

Modification and Quantitative Analysis of the Münch Model in the Integrated System of Water Translocation in Plants

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Abstract. Aiming at making the Münch model more adequate to the biological reality we introduce certain modifications and complements. Considering the model within the framework of so-called integrated system of long-distance water transport in plants we present a quantitative analysis based on the Kedem-Katchalsky formalism. A new mathematical description of the reverse osmosis is also utilized. The work is a starting point for further quantitative studies and simulations of the phloem transport of water and assimilates in plants.

Key words: Water — Assimilates — Phloem — Mass transport — Transport equations

Introduction

Biophysical aspects of phloem transport of water and assimilates in plants are analyzed mainly on the basis of three theories: the theory of diffusion and natural cytoplasm motion, the electroosmotic theory, and the Münch mass transport theory (Preston 1963; Fensom and Spanner 1969; Wilkins 1970; Zimmermann and Brown 1971; Clarkson 1974; Salisbury and Ross 1975; Ziegler 1977; Mengel and Kirkby 1980; Fensom 1981; Amin 1986; Patrick 1990; Bel 1993; Kargol 1994; Kargol et al. 1998). The latter, also known as the theory of pressure induced flows, is the most widely accepting.

The theory is based on the so-called Münch model (Salisbury and Ross 1975; Wilkins 1976; Ziegler 1977; Fensom 1981; Kargol 1994). In its classical form the model consists of two osmometers connected by a tube and submerged in two connected containers. One of the osmometers represents the photosynthesizing cells in leaves, that is places where assimilates are produced (the source). The other osmometer models parts of a plant where assimilates are consumed (the sink), i.e. the root system, bulbs, fruits, or buds. The connecting tube represents the conducting vessels in phloem. According to Münch, the membrane of the first osmometer forms

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a barrier separating the leaves apoplast from the cytoplasm of the photosynthesizing cells. There is an osmotic flow of water to those cells, resulting in the increase of their turgor pressure. Under this pressure the water (with assimilates) is then transported along the plant phloem to places where assimilates are metabolized, that is to places represented by the second osmometer. There water permeates through the membrane by reverse osmosis. Such a model, although sound from a biophysical point of view, is nevertheless far from biological reality. In order to make it more realistic, several modifications were proposed (Preston 1963; Zimmermann and Brown 1971; Clarkson 1974; Ziegler 1977; Mengel and Kirkby 1980; Fensom 1981; Patrick 1990; Kargol 1994; Kargol 1996; Kargol et al. 1998).

Various attempts have also been made at a mathematical description of phloem transport (Preston 1963; Ziegler 1977; Amin 1986; Kargol 1994; Kargol 1996; Kargol and Kargol 1996; Kargol et al. 1998). In these investigations various numerical data obtained from experiments on biological material are used. This is true in particular for the work of Kargol (1996), where the so-called integrated system of water translocation on long distances has been proposed. In that system the classical Münch model constitutes the main element. However, this version of the Münch model is too far from biological reality. That statement follows, among others, from identifying the mechanical pressure in the source osmometer of the classical model with the turgor pressure of leaf photosynthesizing cells. That pressure is however too small to induce the phloem translocation of water and assimilates. Moreover, experimental investigation has shown that in the sieve tubes of leaves, which constitute the beginning of water ducts of phloem, there exists a very high positive mechanical pressure. It may reach the value of +3 MPa (Salisbury and Ross 1975; Wilkins 1976; Mengel and Kirkby 1980). Therefore, one should modify the Münch model appropriately.

On assuming such methodology we have introduced in the present work some new modifications and supplements of the Münch model. We believe that the modified model proposed here is relatively highly adequate to biological reality. More than that, it is being considered herein within the integrated system of water translocation over long distances in the plant (Kargol 1996; Kargol and Kargol 1996; Kargol et al. 1998). This allowed, on the basis of the Kedem-Katchalsky formalism (Katchalsky and Curran 1965) to obtain a detail mathematical description of the Münch model. That description deals with the phloem water and assimilates transport coupled with water transport in the plant over other long distances, i.e. in connection with radial water transport in the root, xylem transport and water permeation across leaf tissue and transpiration into the atmosphere. Due to that also transport equations were obtained concerning the Münch model, which will enable us to do a quantitative simulation of the phloem transport coupled with the root pressure, transpiration, the effectivity of creating assimilates by the plant and the rate of their utilisation.

