

ABOUT THE BIOPHYSICAL MECHANISMS OF THE LONG-DISTANCE WATER TRANSLOCATION IN PLANTS

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A b s t r a c t. The present work discusses the basic mechanisms of water translocation on the so-called long distances. The translocation includes: transfer of water and mineral components across the root (from the soil to the xylem tracheary elements); transport of water through the xylem (along the plant); permeation of water across the leaf tissue, where most of it evaporates into the atmosphere; and the phloem transport of water and assimilates. The last type of long-distance transport of water occurs in opposite direction to its xylem transport. It has been shown that the long-distance transport of water is mutually connected at its various stages, and their mechanisms are numerous and operative in various parts of the plant. Especially broad coverage has been given in this work to further development of the so-called graviosmotic hypothesis, according to which water might be transported along the xylem vessels by using the graviosmotic mechanisms. This presentation is concerned with that version of the hypothesis which is based on the gravidiffusive mechanism of graviosmosis.

Key words: plants, water, mineral components, assimilates, transport mechanisms

INTRODUCTION

The long-distance translocation of water and solutes in plants can be, in principle, divided into four stages [1,5,10,12-14,24,31,32]. In the first of them, water is taken from the soil and transported together with its mineral component across the root (radially) to the xylem tracheary elements. In the second stage, water movement occurs along the xylem to the leaves. In the third stage, water permeates across the leaf tissue and most of it evaporates

into the atmosphere from the mesophyll cells and leaf cuticle. The rest of the water, a relatively small amount, is transferred to the phloem where, together with assimilates, it is transported along the plant; in principle in the direction opposite to its transport in the xylem. The phloem transport constitutes, so to say, the fourth stage of the long-distance translocation of water.

It should be added here that there are many mechanisms of long-distance water translocation which are varied and operative in various parts of the plant. Thus, for instance, in the Dixon-Renner transpiration-cohesion theory, the main driving force site of water transport across the root, of its xylem transport and translocation through the leaf tissue is the leaf [24,31,32]. Instead, the root pressure theory states that the driving force for the cross-root water transport is situated in the root itself; which, moreover, can push water up the xylem to a certain height, by the principle of root pressure [6,10,16,24,27,30-32, and others].

In the realm of the so-called graviosmotic hypothesis of the xylem rise of water, elaborated by Kargol and Przystalski [10,13,23], it is postulated that certain mechanisms (graviosmotic mechanisms) may operate in the xylem vessels. While according to the Munch concept [10,24,31,32, and others] (modified recently by Kargol [14]), and also according to other

theories, the mechanisms that drive the phloem transport of water are located within leaves, phloem and also in places where assimilates are utilised. In general, it should be emphasized that there are in fact many mechanisms of the long-distance transfer of water in plants, they are varied and operate in various parts of the plant. It should also be noted that water transports at those various stages are more or less mutually connected, and subject to various control processes [10,13,14,23].

In view of the current knowledge of the transport, and allowing for the structural complexity of the plant (as regards the water pathways of the various stages) the transport of water should be considered as exceptionally complex. No wonder that it is known a little and still a current object of investigation.

The present work discusses the basic biophysical mechanisms of water transport in all the above mentioned stages. A particular treatment has been given to gravidiffusion, having in view the further development of the hypothesis of the xylem graviosmotic water transport in plants. Our interest in the long-distance translocation of water arises, among others, from the investigation we plan on the biophysical principles of setting and growing of plant bulbs. The present work is a kind of introduction to those studies.

MEMBRANE THEORIES OF RADIAL TRANSPORT OF WATER IN ROOTS

In the biological literature [10,16,19,26,29-32, and others] it is stated that there are three major barriers for water transport on the radial pathway of the root. They are denoted by numbers 1, 2 and 3 in Fig. 1. The first of them is located in the epidermis. The second is an epidermal layer of cells (due to the presence of the casparian strip). The third is present at the entrance to the xylem tracheary elements.

Treating these barriers as membranes, a number of membrane models were devised that imitate the radial pathway of water in the root. The simplest of them is the one-membrane model proposed by Fiscus, subsequently developed by Steudle *et al.* [27,28], Kargol

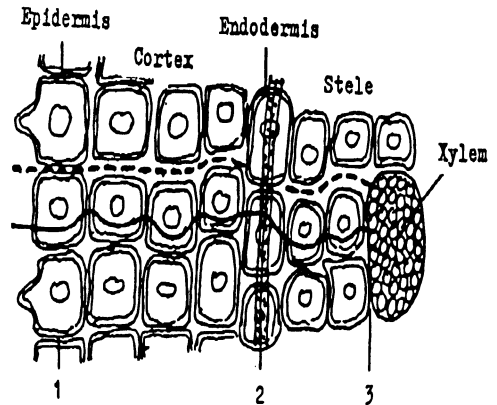


Fig. 1. Fragment of root cross-section.

