# The Plant Root as an Osmo-diffusive Converter of Free Energy

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**Abstract.** This work focuses on the maize root as a one-membrane osmo-diffusive converter of free energy. Energy expenditures of the root on water transport by radial route as well as on xylem water uptake, occurring according to the principle of osmotic root pressure, are analyzed. The so-called practical method of osmo-diffusive energy conversion (Kargol 1990, 1993) and experimental data taken from the work by Steudle et al. (1987) were employed, including coefficients of filtration ($\overline{L}_{\text{pr}}$), reflection ($\overline{\sigma}$) and permeation ($\overline{\omega}$) of the maize root treated as a one-membrane model system. It is shown a.o. that the energy efficiency of the root does not depend (within a certain concentration interval) on the concentration of a given solute in solution into which the root is placed. This suggests a certain independence of environmental conditions. The efficiency is different for different dissolved substances contained in the solution.

**Key words:** Maize root — Water — Osmosis — Diffusion — Energy efficiency

## Introduction

There are different theories to explain water transport across the root (radial route) and the generation of the so-called root pressure (Ginsburg 1971; Fiscus and Kramer 1975; Fiscus 1975, 1977; Pitman 1982; Taura et al. 1987; Michalov 1989; Kargol 1990, 1994). According to the concept of Fiscus (1975, 1977), also developed by other investigators (Steudle et al. 1987; Kargol 1990, 1994; Kargol and Suchanek 1990), water transport across the root (by radial route) is generated in accordance with the osmotic principle. In the light of the literature cited above, root pressure can also be generated according to this principle. This pressure can pump water through the xylem to a certain height ($h$), hence against the force of gravity.

Water transport via both the radial route and the xylem uptake requires definite energy expenditure by the root. This is so because the first of these transports occurs against viscosity forces, and the second one also occurs against gravity force. Developing this problem further we can say that the energy required for this purpose is supplied to the roots by assimilates which are subject to certain processes of energy degradation. Thanks to energy released in these processes, the so-called active substance flows can be generated. They lead to the formation of differences in solute concentrations, and thus, to differences in osmotic pressures. If these differences occur along the radial water route in the root, osmotic water flows can be generated. Furthermore, these differences also represent the principle of root pressure generation.

From physiological aspect it is of interest to analyze energy requirements of the root in relation to radial water transport and water uptake through the xylem under the effect of root pressure. Some introductory investigations of these problems in relation to the maize root have been carried out in earlier works (Kargol and Suchanek 1990; Kargol 1990, 1994; Kargol et al. 1993). They have focused on problems of power output, osmotically dispersed power and diffusively dispersed power generated by the maize root, as well as on root energy efficiency as a one-membrane, osmo-diffusive energy converter. Speaking more precisely, the above mentioned forces and power efficiency have been considered in function of simultaneously changing quantities $C_{\mathrm{m}}$ and $h$. In the present communication a substantial extension and development of these investigations is reported.

These quantities were investigated in relation to the concentrations $C_{\mathrm{m}}$ of various substances contained in the medium solution into which the root is immersed and with respect to height $h$ to which the root pumped water through the xylem according to the principle of root pressure. It was assumed that this pressure is generated osmotically.

## Approximation of the root as a one-membrane system. Equations of power and energy efficiency

The object of the investigations was young maize root cut off from the stalk. The root was treated as a model of osmo-diffusive one-membrane system. The membrane of such a model is conical in shape and it separates the exudate contained in the xylem (concentration $C_{\mathrm{r}}$) from the solution with a concentration $C_{\mathrm{m}}$ into which the root is placed (Fig. 1). The Figure illustrates the radial water route in the root. More detailed information on such an approximation of the root has been reported by Kargol (1990, 1994), Kargol et al. (1993), Fiscus (1975), Fiscus and Kramer (1975), Steudle et al. (1987), a. o.

