The Graviosmotic Hypothesis of Xylem Transport of Water in Plants

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Abstract. This paper presents a full version of the graviosmotic hypothesis postulated earlier in outline (Kargol 1978), which concerns xylem rise of water in plants According to this hypothesis water is transported by xylem vessels (at respective development stages of these vessels) using the graviosmotic mechanisms A detailed description of hypothesis is introduced by a discussion of the development stages of xylem vessels and a presentation of graviosmotic mechanisms postulated to be involved These mechanisms include convective graviosmosis and related effects, gravidiffusional graviosmosis, and osmotic transport aided by gravitational force in multi-membrane systems The presented hypothesis does not contradict the theory of transpiration-cohesion or that of root pressure, rather, it is complementary to them

Key words: Water — Transport — Plant — Xylem — Root pressure — Transpiration — Graviosmosis

Introduction

A number of theories have been devised, so far to explain the long-distance transport of water in the xylem tracheal elements Among them, the most recognized are the transpiration-cohesion theory and the theory of root pressure (Scholander et al 1965, Esau 1967, Salisbury and Ross 1969, Wilkins 1970, Ginsburg 1971, Zimmerman and Brown 1971, Tyree 1972, Fiscus 1975, Anderson 1976, Ziegler 1977, Kargol 1978, 1991, Malinowski 1978, Pitman 1982, Zimmerman and Milburn 1982, Steudle et al 1987, Balling et al 1988, Taura et al 1988, Michalov 1989)

The theories explain well the principles of the xylem water transport Although being mutually complementary, they do not allow for full biophysical interpretation of a number of phenomena connected with the transport For example, one may face difficulties when trying to explain guttation or "weeping" of plants Problems arise concerning the xylem transport of water occurring in spring time when the plant has no leaves and there is no transpiration It is not always easy to explain the processes of filling up the xylem water ducts, after they had been broken by, e.g., excessive transpiration. There have been doubts raised regarding the occurrence of water in liquid state at such high mechanical tensions, theoretically estimated to reach − 3 MPa. Moreover, local mechanical strength of plant leaves capable of withstanding similar high mechanical pressures appears problematic. As a matter of fact there is a high negative pressure in the leaf xylem, whereas there is a turgor pressure in the cells (Balling et al. 1988). Also, high tension value in the leaf xylem, is doubtful despite a successful attempt to measure it (Scholander et al. 1965).

These and other considerations suggest that xylem water transport may be activated not only by the mechanisms postulated by the mentioned theories, but that other mechanisms may be operative as well. In this report, the graviosmotic hypothesis as postulated earlier (Kargol 1978) will be presented in full. According to the hypothesis, the ascent of water in the xylem conducting elements (at respective stages of their development) could be driven by graviosmotic mechanisms. A description of developmental stages of vessels is offered (on the example of Robinia), and certain graviosmotic mechanisms are discussed.

Growth stages of xylem elements

Long-distance water transport in a plant, from root to leaf, occurs along the xylem tracheary elements, i.e. via vessels and tubes (Esau 1967; Salisbury and Ross 1969; Wilkins 1970; Zimmermann and Brown 1971; Ziegler 1977; Kargol 1978; Malinowski 1978; Zimmermann and Milburn 1982).

The graviosmotic hypothesis postulated herein refers to water movement along the xylem vessels, at certain stages of their growth; thus, tracheal elements of this kind will only be considered here.

The vessels develop from a column of meristematic cells. In the process of endogenic growth of a plant, the cells which the vessels develop from first grow sideways and sometimes become elongated. After growth has been completed, secondary walls are formed, the construction material being not deposited on transverse walls (Esau 1967). Moreover, the walls swell to a certain extent, giving off material. As a result, the walls remain a system of loose fibrils. Next, perforation occurs and often the transverse walls disappear completely, the protoplasts degenerate and disappear. First, a vacuole develops at a certain stage of transformation the cytoplasm forms a thin layer around a large vacuole. The nuclei of the cells degenerate as well, followed by complete disappearance of the protoplasts (Esau 1967; Malinowski 1978). Figure 1 illustrates stages (B, C, D, E and F) of the development of the vessel system of Robinia (*Robinia pseudocacia*) according to Eames and MacDaniel (Malinowski 1978). The vessels in their mature final state constitute long water ducts of relatively low hydraulic resistance.

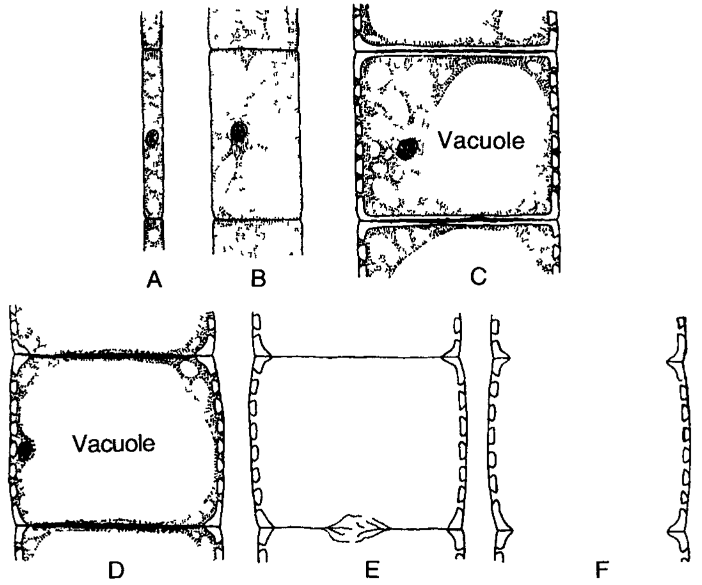


Figure 1. Growth stages of the xylem vessel tube of Robinia, according to Eames and Mac Daniels (Malinowski 1978) *A* – cambium cell, *B* – partly grown cell, *C* – grown cell with lignified secondary walls, *D* – cell with degenerated protoplast (the cytoplasm forms a thin layer around the vacuole), *E* – cell with no protoplast, with end walls forming a net of loose fibrils, *F* – a fragment of vessel tube in mature state

