p is based on such perturbation of the stationary state when the flow through the root ceases and there appears some root pressure [3]. Therewith in some cases they measure the relaxation change in pressure in a capillary attached to a cut root, while in others,

the relaxation change in the flow across the root section. Processing of the resulting curves permits calculation of the relaxation times; on this basis, with a compartmental model (see e.g. [4]) one obtains values identified with root hydraulic conductivity and root permeability for a corresponding solute.

In the present work it is proposed to determine the integral root hydraulic conductivity basing not on a compartmental but on a continual description of mass transfer. The hydraulic conductivity coefficients determined by different methods are compared, the causes of their discrepancy are analyzed. It is shown that the continual model, in contrast to a compartmental one, permits describing the observed peculiarities of the experimental curve.

MODELING BASED ON MEMBRANE THEORY

The scheme of experiment appears as follows [4] (Fig. 1). A cut root id connected with a capillary tube filled partly at the root side with distilled water and partly with oil. The other end of the tube is closed with a piston moved with a micrometer screw. A piezosensor permits registering the liquid pressure in the capillary. Prior to the experiment, the cut root fixed in the measuring system is kept in a nutrient solution till establishment of stationary root pressure. Then, moving the piston one way or the other, or changing the solute concentration, the system is taken out of equilibrium. In the course of experiment, the time change in capillary pressure is measured.
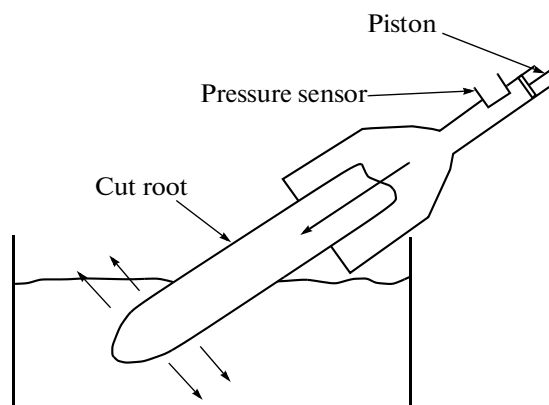
Fig. 1. Scheme of conducting an experiment on measuring hydraulic conductivity.

Replacing the cell layers between the root surface and the xylem vessels with one membrane, following [4], we get a set of equations describing the change in liquid volume in the measuring system under the piston and the change in concentration in xylem vessels:

$$\frac{d(V_s + V_x)}{dt} = -L_p A_r (p_r - \sigma RT(c_{xs} - c_{ms})),$$

$$\frac{d(V_s + V_x)}{\Delta p_r} = \frac{\Delta V_s}{\Delta p_r} = \frac{V_{s0}}{\varepsilon_s}, \left(p_r - p_{r0} = \varepsilon_s \frac{V_s - V_{s0}}{V_{s0}} \right),$$

$$\frac{dc_{xs} V_x}{dt} = P_s A_r (c_{ms} - c_{xs}) + J_a A_r,$$

$$V_x = const, \quad J_a = const.$$

Here V_s is volume of the measuring system; V_x — volume of xylem vessels; A_r — area of root lateral surface; p_r — root pressure; V_{s0} and p_{r0} — stationary values of the measuring system volume and root pressure respectively; c_{xs} — concentration of solutes in xylem vessels; c_{ms} — concentration of solutes in the surrounding medium; ε_s — modulus of elasticity of the measuring system; P_s — integral coefficient of root permeability for solute; J_a — power of active pumps. The set of equations describes exoosmotic experiments (only these will be further considered), in which the flow is directed from xylem vessels outward (with the opposite direction of flow, the last equation must be supplemented with a summand describing the convective efflux of substance from xylem vessels into the capillary). Work [4] disregards the presence of an active pump and brings into consideration a substance not transferred beyond the root. Work [5] shows that an osmotically active substance not transferred by the flow across membranes does not influence the radial transfer of water and ions in the root, and its presence is necessary only to maintain a corresponding root pressure, but would not anyhow tell on the relaxation times.