Using in the solution substances such as saccharose, ethanol and NaCl, Steudle et al. (1987) determined experimentally all the three practical parameters of permeation for the investigated root. According to the formalism of Kedem and Katchal-

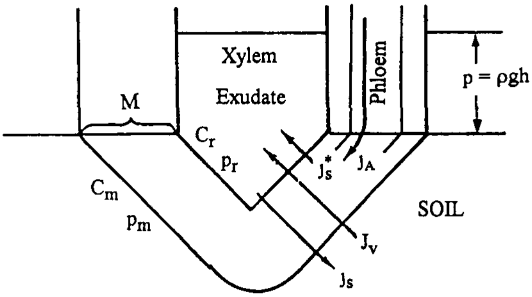

**Figure 1.** Plant root approximated as a one – membrane system (M – membrane; $j_s$, $j_s^*$, $j_A$ – solute streams; $J_v$ – volume stream; $C_m$, $C_r$ – concentrations; $p_m$, $p_r$ – mechanical pressures).

sky (Katchalsky and Curran 1965), those parameters include: filtration coefficient $L_{pr}$ reflection coefficient $\sigma$, and permeation coefficient $\omega$. In accordance with Steudle et al. (1987) the mean values of those parameters are: $\bar{\sigma}_e = 0.27$ and $\bar{\omega}_e = 4.7 \cdot 10^{-8}$ [m.s$^{-1}$] = $18.87 \cdot 10^{-12}$ [mol.N$^{-1}$s$^{-1}$] (for ethanol), $\bar{\sigma}_s = 0.54$ and $\bar{\omega}_s = 1.2 \cdot 10^{-8}$ [m.s$^{-1}$] = $4.82 \cdot 10^{-12}$ [mol.N$^{-1}$s$^{-1}$] (for saccharose), $\bar{\sigma}_N = 0.65$ and $\bar{\omega}_N = 5.7 \cdot 10^{-8}$ [m.s$^{-1}$] = $22.89 \cdot 10^{-12}$ [mol.N$^{-1}$s$^{-1}$] (for NaCl). The value of the third parameter, the filtration coefficient $\overline{L}_{pr}$, was equal to $0.55 \cdot 10^{-7}$ [m.s$^{-1}$MPa$^{-1}$] = $0.55 \cdot 10^{-13}$ [m$^3$N$^{-1}$s$^{-1}$]. Parameter $\overline{L}_{pr}$ is also referred to as hydraulic conductivity. The formula which links parameters $\bar{p}_r$ and $\bar{\omega}$ has the form: $p_r = \omega RT$. The value of parameter $\overline{L}_{pr}$ was averaged from values given by Steudle et al. (1987) for osmotic experiment ($L_{pr}^{en} = 0.94 \cdot 10^{-7}$ [m.s$^{-1}$MPa$^{-1}$]) and hydrostatic experiment ($L_{pr}^{en} = 0.17 \cdot 10^{-7}$ [m.s$^{-1}$MPa$^{-1}$]).

Osmotic and diffusive flows of substances through the radial route of the root were determined from the above values of permeation parameters, concentrations $C_m$ and $C_r$, and mechanical pressure $p_r$ in the xylem. External pressure was $p_m = 1$ [atm]. The numerical data provided above were considered in a previous work (Kargol 1992). They also represented the basis for the present investigations. The investigations were performed using previously derived formulas (Kargol 1990,1993) for power output $M_{uo}$, osmotically dissipated power $M_{ro}$ and diffusively dissipated power $M_{rd}$. These formulas can be written as:

$$M_{uo} = S(p_r - p_m)J_v = S\rho g h J_v, \tag{1}$$

$$M_{ro} = S\frac{J_v^2}{\overline{L}_{pr}}, \tag{2}$$

$$M_{rd} = S\,\bar{\omega}\overline{V}_s(RT)^2(C_r - C_m)^2, \tag{3}$$

where: $S$ is the area of the membrane which imitates the root radial water route; $\rho$ is the density; $g$ is the gravity acceleration; $h$ is the height of water pumped through the xylem according to the principle of root pressure; $J_{\mathrm{v}}$ is the volume stream; $\overline{V}_{\mathrm{s}}$ is the solute mol at volume; $T$ is the temperature; R is the gas constant. Taking into consideration that stream $J_{\mathrm{v}}$ is given by the formula (Katchalsky and Curran 1965):

