

Interaction between Osmotic- and Pressure-induced Water Flow in Plant Roots

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ABSTRACT

When the pressure gradient across a root alters, there is often an apparent change in the permeability of the root to water. Fiscus (Plant Physiol. 1975. 55: 917-922) has suggested that this can be explained by a simple two-compartment model which takes into account rates of solute uptake into the xylem. A method of testing actual data against the Fiscus model is proposed; this shows that in some cases the apparent changes in permeability cannot be explained by the model. The model is not adequate to predict the amounts of solute reaching the xylem by passive drag: a three-compartment model would be more realistic.

When the difference in hydrostatic pressure between the inside of a root and the outside medium changes, there is often an apparent change in the resistance of the root to water flow. Fiscus (5) has presented a model of water and solute entry into a root, which he offers as an explanation for these apparent changes in resistance. In his model, the root has a single inner compartment separated from the external solution by a single membrane, across which active solute transport occurs at a constant rate, J_s^* . The rate of water uptake, J_v , is

$$J_v = L_p(\Delta P - \sigma \Delta \pi) \quad (1)$$

where L_p is the permeability of the membrane and σ its reflection coefficient, ΔP and $\Delta \pi$ are the difference in hydrostatic pressure and osmotic potential, respectively, between the outer solution and inner compartment (π values are taken as positive). In addition to active solute uptake, solute can enter the inner compartment by passive drag, when $\sigma < 1$. By calculating rates of solute entry, Fiscus derives from equation 1

$$J_v = L_p \left(\Delta P - \frac{2\sigma^2 \pi_0}{1 + \sigma} \right) + \frac{2\sigma L_p R T J_s^*}{J_v (1 + \sigma)} \quad (2)$$

where π_0 is the osmotic potential of the external medium, R is the gas constant and T the absolute temperature. Using this formula, the predicted relationship between J_v and ΔP can be plotted, for various values of the other parameters. The relationship is curved (unless $\sigma = 0$); Figure 1, line A, shows one example. Fiscus has given useful illustrations of how the degree of curvature will vary with different values of the parameters in equation 2.

My aim here is to demonstrate that Fiscus' model cannot explain all the reported cases of apparent change of root resistance with changing ΔP . It is worth noting that variable resistance has been demonstrated with fairly young plants, mostly herbaceous species in which L_p is likely to be in the range $0.5 - 10 \times 10^{-7} \text{ cm sec}^{-1} \text{ bar}^{-1}$ (11) and $J_s^* 0.5 - 10 \times 10^{-11} \text{ mole cm}^{-2} \text{ sec}^{-1}$ (based on reference 2). These, according to Fiscus' Figure

5, are values for which the degree of curvature in the J_v versus ΔP graph is relatively small. In actual experiments when J_v and ΔP have been measured, L_p and J_s^* are not known. However, there is a test which can be applied to the data. As J_v increases, the right hand term of equation 2 tends to 0. Therefore, the curve is asymptotic to a straight line, (B in Fig. 1), given by

$$J_v = L_p \left(\Delta P - \frac{2\sigma^2 \pi_0}{1 + \sigma} \right) \quad (3)$$

This cuts the abscissa at

$$\Delta P = \frac{2\sigma^2 \pi_0}{1 + \sigma} \quad (4)$$

The value of σ is usually unknown, but $2\sigma^2/(1 + \sigma)$ cannot be more than 1. Therefore the following test can be applied. Plot J_v against ΔP ; draw a straight line as a tangent to any part of the curve. If any such line cuts the abscissa to the right of $\Delta P = \pi_0$, then the curvature cannot be entirely explained by Fiscus' model.

Fiscus claimed that his model could simulate the data of Lopushinsky (8) for tomato. Applying the above "tangent test" to Lopushinsky's four graphs, the upper part of the curve extrapolates back to $\Delta P = 0.5-0.7$ bar, whereas π_0 was 0.4 bar. Therefore the curvature in Lopushinsky's data cannot be explained by Fiscus' model. If one accepts pressure chamber measurements of leaf water potential as adequate measures of xylem pressure potential, the tangent test can be applied to other data: results for cotton (1) and pear (3) cannot be explained by Fiscus' model. On the other hand, results from detopped root systems of tomato, bean, and cotton (9, 13) are not rejected by the test. Of three experiments on *Vigna sinensis* (7), the results of one do not fit, according to the tangent test, but the other two do.

