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TRANSPIRATION MECHANISM OF CAPILLARY TRANSPORT IN THE XYLEM OF PLANTS

The capillary transport of the aqueous solution of mineral salts in the xylem of plants owing to the transpiration process has been considered. By analyzing the balance of driving forces (capillary forces, gravity forces, and viscous friction), a differential equation describing the liquid flow in the xylem consisting of capillaries with varying cross-sections is derived and integrated. The profile of a vertical capillary with varying cross-section for the maximum water flow is calculated. On the basis of the formula obtained for the minimum capillary cross-section and the Thomson law for the vapor pressure over the concave meniscus of leaf stoma, an expression is obtained for the dependence of the maximum capillary length on the humidity of the atmospheric air.

K e y w o r d s: xylem, transpiration, capillary transport, meniscus radius, leaf stoma, capillary profile, altitude scale.

1. Introduction

At present, the mankind passes from the stage of using the heat from the wood combustion to the stage of using the biomass energy in the form of liquid motor fuel (the biodiesel engine). Therefore, the issue concerning the rates of biomass farm production – e.g., of rape – becomes highly challenging. It is evident that the progress in this domain depends not only on the fertilization, watering, and so on, but also on the presence of novel, intensively growing sorts of plants. At the same time, the selection of the latter requires the understanding of the transpiration mechanism governing the capillary transport of the aqueous solutions of various substances from soil to plant leaves. As early as thirty years ago, the known expert in capillary phenomena A.D. Zimon wrote: "It is owing to the capillary mechanism of water rise that the flora nutrition occurs».

In recent years, the problems of plant "nutrition" and the transport mechanisms of the aqueous solutions of mineral substances from soil to leaves change from the pages of popular scientific editions to those of scientific journals. Even in the leading world scientific journals such as Nature [2] and Science [3], there appeared articles where the parameters of capillary transport in the plant xylem were evaluated. There also emerged highly exotic hypotheses concerning the relatively high flow capacity of xylem with respect to aqueous solutions from soil [4].

2. Brief Review

In my report at the 14th International Scientific Conference "Renewable Energy of the 21-th Century" [5], a review of the current state of researches concerning the transpiration mechanism of capillary transport of aqueous solution of mineral substances in the plant xylem was made. In particular, by analyzing the data published earlier, a number of hypotheses were formulated, which formed a basis for the mathematical model of capillary transport in the plant xylem.

2.1. Hypotheses adopted in the mathematical model

1. The capillary radius is a variable quantity. It is maximal near the root ends, decreases as the distance from the root end increases, and is minimal on the leaf surface (at stomata). This statement is confirmed by the fact that the tree trunk diameter also decreases, as the altitude of its cross-section grows.

2. As the reference (zero) level for the altitude of liquid rising in xylem capillaries, the so-called "soil water level" rather than the earth surface is taken. Water located above this level is in a "capillary" state characterized by a concave meniscus.

3. The "root pressure" is based on the osmosis phenomenon and is not the driving force of capillary transport for the substance solution in xylem. The surface layer of the plant root system is a membrane that selectively transmits only the aqueous solutions of corresponding mineral substances from soil and brings them to the lower cross-section of xylem capillaries.

4. Transpiration or evaporation of water from the surface of meniscuses at the upper ends of xylem capillaries (i.e. from stomata in leaves) occurs exclusively at the expense of heat generated by sunlight absorbed by the leaf surface.

5. Evaporation from the meniscus surface mainly occurs at its edges (along its perimeter). The meniscus edge becomes narrower at that, and the wetting angle θ decreases, which results in an increase in the capillary pressure and, respectively, the water flow through the capillary.

6. Transpiration is the driving mechanism that raises mineral substances in the form of their aqueous solutions in soil from roots to leaves of plants, where water evaporates, whereas mineral substances transform into organic ones in the course of photosynthesis.

In addition, in work [5], a preliminary analysis of the capillary transport in xylem consisting of elements with a constant radius was carried out.