$$J_{\mathrm{v}} = \overline{L}_{\mathrm{pr}}\overline{\sigma}\mathrm{R}T(C_{\mathrm{r}} - C_{\mathrm{m}}) - \overline{L}_{\mathrm{pr}}\rho g h, \tag{4}$$

equations (1) and (2) can be reduced to the form convenient for calculations:

$$M_{\mathrm{uo}} = S\rho g h \overline{L}_{\mathrm{pr}}[\overline{\sigma}\mathrm{R}T(C_{\mathrm{r}} - C_{\mathrm{m}}) - \rho g h], \tag{5}$$

$$M_{\imath\mathrm{o}} = S\overline{L}_{\mathrm{pr}}[\overline{\sigma}\mathrm{R}T(C_{\mathrm{r}} - C_{\mathrm{m}}) - \rho g h]^2, \tag{6}$$

The efficiency of osmo-diffusive conversion of root free energy, associated with radial water transport and its uptake through the xylem, was calculated by:

$$\eta_{\mathrm{od}} = \frac{M_{\mathrm{uo}}}{M_{\mathrm{uo}} + M_{\mathrm{ro}} + M_{\mathrm{rd}}}. \tag{7}$$

## Results of numerical calculations and discussion

In this work the problems of energy conversion in the maize root such as power output $M_{\mathrm{uo}}$, osmotically dissipated power $M_{\mathrm{ro}}$, diffusively dissipated power $M_{\mathrm{rd}}$ and energy efficiency were subjected to theoretical (numerical) investigation. These powers as well as efficiency $\eta_{\mathrm{od}}$ were investigated as functions of solute concentration $C_{\mathrm{m}}$ and height h to which a given root pumps water through the xylem in accordance with the principle of osmotically generated root pressure.

The calculations were made for water solutions of saccharose, ethanol and NaCl.

The calculations were based on equations (3), (5), (6) and (7), the numerical data provided above for parameters $\overline{L}_{\mathrm{p}}$, $\overline{\sigma}$ and $\overline{\omega}$, and the following values of the remaining quantities occurring in the equations: $\overline{C}_{\mathrm{r}} = 60.97$ [mol.m$^{-3}$], $S = 10^{-4}$ [m$^2$], $T = 300$ [K], $\overline{V}_{\mathrm{S}}^{\mathrm{N}} = 0.21 \cdot 10^{-4}$ [m$^3$.mol$^{-1}$] (for NaCl), $\overline{V}_{\mathrm{S}}^{\mathrm{S}} = 2.25 \cdot 10^{-4}$ [m$^3$.mol$^{-1}$] (for saccharose), $V_{\mathrm{S}}^{\mathrm{e}} = 0.57 \cdot 10^{-4}$ [m$^3$.mol$^{-1}$] (for ethanol), $\rho = 1050$ [kg.m$^{-3}$] (exudate density), $g = 9.81$ [m.s$^{-2}$], and R= 8.3 [N.m.mol$^{-1}$.K$^{-1}$]. Some exemplary results of the calculations are shown in the Figures as definite families of curves. They mainly refer to saccharose as a soluble substance.

In Fig. 2 results of the calculation of dependence $M_{\mathrm{uo}} = f(h)_{\mathrm{Cm}}$ are shown, where $M_{\mathrm{uo}}$ is the effective power, and $h$ is the height to which the investigated root pumps water through the xylem according to the principle of osmotically generated root pressure. Curve 1 refers to a situation in which $C_{\mathrm{m}} = 0$. Curves 2, 3, 4, 5 and 6 were obtained for saccharose concentrations $C_{\mathrm{m}}$ of 10 [mol.m$^{-3}$]; 20 [mol.m$^{-3}$]; 30 [mol.m$^{-3}$]; 40 [mol.m$^{-3}$]; 50 [mol.m$^{-3}$]; 60 [mol.m$^{-3}$], respectively.

