

BIOPHYSICAL MECHANISMS OF LONG-DISTANCE TRANSPORT OF LIQUIDS AND SIGNALING IN HIGH PLANTS

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Wave phenomena have been observed in numerous experiments with whole plants. One of possible mechanisms of the long-distance high-speed signaling in high plants is connected with concentration waves that can propagate through the conducting systems of plants. One-dimensional axisymmetrical stationary flow of a viscous liquid with osmotically active dissolved component through a long thin rigid cylindrical tube is considered as a model of the conducting vessel of the plant. Constant concentrations of the component at the inlet and outlet of the vessel are maintained by the live cells of the vegetative organs of the plant. Nonlinear concentration distribution along the tube and the parabolic velocity profiles are obtained. Propagation of small excitations of concentrations and velocities along the tube is considered. Expression for the wave velocity U is presented. The range $U=20-60$ m/s is obtained by numerical estimations at wide variations of the parameters within the physiological limits. The time delay in signal transmission in the system root-leaves corresponds to the experimental data. In that way the concentration waves can mediate high-speed transferring of information between the organs of plants.

KEY WORDS: signaling in plants, concentration waves, long-distance liquid transport, conducting system.

Wave phenomena in long-distance liquid motion in high plants are still under investigated. Two types of conducting vessels provide transport of water and dissolved components in plants. Xylem vessels conduct xylem sap from roots to flowers, leaves and fruits against gravitation. Phloem vessels conduct assimilates from photosynthesizing leaves to the growing leaves, fruits and roots (fig.1). The ascending and descending flows are tightly connected and controlled by the feedback system that is carried out by phytohormones and mineral components delivered by the transport system. The driving force of the transport is the water potential gradient $\nabla\Psi$. Active transport mechanisms and autoregulation of water evaporation by leaves result in non-stationary modes of the liquid flow in the vessels. Continuous registration of ψ at different experimental conditions reveals short- and long-wave oscillations [1]. Auto-oscillatory mode of ground-water absorption by roots has been revealed in experiments [2]. Short-period ($t \sim 15-80$ min) oscillations of water exchange in plants have been observed in many specimens [3]. Rapid variations of osmotic pressure of the root solution cause quick alterations of the stem diameter. The alterations have been observed at rather small variations of the concentration (~ 0.01 M) and pass ahead of the bioelectric reaction that is noticeable at $C \sim 0.3-0.5$ M only. The alterations of the stem diameter propagates along the stem in a wave-like way with velocity $v \sim 10^{-1}-1$ m/s, that considerably exceeds the rate of liquid movement $v \sim 10^{-4}$ m/s. Possible explanation of the quick reaction of the plants is connected with wave propagation in saturated porous media of plant tissues [3-4]. Similar slow waves with $v \sim 96$ cm/s have been observed in experiments [5]. The relation between the rates of movement of the slow waves in longitudinal and transverse directions are the same as for acoustical waves. The waves can carry information (molecules of phytohormones and other regulatory substances) along the plant [5-6]. In the present paper some problems of wave propagation in the conducting systems of plants are considered.

MODEL AND GOVERNING EQUATIONS

Conducting elements of plants can be considered as long thin hollow vertical tubes (xylem vessels) and long chains of elongated cells divided by porous plates (phloem vessels).

The radius a and the length L of the tube are constant values and $a/L \ll 1$ (fig.2). The coordinate $x=0$ ($x=L$) corresponds to the inlet (outlet) of the phloem vessel and the outlet (inlet) of the xylem vessel. The propelling forces of the plant sap motion through the xylem are connected with water pumping by the roots and evaporation by the leaves. As a result the hydrostatic pressure p is much higher at the inlet ($x=0$) than at the outlet ($x=L$) of the xylem vessel. Water pumping due to the osmotic effect at the inlet of the phloem vessels ($x=0$) increases the hydrostatic pressure p at $x=0$ that causes the descending motion of the phloem sap to the roots, growing leaves, flowers and fruits (fig.1) (the Münch hypothesis) [7-8].