2.2. Molecular physics of capillary phenomena [6]

The capillary pressure Δp_σ is connected with the average curvature radius of the meniscus surface, r_0, by the Laplace equation

$$\Delta p_\sigma = \frac{2\sigma}{r_0} = \frac{2\sigma\cos\theta}{r},$$

where $r = r_0/\cos\theta$ is the capillary radius [m], and θ is the contact angle of capillary surface wetting by water [rad]. The pressure difference Δp_g created by the water column in the capillary equals

$$\Delta p_g = \rho g h,$$

where ρ is the water density [kg/m^3], and $g = 9.8$ m/s^2 is the acceleration of gravity.

The height of the capillary rise of a liquid in the cylindrical channel that satisfies the condition $\Delta p_\sigma = \Delta p_g$ is determined by the Jurin formula

$$h = \frac{2\sigma\cos\theta}{\rho g r}.$$

The quantity $\frac{2\sigma}{\rho g}$ is a square of the capillary constant a ($a^2 = \frac{2\sigma}{\rho g}$; for water at 20 °C, $a = 3.8$ mm). Therefore, the Jurin formula can be rewritten as follows:

$$h = \frac{a^2\cos\theta}{r}.$$

The pressure difference in the capillary, Δp_μ, arising owing to the viscous friction forces at the laminar flow is determined by the Hagen–Poiseuille law,

$$\Delta p_\mu = \frac{8\mu V h}{\pi r^4},$$

where μ is the dynamic viscosity (for water at 20 °C, $\mu = 1.0$ MPa $\cdot$ s), and V is the volume flow of water through the capillary [m^3/s].

2.3. Adhesion-assisted rise of water in capillaries with r = const

If we conditionally suppose the capillary radius r to be constant (this is not typical of xylem), the pressure balance equation $\Delta p_\sigma = \Delta p_g + \Delta p_\mu$ brings us to the following expression:

$$\frac{2\sigma\cos\theta}{r} = \rho g h + \frac{8\mu V h}{\pi r^4}.$$

This relation makes it possible to express the water flow in the capillary with a constant cross-section,

$$V = \frac{\frac{2\pi r^3\sigma\cos\theta}{h} - \pi\rho g r^4}{8\mu}. \quad (1)$$

The analysis of this expression showed that it has an extremum at $r = r_{\rm opt}$, which can be found by zeroing the derivative dV/dr. As a result, we obtain the optimum radius value

$$r_{\rm opt} = 1.5\frac{\sigma\cos\theta}{\rho g h} = 0.75\frac{a^2\cos\theta}{h}$$

and the magnitude of the maximum water flow in the vertical capillary,

$$V_{\max} = \frac{27\pi}{2048}\frac{g}{\nu}\left(\frac{a^2\cos\theta}{h_{\max}}\right)^4. \quad (2)$$

3. Formulation of the Problem

The analysis of the analytical expression (2) for a water volume flow $V_{\max}$ shows that its maximum value and, accordingly, the maximum flux of dissolved mineral substances through a separate capillary of xylem is reciprocal to the fourth power of its length. This means that, for instance, the reduction of the capillary length (the plant height) by a factor of two results in the 16-fold ($2^4 = 16$) increase of the maximum water flow through the capillary due to the transpiration! In such a way, it turned out possible to increase the wheat crop capacity by more than an order of magnitude (the "wheat revolution" [7]) by selectively reducing the length of wheat stalk by hybridizing normal and dwarf wheat plants and preserving the ear length of normal wheat (that was the task for geneticists).

Therefore, this work aimed at the mathematical consideration of the transpiration mechanism of capillary transport in xylem and, using it as a basis, at the determination of the adhesion pump productivity for a capillary of variable radius, as well as its dependences on the channel length in xylem and the humidity of atmospheric air, by using the laws of molecular physics for capillary phenomena.

4. Results of Researches

4.1. Model of water rise in capillaries with the variable cross-section

By analyzing the Jurin formula, we can obtain an expression for the meniscus altitude in the capillary, which is valid for the channel with the variable radius and the threshold characteristics. It looks like

$$r = f(h) = \frac{a^2 \cos\theta}{h}.$$

However, this channel cannot provide the capillary transport in the plant xylem, because its profile does not involve losses for the viscous friction at the water flow, i.e. it can be used only in statics.

