Some Compartmental Models of the Root: Steady-state Behavior

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Plots of the pressure difference ($\Delta P$) applied to plant roots vs. the resulting volume flow rate ($Q_v$) often exhibit an anomalous offset that has been difficult to explain. The present analysis suggests that solute build-up in two- and three-compartment models of the root cannot account for this offset. The Ginsburg–Newman three-compartment model explains the offset in terms of differing reflection coefficients for the membranes bounding the intermediate compartment. This model appears more promising, but it predicts a minimum in the plot of xylem-sap osmotic pressure vs. $Q_v$ which is not observed in practice. Fiscus hypothesized that an internal asymmetric distribution of non-mobile solutes is responsible for the offset. In the present study, this hypothesis is incorporated into a four-compartment model of the root that is conceptually related to the three-compartment model of Miller. But according to the four-compartment model, the asymmetric solute distribution does not arise because of solvent drag. Rather the anomalous offset is associated with a concentration gradient of photoassimilates (the non-mobile solutes) that exists in the absence of volume flow, and which drives the diffusive transport of these solutes from the stele to the cortex via endodermal plasmodesmata. This model is consistent with the existence of radial symplastic osmotic-pressure gradients, and it appears to have greater explanatory power than the Ginsburg–Newman model. In particular, it suggests explanations for diurnal variations in $\Delta P$–$Q_v$ curves, as well as the effects of changing external solute concentrations. It also shows how the overall root reflection coefficient can be less than unity, even when the cell membranes are effectively ideally semipermeable, and there is negligible extracellular transport of water and solutes. The model makes a number of experimentally testable predictions.

Introduction

Dalton et al. (1975) and Fiscus (1975) independently proposed a steady-state two-compartment model of the plant root in which a root “membrane” separates an external compartment (the soil or nutrient solution) from an internal compartment (the root xylem). At first, it seemed that this model would explain the nonlinear relationship between $\Delta P$ and $Q_v$ typically observed for excised roots (here $\Delta P$ is the difference in pressure between the external medium and the xylem, and $Q_v$ is the steady-state rate of xylem-sap exudation). However, Newman (1976) pointed out that, in many studies, if a tangent is drawn to the linear portion of the $\Delta P$–$Q_v$ curve (which is approached at high $Q_v$), the intercept on the $\Delta P$ axis ($\Delta P_o$) is greater than the osmotic pressure ($\Pi^o$) of the external medium (Fig. 1). If this observation is interpreted according to the two-compartment model, it implies a reflection coefficient ($\sigma$) for the root membrane that is greater than unity. For a single-membrane model, this is theoretically
impossible (Katchalsky & Curran, 1965). Ficus (1977) countered Newman’s criticism by suggesting that convection within an external unstirred layer would lead to a build-up of solutes at the root membrane. In this case, the osmotic pressure of the solution immediately adjacent to the external face of the membrane would be greater than \( \Pi^o \). Accordingly, one would expect that \( \Delta P_0 > \Pi^o \), which would satisfy Newman’s tangent test. However, Passioura (1984, 1988) concluded that a build-up of solutes at the root membrane would result in a progressive increase in the slope of the \( \Delta P-Q \) curve. Consequently, and contrary to observation, any attempt to draw a tangent to this curve would lead to the conclusion that \( \Delta P_0 < \Pi^o \). The analysis of Passioura (1984, 1988) does not include solute uptake by the root. In the present study, the suggestion of Ficus (1977) regarding solute build-up at the root membrane is reassessed by incorporating solute uptake into the analysis. It is shown that a two-compartment model with solute build-up can account for the fact that \( \Delta P_0 > \Pi^o \). But in doing so, it also predicts that the xylem-sap osmotic pressure approaches \( \Pi^o \) as \( Q_\ell \to \infty \), which is inconsistent with observation. This leads to a consideration of three-compartment models (Ginsburg, 1971; Newman, 1976; Ficus 1981, 1986, 1988; Miller, 1985), and, finally, the introduction of a new four-compartment model. The essentially new feature of this model is the inclusion of solute unloading by the phloem.

The Two-Compartment Model: Solute Build-up at the Root Membrane

The essential features of the two-compartment model with an external unstirred layer are shown in Fig. 2. Following Dalton et al. (1975) and Ficus (1975, 1977), the phenomenological equations developed by Kedem & Katchalsky (1958) and Katchalsky & Curran (1965) are used to describe the volume flow rate \( Q_\ell \) and solute flow rate \( Q_s \) across the root membrane. Then if the membrane is located at a radial distance \( r = a \) from the center of the root, and the unstirred layer extends from \( r = a \) to \( r = b \) \((b > a)\) we have

\[
Q_\ell = 2\pi a l L_p (\Delta P - \sigma \Delta \Pi),
\]

\[
Q_s = (1 - \sigma) C_s Q_\ell + 2\pi a \omega \Delta \Pi + Q_s^*,
\]

where \( l \) is the length of the root, \( L_p \) is the membrane hydraulic conductivity coefficient, \( \sigma \) is the membrane reflection coefficient, \( \omega \) is the membrane permeability coefficient, \( \Delta \Pi \) is the

![Fig. 1. A plot of \( \Delta P \) vs. the average volume flux at the root surface \( J_\ell = Q_\ell/2\pi bl \), data taken from Fig. 2 in Ficus (1977). The horizontal dashed line shows the value of \( \Pi^o \). The dotted line is an extrapolation of the linear portion of the \( \Delta P-Q_\ell \) curve to the \( \Delta P \) axis. It is clear that the intercept \( (\Delta P_0) \) on this axis is greater than \( \Pi^o \). The continuous curve is a nonlinear least-squares fit of eqn (6) with \( \Pi^o(b) = 0.045 \) MPa, \( \gamma = 0.5, \omega = 0 \) and \( T = 295 \) K. Parameter estimates \( \pm \) SEs: \( L_p = (2.80 \pm 0.03) \times 10^{-13} \) m s\(^{-1}\) Pa\(^{-1}\), \( \sigma = 0.644 \pm 0.003, Q_s^*/2\pi bl = (10 \pm 1) \times 10^{-9} \) mol m\(^{-2}\) s\(^{-1}\), \( 2\pi bl k = (7.8 \pm 0.8) \times 10^8 \) s m\(^{-1}\).

