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Studies of Osmo-Diffusive and Energetic Properties of the Maize Root

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Abstract. This work is concerned with osmotic and diffusive transport of water and solutes across the maize root, and also with ascent of substances in the xylem. The root has been modelled as a one-membrane system. For the root treated in this way (and with the stem cut off) all the transport parameters present in the thermodynamic description of transport (Katchalsky and Curran 1965) were determined using the pressure probe method (Steudle et al. 1987). These parameters include coefficients of filtration L_p, reflection σ, and permeability ω. Using numerical values of the parameters and the formalism mentioned, detailed calculations were performed of osmotic volume flows J_v, and solute flows j_s, going across the maize root and pumped by the root up to a certain height h, against the force of gravity. This in turn allowed, with the use of a previously developed analytical method (Kargol 1990) to study the osmo-diffusive conversion of free energy of solutions, and to analyse the root as a free energy converter. In particular, the effective power and energetic efficiency of the root in the radial transport and pumping of water by the root pressure up to a certain height h, were studied. The root pressure has been assumed to be generated osmotically.

Key words: Diffusion — Osmosis — Root — Maize — Energy conversion — Work — Power — Energetic efficiency

Introduction

The movement of water and solutes across the root (radially) is undoubtedly of basic importance for all physiological processes in the entire plant. Views concerning the biophysical mechanism of the movements differ considerably (Anderson 1976; Pitman 1982; Ziegler 1977; Zimmerman and Brown 1971; Kargol 1978; Tyree 1973). According to the so-called membrane theories (Ginsburg 1971; Fiscus 1975, 1977; Kargol 1978; Steudle and Jeschke 1983; Steudle et al. 1987; Taura et al. 1987, 1988) the basic, passive mechanisms of transport (with the exception of e.g. flows induced by transpiration which are due to cohesion mechanism) include: osmosis, diffusion and convection. A necessary condition for these mechanisms to be operative is the existence of adequate concentration gradients in the root. The theories assume the existence of certain barriers for water and dissolved solutes on radial pathways within the root. These barriers are then assigned the role of membranes.

Depending on the number of barriers specified, one-membrane (Fiscus 1975, 1977; Steudle and Jeschke 1983; Steudle et al. 1987) and multi-membrane models (Ginsburg 1971; Kargol 1978; Kargol and Suchanek 1990; Katou and Furumoto 1988; Michalov 1989; Taura et al. 1987, 1988) have been constructed.

These models have been employed to explain water flow along the concentration gradient, against the gradient, and iso-osmotic flows. They may also serve to explain the mechanisms of generation of the root pressure, due to which water (and dissolved substances) is transported along the xylem trachear elements to a certain height against the force of gravity. The pressure can, according to those models, be generated osmotically. In radial direction water is transferred against the forces of viscous drag. Such a transfer, as well as elevation to a certain height (against the gravitation force) induced by the root pressure require definite energy expenditure.

The energy required for the purpose is supplied to the root by metabolites which undergo energy degradation processes. Energy liberated in these processes drives active transport of some solutes, resulting in setting up and maintaining concentration gradients. Passive, radially directed flows of water and dissolved substances are generated due to these gradients. Thus, without going into biochemical details, the root can be treated as an osmotic and diffusive energy transducer.

In the present work a detailed analysis of osmotic volume flows J_v, and solute flows J_s, across the maize root with the stem cut off will be presented; the root is considered as a one-membrane model system. The flows were analysed as functions of the height of elevation h, of water along the xylem trachear elements accomplished by the osmotically generated root pressure.

These studies were made possible by a work by Steudle et al. (1987) who determined (using the method of pressure probe) all the three parameters of the Kedem-Katchalsky formalism (Katchalsky and Curran 1965), i.e. coefficients of filtration L_p, reflection σ, and permeability ω.

