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MODIFICATION OF INTEGRATED SYSTEM OF LONG-DISTANCE TRANSPORT OF WATER IN PLANTS. WHERE THE PLANT HAS ITS HEART?

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This paper presents further attempts at modifying the integrated system of water transport in the plant on long distances. In principle, the modification is concerned with Münch model which is incorporated into the integrated system. That model of the mass flow of assimilates along the phloem is the coupling element for the long-distance water translocation in the plant. The main objective of the modification is to make Münch's model and the whole integrated system closer to the biological reality. On the basis of the investigations an attempt has been made to answer the question where the plant has its heart and how it functions.

INTRODUCTION

The long-distance translocation of water in the plant can be (according to the so-called integrated system of translocation elaborated by M. Kargol and A. Kargol (1996; Kargol, 1996; Kargol, 1994) divided into four interconnected stages. In the first stage water is moved across the root (along the radial path) from the soil to the xylem of the axial cylinder. In the second, water is transported (usually elevation) along the xylem from root to leaves. In the third stage water permeates across the leaf tissue, mainly through the apoplastic channel. Most of that water reaches mezophil cells walls and leaf cuticules, whence it evaporates into the atmosphere. The rest of the water, a relatively small amount, is taken up from the apoplast by the leaf cells. From there water and assimilates, created in photosynthetic cells, are moved into sieve tubes that initiate the water ducts of phloem. Next, the water with assimilates is transported along the plant through xylem, which constitutes the fourth stage of its long-distance translocation, to places where the assimilates are utilised. In the original version of the integrated system by M. Kargol and A. Kargol (1996; Kargol, 1996; Kargol, 1994) the element that connected water movement in the respective stages was the classic Münch's model, which is the basis of the Münch theory (called also the theory of mass or pressure-induced flow) explaining the biophysical basis of the phloem transport of water and assimilates (Kargol, 1994; Salisbury & Ross, 1969; Wilkins, 1969; Ziegler, 1977; Mengel & Kirkby, 1980).

That model constitutes two osmometers connected in a push-pull fashion by a tube that imitates the phloem elements of the plant. According to Münch's theory, one of the osmometers represents the leaf photosynthetic cells, i.e. places where assimilates are created (sources). Whereas the second osmometer imitates places where assimilates are utilised (sinks). The model has been properly incorporated into the integrated model of long-distance translocation of water in the plant (Kargol & Kargol, 1996; Kargol, 1996; Kargol, 1994).

It should, however, be emphasised here that the model in its primary form (as qualitatively correct from the biophysical point of view) was, however, substantially away, in its quantitative aspect, from the biological reality. It was also too general from the point of view of that reality. However, it has crucial significance for grasping the interconnections in plant water transport on various long distances. The above mentioned reservations arise mainly because the photosynthetic cells (represented by the first osmometer of the Münch model) have a too low turgor pressure to induce the phloem water transport on the scale found in the plant. Hence, definite modifications had to be made in the classical version of Münch's model. They should in the first place make allowance for the fact that there is a very large mechanical pressure in the leaf apoplast (relative to atmospheric pressure), which can reach –3 MPa and also that the mechanical pressure in sieve tubes (initiating the water ducts of phloem) may reach +3 MPa (Kargol *et al.*, 2001; Pitman, 1982; Salisbury & Ross, 1969; Wilkins, 1969). Such modifications we introduced in the previous paper (Kargol *et al.*, 2001).

They address not only the pressures but also postulate possible routes and mechanisms for inflow of water and assimilate into the sieve tubes. However there still remained the problem of detailed functioning of representation of the second osmometer of Münch's model embedded in the integrated system. And that is the objective of the present paper. A detailed discussion of the problems occurring here is in the next section.

