General model for osmotic and pressure-induced flow in plant roots

(root exudation/iso-osmotic flow/nonlinear root flow/root resistance changes/standing gradient root flow)

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ABSTRACT This paper presents a general model to describe coupled solute and water flow through plant roots when they are subjected to osmotic or hydrostatic pressure gradients, or both simultaneously. The model is based on well-established membrane transport equations derived from irreversible thermodynamic considerations. A variety of experimentally observed phenomena such as changes in root resistance with flow rate, apparent negative resistance effects, xylem sap dilution, and apparent non-osmotic water transport can be adequately explained with this model. The model also predicts that an exuding excised root system will be very insensitive to changes in the hydraulic conductivity coefficient. Previous work with a flat membrane of unit surface area and uniform properties is confirmed for a cylindrical coordinate system of nonuniform characteristics.

An understanding of the mechanism by which water transport occurs through plant roots is essential to any attempt to describe water movement through the whole plant, and to account for the effects of root environmental parameters on the whole plant water status. However, attempts to formulate a unified theory of water transport have met with a number of difficulties. Foremost among these are the observations of apparent decreases in root resistance to water flow as the rate of water flow through them increases. This phenomenon was first reported by Jost (1) in 1916 and later studied extensively by Brewig (2) and Brouwer (3, 4). Hailey *et al.* (5) have collected a number of more recent observations of their own and other workers on resistance to water flow in whole plants. Several of these suggest that a decrease in resistance occurs with increasing water flow, especially at low rates.

As the conditions in the root systems of intact plants are usually difficult to ascertain or control we will confine ourselves to consideration of detached roots or root systems. In this light, the experiments of Mees and Weatherley (6) and Lopushinsky (7, 8) are nearly ideal for the purposes of our analysis. In these experiments they demonstrated a decrease in resistance to water flow as it was increased by application of hydrostatic pressure. This phenomenon was attributed to the "Erbe effect" by Hylm (9, 10) and others. The "Erbe effect," however, deals with the displacement of a fluid from a system of capillary pores of various sizes by a dissimilar fluid. It is therefore inapplicable to roots, where the presumed pores would already be filled with water. Also, when Mees and Weatherley (6) calculated the total driving force or total water potential difference ($\Delta\psi$) acting in their root systems some of the data indicated a "negative resistance" to water flow relative to $\Delta\psi$. That is, an increase in flow was associated with a decrease in $\Delta\psi$. This cannot be explained

by the Erbe effect. Both Mees and Weatherley (6) and Lopushinsky (7, 8) observed the well-known dilution effect which occurred when water flow through the roots was increased. This dilution of the xylem sap occurs because increasing increments of water flow are not accompanied by compensating increases in the solute flow. Both laboratories reported that at relatively high flow rates the concentration of the xylem sap fell to a small fraction of its original concentration.

Fiscus (11)* demonstrated, using the well-established irreversible thermodynamics of membrane processes, that the phenomena of decreasing apparent resistance, apparent negative resistance, and the dilution effect are all inherent properties of a simple solute-accumulating membrane under the influence of an applied hydrostatic pressure. It was shown on the basis of the membrane transport equations that flow through a membrane of unit area and uniform properties capable of accumulating solutes and subjected to a hydrostatic pressure will increase in a nonlinear fashion with respect to pressure. The degree of the dilution effect and the negative resistance characteristics were shown to be functions of the selectivity of the membrane to solutes.

Another problem of water transport through excised roots arises from the observations of some workers (12-15) of apparent nonosmotic water transport in the absence of an applied hydrostatic pressure gradient. This so-called nonosmotic flow was formerly interpreted as caused by active water transport. Some workers (16) attribute this to the removal of solutes from the xylem in the more basal regions of the root, and still others (17) claim it is a product of a standing gradient flow system.

It is our intention in this paper to present an extension of the unit area membrane treatment of Fiscus (11). When this treatment is extended to a cylindrical system such as a root it satisfactorily explains the phenomena of apparent decreases in root resistance, the dilution effect, and apparent nonosmotic water transport in roots.