The coefficients were determined for young roots cut off the stem and treated as one-membrane systems. This subsequently allowed to analyse the energy relations of maize root using the previously developed analytic method of studying the osmotic and diffusive conversion of free energy of solutions (Kargol 1990).

Treating the root as an energy converter we could study its ability to do useful work connected with the pumping of water against gravitation. The energetic efficiency was also studied. The present work is the first one of a series of systematic studies into these problems of essential importance from the physiological viewpoint.

Maize root as a one-membrane system. Parameter of permeation

In 1987 Steudle et al. published the results of osmotic and hydrostatic experiments, performed on young maize roots cut off the stem. The root together with the bathing solution was treated as one-membrane system. A scheme of such a system, a rough approximation of the real system, is shown in Fig. 1. Membrane M of a conic shape represents the whole root and separates solution with concentration C_m (medium) from another solution with concentration C_r (exsudate). If an osmotic pressure difference occurs on the membrane, $\Delta\Pi = RT(C_r - C_m) > 0$, the root can transfer water radially (across) and up the xylem to a certain height h, against hydrostatic pressure: $\Delta P = \varrho g h$, where ϱ is the exsudate density, g is the gravity acceleration.The root thus modelled can function continuously if the concentration difference $\Delta C = C_r - C_m$ is maintained on membrane M.

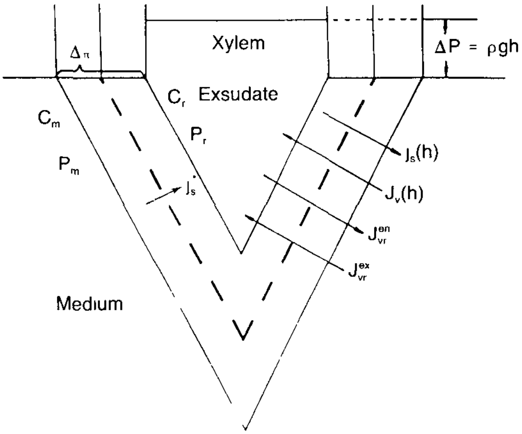


Figure 1. Membrane model of the maize root (for description see the text).

In the given situation one should assume the presence in the root of active solute flows j_s^*, which maintain the concentration difference (Fiscus 1975, 1977). The membrane should be assigned definite permeability parameters, i.e. coefficients of filtration L_P, reflection σ, and permeability ω. These parameters, as used in the Kedem-Katchalsky formalism, unequivocally describe the permeability properties of a given membrane (Katchalsky and Curran 1965).

Steudle et al. (1987) using the pressure probe method measured all the parameters mentioned for young maize roots, treating them as one-membrane systems. Numerical values of the parameters are given in Tables 1 and 2 according to Steudle et al. (1987).

Table. 1. Root pressures P_{ro}, and filtration coefficients, L_{pr}^{ex} and L_{pr}^{en}.

Type of experiment	Root pressure P_{ro} [MPa]	$L_{pr}^{ex} \times 10^7$ $\left[\frac{\text{m}}{\text{s MPa}}\right]$	$L_{pr}^{en} \times 10^7$ $\left[\frac{\text{m}}{\text{s MPa}}\right]$	Mean value $\overline{L}_{pr} \times 10^{13}$ $\left[\frac{\text{m}^3}{\text{N s}}\right]$
1	2	3	4	5
Hydrostatic	0.12 ± 0.08	1.15 ± 0.94	0.94 ± 0.66	0.55
Osmotic	0.14 ± 0.07	0.11 ± 0.11	0.17 ± 0.13	

Table. 2. Mean values of reflection coefficient $\bar{\sigma}$, and permeability coefficients $\overline{P}_r$, and $\bar{\omega}$.