In view of the above, one can assume that there exists such a stage of the vessel system at which the transverse walls possess osmotic properties, and the protoplasm is a thin layer around a large vacuole – see Fig. 1*D* – with effectively no movement within

Graviosmotic phenomena on which the graviosmotic hypothesis has been based

We shall now provide basic information about graviosmotic phenomena taken as a basis for the graviosmotic hypothesis. These phenomena include: convective graviosmosis and related effects, gravidiffusional graviosmosis, and osmotic transport aided by gravitational force as observed in multi-membrane systems.

a. Convective graviosmosis and related effects

The phenomenon of convective graviosmosis was described in 1971 (Kargol 1971; Przestalski and Kargol 1972). Let us consider a two-membrane system in two

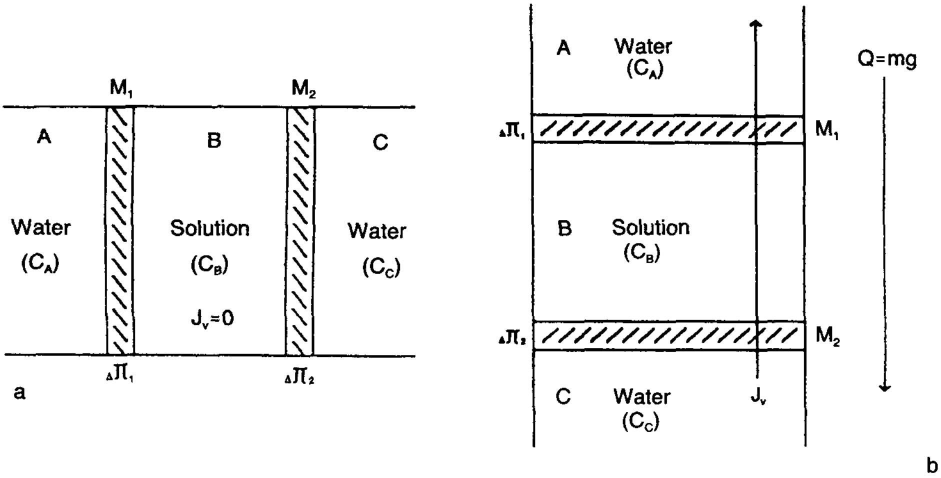


Figure 2. Two-membrane system in positions (*a*) and (*b*): M_1, M_2 – membranes, A, B, C – compartments, C_A, C_B, C_C – concentrations

positions (see Fig. 2*a*, *b*). Let two selective membranes, M_1 and M_2, of equal surfaces ($S_1 = S_2 = S$), equal filtration ($L_{p1} = L_{p2} = L_p$), reflection ($\sigma_1 = \sigma_2 = \sigma$) and permeability ($\omega_1 = \omega_2 = \omega$) coefficients separate three compartments A, B and C, which are filled with solutions of concentrations C_A, C_B and C_C with the density increasing with the concentration. Let, moreover, concentrations of the solutions be $C_A = C_C = C_0$ and $C_B > C_0$. It is obvious that the system is osmotically symmetrical when in position (*a*) (Fig. 2*a*). The differences in osmotic pressure $\Delta\Pi_1$ and $\Delta\Pi_2$ occurring on both membranes balance each other ($\Delta\Pi_1 = -\Delta\Pi_2$). This is confirmed by zero volume flow ($J_v = 0$) in the system.

On repositioning the system to become vertical to position (*b*) with the membranes in horizontal position (Fig. 2*b*) it gets osmotically polarized. A certain uncompensated difference in osmotic pressures occurs: $\Delta\Pi = \Delta\Pi_2 - \Delta\Pi_1$, inducing non-zero volume flow J_v, called graviosmotic flow. This phenomenon and systems where it occurs have been called graviosmosis and graviosmotic systems respectively (Kargol 1971; Przestalski and Kargol 1972).

Graviosmotic flow J_v is directed upwards with solutions with the density increasing with the concentration (e.g. water solutions of glucose), or downwards with the density of the solutions decreasing with the concentration (e.g. water solutions of alcohols).

The flow can be calculated (Kargol 1971; Przestalski and Kargol 1972) using the equation:

$$J_v = \frac{1}{2}L_p\sigma_s\Delta\Pi - \frac{1}{2}L_p\Delta P = \frac{1}{2}L_p(\sigma_s \mathrm{R}T\Delta C - \Delta P), \tag{1}$$

where $\Delta C_2 \approx C_B - C_C$ (for density increasing with the concentration), $\Delta C \approx C_A - C_B$ (for density decreasing with the concentration); R is the gas constant; T is temperature; L_p is the filtration coefficient; σ_s is the pseudoreflection coefficient (Kargol 1985).