THE MODEL

A root can conveniently be treated as a cylindrical membrane system of radius r , and for the purpose of analysis, subdivided into a series of discs of thickness l . The value of r and its relation to root anatomy is still somewhat controversial, but for our purposes we have assumed that the mem-

* Since this paper was prepared, an article by Dalton *et al.* (22) has appeared which agrees with many of the conclusions of Fiscus (11) with regard to the general causes and nature of changes in root resistance and the dilution effect.

FIG. 1. The basic model showing the flows of volume and solutes into and through each subsection.

brane is coincident with the endodermis and have chosen r accordingly.

The flows of solute and water through any of these subsections is illustrated in Fig. 1. At the steady state, in each section there is one equation of continuity for solute flux and another for the total volume flow. We will treat the solute flux first.

In this paper we will not deal with the electrical properties of the membrane nor with any charge separation of the solutes, so that the analysis can only be strictly applied to nonelectrolytes. We further assume throughout that the solutions behave ideally and that the membrane is rigid and capable of accumulating solutes against a potential gradient. Definition of the mechanism by which accumulation occurs is not essential to our analysis. Also it is assumed that there is no gradient of concentration along the length of the disc. If l is taken small enough this condition is virtually assured. In our simulations throughout this paper we have arbitrarily set $l = 0.1$ cm, feeling that any concentration difference across this distance is small enough to be ignored.

For the solute flux through each subsection the equation of continuity is

$$Q_{sBn} = Q_{sBn-1} + J_{sn}2\pi rl \quad [1]$$

where Q_s is the time rate of solute flux in mole sec^{-1} , subscripts refer to the boundaries Bn and $Bn-1$, J_{sn} is the rate of solute flux through the radial walls of segment n in mole $\text{cm}^{-2} \text{sec}^{-1}$, and $2\pi rl$ is the surface area of the radial walls.

Further, the solute flux across the boundary $Bn-1$ is simply the product of the concentration and the volume flow.

$$Q_{sBn-1} = Q_{vBn-1}C_{Bn-1}^i \quad [2]$$

where Q_{vBn-1} is the volume flow across the boundary $n-1$ in $\text{cm}^3 \text{sec}^{-1}$ and C_{Bn-1}^i is the concentration of the solution at the boundary $n-1$ in mole cm^{-3} .

For the rate of radial solute flux we may write, after Katchalsky and Curran (18)

$$J_{sn} = \bar{C}_s(1 - \sigma)J_{vn} + \omega_n\Delta\pi_n + J_{sn}^* \quad [3]$$

where J_{sn}^* is the rate of active uptake in mole $\text{cm}^{-2}\text{sec}^{-1}$, ω is the coefficient of solute mobility in the membrane (19), σ is the reflection coefficient, J_{vn} is the rate of volume flow through the radial walls of segment n , and $\bar{C}_s$ is the average solute concentration on both sides of the membrane. Thus we see that the total solute flux is the sum of the solvent drag component, a diffusive component, and an active uptake term.

The average concentration term $\bar{C}_s$ is defined as (19)

$$\bar{C}_s = \Delta C_s / \Delta \ln C_s \quad [4]$$

We may approximate $\ln C_s$ with a power series (19) and so long as the internal and external concentrations are not too

different, the first term of the series is sufficiently precise and we have

$$\bar{C}_s = (C^o + C^i)/2 \quad [5]$$

where the subscripts "o" and "i" refer to the outside and inside compartments, respectively.