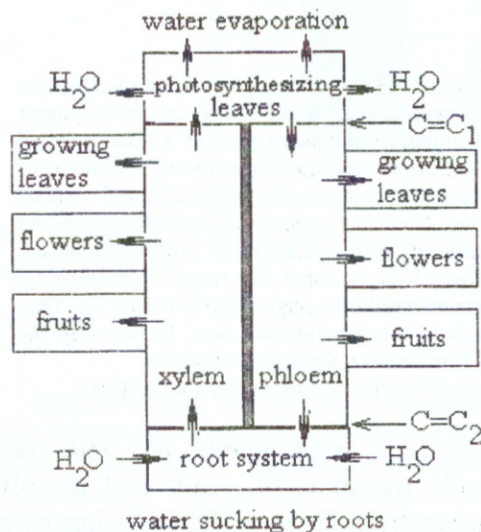


Fig.1. Water and solute fluxes in a plant.

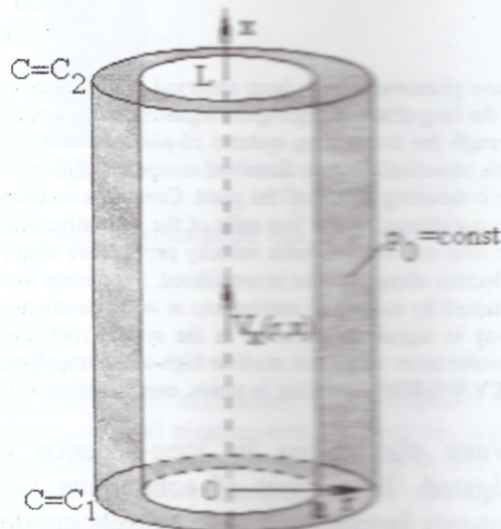


Fig.2. Model of the conducting vessel.

Let us consider the liquid flow through the long thin tube ($a \ll L$) with impermeable rigid wall that correspond to the sap motion along the part of stem or shoot between the side branches so that the sap flow in the radial direction is not taken into consideration. In the case we can consider the one-dimensional axisymmetric flow of a viscous compressible liquid with an osmotically active dissolved component. The governing equations are the following [9]:

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho V_x}{\partial x} = 0 \quad (1)$$

$$\frac{\partial V_x}{\partial t} + V_x \frac{\partial V_x}{\partial x} = -\frac{1}{\rho} \frac{\partial p}{\partial x} + \nu \left(\frac{\partial^2 V_x}{\partial r^2} + \frac{1}{r} \frac{\partial V_x}{\partial r} + \frac{\partial^2 V_x}{\partial x^2} \right) \quad (2)$$

$$\frac{\partial C}{\partial t} + \frac{\partial}{\partial x} (V_x C) = \frac{\partial}{\partial x} \left(D \frac{\partial C}{\partial x} \right) \quad (3)$$

where V_x is the axial velocity, ρ, ν are density and kinematic viscosity of the sap, C, D are concentration and diffusion coefficient of the dissolved component. According to the Münch hypothesis, the hydrodynamic pressure p inside the vessel is maintained by the live cells at an osmotic equilibrium with respect to the surrounding water-containing tissues where the hydrodynamic pressure p_0 is held constant [8,9] so that

$$p = \pi + p_0 \quad (4)$$

Here π is the osmotic pressure that can be calculated from the van't Hoff equation for a dilute solution:

$$\pi = \frac{RT}{M_c} C \quad (5)$$

where M_c is the molar mass of the dissolved component, R is the gas constant, T is the absolute temperature. The problem (1)-(5) for the variables V_x, C, ρ can be solved at the conditions:

$$r = 0: \quad \partial V_x / \partial r = 0, \quad r = a: \quad V_x = 0 \quad (6)$$

$$x = 0: \quad C = C_1(t), \quad x = L: \quad C = C_2(t) \quad (7)$$

$$t = 0: \quad C = C_0(x) \quad (8)$$

INVESTIGATION OF STEADY FLOW IN THE TUBE

When $D, C_{1,2}$ are constant we can introduce the dimensionless parameters $c = C/C^\circ$, $v = V_x/V^\circ$, $X = x/L$, $z = r/a$, $T = t/T^\circ$ and rewrite equations (2)-(3) in the form:

$$\frac{1}{St} \frac{\partial c}{\partial T} + \frac{\partial}{\partial X}(vc) = \frac{1}{Pe} \frac{\partial^2 c}{\partial X^2} \quad (9)$$

