A mechanistic interpretation of root transport of water

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Abstract. The present paper offers a mechanistic interpretation of filtration coefficients L_{pr} in isolated maize roots, measured with the use of the root pressure probe by Steudle and others (Steudle 1990, 1992; Steudle and Brickmann 1989; Steudle and Frensch 1989; Steudle and Jeschke 1983; Steudle et al. 1993) on the basis of the Kedem-Katchalsky equations. Detailed investigations have been based on the mechanistic equations of solute and solvent membrane transport across porous membranes (Kargol 2001; Kargol and Kargol 2003a,b). It must be stressed that transport equations of both these (thermodynamic and mechanistic) formalisms are mutually compatible, which has been demonstrated for instance in the works Kargol and Kargol (2003) and Suchanek (2005, 2006).

Key words: Porous membranes — Root transport of water — Mechanistic equations — Root pressure probe — Filtration coefficient

Introduction

In the 1970s, it was demonstrated (Fiscus and Kramer 1975) that the root – even if isolated from the rest of the plant – is capable of water uptake and transportation through the xylem against gravity. This phenomenon (the so-called root pressure) may be described if the root is treated as an osmometer equipped with a selective membrane. Water is driven across the osmometer membrane by filtration and osmosis, in accordance with thermodynamic equations of the Kedem-Katchalsky (KK) membrane transport (Kedem and Katchalsky 1958, 1961; Katchalsky and Curran 1965). These equations define the measurable coefficients (L_{pr}, σ_r, ω_r) which characterise the root membrane (the index r refers to the root), with the assumption that the membrane is homogenous in terms of transport properties. In the 1980s and 1990s, the parameters L_{pr}, σ_r, ω_r were determined experimentally for isolated roots of various plants with the use of several measurement techniques (Steudle and Jeschke 1983; Steudle et al. 1987, 1993; Steudle and Brickmann 1989; Steudle and Frensch 1989; Steudle 1990, 1992).

In the present article, only the filtration coefficients L_{pr} of isolated maize roots are considered, as determined by Steudle and others with the use of the so-called root pressure probe (Steudle and Frensch 1989; Steudle et al. 1993, 1987). These coefficients determine hydraulic conductivity of the roots, thus characterising root water transport. The data published in Steudle and Frensch (1989) and Steudle et al. (1987) represent outstanding quality. They are also very interesting due to the fact that they cannot be unambiguously interpreted basing on the above-mentioned one-membrane root model.

From the KK formalism (which has provided the basis for the experiment) it follows that the values of independent parameters (L_{pr}, σ_r, ω_r) of the root membrane are not dependent on measurement methods. Yet the measurements taken with the use of the root pressure probe showed that the values of the root filtration coefficients L_{pr} are clearly dependent on the type of stimulus (hydrostatic or osmotic) which induced the radial flow of water through the root. According to Steudle, these results demonstrate the structural complexity of the root which is not formulated by the single-membrane model (Steudle and Jeschke 1983; Steudle et al. 1987, 1993; Steudle 1990, 1992).

The present author believes that an additional reason for the said discrepancy between the model and the experiment may be high generality of the formalism applied to data description (in this case, the thermodynamic KK equations).

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That is why an alternative description of root transport should be provide using mechanistic equations which make allowances for the microscopic structure of the root membrane and are more detailed than the KK equations. Both these approaches (the thermodynamic and the mechanistic), applied jointly, offer a more thorough investigation tool than the KK equations alone, on condition of mutual compatibility of both descriptions (Kedem and Katchalsky 1961; Katchalsky and Curran 1965; Suchanek 2005, 2006).

