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Osmotic, Hydromechanic and Energetic Properties of Modified Münch's Model

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Abstract. In the present work have been made some modifications of Münch's model, which concerns the explanation of biophysical bases of the problem of transport of water and assimilates. Then, by using the thermodynamic formalism of Kedem and Katchalsky (1958), we have made a mathematical description of the model. On this basis it is shown that the model has a series of specific osmotic and hydromechanic properties. Next with the use of the description, the energetic aspect of the model is treated. In this study has been employed an analytical method previously developed (Kargol 1985, 1990, 1993) for studying osmotic and diffusive energy conversion of solutions of different concentrations. The energetic aspect of the study follows from the fact that the phloem transport of water and dissolved assimilates occurring against various forces (including the viscous friction) requires definite expenditure of energy on the part of the plant. Adequate power and energetic efficiency equations have been derived. The equations derived in this work, concerned with Münch's model, offer concrete possibilities for qualitative studies of transport of water and assimilates by phloem in plants.

Key words: Water transport — Phloem — Münch's model — Osmosis — Power — Energetic efficiency — Energy conversion

Introduction

Living cells are supplied with energy by means of assimilates. These high-energy substances are produced in photosynthetic processes in leaves, and distributed throughout the entire plant via phloem. A number of hypotheses have been developed until now in order to explain the mechanisms of the long-distance translocation of assimilates (Peel 1965, Fensom and Spanner 1969, Wilkins 1969, Siddiqui and Spanner 1970, Zimmermann and Brown 1971, Salisbury and Ross 1975, Zurzycki and Michniewicz 1977, Fensom 1981, Bel et al. 1992 and others). Among them there is the electro – osmotic theory, the diffusion and cytoplasm movement hypothesis and the Münch theory of flows under pressure. We are concerned here with the last one, mainly because it is the most accepted, at least in the cited literature; and because this theory can (in the present work) be modified a little and developed by using the thermodynamics formalism (Kedem and Katchalsky 1958, Curran and MacIntosh 1962, Kargol 1978). The theory of flow under pressure states that assimilates are transported through phloem carried along with water (convective mass flow). The flows can be explained in the simplest way by using a proper membrane model developed by Münch. The model consists of two osmometers I and II, connected in opposition (a push-pull way) via a tube R_u and immersed in a solution contained in vessels N_1 and N_2. Fig. 1 shows this in detail.

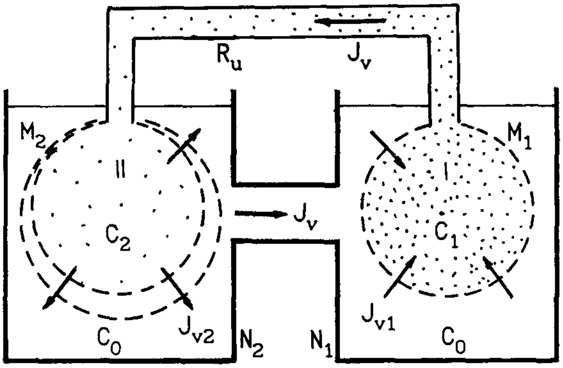


Figure 1. The Munch's model (I, II – osmometers, J_v, J_{v1}, J_{v2} – volume flows, C_1, C_2, C_0 – concentrations, M_1, M_2 – membranes, R_u – tube, N_1, N_2 – vessels).

Let us assume after Münch that osmometer I of the model, filled with concentrated solution C_1, represents in general the photosynthetic cells in leaves where, as a source effect, assimilates are created. Whereas osmometer II, containing a dilute solution C_2, represents the places in the plant where assimilates are utilized. Those can be, for instance, root, fruit, or flower bud cells. In the model it is also assumed that phloem is the generalized cell R_u concerning both hypothetical osmometers, together with sieve tubes and companion cells. The connected vessels N_1, N_2 (together with solution C_0) imitate the plant's apoplast together with the water it contains and the substances dissolved.

This membrane M_1 (of osmometer I) separates solutions C_1 and C_0 and membrane M_2 (of osmometer II) – solutions of concentrations C_2 and C_0. If the membranes are identical (which in fact is assumed in Münch's model) the pressure – driven transport through tube R (from osmometer I to II) can occur under the condition that C_1 is suitably greater than C_2. Under the conditions specified, water will be drawn osmotically by osmometer I (from vessel N_1). This will generate a mechanical pressure P_1 in that osmometer, and thus a transport of water and assimilates (mass transport) will be induced through tube R_u to osmometer II. Since in osmometer II (and apparently to a certain extent during their transport through tube R_u) the assimilates will be returned to the surroundings or incorporated into certain structures of the plant, in osmometer II the concentration C_2 of assimilates will be lower than their concentration C_1 in osmometer I. Hence water can leave osmometer II (across membrane M_2) on the principle of reversed osmosis.

If the dimensions of osmometer II increase, e.g. with local growth of the plant, the mass transport through tube R_u may occur even when there is no flow of water across membrane M_2, or only an adequately small flow.

In case both osmometers are placed in identical solutions, the water flow in the model considered will be understood as the so-called isoosmotic flow (Ginsburg 1971).

The above described properties of the model considered are basic for Münch's theory of the phloemic transport of water and assimilates in plants.

Introducing some modifications of the model in the present paper, we describe it using the practical thermodynamic formalism of Kedem and Katchalsky (1958). Based on that, we show a series of further osmo-hydromechanical properties of the model that are suitable for interpretation of the phloemic transport of water and assimilates.