![Fig. 2. Schematic representation of the two-compartment model with solute build-up within an unstirred layer (most probably the cortical apoplast). The reflection coefficient \( \sigma \) of the root membrane is less than unity. Note that \( \Pi^o \geq \Pi^o(b) \), which is inconsistent with experimental observation.](image-url)
trans-membrane difference in osmotic pressure, $\Delta P$ is the trans-membrane difference in hydrostatic pressure, $Q_v^*$ is the rate of active solute transport and $C_s$ is a mean solute concentration. If the membrane separates an external compartment (o) from an internal xylem compartment (x), then

$$\Delta P = P_o - P_x$$  \hspace{1cm} (3)$$

and

$$\Delta \Pi = \Pi_o(a) - \Pi_x.$$  \hspace{1cm} (4)$$

We specify $\Pi_o$ at $r = a$ (i.e. immediately adjacent to the external face of the root membrane) because in the presence of an external unstirred layer, $\Pi_o$ is a function of $r$ (Fig. 2). For water-cultured plants (as used by Fiscus, 1977), and plants growing in well-watered soils, the most likely site of solute build-up is within the cortical layer, (e.g. at the endodermis), and $b$ is the radius of the root.

Following Barry & Diamond (1984) $C_s$ is expressed as

$$C_s = C_s^o - \gamma \Delta C_s = C_s^o(a) - \gamma(C_s^o(a) - C_s^o),$$  \hspace{1cm} (5)$$

where $\gamma \to 0.5$ as $Q_v \to 0$ (low-flow approximation) and $\gamma \to 0$ as $Q_v \to \infty$ (high-flow approximation). In the linear portion of the $\Delta P - Q_v$ curve, $\gamma$ must approach one of these approximations (otherwise the relationship would be nonlinear). Since the linear relationship is approached at high $Q_v$, it is tempting to choose the high-flow approximation and set $\gamma = 0$. However, this is not necessarily correct. In fact, for models in which the mechanism of trans-membrane solute transport is not specified, it is not possible to say a priori which approximation is appropriate. Accordingly, we consider both the high- and low-flow approximations. It should also be noted that, in general, the high-flow approximation is expected to apply only for sufficiently small $|\Delta C_s|$; otherwise $\gamma$ may not approach a constant value as $Q_v \to \infty$ (Barry & Diamond, 1984).

The following expression for $\Delta P(Q_v)$ is derived in Appendix A:

$$\Delta P = \frac{Q_v}{2\pi a L_p} + \frac{\sigma^2 \Pi^o(b) Q_v - \sigma R T Q_v^*}{Q_v[(1-\gamma)(1-\sigma) + \sigma e^{-kR}]} + \frac{2\pi a L \sigma R T^*}{Q_v}.$$  \hspace{1cm} (6)$$

where $k$ depends on the solute diffusivity ($D_s$) within the unstirred layer and the fraction ($\alpha$) of the area $2\pi rl$ that is available for solute transport:

$$k = \frac{\ln(b/a)}{2\pi l \alpha D_s}.$$  \hspace{1cm} (7)$$

Figure 1 shows a least-squares fit of eqn (6) to some data of Fiscus (1977). There was insufficient data at low $Q_v$ for an estimate of $\omega$, and so $\omega$ was set to zero. The variation of $\gamma$ with $Q_v$ is, of course, unknown; the fit in Fig. 1 was obtained using the constant value $\gamma = 0.5$ (low-flow approximation). An equally good fit is obtained with $\gamma = 0$ (high-flow approximation).

As $Q_v \to \infty$, eqn (6) approaches the straight-line relation

$$\Delta P = \frac{Q_v}{2\pi a L_p} + \Delta P_0, $$  \hspace{1cm} (8)$$

where

$$\Delta P_0 = \frac{\sigma^2 \Pi^o(b)}{(1-\gamma)(1-\sigma)}. $$  \hspace{1cm} (9)$$

For $\gamma = 0.5$, $\Delta P_0 > \Pi^o$ when $0.5 < \sigma < 1.0$, and for $\gamma = 0$, $\Delta P_0 > \Pi^o$ when $0.62 < \sigma < 1.0$. Most estimates of $\sigma$ for excised roots of herbaceous plants are within the range $0.5 \leq \sigma \leq 1.0$ (Steudle, 1992; Steudle & Peterson, 1998). Hence, in principle, the two-compartment model with solute build-up can account for both the form of the $\Delta P - Q_v$ curve (Fig. 1) and the frequent observation that $\Delta P_0 > \Pi^o$. However, for certain choices of parameter values, eqn (6) can exhibit biphasic behavior, which is never observed in practice. Moreover, it can be shown from
FIG. 3. Schematic representation of Miller’s three-compartment model. Solute build-up occurs within a symplastic compartment. The outer (1) and inner (2) membranes have identical reflection coefficients. $P_x$ can be less than $P_o$, but $P_i > P_o$ for large $Q_v$, which seems improbable.

(Mees & Weatherley, 1957; Lopushinsky, 1964; Fiscus, 1977; Munns & Passioura, 1984). In fact, for large $Q_v$ and $P_o(b)$, $P_x$ may approach values that are much less than $P_o(b)$. Furthermore, eqn (9) predicts that $AP_o - P_x \sim P_o$. By contrast, Munns & Passioura (1984) found that for barley plants growing in various concentrations of NaCl, $AP_0 - P_o$ was independent of $P_o$. For models in which external unstirred layer effects are assumed negligible, this can be explained by supposing that NaCl is effectively impermeant in the root membrane(s); see eqn (19) below. But such an explanation is not possible for the two-compartment model with solute build-up, because as pointed out by Passioura (1984, 1988), the presence of impermeant solutes in the external medium would lead to a nonlinear relationship between $AP$ and $Q_v$ for large $Q_v$ [eqn (6) with $\sigma = 1$, $\omega = 0$], which is not observed in practice. On balance, then, it seems that the two-compartment model should be rejected.

The Three-Compartment Model of Miller

According to this model (Miller, 1985), the xylem (x) and external (o) compartments are separated by an intermediate symplastic compartment (i). This symplastic compartment is bounded by outer (1) and inner (2) cell membranes with identical reflection coefficients (i.e. $\sigma_1 = \sigma_2 = \sigma$). Miller (1985) proposed that a build-up of solutes occurs at the inner boundary of the symplastic compartment and that simultaneously solutes are depleted at the outer boundary of this compartment (solute concentration gradients in the bathing medium are ignored; Fig. 3). This radial concentration gradient arises because of a combination of convection and diffusion within plasmodesmata.

