

p in similar pressure units, that R_L and R_V are dimensionally similar; however, nothing is learned by comparing their magnitudes since they refer to physically dissimilar phenomena. What is required is a comparison of the effect on flow of a relative change in R_V with a similar relative change in R_L . From the relation $V_0 dP_w = v_0 dp_w$, where V_0 and v_0 are the specific volumes of liquid water and water vapour respectively,

$$\frac{R_V}{R_L} \cdot \frac{(\partial f/\partial R_V)R_L}{(\partial f/\partial R_L)R_V} = \frac{R_V}{R_L} \cdot \frac{v_0}{V_0}$$

Professor Levitt discusses an example in which $R_V/R_L = 1/2,500$. $v_0/V_0 = 33,000$ (at 30° C), however, and thus a change in resistance to vapour flow will alter the transpiration rate 13 times more than a similar relative change in the resistance to liquid flow. van den Honert's argument exaggerates the relative importance of R_V ; nevertheless, his conclusion remains qualitatively correct. Indeed, were it not for this and the large energy requirement for vaporization, few land plants could survive.

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¹ Levitt, J., *Nature*, **212**, 527 (1966).

Resistance to Water Transport in Plants

DR. LEVITT¹ directly compares a resistance for flow of liquid water with one for gaseous diffusion of water vapour. A comparison of the resistances in the plant tissues with those in the gaseous phase is, however, only possible even as an approximation if both are expressed in terms of the same fluid. If this comparison is made in terms of water vapour we can specify, for each part of the system that is considered separately, an equivalent air path; this is a tube of air of unit cross-sectional area of such a length that, with the equivalent potential difference (ΔP) maintained between its two ends, it would allow the same net flow of water as that observed to pass through the system in the steady state.

For diffusion of water vapour in such a tube of air

$$\frac{P_T V}{t} = \frac{K.A.(P_1 - P_2)}{l}$$

where P_T is the total pressure (atm), $\frac{P_T V}{l}$ is the volume (cm³) of water vapour calculated as at unit pressure passing through the tube in time t (sec), K is the diffusion coefficient for water vapour (cm² sec⁻¹), A is the cross-sectional area (cm²) and l is the length (cm) of the tube and $P_1 - P_2$ is the difference in partial pressure (atm) of aqueous vapour between the two ends. The rate of flow $\frac{P_T V}{t}$ is thus in terms of cm³ sec⁻¹ of aqueous vapour calculated as at unit pressure and at the temperature of the experiment. The resistance is

$$\frac{(P_1 - P_2) t}{P_T V} = \frac{l}{KA} = R \text{ sec cm}^{-3} \tag{1}$$

The expression used by van den Honert² was

$$\frac{dm}{dt} = \frac{P_1 - P_0}{R_r} = \frac{P_2 - P_1}{R_x} = \frac{P_3 - P_2}{R_l} = \frac{P_4 - P_3}{R_g}$$

or for the whole system

$$\frac{dm}{dt} = \frac{P_4 - P_0}{R_r + R_x + R_l + R_g} \tag{2}$$

Here dm/dt (in unspecified units) was the rate of water transport in the steady state, $P_1 - P_0$ to $P_4 - P_3$ were potential differences in terms of diffusion pressure deficit (atm) and R_r, R_x, R_l and R_g were resistances (again in unspecified units) for the roots, xylem, leaves and gaseous phase respectively. dm/dt can be equated to $\frac{P_T V}{t}$ and

the equivalent partial pressures of aqueous vapour (atm) can be substituted for diffusion pressure deficits, with a change of sign.

We can then use equation (1) to calculate the resistance in the plant ($R_r + R_x + R_l$) with potential difference ($P_0 - P_3$) and that in the gas phase (R_g) with ($P_3 - P_4$). The ratio of these resistances is obviously $(P_3 - P_4) \div (P_0 - P_3)$; in the example given by Dr. Levitt this ratio is 13 : 1, whereas for the osmotic potential differences the ratio was 20 : 1. The arbitrary choice of water vapour or liquid water as the basis for comparison thus leads to different values, showing that the method is at best very approximate. The difference arises from the logarithmic relation between osmotic pressure and equivalent vapour pressure; there is, at least, no doubt as to the part of the system with the greatest resistance.

In making these calculations it must be assumed that the environment provides a heat flow to the leaves at a rate just sufficient to maintain the system isothermal, with the production of $P_T V/t$ cm³ sec⁻¹ of water vapour.

Although van den Honert² reached a correct qualitative conclusion as to the relative magnitude of the resistance in the plant and gaseous phase, respectively, he did not state at all clearly the implications for the survival of the plant. He suggested that control of rate of water transport in the plant could only be effective in the gaseous phase, that is, reduction of stomatal aperture, and wrote: "If, for instance, the filtration resistance of the roots is increased, it will have little effect on the rate of water transport; its only effect will be an increase of diffusion pressure deficit in the whole plant". That would, however, depend on the absolute increases in resistance that could be achieved in the two phases, and if equation (2) could be accepted it is obvious that the same absolute increase in any of the resistances would have the same effect on steady state flow. If the resistance in either phase became infinite, water transport would, of course, come to an end. The important difference is that the main effect of resistances in the liquid phase, with the exception of that for the final path from the mesophyll cell to the intercellular space system of the leaf, is to restrict the replacement of the water lost by transpiration; resistances in the gaseous phase restrict that loss. Thus, the former may be considered "harmful" resistances and the latter "protective". A large increase of resistances in the liquid phase would reduce transpiration, but the leaves could be killed and desiccated before a steady state was reached.

Whether water movement through plants obeys the Ohm's law analogy must be tested experimentally by finding whether rate of flow is directly proportional to potential difference. There is some evidence that it is not^{3,4}, and for such a heterogeneous and non-rigid system as a plant perhaps this is not surprising.

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¹ Levitt, J., *Nature*, **212**, 527 (1966).

² Honert, T. H. van den, *Disc. Farad. Soc.*, **3**, 146 (1948).

³ Brouwer, R., *Symp. Soc. Exp. Biol.*, **19**, 131 (1965).

⁴ Mees, G. C., and Weatherley, P. E., *Proc. Roy. Soc.*, **B**, **147**, 367 and 381 (1957).