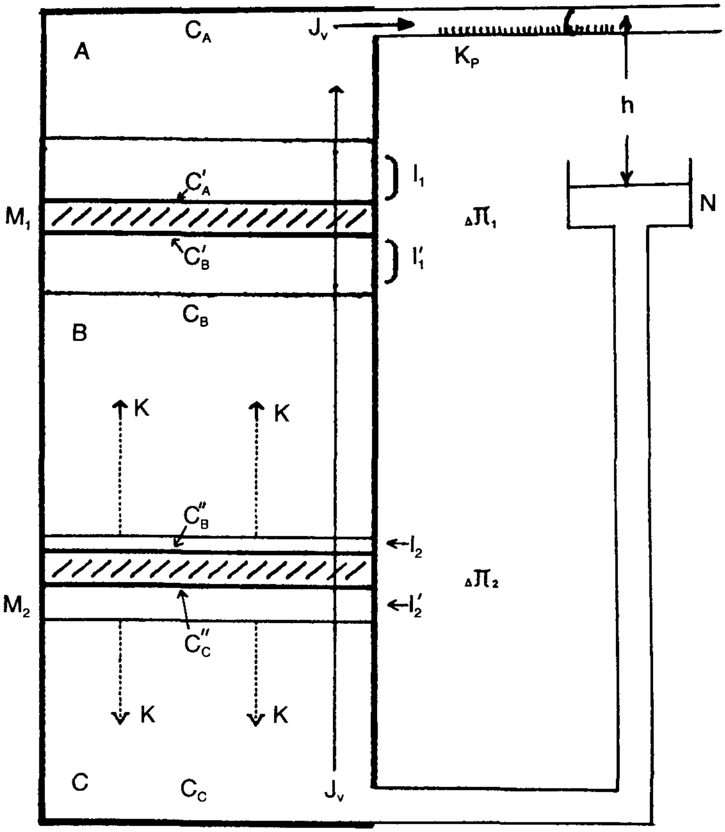


Figure 3. Graviosmotic system. M_1 and M_2 – membranes, A, B, C – compartments, C_A, C_B, C_C – concentrations, l_1, l'_1, l_2, l'_2 – near-membrane layers, K, K – convective currents, J_v – graviosmotic flux, K_p – capillary, N – vessel

Fundamental to the graviosmotic phenomenon is the creation of stable diffusive layers in the vicinity of one of the membranes, and of unstable layers in the vicinity of the other membrane. In Fig. 3 the layers are marked l_1 and l'_1, and l_2 and l'_2, respectively. It should be stated here that layers l_2 and l'_2 are unstable if the density of the solution increases with the concentration. Instability of the layers induces convection in solutions C_B and C_C. The convective currents are indicated with arrows KK (Fig 3) Owing to the currents the solutions are effectively stirred As a consequence of stirring, the osmotic pressure difference $\Delta\Pi_2$ (at membrane M_2) becomes considerably smaller than $\Delta\Pi_1$ (at membrane M_1)

Graviosmosis induced by such a mechanism has been termed convective graviosmosis It has extensively been discused by Kargol (1971, 1978, 1981), Kargol et al (1979) and Przestalski and Kargol (1987)

Let us at least briefly explain, once again the mechanisms of formation of stable layers l_1' and l_1 in M_1 membrane enviroment and of non-stable layers l_2' and l_2 in M_2 membrane Similar layers are formed if the density of solutions in the given graviosmotic system increases with the increasing concentration Let us first consider layers l_1 and l_1' (see Fig 3) which are formed in M_1 membrane enviroment This membrane separates an upper solution of a smaller concentration (C_A) from a lower solution of a higher concentration (C_B) A layer l_1' of the solute diffusing upwards forms just beneath this membrane, with a density smaller than that of solution C_B This layer is stable because gravitation force favors it Particles of the substance which left layer l_1' cross membrane M_1 Next, penetrating the upper solution C_A they form a layer l_1 just above it with a density higher than that of solution C_A This layer is also stable thanks to the action of gravitation force Also it should be added that the thickness of these layers increases slowly in time

The concentration decrease also intensifies This means that the concentration differences C_A' and C_B' (see Fig 3), on the membrane surfaces are small From experiments

$$\Delta C_1 = C_B' - C_A' \approx 0$$

The situation is different in the lower membrane environment (M_2) Here, solute particles leave layer l_2 by diffusion and next they diffuse through membrane M_2 and pass to solution C_C In this way it happens that the density of solution in layer l_2 becomes smaller than that of solution C_B as a whole Water which osmotically crosses membrane M_2 dilutes solution in layer l_2 This layer in the field of gravitational force thus becomes unstable Therefore, convection flows KK arise, they largely destroy this layer and effectively cause mixing of the entire solution C_B

Solute particles which, after crossing membrane M_2, enter solution C_C form a layer l_2' of a density higher than that of solution C_C Thus this layer is also unstable and is being largely destroyed due to the generation of convection flows KK, by gravitational force

In a stationary state the thickness of these layers and as well as the decrements in solution concentrations are negligible and constant in time

The concentration difference ΔC_2 of solutions C_B'' and C_C'' occurring on membrane M_2 (see Fig 3) is much larger than that on membrane M_2

In this way the two-membrane system under consideration undergoes graviosmotic polarization.

Numerous effects are connected with the phenomenon, they have been employed to construct the graviosmotic hypothesis and we shall outline them here.

Graviosmotic pumping of water upwards

Experimental studies (Kargol 1971) have shown that the graviosmotic system is capable of pumping water up to a certain height h. Moreover, a column including multiple systems in series pumps water to a height

$$H = h_1 + h_2 + h_3 + \dots, \tag{2}$$

where $h_1, h_2, h_3, \dots$ are pumping heights by the respective systems. Fig. 4 shows such a column composed of three graviosmotic systems.

