

COMMON PRINCIPLES IN CONSTRUCTION OF BIOLOGICAL NETWORKS

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Complex biological networks govern most functional properties at subcellular, cellular, tissue and organ levels. They appear at the early development stages of a growing organism at different physical and biological conditions, under biochemical and genetic control (Metzger 1999). Recent biophysical and morphometric data give us a detailed description of the topology, function and dynamics of biological networks. The most amazing discovery is the common design principles of the network construction in Nature including animal and plant tissues and organs (La Barbera 1990). One of the most investigated questions is structure of the long-distance transport systems which are designed for transport of liquid and dissolved substances on distances that are comparable to the characteristic size of the system.. The precise data on geometry of arterial and venous beds in mammals (La Barbera 1990; Pries 1995), conducting systems in leaves and roots of higher plants (Mitchison 1980; Kizilova 2001; McCulloh 2003), branches and shoots in trees (Honda 1978; Zhi 2001) trophic fluid transport systems in sponges (La Barbera 1990) and river basins (Pelletier 1999) reveal their similarity. In spite of the complicated topology of the networks a few mathematical principles underlie the patterns of structure, bifurcations and closed bops in the network organization (Zamir 1984; La Barbera 1990; Frame 1995). The principles correspond to the model of optimal branching tree-like pipeline which provide the liquid delivering at the minimal total costs on the liquid motion and the pipeline construction and maintenance.

In the present paper the statistical data on network geometry of the venation system of *Morus alba* leaf are presented. The mathematical model of the sap motion in the conducting system of a leaf is proposed. On the base of the solution of an optimization problem the principle of optimal construction of a bifurcation in plant leaf venation that correspond to Murray's law is obtained.

1. Network geometry description. Regularities in the vascular systems organization are investigated on special plastic casts, radiographic, x-ray images and tinted preparations. The lengths L_i , diameters d_i and branching angles α_i at each bifurcation as well as the number of vessels N_i of the same order i are measured (fig.1). The branching order is determined as follows:

1. The largest (the first) vessel possesses $i = 1$;
2. Two vessels with the branching orders l and k join into a parent vessel with the order

$$i = \begin{cases} l-1 & \text{at } l = k \\ \min \{l, k\} & \text{at } l \neq k \end{cases} \quad (1)$$

The following statistical dependences between the measured parameters have been obtained for different branching long-distance transportation systems in Nature:

1. *Murray's law* $d_0^\gamma = d_1^\gamma + d_2^\gamma$, where $d_{0,1,2}$ – the diameters of the parent and daughter's vessels at the bifurcation. For the most networks $\gamma \approx 3$ ($\gamma = 2.55 - 3.02$ for arterial, $\gamma = 2.76 - 3.02$ for venous, $\gamma = 2.61 - 2.91$ for respiratory systems) and the higher the animal's position at the evolutionary scale, the closer γ to $g = 3$ (Zamir 1986).

2. *Branching angles in a bifurcation*

$$\cos(\alpha_1) = ((1+\xi^3)^{4/3} + 1 - \xi^4) / (2(1+\xi^3)^{2/3}), \quad \cos(\alpha_2) = ((1+\xi^3)^{4/3} + \xi^4 - 1) / (2\xi^2(1+\xi^3)^{2/3}) \quad (2)$$

where $\xi = d_1/d_2 < 1$ – asymmetry of the bifurcation, $d_1 = \min \{d_{1,2}\}$.

3. The length-diameter relation $L_j = ad_j^b$, where a, b characterize the structure of the network.

For mammalian arterial beds $a = 2.60\text{--}7.59$, $b = 0.84\text{--}1.16$. For $b \sim 1$ and $L_i \sim d_i$, Murray's law for the vessels' lengths at a bifurcation is valid as well.

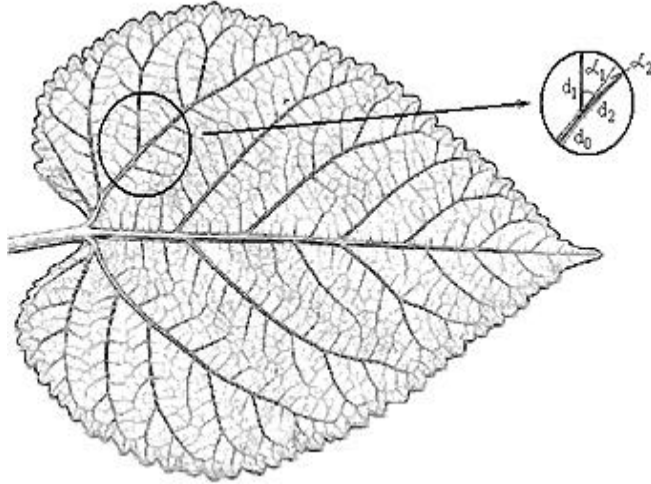


Figure 1. *Morus Alba* leaf venation and a schema of the bifurcation of the veins.