Like Fiscus’s two-compartment model, Miller’s three-compartment model predicts that $AP$ approaches a linear function of $Q_v$ as $Q_v \rightarrow \infty$. From eqns (6) and (7) in Miller (1985), the intercept on the $AP$ axis is given by

$$AP_0 = \frac{4\sigma^2 P_o}{1 + \sigma}$$

from which we conclude that $AP_0 > P_o$ when $\sigma > (1 + \sqrt{17})/8 \approx 0.64$. This is a reasonable lower limit (Steudle, 1992; Steudle & Peterson, 1998). Furthermore, Miller’s model predicts that

$$\lim_{Q_v \rightarrow \infty} P_x = \frac{(1 - \sigma)}{(1 + \sigma)} P_o$$

which is less than $P_o$. This is consistent with experimental observation. However, the model also predicts that

$$\lim_{Q_v \rightarrow \infty} P_i^1 = \lim_{Q_v \rightarrow \infty} P_i^2 = P_o$$

and

$[see his eqns (6) and (7)], where $P_i^1$ and $P_i^2$ are the osmotic pressures of the cell sap immediately adjacent to the outer and inner membranes,
respectively. Since $P^i(r)$ is monotonic decreasing (Miller, 1985) it then follows that throughout the symplastic compartment:

$$\lim_{Q_j \to \infty} P^i = P^o \tag{16}$$

(see Fig. 3). This seems improbable, given that most nutrients are presumably accumulated in, rather than excluded from the symplast (at least at low $P^o$). Furthermore, it follows from eqn (12) that $AP_0 \leq 2P^o$. But in practice $AP_0$ can exceed $2P^o$ [e.g. for the data of Fiscus (1977), $P^o < 0.05$ MPa but $AP_0 > 0.1$ MPa; see Fig. 1].

The above analysis applies to the low-flow approximation ($\gamma = 0.5$), as assumed by Miller (1985). However, assuming the high-flow approximation ($\gamma = 0$) does not improve matters (see Appendix B). Hence it seems that Miller’s model should also be rejected.

The Three-Compartment Model of Ginsburg and Newman

The essential feature of this model (Ginsburg, 1971) is that $\sigma_1 \neq \sigma_2$. Also, unlike Miller’s model, it is assumed that radial gradients of $P^i$ are negligible (Fig. 4). Ginsburg (1971) further assumed that $P^i$ is invariant with $Q_v$. Newman (1976) extended Ginsburg’s model to include solute transport, and obtained the same form of relation, $\Pi^i > \Pi^o$ and $\Pi^i < \Pi^o$ for large $Q_v$. However, $\Pi^i$ and $\Pi^o$ can show complex behavior for intermediate $Q_v$ (see Figs 5 and 6). In this model, the anomalous offset in the $\Delta P - Q_v$ curve arises not because of solute build-up, but because of a difference in $\sigma$ between membranes 1 and 2.

For large $Q_v$, $\Delta P(Q_v)$ approaches a straight-line relation [Figs 5(a) and 6(a)] with an intercept on the $\Delta P$ axis given by

$$\Delta P_0 = \Pi^o + \Pi^o_j(1 - \sigma_j) \left( \frac{\sigma_{j2} - \sigma_{j1}}{1 - \sigma_{j2}} - 1 \right), \tag{19}$$

where $\Pi^o = \Pi^o_i + \Pi^o_j$ is the total external osmotic pressure. Hence, if $\Delta P_0 > \Pi^o$ (as is often the case) an additional requirement is that

$$\sigma_{j2} > 0.5\sqrt{1 + 4(1 + \sigma_{j1}) - 1}. \tag{20}$$
It is hard to know whether eqns (17), (18) and (20) are plausible. Furthermore, \( \Pi_j^0(Q_v) \) and \( \Pi_j^x(Q_v) \) can both exhibit minima [Figs 5(b), 5(c), 6(b) and 6(c)]. As far as the author is aware, this behavior has never been observed for \( \Pi_j^x(Q_v) \), and although data on \( \Pi_j(Q_v) \) are not available, the value of \( \Pi_j^0 \) at the minimum can be rather low [e.g. less than \( \Pi^0 \); Fig. 5(b)]. In fact, for \( Q_j^* > 0 \), \( \Pi_j^0 \) can be negative [see eqns (C6) and (C9)].

On balance, the stringent requirements embodied in eqns (17), (18) and (20), together with the peculiar behavior of \( \Pi_j^0(Q_v) \) and \( \Pi_j^x(Q_v) \) (Figs 5 and 6) must cast doubt on the Ginsburg–Newman model. However, eqn (19) does illustrate a point mentioned above, namely that \( \Delta P_0 - \Pi^0 \) can be independent of \( \Pi^0_{NaCl} \) for barley roots (Munns & Passioura, 1984). For lupin, \( \Delta P_0 - \Pi^0 \) became progressively more negative as \( \Pi^0_{NaCl} \) was increased (at least for \( C^0_{NaCl} > 75 \text{ mol m}^{-3} \)) suggesting the roots had become leaky to NaCl. However, even at these high concentrations, Munns & Passioura (1984) could not detect any increase in the osmotic pressure of petiole-xylem sap; they suggested that the salt may have been extracted from the transpiration stream prior to its arrival at the petiole.