It is more convenient to transform the set of equations to the form:

$$\frac{dV_s}{dt} = -L_p A_r \left(\varepsilon_s \frac{V_s - V_{s0}}{V_{s0}} - \sigma RT(c_{xs} - c_{xs0}) + \sigma RT(c_{ms} - c_{ms0}) \right),$$

$$\frac{dc_{xs} V_x}{dt} = P_s A_r (c_{ms} - c_{xs}) + J_a A_r,$$

where c_{ms0} is the initial concentration of the external solution, and c_{xs0} is the stationary concentration in the xylem.

In hydrostatic experiments, the system is taken out of a stationary state with a jump-wise increase of pressure in the tube above the root section by moving the piston. Then at initial conditions $V_s = V_A$, $c_{ms} = c_{ms0}$, $c_{xs} - c_{ms} = \frac{J_a}{P_s}$ at $t = 0$, taking that at $t > 0$ the external concentration remains constant, $c_{ms} = c_{ms0}$, we get a solution of the form:

$$c_{xs}(t) = c_{ms} + \frac{J_a}{P_s}$$

$$V_s(t) = V_{s0} + (V_A - V_{s0}) \exp(-k_w t),$$

where $k_w = \frac{L_p A_r \varepsilon_x}{V_{s0}}$. Using the law of elasticity, we obtain that

$$k_w = A_r \frac{\Delta p_r}{\Delta V_s} L_p. \tag{1}$$

The $\frac{\Delta p_r}{\Delta V_s}$ value, determined experimentally, characterizes the elasticity of the measuring system and changes insignificantly upon small changes of volume. The solution obtained shows that pressure relaxation in the hydraulic experiment is described by only one exponential, and the rate constant k_w, determined by processing the experimentally obtained plot, serves to find the L_p value, which is further considered the integral root hydraulic conductivity.

Approximation with one exponential of the results of measuring the pressure relaxation in maize roots [4] has shown that the characteristic relaxation time

$$T = 1/k_w \tag{2}$$

on average makes 14—30 s. Despite that the exact solution is represented by one exponential, in [6] it is indicated that one a relaxation curve one should discern three different segments caused by different relaxation times. The first, fast part of the relaxation curve is characterized by a relaxation time about 1.2 s, the second part has a relaxation time 2,7—7 s, and the last, slow — in the range 75—95 s. In the opinion of the authors of [6], the first segment corresponds to an

elastic reaction of the system to an abrupt change of pressure. The third, slowest segment of the curve is associated with rearrangement of the radial flow of liquid as a result of change in the concentration profile. Outflow of liquid from xylem vessels leads to a temporary significant growth of concentration in the extracellular space (apoplast) in the vicinity of Casparian strips in the endodermis (cylindrical layer of cells inside the root), which create an impermeable barrier for radial flow of water and solutes over the extracellular space. The existence of a region of significant inhomogeneity of concentration in the extracellular space in its turn may noticeably influence the radial flow and makes incorrect the use of formulae based on membrane relationships. Therefore the authors of [6] used for determining the integral root conductivity just the second phase of the relaxation curve. Attempts of mathematical modeling of the development of a boundary layer adjacent to the epidermis and of its influence on relaxation times for various experiments are presented in [7, 8].

The main drawback of the compartmental model used is the impossibility of obtaining an experimental relaxation curve containing segments with different relaxation times; therefore, the choice of one or another curve segment in data processing is not quite substantiated. Another drawback of the standard method is that the quantity thus measured characterizes the root radial conductivity only near a state of the system corresponding to no flow. Apart of that, with a compartmental model the processing of data completely ignores the inner structure of the root and the character of flow therein (radial flow on the microlevel, peculiarities of anatomical structure). All this leads to the necessity of considering fuller continual models.