In the mathematical considerations the recently proposed (Kargol 1997) new way of describing reversed osmosis was applied. This was done because that description treats the process as a non-linear one. Moreover, the phloem transport

of water and assimilates undergoes various regulation effects, in which non-linear processes become especially important.

Modification of the Münch model as part of the integrated system of long-distance water transport in plants

In general, the long-distance water transport in plants can be separated into four stages (denoted I, II, III, IV in Fig. 1). The Figure shows the so-called integrated system of water transport in plants proposed recently (Kargol 1996; Kargol and Kargol 1996). At the first stage water with mineral components is transported radially across the root from the soil to the xylem. The second stage is water uptake (through tracheary elements of xylem) from the root to the leaves. The next stage (III) consists of permeation (mainly through apoplast) in the leaf tissue. There, most of the water evaporates to the atmosphere from the surface of mesophyll cells and the leaf cuticles. The remaining water (a relatively small amount) is absorbed from the leaf apoplast by the photosynthesizing cells. Then, it is passed to the conducting elements in phloem (sieve elements). Here, it is (together with assimilates) transported along the plant to places where assimilates are used. This flow is usually opposite to the xylem transport and constitutes the last, fourth stage in the long-distance transport model. The present work concentrates on this fourth stage. First, however, let us summarize basic information on biophysical mechanisms of water transport in the former three stages (I, II, III) in the integrated system shown in Fig. 1 (Kargol 1996). We assume that at the first stage the water flux J_{vr} across the root is generated osmotic (Fiscus 1975; Pitman 1982; Steudle et al. 1987; Kargol and Suchanek 1990; Kargol 1992; Kargol and Markowski 1996), as is the root pressure. At the next two stages (II and III) the water fluxes J_{vx} and J_{vg} (along xylem), J_{vA} (through leaf apoplast) and J_{vt} (the transpiration flux) are determined by the Dixon-Renner transpiration-cohesion theory (Wilkins 1969; Zimmermann and Brown 1971; Ziegler 1977; Kargol 1994; Kargol 1996) and the graviosmotic theory (Kargol 1978; Przystalski and Kargol 1987; Kargol 1992). The graviosmotic transport in xylem is denoted by J_{vg} . One might add that the water transport at those two stages is also influenced by the root pressure, according to the root pressure theory. The amount of water absorbed by the photosynthesizing cells from the leaf apoplast is small compared to the amount transpiring from the leaves. Thus, the following continuity equation can be written (Kargol 1996):

$$S_r J_{vr} = S_x J_{vx} + S_{xg} J_{vg} = S_A J_{vA} \cong S_t J_{vt} \quad (1)$$

where S_r is the active surface of the radial pathway in root, S_x is the total active surface of the tracheary elements in xylem, S_{xg} is the active surface of the xylem vessels in which the flux J_{vg} is generated, S_A is the (total) active surface of the apoplast pathway in leaves, and S_t is the total transpiration surface of the leaves.

