

Effects of Coupled Solute and Water Flow in Plant Roots with Special Reference to Brouwer's Experiment¹

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ABSTRACT

This paper presents a further examination of the effects of coupled solute and water flow as it applies to plant roots. A cylindrical two-compartment membrane root model can account for many diverse root phenomena. Among these are (1) non-linear pressure flow, (2) interval osmotic dilution, (3) negative resistance effects, (4) non-osmotic water flux, and (5) the internal osmotic compensation effect. In addition, we have now demonstrated that the same model is capable of reproducing the complex patterns of root resistance profile change noted by some workers. In none of these instances is there need to invoke any change in the hydraulic conductivity of the system to explain the observed effects. The only features necessary to explain these phenomena are a membrane-like structure and a mechanism for actively accumulating solutes.

INTRODUCTION

Studies of water uptake by roots or root systems have revealed that the relationship between the driving forces, whether osmotic or hydrostatic pressures or both, and water flow, display some rather complex patterns. We can organize these patterns into groups and illustrate them with specific examples.

First are the experiments of Lopushinsky (1961, 1964) and Mees and Weatherley (1957) in which nutrient solution was driven through detached tomato root systems by applying an increased hydrostatic pressure to the outer surface of the roots. The resultant exudate was collected from the cut stump which protruded to the outside of the pressure vessel. In both laboratories it was noted that increases in the applied pressure caused disproportionate increases in flow. That is, it appeared as though the resistance to flow was decreasing with increasing flow rates. We will call this effect non-linear pressure flow.

At the same time, these investigators noted that the concentration of the exudate decreased dramatically with increased volume flow, frequently falling to a small fraction of the concentration in the root medium. This is the so-called internal dilution effect which is caused by greater increases in water transport relative to the transport of solutes.

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Furthermore, Mees and Weatherley (1957) calculated the osmotic pressure difference between the exudate and the root medium ($\Delta\pi$). When this was added to the hydrostatic pressure difference (ΔP) to give the total potential difference ($\Delta\Psi$), they found in at least one experimental instance that an increase in volume flow was associated with an actual *decrease* in the total water potential difference. This *negative resistance* effect has been confirmed in our laboratory (unpublished) with maize (*Zea mays* L. cv. Pioneer 3369A) and soybean (*Glycine max* cv. Ransom).

Most of the other relevant experiments involved the use of excised terminal root segments. In the absence of an hydrostatic pressure gradient, the flow (root pressure exudation) was controlled by changing the external osmotic concentration. The osmotic potential of the exudate may be measured and the osmotic difference across the root calculated. When the osmotic difference is calculated in this manner and plotted against the exudation rate the relationship usually appears to be linear and frequently has a positive intercept on the flow axis (Anderson and Collins, 1969; Anderson and Reilly, 1968; Ginsburg and Ginzburg, 1971; House and Findlay, 1966). This presumed positive flow rate in the absence of an osmotic pressure difference represents the so-called non-osmotic water flux.

This type of experiment is also useful for demonstrating the internal osmotic compensation effect. This effect becomes apparent when the steady state exudation rate is modified by changing the osmotic concentration of the root medium. If the external osmotic concentration is increased the steady state flow rate is decreased due to the decreased osmotic gradient. However, active uptake of solutes will continue with the result that the steady state osmotic gradient is maintained in the proper direction and steady state flow can continue but at a reduced rate and yielding a more concentrated exudate (Klepper, 1967). Thus, barring damage or physiological changes in the root tissue, it should not be possible to completely halt steady state flow by the addition of an external osmotic agent as long as there are solutes available for active accumulation.

The final type of observation is typified by the experiment of Brouwer (1954) in which he demonstrated a rather complex pattern of velocity-dependent permeability changes in the roots of *Vicia faba*. This was accomplished by measuring water uptake through adjacent segments of a single root while the internal suction tension of the root was varied by changing the transpiration rate of the shoot, or the external osmoticum around the rest of the root system. The results of such an experiment showed two basic patterns of permeability changes. In the apical 2.5 cm he found an initial increase in permeability followed by a decrease to a plateau at high rates of flow. In the three more basal segments (2.5 cm each) he found consistent increases in permeability with flow at lower flow rates after which the permeability again reached a plateau at higher flow rates. Any general model describing water flow through root systems must account at least in principle for all of the above observations.