The phloemic transport of water and assimilates occurs against various forces, viscous friction including. Hence it requires energy expenditure on the part of the plant. Therefore, the energetic aspect of Münch's model has also been considered. To this end has been used the previously developed practical method (Kargol 1985, 1990, 1991) for analytic and quantitative study of osmo-diffusive conversion of free energy.

Modification of Münch's model and its mathematical description

Modifying Münch's model, we assume that membranes M_1 and M_2 of the respective osmometers (see Fig. 1), differ in their filtration coefficients ($L_{p1} \neq L_{p2}$), reflection coefficients ($\sigma_1 \neq \sigma_2$) and permeability coefficients ($\omega_1 \neq \omega_2$). We also assume that the membranes separate solutions of different concentrations, with $C_1 \neq C_2$ and $C_{01} \neq C_{02}$. In addition, let the mechanical pressures be different in the vicinity of both osmometers ($P_{01} \neq P_{02}$).

Having in view a detailed investigation of the osmotic properties of a model thus modified, whose schematic diagram is shown in Fig. 2, let us make use of the thermodynamic formalism of Kedem and Katchalsky (1958), practical equation for volume flow.

That equation has the form:

$$J_v = L_p \cdot \sigma \cdot \Delta\Pi + L_p \cdot \Delta P, \tag{1}$$

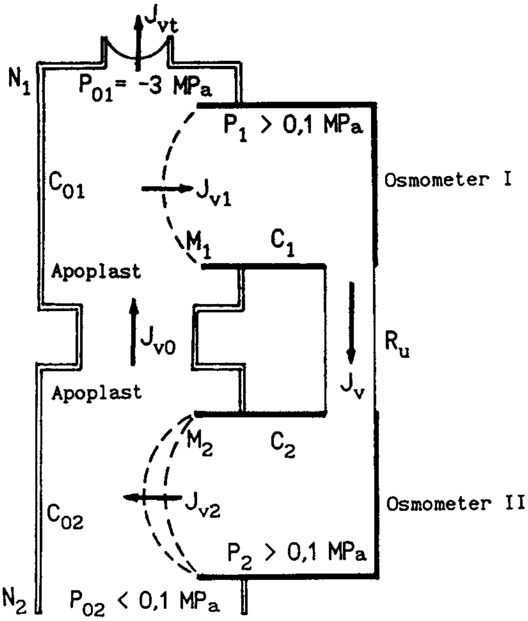


Figure 2. The generalized Münch's model describing the transport of water and assimilates through the phloem (C_1, C_2, C_{01}, C_{02} – concentrations, M_1, M_2 – membranes, R_u – tube, N_1, N_2 – vessels, P_{01}, P_{02}, P_1, P_2 – mechanical pressures, J_v, J_{v0}, J_{v1}, J_{v2} – volume flows, J_{vt} – transpirating water flux).

where: J_v – volume flow, $\Delta\Pi$ – difference in osmotic pressure, ΔP - difference in mechanical pressure.

Using this equation for membranes M_1 and M_2 of the model and allowing for the fact that we are dealing with n-component solution we can write:

$$J_{v1}^n = L_{p1} \sum_1^n (\sigma_{1i} \cdot \Delta\Pi_{1i}) + L_{p1} \cdot \Delta P,$$

$$J_{v2}^n = L_{p2} \sum_1^n (\sigma_{2i} \cdot \Delta\Pi_{2i}) + L_{p2} \cdot \Delta P,$$

where: J_{v1}^n, J_{v2}^n – fluxes, σ_{1i}, σ_{2i} – reflection coefficients of i-th solute, $\Delta\Pi_{1i}$, $\Delta\Pi_{2i}$ – differences in osmotic pressure of i-th solute.

In order to simplify the considerations, let us assume that there is only one solute in the solution. Using this and van't Hoff's formula, we can write the above equations as follows:

$$J_{v1} = L_{p1} \cdot \sigma_1 \cdot \mathrm{R}T \cdot (C_1 - C_{01}) - L_{p1} \cdot (P_1 - P_{01}) \tag{2}$$

$$J_{v2} = L_{p2} \cdot \sigma_2 \cdot \mathrm{R}T \cdot (C_2 - C_{02}) + L_{p2} \cdot (P_2 - P_{02}) \tag{3}$$

where: C_{01}, C_{02} and P_{01}, P_{02} are concentrations and pressures, respectively, in the apoplasts that constitute the neighbourhood of the generalized osmometers I and II (see Fig. 2), R – the gas constant, T – the temperature.

From equation (2) it follows that the photosynthetizing cells of leaves, which imitate osmometer I, can draw water osmotically from the surrounding apoplast, provided the following condition is met:

$$\sigma_1 \cdot \mathrm{R}T \cdot (C_1 - C_{01}) > (P_1 - P_{01}). \tag{4}$$

It should be added here that in high plants the negative pressure P_{01} is very great. Its value may reach -3 MPa, by theoretical estimates. Changes in that pressure, induced by increased or decreased transpiration effect the phloem transport. That effect is of course allowed for in equation (2). Pressure P_1 is the turgor pressure of photosynthetizing cells. It is greater than the atmospheric pressure ($P_1 > 0{,}1$ Pa). Equation (3), referring to osmometer II, says that water can permeate across membrane M_2 by reversed osmosis if:

$$\sigma_2 \cdot \mathrm{R}T \cdot (C_2 - C_{02}) < (P_2 - P_{02}), \tag{5}$$

where P_2 is the turgor pressure in the plant cells the equivalent of which is osmometer II and P_{02} – negative pressure in the xylem that belongs to the apoplast surrounding the cells (see vessel N_2 in Fig. 2).