Substance	Reflection coefficient $\bar{\sigma}$	Permeability coefficients $\overline{P}_r \times 10^8$ $\left[\frac{\text{m}}{\text{s}}\right]$	$\bar{\omega} \times 10^{12}$ $\left[\frac{\text{mol}}{\text{N s}}\right]$
Ethanol	0.27 ± 0.01	4.7 ± 1.1	18.87
Sucrose	0.54 ± 0.22	1.2 ± 0.8	4.82
NaCl	0.64 ± 0.28	5.7 ± 3.7	22.89
KNO_3	0.67 ± 0.04	–	–
Mannitol	0.74 ± 0.20	–	–

Data given in Tables 1 and 2 mean the following:

1. The filtration coefficient L_p determined for fluxes J_v^{ex} out of the root and denoted L_{pr}^{ex}, has been termed exoosmotic hydraulic conductivity. The coefficient determined for fluxes J_v^{en} entering the root, denoted L_{pr}^{en}, has been termed endoosmotic hydraulic conductivity.
2. The parameter $\overline{L}_{pr}$ (column 5, Table 1) is an average of the coefficients L_{pr}^{ex} and L_{pr}^{en}.
3. The coefficient $\bar{\omega}$, which appears in the Kedem-Katchalsky formalism, was calculated according to Steudle et al. (1987) using the expression:

$$\overline{P}_r = \bar{\omega} RT,$$

where $\overline{P}_r$ is the average permeability coefficient, R is the gas constant, and T is the temperature.

4. Coefficient $\bar{\sigma}$ is the average of several measurements.

Studies of volume and solute flows across the maize root

The parameters $\bar{L}_{pr}$, $\bar{\sigma}$ and $\bar{\omega}$ given in Tables 1 and 2 will now be used for a quantitative analysis of volume flows J_v, and solute flow j_s, across the maize root and then up the xylem to a height h.

We shall study the flows using the practical equations of Kedem-Katchalsky (Katchalsky and Curran 1965). For the root considered as a one-membrane system (see Fig. 1) these equations can be written as:

$$J_v(h) = \bar{L}_{pr}\bar{\sigma}RT(C_r - C_m) - \bar{L}_{pr}\varrho gh, \tag{1}$$

$$j_s(h) = -\bar{\omega}RT(C_r - C_m) + (1-\sigma)\frac{C_r + C_m}{2}J_v(h), \tag{2}$$

where $J_v(h)$, $j_s(h)$ is the volume and solute flux as function of h, $\Delta P = \varrho gh$; ϱ is the exsudate density; g is the gravity acceleration.
Introducing the notation

$$j_D = -\bar{\omega}RT(C_r - C_m), \tag{3}$$

$$j_u(h) = (1-\sigma)\frac{C_r + C_m}{2}J_v(h), \tag{4}$$

equation (2) can be rewritten as

$$j_s(h) = j_D + j_u(h), \tag{5}$$

where j_D is the diffusive flux; $j_u(h)$ is the flux of the dissolved substance carried along the pores by flux J_v; and $j_s(h)$ is the net flux.

To be more specific, now we shall assume that the active flux j_s^*, of solute results in the development of concentration difference $\Delta C = C_r - C_m$ on the membrane, giving rise to osmotic pressure difference $\Delta\Pi = 1.5 \times 10^5$ [N m^{-2}] (60 mOsmol) as calculated by the Van't Hoff formula.

It should be added here that Ginsburg (1971) dealing with a two-membrane model of the maize root considered concentration differences taken for the calculations of the same order of magnitude. Making use of the above given value of osmotic pressure difference, data given in Tables 1 and 2, and equations (1), (2) and (4), the following dependences were calculated: $J_v(h), j_s(h), j_u(h)$. These are shown in Figures 2, 3 and 4. Plots 1, 2, 3, 4 and 5 and Fig. 2 show relations $J_v(h)$ obtained for ethanol, sucrose, NaCl, KNO_3 and mannitol, respectively. As seen in Figure, the osmotic flow, J_v, diminishes rather strongly (linearly) with the increasing height (h) for all the substances studied, reaching zero at $h = 3.8$ [m]; 7.7 [m]; 9.3 [m]; 9.7 [m]; and 10.7 [m], respectively.