$$\frac{1}{St} \frac{\partial v}{\partial T} + v \frac{\partial v}{\partial X} = -\frac{1}{\alpha} \frac{\partial c}{\partial X} + \frac{1}{Re} \left(\frac{\partial^2 v}{\partial z^2} + \frac{1}{z} \frac{\partial v}{\partial z} + \left(\frac{a}{L} \right)^2 \frac{\partial^2 v}{\partial X^2} \right) \quad (10)$$

where $St = V^\circ T^\circ / L$, $Pe = V^\circ L / D$, $Re = V^\circ a / v$, $\alpha = \rho M_c (V^\circ)^2 / (RT C^\circ)$. Typical values for the parameters are $a = 10^{-5} - 10^{-4}$ m, $L = 10^{-2} - 10^{-1}$ m, $D = 10^{-10} - 10^{-9}$ m²/s, $V^\circ = 10^{-4} - 10^{-3}$ m/s, $v = (0.9 - 3) \cdot 10^{-6}$ m²/s [8,10]. One can obtain here the estimations of the Reynolds and Peclet numbers $Re = 10^{-3} - 10^{-1}$, $Pe = 10^4 - 10^5$. When $Re \ll 1$ the derivatives of v with respect to X can be neglected as compared to the derivatives of v with respect to z and the nonlinear term in (10) can be omitted. Solution of (1)-(9) can be considered as expansion in terms of the small parameter $\varepsilon = 1/Pe$ in the form:

$$c = c_0 + c_1 \varepsilon + c_2 \varepsilon^2 + \dots, \quad v = v_0 + v_1 \varepsilon + v_2 \varepsilon^2 + \dots \quad (11)$$

Substituting (11) in (9)-(10), assuming $\partial v / \partial T = 0$ and comparing the values of the same order on ε give the equations for c_0, v_0 instead of (9)-(10) (subscripts are omitted for simplicity):

$$\frac{1}{\alpha} \frac{\partial c}{\partial X} = \frac{1}{Re} \left(\frac{\partial^2 v}{\partial z^2} + \frac{1}{z} \frac{\partial v}{\partial z} \right) \quad (12)$$

$$\frac{1}{St} \frac{\partial c}{\partial T} + \frac{\partial}{\partial X}(vc) = 0 \quad (13)$$

The system (12)-(13) describes Poiseuille-like flow with concentration gradient as a driving force instead of the pressure drop. In that way the solution of the system is:

$$v(Z, X) = \frac{Re}{4\alpha} (1 - Z^2) \frac{\partial c}{\partial X}, \quad c = \sqrt{s_1^2 - (s_1^2 - s_2^2)X} \quad (14)$$

where $s_{1,2} = C_{1,2}/C^0$. The model (1)-(5),(7)-(9) has been used in [8] for investigation the stationary flow of the phloem sap at some simplifying conditions. Now we can substitute (14) into the equations for c_1, c_2, \dots and calculate the high-order terms in (9)-(10). Some results of numerical calculations of distributions $c(X), v(X)$ are presented in fig.3-4.

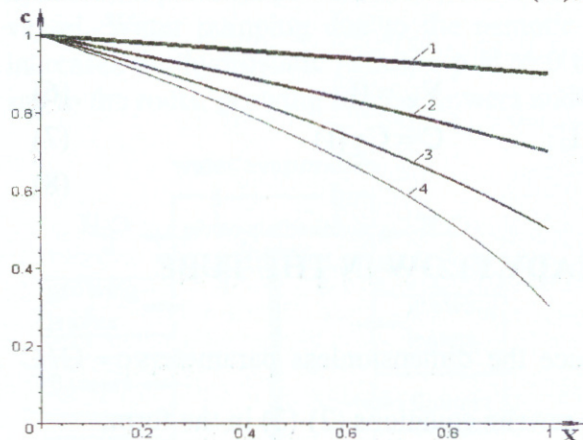


Fig.3. Dependences $c(X)$ for $C_2/C_1=0.9$, 0.7, 0.5, 0.3 (curves 1-4 respectively).

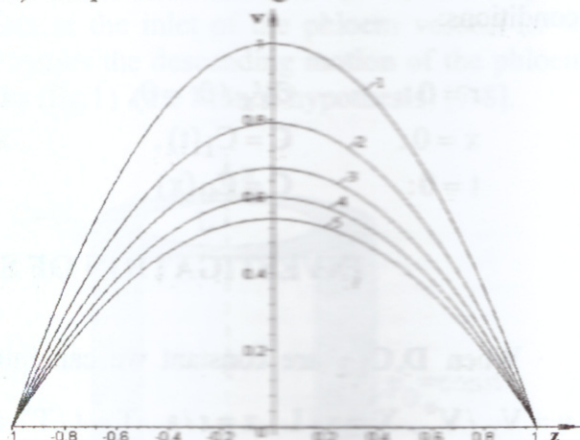


Fig.4. Dependences $v(X)$ for $X=1, 0.8, 0.6, 0.4, 0.2$ (curves 1-5 respectively).