The Three-Compartment Model of Fiscus

Fiscus (1981) found that supplying abscisic acid (ABA) in the solution bathing excised roots of Phaseolus caused a transient release of solutes to the xylem. Concurrently, the \( \Delta P - Q_v \) curve was

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**FIG. 5.** Plots of \( \Delta P \) [a; eqn (C2)], \( \Pi_j^0 \) [b; eqn (C6)] and \( \Pi_j^x \) [c; eqn (C7)] vs. \( Q_v/A_1 \) for the Ginsburg–Newman three-compartment model. For this limited range of \( Q_v/A_1 \) values \( \Delta P_0 < \Pi^0 (0.1 \text{ MPa}) \) for both \( \Delta P(Q_v) \) curves (a). \( \Pi_j^0 \) and \( \Pi_j^x \) both exhibit minima (b and c). Continuous curves: \( \sigma_{j1} = 0.90, \sigma_{j2} = 0.99 \). Dashed curves: \( \sigma_{j1} = 0.80, \sigma_{j2} = 0.90 \). Other parameter values: \( \gamma_1 = \gamma_2 = 0, L_{P1} = L_{P2} = 10^{-12} \text{ m s}^{-1} \text{ Pa}^{-1}, \omega_{j1} = \omega_{j2} = 10^{-14} \text{ mol m}^{-2} \text{ s}^{-1} \text{ Pa}^{-1}, Q_j^*/A_1 = 5 \times 10^{-5} \text{ mol m}^{-2} \text{ s}^{-1}, Q_j^*/A_2 = 0, A_1/A_2 = 10, T = 295 \text{ K}, \Pi_j^0 = 0.1 \text{ MPa}, \Pi_j^x = 0 \).
shifted downward, so that ΔP₀ approached Π°. The two- and three-compartment models considered above can account for these observations if it is supposed that ABA causes a reduction in σ (σ₂ in the case of the Ginsburg–Newman model). This would lead to a decrease in ΔP₀ and a “burst” of solute release into the xylem associated with increased “solvent drag”. Fiscus (1986, 1988) proposed a different explanation: that the offset in the ΔP–Qᵥ curve (ΔP₀ > Π°) seen in the absence of ABA results from an asymmetric distribution of nonmobile solutes within an intermediate compartment (by “nonmobile” Fiscus apparently meant solutes not normally released to the xylem). Application of ABA somehow renders these solutes mobile, and their consequent release to the xylem abolishes the internal concentration gradient. It can be shown from eqns (4) and (5) in Fiscus (1986) that consistent with observation, Π°(∞) = (1 − σ)Π° < Π° where σ is the reflection coefficient of the composite root membrane. [Fiscus (1986) assumed the high-flow approximation (γ = 0), but this can only overestimate Π°(∞); hence the conclusion Π°(∞) < Π° applies also to the low-flow approximation (γ = 0.5).]

Fiscus’s three-compartment model is reminiscent of Miller’s model, except that in Fiscus’s model the relevant solutes do not permeate the inner membrane. In this case the putative asymmetric solute distribution cannot be attributed to convection within an unstirred intermediate compartment, because this would lead to a nonlinear relationship between ΔP and Qᵥ for large Qᵥ [Passioura, 1984, 1988; eqn (6) with σ = 1, ω = 0]. So where do the putative nonmobile solutes come from and why is their distribution asymmetric? Possible answers to these questions are discussed in the following section.
A Four-Compartment Model with Phloem Unloading

There is evidence for significant osmotic pressure gradients across the endodermis, possibly associated with the transport of photoassimilates from the stele to the cortex (Warmbrodt, 1986, 1987; Pritchard et al., 1989). In the light of this possibility, we now introduce a four-compartment model of the root that includes phloem unloading (Fig. 7). The four compartments are: the external medium (o), the cortical symplast (c), the stelial symplast (s) and the xylem lumina (x). Compartments o and c are separated by an ideally semipermeable membrane (oc) which corresponds to the epidermal and/or cortical cell membranes. Similarly, compartments s and x are separated by an ideally semipermeable membrane (sx) which corresponds to the stelial-parenchyma cell membranes. The assumption that σ = 1 for membranes oc and sx is consistent with experimental observation (e.g. Murphy & Smith, 1994a, b). By contrast, the endodermal membrane (cs) separating compartments c and s contains plasmodesmata, and so may have reflection coefficients (σcs) significantly less than unity (Zhang & Tyerman, 1991; Tyerman et al., 1992; Murphy & Smith, 1998). We suppose that two classes of solutes are transported across membrane cs: solutes (i) impermeant in membranes oc and sx but permeant in membrane cs; and solutes (j) permeant in all three membranes. The i solutes are presumed to derive from the phloem, and are transported from s to c via plasmodesmata in membrane cs. The j solutes derive from the external medium (via membrane oc). They are transported in the opposite direction to i (i.e. from c to s via plasmodesmata in membrane cs), and are then unloaded into the xylem (via membrane sx). Finally, we suppose that there may also be impermeant solutes (i) in compartment o, although these will generally be chemically different from those in compartments c and s. It is assumed that compartment x contains only permeant solutes (j). Solute concentration gradients (apoplastic and symplastic) within the cortex and stele are ignored, as are gradients in the bathing medium. In principle they can be included, but this would only introduce unnecessary complications. Here we wish to emphasize the possible effect of a step change in symplastic osmotic pressure across the endodermis. Apoplastic transport of water and solutes across the endodermis is assumed negligible.

In the steady state we have

\[
Q_v = Q_v^{oc} = A^{oc}L_p^{oc} (P^o - P^c + \Pi_i^c + \Pi_j^c - \Pi_i^s - \Pi_j^s),
\]

(21)

\[
Q_v = Q_v^{cs} = A^{cs}L_p^{cs} [P^c - P^s - \sigma_j^{cs}(\Pi_i^c - \Pi_j^c)]
- \sigma_i^{cs}(\Pi_j^c - \Pi_j^s)],
\]

(22)

\[
Q_v = Q_v^{sx} = A^{sx}L_p^{sx} (P^s - P^x - \Pi_i^s - \Pi_j^s + \Pi_j^x),
\]

(23)

from which we obtain

\[
\Delta P = Q_v R_p + \Pi_i^c + \Pi_j^c - \Pi_j^s
\]

\[
- (1 - \sigma_i^{cs}) A \Pi_i^{cs} - (1 - \sigma_j^{cs}) A \Pi_j^{cs},
\]

(24)

where the radial hydraulic resistance of the root \((R_p)\) is given by

\[
R_p = \frac{1}{A^{oc}L_p^{oc}} + \frac{1}{A^{cs}L_p^{cs}} + \frac{1}{A^{sx}L_p^{sx}}.
\]