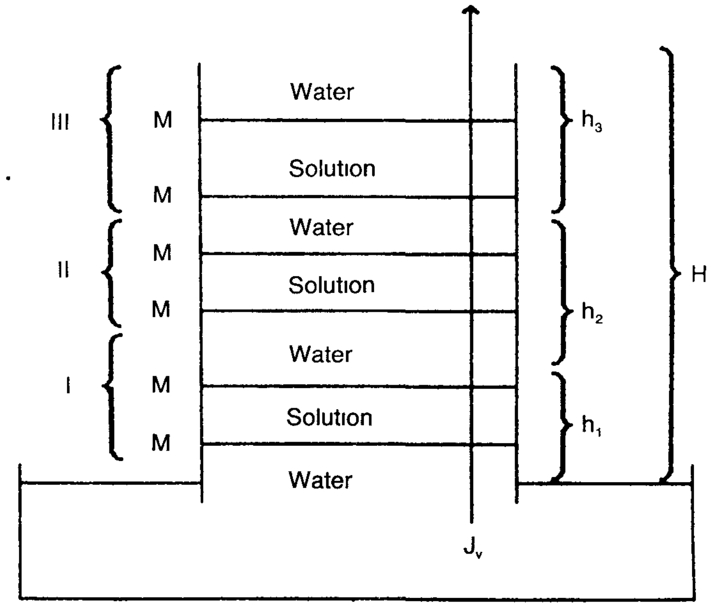


Figure 4. A column of three graviosmotic systems connected in series. I, II, III – graviosmotic systems, H, h_1, h_2, h_3 – heights of water elevation ($H = h_1 + h_2 + h_3$).

In view of the above the system can be assumed to be able to pump water to any height provided the column contains a sufficient number of graviosmotic systems connected in series. It should also be emphasized that graviosmotic transport can be directed against gravity as well.

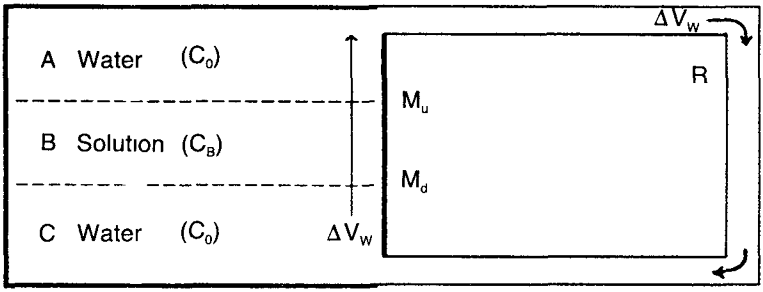


Figure 5a. Graviosmotic circulation of water M_u, M_d - membranes, A, B, C compartments, J_v - volume flux, R - tube

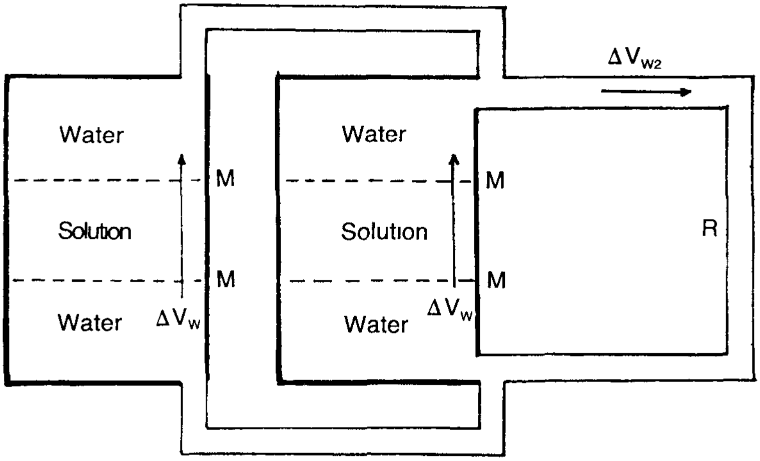


Figure 5b. A system of two graviosmotic units connected in parallel

Graviosmotically induced circulation of water

Graviosmotically induced circulation of water can be observed when the outer compartments (A and C) of a graviosmotic system are connected with each other R_u (Kargol 1971) (Fig 5a, the flow of water is indicated by the arrows) The volume of water ΔV_u is given by

$$\Delta V_u = \frac{1}{2} S \Delta t L_p \mathrm{R} T \sigma_s (C_B - C_0) \qquad (3)$$

where C_B, C_0 are concentrations, S is the active surface of each membrane, Δt is time and σ_s is the coefficient of reflection From the above formula, as well as from experimental studies (Kargol 1971), it follows that with series connection of e.g. two graviosmotic systems, in parallel (Fig. 5*b*) (implying increased effective surface S) the amounts of circulating water increase. With two identical graviosmotic systems $\Delta V_{w2} = 2\Delta V_w$.

Amplification of graviosmotic transport

Amplification of transport in a graviosmotic system occurs when a proper three-component solution is employed in the graviosmotic system (Kargol 1978; Kargol et al. 1979). This requires that the density of one solution increases with the increasing concentrations of one solute while the density of the other one decreases with the increasing concentration of the other solute. A good example of such a system are water solutions of glucose and ethanol.