From equation (3) it also follows that efflux of water from the cells (whose equivalent is osmometer II), where assimilates are used to the apoplast, depends on pressure P_{02}. This conclusion is a line with the data in a paper by Peel (1965).

With reference to the above considerations one should add that pressure flow along the phloem (whose equivalent is tube R_u) can occur when pressure P_1 is higher than P_2.

If water efflux from osmometer II is equal to the osmotic intake of water by osmometer I, we can write down that:

$$J_{v1} = J_{v2} = J_v \tag{6}$$

Allowing for this condition and using equations (2) and (3), one can easily obtain the following equation for volume flows occurring in the model under discussion:

$$J_v = L \cdot [\mathrm{R}T\sigma_1 (C_1 - C_{01}) - \mathrm{R}T\sigma_2 (C_2 - C_{02}) - (P_1 - P_2)] + L \cdot (P_{01} - P_{02}) \tag{7}$$

where $L = L_{p1} \cdot L_{p2} \cdot [L_{p1} + L_{p2}]^{-1}$ and $(P_1 - P_2)$ is the mechanical pressure head on the tube R_u, whereas $(P_{01} - P_{02})$ – the mechanical pressure head on the vessels N_1, N_2 which imitates plant's apoplast.

The above equation allows to analyse in detail the osmo-hydromechanical properties of the model considered. Now we shall consider some of those properties in some selected cases.

Case 1.
To start with let us consider the simplest case, assuming that the membranes M_1 and M_2 of both osmometers are semipermeable ($\sigma_1 = 1$ and $\sigma_2 = 1$) and the concentrations C_{01} and C_{02} as well as pressures P_{01} and P_{02} are identical ($C_{01} = C_{02} = C_0$, $P_{01} = P_{02} = P_0$). Under these assumptions equation (7) is reduced to the form:

$$J_v = L \cdot \mathrm{R}T \cdot (C_1 - C_2) - L \cdot (P_1 - P_2) \tag{8}$$

Assuming also that the hydraulic permeability L_u of the tube R_u is very large, we can put $(P_1 - P_2) \approx 0$ (since $P_1 - P_2 = \frac{J_v}{L_u \to \infty} \approx 0$). Thus the last equation can be written as:

$$J_v = L \cdot \mathrm{R}T \cdot (C_2 - C_1) \tag{9}$$

From this equation it follows that volume flow J_v can occur in the model considered if $C_1 \neq C_2$. It will be, for instance, from osmometer I to osmometer II if $C_1 > C_2$. Since we have assumed that $C_{01} = C_{02}$, the flow J_v will be understood as an isoosmotic flow (Ginsburg 1971).

Case 2.
Let us now assume that membranes M_1 and M_2 differ in their filtration coefficients ($L_{p1} \neq L_{p2}$) and reflection coefficients ($\sigma_1 \neq \sigma_2$). Then, with all other assumptions of case 1 kept, the equation for volume flow has the form:

$$J_v = L \cdot \mathrm{R}T \cdot [\sigma_1 (C_1 - C_0) - \sigma_2 (C_2 - C_0)] \tag{10}$$

In order to discuss this equation, let us further assume that $\sigma_2 < \sigma_1$, with $\sigma_1 = 1$. Under these conditions the transport may proceed from osmometer I to II ($J_v > 0$) when $C_1 > C_2$ and also when $C_1 = C_2$ if, of course, is met the inequality:

$$\sigma_1 (C_1 - C_0) > \sigma_2 (C_2 - C_0) \tag{11}$$

In accordance with this inequality a transport J_v from osmometer I to II is possible even when $C_1 < C_2$. This may, of course, occur when the coefficient σ_1 is greater enough than σ_2.

Case 3.
Let us still take up the most general case,assuming that $C_1 > C_2$, $\sigma_1 > \sigma_2$, $P_1 > P_2$, $P_{01} < P_{02}$ and $C_{01} \neq C_{02}$. With these assumptions the volume transport J_v

is described by equation (7). According to this equation flow J_v is possible from osmometer I to II (along tube R_u) if the inequality is satisfying:

$$\mathrm{R}T\sigma_1 (C_1 - C_{01}) > \mathrm{R}T\sigma_2 (C_2 - C_{02}) + (P_1 - P_2) - (P_{01} - P_{02}) \qquad (12)$$

Performing a detailed discussion of this case, it is easy to notice that, with σ_1 greater enough than σ_2, the above inequality can be fulfilled when:

$C_{01} < C_{02}$, meaning flow J_v in accordance with concentration gradient.

$C_{01} = C_{02}$, meaning the occurrence of isoosmotic flow.

$C_{01} > C_{02}$, meaning that the model is able to pump water against concentration gradient (Curran and MacIntosh 1962, Patlak et al. 1963, Kargol 1978).

In general it should be noticed that in the situation of Fig. 2 osmometer I is above osmometer II. Under these conditions the transport along the phloem – imitating tube R_u is directed downwards. The model considered will also exhibit the same properties if osmometer is situated below osmometer II. Then the transport along tube R_u will proceed upwards. On this basis one can model the transport of assimilates through phloem occurring in two directions: upwards and downwards (Wilkins 1969, Zimmermann and Brown 1971, Salisbury and Ross 1975, Zurzycki and Michniewicz 1977).

It should also be added here that the phloem transport J_v described by equation (7) is a function of many variables, a function of the negative pressure P_{01}, whose value in plants depends on the intensity of transpiration.

The above analysis, although not complete, can still furnish some new information about the osmo-hydromechanical properties of modified Münch's model. Those properties, that follow from equation (7), make the model more universal as far as interpretation of phloem water and assimilates transport is concerned. They also make it more convincing from the biological point of view.