[12,15,16], and Kargol *et al.* [18]. In this model, shown schematically in Fig. 2, the three above mentioned barriers have been replaced by one membrane M of filtration coefficient L_p , reflection coefficient $\bar{\sigma}$ and permeability coefficient $\bar{\omega}$. It is interesting, from the biophysical point of view, that it was possible, in suitable experimental investigations, to determine mean values of the parameters L_p , $\bar{\sigma}$ and $\bar{\omega}$ for roots of some plants and some substances [6,27,28]. Thus it was possible to describe the osmotic, hydromechanical and diffusive properties of a model root by using the Kedem-Katchalsky formalism. Appropriate equations of the formalism for volume flux J_v and solute flux j_s have the form:

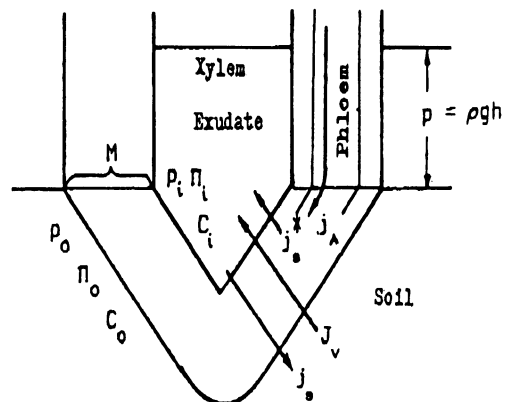


Fig. 2. One-membrane model of the root (explanations in the text).

$$J_v = L_{pr} \bar{\sigma}_r RT(C_i - C_o) - L_{pr}(p_i - p_o), \quad (1)$$

$$j_s = -\bar{\omega} RT(C_i - C_o) + (1 - \bar{\sigma}_r) \frac{C_i + C_o}{2} \cdot J_v \quad (2)$$

where C_i , C_o - concentrations; p_i , p_o - mechanical pressures, R and T - the gas constant and absolute temperature.

From these equations it follows that the fluxes J_v and j_s are functions of both concentration differences ($C_i - C_o$) and the pressure difference ($p_i - p_o$). Fundamental to the model are thus osmosis, diffusion and hydromechanical flows. The one-membrane model of the root radial water pathway describes flows that occur in accordance with concentration gradients only, i.e., from higher to lower concentration. That simple model is only a relatively coarse approximation of reality, as the structures conducting water in the root are immensely complicated. Nonetheless, the model explains relatively well certain biophysical mechanisms that drive water across the root. It explains also the mechanism of root pressure generation that drives water against the hydrostatic pressure $p = \rho gh$ (see Fig. 2). According to the model, root pressure is induced by the osmotic principle, as the coefficient σ_r is larger than zero. The model also allows water transport driven by the pressure $p_i < p_o$. According to the Dixon-Renner theory, presented below in detail, the tension p_r may develop by the cohesion-transpiration principle.

The above presented biophysical concepts of water transport across the root, from the soil to the xylem tracheary elements, explain water transfer occurring in accord with its concentration gradient only. There are, however, experimental data showing that water in the root can be transported isoosmotically (i.e., at zero concentration gradient) and opposite to the concentration gradient.

In order to explain that phenomenon, Ginsburg [7] worked out in 1971 a two-membrane model to imitate the symplastic pathway of water, comprising the epidermis, bark and endodermis. That model is shown schematically in Fig. 3. Ginsburg assumed that on the

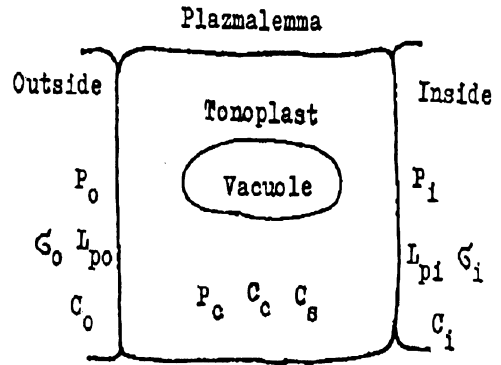


Fig. 3. Two-membrane model by Ginsburg [7] that imitates the symplastic water pathway across the root.

considered symplastic pathway water encounters two barriers. One of them is the border of the root cytoplasmic continuum, from the soil side, which is the epidermis. The other is the endodermal layer. Ginsburg assigned to the barriers the significance of membranes M_o and M_i with filtration coefficients (L_{po} and L_{pi}) and reflection coefficients (σ_o and σ_i), respectively. Next he assumed that the cytoplasmic bridges are permeable to water and solutes. Owing to that, and to the natural movement of cytoplasm in the cells of the bark, one may assume that there are no concentration gradients within its area. The presented model is thus a two-membrane system in which the membrane M_o separates two solutions of concentrations C_o and C_c , and the membrane M_i - solutions of concentrations C_c and C_i . The vacuole present in the model represents vacuoles of the respective cells.

Performing, with respect to Ginsburg model, the same analytical considerations as in papers [3,10,19,22] for a typical two-membrane model, one may obtain the following equations for osmotic volume flux:

$$J_v = -L RT(\sigma_i - \sigma_o) C_o + L RT(\sigma_i C_i - \sigma_o C_o) \quad (3)$$

where $L = L_{po} L_{pi} (L_{po} + L_{pi})^{-1}$.

Analysing this equation, it is easy to show that, depending on the concentration C_i (which can be regulated by the active solute flux j_s^*)

the volume flux J , can occur according to concentration gradient (when $C_o < C_i$), in isosmotic layers (when $C_o = C_i$) and opposite to concentration gradient (when $C_o > C_i$). These conclusions, when referred to water transport across the root, constitute the main result of Ginsburg model.

The model presented, which imitates the symplastic water pathway across the root, is able to explain pumping of water to a certain height h^{\max} against hydrostatic pressure $\Delta p < \rho gh^{\max}$. It means that within a root, that operates according to this model, a root pressure Δp is generated (by the osmotic principle). This model has been developed considerably by Kargol and Suchanek [19].