To explain the amplification effect, let us consider a graviosmotic system in which the middle compartment (B) is filled with a glucose solution and the outer compartments (A and C) with pure water. Under these conditions the graviosmotic flux J_{v2} is a linear function of glucose concentration C_g in compartment (B). This is illustrated in Fig. 6. It follows that a change ΔJ_{v2} of flux J_{v2} induced by a small change of concentration ΔC_g of solution C_g is relatively small and constant over the entire concentration range studied.

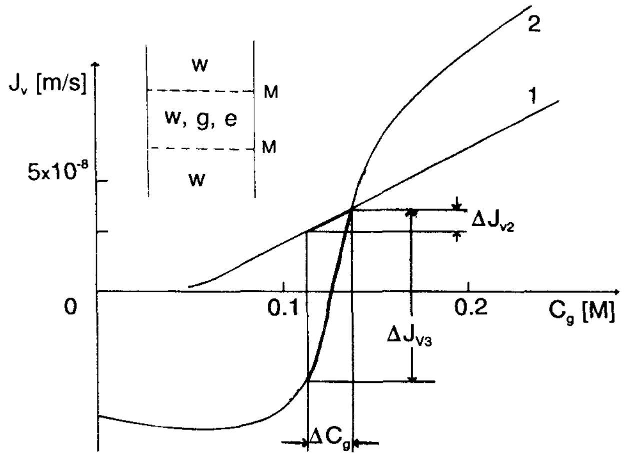


Figure 6. Plots of relationships: $J_{vg2} = f(C_g)_{Ce=0}$ – curve 1 and $J_{vg3} = f(C_g)_{Ce}$ – curve 2

Another situation occurs when the middle compartment is filled with water solution of glucose suplemented by a certain (constant) concentration of ethanol

(C_e = const). In this case, the dependence of graviosmotic flux J_{v3} on concentration C_g is as shown by curve 2 in Fig. 6. From the shape of the curve it follows that changes ΔJ_{v3} of the flux J_{v3}, induced by the same concentration change ΔC_g, differ for different concentration intervals. Moreover, changes ΔJ_{v2} can be several times larger than the changes ΔJ_{v2}. This means that the system has amplification properties. A measure is amplification coefficient defined as:

$$K = \frac{\Delta J_{v3}}{\Delta J_{v2}} \tag{4}$$

It has been shown that with a system composed of two nephrophane membranes the maximal value of the coefficient is $K \cong 5$.

From curve 2 in Fig. 6 it also follows that the graviosmotic flow J_{v3} can be varied both in its magnitude and direction by changes in concentration C_g. This fact is significant for the graviosmotic hypothesis. The regulation and amplification effects refer also to the phenomenon of graviosmotic circulation of water and to the upward graviosmotic pumping of water.

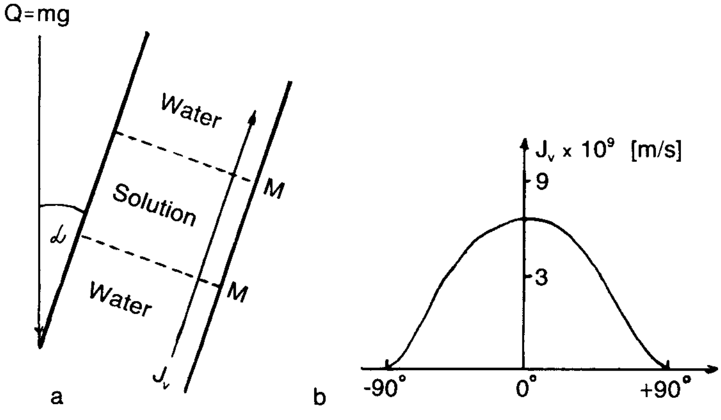


Figure 7. Graviosmotic system positioned at angle α with respect to the vertical (*a*). Plot of the relationship $J_v = f(\alpha)$ (*b*)

Graviosmotic transport as a function of the angle of inclination of the graviosmotic system

Graviosmotic transport J_v (as well as the amount of circulating water) depends on angle α by which the system deviates from the direction of the force of gravity. To investigate the dependence, the graviosmotic system shown in Fig. 7*a* was positioned at various angles. The graviosmotically generated volume flow J_v was measured yelding the relationship $J_v = f(\alpha)$ (Fig. 7*b*). It can be seen that J_v has a maximal value at $\alpha = 0$. Flux J_v decreases with the increasing absolute value of the angle $|\pm\alpha|$, and is zero at $+90°$ and $-90°$. This fact is significant for the graviosmotic hypothesis formulated here in as it allows drawing some conclusions referring to the experimental method of studying the graviosmotic mechanisms in biological systems.

b. Graviosmosis determined by gravidiffusion

Theoretical studies of diffusion in gravity fields (Chandrasekhar 1943; Etori 1986; Hładyszowski et al. 1986,1989) and also some experimental studies on electrolyte transport in membrane systems (Custard and Faris 1965, Kargol 1978; 1988) have indicated that the force of gravity can be a factor able to augment or diminish vertical free diffusion of solutes in liquids. Diffusion thus modified is called gravidiffusion. It has been shown theoretically (Hładyszowski et al. 1986) that times τ_1 and τ_2 of gravidiffusion-induced displacement l of a substance in upward or downward direction respectively, are given by

$$\tau_1 = \frac{l^2}{2\mathrm{D}}\left(1 - \frac{lF}{3\theta}\right), \tag{5}$$

$$\tau_2 = \frac{l^2}{2\mathrm{D}}\left(1 + \frac{l\mathrm{F}}{3\theta}\right) \tag{6}$$

where D is the diffusion constant, F is the force and θ is the temperature in energy limits.