(25)
and as usual $\Delta P_0$ is the intercept of the limiting linear portion of the $\Delta P(Q_\nu)$ curve on the $\Delta P$ axis:

$$\Delta P_0 = \Pi^o - [1 - (\sigma_j^o)^2] (\Pi_j^* + \frac{J_j^*}{\omega_j^o}) \frac{A^{cs}\omega_j^{cs}}{A^{cs}\omega_j^{cs}} - (1 - \sigma_j^o) \left(\frac{J_j^*}{\omega_j^o}\right),$$

and, as usual, $\Delta P_0$ is given by eqn (3), and

$$\Delta P = Q_v R_p + \Delta P_0 - \frac{RT A^{cs}\omega_j^{cs}}{Q_v} \left(\Pi_j^* + \frac{J_j^*}{\omega_j^o}\right),$$

where $R_p$ is apparent root hydraulic resistance:

$$R_p = R_p + \frac{(1 - \sigma_j^o)^2}{RT A^{cs}\omega_j^{cs}} \Pi_i^c,$$

and

$$Q_j^{oc} = Q_j^{*} + A^{uc}\omega_j^{uc} (\Pi_j^* - \Pi_j'),$$

$$Q_j^{sx} = A^{sx}\omega_j^{sx} (\Pi_j^* - \Pi_j'),$$

where the $\omega$'s are permeability coefficients and $Q_j^{*}$ is the rate of active transport across membrane $oc$ (transport across membrane $sx$ is assumed to be entirely passive). Transport of solutes $i$ and $j$ across membrane $cs$ is described by the relations

$$Q_i^{cs} = (1 - \sigma_i^c) \bar{C}_i Q_v + A^{cs}\omega_i^{cs} \Delta \Pi_i^c,$$

$$Q_j^{cs} = (1 - \sigma_j^c) \bar{C}_j Q_v + A^{cs}\omega_j^{cs} \Delta \Pi_j^c,$$

where

$$\bar{C}_i = C_i - \gamma_i (C_i^c - C_i^o),$$

$$\bar{C}_j = C_j - \gamma_j (C_j^c - C_j^o),$$

and as usual $0 \leq \gamma_i \leq 0.5$ and $0 \leq \gamma_j \leq 0.5$.

In deriving expressions for $\Pi_j^*(Q_\nu)$ and $\Delta P(Q_\nu)$, it is useful to define a dimensionless variable

$$y = \frac{Q_v}{RT A^{cs}\omega_j^{cs}}.$$

The derivation is given in Appendix D, where it is shown that if $A^{cs}\omega_j^{cs}/A^{cs}\omega_j^{cs} < 1$ and $A^{sx}\omega_j^{sx}/A^{sx}\omega_j^{sx} < 1$, there will be a range of $y$ values (e.g. $0.1 \leq y \leq 10$) for which $\Pi_j^*(Q_\nu)$ and $\Delta P(Q_\nu)$ can be approximated as

$$\Pi_j^* = A^{sx}\omega_j^{sx} \left(\Pi_j^* + \frac{J_j^*}{\omega_j^o}\right) \frac{RT}{Q_v} + \frac{1 - \sigma_j^o}{A^{cs}\omega_j^{cs}} \left(\frac{J_j^*}{\omega_j^o}\right).$$

The predicted variation of $\Pi_j^*$ with $Q_\nu$ [eqn (35); Figs 9(a) and 11(a)] is qualitatively of the correct form (i.e. hyperbolic). And if $A^{cs}\omega_j^{cs}/A^{cs}\omega_j^{cs} \ll 1$, $\Pi_j^*$ may fall to values less than $\Pi_j^o$ even when $y$ is restricted to an intermediate range (so that the simplified model applies). Similarly, eqn (36) is identical in form to the solution for $\Delta P(Q_\nu)$ for a two-compartment model in the absence of unstirred layer effects and with $\omega = 0$ [eqn (6) with $\omega = 0$, $k = 0$; Figs 9(b) and 11(b)]. Clearly, however, the parameters in eqn (36) have a different meaning from their counterparts in the two-compartment case. Note first that since photoassimilates are transported from the stele to the cortex via the endodermis (membrane $cs$), $J_i^o < 0$. By contrast, inorganic nutrients
FIG. 8. Four-compartment model with assimilate unloading. Plots of $P_{ci}$, $P_{sj}$ [a; eqns (D3), (D4)] and $P_{ci}$, $P_{si}$ [b; eqn (D10), $P_{ci}$ held constant] vs. the dimensionless volume $\#_{ux}y$ [eqn (34)]. Parameter values: $P_{oi}$ = 0, $P_{oj}$ = 0.1 MPa, $P_{ci}$ = 0.3 MPa, $(J^{\ast}_{j}/\sigma^{\ast}_{j})$ = 0.5 MPa, $R_{P}$ = 0.1 MPa, $(A^{sx}_{u}u^{sx}_{j}/A^{cs}_{u}u^{cs}_{j})$ = 0.01, $(A^{sx}_{u}u^{sx}_{j}/A^{cs}_{0}u^{cs}_{j})$ = 0.1, $(\sigma^{\ast}_{i}/\sigma^{\ast}_{j})$ = 1, $\Delta P_{csi}(0)$ = 0.2 MPa, $\sigma^{\ast}_{i}$ = $\omega^{\ast}_{i}$ = 0.5.

FIG. 9. Four-compartment model with assimilate unloading. Plots of $\Pi^{\prime}_{j}$ (a) and $\Delta P$ (b) vs. the dimensionless volume flux y. Continuous curves: full model [eqns (24)–(27) and (D3)–(D10)]; dashed curves: simplified model [eqns (35) and (36)]. Parameter values as in Fig. 8. The horizontal dotted lines show the value of $P_{oi}$ (0.1 MPa).

Imported from the bathing medium are then transported from the cortex to the stele, so that $J^{\ast}_{j} > 0$. But, by hypothesis, $A^{sx}_{u}u^{sx}_{j}/A^{cs}_{u}u^{cs}_{j}$ < 1, and so from eqn (38), $\Delta P_{0}$ may be greater than $\Pi^{\ast}_{0}$. An upper limit for $\Delta P_{0}$ is given by

$$\Delta P_{0} \leq \Pi^{\ast}_{0} - (1 - \sigma^{\ast}_{i})(J^{\ast}_{i}/\omega^{\ast}_{i})$$

$$= \Pi^{\ast}_{0} - (1 - \sigma^{\ast}_{i})\Delta P_{csi}(0),$$

(39)

where $\Delta P_{csi}(0)$ is the trans-endodermal difference in osmotic pressure for solute i in the absence of volume flow [eqn (30)]. Plasmolysis studies by Warmbrodt (1986, 1987) suggest values for $\Delta P_{csi}(0)$ of −0.2 to −0.6 MPa in barley roots and around −0.25 MPa in maize roots. For wheat roots, pressure-probe measurements by Pritchard et al. (1989) yielded estimates of around −0.2 MPa. There are no estimates of $\sigma$ for endodermal cells, but pressure-probe measurements on other cells suggest values for $\sigma^{\ast}_{i}$ of around 0.5 (Murphy & Smith, 1998). Tentatively combining these values gives $\Delta P_{0} - \Pi^{\ast}_{0} \leq 0.1$–0.3 MPa, which might be regarded as a reasonable range (e.g. see Newman, 1976; Fiscus, 1977, 1986; Passioura & Munns, 1984).