CONTINUAL MODELING

Assuming that the root is axially symmetrical, consider its tissue as a porous continuous medium occupying the region $r_0 \leq r \leq r_1$, where r_0 and r_1 are coordinates of boundaries with the region of xylem vessels and surrounding medium. The porous medium is filled by two fluid phases, formed by viscous liquids being respectively in the apoplast (first phase) and symplast (second phase) and filtered though a rigid undeformable carcass. In the framework of a macroscopic model, each of these liquids spatially separated at the microlevel is held to fill the entire tissue space. It is assumed that in each phase a low-molecular component is dissolved at bulk concentrations c_1 and c_2 respectively. In the capacity of solute in the given case we will consider NaCl, capable of moving in the medium both as a result of active transfer across membranes and by means of convection and diffusion. NaCl also creates an osmotic force connected with the presence of semipermeable cell membranes. The water flow between phases is regulated by membrane-type relationships with account of difference in osmotic pressures created by solute. In writing down the macroscopic dynamic relationships, account was taken of the notion of flow organization at the cellular level. In the extracellular fluid phase, a purely viscous flow is assumed, whereas in the intracellular one there is also a distributed osmotic force. A closed set of equations describing radial mass transfer in the root has the form [5, 9]:

$$\rho_1 \frac{1}{r}\frac{\partial v_1 r}{\partial r} = J, \quad \rho_2 \frac{1}{r}\frac{\partial v_2 r}{\partial r} = -J,$$

$$J = L_w[p_2 - p_1 + RT(c_1 - c_2)],$$

$$v_1 = -\beta_1 \frac{\partial p_1}{\partial r}, \quad v_2 = \beta_2\left(-\frac{\partial p_2}{\partial r} + \zeta Rt\frac{\partial c_2}{\partial r}\right),$$

$$\rho_1\left(\frac{\partial c_1}{\partial t} + \frac{1}{r}\frac{\partial c_1 v_1 r}{\partial r}\right)$$

$$= -k - \lambda(c_2 - c_1) + \rho_1 D_1\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial c_1}{\partial r}\right),$$

$$\rho_2\left(\frac{\partial c_2}{\partial t} + \frac{1}{r}\frac{\partial(1-\zeta)c_2 v_2 r}{\partial r}\right)$$

$$= k - \lambda(c_2 - c_1) + \rho_2 D_2\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial c_2}{\partial r}\right),$$

$$\frac{dP_r}{dt} = -2\pi r_0 L\alpha v_1(r_0)E_v,$$

$$\frac{d(c_{xyl}V_{xyl})}{dt} = 2\pi r_0 L\left(-\alpha v_1(r_0)c_{xyl} + \frac{\lambda_{xyl}}{\rho}(c_2(r_0) - c_{xyl})\right).$$

Here ρ_1 and ρ_2 are bulk densities of the phases; v_1 and v_2 — liquid velocities in the apoplast and symplast respectively; p_1 and p_2 — hydrostatic pressures in the apoplast and symplast; L_w — bulk coefficient of tissue hydraulic conductivity; J — interphase flow; T — absolute temperature; $R = \rho_0 R_0/\mu_0$ (R_0 — universal gas constant; μ_0 — molar mass of low-molecular solute; ρ_0 — water density); β_1 and β_2 — conductivities of the apoplast and symplast, ζ — distributed reflection coefficient of the symplast (its expression through parameters at the cellular level is given in [5], further used is the value $\zeta = 0,899$); λ — cell membrane permeability for solute; k — interphase active flux of substance (further assumed piecewise constant—zero in the region internal relative to Casparian strips and nonzero in the external region); D_1 and D_2 — diffusion coefficients for solutes in apoplast and symplast; V_{xyl} — xylem volume. The last two equations describe the change in root pressure P_r at the expense of an elastic change in volume and the change in substance concentration in the xylem c_{xyl} at the expense of outflow from xylem vessels into the apoplast space and diffusion mass exchange with the symplast through cell walls. Here L and α are root length and the volume fraction of the apoplast;

E_v – coefficients of elasticity of the measuring system; λ_{xyl} – permeability of xylem vessels for solute.