There have been more membrane models developed [16,29,30]. We are not going to present them here, however; adding that besides passive there are postulated also active mechanisms of water transport. The existence of the latter is highly improbable.

THEORIES OF XYLEM WATER MOVEMENT IN PLANTS

Until now many biophysical theories of xylem water transport in plants have been elaborated. The most accepted of them are: the root pressure theory [1,6,12,16,18,19,24,26,27,31,32 and others], the transpiration-cohesion theory [10,13,24,26,31,32] and the graviosmotic theory [9,10,13,23]. The first of them, i.e., the root pressure theory, has already been presented above. According to this theory, in the root develops osmotically a certain mechanical pressure, which is bigger than the atmospheric pressure. Owing to this, water in the plant can be elevated through xylem to a height h (against the force of gravity).

Thus, in the following, we shall discuss the remaining theories, i.e., the transpiration-cohesion theory and the graviosmotic theory.

Transpiration-cohesion theory of Dixon-Renner

The xylem transport occurs through vessels and/or tubes. In a mature state those tracheary

elements are lignified and have good hydraulic permeability. The transport occurs in continuous conducting tubes which branch along the length of the plant, and thus the conducting bundle becomes thinner and thinner. Conducting bundles branch also within leaves, thinning gradually until they become single vessel elements. Further on, water permeates across the leaf wall and evaporates into the atmosphere [10,24,26,31,32, and others].

When talking about evaporation into the atmosphere, mostly from the surface of mesophyll cells, we mean evaporation of water contained in pores of the wall of these cells. In the pores the water surface forms a concave meniscus. So, due to the forces of surface tension, an additional negative pressure called capillary pressure is generated under the surface. Due to that pressure water is elevated up the xylem as high as the plant grows. The pressure can be calculated from the formula:

$$\Delta p = \rho gh = \frac{2u}{r} \quad (4)$$

where u - surface pressure, r - mean pore radius in walls of mesophyll cells. Assuming $u = 7.5 \cdot 10^{-2}$ (Nm⁻¹) and $r = 10^{-9}$ (m), we get $\Delta p \approx -30$ (atm).

It should be added here that microscopic studies have confirmed the existence of pores of this radius in the walls of mesophyll cells [31]. The negative pressure thus calculated is sufficiently large to elevate water up the xylem to great heights. Transport of water due to that pressure, i.e., by the principle of Dixon-Renner theory, only occurs when there is transpiration.

The hypothesis of the graviosmotic transport of water along the xylem vessel and its discussion

The fundamentals of the graviosmotic xylem transport of water have been presented in papers by Kargol and Przystalski [9,10,23]. These postulate that water might be raised up the xylem vessels, at the proper phase of their development, by the principle of the graviosmotic phenomenon. The hypothesis was first

based on convective graviosmosis and connected effects such as: pumping of water against the force of gravity, water circulation, asymmetry of the graviosmotic transport and its amplification [10,13,16,23]. Recently, the graviosmotic hypothesis has been considerably developed in [13], where the version based on gravidiffusion is considered.

In the present work we present both versions of the hypotheses. Having in view further development of the graviosmotic hypothesis based on the gravidiffusive mechanism, we have presented in this work some of our new studies on the process of gravidiffusion.

THE ESSENCE OF GRAVIDIFFUSION

Fundamental for the graviosmotic phenomenon may be either convection or gravidiffusion. Hence we distinguish between convective and gravidiffusive graviosmosis.

In order to present the essence of the convective graviosmotic phenomenon (first noticed in 1971 by Kargol and Przestalski [9,21]), let us take into account the membrane system shown in Fig. 4a,b. It is composed of two selective membranes (M_1, M_2) with the same permeability parameters ($L_{p1} = L_{p2} = L_p, \sigma_1 = \sigma_2 = \sigma$ and $\omega_1 = \omega_2 = \omega$). Let the membranes separate three compartments, of which the external ones are filled with a solution of concentration C_o , and the middle one with

concentration C_m . It is obvious that the system, when situated in position (a) of Fig. 4a, is osmotically symmetrical. The differences in osmotic pressures, $\Delta\pi_1$ and $\Delta\pi_2$, compensate each other ($\Delta\pi_1 = \Delta\pi_2$). Also the differences in mechanical pressures on the membrane compensate ($\Delta p_1 = \Delta p_2$). This is confirmed by the absence of volume flow in the system ($J_v = 0$). On reorientating the system relative to the vertical, to position (b), with membranes situated horizontally, it ceases to be osmotically symmetrical. A certain resultant pressure difference develops:

$$\Delta\pi = \Delta\pi_1 - \Delta\pi_2 \approx 0 \quad (5)$$

As a result, a non-zero volume flow J_{vg} arises, which is called the graviosmotic flux. The generation of that flow is called graviosmosis, and the systems where such flows occur are called graviosmotic systems [10,13,23]. The graviosmotic flow is directed upwards if solutions with density of increasing concentration are employed (e.g., water solutions of glucose), and downwards - if the solution density decreases with concentration (e.g., water solutions of ethanol). Detailed information about that graviosmosis and connected effects is given in papers [9,10,13,16,21,23]. We shall emphasize here only that any graviosmotic system is able to pump water to a certain height against the force of gravity.