The considerations get complicated when the size of osmometer II increases, which can correspond to local growth of the plant. Under these conditions flux J_{v2} may be smaller than J_{v1}, or even equal to zero ($J_{v2} = 0$).

The energetic aspect of Münch's model

In the light of Münch's model the phloem transport of water and assimilates in it is driven osmotically. According to equation (2) that driving is brought about by the effective osmotic pressure difference:

$$\sigma_1 \cdot \Delta\Pi_1 = \sigma_1 \cdot \mathrm{R}T \cdot (C_1 - C_{01}) \qquad (13)$$

Since the transport occurs against various forces the viscous ones including, it thus requires definite energy expenditure on the part of the plant. From the biological point of view it is interesting to consider the energetic aspect of the transport. We can do that by using equation (7) and the previously developed method (Kargol 1985, 1990, 1993) for studying the osmo-diffusive conversion of energy of solutions of various concentrations. Proceeding in line with the method, let us transform equation (7) to the form:

$$\sigma_1 \cdot \Delta\Pi_1 = \frac{J_v}{L} + \sigma_2 \cdot \Delta\Pi_2 + \Delta P - \Delta P_0 \tag{14}$$

where: $\Delta\Pi_1 = \mathrm{R}T \cdot (C_1 - C_{01})$, $\Delta\Pi_2 = \mathrm{R}T \cdot (C_2 - C_{02})$, $\Delta P_0 = P_1 - P_2$ and $\Delta P_0 = P_{02} - P_{01}$.

Next, multiplying this equation by $S \cdot J_v$, where S is a unit effective surface of each of the membranes M_1 and M_2 of Münch's model and also a unit surface of phloem transverse section (pipe R_u see Fig. 2), we obtain the so-called global power equation:

$$S \cdot J_v \cdot \sigma_1 \cdot \Delta\Pi_1 = S \cdot \frac{J_v^2}{L} + S \cdot \sigma_2 \cdot \Delta\Pi_2 \cdot J_v + S \cdot \Delta P \cdot J_v - S \cdot \Delta P_0 \cdot J_v \tag{15}$$

It should be emphasized here that each term of this equation satisfies the mechanics equation $M = F \cdot v$, where M – power, F – force and v – velocity.

Introducing the notations:

$$M_c' = S \cdot \sigma_1 \cdot \Delta\Pi_1 \cdot J_v = S \cdot \sigma_1 \cdot \mathrm{R}T \cdot (C_1 - C_{01}) \cdot J_v \tag{16}$$

$$M_{r0} = S \cdot \frac{J_v^2}{L} \tag{17}$$

$$M_{u\pi} = S \cdot \sigma_2 \cdot \Delta\Pi_2 \cdot J_v = S \cdot \sigma_2 \cdot \mathrm{R}T \cdot (C_2 - C_{02}) \cdot J_v \tag{18}$$

$$M_{u0} = S \cdot \Delta P \cdot J_v \tag{19}$$

$$M_{ua} = S \cdot \Delta P_0 \cdot J_v = S \cdot (P_{02} - P_{01}) \cdot J_v \tag{20}$$

equation (15) can be rewritten:

$$M_c' = M_{r0} + M_{u\pi} + M_{u0} - M_{ua} \tag{21}$$

where: M_c' – total power of osmotic origin, M_{r0} – power dissipated in the pores of membranes M_1 and M_2, determined by the forces of friction, $M_{u\pi}$ – power spent on pushing water against the osmotic pressure $\sigma_2 \cdot \Delta\Pi_2$, M_{u0} – useful power spent on pushing water through the tube R_u (against mechanical pressure $\Delta P = P_1 - P_2$), and M_{ua} – power spent on pushing water through the apoplast from osmometer II to I, effected by the pressure $\sigma_1 \cdot \Delta\Pi_1$. Formulas (16)–(21) allow to consider quantitatively the respective powers in the phloem transport of water and assimilates.

All the above named powers are, as seen in formulas (16)–(21), functions of volume flux J_v. Since this flux is, according to formula (7), dependent on the pressure P_{01} (see Fig. 2) determined by the intensity of transpiration, those powers are thus dependent on transpiration.

This refers also to the power M_{u0}, which we have called useful power. Such a name is justified by the fact that the phloem transport occurs against the pressure $\Delta P = P_1 - P_2$ (see Fig. 2), which we can treat as an external pressure. On introducing a quantity $\mathcal{L}$, called hydraulic conductivity of phloem, and defined as:

$$\mathcal{L} = \frac{J_v}{\Delta P} \tag{22}$$

the equation of useful power can be written as:

$$M_{u0} = S \cdot \frac{Jv^2}{\mathcal{L}} \tag{23}$$

Thus we have shown that the useful power M_{u0}, like the dissipated power M_{r0}, is a square function of flux J_v.

Under the assumption that the membranes M_1 and M_2 in the considered Münch's model are selective, i.e. the values of the parameters σ_1 and σ_2 are in the intervals: $0 < \sigma_1 < 1$ and $0 < \sigma_2 < 1$, fluxes of solutes will occur across the membranes. Those fluxes can be described, according to the thermodynamic formalism (Kedem and Katchalsky 1958), by the equations:

$$j_{s1} = -\omega_1 \cdot \Delta\Pi_1 + (1 - \sigma_1) \cdot \overline{C}_1 \cdot J_v \tag{24}$$

$$j_{s2} = -\omega_2 \cdot \Delta\Pi_2 + (1 - \sigma_2) \cdot \overline{C}_2 \cdot J_v \tag{25}$$

where: ω_1, ω_2 – permeability coefficients, $\overline{C}_1$, $\overline{C}_2$ — mean concentrations.