Fiscus suggested that his model could explain the data of Mees and Weatherley (9) for tomato, by choice of a suitable value of σ . Although the tangent test applied to these data does not reject Fiscus' model, there is other evidence to reject it. Mees and Weatherley's data (10) allow calculation of σ for some tomato plants; it averaged 0.76. In their results values for all the other parameters in equation 1 except L_p are given, and one can easily show that L_p must have changed as ΔP was increased. I have published an example of the calculations elsewhere (Table 14.10 in ref. 12). Even if one assumes that the value $\sigma = 0.76$ may not apply to these plants, one can solve equation 1 simultaneously for two values of ΔP . Applied to each of the three sets of data of Mees and Weatherley (Fig. 5 in ref. 9) this gives impossible values of σ (i.e. above 1 or below 0) for part of the measured range, and for two of the three sets L_p is not even approximately constant between different pairs of ΔP values. Thus unless we assume Mees and Weatherley's measurements of xylem osmotic potential to be seriously wrong, there is no way of making their data fit Fiscus' model.

Fiscus also predicts the total solute flux into the xylem, for

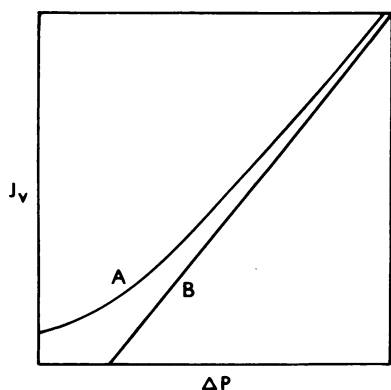


FIG. 1. Line A shows a predicted relationship of rate of water flow into root (J_v) to hydrostatic pressure difference between external medium and xylem (ΔP); this curve is asymptotic to line B.

different values of σ and ΔP . Here I believe his model is inadequate for quantitative predictions. He has presented a two-compartment model, *i.e.* a single membrane separates the outside solution from the xylem contents. It is almost certain that in real roots most water reaches the xylem by crossing two membranes, possibly more. There is a middle compartment, which may for example be the cells of the endodermis, in which the osmotic potential, π_m , is much higher than in the external solution or the xylem. There are two reasons why a root might have $\sigma < 1$ for transport from the outside to the xylem: (1) there might be pathways by which some of the water avoids crossing any membrane; (2) the membranes themselves might have $\sigma < 1$. On the three-compartment model the amount of solute reaching the xylem by passive drag will differ between these two cases, since in the first case the external solution is involved in drag into the xylem, whereas in the second case the much higher concentration from the middle compartment is involved. Ginsburg (6) has suggested a three-compartment model in which the reflection coefficient of the inner membrane is lower than that of the outer membrane. If $\sigma = 1$ for the outer membrane and $\sigma < 1$ for the inner, this could explain how solute transport into the xylem can be influenced by the rate of water uptake, due to drag across the inner membrane, and yet leakage from cells or xylem to the outside, which would be expected in a root when $\sigma < 1$, fails to occur.

It is unlikely that this three-compartment model can offer any further explanation for apparent changes in root resistance to water flow. If we assume, following Ginsburg (6), that π_m , the osmotic potential of the middle compartment, remains constant, and also, for the sake of simplicity, that the two membranes have equal L_p , then the corresponding equation to equation 2 is

$$J_v = L_p \left(\Delta P - \frac{2\sigma_2^2 \pi_m}{1 + \sigma_2} - \sigma_1(\pi_0 - \pi_m) \right) + \frac{2\sigma_2 L_p R T J_s^*}{J_v(1 + \sigma_2)} \quad (5)$$

where σ_1 and σ_2 are for the outer and inner membranes, respectively. Applying the tangent test, this extrapolates to the abscissa where

$$\Delta P = \frac{2\sigma_2^2 \pi_m}{1 + \sigma_2} + \sigma_1(\pi_0 - \pi_m) \quad (6)$$

This could only be $> \pi_0$ if $\sigma_1 < \sigma_2$ which is unlikely, so the tangent test is still likely to be valid. Fiscus assessed the degree of curvature in the J_v versus L_p relationship by changes in $d\Delta P/dJ_v$. From equation 5

$$\frac{d\Delta P}{dJ_v} = \frac{1}{L_p} + \frac{2\sigma_2 R T J_s^*}{(1 + \sigma_2) J_v^2} \quad (7)$$

which is identical to Fiscus' equation 15, except that σ_2 replaces σ . Therefore the changes in curvature predicted by the two-compartment and three-compartment models are essentially the same.

Dalton *et al.* (4) have independently proposed a model which is similar to Fiscus' and is open to similar criticisms.

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