Before solving the problem on root pressure relaxation, let us determine the pressure and concentration in xylem vessels having formed by the start of experiment in the absence of flow through the root. For this we solve the first six equation of the given set written in stationary form, with boundary conditions for the lack of flow of liquid and solute across the inner and outer borders of the root and the extracellular pressure and concentration specified at the outer root border:

$$r = r_1: p_1 = p_e = 0, c_1 = c_e, v_1 = 0, v_2 = 0,$$
$$\frac{\partial c_2}{\partial r} = 0, r = r_0: v_1 = 0, v_2 = 0, \frac{\partial c_2}{\partial r} = 0. \quad (3)$$

As a result, the pressure and concentration in xylem vessels will be found from conditions: $P_r = p_1$ and $c_{xyl} = c_1$ at $r = r_0$. Taking v_1 and v_2 to be zero, one can find the following solution of the set:

$$p_1 = \begin{cases} P_r, r < r_c \\ 0, r > r_c \end{cases}$$

($r = r_c$ is the location of Casparian strips),

$$p_2 = p_1 + RT(c_2 - c_1), \; c_1 = \begin{cases} c_e + k/\lambda, r < r_c, \\ c_e, r < r_c, \end{cases}$$

$$c_2 = c_e + k/\lambda, \; p_r = RT\frac{k}{\lambda}, \; c_{xyl} = c_e + \frac{k}{\lambda}.$$

Solution of the nonstationary set of equations gives the experimentally registered change in pressure under the piston. Specifying the boundary conditions, consider a somewhat simplified situation in which we neglect the flux of water and solutes across the outer and inner borders of the symplast as compared with fluxes between the symplast and apoplast. In this case $\lambda_{xyl} = 0$, and the conditions for water and solute fluxes in the intracellular space convert to no-flow conditions. In solving the nonstationary problem, we replace the no-flow conditions for outer and inner surfaces of the apoplast in boundary conditions (3) with conditions $c_1 = c_{xyl}(t)$ and $p_1 = p_r(t)$ at $r = r_0$.

The boundary conditions on Casparian strips (at $r = r_c$), not presented here, take into account the absence of flow through the apoplast and the continuity of the sought-for functions and fluxes in the symplast. The initial concentration in xylem vessels was taken to be the value found above in the absence of flow. The initial pressure in the xylem was taken to be a value perturbed relative to the above-found stationary pressure.

The coefficients used in the set of equations, L_w, λ, k, β_2 and D_2, are expressed through the cell-level parameters given in literature sources (in more detail this is discussed in [10]): $L_w = 2.5L_{p(cell)}\rho_0/l$, $\lambda = $ $2.5P_{s(cell)}\rho_0/l$, $k = 2.5I_s\mu/l$, $\beta_2 = 2L_{p(cell)}l$, $1/D_2 = 1/D_1 + 1/(2P_sl)$. Here $L_p(cell)$ is the hydraulic conductivity coefficient of cell wall unit surface; $P_{s(cell)}$ – permeability coefficient of cell wall unit surface for solute; l – mean cell radius; μ – molar mass of transferred substance; I_s – active ion flux through cell surface.

The relaxation curve was obtained at the set of parameters corresponding to maize roots. In numerical modeling, the following values were chosen: $L_{p(cell)} = 8.8 \times 10^{-13}$ m s^{-1} Pa^{-1}, $r_0 = 1.3$ mm, $r_c = 1.9$ mm, $r_1 = 0.5$ mm, $D_1 = 3 \times 10^{-10}$ m^2 s^{-1}, V_x constitutes 3% of root volume, $\rho_1/\rho_0 = 0.07$, $L = 85$ mm ([7]), $E_r = 2.9 \times 10^{15}$ Pa m^{-3}, $I_s = 150 \times 10^{-9}$ mol m^{-2} s^{-1}, $l = 15$ μm ([6]). The cell wall permeability coefficient for solute was chosen to be: $P_s = 1.5 \times 10^{-8}$ m s^{-1}. This is almost five times greater than the average permeability given in the literature. Such a choice is connected with that in experimental works they usually give the values of integral permeability for the whole root.