Returning to Eq. 3, we wish to consider further the diffusive term $\omega\Delta\pi$. Tyree (20) has collected values of ω for a variety of solutes and plant membranes. His figures indicate that for electrolyte species of major interest to plant scientists the values of $\omega\Delta\pi$ are frequently much less than the solvent drag or active uptake components which one encounters in root systems. Therefore, for the purpose of this analysis we will ignore the diffusive term and write

$$J_{sn} = \bar{C}_s(1 - \sigma)J_{vn} + J_{sn}^* \quad [6]$$

The equation of continuity for the volume flow through each subsection is

$$Q_{vBn} = Q_{vBn-1} + J_{vn}2\pi rl \quad [7]$$

where J_{vn} is the rate of volume flow through the radial walls of segment n in $\text{cm} \text{sec}^{-1}$ and the other terms are as before. Further, the rate of volume flow through the radial walls may be written as

$$J_{vn} = L_{pn}\Delta P - \sigma L_{pn}RT(C^o - C_{Bn}^i) \quad [8]$$

where R is the gas constant in $\text{ml atm deg}^{-1}\text{mole}^{-1}$, T is the absolute temperature, L_{pn} is the hydraulic conductivity of segment n , C is the concentration in mole cm^{-3} , and ΔP is the hydrostatic pressure difference across the membrane in atm.

Eqs. 6 and 8 show us that a further analysis of the term C^i is necessary in order to write an explicit expression for coupled solute and water flow through our system.

We see that the internal concentration of the solution leaving the segment through boundary n is the ratio of the solute flow to the volume flow across the boundary. Thus

$$C_{Bn}^i = Q_{sBn} / Q_{vBn} \quad [9]$$

and substituting from Eqs. 1, 2, and 7 we get

$$C_{Bn}^i = \frac{Q_{vBn-1}C_{Bn-1}^i + 2J_{sn}\pi rl}{Q_{vBn-1} + 2J_{vn}\pi rl} \quad [10]$$

Substituting from Eq. 6 for J_{sn} and rearranging yields

$$C_{Bn}^i = \frac{\pi r l [J_{vn}(1 - \sigma)C^o + 2J_{sn}^*] + Q_{vBn-1}C_{Bn-1}^i}{J_{vn}\pi r l(1 + \sigma) + Q_{vBn-1}} \quad [11]$$

Finally, substituting Eq. 11 into Eq. 8 and rearranging, we find

$$J_{vn}^2\pi r l(1 + \sigma) + J_{vn}\{Q_{vBn-1} - \pi r l L_{pn}[\Delta P(1 + \sigma) - 2\sigma^2\pi^o]\} - L_{pn}\{Q_{vBn-1}(\Delta P - \sigma\pi^o) + \sigma RT(2J_{sn}^*\pi r l + Q_{vBn-1}C_{Bn-1}^i)\} = 0 \quad [12]$$

which is quadratic in J_{vn} and is easily solved by the quadratic formula. The solution to this equation is then inserted in Eq. 7 to find the rate of flow of volume across the boundary n in $\text{cm}^3 \text{sec}^{-1}$. The calculations must be repeated for each succeeding section until the base or cut end of the root is reached. The boundary conditions for the first (apical) segment are simply

FIG. 2. Profile of volume flow, osmotic pressure difference, and active uptake rate over a 10 cm root. $L_p = 0.1 (10^{-6}) \text{ cm sec}^{-1} \text{ atm}^{-1}$, $\pi^0 = 0.5 \text{ atm}$. The numbers on the figure indicate σ .

$$Q_{vBn-1} = C_{Bn-1}^i = 0. \quad [13]$$

Thereafter, any of the independent variables, L_{pn} , σ_n , r , l , π^0 , ΔP , or J_{sn}^* may be varied along the root axis in any manner desired. In most experimental situations π^0 and ΔP are usually held constant, or nearly so, over the length of the root, as is r to a very good approximation. The values for L_{pn} , σ_n , and J_{sn}^* are usually unknowns calculated from experiment. These calculated values are generally assumed to be averages for the entire root surface.

The values of the variables used for the various simulations in this paper are indicated in the figures. The calculations were carried out with a FORTRAN program on an IBM 370/165 computer.

RESULTS AND DISCUSSION

As an example of how the system works, Fig. 2 shows a root axis profile of values for radial volume flow and $\Delta\pi$ for the case where $\Delta P = 0$. All of the variables in this case were held constant except for the active uptake rate. J_{sn}^* was held constant for the first 5 mm from the tip and then decremented by 10% at each succeeding 1 mm segment.