On the basis of these equations one can obtain, according to the analytic method of osmo-diffusive conversion of energy (Kargol 1990, 1993) the following equations for diffusive dissipation of power:

$$M_{rD1} = S \cdot \omega_1 \cdot \overline{V}_s \cdot \Delta\Pi_1^2 \tag{26}$$

$$M_{rD2} = S \cdot \omega_2 \cdot \overline{V}_s \cdot \Delta\Pi_2^2 \tag{27}$$

where: $\overline{V}_s$ – mole volum of assimilates.

Taking into account all the above explicit power equations one can easily derive an expression for energetic efficiency η_{0D} of osmo-diffusive conversion of energy, occurring in Münch's model. In accordance with the general definition of that quantity,taking as the ratio of useful to total power, it can be written as:

$$\eta_{0D} = \frac{M_{u0}}{M_{u0} + M_{r0} + M_{u\pi} + M_{ua} + M_{rD1} + M_{rD2}} \tag{28}$$

Simulative studies on modified Münch's model

Analytic considerations, performed in the present work, on generalized Münch's model create new possibilities in the research of the phloem transport of water and assimilates. They comprise, namely, osmo-hydromechanical and energetic possibilities of the transport. In order to carry out such studies, it is necessary to measure on biological objects such quantities as: C_1, C_2, C_{01}, C_{02}, L_{p1}, L_{p2}, σ_1, σ_2, ω_1, ω_2 and φ. For the most, part such data have not been determined up to now. So, in the present situation, we have to restrict the studies to some simulative attempts concerning the model. They will be based on some arbitrary or estimated data shown in the table below (Peel 1965, Wilkins 1969, Ginsburg 1971, Zimmermann and Brown 1971, Salisbury and Ross 1975, Zurzycki and Michniewicz 1977, Fensom 1981, Kargol 1992, Meshcheryakov et al. 1992 and other).

Table 1. Data assumed in the calculations.

$L_{p1} = L_{p2}$ $[\mathrm{m^3N^{-1}s^{-1}}]$	σ_1	σ_2	$C_{01} = C_{02}$ $[\mathrm{mol.m^{-3}}]$	C_1 $[\mathrm{mol.m^{-3}}]$	C_2 $[\mathrm{mol\ m^{-3}}]$	$\overline{V}_s$ $[\mathrm{m^3.mol^{-1}}]$
$5 \cdot 10^{-12}$	0.98	0.8	$0.01 \cdot 10^3$	$1.2 \cdot 10^3$	$0\,1 \cdot 10^3$	$0.115 \cdot 10^3$

P_1 $[\mathrm{N.m^{-2}}]$	P_2 $[\mathrm{N.m^{-2}}]$	P_{01} $[\mathrm{N.m^{-2}}]$	P_{02} $[\mathrm{N.m^{-2}}]$	ω_1 $[\mathrm{mol.N^{-1}s^{-1}}]$	ω_2 $[\mathrm{mol.N^{-1}\ s^{-1}}]$	S $[\mathrm{m^2}]$	T $[K]$
$1.25 \cdot 10^5$	$1.1 \cdot 10^5$	$-3 \cdot 10^6$	$-2 \cdot 10^6$	$0.1 \cdot 10^{-11}$	$0.5 \cdot 10^{-11}$	10^{-4}	300

In the present paper we shall present detailed results on osmo-hydromechanical and energetical properties of modified Münch's model.

a. Osmo-hydromechanical properties

According to the transpiration-cohesion theory let us assume that the mechanical pressure in the surroundings of osmometer I, i.e. in the apoplast surrounding the photosynthetizing cells, is $P_{01} = -3$ MPa. In the osmometer itself that imitates those cells, the mechanical pressure $P_1 > 0,1$ MPa (turgor pressure). For the osmo-mechanical equilibrium to occur between the photosynthetizing cells and the surrounding apoplast, a concentration $C_1 \approx 1,2$ [mol/l] must occur in the cells. This follows directly from the formula: $P_{01} = \sigma \cdot \mathrm{R}T \cdot (C_1 - C_{01})$, under the assumption that $C_{01} = 0$ and $\sigma = 1$. If the pressure P_{01} decreases, in osmometer I shall develop a volume flow given by equation (7). Flow J_v may also be induced by concentration C_1 rising above 1,2 [mol/l]. It should be added here that increase in pressure P_{01} in a plant may be due to increased transpiration, and increase in concentration C_1 – to increased efficiency of photosynthetic processes.

Having the above in mind, on the basis of equation (7) we have performed detailed numerical calculations of the functions J_v (P_{01}) and J_v (C_1). In the calculations it was assumed that the remaining quantities in formula (7) are constant. Their values are given in Table 1. Plots of the calculated functions are shown in Figs. 3*a* and 3*b* respectively.