2. Statistical data on organization of the conducting system in plant leaves.

Geometry of a conducting system of fresh-cut *Morus Alba* leaves have been investigated on the scanned images using the computer methods of image analysis (SciImage 3b software). The branching orders of different veins have been established by the rules (1). The diameters, lengths and branching angles of the veins at different bifurcations have been measured. The dependences $\xi(d_0)$, $\lambda(d_0)$, $d(L)$, $A(K)$ where $\lambda = (d_1^3 + d_2^3)/d_0^3$, $K = (d_1^2 + d_2^2)/d_0^2$, $A = \cos(\alpha_1 + \alpha_2)$ have been investigated

and the corresponding coefficients a, b have been calculated with least squares method. As an illustration the dependences for one leaf (approximately 200-250 vein bifurcations) is presented in fig.2-5.

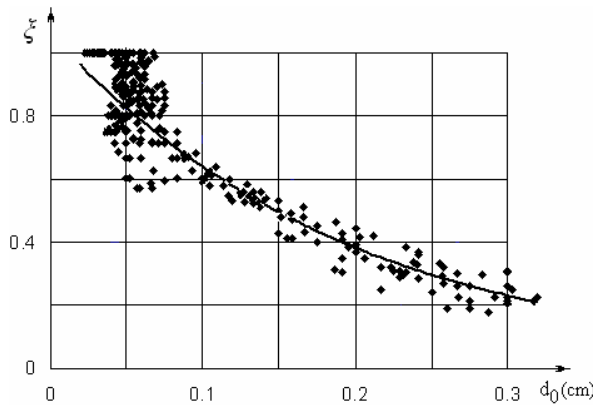


Figure 2. Dependence $\xi(d_0)$, $i = 1-3$.

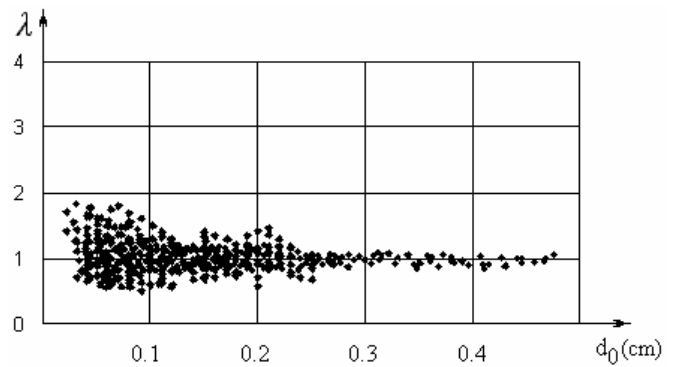


Figure 3. Dependence $\lambda(d_0)$, $i = 1-5$.

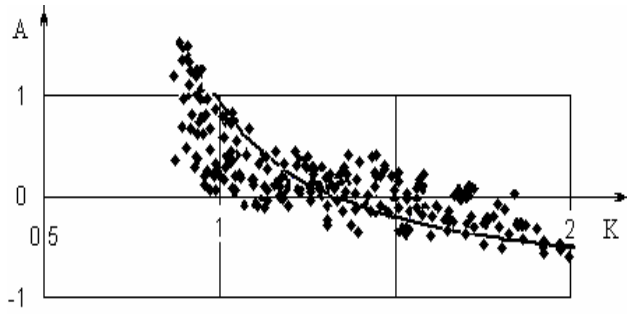


Figure 4. Dependence $A(K)$, $i = 1-4$.

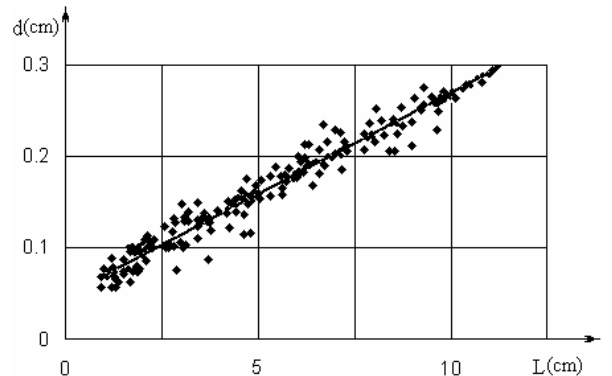


Figure 5. Dependence $d(L)$, $i = 1-3$.