To discuss the process in more detail and to determine its effect on osmotic transport of water, let us consider a system in which a selective, horizontal membrane separates two solutions, C_1 and C_0 . Let the concentrations meet the condition $C_1 > C_0$ with their densities increasing with the increasing concentration. Moreover, let the solutions be dilute enough, so that no convective flow develops upon inverting the concentration gradient (in relation to the force of gravity). The system can be positioned in two opposite positions (a) and (b) (Fig. $8a, b$).

Let us first discuss position (a), with the more concentrated solution (C_1) sited below the membrane and the less concentrated (C_0) one above it. In view of the concentration difference on the membrane ($\Delta C_{a0} = C_1 - C_0$ at time zero), there will be osmotic permeation of water and gravidiffusive permeation of solute. This results in the formation of near-membrane diffusion layers l_a and l_a^x (see Fig. $8a$). These layers are stable since the force of gravity favors it. The thickness of the layers and the concentration decrements will grow over in time. Meanwhile the concentration difference ΔC_a on the membrane will decrease, first quickly with subsequent slowing down. After a relatively short interval, the concentration difference will be very small, as will become gravidiffusion flows (across the membrane)

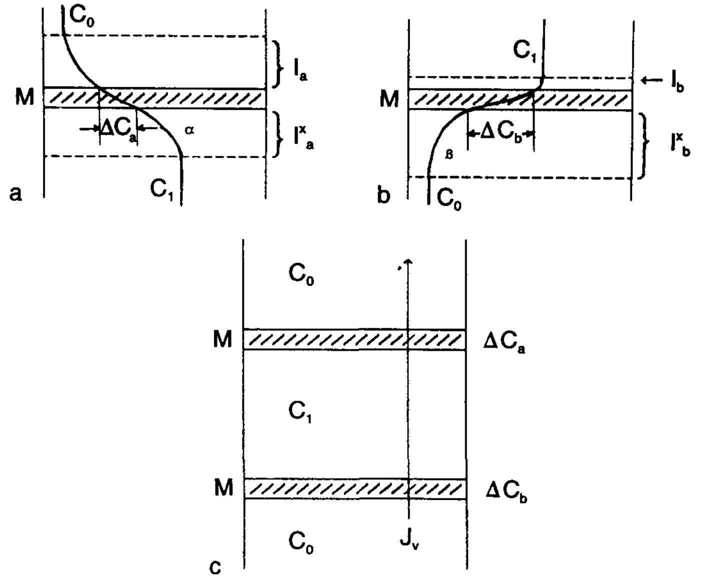


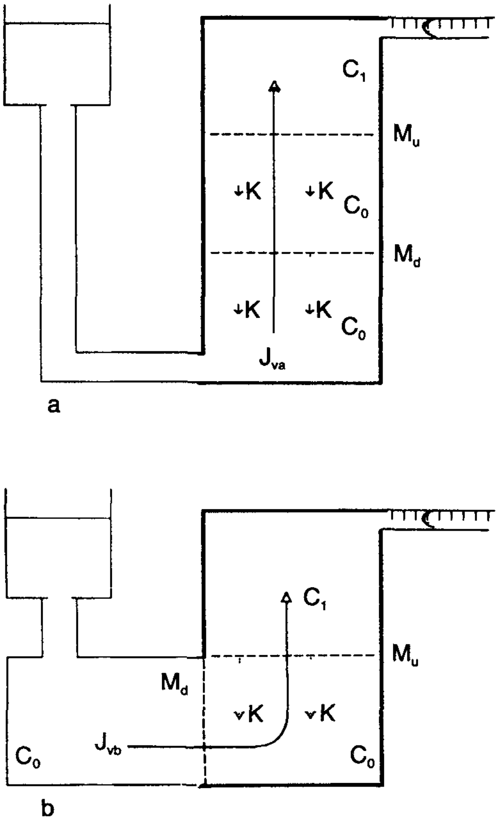
Figure 8. One-membrane system in positions (a) and (b). Graviosmotic system (c): C_1 and C_0 – concentrations, ΔC_a and ΔC_b – concentration differences, l_a, l_a^x, l_b, l_b^x – near-membrane layers

of solute and osmotic flow of water. It can be postulated that after time t the concentration distribution in the solution will similar to that shown by curve α in Fig. 8a.

When the system is in position (b) (Fig. 8b) a different situation will ensue: the diffusive transport of the solute is now enhanced by the force of gravity. The diffusion layer l_b^x (below the membrane) will be more developed (larger thickness and higher concentration difference) than layer l_a^x as compared to position (a). The thickness and the concentration decrement of diffusion layer l_b (above the membrane) will be relatively moderate. Fig. 8b illustrates this in more detail; the near-membrane layers are indicated and the postulated concentration distribution throughout the system is shown by curve β. From various experimental studies it follows that the concentration difference ΔC_b on a membrane is large, much larger than ΔC_a . Accordingly, the osmotic flows of water and gravidiffusion fluxes of solute are large (Kargol 1978; Ślęzak and Turczyński 1986).