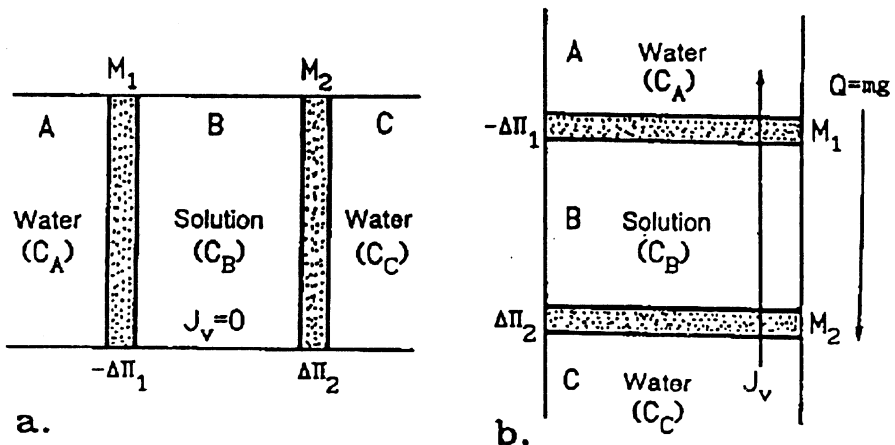


Fig. 4. Two-membrane system in positions (a) and (b).

PHASES OF XYLEM VESSEL DEVELOPMENT

Since the graviosmotic hypothesis refers to the xylem vessels, we shall discuss briefly the phases of development of these tracheary elements. The vessels develop from a column of the meristematic cells. In the process of plant development the cells from which vessels develop first grow broader and sometimes longer. When their growth stops, secondary walls are formed without the building material being deposited on the cross walls. What is more, the walls swell and then material is washed away from them. As a result, the cross walls become loose fibrils. Next, perforations appear and often the cross walls disappear completely. At the same time, protoplasts degenerate and disappear. First, the vacuole increases. At a certain stage the cytoplasm forms a thin layer around the vacuole. The cell nucleus degenerates also and then the protoplasts disappear completely. As an example, Fig. 5 shows the phases A, B, C, D, E and F of development of the conducting vessels of robinia (*Robinia pseudocacia*) according to Eames and MacDaniels, as in [20]. As a result, the vessels in their mature state constitute long watery pathways in the plant of relatively low hydraulic resistance to water.

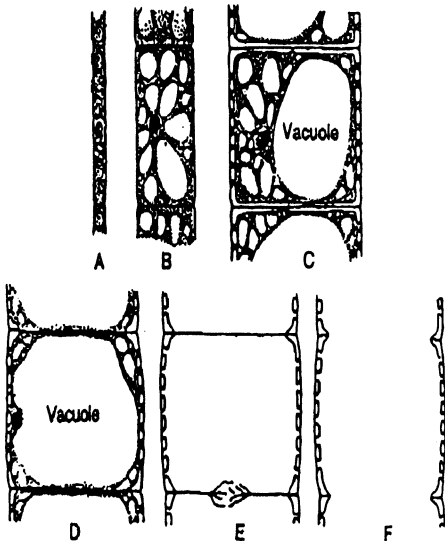


Fig. 5. Phases of robinia xylem vessel development according to Eames and MacDaniels (after Malinowski [20]).

THE BASIS OF THE GRAVIOSMOTIC HYPOTHESIS

In view of what has been said above, one can assume that there exists a phase of the xylem vessel development (phase D) when the cross walls still have osmotic properties, but the protoplasm constitutes only a thin layer around a large vacuole, and does not perform its natural movements. It is on the basis of this phase that the graviosmotic hypothesis of xylem movement of water has been constructed.

In order to present that hypothesis, let us take into account a fragment of the vessel duct illustrated in Fig. 6. Let the respective cells A and B of the duct be just in phase D in which (as mentioned above) one can assume that the protoplasm does not perform its natural movements. Moreover, let the cross walls separating sections A and B still exhibit osmotic properties, i.e., have reflection coefficients σ bigger than zero for the osmotically active substances. Due to the existence of protoplasts one can also assume that active flows J_s^* of solutes are present in the elements of the duct. Those fluxes are denoted as arrows in Fig. 6. Owing to the active flows, one can assume that in, say, sections (vessels) B the solute concentrations

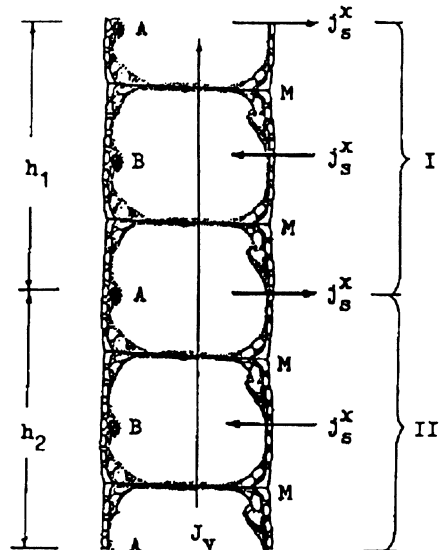


Fig. 6. Fragment of xylem vessel duct.

are greater than in sections A ($C_B > C_A$). In the situation presented, a given fragment of the xylem vessel duct, shown in Fig. 6 (composed of four vessels), can be treated as a system of two joined graviosmotic systems in series (I and II) [10,13,23]. This system is able to transport water against the force of gravity (by the graviosmotic principle) to the height $H = h_1 + h_2$, where h_1 and h_2 are heights of pumping by the respective systems I and II.