In the present article, the author attempts to approach the root as an osmometer equipped with a membrane of a certain (porous) structure, heterogeneous in terms of its transport properties. In this model, water and the solute move from the root's environment into its interior across the pores with varied cross-section radiuses. The dimensions of some of these pores are too small to contain solute particles (hence they are semi-permeable). The remaining pores (with larger dimensions) are permeable to solute particles. The membrane transport is also subject to the Kargols mechanistic equations (Kargol 2001; Kargol and Kargol 2003a,b) which – as has been demonstrated (Kargol and Kargol 2003a,b; Suchanek 2005, 2006) – are mutually compatible with the KK equations. Basing on the model of a root as a porous membrane, an explanation shall be offered for the above-mentioned relationship of the root filtration coefficients and the method of their measurement.

Results

Root filtration coefficients determined by the root pressure probe

According to the literature (Fiscus and Kramer 1975; Steudle 1990, 1992; Steudle and Brickmann 1989; Steudle and Frensch 1989; Steudle and Jeschke 1983; Steudle et al. 1987, 1993), the root is permeable (to a certain extent) for some mineral salts, apart from water. Thus, the single model membrane is a selective membrane, and the root transport is formulated by the KK equations (Kedem and Katchalsky 1958, 1961; Katchalsky and Curran 1965):

$$J_{vr} = L_{pr}\Delta P_{xg} - L_{pr}\sigma_r\Delta\Pi_{xg} \tag{1}$$

$$j_{sr} = (1-\sigma_r)\overline{c}_s J_{vr} + \omega_r\Delta\Pi_{xg} \tag{2}$$

where J_{vr}, j_{sr} are water and solute flows, respectively, moving across the root; ΔP_{xg}, $\Delta\Pi_{xg}$ are pressure differences between the xylem (x) and the medium (g); L_{pr}, σ_r, ω_r are practical root coefficients.

From Eq. (1) it follows that the root filtration coefficient L_{pr}, which characterises root permeability to water, can be measured in two ways:

$$L_{pr}^{hydro} = \left(\frac{J_{vr}}{\Delta P_{xg}}\right)_{\Delta\Pi_{xg}=0} \text{ or } \sigma_r L_{pr}^{osmo} = \left(\frac{J_{vr}}{\Delta\Pi_{xg}}\right)_{\Delta P_{xg}=0} \tag{3}$$

where the reflection coefficient $\sigma_r = \left(\dfrac{\Delta P_{xg}}{\Delta\Pi_{xg}}\right)_{J_{vr}=0}$ is determined separately.

As the coefficients L_{pr}, σ_r, ω_r in Eqs. (1) and (2) are mutually independent, the value of the coefficient L_{pr} should not depend on the measurement method (3).

More precisely, the filtration coefficients L_{pr} of isolated roots of various plants have been measured with the use of the root pressure probe connected to the tip of the root excised from the rest of the plant (Steudle and Jeschke 1983; Steudle et al. 1987, 1993; Steudle and Brickmann 1989; Steudle and Frensch 1989; Steudle 1990, 1992). In these experiments, the volume flow J_{vr} (t) and pressure differences $\Delta P_{xg}(t)$, $\Delta\Pi_{xg}(t)$ change in time, and Eqs. (1) and (2) take the differential form, while the coefficients L_{pr}, σ_r, ω_r remain constant.

In the experiments conducted by Steudle and others (under precisely specified conditions), the value of root pressure (P_{ro}) was initially determined. Subsequently, with the use of the probe, over a short period of time, the hydrostatic pressure in the xylem was increased or decreased (so-called hydrostatic experiments), or the medium concentration was changed (osmotic experiments). In this way, the water volume flow $J_{vr}(t)$ was induced between the medium and the root xylem, which consequently brought a change in the xylem hydrostatic pressure. This pressure exponentially decreased (or increased) in time (Fig. 1), and its changes were recorded in a constant manner by the pressure probe in the form of the so-called pressure relaxation curve. This curve illustrates the process of the root-probe system reaching a state of equilibrium.