The profile of a capillary with variable radius, which can supply water from its lower cross-section to the upper one (the leaf stoma) owing to the water surface tension can be determined from the pressure difference balance between two capillary cross-sections located at the altitudes 0 and h: $\Delta p_\sigma = \Delta p_g + \Delta p_\mu$. Whence, at $r = f(h)$, we have

$$\frac{2\sigma\cos\theta}{r(h)} = \rho g h - \int_0^h \left(\frac{\partial p}{\partial h}\right)_\mu dh, \tag{3}$$

where the derivative in the integrand is determined from the Hagen–Poiseuille law in the differential form,

$$\left(\frac{\partial p}{\partial h}\right)_\mu = -\frac{8\mu V}{\pi r^4}.$$

The term-by-term differentiation of the expression obtained for the pressure balance with respect to the variable h (the current capillary length) results in the differential equation

$$\frac{dr}{dh} = -\frac{\frac{8\mu V}{\pi\rho g} + r^4}{r^2 a^2 \cos\theta}. \tag{4}$$

Separating the variables and integrating the differential equation that describes liquid laminar liquid flow against the gravitational forces in a cylindrical channel with variable radius, we obtain the capillary profile in the form of the dependence of the altitude of the meniscus rise in xylem, h, on the water volume flow V and the current capillary radius r,

$$h = \frac{b}{2c\sqrt{2}}\left(\operatorname{arctg}\frac{rc\sqrt{2}}{r^2 - c^2} + \operatorname{arcth}\frac{rc\sqrt{2}}{r^2 + c^2}\right), \tag{5}$$

where h is the distance from the groundwater line to the current capillary cross-section [m], r the current capillary radius [m], $b = a^2\cos\theta$ [m^2], $c = \sqrt[4]{\frac{8V\nu}{\pi g}}$ [m], and $v = \mu/\rho$ [m^2/s]. It is evident that, for $r \to \to r_{\min} = c$, we have $h \to h_{\max}$. Taking into account that $\operatorname{arctg}\infty = \frac{\pi}{2}$ and $\operatorname{arcth}\frac{\sqrt{2}}{2} \approx 0.8814$ [8], we obtain the expression

$$h_{\max} = \frac{b\left(\frac{\pi}{2} + 0.8814\right)}{2c\sqrt{2}} \approx 0.867\frac{b}{c}.$$

For the maximum liquid volume flow $V_{\max}$ through the capillary with the variable cross-section, we obtain the final expression

$$V_{\max} = \frac{2}{9}\frac{g}{\nu}\left(\frac{a^2\cos\theta}{h_{\max}}\right)^4. \tag{6}$$

A detailed analysis of the expressions obtained for $V_{\max}$ in the cases of an optimum capillary with the constant cross-section and a capillary with the variable cross-section showed that, provided other identical conditions, the maximum water flow through the capillary with the variable radius is 5.36 times larger than that through the optimum capillary with the constant radius. The analytical expressions for $V_{\max}$ do not contain the upper limit of the capillary length, i.e. the threshold tree height, in the both cases. However, it is well known that the capillary length in the xylem of high trees is confined: it amounts to about 150 m (for instance, the maximum height of eucalyptus reaches 120 m, and about 30 m fall to the share of its roots). At the same time, the dependence obtained above for the maximum water flow through the capillary does not give any limiting value for the minimum radius at its upper cross-section (the radius of a stoma at the leaf surface).