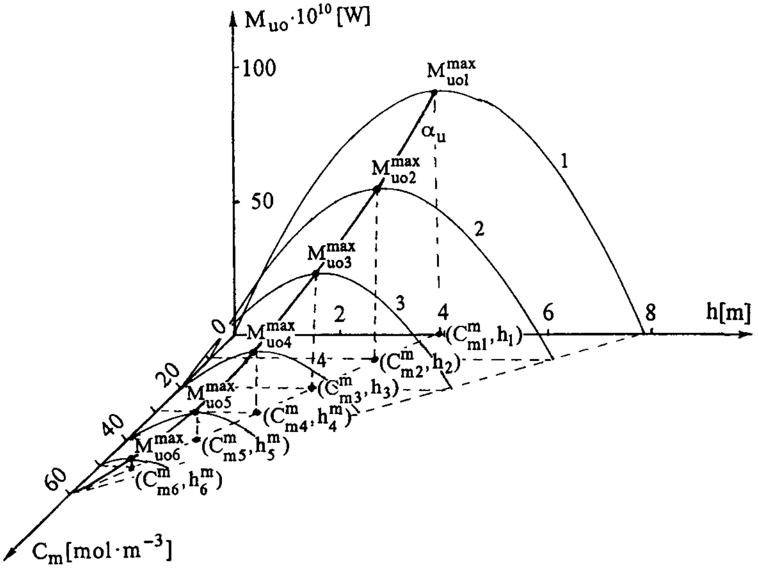

**Figure 2.** Results of the investigation of effective power $M_{uo}$ as a function of simultaneous changes in saccharose concentration $C_m$ in medium solute and height $h$.

The curves run through characteristic points $M^{max}_{uo1}$, $M^{max}_{uo2}$, $M^{max}_{uo3}$, $M^{max}_{uo4}$, $M^{max}_{uo5}$, $M^{max}_{uo6}$ which express the respective maximum values of power output. The points have coordinates $(C^m_{m1}, h^m_1)$, $(C^m_{m2}, h^m_2)$, $(C^m_{m3}, h^m_3)$ etc. Obviously, an many those points can be determined arbitrarily for different $C^m_m$ and $h^m$. By connecting them we obtain curve $\alpha_u$ which expresses the dependence:

$$M^{max}_{uo} = f\left(C^m_m, h^m\right).$$

It is obvious from the above formula in general that the maximum power output $(M^{max}_{uo})$ decreases with the increasing $C_m$ and increases with the increasing $h$.

Fig. 3 illustrates the results of the calculations of osmotically dissipated power $M_{ro}$ as a function of height $h$ for different constant concentrations $C_m$ of saccharose in the medium solution. Curves 1, 2, 3, 4, 5 and 6, which express the dependence $M_{ro} = f(h)_{Cm}$ were obtained for saccharose solute concentrations $C_m$ of 0 [mol.m$^{-3}$]; 10 [mol.m$^{-3}$]; 20 [mol.m$^{-3}$]; 30 [mol.m$^{-3}$]; 40 [mol.m$^{-3}$]; 50 [mol.m$^{-3}$]; and 60 [mol.m$^{-3}$].

Taking into consideration coordinates for which the power output reaches maximum values $(M^{max}_{uo})$, i.e. coordinates $(C^m_{m1}, h^m_1)$, $(C^m_{m2}, h^m_2)$, $(C^m_{m3}, h^m_3)$ etc., it is easy to find the respective osmotically dissipated powers: $M^m_{ro1}$, $M^m_{ro2}$, $M^m_{ro3}$, $M^m_{ro4}$, $M^m_{ro5}$ and $M^m_{ro6}$. Connecting these points we obtain curve $\alpha_r$ which is a graphic