As mentioned above, we concentrate here on the last stage of the water translocation, i.e. the phloem transport of water and assimilates. Our considerations are

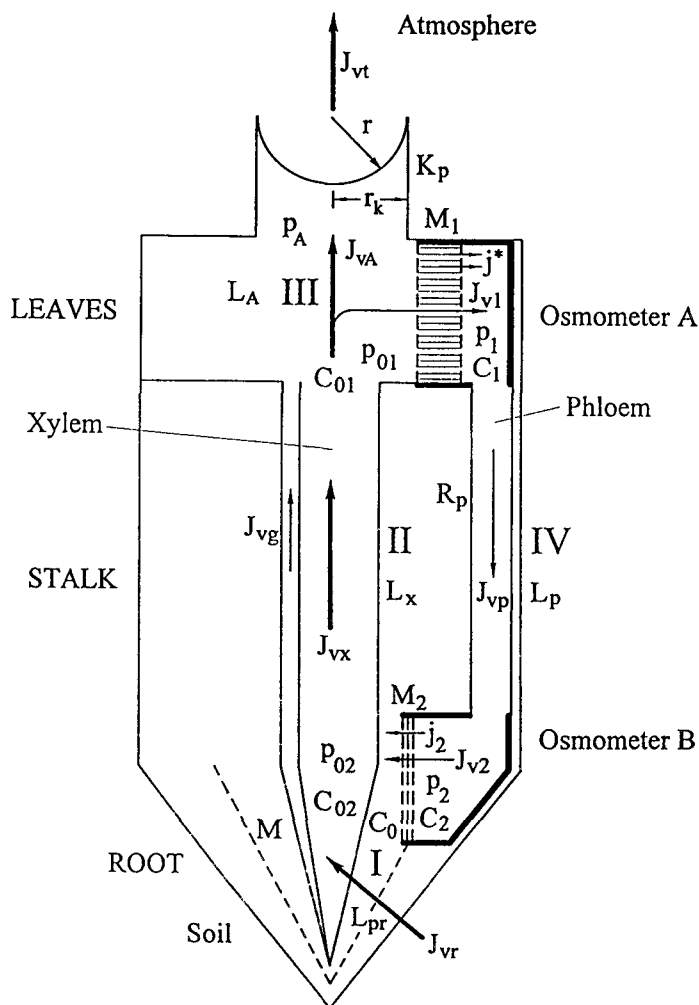


Figure 1. Munch model in the integrated system of water translocation in plants, (I, II, III, IV – stages of water translocation in plants, L_{pr} , L_{px} , L_{pA} , L_p – hydraulic permeability, J_v , J_{vx} , J_{vA} , J_{vp} – volume flows, J_{vt} – flow of transpiring water, M_1 , M_2 – membranes of osmometers of Munch model (I and II respectively), L_{p1} , L_{p2} – filtration coefficients of membranes M_1 and M_2 , C_1 , C_2 – solution concentrations in osmometer I and II respectively, C_{01} – concentration of solution in leaf apoplast, C_{02} – concentration of solution in xylem of a root, C_0 – concentration of solution in stem of the root, P_1 , P_2 , P_{01} , P_{02} , P_A – mechanical pressures)

based on the Munch model. The model, modified here from its original version (as we explain below) consists of two osmometers A and B connected by a tube R_p representing the conducting elements of plant phloem. As Fig. 1 shows the Munch

model is an integral part of the long-distance water translocation (Kargol 1996). Therefore, the phloem transport can be analyzed in connection with the transport in the first three stages, and in particular we can determine its dependence on e.g., transpiration, assimilate production rate, root pressure, and the assimilate metabolism rate. Some introductory statements can be found in Kargol (1994). Our modifications were inspired by several earlier papers (Preston 1963; Wilkins 1969; Tyree 1970; Clarkson 1974; Ziegler 1977; Mengel and Kirkby 1980; Fensom 1981; Starck 1983; Niemyska 1986; Amin 1986; Balling and Zimmermann 1990; Patrick 1990; Bel et al. 1992; Bel 1993; Kargol 1994; Kargol 1996).