4.2. Estimation of the minimum capillary radius in the stomata of leaves

In order to calculate the minimum capillary radius in the stomata of leaves, let us use the well-known Thomson (Lord Kelvin) equation for the equilibrium vapor pressure P_s above a curved meniscus surface,

$$P_s = P_\infty \exp\left(-\frac{2\sigma M}{\rho R T r_0}\right), \tag{7}$$

where P_∞ is the equilibrium pressure of saturated vapor over the plane water surface at a given temperature (this parameter grows with the temperature, being equal to 1.4 and 1.6 kPa at temperatures of 12 and 14 °C, respectively), $r_0 = r/\cos\theta$ is the meniscus surface radius, r the stoma radius [m], θ the wetting angle of water on the capillary surface [deg], σ the water surface tension [N/m], ρ the water density [kg/m^3], $M = 18$ g/mol is the molar mass of water, T the absolute temperature [K], and $R = 8.3144$ J/(mol $\cdot$ K) is the universal gas constant. From this equation, we can determine the stoma radius,

$$r = \frac{2M\sigma\cos\theta}{\rho R T \ln\frac{P_s}{P_\infty}}. \tag{8}$$

It is evident that, in the course of transpiration, the pressure of saturated vapor over the meniscus, P_s, has to exceed the partial pressure of water vapor in the surrounding air, P_{part}. Its magnitude is usually given by the relative air humidity $\varphi = P_{\text{part}}/P_\infty$. Moreover, on the way of vapor from the meniscus surface to the surrounding air, there exists a pressure drop $\Delta P_D = P_s - P_{\text{part}}$, which is determined by the water flow in the stomata of leaves, $V_{\max}$, and the diffusion resistance R_D for vapor on its way from the meniscus surface to the surrounding air,

$$\Delta P_D = R_D V_{\max}\left(\frac{\rho''}{\rho'}\right),$$

where ρ'' and ρ' are the densities of vapor and liquid, respectively. Hence, the expression for P_s looks like

$$P_s = \varphi P_\infty + \Delta P_D. \tag{9}$$

Substituting it into expression (8), we ultimately obtain

$$r_{\min} = \frac{2M\sigma\cos\theta}{\rho R T \ln\left(\varphi + \frac{\Delta P_D}{P_\infty}\right)}. \tag{10}$$

The analysis of this formula shows that the minimum radius of stoma $r_{\min}$ is a positive value only in the case where the expression in the parentheses is larger than 1.

4.3. Estimation of threshold xylem parameters

The analysis of the results obtained above for the minimum capillary radius calculated from the Jurin and Thomson formulas shows that, on this basis, it is possible to find the final result of this research: the maximum length of capillaries in xylem, $h_{\max}$. As was shown above, $h_{\max}$ is obtained at $r_{\min} = c = \sqrt[4]{\frac{8V\nu}{\pi g}}$. Equating this value to expression (10) obtained from the Thomson formula and taking formula (6) into account, we obtain after some transformations that

$$h_{\max} = \frac{1}{C}\frac{RT}{Mg}\ln\frac{1}{\varphi + \frac{\Delta P_D}{P_\infty}}, \tag{11}$$

where the constant $C = \sqrt[4]{36\pi} \approx 3.26$. The dimensionless quantity $\frac{RT}{Mg}$ enters the well-known "barometric formula" (obtained for the first time by Laplace [10]) that looks like

$$p = p_0 \exp\left(-\frac{Mg}{RT}h\right) = p_0 \exp\left(-\frac{h}{H_{\text{as}}}\right), \tag{12}$$

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where $H_{\rm as} = \frac{RT}{Mg}$ is a characteristic size for the atmosphere (along the vertical), which is called the "altitude scale" and serves as the scale for the height h above the sea level.

A comparison of those formulas demonstrates that the expression for the total capillary length $h_{\rm max}$ contains, as a multiplier, the "altitude scale" that differs from the atmospheric "scale" by the absolute temperature value (for the atmospheric scale, this value is taken to equal 250 K) and the molar mass M ($M = 29$ g/mol for air). As a result, the calculation of the atmospheric "altitude scale" gives the value $H_{\rm as} = 7.5$ km. At the same time, the calculation for H_2O ($M = 18$ g/mol and, e.g., $t = 12$ °C) gives an even larger value, $H_{\rm vap} = 13.5$ km.