The value of osmotic pressure of the surrounding solution π_{ext} created by NaCl can be obtained on the basis of indirect data. Thus as the concentration in the inner region of apoplast in the absence of flow, work [7] gives $c_{bulk} = 50$ mol m^{-3}. Then the concentration of the surrounding solution can be found from the estimate $c_{ext} - c_{bulk} = I_s/P_s$. As a result we get $c_{ext} = 40$ mol m^{-3}, which corresponds to $\pi_{ext} \approx 0.1$ MPa. There are no data at all regarding the fraction of intracellular space suitable for effective flow from cell to cell (here one should take into account both the presence of cellular organelles and the viscous adhesion on solid surfaces inside the cell, and possibly many other things). Let us take $\rho_2/\rho_0 = 0.7$, where ρ_0 is water density.

DETERMINATION OF HYDRAULIC CONDUCTIVITY COEFFICIENT

The flux of liquid depends on the difference of hydrostatic and osmotic pressures between the surrounding medium and the xylem vessels Δp and $\Delta \pi$. The use of relationship $J_w = L_p(\Delta p - \sigma \Delta \pi)$ is a linearization of this dependence in the vicinity of a point corresponding to no flow. The hydraulic conductivity coefficient thus obtained, therefore, does not characterize the flux at Δp and $\Delta \pi$ substantially differing from zero.

Let us determine the integral hydraulic conductivity of the root L_p as a measure of change in the flux through unit root lateral surface J_w upon a change of hydrostatic pressure difference between the surrounding medium and the xylem and at constancy of all other factors. In this way, we determine the integral hydraulic conductivity coefficient as a partial derivative of the flux through unit root lateral surface with respect to the hydrostatic pressure difference at fixed
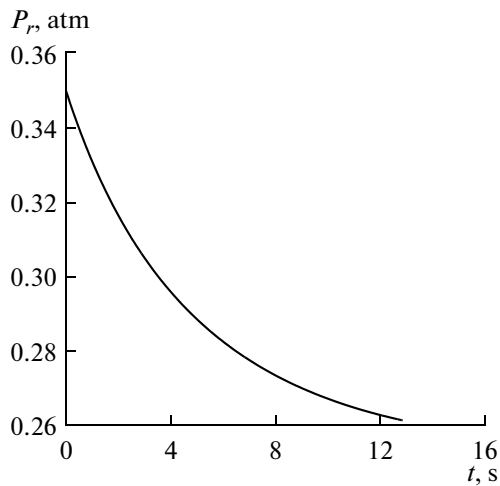
P_r, atm

Fig. 2. Example of a relaxation curve of root pressure P_r at $\beta_1/\beta_2 = 1000$.

osmotic pressure difference between the xylem vessels and the surrounding medium:

$$L_p = \left.\frac{\partial J_w}{\partial \Delta p}\right|_{\Delta\pi = \text{const}}.$$

For this one should solve a problem in which the concentration in the extracellular space is specified both on the outer and on the inner (at site of contact with xylem vessels) borders. From the solution of the problem one will obtain the dependence $J_w = J_w(\Delta p)$ ($\Delta\pi = \text{const}$). The above-presented set of differential equations (without the two last equations for root pressure and concentration in xylem) was solved at previous conditions on Casparian strips and conditions on the outer and inner borders obtained from (3) by replacement of $v_1 = 0$ at $r = r_0$ and $r = r_1$ with conditions $c_1 = c_{xyl} = \text{const}$ и $p_1 = \Delta p$ at $r = r_0$.