We assume that membrane M_1 in osmometer A represents the water pathway from the leaf apoplast to the inside of the sieve tubes at the beginning of the phloem water ducts. This conduit includes the photosynthesizing cells, sieve elements' cells, and companion cells forming the sieve tubes. Within that pathway the transport can take place along the apoplast or the symplast route. According to the literature data we assume that the pressure in the leaf apoplast is negative relative to the atmospheric pressure and can reach values up to $P_{01} = -3$ MPa. On the other hand, the pressure in the sieve tubes in leaves also has large values but positive relative to the atmospheric pressure. It can reach $P_1 = +3$ MPa (Salisbury and Ross 1975; Wilkins 1976; Ziegler 1977; Mengel and Kirkby 1980; Kargol 1994). Water and the assimilates are transported across membrane M_1 to the inside of osmometer A. It models the insides of the sieve tubes from which the phloem water ducts begin in leaves. Membrane M_1 represents the transport route from leaves' apoplast to the insides of these tubes. The water volume flux is denoted J_{v1} and the assimilate flux j^* in Fig. 1. We have to assume that the assimilates are transported actively. It is a trans-cell transport, *via* the symplast route, from the photosynthesizing cells, through the layers of cells, to the inside of the sieve tubes. Along that conduit the assimilate concentration increases and is the largest in the sieve tubes. Such concentration gradient causes water taken from the apoplast (and supplied there by xylem) to be transported osmotically through layers of cells. In the last phase it is pumped to the sieve tubes. In general, transport along this route (represented by membrane M_1) can take place both along the apoplast and symplast route. However, the apoplast route becomes less accessible to water in the proximity of the sieve tubes. The osmotic flux J_{v1} into the sieve tubes in the last phase occurs only in symplast.

Keeping in mind biological interpretation of the membrane M_1 in the Münch model, we describe its transport properties. The passive transport properties can be determined, within the Kedem-Katchalsky formalism (Katchalsky and Curran 1965), by the transport coefficients: of filtration L_{p1} , reflection σ_1 , and permeation ω_1 . The values are: $L_{p1} > 0$, $\sigma_1 = 1$, $\omega_1 = 0$. With these values of σ_1 and ω_1 , the solutes do not permeate from the leaf symplast to the apoplast. We may add that the solutes (mineral components) supplied to the leaf apoplast with water (through xylem) have to be completely absorbed from there (in an active process) by the leaf cells where they are metabolized. Otherwise, water evaporation would quickly lead to a significant concentration increase in the apoplast solution, a situation

that is clearly physiologically disadvantageous. Also, situations exist when there is an excessive intake of the solutes from the apoplast by the leaf cells. In that case the solutes are appropriately stored (Clarkson 1974).

Next, in the Münch model, water with the assimilates flows from osmometer A through the tube R_p to osmometer B. This volume flux J_{vp} is generated by the hydraulic pressure difference $\Delta P = P_1 - P_2$, where P_1 , P_2 are the pressures in osmometers A and B, respectively. As already mentioned, osmometer B is supposed to represent the parts of plant where assimilates are used. In particular, let us assume that this happens mainly in the root system. It is a biologically realistic assumption, e.g., in the case of plants that do not produce fruits in the given vegetation period, or already did so. There is a volume flux J_{v2} across membrane M_2 of this osmometer consisting of water and some solutes, including assimilates.

We observe here a reverse osmosis generated by hydraulic pressure $\Delta P_2 = P_{02} - P_2$, where – as shown in Fig. 1 – P_{02} is the pressure on the outside of membrane M_2 . Just as membrane M_1 generalizes a fairly complex biological system, membrane M_2 represents a certain transport conduit. In particular, the inside of osmometer models the sieve tubes at the end of the phloem water ducts. From there, water (with dissolved assimilates) is transported through plasmodesm to the cytoplasmic continuum of the stele. There, the assimilates are partially used. Water and the rest of assimilates permeate then through the cell walls of the continuum, to the stelar apoplast, where the assimilate concentration is denoted by C_0 (see Fig. 1). Membrane M_2 generalizes this entire water pathway from the sieve tubes to the apoplast of the stele. Along that pathway the assimilates can be transported both actively and passively. Again, within the framework of Kedem-Katchalsky formalism, we ascribe to the membrane M_2 the transport coefficients L_{p2} , σ_2 , ω_2 , such that $L_{p2} > 0$, $1 > \sigma_2 > 0$, $\omega_2 > 0$.