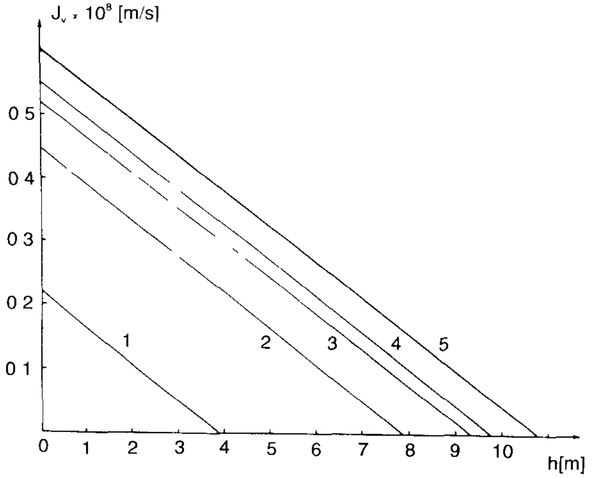


Figure 2. Plots of the relation $J_v(h)$ for ethanol (curve 1), sucrose (curve 2), NaCl (curve 3), KNO_3 (curve 4) and mannitol (curve 5).

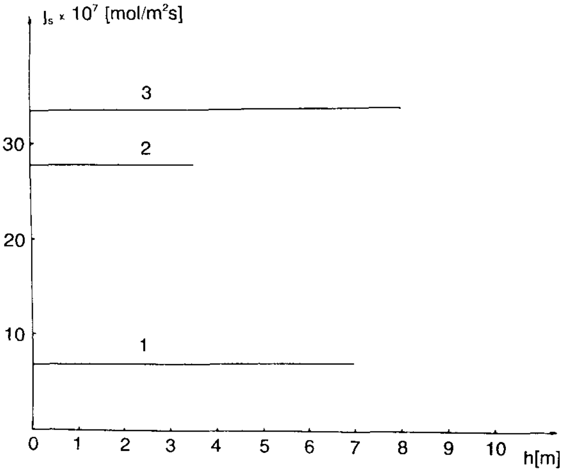
Columns 1 and 2 of Table 3 give numerical values of $J_v(h = 0)$ obtained for the above mentioned solutes. Column 3 contains values of $J_v(h = 0)$ taken from Ginsburg (1971).

Plots 1, 2 and 3 of Fig. 3 show relations $j_s(h)$ obtained from equation (2) for sucrose, ethanol, and NaCl, respectively. We performed the calculations assuming $\bar{C} = \frac{1}{2}C_r$; $C_m = 0$; and $C_r = 60.97$ [mol.m^{-3}]. From the plots obtained it follows

Table. 3. Values of volume fluxes, $J_v(h = 0)$, in maize root determined for $h = 0$

Calculated values of $J_v(h = 0) \times 10^8$ $\left[\frac{m}{s}\right]$		Values of $J_v(h = 0) \times 10^8$ $\left[\frac{m}{s}\right]$
for $\Delta\Pi = 0.1 \times 10^6$ $\left[\frac{N}{m^2}\right]$	for $\Delta\Pi = 0.15 \times 10^6$ $\left[\frac{N}{m^2}\right]$	reported by Ginsburg(1971)
1	2	3
0.15 (ethanol)	0.22 (ethanol)	
		0.13
0.29 (sucrose)	0.44 (sucrose)	
		0.15
0.35 (NaCl)	0.52 (NaCl)	
		0.20
0.37 (KNO_3)	0.55 (KNO_3)	
		0.71
0.40 (mannitol)	0.60 (mannitol)	

Figure 3. Plots of relations $j_s(h)$ obtained for sucrose (curve 1), ethanol (curve 2) and NaCl (curve 3).



that there is but a relatively weak dependence of fluxes of the respective substances on h.