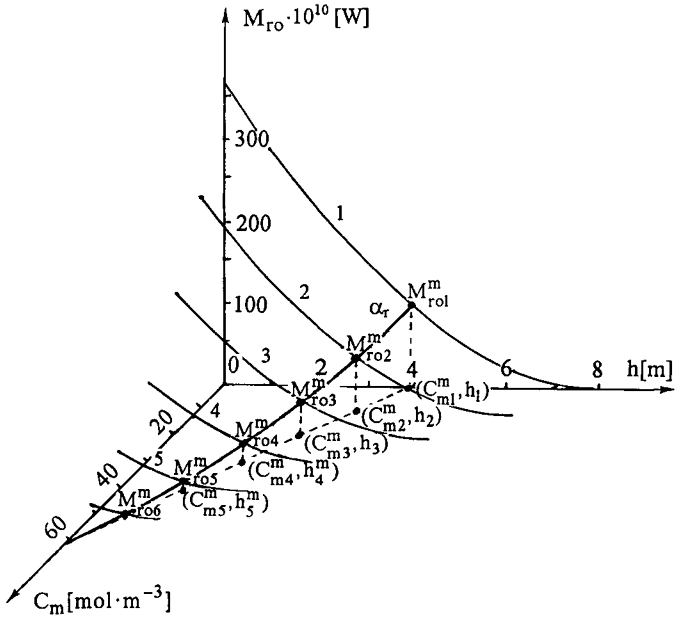

**Figure 3.** Results of the investigation of osmotically dissipated power ($M_{ro}$) in dependence on simultaneous changes in saccharose concentration $C_m$ in medium solute and height $h$.

expression of the function:

$$M^{m}_{ro} = f\,(C^{m}_{m},\ h^{m}).$$

This curve, similarly as curve $\alpha_u$ in Fig. 2, will be necessary to carry out a proper investigation into the energy efficiency of osmo-diffusive conversion of free energy of a given plant root. However, we first have to consider the results of calculations concerning the diffusively dissipated power ($M_{rd}$). This power calculated from equation (3) depends on concentration $C_m$ (curve $\alpha_{do}$ in Fig. 4). It does not depend, however, on height $h$. Nevertheless, definite values of power: $M^{m}_{rd1}, M^{m}_{rd2}, \dots, M^{m}_{rd6}$ can be found for coordinates $(C^{m}_{m1},\ h^{m}_{1})$, $(C^{m}_{m2},\ h^{m}_{1}), \dots, (C^{m}_{m6},\ h^{m}_{6})$, (Fig. 4) yielding curve $\alpha_d$.

Using formula (7), the curves $\alpha_u$ (Fig. 2), $\alpha_r$ (Fig. 3) and $\alpha_d$ (Fig. 4) permit to find the graphic image of the function:

$$\eta^{ms}_{od} = f\,(C^{m}_{m},\ h^{m}).$$

where: $\eta^{ms}_{od}$ is the energy efficiency of the root when generating maximum power output.

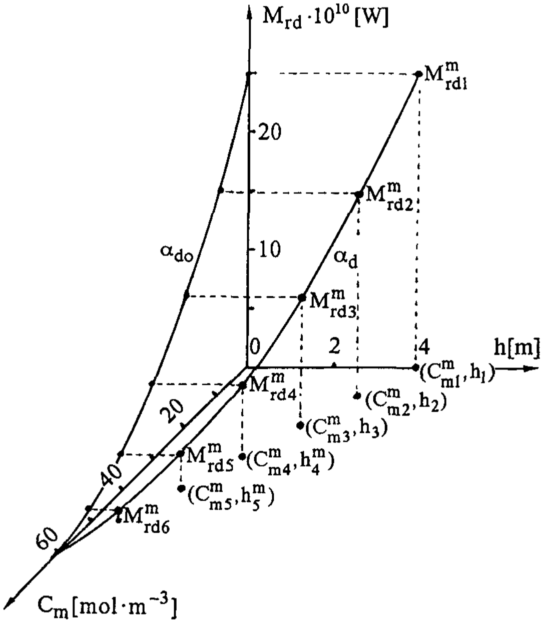

**Figure 4.** Results of the investigation of diffusively dissipated power ($M_{\rm rd}$) in dependence on saccharose concentration $C_{\rm m}$. Power $M_{\rm rd}$ is not dependent on $h$.