Dalton, Raats, and Gardner (1975) and Fiscus (1975) have proposed very similar models for coupled solute and water flow through plant roots which are based on two frequent observations: (1) there is a structure or combination of structures in the root which functions as a differentially permeable membrane; and (2) this mem-

brane has the ability to bring about accumulation of solutes in the root interior far in excess of the external concentrations. By taking the concentration of solutes in the root interior as the ratio of the entry rates of solute and water we have

$$C^i = J_s / J_w \quad (1)$$

Where C^i is the concentration of the inside compartment in mol cm⁻³, J_w is the flow of water in cm s⁻¹ which is taken as the total flow of volume J_v , and J_s is the total solute flux in mol cm⁻² s⁻¹ which includes terms to account for the diffusive, drag, and active solute uptake (J_s^*) components. From this we were able to derive relationships which could account for the non-linear nature of the water flow as well as the internal dilution and negative resistance effects noted above for systems subjected to hydrostatic pressures. Also, for those systems not under external hydrostatic pressures, the internal osmotic compensation effect is a natural consequence of this treatment (Fiscus, 1975). Extension of this simple membrane model to a cylindrical system led Fiscus and Kramer (1975), in agreement with the previous work of Anderson, Aikman, and Meiri (1970), to suggest that these principles could also account for the so-called non-osmotic water uptake in excised root segments. We now propose that the use of these same principles can supply a logical and straightforward explanation of the complex root resistance profile changes reported by Brouwer (1954).

MATERIALS AND METHODS

With regard to Brouwer's experiments, the problem reduces to the question of what factor or combination of factors could lead to increases in apparent permeability at low flow rates followed by decreases at higher flow rates in one segment, and more consistent increases in permeability over the entire range of flows in the adjacent segment. To answer this question we may turn again to the cylindrical model of Fiscus and Kramer (1975) which is based on the diversion of the root into cylindrical subunits of arbitrary length l , and sequential summing of the solute and water flows for each subunit. Volume flow (J_v) through the radial walls of each subunit is based on the well-known membrane transport equation:

$$J_v = L_p[\Delta P - \sigma RT(C^o - C^i)] \quad (2)$$

where J_v is the total flow of volume in cm s⁻¹ (assumed equal to the water flux J_w), L_p is the hydraulic conductivity coefficient in cm s⁻¹ Pa⁻¹, ΔP is the hydrostatic pressure difference in Pa, σ is the dimensionless reflection coefficient, R is the gas constant in cm³ Pa⁻¹ mol⁻¹ deg⁻¹, T is the temperature in A^o, and C^o and C^i are the outside and inside concentrations respectively in mol cm⁻³. Then by solving equation (1) for C^i and inserting in equation (2) we found the following relationship (Fiscus and Kramer, 1975: equation 12) for the total volume flow through the radial walls of each subunit (n):

$$J_{vn}^2 \pi r l (1 + \sigma) + J_{vn} \{ Q_{vBn-1} - \pi r l L_{pn} [\Delta P (1 + \sigma) - 2\sigma^2 \pi^o] \} - L_{pn} [Q_{vBn-1} (\Delta P - \sigma \pi^o) + \sigma RT (2J_{sn}^* \pi r l + Q_{vBn-1} C_{Bn-1}^i)] = 0 \quad (3)$$

where Q_{vBn-1} is the volume of solution passing the apical boundary (Bn - 1) of each subunit in cm³ s⁻¹, C_{Bn-1}^i is the osmotic concentration of that solution in mol cm⁻³, and r is the radius in cm.

Within the context of this cylindrical model there are several parameters which we might expect to vary along the axis of the root. The most obvious are the hydraulic conductivity L_p , the active solute uptake rate J_s^* , and the selectivity or reflection coefficient, σ .

To gain more insight into the way in which changing these variables might affect the permeability patterns of a cylindrical root segment we simulated, using the cylindrical model, the effects of hydrostatic pressure increases in a 10 cm segment. For this particular simulation the

active uptake rate was arbitrarily held constant for the apical 5 mm then decreased by 10 per cent for each succeeding 1 mm segment until it reached approximately 10 per cent of the maximum after which it was held constant. The hydraulic conductivity was held constant over the entire 'root' length as was σ for each pressure series.

The root permeability was then calculated in a manner similar to that of Brouwer (1954) by dividing the total flow by the driving force. For the purposes of this simulation the driving force was taken as ΔP which would be equivalent to the tension in the xylem of a plant. Using the total water potential difference, calculated as the sum of the hydrostatic and osmotic differences, results in no substantial change in the salient features of the resultant permeability patterns. This procedure was followed for several series of pressure increases at various specified values for σ .