Plots 1, 2 and 3 shown in Fig. 4 illustrate the relations $j_u(h)$ obtained for ethanol, sucrose and NaCl, with the use of equation (4). It follows from these plots that height (h) - dependent absolute changes of flux $j_u(h)$ are considerable.

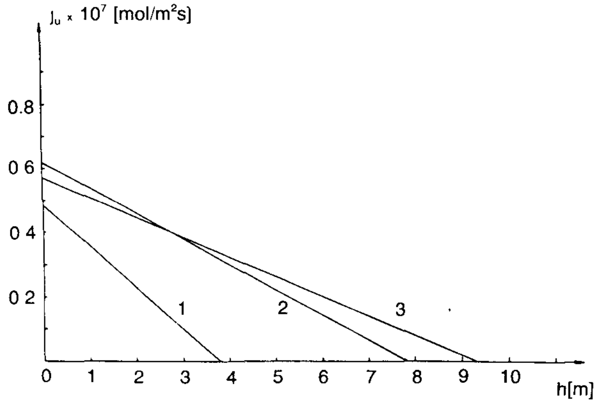


Figure 4. Relations $j_u(h)$ obtained for ethanol (curve 1), sucrose (curve 2) and NaCl (curve 3).

Energetic analysis of the maize root

a. *The nature of the problem. Equation for power and energetic efficiency*

The finite, non-zero value of the filtration coefficients L_{pr}^{ex}, and L_{pr}^{en}, and thus also their mean value. $\bar{L}_{pr}$ means that the radial transfer of water (affected osmotically according to the assumed one-membrane model, see Fig. 1) requires a definite energy expenditure. Since values of the coefficients are determined mostly by viscous forces (dissipative forces) the energy used by the root for that purpose will be treated as dissipated energy. This energy per unit time can be referred to as osmotically dissipated power M_{ro}. Moreover, in the root there is a diffusively dissipated power M_{rD}. This follows from the fact that the mean value of the reflection coefficient $\bar{\sigma}$, of the root-imitating membrane M is less than unity. Energy consuming is also the pumping of water through the root xylem trachear elements up to a certain height h, against hydrostatic pressure $\Delta P = \varrho g h$. This pressure should be treated as an external pressure, and work done against it as effective work. The work per unit time is the effective power M_{uo}, generated by the root. The above mentioned energy expenditures are covered by the root via the metabolites. Due to their degradation proper concentration difference ΔC is generated and maintained in the root by active transport j_s^*, of solutes. These in turn induce passive osmotic flows J_v, and solute flows j_s. In view of what has been said, the root can be treated as an osmotic-and-diffusive energy converter. From the physiological viewpoint, it is of interest to know the energetic ability of the converter. In particular, we are concerned here with the energetic ability of the root to transfer water and solutes radially, as well as with the raising of water in the xylem caused by osmotically generated root pressure. Knowledge of these abilities was made possible due to the work by Steudle et al. (1987) and also thanks to the analytic method developed by Kargol (1990) allowing to study the osmotic-and-diffusive conversion of free energy of solutions. Now we shall attempt to investigate the energetic possibilities of the root. For that purpose we shall make use of the above numerical data concerning the maize root as a one-membrane system (Steudle et al. 1987). We shall also use the equations for effective power M_{uo}, produced osmotically in the root; dissipated power M_{ro}, used for radial transfer of water; power M_{rD} dissipated by diffusion in the process of solute permeation; and the equation for energetic efficiency η_{oD}, of osmotic-and-diffusive energy conversion (Kargol 1990). These equations are:

$$M_{uo} = S \Delta P J_v(h), \tag{8}$$

$$M_{ro} = S \frac{[J_V(h)]^2}{\bar{L}_{pr}}, \tag{9}$$

$$M_{rD} = S \frac{\bar{\omega}}{\bar{C}} \Delta \Pi^2 = S \frac{\bar{\omega}}{\bar{C}} (RT)^2 (C_r - C_m)^2, \tag{10}$$