In hydrostatic experiments, from the courses of relaxation curves, conclusions were drawn as to the values of the filtration coefficient L_{pr}^{hydro}. In osmotic experiments, in turn, these curves reflected two phases of the experiment. The first (so-called "water" phase) corresponded to rapid movement of water as driven by the osmotic pressure difference between the medium (i.e. solutions of selected solutes) and the root xylem. The second, later "solute" phase corresponded to the water flow as driven by diffusion of the solute to (or from) the xylem. From the "water" phase, the product $L_{pr}^{osmo}\sigma_r$ was determined, and from the "solute" phase – the coefficients σ_r and ω_r.

Table 1 shows standard values of filtration coefficients L_{pr} as obtained with the use of the pressure probe (Steudle et al. 1987, 1993; Steudle and Frensch 1989) It can be seen that the filtration coefficients L_{pr}^{hydro} of various roots (determined in hydrostatic experiments) exceed by almost one order of magnitude the coefficients L_{pr}^{osmo} (measured in osmotic ex-
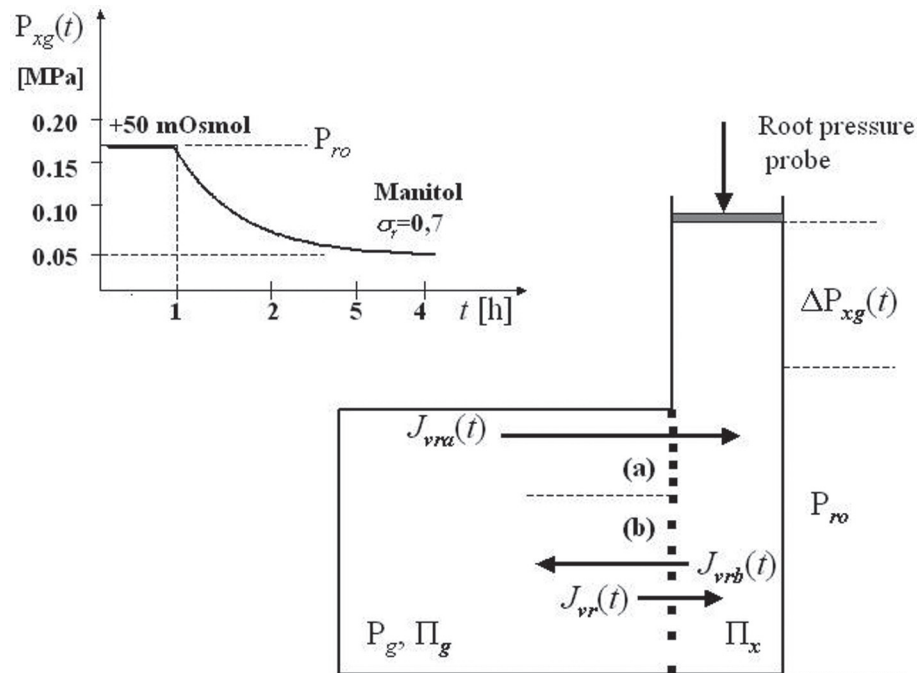
Figure 1. Model of the root as a porous membrane. M, root membrane; Π_x and Π_g, osmotic pressures in the medium and in the xylem, respectively; J_{vra} and J_{vrb}, water volume flows across the semi-permeable (a) and permeable (b) parts of the membrane; $J_{vr}(t)$, total volume flow across the membrane; P_{ro}, root pressure at the outset of the experiment; $\Delta P_{xg}(t)$, mechanical pressure in the xylem as recorded by the pressure probe (the top left-hand corner shows a sample relaxation curve as recorded in the osmotic experiment – the "water phase" (Steudle at al. 1993).