The analysis of formula (11) showed that the maximum length of capillaries in xylem is practically independent of the physical properties of water: the density, surface tension, and kinematic viscosity (except for M). Using this formula, one can estimate the maximum humidity of air, $\varphi_{\rm max}$, that can block the processes of transpiration and capillary transport in xylem. Exponentiating the both sides of Eq. (11), we obtain the expression

$$\varphi + \frac{\Delta P_D}{P_\infty} = \exp\left(-C\frac{h}{H_{\rm vap}}\right). \qquad (13)$$

Whence it is possible to obtain an expression for the maximum water flow through a capillary depending on the atmospheric air humidity φ,

$$V_{\rm max} = \left[\exp\left(-C\frac{h}{H_{\rm vap}}\right) - \varphi\right]\frac{\rho' P_\infty}{\rho'' R_D}. \qquad (14)$$

For the threshold air humidity $\varphi_{\rm max}$, we evidently have $V \to 0$, so that the diffusion pressure drop $\Delta P_D \to 0$. Therefore, we may write

$$\varphi_{\rm max} = \exp\left[\left(-C\frac{h}{H_{\rm vap}}\right)\right]. \qquad (15)$$

Whence, for the maximum height of giant trees (e.g., an eucalyptus or a sequoia) with the capillary length $h_{\rm max} = 150$ m, we obtain

$$\varphi_{\rm max} \approx \exp(-0.03623) \approx 96.44\%.$$

Hence, it is evident that even a high air humidity cannot block the transpiration process in the plant xylem.

5. Conclusions

In this work, a mathematical model for the transpiration mechanism of the capillary transport of water in a plant xylem is formulated. For its substantiation, a number of hypotheses are proposed to estimate the driving forces of the water flow both in soil and the plant xylem. By analyzing the balance of driving forces (capillary, gravitational, and viscous friction forces), a differential equation is derived for the liquid flow against the gravitational forces in a capillary with a variable radius depending on the channel coordinate. By integrating this equation, the profile of a capillary that provides the maximum transport capability for the aqueous solution of mineral substances in xylem is found. The corresponding maximum value is calculated to be 5.36 times larger than the optimum volume flow for a capillary with a constant cross-section. In addition, it turns out that the expression for the profile does not contain the threshold capillary length in xylem.

The maximum water flow in xylem elements is found to depend very strongly on the plant height: it is reciprocal to the fourth power of the capillary length. Therefore, the reduction of the capillary length (e.g., the tree trunk or the plant stern) by a factor of two increases the productivity of the adhesion pump by more than an order of magnitude (by a factor of 16). By analyzing the expression for the maximum capillary length, which was obtained with the use of the Thomson law, it was found that the length of elements in the plant xylem is practically independent of the physical properties of water: its density, surface tension, and kinematic viscosity (except for the molar mass). By analyzing the process of transpiration from the stoma of leaves in the framework of the Thomson law, it is established that the atmospheric air humidity practically does not affect the productivity of the adhesion pump and does not confine the maximum length of capillaries in xylem. Hence, it is proved that the threshold height of giant trees is, in effect, not confined by the transpiration mechanism of capillary transport in xylem. Therefore, it is evidently confined by absolutely different mechanisms associated with the sunlight energy absorbed by leaves within the daylight hours or with the strength of xylem (wood) structure.

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ТРАНСПІРАЦІЙНИЙ МЕХАНІЗМ КАПІЛЯРНОГО ТРАНСПОРТУ В КСИЛЕМІ РОСЛИН

Р е з ю м е

Стаття присвячена проблемі капілярного транспорту водного розчину мінеральних речовин у ксилемі рослин за рахунок процесу транспірації. На основі аналізу балансу рушійних сил (капілярних сил, сил тяжіння та сил в'язкого тертя) отримано та проінтегровано диференціальне рівняння течії рідини в ксилемі, що складається з капілярів змінного перетину. Отримано профіль вертикального капіляра змінного перетину для максимальних витрат води. На основі отриманої формули для мінімального перетину капіляра і закону Томсона для тиску пари над увігнутим меніском стоми листя отримано вираз для продуктивності адгезійного насосу в залежності від довжини капілярів ксилеми та вологості атмосферного повітря.