THE INVESTIGATED PROBLEMS AND ATTEMPTED SOLUTION

Having in view detailed presentation of the research problems of this work and their attempted solution, let us begin with the integrated system of long-distance translocation of water in the plant presented in (Kargol, Suchanek & Kargol, 2001). It is illustrated in Fig. 1. Already there the system is substantially modified with respect to its original version formulated by M. Kargol and A. Kargol (1996; Kargol, 1996; Kargol, 1994). At the basis of the system are biophysical mechanisms of active transport of water in the plant that fit into the realm of the membrane theories of root pressure (e.g. Amin, 1986; Anderson, 1976; Fiscus & Kramer, 1975; Fiscus, 1975; Fiscus, 1986; Fiscus, 1989; Ginsburg, 1971; Kargol & Suchanek, 1990; Kargol, Markowski, Suchanek & Przestalski, 1993; Kargol, 1992a; Katou & Taura, 1989; Katou, Taura & Furumoto, 1987; Pitman, 1982; Steudle, Oren & Schultze, 1987; Taura, Iwaikawa, Furumoto & Katou, 1988; Tyree, 1973; Tyree, 1970), and the transpiration-cohesion theory of Dixon and Renner, developed by A. Kargol (1996), the graviosmotic theory of A. Kargol and Przestalski (Kargol, 1978; Kargol, 1992b; Przestalski & Kargol, 1987) and Münch's theory of phloem transport of water and assimilates, developed and modified by M. Kargol and coworkers (Kargol *et al.*, 2001; Kargol, 1994).

The integrated system presented here (Fig. 1) represents the whole plant. According to the system (like in its former versions (Kargol & Kargol, 1996; Kargol, 1996; Kargol *et al.*, 2001; Kargol, 1994) the long-distance water transport in the plant has been divided into four linked stages. They are denoted as follows:

I radial transport in the root
II xylem transport along the plant
III water translocation in leaves and its evaporation to the atmosphere
IV phloem transport.

Volume fluxes of water and assimilates in the respective stages are denoted as J_{pr}, J_{vx}, J_{vA}, J_{vp}, whereas the flux of transpirated water is J_{vt}.

It was also assumed that the hydraulic conductivities at the respective stages are L_{pr}, L_{px}, L_{pA} and L_p (Fig. 1).

The element that connects water transport at the respective stages is, according to the concept by M. Kargol and A. Kargol (1996; Kargol, 1996; Kargol *et al.*, 2001; Kargol, 1994), the Münch model which explains the biophysical basis of the floem transport of water and assimilates. That model consists of two osmometers *A* and *B* connected in a push-pull way by a tube R_p which imitates the phloem conducting elements. When modifying the model it was assumed in (Kargol *et al.*, 2001) that the inside of osmometer *A* does not represent (in a generalized way) the photosynthetic cell of the leaf (i.e. places where assimilates are created, as postulated by Münch), but the inside of sieve tubes at the start of phloem water ducts.

Membrane M_1 of the osmometer separates solutions C_1 from C_{01}, where C_1 is concentration of solution in sieve tubes at the start of phloem water ducts, and C_{01} — concentration of solution in the leaf apoplast. The solutions are under mechanical pressures P_1 and P_{01} (see Fig. 1) which can reach values up to +3 MPa and –3 MPa (Kargol, 1994; Salisbury & Ross, 1969; Wilkins, 1969; Kargol *et al.*, 2001). Operation of that osmometer with respect to the plant (including water and assimilates transport to the inside of leaf sieve tubes) was extensively explained in paper (Kargol *et al.*, 2001).

A still open question, that require detailed analysis and explanations, constitutes the operation of osmometer *B*, which according to Münch imitates the place were assimilates are utilised. According to Fig. 1 that place is the plant root (root system). It should be explained here that there are such periods in the plant vegetation when the root system is indeed the main „receiver" of assimilates.

Modifying and specifying the operation of that osmometer we assume that its interior (containing assimilates solution of concentration C_2 under pressure P_2) represents the interior of the sieve tubes that terminate the water ducts in phloem. Whence, across the membrane M_2, water together with assimilates is, within the volume flux J_{v2}, transported to nearest cells owing to reversed osmosis, especially to the area of the axial cylinder apoplast which surrounds the phloem conducting

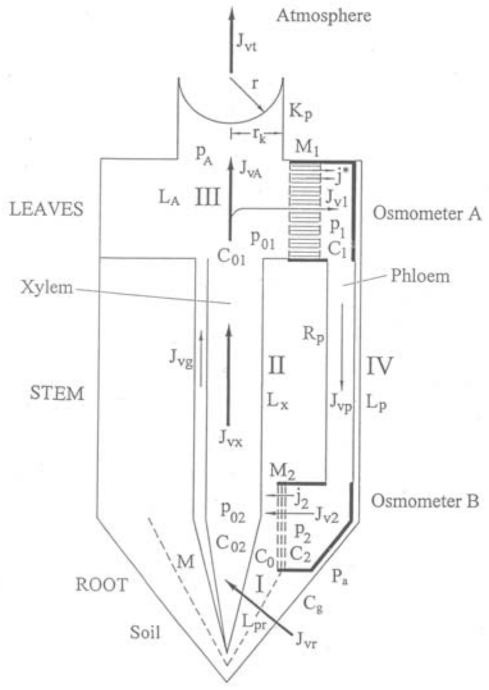

Fig. 1. Scheme of the integrated system of water translocation in the plant, after (Kargol, Suchanek & Kargol, 2001), (Description in the text).