RESULTS AND DISCUSSION

The results (Fig. 1) show two interesting features. First, all of the permeability curves seem to approach a similar value at high rates of flow. This value is the one specified as the hydraulic conductivity in the simulation. Secondly, the shape of the permeability curves is very profoundly influenced by the membrane selectivity (σ). At high σ we see a steady decrease in the apparent permeability with increasing flow rates. At higher flow rates, the permeability seems to be levelling off. At intermediate values of σ we can see increases in permeability at low flow rates followed by decreasing values until at high flow rates the permeability again seems to be ap-

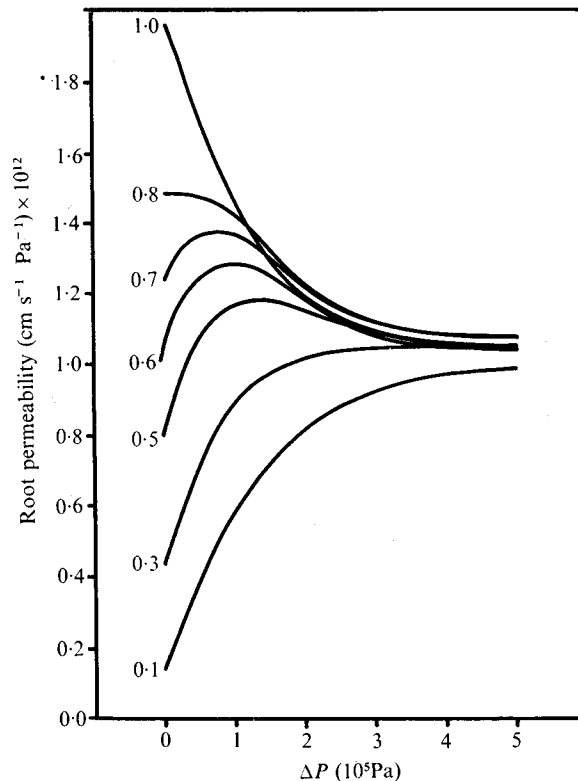


FIG. 1. Apparent root permeability of a simulated 10 cm root segment as affected by increasing hydrostatic pressures. The influence of the reflection coefficient (numbers on figure) on the shape of the curves is also shown. $L_p = 0.1 \times 10^{-1} \text{ cm s}^{-1} \text{ Pa}^{-1}$; $\pi^0 = 10^5 \text{ Pa}$.

proaching a constant value. At lower values of σ we see consistent increases in permeability with increases in flow which seem again to approach the same constant value at high flow rates.

The qualitative interpretation of Brouwer's data on the basis of this model then is fairly straightforward. At high flow rates the apparent permeability in all of the root segments appears to approach a constant value which we might infer, from our model and Fig. 1, represents the true value of the hydraulic conductivity of the 'root membrane'. Since in Brouwer's data this plateau value approximately doubles from the first to the second segments we may infer that the hydraulic conductivity is twice as high in the region 3 to 6 cm behind the root tip as it is in the apical 3 cm. Also, his data seems to show that the conductivity changes little in the entire region between 3 and 12 cm from the root tip.

On a quantitative basis Brouwer's data are more difficult to interpret because the diameter of each root segment is not known. However, we are probably safe in assuming that they were between 0.1 and 0.01 cm in diameter. Given these extreme dimensions and estimates of the plateau values from Brouwer's data (his Fig. 2) we can calculate the hydraulic conductivity of his root segments. Table 1 shows the extremes and the values based on a midpoint diameter of 0.05 cm. Comparing these midpoint values for the various sections shows L_p values of 2.5×10^{-11} cm s⁻¹ Pa⁻¹ for the terminal segment and approximately 5.0×10^{-11} cm s⁻¹ Pa⁻¹ for the three more basal segments which all seem to be similar.

TABLE 1. Comparison of extreme and midpoint values for the hydraulic conductivity (L_p) calculated from Brouwer's data

Diameter (cm)	Estimated L_p (cm s ⁻¹ Pa ⁻¹) 10 ⁶	
	Basal segments (II, III, IV)	Terminal segment (I)
0.1	0.25	0.125
0.05 (midpoint)	0.50	0.25
0.01	2.5	1.25

Also, on the basis of our model the shape of Brouwer's permeability-suction tension curves may be interpreted as indicating a lower selectivity in the more basal regions of the root than exists in the apical 3 cm segment. In this regard it is important to caution that the external osmotic concentration (π^0) also has a strong influence on the shape of these curves. This is apparent in Fig. 2A where we have used the same simulation as before but have arbitrarily chosen $\sigma = 0.7$ and changed π^0 for each pressure series. Here we note that increasing π^0 serves to accentuate the peak in permeability at low ΔP and with higher values of σ (Fig. 2B) tends to produce a peaking effect where none was evident at lower π^0 . It is also worthy of note that increasing π^0 at constant ΔP tends to increase the apparent permeability, especially at low values of ΔP .