In a real plant a single vessel duct is composed of a large number of cells (vessels A and B). Adequately large is also the number of hypothetical graviosmotic systems able to pump water to a suitable large height H .

GRAVIOSMOSIS BY THE GRAVIDIFFUSIVE MECHANISM

As two kinds of graviosmosis are distinguished, i.e., convective graviosmosis [10,13,16, 23] and graviosmosis of gravidiffusive mechanism, two versions of the graviosmotic hypothesis are possible [13]. The former, based on convective graviosmosis, may refer to plants with adequately large xylem vessels only. It has been proven experimentally that the convective graviosmosis may be observed in graviosmotic systems with vessels of inner diameter ($2r$) greater than about 0.35 mm [10]. This is an essential restriction of that version of the hypothesis; mostly because there are relatively few plants with the xylem vessels of such a large size. Here belong such plants like elm, oak, or some species of liana.

In the case of graviosmosis based on the gravidiffusive mechanism there is no such restriction. This type of graviosmosis can operate in small size xylem vessels. This, however, requires further studies related mainly to the process of gravidiffusion in liquids, and thus modified by the force of gravity. Such diffusion was considered by many authors [2,4, 8,13,25].

Now we take the gravidiffusive transport through a horizontally situated membrane M which separates two well stirred solutions of different concentrations. Figure 7 illustrates this in detail.

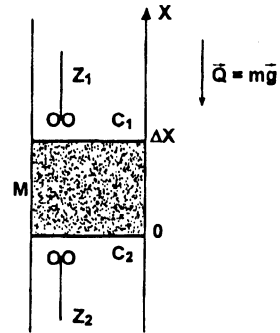


Fig. 7. Membrane system (M - membrane, C_1 , C_2 - concentrations of the solutions, x - membrane thickness, Z_1 , Z_2 - stirrers).

According to the Kedem-Katchalsky formalism, the permeability properties of the membrane are described by the parameters L_p , σ and ω . We are, of course, interested in a membrane for which the σ parameter value is within the interval $0 \leq \sigma < 1$. Then, besides water, also permeates the solute. Let the solute together with its hydration shell have density ρ_s different from water density ρ_w . We can assume that to the solute (within membrane) is applied a non-zero resultant force of the forces of gravity Q and a buoyancy force F_w . That force can be expressed by the formula:

$$F_g = -\left(1 - \rho_w/\rho_s\right)\bar{m}g \quad (6)$$

where \bar{m} is the mass of the solute together with the hydration shell.

That force generates the phenomenon of gravidiffusional migration (gravidiffusion) of the solute. It is 'imposed' on the diffusion process inducing additional flux of solute J_s . The phenomenon of gravitational migration has already been considered in the description of movement of molecules in the field of gravity [2,4,10,13,17,25]. In the work [4] it was assumed that the random force $R(t)$, which occurs in Langevin's equation, on a solute molecule in gravitational field is isotropic. This however, is the case when there is no effective force of gravity on the water molecules. And this condition is met.

The main problem with deriving Kedem-Katchalsky's equations, that allow for the gravidiffusion effect, is formulating proper expressions

for the difference of chemical potentials of solute. In order to solve this problem, let us assume at the outset that the solute molecules in a dilute solution have, from the thermodynamic point of view, properties analogous to the ideal gas. Thus we can assume the following expression for chemical potentials:

$$\mu_s = \mu_s^0(T, P, C_s) + \mu_s^1 \quad (7)$$

where $\mu_s^0(T, P, C)$ is that part of the chemical potential which depends explicitly on temperature (T), pressure (P) and concentration (C) of the solution. The quantity:

$$\mu_s^1 = (\partial U / \partial n_s)_{S, V, n_w} \quad (8)$$

is an additional part of chemical potential connected with the pressure of the field of gravity. The symbol U expresses the potential gravitational energy of solute molecules (corresponding to the force F_g of Eq. (12) in a certain small volume V . Let the symbols n_s and n_w denote the numbers of moles of solute and water contained in that volume, while S - entropy of the solution element of volume V .

We are concerned with a rectangular volume of thickness $2d$, which is positioned horizontally as shown in Fig. 8.

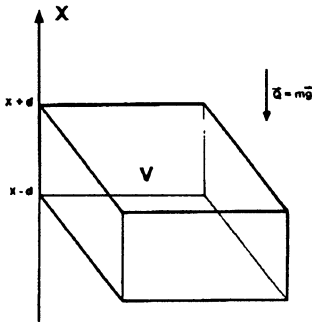


Fig. 8. Elementary volume of solution in the form of a horizontally placed parallelepiped of thickness $2d$.

It is easy to show that the mean gravitational energy of one solute molecule (assuming homogeneous concentration within the volume) is:

$$E_p = mgh(1 - \rho_w / \rho_s) \quad (9)$$

where h is height of column of solution.

Thus the total potential energy of cell solute molecules within the volume V is:

$$U = N_s mgh(1 - \rho_w / \rho_s) \quad (10)$$

where N_s is the number of solute molecules in the volume.

Hence the relation can be obtained:

$$U = n_s N mgh(1 - \rho_w / \rho_s) \quad (11)$$

where N is the Avogadro number.