PROPAGATION OF SMALL EXCITATIONS

We consider here the wave propagation through the tube as possible biophysical mechanism of long-distance signaling in high plants. The linearized equations (1)-(2) when they are considered as a system for $V_x, p, \rho(p)$ describe propagation of small excitations in the form $f = f' e^{i\omega(t-x/w)}$, where $f = \{V_x, p\}$, f' are small amplitudes, $w = (dp/dp)^{-1}$ is the wave velocity. Numerical estimations give the values $w \sim 10^3$ m/s. That sort of waves can carry information between the leaves and the roots of the plant at rapid variations of the pressure conditions at the ends of the tube, for instance in experiments with plants in pressure bomb chamber [11]. The relatively slow concentration waves can be investigated by assuming $c = s_c + c'$, $v = v_c + v'$ in (9)-(10), where $s_c = s_1 = s_2$ and $v_c = 0$ are unperturbed values, c', v' are small perturbations that can be introduced as

$$c' = c^* e^{i\omega(T-X/u)}, \quad v' = v^* e^{i\omega(T-X/u)} \quad (15)$$

where u is the wave velocity. Substituting (15) in (12)-(13) we obtain the uniform algebraic system of equations for the small amplitudes c^*, v^* in the form:

$$A \begin{pmatrix} c^* \\ v^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad A = \begin{pmatrix} \frac{1}{St} & -\frac{s_c}{u} \\ -\frac{1}{\alpha u} & 1 \end{pmatrix} \quad (16)$$

The solvability condition for (16) is $\det(A) = 0$ that gives the next expression for the wave velocity (in dimension form):

$$U = \sqrt{\frac{RTC_1}{M_c \rho}} \quad (17)$$

Mechanisms of long-distance transport of liquids and signaling in high plants

In the phloem vessels the sucrose solution moves through the tubes and for that case $M_c = 0.3423 \text{ kg/mol}$, $\rho = 1300 \text{ kg/m}^3$, $C_1 = 200 - 300 \text{ kg/m}^3$ [8,10]. Assuming the temperature variations $T = 283 - 303 \text{ K}$ we can obtain from (17) the range of the wave velocities $U = 20 - 60 \text{ m/s}$. The wave is rather small one as compared to the longitudinal wave in compressible liquid. When the plant stem has the total length $L_\Sigma = 0.1 - 1 \text{ m}$, the slow wave passes the distance L_Σ in $t \sim 1.7 - 50 \text{ ms}$.

CONCLUSIONS

At dynamical equilibrium conditions the concentration gradient between the inlet and outlet of the conducting vessel that is maintained by active synthesis (absorption) of the dissolved component in different vegetative organs of the plant defines the propelling force of the liquid motion through the vessel. The governing equations give the parabolic velocity profiles and nonlinear concentration distribution along the vessel for the stationary flow.

Slow concentration waves can be caused by variation of the concentration of the dissolved component at the inlet of the tube. At variation of the parameters of the model within the physiological limits for high plants the wave velocity $U = 20 - 60 \text{ m/s}$ is obtained. For the stem length $L_\Sigma = 0.1 - 1 \text{ m}$ the time delay between application of the stimuli and reaction of the distant vegetative organs is $t \sim 1.7 - 50 \text{ ms}$ that is comparable to the experimental data [4]. In that way the slow waves can mediate long-distance high-speed transferring information between the organs that can not be carried by convective flow of the liquid which moves at $V \sim 10^{-5} - 10^{-4} \text{ m/s}$ and reaches its maxima $V = 0.02 - 0.04 \text{ m/s}$ in lianas.

Propagation of the concentration jump δC_1 along the vessel as well as non-stationary conditions $C_1(t), C_2(t)$ at the ends of the vessel can be investigated on the basis of the developed model. The results can be generalized for the model of the conducting system as a bundle of thin tubes with porous walls [12] with different mechanical parameters [13].

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