Table 1. Reflection coefficients σ_r of excised maize root for different solutes, measured using the root pressure probe

Medium	σ_r	References
Etanol	0.3	
KCl	0.5	Steudle and Frensch (1989)
KNO$_3$	0.5	
Mannitol	0.74	
Sacharoza	0.54	Steudle et al. 1987
PEG 1000	0.82	
NaCl	0.64	Steudle et al. 1993

Filtration coefficients L_{pr}^{osmo} (osmotic) and L_{pr}^{hydro} (hydrostatic) for different solutes are in the range 0.85–2.27 and 1.9–8.9 ms^{-1}MPa^{-1}, respectively.

periments). The observed inequality $L_{pr}^{osmo} < L_{pr}^{hydro}$ does not result from application of the KK formalism.

In the present article, the above data, based on a single-membrane root model in which the membrane has a porous structure are analysed. To begin with, basic information on water and solute transport across this type of membrane are presented.

Transport across a porous membrane

Let us consider a porous membrane M (Fig. 2), which separates solute (s) solutions, diluted and well-stirred. Across this membrane, driven by the mechanical pressure difference (ΔP) and the osmotic pressure difference ($\Delta\Pi$) on both sides, the solvent volume flow ($J_v \approx J_{vw}$) and the solute volume flow j_s pass, both directly proportional to pressure differences. The flows J_v and j_s (defined in a manner identical to that of the KK formalism) move across the pores with varied cross-section radiuses, which are placed randomly within the membrane. Water permeates across all the membrane's pores, while the solute (s) – only across those whose radiuses are larger than the radius r_s of the solute particle.

The membrane M in Fig. 2 has been conventionally divided into Part (a), in which the pore radiuses fulfil the relation $r < r_s$, and Part (b), where the relation $r > r_s$ is valid. The pores in Part (a) of the membrane constitute an impenetrable barrier for solute (s) particles, hence they are semi-permeable and may be (locally) assigned the reflection coefficient $\sigma_a = 1$. The pores in Part (b) of the membrane, across which both water and the solute (s) diffuse, are to be assigned the local reflection coefficient $\sigma_b = 0$. The membrane is selective if it contains both types of pores. Then the global reflection

coefficient of the membrane fulfils the inequality $0 < \sigma < 1$ (despite the fact that local reflection coefficients of the pores only equal $\sigma_a = 1$ or $\sigma_b = 0$).

Transport across this membrane is described by the Kargols mechanistic equations (Kargol 2001; Kargol and Kargol 2003a,b). It has been demonstrated that these equations are fully compatible with the KK equations (Kargol and Kargol 2003a,b; Suchanek 2005, 2006). Because in both (thermodynamic and mechanistic) approaches, the stimuli and the flows are defined in the same way, the practical coefficients L_p, σ, ω of the KK equations may be compared to corresponding proportion coefficients in the mechanistic equations. In this way, a complete description of transport across porous membranes is obtained. The description (Suchanek 2005) also includes mechanistic equations in the following form:

$$J_v = L_p \Delta P - L_p \sigma \Delta \Pi \qquad (4)$$

$$j_s = L_p (1 - \sigma) \Delta P + \omega_d \Delta \Pi \qquad (5)$$

as well as the mechanistic notation of the coefficients L_p, σ, ω_d of the porous membrane written as follows:

$$L_p = L_{pa} + L_{pb}, \qquad \sigma = \frac{L_{pa}}{L_p} \qquad (6a)$$

$$\omega_d = \overline{c}_s L_D \text{ and } \omega_d \approx \overline{c}_s L_p (1 - \sigma) \qquad (6b)$$

where L_{pa}, L_{pb} are filtration coefficients of Parts (*a*) and (*b*) of the root membrane, respectively; ω_d is the practical coefficient which formulates diffusion of the solute permeating across the pores (b) only; L_D is the phenomenological diffusion coefficient.