As one would expect, the radial flow decreases with increasing distance from the tip because $\Delta\pi$ decreases. The decrease in $\Delta\pi$ is caused by the combined effects of decreasing solute uptake along the root and dilution by the influx of water. As the root becomes longer, of course, $\Delta\pi$ will approach zero under these conditions. In this way the model is similar to the standing gradient models proposed by Diamond and Bossert (21) for water transport in epithelia and by Anderson *et al.* (17) for excised root exudation. This is indeed another standing gradient model for excised root exudation but it incorporates provision for the influence of applied hydrostatic pressure gradients.

An interesting effect of the reflection coefficient in this system is also partially brought out in Fig. 2 and will be mentioned again later. This is that lowering σ results in both an increase in the rate of radial volume flow through the more basal segments of the root, and an increase in $\Delta\pi$ all along the root axis.

An important test of the applicability of our model to roots in general is the effect of hydrostatic pressure on the volume flow rate out of the cut end of the root and the osmotic pressure difference between the emerging sap and the root medium. When such an experiment is simulated with

FIG. 3. Exudation of a 10 cm root under the influence of applied hydrostatic pressure illustrating the nonlinear response to pressure and the dilution effect. $L_p = 0.1 (10^{-6}) \text{ cm sec}^{-1} \text{ atm}^{-1}$. J_{sn}^* profile same as for Fig. 2.

our model the results, shown in Fig. 3, bear a striking resemblance to those reported by Lopushinsky (7, 8) and Mees and Weatherly (6) for pressure flow through root systems. Two important features should be noted. First, there is an apparent decrease in the resistance to water flow as the hydrostatic pressure is increased and secondly, the internal solution concentration decreases rapidly with increases in flow rate. This latter phenomenon is the widely known dilution effect.

When these same simulated data are expressed in terms of the total inwardly directed driving force ($\Delta P - \Delta\pi$), Fig. 4, one sees that it is possible for such a system to possess a "negative resistance" region under the proper conditions. This

FIG. 4. Effect of total inwardly directed driving force ($\Delta\psi = \Delta P - \Delta\pi$) on exudation from a 10 cm root. The numbers on the figure indicate σ . The curved horizontal lines are levels of equal pressure. J_{sn}^* profile same as Fig. 2.

FIG. 5. Effect of changes in π° on exudation rate and $\Delta\pi$ of the exuded xylem sap. Note the two different scales for $\Delta\pi$. The arrows near the numbers indicating σ refer the curves to the proper scale. J^* , profile same as Fig. 2.

negative resistance characteristic was noted experimentally by Mees and Weatherly (6) and more recently in this laboratory (unpublished). Both the apparent changes in resistance and the negative resistance effect have been explained theoretically by Fiscus (11) on the basis of well-established membrane transport equations. It was shown that the negative resistance effect is due to the interplay between the hydrostatic and osmotic driving forces, which leads to a proportionately larger decrease in the less effective osmotic driving force with increases in the hydrostatic component. It is sufficient to note here that the same effects occur in a simulated root with cylindrical geometry as occur in a flat membrane of unit surface area and uniform properties.

It is now evident that water transport through a membrane system such as we have described will be linearly related to the total water potential difference ($\Delta\psi$) only in special circumstances, most notably when $\sigma = 1$ and π° is constant. Therefore, in describing the flow patterns in such a membrane system it is not sufficient to know only $\Delta\psi$, but the proportions of the components ($\Delta P:\Delta\pi$) and their relative effectiveness must also be known.

Another anomaly of excised root exudation is the apparent nonosmotic water flow that has been reported by some workers (12–15). Such experiments are easy to simulate with our model and for simplicity we have used the same root parameters as for Fig. 2. The root was subjected to successive levels of π° ranging from 0.25 to 3.0 atm in 0.25 atm steps at various levels of σ . The calculations were carried out as before and the resultant flow from the most basal segment was divided by the entire root surface area to give an average flow rate of the type usually reported in the literature. The results of this experiment, Fig. 5, show that for highly selective membranes the data appear linear down to quite small values of $\Delta\pi$, where J_v drops off very rapidly and approaches zero as $\Delta\pi$ also approaches zero. For less selective mem-