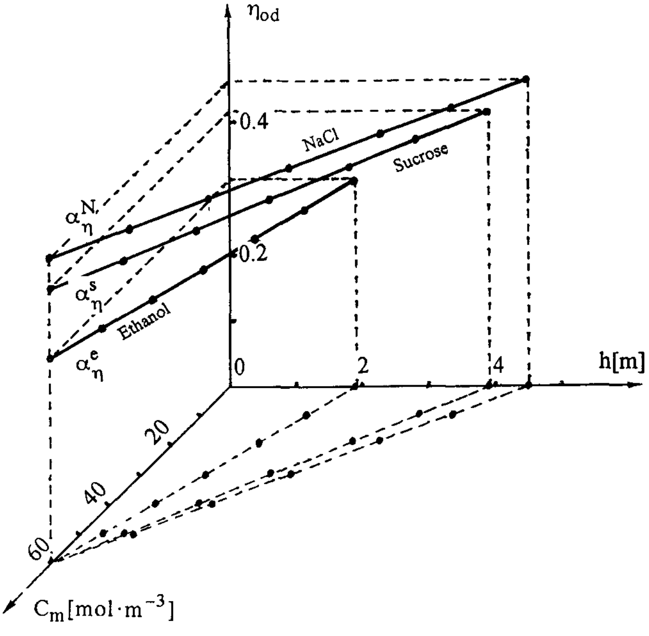

**Figure 5.** Dependences $\eta^{\rm m}_{\rm od} = f\,(C^{\rm m}_{\rm m}, h^{\rm m})$ for saccharose (plot $\alpha^{\rm S}_\eta$), ethanol (plot $\alpha^{\rm e}_\eta$) and NaCl (plot $\alpha^{\rm N}_\eta$).

It is represented by the plot $\alpha_\eta^S$ given in Fig 5 Obviously, it refers to water solutions of saccharose

It follows from an analysis of this plot that if the root generates maximum power output $M_{uo}^{max}$, it operates at a constant energy efficiency Moreover, this efficiency does not depend in these conditions either on concentration $C_m$ of solution or the height $h$ of water pumping through the xylem This can be checked by projecting the plot $\alpha_\eta^S$ on planes $(0, C_m, \eta_{od})$ and $(0, h, \eta_{od})$ (see Fig 5)

Analogous calculations were also done for ethanol and NaCl as substances dissolved in solution into which the root is placed Qualitatively analogous results were obtained Therefore, we only restricted the presentation of those results to graphic form of the function

$$\eta_{od}^{me} = f\left(C_m^m, h^m\right) \quad \text{and} \quad \eta_{od}^{mN} = f\left(C_m^m, h^m\right)$$

(plots $\alpha_\eta^e$ and $\alpha_\eta^N$ in Fig 5) It arises from the plots that also for ethanol and NaCl the plant root operates with a constant energy efficiency (independent of either $C_m^m$ or $h^m$) upon generating maximum power output $(M_{uo}^{max})$

Fig 6 shows the results of the calculations of efficiency $\eta_{od}^S$ (for saccharose) as a function of simultaneous changes in $C_m$ and $h$ The family of curves represented

