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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 mineral and organic components in plants. Xylem vessels conduct xylem sap from roots to flowers, leaves and fruits opposite the gravitation force. Phloem vessels conduct assimilates from photosynthesizing leaves to growing leaves, fruits and roots (fig.1). The ascending and descending liquid flows are tightly connected and controlled by the feedback system that is carried out by phitohormones and mineral components which are delivered by transport system. The driving force of the transport is 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~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) and pass ahead of the bioelectric reaction that is noticeable at ~0.3-0.5 only. The alterations of the stem diameter propagates along the stem in a wave-like way with velocity $v\sim10^{-1}$-1 m/s, that considerably exceeds the rate of liquid movement $v\sim10^{-4}$ m/s along the stem. 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~96 cm/s have been revealed 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].

Hydrodynamical phenomena that are connected with wave propagation along the conducting pathways of plants, concentration waves, elastic waves in the porous skeleton of the plant tissues have not been sufficiently investigated. 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 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 is much higher at the inlet (x=0) then at the outlet (x=L) of the vessel. Water pumping due to the osmotic effect at the inlet (x=L) of the phloem vessels increases the hydrostatic pressure at x=L that causes the motion of the phloem sap to the roots, growing leaves, flowers and fruits (fig.1) of the plant (the Munch hypothesis) [7-8].

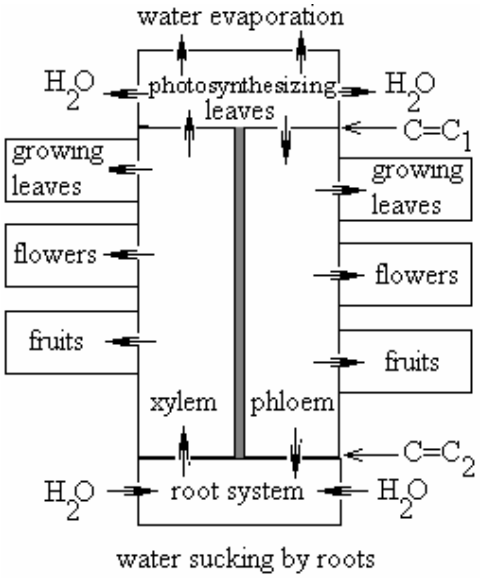

Fig.1. Water and solute fluxes in a plant.

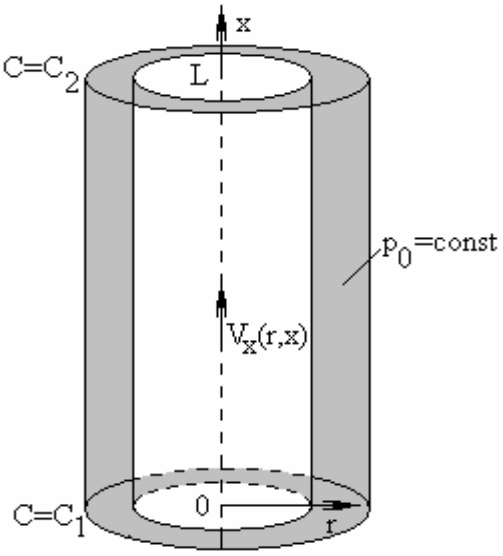

Fig.2. Model of the conducting vessel.

The governing equations of one-dimension axisymmetric flow of a viscous compressible liquid with an osmotically active dissolved component through the tube are the following [9]:

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho V_x}{\partial x} = 0 \tag{1}$$

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

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

where V_x is axial velocity, ρ, ν are density and kinematic viscosity of the sap, p is hydrostatic pressure, C,D are concentration and diffusion coefficient of the dissolved component. The Munch hypothesis can be formulated as [8]:

$$p = \pi + p_0 \tag{4}$$

where π is osmotic pressure, $p_0 = \text{const}$ is the hydrostatic pressure in the surrounding tissues. The balance between the hydrostatic and osmotic pressures is maintained by the live

cells and can be regarded as a dynamical equilibrium [9]. For the osmotic pressure π the van't Hoff equation for a dilute solution can be used in the form:

$$\Pi = \frac{RT}{M_c} C \tag{5}$$

where M_c is 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:

$$r = 0: \quad \partial V_x / \partial r = 0, \qquad r = a: \quad V_x = 0 \tag{6}$$