COMPARISON OF TWO METHODS FOR PROCESSING EXPERIMENTAL DATA

Using the above-described mathematical model, let us model an experiment on relaxation of root pressure after a sharp rise of pressure in the capillary tube of the measuring system. The relaxation curve obtained in a numerical experiment we will, as in the standard method [4], approximate with several exponentials and, choosing the corresponding relaxation time T, determine the hydraulic conductivity from relationship $\dfrac{1}{T} = A_r \dfrac{\Delta p_r}{\Delta V_s} L_p$, which follows from relationship (1) and (2).

Having modeled the hydrostatic exoosmotic experiments at various ratios of apoplast and symplast conductivities β_1/β_2, we approximate the obtained root pressure relaxation plots with a function of form $P_r =$
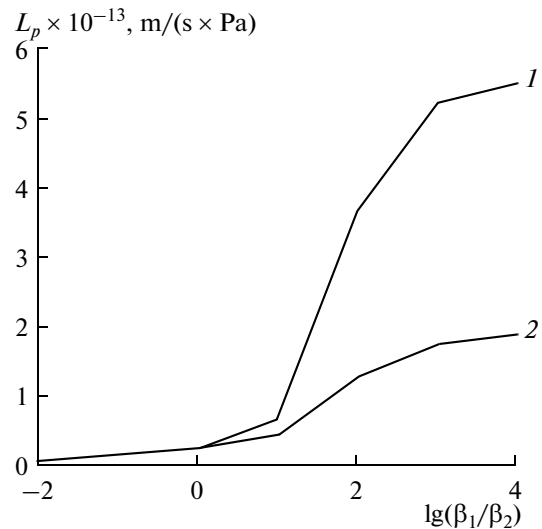

Fig. 3. Comparison of hydraulic conductivities obtained after processing of relaxation curves: *1* − by standard method using the smaller relaxation time; *2* − using the greater relaxation time.

$a_1 e^{-t/T_1} + a_2 e^{-t/T_2} + b$ (relaxation curve at $\beta_1/\beta_2 = 10^3$ is presented in Fig. 2). For this purpose a Matlab 6.5 package was used. First we conducted approximation of some initial and final segments of the relaxation curve using one exponential. The relaxation time values thus found were used as an initial approximation in the iterative process of finding the parameters of the initial curveâ. The relaxation times obtained and the weight factors at the exponentials are presented in the table.

With the aid of the data obtained we calculated the root hydraulic conductivity at different values of $\log(\beta_1/\beta_2)$. Figure 3 presents the results of comparing the conductivity obtained with the standard method [6] using the smaller of the two relaxation times (curve *1*) with the conductivity calculated with the use of the larger relaxation time T_2, (curve *2*) (the elastic response of the system in response to a pressure jump

Values of parameters of function $P_r = a_1 e^{-t/T_1} + a_2 e^{-t/T_2} + b$ in approximation of relaxation curves

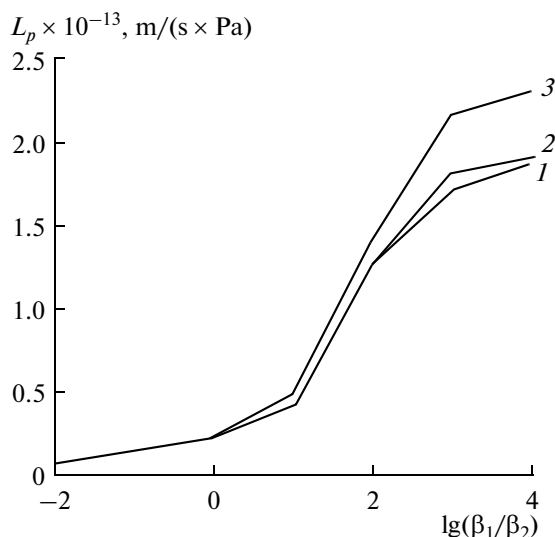| $\log(\beta_1/\beta_2)$	T_1, s	T_1, s	a_1, atm	a_2, atm
−2	164	174	0.04	0.06
−1	83	88	0.04	0.06
0	52.1	56.3	0.04	0.06
1	20	30	0.02	0.08
2	3.6	10.3	0.02	0.08
3	2.5	7.24	0.03	0.07
4	2.35	6.9	0.03	0.066