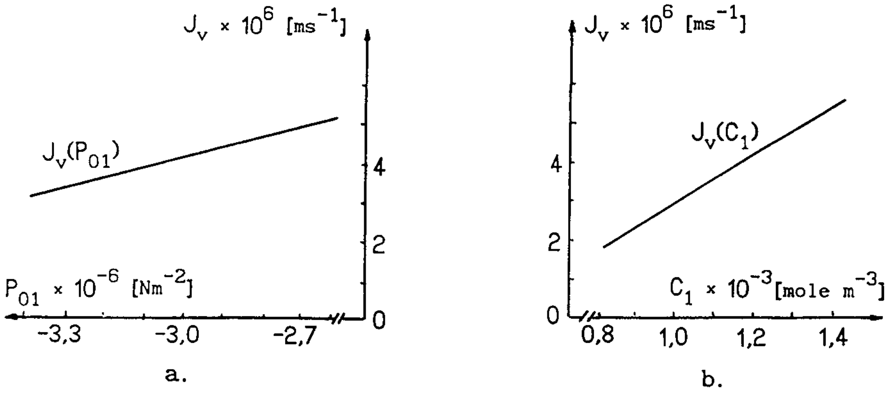


Figure 3. *a*. Dependence $J_v(P_{01})$, *b*. Dependence $J_v(C_1)$.

From the plot in Fig. 3*a* it follows that increased negative value of P_{01}, due to increased transpiration, brings about increased volume flux J_v which includes water and assimilates. Flux J_v increases also with increasing concentration of C_1. This is shown in detail in Fig. 3*b*. Both the dependences are linear in the studied pressure and concentration intervals.

Since root pressure can be generated in the root, pressure P_{02} (see Fig. 2) may change. Numerical calculations of J_v as a function of pressure P_{02} (by using equation (7)) were made, assuming that the intensity of transpiration is constant in time. The plot of the function is shown in Fig. 4*a*.

There, it can be seen that the flow J_v decreases with increasing P_{02} caused by increasing root pressure. Assuming next that increased intensity of assimilates utilization brings about decreased concentration C_2, the relationship J_v (C_2) has been calculated and plotted. That plot is shown in Fig. 4*b*, where we can see that a decrease in concentration C_2 induces an increase in J_v.

Thus some abilities of the plant were determined concerning the generation and regulation of the phloem transport of J_v. These are: adequate changes in

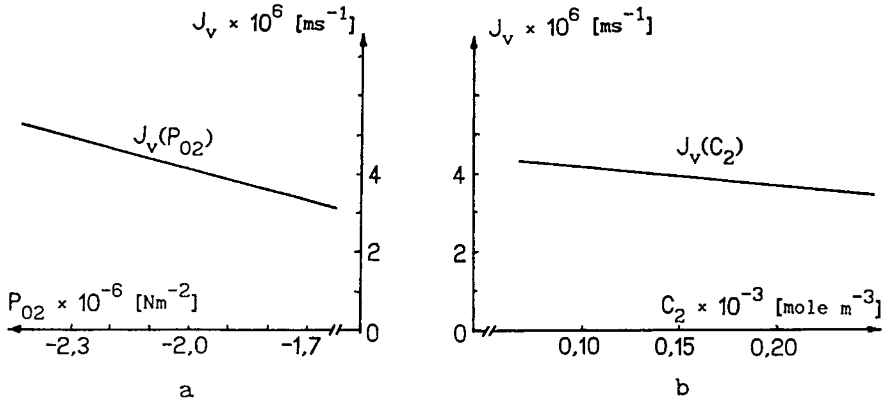


Figure 4. *a* Dependence J (P_{01}) *b* Dependence J (C_1)

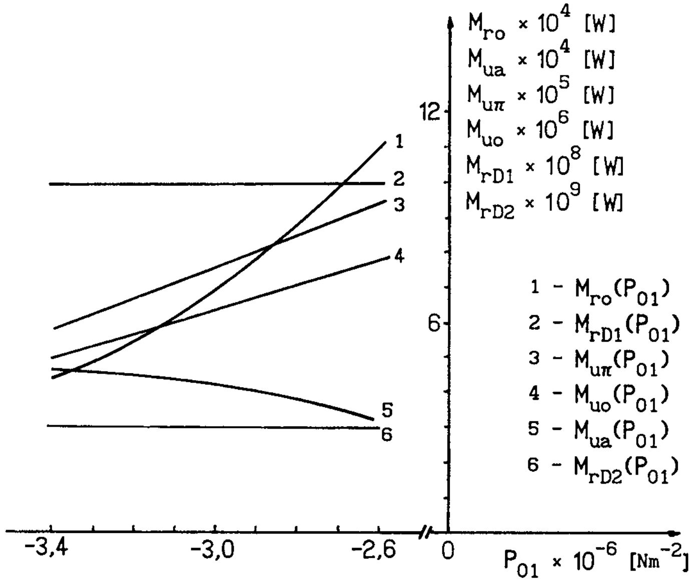


Figure 5. Dependences $M_{r0}(P_{01})$ graph 1, $M_{rD1}(P_{01})$ graph 2, $M_{u\pi}(P_{01})$ graph 3, $M_{u0}(P_{01})$ - graph 4 $M_{ua}(P_{01})$ graph 5 and $M_{rD2}(P_{01})$ - graph 6

intensity of transpiration, in efficiency of photosynthetic processes, changes in the root pressure and in intensity of utilization of assimilates

In a real plant the changes in P_{01} and P_{02} and in concentrations C_1 and C_2 may occur simultaneously Then the flow J_v will be determined by the resultant change