$$\eta_{oD} = \frac{\varrho g h J_v(h)}{\varrho g h J_v(h) + \frac{[J_V(h)]^2}{L_{pr}} + \frac{\bar{\omega}}{\bar{C}}(RT)^2(C_r - C_m)^2} \tag{11}$$

where: $\varrho gh = \Delta P$ is the hydrostatic pressure difference; $RT(C_r - C_m) = \Delta\Pi$ is the osmotic pressure difference; $\bar{C} \approx \frac{2}{3}C_r$, $C_r > C_m$ ($C_m \approx 0$); and S is the active surface of a conically shaped membrane to model the root.

b. *Calculations of effective power*

The ascent of water to height h (against gravitation) induced by osmotically generated root pressure means performance by the root of useful work or, in other words, production of effective power M_{uo}. This power is described by equation (8). Using this equation and the calculated relation $J_v(h)$, the power has been calculated for different values of h. Based on this, plots of the relation $M_{uo}(h)$ were constructed for ethanol, sucrose, NaCl and KNO_3. It was assumed in the calculations that concentration differences $\Delta C = C_r - C_m$ of the substances were 60.5 [mol.m^{-3}] with $C_m = 0$. The active surface of the root was assumed to be $S = 10^{-4}$ [m^2], the exsudate density $\varrho = 1050$ [kg.m^{-3}], the gravity acceleration $g = 9.81$ [m.s^{-2}]. Plots 1, 2, 3 and 4 in Fig. 5 show the relations obtained. The plots have similar shapes. They show that the effective power M_{uo}, reaches zero at $h = h_o = 0$, and at $h = H = 3.9$ [m] for ethanol 7.8 [m]; for sucrose; 9.3 [m] for NaCl; and 10 [m] for KNO_3. Values $0 < h < H$ exist (different for different substances) for which $M_{uo} > 0$. From the curves it follows that there are values of h for which the maize root produces maximal effective power ($M_{uo} = M_{uo}^{\max}$). Maximal effective powers are produced at $h = 1.95$ [m] for ethanol; 3.95 [m] for sucrose; 4.65 [m] for NaCl; and 5 [m] for KNO_3.

The curve shown in Fig. 5 indicates also that different substances affect to different degrees the root's ability to produce effective power M_{uo}, and maximal power $M_{uo}^{\max}$.

c. *Calculation of dissipated power*

In the process of radial transport of water within the maize root, the power M_{ro}, is dissipated. The dissipation occurs due to viscous forces on the osmotically transported water. The result of calculations of this power, by equation (9) and data taken from the curves shown in Fig. 2, are shown graphically in Fig. 6. The respective curves 1, 2, 3, and 4 represent relations $M_{ro}(h)$ obtained for ethanol, sucrose, NaCl and KNO_3. They show that power M_{ro} decreases (parabolically) with the increasing h. This is reasonable since, as seen in Fig. 2, with the increasing height the value of osmotic volume flow J_v, decreases. Besides M_{ro}, also M_{rD} dissipated. This occurs as a result of diffusion of dissolved substances across membrane M

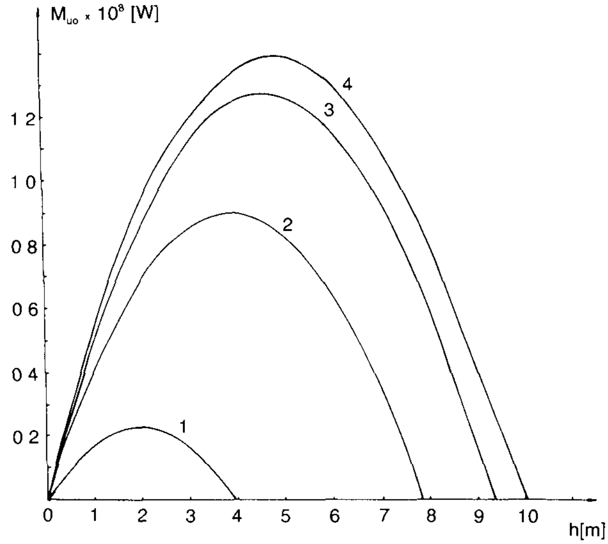


Figure 5. Relations $M_{uo}(h)$ obtained for ethanol (curve 1), sucrose (curve 2), NaCl (curve 3) and KNO_3 (curve 4).