Fig. 4. Comparison of hydraulic conductivities obtained with the aid of different methods. Curve *1* − calculation by compartmental model using the greater relaxation time. Two other curves obtained from the continual model at an osmotic pressure in the xylem equal to the osmotic pressure in the surrounding medium (*2*), and equal to zero (*3*).

observed in the experiment in the given case is absent). It is seen that at $\beta_1/\beta_2 \gg 1$ the differences in conductivities determined on the basis of different relaxation times become significant. From the table it is evident that the weight factor at the exponential with the smaller relaxation time is several times smaller than the corresponding factor at the second exponential (the difference is especially great if $\beta_1/\beta_2 \approx 1$).

Let us compare the values of conductivity obtained on the basis of the membrane model and the theoretical value calculated with the use of the continual model of substance transfer in the root. To obtain the theoretical hydraulic conductivity $L_{\mathrm{p}} = \left.\dfrac{\partial J_{\mathrm{w}}}{\partial \Delta p}\right|_{\Delta \pi \,=\, \mathrm{const}}$ from the numerical solution of the corresponding problem we obtained dependences $J_{\mathrm{w}} = J_{\mathrm{w}}(\Delta p)$ ($\Delta \pi =$ const) which are well approximated by a straight line. Therefore the value of hydraulic conductivity was easily determined as the angle coefficient in the linear regression equation. The result of comparing the calculated theoretical conductivity coefficient and the conductivity coefficient obtained on the basis of the formula ensuing from the compartmental model but with the use of not the smaller but the larger relaxation time is presented in Fig. 4. Curve *1* was obtained by the standard method with the use of the larger relaxation time, curves *2* and *3* are variants of calculations on the basis of the continual model with a choice of the osmotic pressure in the xylem equal to the value of osmotic pressure in the surrounding medium and to zero respectively. The result of calculations at the osmotic pressure difference at no flow through the

root is practically indistinguishable from curve *1*. The value of the theoretical conductivity coefficient at $\beta_1/\beta_2 \gg 1$ proves to some extent dependent on the concentration difference between xylem vessels and the surrounding medium.

At a high conductivity of the apoplast space, inherent particularly in maize roots, the integral root conductivity calculated in the standard way (based on smaller time) proves close to the conductivity of a solitary cell. Therefore, as pointed out in [11], the value thus calculated characterizes only the mean conductivity of the outer layers of cell walls, but in no measure the radial conductivity of the entire root. In its turn, the slow part of the relaxation curve reflect the change in root pressure caused by radial flow of water against the background of a weakly changing concentration profile. In fact it is this that is taken into account when using the continual model for calculating the hydraulic conductivity coefficient.

In the study of substance transfer in the root, of interest is the question of the relationship of conductivities of different root structure and how the existing methods of measurement can be used to obtain such information.

On the basis of the method of conducting an experiment used by us, a means can be proposed for estimating the ratio of extracellular and intracellular conductivities. Measuring the conductivity of cell walls in the outer layers of the root and using the continual model, we obtain a plot of dependence L_{p} vs. $\log\beta_1/\beta_2$ (it is assumed that cell wall conductivities of the outer and inner cell layers differ insignificantly). Having determined experimentally the value of whole root conductivity, with the plot (Fig. 4) we can find the ratio β_1/β_2.

As a result of collating two methods of processing a nonstationary experiment on measuring the root conductivity on the basis of the traditional membrane and the continual models it is demonstrated that the radial root conductivity should be determined with the slow rather than the fast segment of the relaxation curve. In the framework of the existing experimental method, noted is the possibility of evaluating the ratio of intracellular and extracellular conductivities by the experimental relaxation curve. It is shown that the peculiarities of experimental curves connected with the existence of relaxation curve segments characterized by different sets of parameters can be obtained only in the framework of the full continual multiphase mathematical model.

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