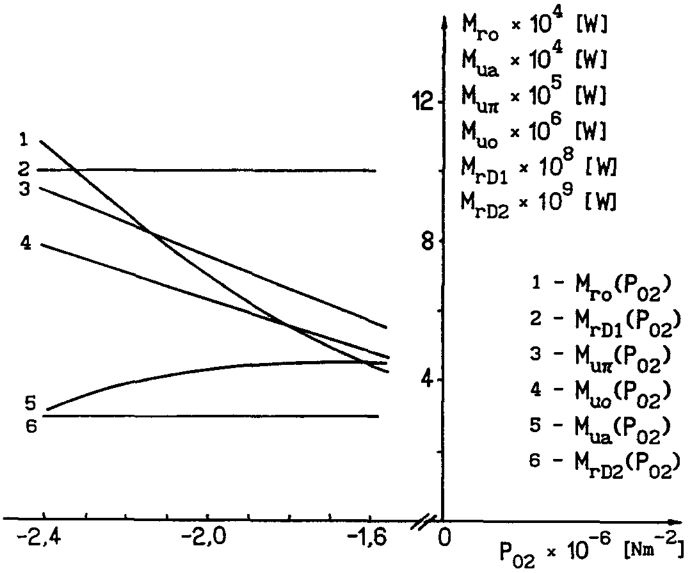


Figure 6. Dependences: $M_{r0}(P_{02})$ – graph 1, $M_{rD1}(P_{02})$ – graph 2, $M_{u\pi}(P_{02})$ – graph 3, $M_{u0}(P_{02})$ – graph 4, $M_{ua}(P_{02})$ – graph 5, $M_{rD2}(P_{02})$ – graph 6.

b. Energetical properties

The phloem transport of water and assimilates is connected with a definite expenditure of energy. In other words, it is connected with expenditure of: power M_{r0} which is osmotically dissipated in pores of membrane M_1 and M_2, power $M_{u\pi}$ – spent against the osmotic pressure $\sigma_2 \Delta\Pi_2$, useful power M_{u0}, power M_{ua} spent on pumping water along the xylem and apoplast from osmometer II to osmometer I against the pressure $(P_{02} - P_{01})$ – see Fig. 2, and powers dissipated on diffusion, i.e. M_{rD1} and M_{rD2}. All those powers are expressed by formulae (17), (18), (19), (20), (26) and (27). By using these formulae and equation (7), as well as the data given in Table 1, numerical studies of the powers as functions of P_{01} and P_{02} have been made, as well as of C_1 and C_2. The results of these studies are shown in the consecutive figures, i.e. Figs. 5, 6, 7 and 8. From the plots in Fig. 5 and 6 it follows that powers M_{rD1} and M_{rD2}, practically, do not depend on pressure P_{01} or P_{02}. However, markedly depend on those pressures the powers M_{r0} and M_{u0} and also M_{ua} and $M_{u\pi}$. With increasing pressure P_{01} powers M_{r0}, M_{u0} and $M_{u\pi}$ increase, while power M_{ua} decreases (see Fig. 5). The situation is quite different when pressure P_{02} increases (see Fig. 6). Then the powers M_{r0}, M_{u0} and $M_{u\pi}$ decrease while the power M_{ua} increases. Powers M_{rD1} and M_{rD2} do not depend on pressure P_{02}.

Practically all the powers considerated depend, more or less, on concentrations

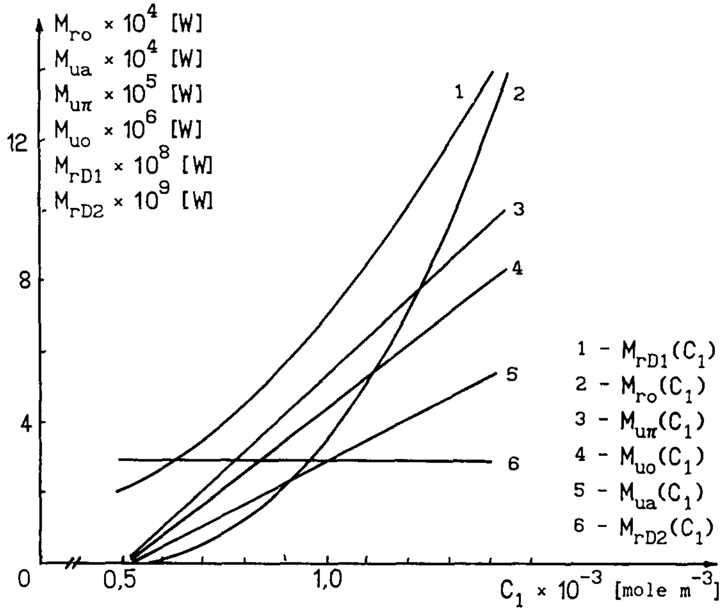


Figure 7. Dependences: $M_{rD1}(C_1)$ – graph 1, $M_{r0}(C_1)$ – graph 2, $M_{u\pi}(C_1)$ – graph 3, $M_{u0}(C_1)$ – graph 4, $M_{ua}(C_1)$ graph 5 and $M_{rD2}(C_1)$ – graph 6.