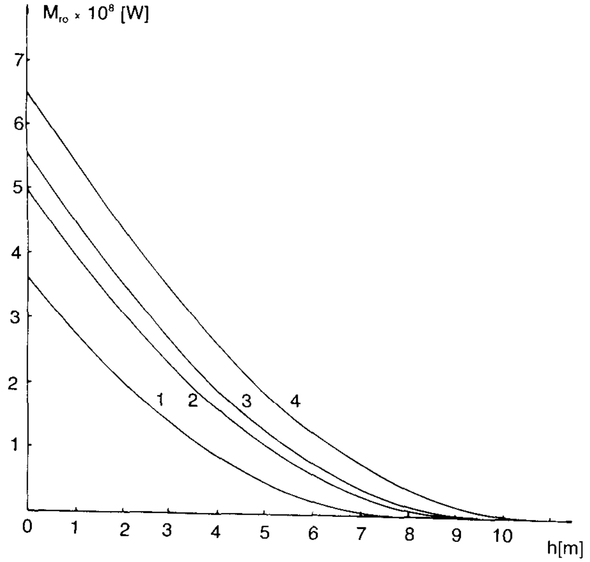


Figure 6. Relations $M_{ro}(h)$ obtained for ethanol (curve 1), sucrose (curve 2), NaCl (curve 3) and KNO_3 (curve 4).

(imitating the root). The membrane has, as shown by Steudle et al. (1987), reflection coefficient $\bar{\sigma}$, lower than unity, implying non-zero permeability coefficient

$\bar{\omega}$. The power can be calculated from equation (10) for substances with a known coefficient $\bar{\omega}$. It should be noted here that the power does not depend on the height h. The powers calculated for ethanol, NaCl and sucrose are given in Table 4. For the calculations it was assumed that $S = 10^{-4}$ [m^2], $\Delta\Pi = 1.5 \times 10^5$ [N m^2] and, by estimation, $C_m \approx 0$, $\bar{C} = \frac{2}{3}C_r$ with $C_r = 60.97$ [mol m^{-3}].

The data in Table 4 indicate that the power dissipated by diffusion (M_{rD}) is considerably greater than the osmotically dissipated power M_{ro} at $h = 0$.

Table. 4. Calculated powers M_{rD} and $M_{ro}(h = 0)$

Substance	M_{rD} [W]	M_{ro} [W]
Ethanol	1.04×10^{-6}	0.88×10^{-8}
NaCl	0.27×10^{-6}	3.60×10^{-8}
Sucrose	1.27×10^{-6}	4.91×10^{-8}

d. *Calculation of energetic efficiency of the maize root, for osmotic-and-diffusive free energy conversion*