From the above equations, allowing also for Eqs (7) and (8), we obtain:

$$\mu_s = \mu_s^0(T, P, C_s) + N mgh(1 - \rho_w / \rho_s). \quad (12)$$

Using the equations, we derive the following expressions for differences of chemical potentials on either side of the membrane:

$$\Delta \mu_s = \bar{V}_s \Delta P + \frac{\Delta \pi}{c} + \bar{V}_s \Delta P_G, \quad (13)$$

where

$$\Delta P_G = \frac{N m g \Delta x (1 - \rho_w / \rho_s)}{\bar{V}_s}, \quad (14)$$

and

$$\Delta \mu_w = \bar{V}_w (\Delta P - \Delta \pi) \quad (15)$$

where Δx - membrane thickness, \bar{V}_s , and \bar{V}_w are molar volumes of solute and water, respectively.

The quantity ΔP_G can be called 'difference of gravitational pressures'. However, this quantity has nothing to do with mechanical pressure, as it is applied to solute molecules only.

On making allowance for the above equations, the dissipation function takes the form:

$$\Phi = (J_s' \bar{V}_s + J_w \bar{V}_w) \Delta P + (J_s' / c - J_w \bar{V}_w) \Delta \pi + (J_s' \bar{V}_s) \Delta P_G \quad (16)$$

where J_s' is the solute flux generated by the mechanical and osmotic pressure difference; while J_s'' is the solute flux generated by the gravitational pressure difference on the membrane.

With the notation:

$$J_G = J_s \bar{V}_s \quad (17)$$

the dissipation function can be written:

$$\Phi = J_V \Delta P + J_G \Delta P_G + J_D \Delta \pi, \quad (18)$$

where J_G we call 'gravitational volume flux'.

The phenomenological equations for the fluxes J_V , J_G and J_D are thus as follows:

$$J_V = L_P \Delta P + L_{PG} \Delta P_G + L_{PD} \Delta \pi \quad (19)$$

$$J_G = L_{GP} \Delta P + L_G \Delta P_G + L_{GD} \Delta \pi \quad (20)$$

$$J_D = L_{DP} \Delta P + L_{DG} \Delta P_G + L_D \Delta \pi. \quad (21)$$

From the Onsager relations we have:

$$L_{PG} = L_{GP}, L_{PD} = L_{DP}, L_{GD} = L_{DG}.$$

It can be shown that the total solute flux J_s satisfies the equation:

$$\frac{J_s}{c} = J_V + J_G + J_D. \quad (22)$$

Let us determine the values of ΔP and $\Delta \pi$ from (Eqs (19) and (21)), and then introduce them - together with (Eqs (19), (20) and (21)) - into (Eq. (22)). The result is the following relation:

$$\begin{aligned} \frac{J_s}{c} = & \left(1 - \frac{L_{GD}L_{DP} - L_D L_{GP}}{L_P L_D - L_{DP}L_{PD}} \right) J_V + \\ & \left(1 - \frac{L_{GP}L_{PD} - L_{GD}L_P}{L_P L_D - L_{DP}L_{PD}} \right) J_D + \\ & \frac{\det A}{L_P L_D - L_{DP}L_{PD}} \Delta P_G. \end{aligned} \quad (23)$$

Let us now calculate ΔP and ΔP_G from Eqs (19) and (20), and then put them, together with (19), (20) and (21) into Eq. (22). Now, the following equation results:

$$\begin{aligned} \frac{J_s}{c} = & \left(1 - \frac{L_{GP}L_{DG} - L_G L_{DP}}{L_P L_G - L_{GP}L_{PG}} \right) J_V + \\ & \left(1 - \frac{L_{PG}L_{DP} - L_P L_{DG}}{L_P L_G - L_{GP}L_{PG}} \right) J_G + \\ & \frac{\det A}{L_P L_G - L_{GP}L_{PG}} \Delta \pi \end{aligned} \quad (24)$$

where $\det A$ is the determinant of a matrix formed from the phenomenological coefficients of Eqs (19), (20) and (21).

In the limit of zero gravitational effect, (Eqs (23) and (24) must assume the form of the respective equations without the field of gravity. This leads to the relations:

$$L_{DP}L_{GD} + (-L_D)L_{GP} = 0 \quad (25)$$

$$(-L_P)L_{GD} + L_{PD}L_{GP} = 0. \quad (26)$$

The above set of equations has non-zero solution with respect to L_{GD} and L_{GP} only when the condition is met:

$$L_{PD}L_{DP} - L_D L_P = 0.$$

However, this condition means that:

$$\omega = 0$$

which corresponds to a totally non selective membrane (for which the gravitational flux is also zero). Hence the only solution of Eqs (25) and (26) that have physical sense is:

$$L_{GD} = L_{GP} = 0. \quad (27)$$

From the Onsager relations it follows also that:

$$L_{GD} = L_{PG} = 0. \quad (28)$$

Allowing for relations (27) and (28), the phenomenological equations take the form:

$$J_V = L_P \Delta P + L_{PD} \Delta \pi \quad (29)$$

$$J_G = L_G \Delta P_G \quad (30)$$

$$J_D = L_{DP} \Delta P + L_D \Delta \pi. \quad (31)$$

On the basis of these equations and Eq. (24) we finally get:

$$J_V = L_P \Delta P - \sigma L_P \Delta \pi, \quad (32)$$

$$J_s = \bar{c}(1-\sigma)J_V + \bar{c}L_G \Delta P_G + \omega \Delta \pi. \quad (33)$$

The two equations are just the sought for Kedem-Katchalsky equations that allow for the process of gravidiffusion. The coefficient L_G can by analogy to the coefficient L_P - be called 'coefficient of gravidiffusional filtration'.