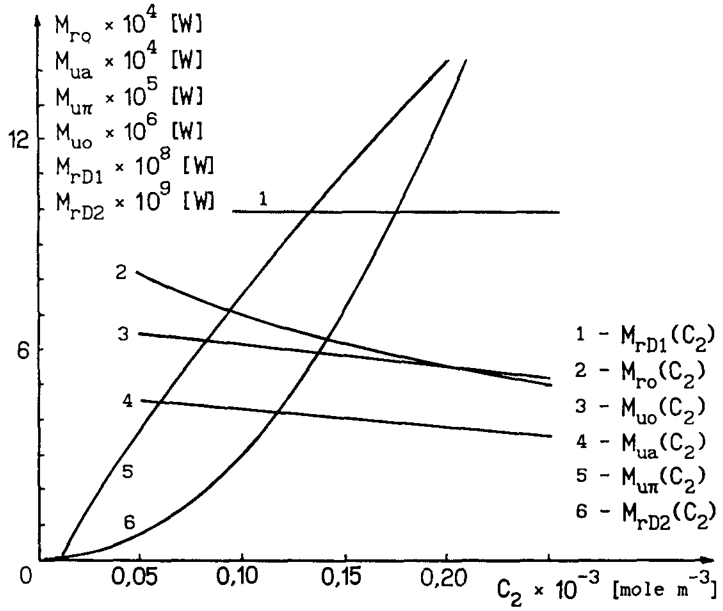
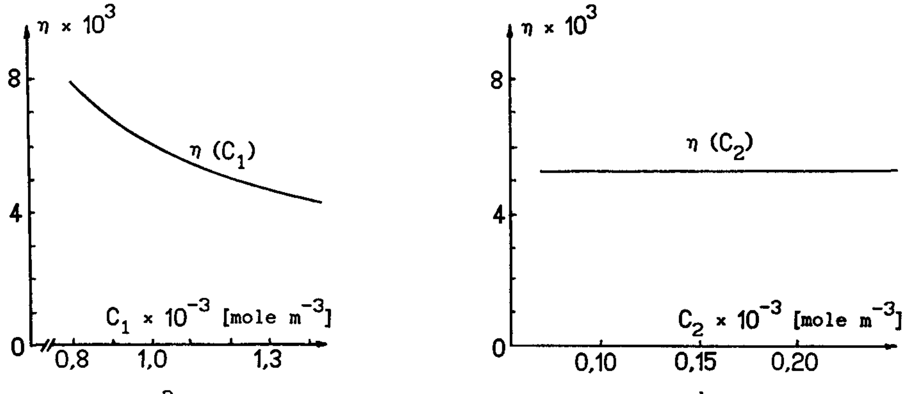


Figure 8. Dependences: $M_{rD1}(C_2)$ – graph 1, $M_{r0}(C_2)$ – graph 2, $M_{u0}\,(C_1)$ – graph 3, $M_{ua}\,(C_2\,)$ – graph 4, $M_{u\pi}\,(C_2)$ – graph 5 and $M_{rD2}\,(C_2)$ – graph 6.



a.

b.

Figure 9. *a.* Dependence $\eta(C_1)$, *b.* Dependence $\eta(C_1)$.

C_1 and C_2, and thus they can be seen in Figs. 7 and 8. An exception is the power M_{rD2} which does not depend on concentration of C_1 (Fig. 7) and power M_{rD1} which does not depend on concentration C_2 (Fig. 8). It is remarkable here that power M_{rD2} depends very strongly on concentration C_1 (see Fig. 7) and thus on the intensity of photochemical processes. Power M_{rD2} depends also very strongly on concentration C_2 (see Fig. 8) so it depends on the intensity of assimilates use.

c. Energetical efficiency

The results of calculations of the respective powers allow, with the use of equation (28), to modify Münch's model, as a function of C_1, C_2, P_{01} and P_{02}. Appropriate results of the study are shown in graphic form in Figures 9*a*, *b* and 10*a*, *b*. From these plots it follows that the energetical efficiency η depends in a considerable way on concentration C_1 only. It decreases with increasing concentration C_1 (see Fig. 10*a*). This means that, provided in a real plant the transport of water and assimilates occurs according to Münch's model, the energetical efficiency of that transport depends on the intensity of photochemical processes only.

Concluding remarks

1. It has been shown that if the phloem transport of water J_v (comprising transport of water and assimilates) occurs in a real plant according to Münch's model, it can be studied by using the thermodynamic formalism of Kedem and Katchalsky (1958).
2. By using that formalism and modifying the model, it has been shown that it possesses a series of specific osmo-hydromechanical and energetical properties. These refer to the conditions of generation and regulation of the phloem transport of water and assimilates, and the necessary expenditure of energy. From the studies

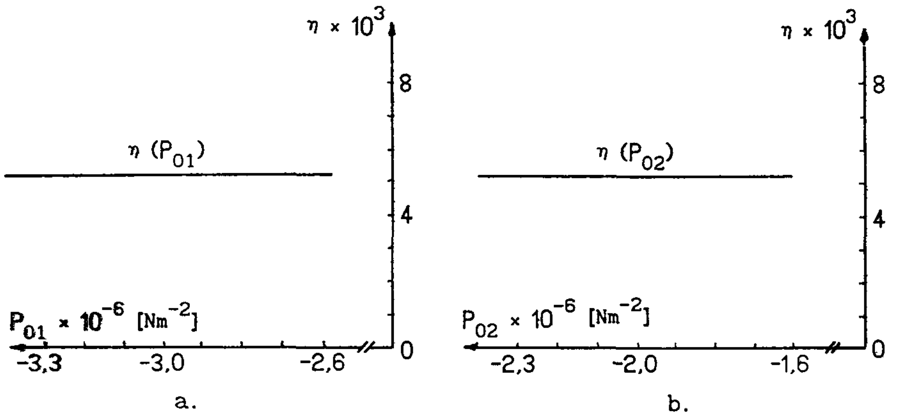


Figure 10. *a.* Dependence $\eta(P_{01})$, *b.* Dependence $\eta(P_{02})$.

performed it follows that the phloem transport J_v can be affected by: transpiration, intensity of photosynthetic processes, root pressure and the rate assimilates are utilized.

3. The energetic aspects of the phloem transport have been studied by using the previously elaborated method (Kargol 1990) of analysing the osmo-diffusive conversion of free energy of solutions of different concentration.

4. The present study makes Münch's model more universal as regards the interpretational possibilities concerning the phloem transport of water and assimilates. It also makes the model more convincing from the biophysical point of view.

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