Finally, water from the stelar apoplast can be taken up by the tracheary elements of xylem and transported along a plant from the roots to the leaves. Thus, to a certain degree water circulates in plants.

The above remarks on the transport of water and assimilates through membrane M_2 do not contradict theories of radial water transport in roots, i.e. from the soil to the xylem of the stele (Ginsburg 1971; Fiscus 1975; Pitman 1982; Steudle et al. 1987; Taura et al. 1988; Michalov 1989; Kargol and Suchanek 1990; Kargol 1992; Kargol and Markowski 1996).

Quantitative description of the modified Münch model

In this section, we present a quantitative analysis of the modified Münch model. We consider the model within the framework of the integrated water translocation system shown in Fig. 1. Using the notation as in the Figure, the volume fluxes J_{v1} and J_{v2} can be written as:

$$J_{v1} = L_{p1}\sigma_1 RT(C_1 - C_{01}) - L_{p1}(P_1 - P_{01}) \quad (2)$$

$$J_{v2} = -L_{p2}\sigma_2 RT(C_2 - C_0) + L_{p2}(P_2 - P_{02}) \quad (3)$$

where L_{p1} , L_{p2} are the filtration coefficients, $\sigma_1 = 1$, σ_2 are the reflection coefficients, P_1 , P_{01} , P_2 , P_{02} are hydraulic pressures, C_1 , C_{01} , C_2 , C_{02} , C_0 are concentrations (see Fig. 1) where C_0 is the concentration in the vicinity of osmometer B (i.e. in the stelar apoplast of the root). Flux J_{v1} permeating osmotically to the inside of osmometer A generates mechanical pressure P_1 there. The pressure forces water and assimilate flow J_{vp} (mass transport) along the conducting ducts of phloem (represented by R_p). Denoting the hydraulic conductivity of phloem L_p , we obtain

$$J_{vp} = L_p \Delta P \quad (4)$$

where

$$\Delta P = P_1 - P_2 \quad (5)$$

We assume that the amount of water accumulated in the parts of plant where assimilates are used (osmometer B) is much smaller than the amount of water pumped across membrane M_2 (reverse osmosis). Then, the following continuity law holds (Kargol 1996)

$$S_1 J_{v1} = S_p J_{vp} = S_2 J_{v2} \quad (6)$$

where S_1 , S_2 are active surfaces of membranes M_1 and M_2 , S_p is the active cross-section area of the conducting elements of phloem. From (2)–(6) we get the following expression for the phloem mass transport

$$S_p J_{vp} = \mathcal{L} [RT(C_1 - C_{01}) - \sigma_2 RT(C_2 - C_0)] + \mathcal{L}(P_{01} - P_{02}) \quad (7)$$

where \mathcal{L} is given by

$$\mathcal{L} = S_p L_p L_{ps} (S_p L_p + L_{ps})^{-1} \quad (8)$$

and

$$L_{ps} = S_1 L_{p1} S_2 L_{p2} (S_1 L_{p1} + S_2 L_{p2})^{-1} \quad (9)$$

The quantity $S_p J_{vp}$ is the volume of water and assimilates transported in phloem *per unit time*. As eq. (7) shows it is a function of concentrations C_1 , C_{01} , C_2 , C_0 and pressures P_{01} , P_{02} . The value of C_1 depends on the photosynthesis rate, active transport j^* (see Fig. 1) and the rate of assimilate transport from osmometer A through the tube R_p . On the other hand, concentration C_2 depends on the rate of assimilate usage by a plant and the speed of their transport through membrane M_2 to the outside of osmometer B. One might assume that the transport across M_2 may be both active and passive. As we show below the latter determines concentration C_0 .