elements.It was assumed that assimilates concentration in the phloem area is C_0 (Fig. 1). Thus membrane M_2 imitates in the plant the membrane and cell wall of the root sieve tubes (terminating here the phloem water ducts).

This is illustrated in detail in Fig. 2 where root cross section is represented in its vascular region. This cross-section was made on the basis of the literature we had access to (e.g. Anderson, 1976; Fiscus, 1989; Ginsburg & Ginsburg, 1971; Pitman, 1982; Steudle *et al.*, 1987; Taura *et al.*, 1988; Tyree, 1973; Wilkins, 1969; Ziegler, 1977; Zimmerman, 1971). In should be added here that assimilates from the near-phloem region of the axial cylinder apoplast (at concentration C_0) are absorbed actively by cells nearest to the cylinder. Moreover, the assimilates are further distributed to all living cells of the root. And this, we think, occurs via the symplastic route.

However the water transported (in J_{v2}) to apoplast of the axial cylinder is then together with water of the flux J_{vr} (i.e. water moved through the radial path of root) taken by the xylem tracheary elements of axial cylinder and next transported (elevated) along the plant. This state of affairs means that water circulates inside the plant. So one can ask where the plant's heart is. An attempt at answering this question is made in the appendix of this paper.

MATHEMATICAL DESCRIPTION OF THE FLUXES

Let us now consider the basic problem of the mathematical description of volume and assimilates flows in the realm of the long-distance water translocation considered here. In that task we'll be using the mechanistic transport equations by M. Kargol and A. Kargol (2000; Kargol, 2001; Kargol & Kargol, 2003). The equations have the form:

$$J_v = J_{VM} = L_p \Delta P - L_p \sigma \Delta \Pi, \qquad (1)$$

$$j_s == j_{SM} = \omega_d \Delta \Pi + (1-\sigma)\bar{c}\Delta P, \qquad (2)$$

where: J_v and j_s - volume flux and solute flux, respectively; L_p, σ and ω_d - coefficients (filtration, reflection and diffusive permeation) ΔP and $\Delta\Pi$ - pressure differences (mechanical and osmotic), and $\bar{c} = 0.5(C_1 + C_2)$ - mean value of concentrations $C_1$and C_2.

A special advantage of the equations is their total interpretational clarity, which cannot be said about the phenomenological Kedem-Katchalsky equations (Katchalsky & Curran, 1965). This is why we are interested in this problem. One should add here that equation (1) for volume flux is identical with that of Kedem-Katchalsky equation. However, there is a significant difference in the expression for j_s. Let us recall that the Kedem-Katchalsky equation (Katchalsky & Curran, 1965) has the form:

$$j_s = \omega \Delta \Pi + (1-\sigma)\bar{c}J_v, \qquad (3)$$

where ω is the solute permeation coefficient meas-

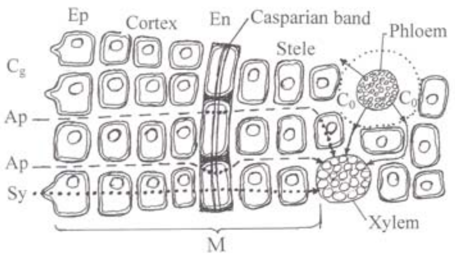

Fig. 2. Illustration of root cross section at the root hair region (a_p - apoplast water route, s_y - symplastic water route).

ured when osmotic pressure is compensated by mechanical pressure difference $\Delta P=\sigma\Delta\Pi$.