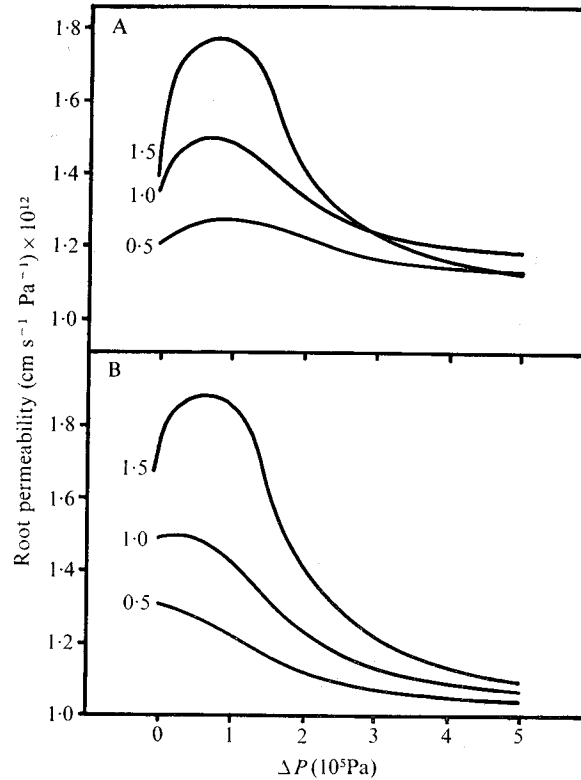


FIG. 2. A. Influence of π^0 (numbers on figure in units of 10^5 Pa) in accentuating the permeability peak at lower hydrostatic pressures
 B. Influence of π^0 (numbers on figure in units of 10^5 Pa) in producing the permeability peaking effect at higher values of σ . $L_p = 0.1 \times 10^{-11}$ cm s $^{-1}$ Pa $^{-1}$ for A and B. A, $\sigma = 0.7$; B, $\sigma = 0.8$.

The interpretation of Brouwer's permeability profile changes on the basis of differences in L_p and σ between the different root segments seems reasonable when considering the developmental differences which are likely between the apical 3 cm segment and the rest of the root. A portion of the apical segment would be expected to consist of tightly packed tissue with poorly developed vascular elements and thus present a pathway with lower conductivity than the older more basal tissue which may have become disrupted by the development of secondary root primordia. Within this same context it is easy to see how the young, actively growing tissue near the root tip might exhibit a greater effective selectivity due to its own growth requirements. That is, the removal of solutes by the young cells along the pathway would have the same apparent effect as a more selective membrane barrier. Again we might expect the older tissue to appear less selective due to both an increase in leakiness of the actual ion barrier and to the lower growth requirements of the cells along the radial pathway.

Now, it is possible to account, in principle at least, for what has become a large body of data which was previously difficult to reconcile on a reasonable basis. Observations including (1) non-linear pressure flow, (2) internal osmotic dilution, (3) negative resistance effects, (4) non-osmotic water flux, (5) internal osmotic

compensation, and (6) root resistance profile changes may all now be explained on the basis of three fundamental observations which appear to apply to nearly all root systems. These are: (1) there is some structure in the root which acts as a differentially permeable membrane; (2) somehow the root is able to move some solutes from one side of this membrane to the other against a potential gradient; and (3) there is interaction between the flows of solutes and solvent. These three properties have been known for a considerable period of time but it has not been clear just how they interacted with each other to produce the variety of phenomena which we have been discussing without invoking a change in L_p . However, the general nature of this treatment must be emphasized and we recognize the inadequacy of this particular model in identifying any specific anatomical structures as the effective agents for any of the model parameters.

It is evident from Fig. 2A and B that the interaction between the various parameters is such that we can produce particular effects (i.e. permeability peaking) through the manipulation of more than one of the major terms. For example the permeability peaking effect may be produced by manipulating either σ or π^0 to a certain degree. Obviously a more sophisticated experimental approach is needed to isolate and measure these interactions than has been used in the past.

An additional problem is that the anatomical nature of the root ion barrier is still largely uncertain and this type of treatment tells us only that a single membrane having certain properties will act in a manner similar to a root. The overall effect may be described in terms of a single membrane but the barrier may actually consist of more than one membrane in series of a combination of membranes and/or cell walls or some other structure that we do not ordinarily identify as a membrane. After all, the broad definition of a membrane is largely functional and need not necessarily indicate a plasmalemma or tonoplast:

Regardless of the details of the model, which will doubtless change with time, species, and environment, the explanation in principle of the various phenomena we have mentioned lends much credence to the functional concept of the root as a relatively simple semipermeable membrane system.

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