R. Takaki

(b)

1 magnolia hydrangea 1 2 3 order

Fig. 10. Examinations of Horton's law for three leaf veins. (a) Single leaves of fern, magnolia and hydrangea. The fern leaf is divided into many parts and forms a tree shape, while the other two leaves include network structures. (b) Horton's law with a common bifurcation ratio of about 14 (reproduced from Takaki (1978)).

has been investigated since many years. In the following a short review is given based on the article by Kamiya and Togawa (1973). As for the branching of blood vessels, Thompson (1917) gave some qualitative rules as follows, which are seen in most blood vessels:

(1) When a mother vessel branches to two daughter ones, cross-sectional area of the mother is smaller than the sum of the daughters' areas.

(2) When the cross-sectional areas of daughters are equal, their angles of deviations from the direction of the mother are equal.

(3) When one daughter has smaller cross-sectional area than the other, it has a larger deviation angle than the other daughter.

More precise study of the branching rule was made by Murray (1926a, b). He considered two kinds of cost for blood vessels to maintain its roles; one is the power to transport the blood and the other is a metabolic cost to refresh the blood. If these costs are considered for a single duct with radius r and length l filled with blood, the former is a product of flow rate f and the pressure difference Δp , while the latter is proportional to the volume V of the duct, hence the cost function CF is expressed as

$$CF = f\Delta p + kV$$
, where $\Delta p = \frac{8\mu}{\pi} \frac{fl}{r^4}$, $V = \pi r^2 l$, (5)

and μ and k are the blood viscosity and an unknown constant, respectively. The formula for the pressure difference is derived by minimizing CF, i.e. from $\partial CF/\partial r = 0$, and we have the following expression for the flow rate:

$$f = \sqrt{\frac{\pi^2 k}{16\mu}} \cdot r^3 \propto r^3. \tag{6}$$

If we consider a branching of vessels as shown in Fig. 11 with radii and flow rates of mother and daughters r_0 , r_1 , r_2 and f_0 , f_1 , f_2 , respectively, we have $f_0 = f_1 + f_2$, hence we have

$$r_0^{3} = r_1^{3} + r_2^{3}.$$
 (7)

From this result we can derive $r_0^2 = r_1^2 \cdot r_1 / r_0 + r_2^2 \cdot r_2 / r_0 <$ $r_1^2 + r_2^2$, which agrees with the assertion (1) of D. Thompson. An experimental value 2.7 of the index in Eq. (7) was obtained (instead of 3) by Suwa and Takahashi (1971). A comment is given here on the index 3 in Eq. (7). If it is 2, the sum of cross sectional areas of daughters after branching is equal to that before branching. However, owing to the viscosity of blood the flows in narrow daughters the blood receives strong resistance, which results in loosing much energy. Therefore, the value 3 of the index assures an effective flow distribution.

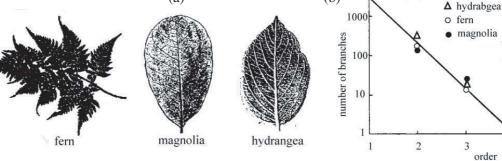
Furthermore, by minimizing the CF for the combination of three ducts as shown in Fig. 11 through varying the coordinates (x, y) of the connection point B, Murray (1926a, b) obtained the relations between θ_1 , θ_2 and r_0 , r_1 , r_2 , as follows:

$$\cos\theta_{1} = \frac{r_{0}^{4} + r_{1}^{4} - r_{2}^{4}}{2r_{0}^{2}r_{1}^{2}}, \quad \cos\theta_{2} = \frac{r_{0}^{4} + r_{2}^{4} - r_{1}^{4}}{2r_{0}^{2}r_{2}^{2}}, \cos(\theta_{1} + \theta_{2}) = \frac{r_{0}^{4} - r_{1}^{4} - r_{2}^{4}}{2r_{1}^{2}r_{2}^{2}}.$$
(8)

These results agree with the assertions (2) and (3) of Thompson (1917).

Kamiya and Togawa (1972, 1973) proposed another theory for the condition at the branching for the following reason. Blood vessels are connected at the end to tissues through the capillary system, where the blood pressure must balance with the pressure of tissue or osmotic pressure there. On the other hand, the pressure at the beginning, i.e. the heart, is also fixed. In addition, the flow rate of blood must be adjusted to the needs from tissues. Therefore, in order to consider the optimal design of blood vessels, it is not meaningful to include the transportation cost of blood. Hence, they considered only the volume of blood. They chose three quantities x, y and r_0 in Fig. 11 as variables for optimization. Reason of the choice of r_0 for optimization is not mentioned in their paper. According to the guess of the present author, they fixed the sizes of narrow vessels at tissues and tried to construct thicker blood vessels.





(a)