The diameters $d_{j,0-2}$ in the bifurcations obey Murray's law at $\gamma \approx 3$ (fig.2-3). The numerical solution of the equation $(1 + (d_2/d_1)^\gamma)(d_1/d_0)^\gamma = 1$ that follows from Murray's law, give $\gamma = 2.72 - 3.08$ for 42 specimens of *Morus Alba* leaf. The branching angles correspond to the optimal values (2) (solid line in fig.4). The relation $d(L)$ between the geometrical parameters L , d of the separate conducting elements is linear (fig.5). Comparative analysis of the data for *Morus Alba* (fig.2-5), *Cotinus obovatus* (Kizilova 2003) as well as for some other leaves (Kizilova 2000) and mammal vascular systems (Zamir 1984, 1986) shows, that both transport structures are characterized by a similar kind of statistical dependences. It means that construction of long-distance transport systems governs by the same design principles in animals and high plants. The conclusion is quite amazing for the developmental ways of the plants and animals have been departed since the earliest stages of evolution at single-cellular level.

3. Model of an optimal bifurcation of the tubes with permeable walls. Axisymmetric steady motion of a viscous fluid through a single bifurcation (fig.1) of vessels with permeable walls is considered. Each vessel is represented as a thin long round tube ($d_j / L_j \ll 1, j = 0 - 2$). At $Re \ll 1$ the mass and impulse continuity conditions in the cylindrical coordinate system (r, ϑ, x) that is connected with the tube are the followings

$$\frac{1}{r} \frac{\partial}{\partial r}(rV_r) + \frac{\partial V_x}{\partial x} = 0, \quad \frac{dp}{dx} = \mu \left(\frac{\partial^2 V_x}{\partial r^2} + \frac{1}{r} \frac{\partial V_x}{\partial r} \right) \quad (3)$$

where p is pressure, $\vec{V} = (V_r, 0, V_x)$ is velocity, μ is viscosity of the fluid. The boundary conditions are defined as:

$$\begin{aligned} V_x|_{r=R} &= 0, & \frac{\partial V_x}{\partial r}|_{r=0} &= 0, \\ V_r|_{r=0} &= 0, & V_r|_{r=R} &= w \end{aligned} \quad (4)$$

$$p|_{x=0} = p_1, \quad p|_{x=L} = p_2 \quad (5)$$

where w is the outflow speed. By integrating (3) with respect to r taking into account (4), we shall receive:

$$V_x = -\frac{1}{4\mu} \frac{dp}{dx} (R^2 - r^2), \quad V_r = \frac{1}{16\mu} \frac{d^2 p}{dx^2} (2R^2 r - r^3) \quad (6)$$

and the equation for the pressure field:

$$\frac{d^2 p}{dx^2} = \frac{16\mu w}{R^3} \quad (7)$$

Pressure is obtained from (7), (5) as

$$p^{(1)}(x) = p_1 - Z^p \left(\left(\frac{p_1 - p_2}{Z^p} + \frac{\Phi}{2} \right) y - \frac{\Phi}{2} y^2 \right) \quad (8)$$

at $w = w_0 = \text{const}$ and

$$p^{(2)}(x) = p_1 - Z^p \left(\frac{p_1 - p_2}{Z^p} y + \Phi \left(\frac{2}{3} y - y^2 + \frac{y^3}{3} \right) \right) \quad (9)$$

at $w = 2w_0(1 - y)$, where $y = x/L$ or, in other form

$$p^{(1)}(x) = p_1 - Z^p (Qy - \Phi y^2 / 2), \quad p^{(2)}(x) = p_1 - Z^p (Qy - \Phi(y^2 - y^3 / 3))$$

where $Q = 2\pi \int_0^R r V_x(r,0) dr$, $Z^P = 128\mu L / (\pi d^4)$, $\Phi = \Sigma w_0$. In both cases of w distribution

along the wall the full outflow $\Phi = \pi d L w_0$ remains the same. Substitution (8), (9) in (6) gives the velocity fields. Hence it follows that the hydraulic resistance $Z = (p_1 - p(L)) / Q$ of the tube is $Z^{(1)} = Z^P (1 - \Phi / (2Q))$, $Z^{(2)} = Z^P (1 - 2\Phi / (3Q))$

For a symmetrical bifurcation ($L_2 = L_1$, $d_2 = d_1$) of the tubes with diameters $L_{0,1}$ and lengths $d_{0,1}$, Poiseuille's law for the tubes in a bifurcation is $p_1 - p_2 = Q_1 Z_1$, $p_2 - p_3 = Q_2 Z_2$, where Q_1 , $Q_2 = (Q_1 - \Phi_1) / 2$, $Z_{1,2}$ are the volumetric rates at the inlet and the hydraulic resistances of the tubes with $i=1$ and $i=2$, $p_1 = p(0)$, $p_2 = p(L_1)$, $p_3 = p(L_1 + L_2)$. The x -axis is continuous along two tubes and $x \in [0, L_1]$ for the first-order tube and $x \in [L_1, L_1 + L_2]$ for the second-order ones. Hence it follows for the total hydraulic resistance $Z = (p_1 - p_3) / Q_1$ of the bifurcation:

$$Z^{(1)} = Z_1^P + Z_2^P \frac{\Phi_1}{2Q_1}, \quad Z^{(2)} = Z_1^P + Z_2^P \frac{2\Phi_1}{3Q_1}$$