Equations (29) and (31) do not contain a term connected with ΔP_G (like Eq. (30) that

does not contain terms connected with ΔP and $\Delta\pi$). This means that the total solute flux J_s across the membrane can be presented as sum of two 'component' fluxes:

$$J_s = J'_s + J''_s, \quad (34)$$

where $J'_s = \bar{c}(J_D + J_V)$ is the solute flux generated by the concentration difference and mechanical pressure difference. The flux $J''_s = \bar{c}J_G$ is the solute flux generated by the field of gravity.

This also means that the fluxes J'_s and J''_s do not affect each other. They can thus be treated as independent fluxes. The above considerations refer to a membrane for which $0 \leq \sigma < 1$. As a matter of course, we were not interested in the case of an ideally selective membrane, for which the flux J_s is equal to zero (as with $\sigma = 1$ the quantity $\omega = 0$).

The problem of gravidiffusion in membrane systems is much more complicated if the solutions separated by the membrane are not stirred by external agents. Its solution is, however, necessary for further development of the hypothesis of gravidiffusional xylem water elevation in plants based on graviosmosis of gravidiffusional mechanism. It is expected to show that a concentration difference (and thus osmotic pressure difference) on a membrane of a given membrane system may depend on the position of the system with respect to the vertical. This effect may be the cause of generating graviosmotic volume flows in a graviosmotic system (Fig. 4b).

BIOPHYSICAL THEORIES OF THE PHLOEM TRANSPORT OF WATER AND ASSIMILATES

The energy supply of living plant cells occurs via assimilates. Those energy-containing substances are produced in the leaves (in the photosynthetic processes occurring there) and distributed throughout the plant via the phloem. A number of hypotheses have been developed that try to explain the mechanisms of their long-distance translocation. Among them one can name the electroosmotic theory, the hypothesis of diffusion and cytoplasm movement, and the Münch theory of flows under pressure

[5,12,14,24,31,32]. We focus here our attention on the last one, mainly because it is the most accepted in the biological literature and because that theory can - as shown by Kargol [14] - be markedly modified and developed due to the Kedem-Katchalsky thermodynamic formalism.

The theory of flows under pressure assumes that assimilates are transported via phloem by being carried along with water (mass flow). Those flows find simple explanation in a membrane model elaborated by Münch [14,24,31,32]. It is composed of two osmometers I and II, connected with a tube R_u , in a push-pull way, and immersed in a solution of the containers N_1 and N_2 of Fig. 9. Tube R_x , which connected the vessels N_1 and N_2 , represents xylem. J_{vo} is the xylem flow.

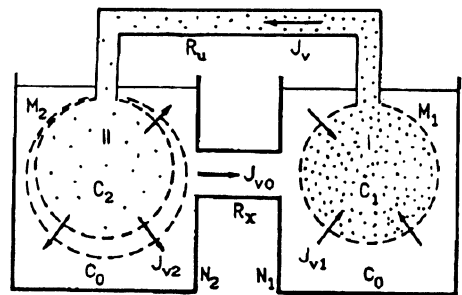


Fig. 9. Münch model.

Let us assume, after Münch, that osmometer I of the model filled with a concentrated solution (C_1) represents in a generalised way the photosynthetic cells of the leaves. Here the assimilates are created. Instead, osmometer II, containing a dilute solution (C_2), represents the places in the plant where assimilates are utilised. They can be, e.g., root cells, fruit cells or bud cells. In the model it is also assumed that the generalized link R_u connecting both hypothetical osmometers is the phloem with sieve tubes and accompanying cells. The connected vessels N_1 N_2 (with solution C_0) imitate the plant apoplast together with the water and solutes contained in it. From the above model it follows, most of all,

that with $C_1 > C_2$ transport of water and assimilates can occur by the osmotic principle. Xylem is represented by tube R_x and J_{v0} is the xylem flow.

MODIFIED MÜNCH MODEL AND ITS MATHEMATICAL DESCRIPTION

The Münch model has been recently modified by Kargol in a substantial way [14]. In that modification it was assumed that membranes M_1 and M_2 of the osmometers differ in their filtration coefficients ($L_{p1} \neq L_{p2}$), reflection coefficients ($\sigma_1 \neq \sigma_2$) and permeability coefficients ($\omega_1 \neq \omega_2$).

It was assumed also that the membranes separate solutions of different concentration, with $C_1 \neq C_2$ and $C_{01} \neq C_{02}$, where C_{01} and C_{02} are concentrations of the solutions in vessels N_1 and N_2 . Also the mechanical pressures near both osmometers were assumed to be different ($P_{01} \neq P_{02}$).

Having in view a detailed investigation of the osmotic properties of the model thus modified, shown schematically in Fig. 10, let us make use of the practical Kedem-Katchalsky equation for the volume flow.