A more complete information on the osmo-diffusive free energy conversion can be obtained by finding the energetic efficiency of the conversion given by equation (11). In the present work this quantity has been determined as a function of h for ethanol, NaCl and sucrose using the above given numerical data. The results are graphically shown in Fig. 7. The curves 1, 2 and 3 represent relations $\eta_{oD}(h)$ obtained for ethanol, sucrose and NaCl, respectively. From the course of the curves it follows that $\eta_{oD} = 0$ for $h = 0$, and for $h = 3.9$ [m] for ethanol; 7.8 [m] for sucrose; and 9.3 [m] for NaCl. For h in the range $0 < h < H$, the efficiency $\eta_{oD} > 0$. Maximal values $\eta_{oD}^{\max}$ are obtained at $h = 1.95$ [m] for ethanol; 3.9 [m] for sucrose; and at 4.65 [m] for NaCl. From curves in Fig. 5 and 7 it follows that the maize root has maximal energetic efficiency at such heights h, for which the effective power $M_{uo}^{\max}$, reaches a maximum. The results given in Fig. 7 indicate also that various substances affect the efficiency $\eta_{oD}(h)$, and thus also $\eta_{oD}^{\max}(h)$, differently. Different are also the heights h, for which maximal energetic efficiency is attained. Similar results for $\eta_{oD}(h)$ were reported by Suchanek (1989), who studied η_{oD} as a function of ΔP. She has employed a different analytical method in her study of osmotic-and-diffusive energy conversion.

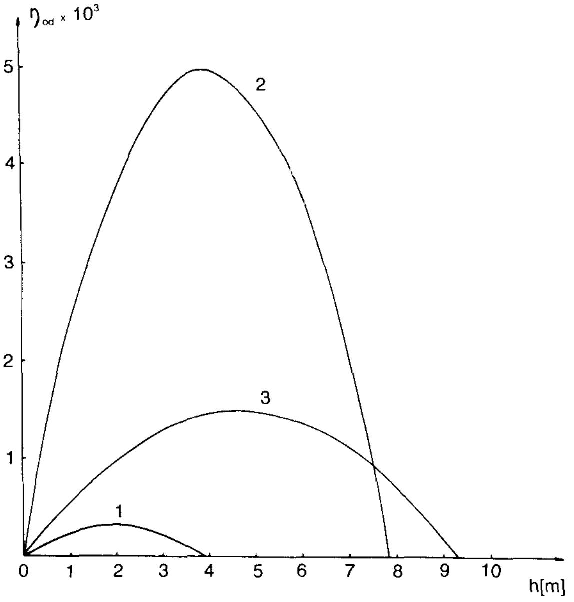


Figure 7. Relations $\eta_{oD}(h)$ obtained for ethanol (curve 1), sucrose (curve 2) and NaCl (curve 3).

Concluding remarks

The present work contains a comprehensive study of the osmotic and diffusive properties of young maize root with the stem cut off. The root was considered as a one-membrane system. The analysis and calculation performed were based on the results of studies of the roots by Steudle et al. (1987), and on the previously developed analytical method (Kargol 1990). This method refers to basic problems of osmo-diffusive conversion of free energy of solutions of different concentration.

It should be also noted that the maize root has a very complex structure. The transport processes of substances across the root are numerous and complicated. Therefore, the one-membrane model is only an approximation of the transport route for substances across the root. This implicates some problems, which have also been recognized by other authors (Fiscus 1975; 1977; Steudle et al. 1987; Taura et al. 1988). Despite all these problems, Steudle et al. (1987) have experimentally determined the transport parameters (L_P, σ and ω) for the maize root. This should be considered as a significant scientific achievement invaluable for the present work.

Certain biophysical aspects of water and solute transport across the root are discussed, and the ascent of water through the xylem to a certain height h, induced by the root pressure. It has been assumed that the pressure is osmotically generated. The ability of the maize root to convert free energy is discussed considering the root as a one-membrane system. A quantitative analysis was performed of the effective power M_{uo}, osmotically produced by the root, of the osmotically dissipated power M_{ro}, and of the power dissipated by diffusion M_{rD}. The energetic efficiency η_{oD}, of the osmotic-and-diffusive energy conversion was also studied. This provided the basis for some additional observations. Among others, it was noted that for certain heights of water elevation in the xylem (different for different substances) the maize root produces maximal effective power $M_{uo} = M_{uo}^{\max}$. For these heights it functions with maximal energetic efficiency.

The study presented in this paper may have practical, in addition to cognitive, aspects which may be of interest for biomass production.

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