The Munch model we consider functions (i.e. the flux J_{vp} flows from osmometer A to B) if

$$RT(C_1 - C_{01}) > (P_1 - P_{01}) \quad (10)$$

$$\sigma_2 RT(C_2 - C_0) < (P_2 - P_{02}) \quad (11)$$

and

$$\Delta P = P_1 - P_2 > 0 \quad (12)$$

Condition (11) means that reverse osmosis takes place on membrane M_2 . Assuming $\sigma_2 < 1$, in addition to the volume flux J_{v2} there is a solute (assimilate) flux j_2 . It can be written as:

$$j_2 = \omega_2 RT(C_2 - C_0) + (1 - \sigma_2) \frac{C_2 + C_0}{2} J_{v2} \quad (13)$$

Dividing (3) by (13) we get:

$$\frac{j_2}{J_{v2}} = \frac{\omega_2 RT(C_2 - C_0)}{L_{p2}[(P_2 - P_{02}) - \sigma_2 RT(C_2 - C_0)]} + (1 - \sigma_2) \frac{C_2 + C_0}{2} \quad (14)$$

One can show (Kargol 1996):

$$\frac{j_2}{J_{v2}} = C_0 \quad (15)$$

This relation results from the following rearrangements:

$$\frac{j_s}{J_v} = \frac{j_s}{j_s \bar{V}_s + j_w \bar{V}_w} = \frac{\frac{\Delta m_s}{S \Delta t}}{\frac{\Delta m_s}{S \Delta t} \bar{V}_s + \frac{\Delta m_w}{S \Delta t} \bar{V}_w} = \frac{\Delta m_s}{\Delta V} = \frac{\Delta m_s}{V} = C_0$$

where Δm_s and Δm_w are masses (of solute and of the water), \bar{V}_s and \bar{V}_w are the molar volumes.

Then, eq. (14) can be rewritten as:

$$C_0 = \frac{\omega_2 RT(C_2 - C_0)}{L_{p2}[(P_2 - P_{02}) - \sigma_2 RT(C_2 - C_0)]} + (1 - \sigma_2) \frac{C_2 + C_0}{2} \quad (16)$$

It is a simple quadratic equation in C_0 :

$$\alpha C_0^2 + \beta C_0 + \gamma = 0 \quad (17)$$

where

$$\begin{aligned} \alpha &= L_{p2} \sigma_2 RT (1 + \sigma_2) \\ \beta &= L_{p2} [(P_2 - P_{02})(1 + \sigma_2) - 2\sigma_2 RT C_2] + 2\omega_2 RT \\ \gamma &= L_{p2} \sigma_2 (1 - \sigma_2) [\sigma_2 RT C_2 - (P_2 - P_{02})] - 2\omega_2 RT C_2 \end{aligned}$$

A physical solution to (17) is:

$$C_0 = \frac{-L_{p2} [(P_2 - P_{02})(1 + \sigma_2) - 2\sigma_2 RT C_2] - 2\omega_2 RT + \sqrt{\Delta}}{2L_{p2} \sigma_2 RT (1 + \sigma_2)} \quad (18)$$

where

$$\Delta = \{L_{p2}[(P_2 - P_{02})(1 + \sigma_2) - 2\sigma_2 RTC_2] + 2\omega_2 RT\}^2 - 4L_{p2}\sigma_2 RT(1 + \sigma_2)\{L_{p2}C_2(1 - \sigma_2)[\sigma_2 RTC_2 - (P_2 - P_{02})] - 2\omega_2 RTC_2\}$$

Expression (18) gives an explicit dependence of C_0 on the membrane transport parameters (L_{p2} , σ_2 , ω_2), the concentration C_2 and the hydraulic pressure $\Delta P_2 = P_2 - P_{02}$. It follows that if $\sigma_2 = 1$, then $C_0 = 0$ (since then $\omega_2 = 0$). If, on the other hand, $\sigma_2 = 0$, then $C_0 = -\gamma/\beta = C_2$. As it is easy to see C_0 decreases with the increasing σ_2 .