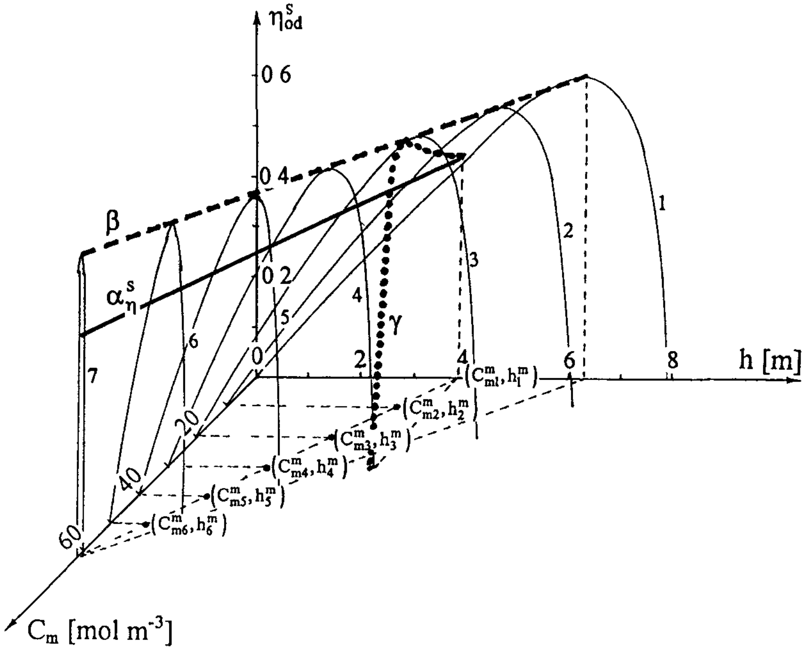

**Figure 6.** A family of dependences of $\eta_{od}^S$ on simultaneous changes in saccharose concentration $C_m$ and height $h$

here, illustrates in a complex way the energy – related properties of a root as a one-membrane osmotically-diffusive transducer of free energy. These properties concern the efficiency of using free energy by the root to transport water across the root (against viscosity forces) and to uptake it through the xylem at a certain height (against viscosity forces and against gravity force).

## Conclusion

This paper deals with the energy aspect of water transport across the maize root and its uptake in the plant (through the xylem) under the influence of osmotically generated root pressure. The root of this plant is treated as a one-membrane, osmotically-diffusive energy converter model. Utility force ($M_{\mathrm{uo}}$), osmotically dissipated force ($M_{\mathrm{ro}}$), diffusively dissipated force ($M_{\mathrm{rd}}$), and the so-called energy efficiency $\eta_{\mathrm{od}}$ of osmotically-diffusive energy conversion were investigated. In previous works (Kargol 1992, 1994; Kargol et al. 1993), these quantities were investigated in dependence on the medium solute concentration $C_{\mathrm{m}}$ and/or on height h of water pumping along the plant (through the xylem). In the present paper the dependences of these quantities on simultaneously changing concentration, $C_{\mathrm{m}}$ and height, $h$ were investigated. Particular attention was paid to the energy efficiency $\eta_{\mathrm{od}}^{\mathrm{m}}$ of a root in conditions of maximum effective power. Effective power ($M_{\mathrm{uo}}^{\mathrm{max}}$) is independent of either the concentration $C_{\mathrm{m}}$ of a given substance or of height $h$. This is illustrated by diagrams $\alpha_{\eta}^{\mathrm{S}}$, $\alpha_{\eta}^{\mathrm{N}}$ and $\alpha_{\eta}^{\mathrm{e}}$ in Fig. 5, and diagram $\alpha_{\eta}^{\mathrm{S}}$ in Fig. 6.

This investigation was possible thanks to the determination (by Steudle et al. 1987) of parameters $\overline{L}_{\mathrm{pr}}$, $\overline{\sigma}$ and $\overline{\omega}$ for maize root. Parameters $\overline{L}_{\mathrm{pr}}$, $\overline{\sigma}$ and $\overline{\omega}$ are loaded by error. The influence of these errors on powers $M_{\mathrm{ro}}$, $M_{\mathrm{uo}}$ and $M_{\mathrm{rd}}$ as well as on energy efficiency $\eta_{\mathrm{od}}$ was estimated. Assuming, these errors to be $\Delta\overline{L}_{\mathrm{pr}} = 0.44 \cdot 10^{-13}$ [m$^3$.N$^{-1}$s$^{-1}$], $\Delta\overline{\sigma} = 0.2$ and $\Delta\overline{\omega} = 3.8 \cdot 10^{-12}$ [mol.N$^{-1}$s$^{-1}$] an error $\Delta\eta_{\mathrm{od}}^{\mathrm{S}}$ of 0.4 is obtained for saccharose. Furthemore, it was assumed that $C_{\mathrm{m}} = 0$ and $h = 4$ [m]. As can be seen, the error $\Delta\eta_{\mathrm{ed}}^{\mathrm{S}}$ is large. However, the focus of this work was the nature of changes $\eta_{\mathrm{od}}$ as a function of $C_{\mathrm{m}}$ and $h$.

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