Our detail considerations we will begin with a mathematical description of the flow J_{vr} at the 1st stage of the long-distance water translocation in the plant. That flow includes water transfer (and mineral components) through the radial path of root to xylem tracheary elements of the central cylinder. According to the Fiscus concept (Fiscus & Kramer, 1975; Fiscus, 1975; Fiscus, 1986; Fiscus, 1989; Frensch & Steudle, 1989), developed also by other researchers (Frensch & Steudle, 1989; Kargol, 1978; Kargol & Suchanek, 1990; Kargol *et al.*, 1993; Kargol, 1992; Steudle & Brickmann, 1988; Steudle *et al.*, 1987), that route can be approximated to a one-membrane system, where membrane M separates two solutions of concentrations C_{02} and C_g (pictured in Figs 1 and 2). Applying equation 1 to that system we have:

$$J_{vr} = L_{pr}RT(C_{02} - C_g) - L_{pr}(P_{02} - P_a)\,, \qquad (4)$$

where L_{pr} and σ_r=1 coefficients (filtration and reflection) of membrane M which divides soil solution C_g and solution C_{02} in apoplast of the axial cylinder, R and T - gas constant and temperature. P_{02} - mechanical pressure in the xylem elements and P_a atmospheric pressure. It should be noted here that water contained in the flux J_{vr} is first transported to apoplast of the axial cylinder and then to tracheary elements of the xylem. At that moment we have to emphasise that to that apoplast is transported water carried by the flux J_{v2} which flows across membrane M_2 of the osmometer owing to reverse osmosis (Fig. 1). This water is also taken up by conducting elements of the xylem of the axial cylinder (after assimilates have been removed by cells of the axial cylinder).

Thus we assume that the volume flow transported through xylem is expressed as:

$$J_{vx} = J_{vr} + J_{v2}. \qquad (5)$$

Since the xylem transport (II stage of long-distance translocation) is driven by the pressure difference ($P_{02} - P_{01}$), the expression for the xylem volume flow can be written:

$$J_{vx} = L_{px}(P_{02} - P_{01}). \qquad (6)$$

where: L_{px} is the xylem hydraulic conductivity. The flux J_{vx} penetrates into the leaf apoplast, whence a small amount of water permeates across membrane M_1 into osmometer A, which imitates the inside of the sieve tubes where the water duct of phloem begins.

The remaining (major) part of the water is transported by apoplast to the cell walls of leaf mesophyll and cuticles. That water transport can be expressed by the relation

$$J_{vA} = L_{pA}(P_k - P_{01}), \qquad (7)$$

where: L_{pA} - hydraulic conductivity of the apoplast and P_k - capillary pressure (Kargol & Kargol, 1996; Kargol, 1996). That water transpirates (evaporates) to the atmosphere as part of the flux J_{vt}.

The problem of the phloem water and assimilates transport, i.e. J_{vp} transport (IV stage) are more complicated. We showed it earlier (Kargol & Kargol, 1996; Kargol, 1996; Kargol *et al.*, 2001; Kargol, 1994) that the basic equation for that transport has the form:

$$\begin{aligned} S_p J_{vp} &= A[RT(C_1 - C_{01}) - \sigma_2 RT(C_2 - C_0)] + \\ &+ A(P_{01} - P_{02}), \end{aligned} \qquad (8)$$

where: $A = S_p L_p L_{ps}(S_p L_p + L_{ps})^{-1}$ with $L_{ps} = S_1 L_{p1} S_2 L_{p2}(S_1 L_{p1} + S_2 L_{p2})^{-1}$.

Let us explain it here that S_p is the total active surface of the xylem conducting element, L_p - phloem hydraulic conductivity, S_1 and S_2 are active areas of membranes M_1 and M_2, and L_{p_1} and L_{p2_1} are the membranes' filtration coefficients. We recall here that flux J_{vp} is according to formula (8) a function of concentration C_1 which depends on the rate of assimilates creation, concentration C_2 dependent on effectivity of their utilisation by the plant and pressures P_{01} and P_{02} dependent on intensity of transpiration (J_{vt}) and on root pressure.

An unknown quantity of this equation is concentration C_0. Its value can, however, be found solving the problem of reverse osmosis (occurring on membrane M_2 of osmometer B) according to a procedure proposed by A. Kargol (Kargol, 1997).

Using the notation of fig. 1 one can, applying equations (1) and (2), write the following expressions:

$$J_{v2} = L_{p2}\Delta P - L_{p2}\sigma_2 RT(C_2 - C_0), \qquad (9)$$

$$\begin{aligned} J_{s2} &= \omega_d RT(C_2 - C_0) + \\ &+ (1-\sigma)\frac{C_2 + C_0}{2} L_{p2}\Delta P, \end{aligned} \qquad (10)$$

where: $\Delta P = P_2 - P_{02}$.