Now, it should be stressed that concentration C_0 (concentration of solution in the apoplast of the root axial cylinder) appears both in Eq (18) and (7). Taking together, the equations constitute a non-linear mathematical relation that describes the phloem transport of water and assimilates. Due to that nonlinearity it gives, broader than previously, interpretational possibilities of the considered transport (Kargol 1994, Kargol and Kargol 1996, Kargol 1996). That broadening of the possibilities refers to just regulation of the phloem transport by external factors (just *via* changes in C_0).

Discussion and final conclusions

In this work, the Munch model was considered as a component of the so-called integrated system of water translocation in the plant over long distances. A number of modifications and supplements were introduced to that model to make it more adequate to biological reality. They refer mainly to assigning a biological interpretation to membranes M_1 and M_2 of osmometers I and II. Sufficient to say that membrane M_1 imitates water transport pathway that begins at the leaf apoplast and ends at sieve tubes that initiate the phloem water tracts in leaves. Whereas membrane M_2 (osmometer II) represents, with respect to the plant root, water transport pathway from the inside of the root sieve tubes to the apoplast of the axial cylinder.

In the present work, also a mathematical description was made of transport processes occurring in it. The main new element in it is adaptation of a new mathematical treatment of reversed osmosis (proposed recently (Kargol 1997)) for the description of transport processes across membrane M_2 of osmometer B. Owing to that the interpretational possibilities of the Munch model were enriched (*via* formula 18). In order to explain it somehow, let us assume for instance that the membrane M_2 has the following transport parameters $L_{p2} = 3.9 \times 10^{-12} \text{ m}^3/\text{N s}$, $\sigma_2 = 0.015$ and $\omega = 46 \times 10^{-10} \text{ mol/N s}$. Taking these data and the values of the other quantities in formula (18) $R = 8.3 \text{ N m/mol K}$, $T = 300 \text{ K}$ and $C_2 = 100 \text{ mol/m}^3 = 100 \text{ mmol/l}$, a numerical relation was found between concentration C_0 and pressure difference $\Delta P_2 = (P_2 - P_{02})$. The curve in Fig. 2 presents that dependence, and its course indicates that concentration C_0 depends (decreases) strongly on pressure difference ΔP_2 for its small values. For larger values of the difference

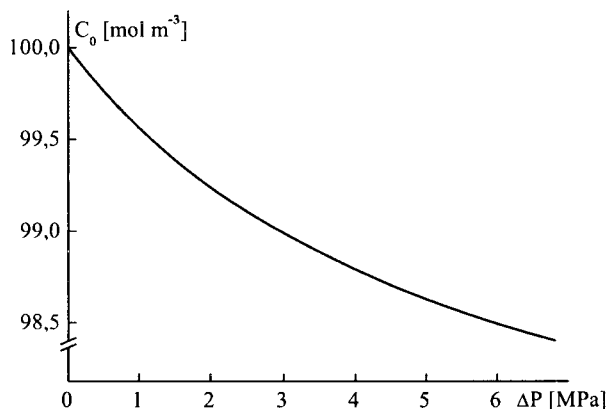


Figure 2. Dependence of concentration C_0 in apoplast of the root axial cylinder on mechanical pressure difference (see Fig 1)

the dependence $C_0 = f(\Delta P_2)$ gets progressively weaker. Plots of this kind are the steeper the larger the values of reflection coefficients of the membranes (10). For σ approaching unity the concentration C_0 goes to zero.

That example indicates that on taking into account reversed osmosis in the Munch model its functioning ceases to be determined by linear processes only. This means that the mathematical description of the Munch model developed here should exhibit a more complicated functioning than previously thought (Kargol 1994, Kargol 1996). In particular, this may concern new interpretational possibilities as regards controlling the phloem transport of water and assimilates in the plant

The developed Munch model description presented here will constitute the basis of our detailed and complex simulation studies. Such studies will be possible after collecting the necessary numerical data obtainable on biological material, concerning water translocation (and solutes contained in it) in the plant on all long distances. At present, we are collecting such data.

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