Passioura & Munns (1984) found that for both barley and lupin, $\Delta P_{0} - \Pi^{\ast}_{0}$ increased in the afternoon. Fiscus (1986) observed a similar increase for Phaseolus roots, and speculated that it might arise from increased solute uptake and sequestration within an intermediate compartment. The four-compartment model suggests an alternative explanation; the diurnal variation in
$\Delta P_0 - \Pi^o$ might reflect a variation in the rate of assimilate import via the phloem (low in the morning, high in the afternoon), and a concomitant variation in $J_{si}^o$ and therefore $\Delta P_{si}^o(0)$ [see eqn (39)]. In principle, this hypothesis can be tested experimentally by measuring the diurnal variation in assimilate import and/or $\Delta P_{si}^o(0)$; both should be correlated with changes in $\Delta P_0 - \Pi^o$. Another prediction of the model is that $\Delta P_0 - \Pi^o$ should decrease to negative values in starved root systems, when $J_{si}^o \rightarrow 0$ [eqn (38)]. Of course the detopped root systems used in many studies (e.g. Fiscus, 1977, 1986) are starved, but it will presumably take some time for $J_{si}^o$ to decay. In fact, in mature plants, starch reserves in the older parts of the root system as well as the stem base might sustain phloem transport and hence $J_{si}^o$ during the experimental period. For seedlings, where reserves are more limited, the decay in $J_{si}^o$ is expected to be more rapid. It should be noted that Munns & Passioura (1984) and Passioura & Munns (1984) used intact plants, and so the possibility of root starvation does not arise.

According to eqn (37), the slope ($R_p$) of the linear portion of the $\Delta P-Q_v$ curve should be positively correlated with $\Pi_j^o$. This was observed by Munns & Passioura (1984) for $\Pi_{NaCl}^o$ in lupin roots but not barley roots. Also for lupin (but not barley) they found that $\Delta P_0 - \Pi^o$ was negatively correlated with $\Pi_{NaCl}^o$ and that $\Delta P_0 < \Pi^o$. One possibility is that the terms in $\Pi_j^o$ (specifically $\Pi_{NaCl}^o$) in eqns (37) and (38) are significant in lupin but not in barley. Remembering that $\Pi_j^o$ is the osmotic pressure due to permeant solutes, this is consistent with the suggestion of Munns & Passioura (1984) that the lupin (but not barley) roots were leaky to NaCl, at least for $C_{NaCl}^o > 75$ mol m$^{-3}$. The decrease in $R_p$ observed by Passioura & Munns (1984) for lupin during the afternoon is more difficult to explain. Passioura & Munns (1984) point out that at least part of the

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**Fig. 10.** As Fig. 8 except that $(A^{vs}o_f^{vs}/A^{ls}o_f^{ls}) = 0.1$ and $(A^{ls}o_f^{ls}/A^{oc}o_f^{oc}) = 1.

**Fig. 11.** As Fig. 9 except that $(A^{vs}o_f^{vs}/A^{ls}o_f^{ls}) = 0.1$ and $(A^{ls}o_f^{ls}/A^{oc}o_f^{oc}) = 1.
decrease may be an artefact arising from the diurnal variation in $\Delta P_0$. But it is also possible that diurnal variations in $J_f^*$ and/or $\Pi^*_j$ contributed to a genuine decrease in $R_p$ [eqn (37)]. In principle, the latter possibilities are experimentally testable.

The above analysis applies to an intermediate range of $y$ values which, however, might be quite large (e.g. $0.1 \leq y \leq 10$). In fact, an upper limit on $y$ is necessary to avoid unreasonably low values of $\Pi_j^*$ (see Appendix D) as well as very large values of $\Delta \Pi^*_j$ [eqn (D12); Figs 8(a), 10(a)] and $\Delta \Pi^*_j$ [eqn (D10); Figs 8(b), 10(b)]. Furthermore, while the mechanism of plasmodesmal transport is deliberately not specified, the putative linear relationship between $\Delta \Pi^*_j$ and $y$ [eqn (D10); Figs 8(b), 10(b)] will presumably apply only for sufficiently low $y$. On the other hand, the validity of the simplified model also depends on the assumptions $A^{xs} w_j^{xs}/A^{cs} w_j^{cs} \ll 1$ and $A^{xs} w_j^{xs}/A^{os} w_j^{os} \ll 1$. It is argued in Appendix D that these assumptions are reasonable. But in any case, plots of the full-model equations suggest that the essential qualitative features of the simplified model can be retained even when $A^{xs} w_j^{xs}/A^{cs} w_j^{cs}$ and $A^{xs} w_j^{xs}/A^{os} w_j^{os}$ are increased to values where the simplified model no longer applies quantitatively. Thus, in Figs 8 and 9, $A^{xs} w_j^{xs}/A^{cs} w_j^{cs} = 0.01$, $A^{xs} w_j^{xs}/A^{os} w_j^{os} = 0.1$ and the simplified model (dashed curves in Fig. 9) is a good approximation to the full model (continuous curves in Fig. 9). In Figs 10 and 11, $A^{xs} w_j^{xs}/A^{cs} w_j^{cs} = 0.1$, $A^{xs} w_j^{xs}/A^{os} w_j^{os} = 1$ and the simplified model is a poor approximation to the full model (compare dashed and continuous curves in Fig. 11). Yet the qualitative behavior of the full-model (continuous) curves in Fig. 11 is very similar to that of the simplified-model (dashed) curves in Fig. 9.