Reverse osmosis will occur here when $|\Delta P| > |-\sigma_2 RT(C_2 - C_0)|$.

In order to solve the problem of reverse osmosis let us note that

$$J_{v2} = j_w \overline{V_w} + j_s \overline{V_s},$$

where $\overline{V_w}$ and $\overline{V_s}$ – molar volumes of water (w) and solute (s).

Knowing that $j_{w2} = \dfrac{\Delta m_w}{S_2 \Delta t}$ and $j_{s2} = \dfrac{\Delta m_s}{S_2 \Delta t}$, (where Δm_w i Δm_s - masses of solvent and solute), we find that (Kargol, 1997):

$$\frac{J_{s2}}{J_{v2}} = C_0. \tag{11}$$

Now, taking into account the Eqs. (9), (10) and (11) we obtain:

$$C_0 = \frac{\omega_{d2} RT(C_2 - C_0) + (1-\sigma_2)\dfrac{C_2 + C_0}{2} L_{p2}\Delta P}{L_{p2}\Delta P - L_{p2}\sigma_2 RT(C_2 - C_0)}. \tag{12}$$

Hence, after using the correlation between the parameters L_p, σ, ω_d (Kargol, 2001):

$$\omega_{d2} = (1-\sigma_2)\frac{C_2 + C_0}{2} L_{p2},$$

we find:

$$\alpha C_o^2 + \beta C_o + \gamma = 0. \tag{13}$$

where:

$$\alpha = RT(1+\sigma_2), \tag{14}$$

$$\beta = \Delta P(1+\sigma_2) - 2\sigma_2 RTC_2, \tag{15}$$

$$\gamma = (\sigma_2 - 1)(RTC_2^2 + C_2 \Delta P). \tag{16}$$

It is a quadratic equation with respect to C_0 with the discriminant

$$\begin{aligned}\Delta = {} & [\Delta P(1+\sigma_2) - 2\sigma_2 RTC_2]^2 - \\ & - 4RTC_2(\sigma_2^2 - 1)(RTC_2 + \Delta P).\end{aligned} \tag{17}$$

The solution with physical sense has the form:

$$C_0 = \frac{2\sigma_2 RTC_2 - \Delta P(1+\sigma_2) + \sqrt{\Delta}}{2RT(1+\sigma_2)}. \tag{18}$$

It is an explicite form of the function:

$$C_0 = f(C_2, \Delta P, \sigma_2).$$

Thanks to that description of reverse osmosis it will be possible to determine either C_0 or C_2 (as required) with reference to the integrated system we consider. That system, treating water translocation within plant, can be studied quantitatively after the necessary data on biological material are accumulated. And this is the aim of our research.

WHERE THE PLANT HAS ITS HEART?

In the context of this paper it is opportune to answer the question: where the plant has its heart?

Let us begin that task with recalling the basic knowledge about the biophysics of heart functioning. As an example let us take the human heart illustrated schematically in Fig. 3. From the biophysical point of view it is a specialised organ operating as a suction and force pump, operating according to hydrodynamics. During heart diastole a certain negative pressure is generated in the chambers (*PK* and *LK*) and in the auricles (*PP* and *LP*) that sucks the venous blood (of the superior and lung vein). It happens when the aorta valve (a) and pulmonary artery valve (b) are closed. Let us

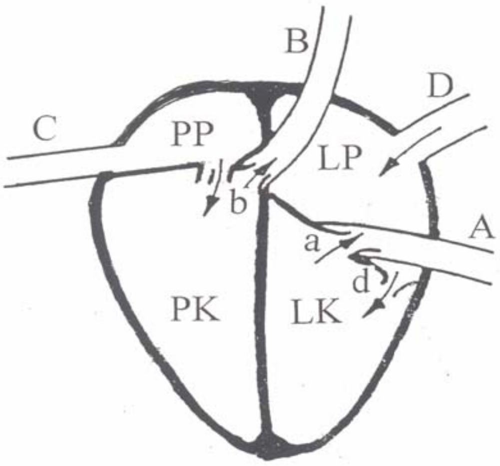

Fig. 3. A scheme of the human heart (PP and LP - vestibules (right and left), PK and LK - chambers (right and left) a, b, c and d - valves (of aorta A, pulmonary artery B, double and triple, C - main vein, D - pulmonary vein).

denote the minimum value of that negative pressure by $P^{\min}$.