The equation has the form:

$$J_v = L_p \sigma \Delta \pi - L_p \Delta P$$

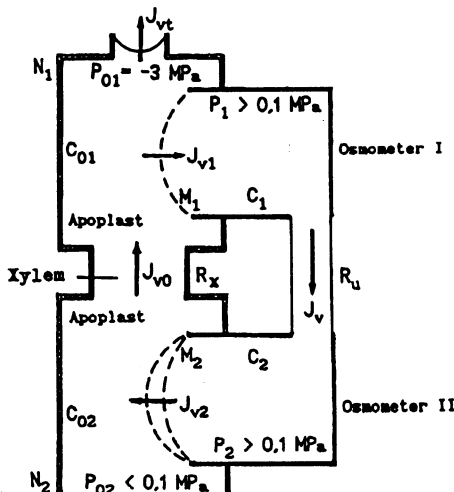


Fig. 10. Münch model modified by Kargol [14].

where J_v - volume flow, $\Delta \pi$ - osmotic pressure difference, ΔP - mechanical pressure difference.

Applying this equation to membranes M_1 we can write:

$$J_{v1}^n = L_{p1} \sum_1^n (\sigma_{1i} \Delta \pi_{1i}) - L_{p1} \Delta P \quad (35)$$

$$J_{v2}^n = L_{p2} \sum_1^n (\sigma_{2i} \Delta \pi_{2i}) - L_{p2} \Delta P \quad (36)$$

where J_{v1}^n, J_{v2}^n - fluxes, σ_{1i}, σ_{2i} - reflection coefficients of the i -th solute, and $\Delta \pi_{1i}, \Delta \pi_{2i}$ - osmotic pressure differences of that solute.

In order to simplify the calculations we assumed [14,16] that there is only one (generalised) solute in the solution. With this and the Vant Hoff's formula for osmotic pressure, the above equations can be written:

$$J_{v1} = L_{p1} \sigma_1 RT (C_1 - C_{01}) - L_{p1} (P_1 - P_{01}) \quad (37)$$

$$J_{v2} = L_{p2} \sigma_2 RT (C_2 - C_{02}) - L_{p2} (P_2 - P_{02}) \quad (38)$$

where C_{01}, C_{02} and P_{01}, P_{02} are concentrations and mechanical pressures in vessels N_1 and N_2 , respectively; which represent apoplast that constitutes the environment of osmometers I and II, R - gass constant, T -temperature.

If the amount of water leaving osmometer II is equal to the amount taken osmotically by osmometer I, then we can write:

$$J_{v1} = J_{v2} = J_v \quad (39)$$

Allowing for this condition and for Eqs (37) and (38), it is easy to obtain the following equation which describes volume flow J_v in the model considered [14,16]:

$$J_v = L [RT \sigma_1 (C_1 - C_{01}) - RT \sigma_2 (C_2 - C_{02}) - (P_1 - P_2)] + L (P_{01} - P_{02}), \quad (40)$$

where $L = L_{p1} L_{p2} (L_{p1} + L_{p2})^{-1}$ and $(P_1 - P_2)$ is the drop of mechanical pressure occurring in tube R_u , whereas $(P_{01} - P_{02})$ - drop of mechanical pressure occurring in vessels N_1 and N_2 which imitate the plant apoplast. Tube R_x represents xylem.

On the basis of formula (40) it has been shown [14,16], among others, that:

1. An increase in pressure P_{01} (caused mainly by decreased intensity of transpiration) induces an increase in the phloem mass transport J_v .
2. With increased pressure P_{02} (which depends mainly on the root pressure) the flux J_v decreases.
3. The flux J_v increases with increasing concentration C_1 , which in turn is the higher the more intensive are the photosynthetic processes in the leaves.
4. The flux J_v depends also on concentration C_2 , which is the smaller the more intensive is the utilisation of the assimilates. As the concentration increases, the flux J_v decreases.

It should be added here that in a real plant the changes in P_{01} and P_{02} occur simultaneously with changes in C_1 and C_2 . In that situation the mass flux J_v is a resultant of changes in all of those quantities [14].

Let us note also that in the situation shown in Fig. 10 the osmometer I is placed above osmometer II. Under these conditions transport through the phloem imitating tube R_u occurs downwards. The model considered will also display the same properties if osmometer I is placed below osmometer II. Then transport through tube R_u is directed upwards. On that basis the transport of assimilates through phloem upwards and downwards can be modelled.

The above considerations, though not complete, supply important information about the osmotic and hydromechanical properties of the modified Münch model. The information, that follows from Eq. (40), makes the model more universal as regards interpretational possibilities referring to the phloem translocation of water and assimilates. It also makes the model more convincing from the biological point of view [14].

CONCLUSION

In this paper we have presented the basic mechanisms which drive the long-distance water translocation in plants, including the uptake of water from the soil, its movement across the root, elevation up the xylem and the phloem transport of water and assimilates contained in it. In the main, further modification and development of the graviosmotic hypothesis of the gravidiffusive mechanism has been of prime concern.

The present work considers in the realm of the Kedem-Katchalsky formalism the gravidiffusive transport across a selective membrane ($0 < \sigma < 1$) which is situated horizontally and separates two well-stirred solutions, the upper one of concentration C_1 and the lower one of concentration C_2 .

Using the Kedem-Katchalsky procedure, an equation for volume flux J_v and an equation for solute flux J_s has been derived.

The considerations on those topics initiate a further study we plan on the gravidiffusive transport in membrane systems with no external stirring agents. The problems dealt with in this work constitute an introduction to the investigation we plan on the basic problems of the biophysics of bulbing and bulb growth in plants.

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