Here $Z = Z(L_{1,2}, R_{1,2}, w_0, Q_1)$ at the constant w_0, Q_1 depends on the bifurcation geometry only. The extreme problem for a bifurcation can be considered in the form of

$$Z(L_{1,2}, R_{1,2}) \rightarrow \min, \quad G(L_{1,2}, R_{1,2}) = \text{const} \quad (10)$$

where G is a geometrical restriction. Problem (10) for $G = \{V, S, D\}$, where V - full volume, S - full lateral surface, D - full dissipation in the system, and a few other criteria was solved for a single tube and a bifurcation of tubes with non-permeable walls as applied to the arterial vessels. As a result the criteria $G = \{V\}$ fit the experimental data best of all. Problem (10) with a number of criteria G was solved for a single tube with permeable walls as applied to plant leaves and the same result was obtained (Kizilova 2000, 2003). Taking into account this conclusion, we consider here the problem (10) with $G = \{V\}$ as applied to the bifurcation of tubes with permeable walls. The Lagrange function is $\Omega = Z + \lambda G$. The conditions $\Omega'_{L_{1,2}, R_{1,2}} = 0$ bring finally to the nonlinear system of equations $\{f_i(r, l) = 0\}$, where $r = d_0 / d_1$, $l = L_0 / L_1$. In contrast to the tubes with non-permeable walls the relative diameters and lengths are not independent here. The results of the numerical solution of this system are presented in Fig.6. Different curves correspond to the different pairs (Z_j, V) of optimal criteria in (10), where $j=0$ correspond to the motion in the tube with non-permeable walls, $j=1,2$ - the tube with permeable walls at $w = w_0 = \text{const}$ and $w = 2w_0(1-y)$ respectively. Two solid lines in fig.6 correspond to the upper and lower boundaries of the measured data ($r \in [1.35; 1.89]$, $l \in [0.25; 2.97]$) (Kizilova 2000) for a number of leaves with different venation types including *Morus Alba* leaf.

The models of the optimal bifurcation of the tubes with permeable walls both at constant and linearly decreasing functions w agree closely with the measured data. Two cases of $w(y)$ slightly differ. For comparison the results of solution of the problem (10) at $G = S$ are presented in fig.6 as well. All these curves lie closely to parameters of the optimal bifurcation of tubes with impermeable walls and do not agree with the real data. Consequently the model of optimal bifurcation of the tubes with permeable walls, which deliver the liquid with a minimal hydraulic

resistance at a given volume is best suited to the measured data. This model perfectly corresponds to physics of the sap motion through the vein systems of the leaves.

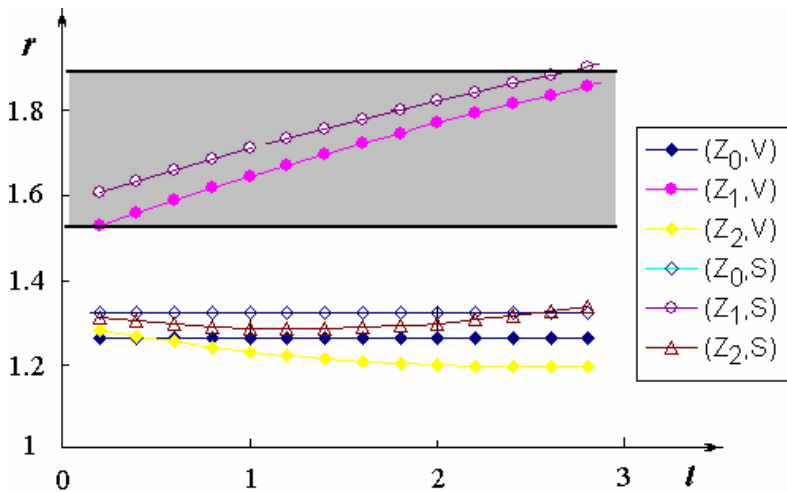


Figure 6. The dependences $r(l)$ for different optimal symmetrical bifurcations.

Conclusions. The branching long-range transport systems in mammal tissues and high plants are statistically identical, obey some relations including Murray's law and correspond to the model of the optimal pipeline which provided liquid delivering at the minimal total cost. The validity of Murray's law can be explained within the frames of the presented mathematical model of sap motion in plant vessels and the solution of the optimization

problem. The solutions for the optimal pipelines which deliver water at minimal hydraulic resistance at a given total volume of the pipeline with either permeable or impermeable walls lie quite close each other and approximate the measured data perfectly.

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