Equations (6) demonstrate that the practical coefficients L_p, σ, ω of the porous membrane may be expressed through the filtration coefficients L_{pa}, L_{pb} of the semi-permeable Part (*a*) and permeable Part (*b*) of the membrane, respectively. It can be seen that the total filtration coefficient L_p of the porous membrane equals the sum-total of filtration coefficients in both parts ((a) and (b)) of the membrane. The reflection coefficient σ, which formulates membrane selectivity with respect to the solute, depends on the relative content of semi-permeable pores in the membrane. The coefficient σ of a semi-permeable membrane (for which $L_p = L_{pa}$) equals one, while σ of a permeable membrane (for which $L_{pa} = 0$) equals zero.

Mechanistic interpretation of root filtration coefficients L_{pr}

Below it is demonstrated that an inequality $L_{pr}^{osmo} < L_{pr}^{hydro}$ may be explained with the use of the mechanistic approach to root transport. To this end, a root model will be used (Fig. 1), in
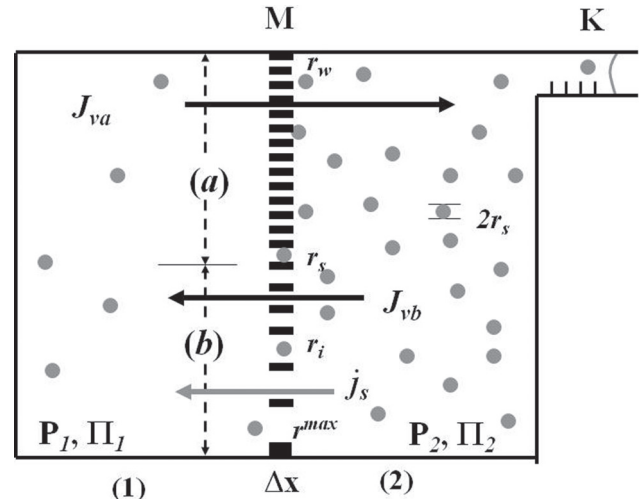
Figure 2. Model membrane system. M, heterogeneous membrane; Δx, membrane thickness; K, capillary; (1) and (2), compartments; Π_1 and Π_2, osmotic pressures; P_1 and P_2, mechanical pressures; J_{va} and J_{vb}, volume flows permeating across Parts (a) and (b) of the membrane; r_w, r_s, r_i, r_N^{max}– pore radiuses; $2\,r_s$, diameter of the solute particle; j_s, „net" solute flow.

which the porous membrane emulates the entire root tissue between the medium and the stele xylem.

According to this model, radial root transport is formulated using the mechanistic equations (1, 2, 3). Water transport across the root is described by the relations:

$$J_{vr} = L_{pr} \Delta P_{xg} - L_{pr} \sigma_r \Delta \Pi_{xg} \qquad (4')$$

$$L_{pr} = L_{pra} + L_{prb} \qquad (6'a)$$

$$\sigma_r = \frac{L_{pra}}{L_{pr}} \qquad (6'b)$$

where ΔP_{xg} and $\Delta \Pi_{xg}$ are pressure differences between the root xylem (*x*) and the medium (*g*); *r* indicates the root. It is assumed that the volume flow in Eq. (4') approximates the resultant water volume flow across the root membrane ($J_v \approx J_{vr}$).

Upon insertion of expressions (6'a) and (6'b) into Eq. (4'), the following formula for the resultant radial water volume flow J_{vr} which flows through the root is obtained:

$$J_{vr} = (L_{pra} + L_{prb}) \Delta P_{xg} - L_{pra} \Delta \Pi_{xg} =$$
$$= L_{pra} (\Delta P_{xg} - \Delta \Pi_{xg}) + L_{prb} \Delta P_{xg} = J_{vra} + J_{vrb} \qquad (7)$$

where $J_{vra} = L_{pra}(\Delta P_{xg} - \Delta \Pi_{xg})$ is the (water) volume flow across the semi-permeable Part (*a*) of the porous root membrane; $J_{vrb} = L_{prb}\Delta P_{xg}$ is the flow across the permeable Part (*b*) of the membrane.