Setting $y$ equal to zero also poses no problem for the model. Thus, on setting $y = 0$ in eqns (D3)–(D5) we find that

$$\Pi_j^*(0) = \Pi_j^*(0) = \Pi_j^*(0) = \Pi_j^*(0) + (J_f^*/w_j^*)$$

whence $\Delta \Pi_j^*(0) = \Pi_j^*(0) - \Pi_j^*(0) = 0$. Then from eqn (24)

$$\Delta P(0) = \sigma^{\text{root}} (\Pi^* - \Pi_j^*(0))$$

where the root reflection coefficient (determined at $Q_r = 0$) is given by

$$\sigma^{\text{root}} = 1 + \frac{(1 - \sigma^{\text{cs}}) \Delta \Pi_j^*(0)}{\Pi_j^*(0) - \Pi^*}. \quad (42)$$

Now in general $\Pi_j^*(0) > \Pi^*$; this is the presumed cause of “root pressure” ($-\Delta P(0) > 0$). Then remembering that $\Delta \Pi_j^*(0) \leq 0$ it follows that $\sigma^{\text{root}} \leq 1$. It has been argued that values of $\sigma^{\text{root}}$ less than unity might be explained by an apoplastic pathway for the transport of water and solutes across the endodermis (Steudle, 1992, 1994; Steudle & Peterson, 1998). This possibility cannot be discounted, but in some root systems such apoplastic transport appears negligible (Perry & Greenway, 1973; Moon et al., 1986). According to the four-compartment model $\sigma^{\text{root}}$ can still be less than unity in such cases. This can be seen from eqn (42); low values of $\sigma^{\text{root}}$ result from a difference in symplasmic osmotic pressure $|\Delta \Pi_j^*(0)|$ across the endodermis, which has a low reflection coefficient ($\sigma^{\text{cs}}$) because of the presence of plasmodesmata. A prediction of eqn (42) is that in starved (e.g. excised) root systems, $\sigma^{\text{root}}$ should increase with time, approaching unity as phloem unloading falls and $\Delta \Pi_j^*(0) \to 0$. In practice, $\sigma^{\text{root}}$ will never literally reach unity because the cell membranes are permeable to solutes, but cell-membrane reflection coefficients can be very close to unity (e.g. Murphy & Smith, 1994b).

Various other observations have been interpreted in terms of apoplastic transport across the endodermis, but these can also be explained by the four-compartment model. Thus, a significant interaction between solute and water fluxes (“solvent drag”; Freundl et al., 1998, 2000) might occur within endodermal plasmodesmata [eqn (31)] rather than the endodermal apoplast. Nor does the effect of decreasing external pH on ABA transport (Freundl et al., 1998) imply apoplastic transport of ABA across the endodermis. Lowering external pH would increase the concentration of protonated ABA, which would promote transport in the cortical apoplast and uptake across cortical cell membranes. But transport across the endodermis could be entirely symplasmic. Similarly, the reduction in ABA transport (Freundl
et al., 2000) and root hydraulic conductivity (Zimmermann & Steudle, 1998) associated with the development of an exodermis does not imply reduced apoplastic transport across the endodermis. It might simply reflect impeded access to the cortical apoplast and hence cortical cell membranes. This possibility is not explicitly allowed for in the four-compartment model, but to a first approximation the effects of an exodermis can be included in the transport parameters \( L_p^a \) and \( \omega f^p \) \cite{eqns (21) and (28)}, both of which would be reduced by an exodermis.

Furthermore, while the calculations of Zhu & Steudle (1991) might suggest a high apoplastic hydraulic conductivity for layers 1–9 of the maize-root cortex, this need not apply to the endodermis. Moreover, their measurements suggest intercellular transport occurs via membranes with reflection coefficients less than unity, while transport between the symplast and apoplast occurs via a membrane with reflection coefficients close to unity (at least in the case of the epidermis). These conclusions regarding reflection coefficients are consistent with the four-compartment model presented here, and are supported by subsequent work \cite{Murphy & Smith, 1994a, b, 1998}.

The four-compartment model may be seen as one expression of the hypothesis of Fiscus \cite{1981, 1986, 1988} that the offset in the \( \Delta P-Q_v \) curve \( (\Delta P_0 > \Pi^a) \) is due to an internal asymmetric distribution of “nonmobile” solutes. But according to the four-compartment model, the nonmobile solutes are derived from the phloem. Hence, a further prediction of the model is that the solute efflux elicited by ABA \cite{Fiscus, 1981} should include an efflux of phloem-derived organic compounds such as sugars.

**Discussion**

The present analysis suggests that solute build-up in two- and three-compartment models of the root \cite{Dalton et al., 1975; Fiscus, 1975, 1977; Miller, 1985} cannot account for the anomalous offset \( (\Delta P_0 > \Pi^a) \) frequently observed in plots of \( \Delta P \) vs. \( Q_v \). The three-compartment model of Ginsburg \cite{1971} and Newman \cite{1976} appears more promising, but it predicts a minimum in the plot of \( \Pi^a \) vs. \( Q_v \) which is not observed in practice. The symplastic osmotic pressure also exhibits a minimum which can be rather low, and sometimes negative. Fiscus \cite{1981, 1986, 1988} hypothesized that an internal asymmetric distribution of nonmobile solutes is responsible for the offset. In the present study, this hypothesis is incorporated into a four-compartment model of the root that is conceptually related to the model of Miller \cite{1985}. But according to this four-compartment model, the asymmetric solute distribution does not arise because of solvent drag. Rather the anomalous offset is associated with a concentration gradient of photoassimilates (the nonmobile solutes) that exists in the absence of volume flow, and which drives the diffusive transport of these solutes from the stele to the cortex via endodermal plasmodesmata. This model appears to have greater explanatory power than the Ginsburg–Newman model. In particular, it suggests explanations for the diurnal variation in \( \Delta P-Q_v \) curves and the effects of changing external NaCl concentration reported by Munns & Passioura \cite{1984} and Passioura & Munns \cite{1984}. The model also shows how the overall root reflection coefficient can be less than unity, even when the cell membranes are effectively ideally semipermeable, and there is negligible apoplastic transport of water and solutes across the endodermis. Data that have hitherto been interpreted in terms of such apoplastic transport \cite{Zhu & Steudle, 1991; Zimmermann & Steudle, 1998; Freundl et al., 1998, 2000} can also be explained by the model.