In the next stage of heart's operation, i.e. during contraction, a pressure is created in the chambers (*PK* and *LK*) of maximum value $P^{\max}$. During that act blood is pumped (with valves (c) and (d) closed - see fig. 3) to aorta and pulmonary artery. Thus it can be said in general that the essence of heart's action is a rhythmic creation of successive pressures $P^{\min}$ and $P^{\max}$, and pumping blood from pressure $P^{\min}$(negative pressure) to where the pressure is $P^{\max}$(positive pressure), i.e. from lower to higher pressure.

The basic problem now is to find an analogical place in the plant.

Analysing the operation of the integrated system of long-distance water transport in the plant, presented in Fig. 1, it is not difficult to note that such a place is situated in the leaves. It is composed of membrane M_1 (of osmometer *B*) and the bathing solutions C_{01} and C_1 where C_{01} is concentration in the leave's apoplast, and C_1 - concentration of the solution inside osmometer *B*, which imitates in a general way the inside of the sieve tubes that initiate here the water ducts of phloem. The solution in the leaf apoplast (C_1) is under very high negative pressure P_{01} (suction). This negative pressure can reach the value $P_{01} \approx -3$ MPa (relative to atmospheric pressure P_a).

In the sieve tubes of leaves, however, the solution (C_1) is under a very high pressure head, which can reach the value $P_1 \approx +3$ MPa. Moreover, the water here is also pumped from a place with lower mechanical pressure P_{01} (to which corresponds pressure $P^{\min}$ in the heart) to higher mechanical pressure P_1. The latter corresponds to the $P^{\max-}$ pressure in the heart. That transport occurs osmotically, induced by the osmotic pressure difference $\Delta\Pi_1 = RT(C_1 - C_{01})$ from solution C_{01} to solution C_1.

The transport of blood in living organisms is at the expense of work performed by the heart muscle whereas in the plant the phloem transport of water is forced at the expense of osmotic work done by osmometer *A*. One can also add here that the system of the phloem sieve tubes in the plant corresponds to aorta, and the system of tracheary elements corresponds to veins.

CONCLUSIONS

In the present paper we continue the modifications began earlier (Kargol *et al.*, 2001) of the integrated system, developed by M. Kargol and A. Kargol (Kargol & Kargol, 1996; Kargol, 1996; Kargol, 1994), that simulates water translocation in the plant on long distances. The aim of the modification is to make the integrated system closer to the biological reality. The main element of the system is the Münch model, constituting the basis of Münch's theory of mass transport of assimilates in the phloem. That model, from the physical point of view, constitutes a push-pull system of two osmometers (*A* and *B*) connected with a tube imitating the phloem elements of the plant. It should be emphasized here that the model connects the phloem water transport with its translocation on the remaining long distances (I, II and III) in the plant.

In the previous paper we have shown that the inside of osmometer (*A*) does not represent the inside of a photosynthesising cell (as assumed by Münch), but the inside of sieve tubes which initiate here the water ducts of phloem.

In this paper we dealt with the second osmometer (*B*). Referring that osmometer to the plant root as a place where assimilates are utilized, we substantiated the view that its inside represents the inside of the root sieve tubes that terminate here the water ducts of phloem. We have also modified the mathematical description of water flow (and dissolved substances) on the respective long distances. This time use has been made of the so-called mechanistic transport equations of M. Kargol and A. Kargol (2000; Kargol, 2001; Kargol & Kargol, in press).

An advantage of the equations is their interpretational clarity, which cannot be said about the Kedem-Katchalsky equations used until now (Katchalsky & Curran, 1965).

Analysing water translocation in the plant on all long distances we concluded that it makes sense to speak about water circulation in a plant, to some extent similar to blood circulation in an animal organism. Moreover, in this paper an attempt has been made to localise the plant's heart and formulate the mechanism of its operation. As a result of the studies performed it was postulated that the plant's heart is in the leaves and operates on the osmotic principle. As a generalised contrivance it extends on all the plant's leaves. That heart pumps water from leaf apoplast (where mechanical pressure may reach –3 MPa) into sieve tubes where the pressure reaches very high values (up to +3 MPa). The second pressure, corresponding to that during heart contraction, is the cause of phloem water and assimilates transport (mass transport called also pressure transport).

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