From Eq. (7) it follows that the flow is the sum-total of partial flows J_{vra} and J_{vrb} which pass across Parts (*a*) and (*b*) of the root membrane, respectively. The flow J_{vra} depends on mechanical and osmotic pressure differences on both sides of the membrane, while the flow J_{vrb} depends exclusively on the mechanical pressure difference.

Now, the expression (7) will be applied to the description of transport phenomena which occur during the measurement of the filtration coefficients L_{pr} in hydrostatic and osmotic experiments. Let us remember that in both types of experiments, conducted with the use of the pressure probe, at the outset, the "equilibrium" value of root pressure (P_{ro}) was determined in the stele xylem (Steudle and Jeschke 1983; Steudle et al. 1987, 1993; Steudle and Brickmann 1989; Steudle and Frensch 1989; Steudle 1990, 1992).

In the hydrostatic experiment, at the moment t_o, over a short time, the pressure P_{ro} was increased (or decreased) by the quantity $\Delta P_{xg}(t_o)$. The difference then lessened exponentially to zero and, after a certain time $t = t_s$, the root returned to the state of equilibrium. As the change occurred rapidly (Steudle and Jeschke 1983; Steudle et al. 1987, 1993; Steudle and Brickmann 1989; Steudle and Frensch 1989; Steudle 1990, 1992), it may be assumed that in its course the osmotic pressure difference between the xylem and the medium did not change significantly ($\Pi_{xg} \approx$ const, i.e. $\Delta\Pi_{xg}(t) \approx 0$, where t is time). The radial water flow $J_{vr}(t)$ across the root and the mechanical pressure difference $\Delta P_{xg}(t)$ in the xylem are functions of time, but the coefficient L_{pr}, which connects both these values, remains constant.

In accordance with the definition (3) and the relation (7), the following is obtained:

$$L_{pr}^{hydro} = \left(\frac{J_{vr}(t)}{\Delta P_{xg}(t)}\right)_{\Delta\Pi_{xg}=0} = \frac{J_{vra}(t) + J_{vrb}(t)}{\Delta P_{xg}} =$$

$$= \left(\frac{L_{pra}(\Delta P_{xg}(t) - \Delta\Pi_{xg}(t)) + L_{prb}\Delta P_{xg}(t)}{\Delta P_{xg}(t)}\right)_{\Delta\Pi_{xg}=0} = \quad (8a)$$

$$= L_{pra} + L_{prb} = L_{pr}$$

In the hydrostatic experiment, it can be seen that both partial flows (J_{vra} and J_{vrb}) move in the same direction, so the resultant flow ($J_{vr}(t) = J_{vra}(t) + J_{vrb}(t)$) formulates the entire water transport across the root membrane. Therefore, this expression proves that the filtration coefficient L_{pr}^{hydro}, as determined in the hydrostatic experiment, represents the total filtration coefficient L_{pr} of the root membrane.

In the osmotic experiment (in its "water" phase), the root pressure P_{ro} is disturbed as a result of occurrence (at the moment t_o) of the non-equilibrium osmotic pressure difference $\Delta\Pi_{xg}(t_o)$. While returning to the state of equilibrium (to be more precise, to the stationary state), the root acts as an osmometer with a porous membrane.

At $\sigma_r = 1$ (i.e. when the membrane is semi-permeable), $L_{pr}^{osmo} = L_{pra} = L_{pr}$, i.e. the coefficient L_{pr}^{osmo} is the total root filtration coefficient. This situation is observed when, for instance, the solution of PEG 1000 is used as the medium. Yet, at $\sigma_r \neq 1$, the coefficient L_{pr}^{osmo} (understood as a value independent of σ_r) has no explicit mechanistic interpretation. This is visible when the behaviour of the root-probe system is described with the following expression:

$$\left(\frac{J_{vr}(t)}{\Delta\Pi_{xg}(t)}\right)_{\Delta P_{xg}^o=0} = \frac{J_{vra}(t) - J_{vrb}(t)}{\Delta\Pi_{xg}} =$$

$$= \frac{L_{pra}[\Delta\Pi_{xg}(t) - \Delta P_{xg}(t)] - L_{pbr}\Delta P_{xg}(t)}{\Delta\Pi_{xg}(t)} \quad (8b)$$