FIG. 6. Predicted influence of L_p on the exudation rate from a 10 cm root. Note the two scales for J_v . The numbers on the figure indicate σ . The arrows refer the curves to the proper J_v scale. J^* , profile same as Fig. 2.

branes ($\sigma = 0.3$ in Fig. 5) the lower levels of $\Delta\pi$ are never attained and the data are nearly perfectly linear. The dashed line in Fig. 5 is at $\Delta\pi = 0.05$ atm. If one excludes from consideration our data below 0.05 atm the result is an apparently straight line having a positive intercept on the J_v axis. This feature is even more striking at lower values of σ since in these cases the operation of the model was such that no data near the 0.05 atm level was ever generated in the experiment. Of the experiments listed above, Ginsburg and Ginsburg (14) and Anderson and Reilly (13) have no data for $\Delta\pi < 0.1$ atm, and House and Findlay (15) show standard errors on their data in this range on the order of ± 0.1 atm. Only Anderson and Collins (12) show data closer than this to zero. In fact, they have data indicating that at the lowest flow rates they achieved, C^o was indistinguishable from C^i . Anderson *et al.* later attributed this phenomenon to the effect of a standing gradient osmotic flow system.

Whether or not $\Delta\pi$ approaches zero very closely depends on several factors. Among these are the geometrical distribution of the root properties L_p , σ , and J^*_{sm} and the external properties π° and ΔP . Of course, any definitive test of this hypothesis depends on the accurate determination of the distribution of these properties along the root axis. So, it would seem that the root permeability, selectivity, solute accumulation rates, or the difficulties in measuring very small $\Delta\pi$ or all of these factors could lead to apparent nonosmotic water transport. In short, taking the data that can be reasonably expected from experimentation, treating them as linear, and extrapolating the lines back to $\Delta\pi = 0$, would make it appear that nonosmotic water transport was occurring when in fact there was none. As Anderson *et al.* pointed out, it is the basic assumption that J_v and $\Delta\pi$ are linearly related that leads to the erroneous conclusion that there is nonosmotic water transport. This is not to say that reabsorption of solutes from the xylem sap as proposed by Klepper (16) is not also possible. The two processes operating simultaneously would make the effect even more pronounced.

One other very interesting feature of this model is the effect of changing the hydraulic conductivity of the root on the exudation rate at $\Delta P = 0$. Fig. 6 shows the results of another simulation where all of the parameters were held constant except L_p , which was varied through nearly 5 orders of magnitude at various levels of σ . The results are quite striking in that they predict a great degree of insensitivity to

changes in L_p . These data show differences in flow rate from as little as 4-fold for the ideal membrane to 200-fold for the relatively nonselective one ($\sigma = 0.1$). In all cases the change in exudation rate per unit change in L_p was negligible. In general, a decrease in the selectivity resulted in a somewhat increased dependence on L_p . At higher levels of L_p it is interesting to note that decreasing σ , over the range shown, resulted in increased exudation. This type of simulation again illustrates the need for more determinations of the distribution of the parameters L_p , σ , and J_{sn}^* along the root axis. The reflection coefficient is rarely measured in plant roots and L_p and J_{sn}^* are usually averaged over the entire root or stelar surface areas, giving no indication of their distribution.

We have dealt only with transport of nonelectrolytes in this paper, although most of the solutes in the root xylem sap usually are electrolytes. As the normal difference in electrical potential between the root xylem sap and the external medium has negligible effect on water flow, we have not dealt with it. The osmotic effect of the solutes in the xylem sap depends on their colligative properties and not on the method of transport. We have, therefore, treated the active uptake term as if it were composed of both the metabolically supported transport and the flow of ions down the resultant electrochemical gradient. Further, we have assumed that the active transport term remains constant during variations in flow rate of water and external concentration, although these assumptions are not strictly correct either. Nevertheless, our model predicts several observed phenomena and we therefore feel that taking into account the effects of electrical potential gradients and changes in active uptake of ions will not materially change its general character.

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