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

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

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:

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

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

where $St = V^\circ T^\circ / L$, $Pe = V^\circ L / D$, $Re = V^\circ a / \nu$, $\alpha = \rho M_c (V^\circ)^2 / (RTC^\circ)$. Typical values for the parameters are $a = 10^{-5} - 10^{-4}$ m, $L = 10^{-2} - 10^{-1}$ m, $D = 10^{-10} - 10^{-9}$ m^2/s, $V^\circ = 10^{-4} - 10^{-3}$ m/s, $\nu = (0.9 - 3)\cdot 10^{-6}$ m^2/s [8,10]. One can obtain here the estimations $Re = 10^{-3} - 10^{-1}$, $Pe = 10^4 - 10^5$. When $Re << 1$ 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:

$$c = c_0 + c_1\varepsilon + c_2\varepsilon^2 + \ldots, \quad v = v_0 + v_1\varepsilon + v_2\varepsilon^2 + \ldots \tag{11}$$

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):

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

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

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:

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

where $s_{1,2} = C_{1,2} / C^{\circ}$. 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 $c_1, c_2, \ldots$ 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.

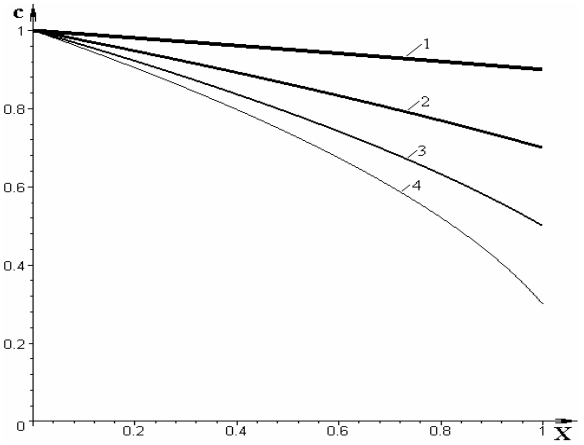

Fig.3. Dependences $c(X)$ for C_2 / C_1=0.9, 0.7, 0.5, 0.3 (curves 1-4 respectively).

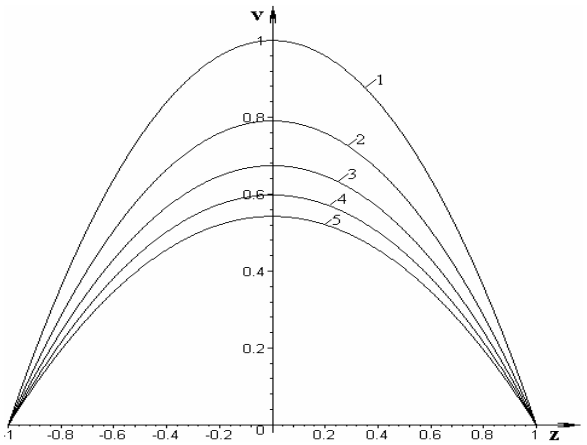

Fig.4. Dependences $v(X)$ for X=1, 0.8, 0.6, 0.4, 0.2 (curves 1-5 respectively).

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, $w = (d\rho / dp)^{-1}$ is wave velocity. The values $w \sim 10^3$ m/s can be obtained here by numerical estimations. 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

$$c^{/} = c^{*} e^{i\omega(T - X/u)}, \quad v^{/} = v^{*} e^{i\omega(T - X/u)} \tag{15}$$

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

$$A \begin{pmatrix} c^{*} \\ v^{*} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \qquad A = \begin{pmatrix} \dfrac{1}{St} & -\dfrac{s_c}{u} \\ -\dfrac{1}{\alpha u} & 1 \end{pmatrix} \tag{16}$$

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

$$U = \sqrt{\frac{RTC_1}{M_c \rho}} \tag{17}$$

In the phloem vessels the sucrose solution moves through the tubes and for the 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 possesses the total length $L_\Sigma = 0.1 - 1\ \text{m}$, the slow wave passes the distance L_Σ in $t \sim 1.7 - 50$ 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.

Slow concentration waves can be caused by variation of the concentration of the dissolved component at the end of the tube. At wide 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 $t \sim 1.7 - 50$ 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 $V \sim 10^{-5} - 10^{-4}$ m/s and reaches its maxima $V = 0.02 - 0.04$ 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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