From this formula, it follows that at the moment t_o there exists no non-equilibrium hydrostatic pressure difference between the medium and the root xylem ($\Delta P_{xg}^o = 0$). Yet the osmotic flow $J_{vra}(t)$, when entering the xylem through the semi-permeable pores (a) of the root membrane, generates the hydrostatic pressure difference $\Delta P_{xg}(t)$ on it, recorded by the pressure probe. This difference drives the water flow $J_{vrb}(t)$ across the permeable pores (*b*) of the membrane from the xylem to the root's surroundings. It also reduces the flow $J_{vra}(t)$, induced by the pressure difference ($\Delta\Pi_{xg}(t) - \Delta P_{xg}(t)$), which enters the xylem. In this way, across the root, there are two simultaneous partial flows in opposite directions, and the resultant water volume flow (at any moment) equals their difference ($J_{vr}(t) = J_{vra}(t) - J_{vrb}(t)$). As has been shown, in the "water" phase of the osmotic experiment, the course of the function $\Delta P_{xg}(t)$ as recorded by the probe, depends on the relative content of semi-permeable pores in the root membrane, i.e. membrane selectivity. In this situation, the coefficient L_{pr}^{osmo} does not express the total hydraulic conductivity (L_{pr}) of the root membrane, despite the fact that during the experiment the water flows through all its pores. While comparing the expressions (8a) and (8b), it can be seen that – in the mechanistic approach – the coefficients $L_{pr}^{hydro} = L_{pr}$ and L_{pr}^{osmo} are not equal, unless the membrane is semi-permeable.

In my opinion, in the osmotic experiment, it is impossible to isolate the parameter L_{pr}^{osmo} which would simultaneously constitute a measure of filtration properties of the root and be independent of the membrane's selective qualities with respect to the solute. A more explicit value seems to be the product $\sigma_r L_{pr}^{hydro} = L_{pra}$, which represents (on the strength of the relation (6')) the filtration coefficient L_{pra} of the semi-permeable Part (*a*) of the root membrane. Most probably, it expresses the hydraulic conductivity of the pathway along which the water – on its way to the xylem – passes through the membranes of root cells.

To conclude, from the mechanistic viewpoint, in hydrostatic experiments, the global filtration coefficient of the

root membrane (L_{pr}) is determined, but the understanding of the reflection coefficient σ_r enables the calculation of the filtration coefficient (L_{pra}) for the semi-permeable part of the membrane.

Discussion

The present article has drawn on the measurement results of filtration coefficients L_{pr} of isolated roots, obtained in the 1980s and 1990s by Steudle and others, with the use of the root pressure probe (Steudle et al. 1987, 1993; Steudle and Frensch 1989). The objective has been to explain the diversification of values of the maize root coefficients L_{pr} depending on whether they were determined through "hydrostatic" or "osmotic" experiments.

In the present paper, it has been assumed that the root – in the course of water uptake from the environment – acts as an osmometer with a porous membrane, and that root transport fulfils the mechanistic Eqs. (4), (5) and (6). Basing on this model, water root transport has been analysed in both types of the above-mentioned experiments conducted with the use of the root pressure probe.

It has been found that in the "water" phase of the hydrostatic experiment, water moves across all the pores ((a) and (b)) of the root membrane in the same direction ($J_{vr}(t) = J_{vra}(t) + J_{vrb}(t)$). Hence, the coefficient L_{pr}^{hydro}, as measured in this experiment, expresses the total hydraulic capacity of the root membrane. Thus it is identical with the resultant root filtration coefficient L_{pr}.