Let us now connect the systems (a) and (b) of Fig. 8a, b to form a graviosmotic system. Such a system is schematically represented in Fig. 8c. Since of the system there is a large concentration difference (ΔC_b) at the lower membrane and a small one (ΔC_a) on the upper membrane, a graviosmotic volume flow J_v will develop in

Figure 9. Membrane systems for studying the enhancement of osmotic transport by the force of gravity



upward direction. We shall term the phenomenon gravidiffusive graviosmosis.

c. Osmotic transport enhanced by the force of gravity

Now, we shall describe how osmotic transport can be enhanced by the force of gravity. This phenomenon will be exemplified a two-membrane system shown in Fig. 9*a*. The system contains two horizontal membranes (one above the other) which separate three compartments A, B, C; they are filled with solutions the densities of which increases with the increasing concentration. The upper membrane (M_u) separate solutions C_1 from C_0 ($C_1 > C_0$), whereas the lower membrane is a partition between solutions of equal concentration, C_0. An experimental study has shown that osmotic volume flux J_{va} depends linearly on concentration C_1 of the solution (Fig. 10). After reorientating the membrane (M_u) from horizontal to vertical position (Fig. 9*b*), volume flux J_{vb} depends on concentration C_1 in the way shown by curve 2 in Fig. 10. From the plots it follows that volume flows J_{va} are

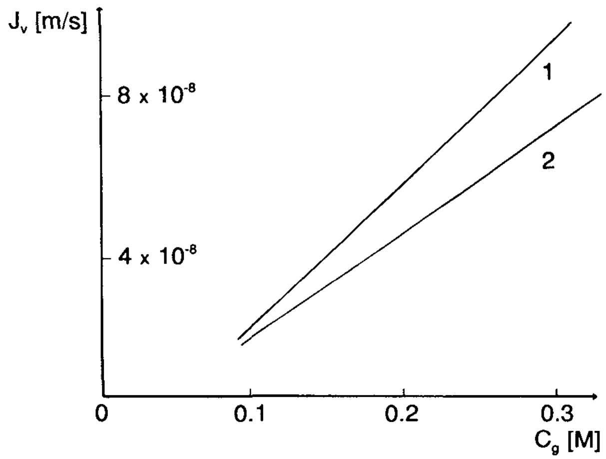


Figure 10. Volume flow J_v versus concentration C_1: plot 1 – relationship $J_v(C_1)$ with enhancement, plot 2 – relationship $J_v(C_1)$ without enhancement

larger than flows J_{vb}. The osmotic pressure differences $\Delta\Pi_u$ at the upper membranes of both systems are equal; thus to explain why $J_{va} > J_{vb}$ one has to assume that an additional osmotic pressure difference $\Delta\Pi_d$ must form at the lower membrane in system (a). This is induced by convective flows generated by the force of gravity (KK in Fig. 9a). The development of the pressure difference $\Delta\Pi_d$ points to some enhancement of the osmotic transport. Such an effect can be observed also in multi-membrane systems.

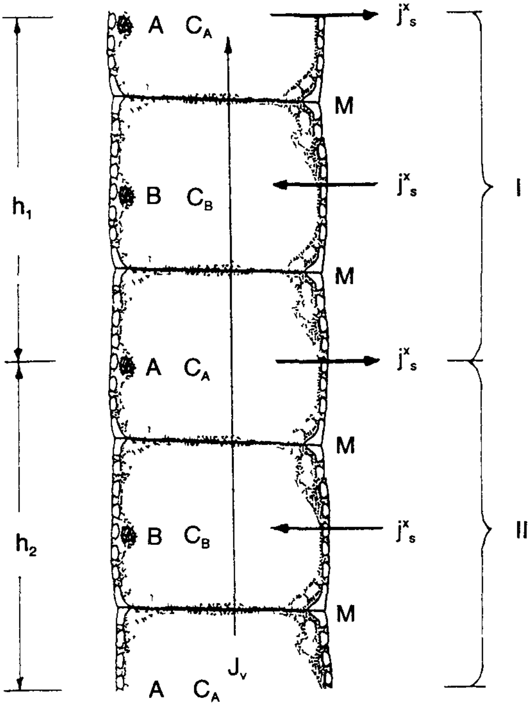
Graviosmotic studies have indicated that enhancing effect should also be observed with concentrations of the solutions small enough to not allow convective flows. In a similar case, the enhancing effect can arise due to gravidiffusion.

Graviosmotic hypothesis

As has been said earlier, the graviosmotic hypothesis refers to water rise through xylem vessels using definite graviosmotic mechanisms. The hypothesis has been developed on the basis of literature data concerning trachear elements, and using graviosmotic phenomena described above.

To present this hypothesis, let us consider a fragment of a vessel draught as shown in Fig. 11. Let particular cells A and B, which represent elements of this sequence, be in the stage of a fairly advanced development. The most interesting seems stage D (Fig. 1). At this stage the cytoplasm in each vessel segment has already formed as a thin layer around a strongly expanded vacuole, so that it may be assumed that it effectively does not perform its natural movements. Moreover, let the transverse walls which separate segments A and B exhibit (in spite of swelling)

Figure 11. Fragment of a vessel element at stage D of growth: I, II, – graviosmotic systems, h_1, h_2 – heights of water elevation, A, B – vessels, J_v – graviosmotic flow, C_A, C_B – concentrations, M, M – transverse walls, j_s^x – active flux of solute



osmotic properties: they have a reflection coefficient σ greater than zero In connection with the existence of protoplasts, active flows j_s^x of diluted substances in a given draught can also be assumed. They are denoted by the arrows in Fig. 11.