In the osmotic experiment, in turn, the resultant water volume flow, at any moment, equals the difference of the partial flows ($J_{vr}(t) = J_{vra}(t) - J_{vrb}(t)$) and depends on the relative quantity of semi-permeable pores in the root membrane, i.e. membrane selectivity with respect to the solute. A comparison of the expressions (5a) and (5b) demonstrates that in the mechanistic approach the coefficients $L_{pr}^{hydro} = L_{pr}$ and L_{pr}^{osmo} cannot be equal, with the exception of the case when the coefficient σ_r of the membrane equals 1. The membrane is then semi-permeable and $L_{pr}^{hydro} = L_{pr}^{osmo} = L_{pr}$. In other cases, the coefficient L_{pr}^{osmo} does not formulate the total volume of the water which flows through the membrane over a unit of time and is not equal to the coefficient L_{pr}. To conclude, according to the mechanistic approach, the total root filtration coefficient (L_{pr}) is determined in hydrostatic experiments, and not in osmotic ones.

An explicit mechanistic interpretation is attached to the product $\sigma_r L_{pr}^{hydro}$, which is equal to the filtration coefficient L_{pra} of the semi-permeable pores of the root membrane, as well as the reflection coefficient of the root (σ_r) as a ratio of the filtration coefficient of the membrane's semi-permeable part (L_{pra}) to the filtration coefficient of the membrane

(L_{pr}) as a whole. For most solutes (see Table 1), the ratio approximates 1/2.

The above findings, in the author's opinion, enhance the precision of the image of root water transport, without excluding previous interpretations. Steudle believed that the inequality $L_{pr}^{hydro} > L_{pr}^{osmo}$ proves the existence of alternative root transport pathways characterised by various permeability for water moving across the root (Steudle and Jeschke 1983; Steudle et al. 1987, 1993; Steudle 1990, 1992).

In the mechanistic approach, the assumption concerning the (porous) structure of the root is an indispensable part of root transport description. However, selection of appropriate root structures to act as the pores (a) and (b) of the root membrane remains an open question. These may be both macroscopic structures (e.g. various water root pathways), and microscopic structures (e.g. plasmodesmas which join successive cells of the bark) of varying hydraulic capacity.

Finally, let me take a stand on the general problem, i.e. the role of the KK formalism in biophysical investigations. The KK equations were developed on the basis of phenomenological thermodynamics of irreversible processes (Kedem and Katchalsky 1958, 1961; Katchalsky and Curran 1965), with the assumption that the model membrane is a thermodynamic "black box". Due to that, they are very general, which is both their considerable advantage and disadvantage. On the one hand, the application scope of the KK equations is very broad (as it covers both natural and artificial membranes), and the quantity of experimental data obtained on this basis is enormous. The possibilities of theoretical and experimental application of these equations to biophysical issues are limited and being gradually exhausted. Consequently, the KK equations are used less and less frequently. Due to that, access to the vast experimental output obtained on the basis of these equations over several decades is becoming increasingly limited.

The present author believes that this output – not infrequently characterised by excellent quality – holds a much larger research potential than it would follow from the KK equations themselves. Namely, the results of these investigations may be reconsidered, treating the KK formalism as a thermodynamic model in its own right. Mechanistic models make allowances for the structure of model membranes, and microscopically formulate transport mechanisms, while the equations which describe them are more detailed than the KK equations. The description of the model based on the general KK equations may be compared (according to precisely defined principles (Kedem and Katchalsky 1961; Katchalsky and Curran 1965; Suchanek 2005, 2006)) with its mechanistic description. This enables a more detailed interpretation of data (obtained previously on the basis of the KK formalism), which expands the scope of phenomena liable to quantitative description. In the present paper, we have attempted to prove this on the basis of biophysical in-

vestigations into root water transport. Still, we are convinced that the scope of research to which this procedure may be applied is much broader.

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