Due to these flows, it is possible to assume that the concentration of diluted substances in vessel segments B may be assumed by larger than the concentrations of these substances in segments A ($C_B > C_A$). In the situation presented, a fragment of the vessel sequence of xylem, represented schematically in Fig. 11 (consisting of 4 vessels), can be treated as a system connected in series (I and II). This system is capable of pumping water against gravitational force (according to the graviosmotic principle) to the height $H = h_1 + h_2$, where h_1 and h_2 are respective pumping heights in systems I and II. If segments B of the system contain substances of decreasing solution density in addition to solutes which increase solution density, graviosmotic water rise can be regulated of movement by active streams j_s^x, values and directions hence by internal elements of the plant. Furthermore, to be effective, graviosmotic transport regulation (rise) of water through xylem vessels can use the effects of transport enhancement.

In a real plant a single vessel sequence contains a great number of cells (segments A, B). It also contains a relatively high number of hypothetical serial graviosmotic systems which are capable of pumping water to a respective height H. In a real plant, there are many parallel vessel draughts. This may mean that there are many graviosmotic systems connected in parallel capable of pumping water (regardless of gravitation force) in large amounts: $\Delta V_{nW} = n\Delta V_W$, where n is the number of graviosmotic systems connected in parallel, ΔV_W is the amount of water transported by a single hypothetical graviosmotic element (system).

This is the approach allowing to analyse the problem of water pumping by xylem on the graviosmotic principle, to any height H and in any amount ΔV_{nW}.

Recognizing two kinds of graviosmosis within a gravidiffusional model makes us to allow for two variants of the graviosmotic hypothesis. One, based on convective graviosmosis, may refer only to plants of adequately large xylem vessels. Our previous experimental investigations (Kargol 1978) suggested that convective graviosmosis can be considered in graviosmotic systems with internal diameter ($2r$) of vessels greater than approx 0.3 mm. This is an essential limitation of this variant of the hypothesis, predominantly since there are relatively few plants with such large xylem vessels, such as elm, oak, or some lianas.

There is no similar restriction with the other variant of the graviosmotic hypothesis based on graviosmosis. This mechanism can be operative in xylem vessels with arbitrarily small dimensions.

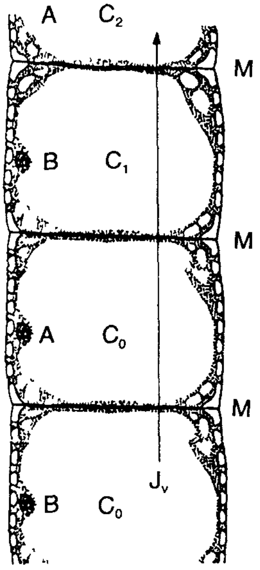


Figure 12. Fragment of a vessel element at stage D of growth, where the enhancement effect may occur: J_v – osmotic flow, A, B – vessels, C_2, C_1, C_0 – concentrations, M, M, M – transverse walls

The above graviosmotic hypothesis can be modified by considering i.a. gravitation force – induced enhancement of upwards to the osmotic transport of water in xylem vessels. To explain it, let us consider a fragment of a vessel draught

(Fig. 12) being at stage D of development (see Fig. 1). Let, there be in connection with a daily cycle of assimilant production (cyclically) a state with concentrations $(\quad > C_2 > C_1 = C_0 = C_0 \quad)$ in every higher segment being higher. This is expected to involve periodical formation of upward osmotic water flows. Moreover, the effect of gravitation force – assisted flows, can be expected to appear in analogue with systems with artificial membranes (Kargol 1990). This effect will appear both in small and large vessels as it can be generated (see under *C*) on the convection and the gravidiffusion principles.

Discussion and Conclusions

The graviosmotic hypothesis of water rise in plants through xylem vessels presented herein remains a hypothesis, and has to be experimentally verified on biological systems. Support to the hypothesis may be drawn from an obviously considerable probability of the occurrence of graviosmotic mechanisms in plants, and from the fact that it does not contradict the transpiration-cohesion theory or the theory of root pressure, rather it is complementary to these theories. This hypothesis allows to explain different phenomena observed in plants, such as input of xylem water transport in a plant during spring when the plant has no leaves and it does not transpire: guttation, plant "tears" or filling the broken water draughts of xylem as a result of excessive transpiration. Thanks to the graviosmotic mechanism, no large negative pressure has to be generated in the plant xylem (theoretically estimated to reach −3 MPa). Graviosmosis - induced water rise in xylem vessels can help e.g. young vessels in a plant when the hydraulic conductivity is too high for water to be raised under the pressure generated by transpiration.

Two variants of the graviosmotic hypothesis are introduced: one based on convective graviosmosis, and the other on graviosmosis of a gravidiffusional model.

The first variant can only be operative in plants with relatively large vessels. Such a restriction does not apply to the second variant based on graviosmosis determined by gravidiffusion. Both variants can be modified by ordinary osmosis and by effects of enhancement of graviosmotic transport and by effects of gravitational force - aided osmotic transport. These latter effects are observed, as has been shown above, in multi-membrane systems. Generally, long-distance water circulation exists in plants. It includes water intake from the environment, its displacement across the root, and rise through the xylem up to the leaves where it partly gets evaporated, and partly transferred again to xylem.

Enhancement of this circulation can also be explained in a different way including graviosmosis.

Graviosmotic transport has been shown to be most effective with the graviosmotic system situated vertically. Referring to plants, graviosmotic principles may be suggested to be involved in a slower growth of plant offshoots at angles in relation to the vertical growth of the main stem. It can be inferred that the more intensive the water transport in a given fragment of a plant, the more effective the physiological processes. The graviosmotic hypothesis proposed herein, similarly as the theory of transpiration-cohesion (Scholander et al. 1965; Salisbury and Ross 1969) has to be verified on biological objects. Investigations are under way by the author of the present paper.

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