The four-compartment model is also consistent with the occurrence of radial symplastic osmotic-pressure gradients, which the Ginsburg–Newman model is not. However, in developing the model, it was assumed that the only change in symplastic osmotic pressure occurs across the endodermis. The studies of Warmbrodt \cite{1986, 1987} and Pritchard et al. \cite{1989} support this assumption, and the magnitude of the osmotic-pressure difference appears to be compatible with the size of the anomalous offset often seen in \( \Delta P-Q_v \) curves. But other studies show that significant turgor- and osmotic-pressure gradients can occur in the cortex \cite{Rygol & Zimmermann, 1990; Zimmermann et al., 1992; Rygol et al., 1993}. If the four-compartment model with assimilate unloading appears promising, it may be necessary
in future to generalize it to the multi-compartment (many-cell-layer) case. In the meantime, the model makes a number of experimentally testable predictions, and it may seem prudent to test at least some of these prior to further theoretical developments. The predictions of the four-compartment model may be summarized as follows:

1. The offset often observed in plots of $\Delta P$ vs. $Q_s$ ($\Delta P_0 - \Pi^o$ in Fig. 1) should be positively correlated with rate of assimilate import into roots [$J_{\text{ass}}^s$; eqns (38) and (39)].

2. The offset should also be positively correlated with the magnitude of radial symplastic concentration gradients in the cortex and/or across the endodermis [$\Delta \Pi^s(0)$; eqns (38) and (39)]. Strictly these gradients should be determined when $Q_s = 0$.

3. In starved root systems, $\Delta P_0 - \Pi^o$ should decrease to negative values [eqn (38) with $J_{\text{ass}}^s = 0$]. This process may be slow in mature plants with abundant starch reserves, but should be rapid in seedlings.

4. Also in starved plants, the overall root reflection coefficient ($\sigma_{\text{root}}$) should increase with time (slowly in mature plants, rapidly in seedlings), eventually approaching a value close to unity when $\Delta \Pi^s(0) = 0$ [eqn (42)]. $\sigma_{\text{root}}$ should be estimated as the ratio of root pressure to the difference in osmotic pressure between the bathing medium and the xylem [$\sigma_{\text{root}} = \Delta P/(\Pi^o - \Pi^s)$] when solute and water fluxes are both zero.

5. If ABA reduces the offset in the $\Delta P - Q_s$ curve and concurrently induces an efflux of solutes into the xylem (Fiscus, 1981), this efflux should include photoassimilates (the putative nonmobile solutes).

6. The slope ($R_p'$) of the linear portion of the $\Delta P - Q_s$ curve should be positively correlated with the osmotic pressure ($\Pi^o$) due to permeant solutes in the bathing medium [but not impermeant solutes; eqn (37)].

7. Diurnal variations in $R_p'$ should be correlated with changes in the rate of active solute uptake ($J^s$) and/or changes in symplastic osmotic pressure [$\Pi^s$; eqn (37)].

A crucial assumption in the four-compartment model is that intercellular transport occurs via membranes with reflection coefficients significantly less than unity, while transport between the symplast and apoplast occurs via a membrane that is effectively ideally semipermeable (i.e. $\sigma = 1$). Pressure-probe measurements support this view (Zhu & Steudle, 1991; Murphy & Smith, 1994a, b, 1998), but the question arises as to why the intercellular reflection coefficients are less than 1.0. In principle, aquaporins could have reflection coefficients of around 0.5 (Welling et al., 1996), but in this case the reflection coefficients of the plasmamembrane should also be around 0.5, which is not observed in practice. Murphy & Smith (1998) suggested that plasmodesmata were the cause of the low intercellular reflection coefficients. But this implies a large hydraulic conductance for the plasmodesmal pathway (Kedem & Katchalsky, 1963a; Murphy & Smith, 1998), and here the evidence appears contradictory. On the one hand, the studies of Zhang & Tyerman (1991), Tyerman et al. (1992) and Murphy & Smith (1998) suggest significant water flow through plasmodesmata. On the other hand, the studies of Tyerman and colleagues show that anoxia reduces $L_p$ and increases $\sigma$. If this is interpreted in terms of plasmodesmal constriction, one would then predict a reduction in the size exclusion limit (SEL) of plasmodesmata and an increase in intercellular electrical resistance. In fact, the data so far show an increase in SEL and no effect on electrical resistance (Cleland et al., 1994; Zhang & Tyerman, 1997). There is at least one way in which these seemingly contradictory results can be reconciled. If anoxia results in gelling of the plasmodesmal contents (e.g. by the intrusion of macromolecules into widened plasmodesmal channels), then $L_p$ will fall and $\sigma$ will rise. However, the effect on solute permeability and electrical conductivity might be small (at least for small molecules and ions; Tyree, 1970), especially given the increase in the plasmodesmal cross section (as indicated by the larger SEL). This hypothesis may be difficult to test at present, but it at least points to the need for a much better understanding of transport through plasmodesmata.
aquaporins, and this agent substantially reduces plant-cell and root $L_p$. However, there is evidence that HgCl$_2$ can have additional effects, which might conceivably include indirect effects on plasmodesmata (Zhang & Tyerman, 1999). In short, it seems that the relative contributions of the symplastic, transcellular and apoplastic pathways for water movement in plant tissues have still not been resolved. As far as the four-compartment model of the root is concerned, a major symplastic component is predicted, with negligible apoplastic transport across the endodermis.

Analysis of the two-compartment model was conducted in the laboratory of Prof. J. S. Boyer (University of Delaware), to whom I am grateful for helpful discussions.

REFERENCES


**Appendix A**

**Derivation of eqn (6)**

For a sufficiently dilute solution, the osmotic pressure (II) is related to the solute concentration (*Cₙ*) by the van’t Hoff equation

\[
\Pi = RT C_\text{s},
\]

(A1)

where *R* is the universal gas constant and *T* is the absolute temperature. Then using eqns (4) and (5), eqn (2) can be written as

\[
Q_\text{s} = [(1 - \gamma)(1 - \sigma)(Q_v/RT) + 2\pi \rho \omega \Pi^u(a)] + [(\gamma(1 - \sigma)(Q_v/RT) - 2\pi \rho \omega \Pi^s + Q^s_\text{x}].
\]

(A2)

But in the steady state, and assuming solute transport in the xylem is dominated by convection, we also have

\[
Q_\text{s} = C_\text{x}Q_v = \Pi^s(Q_v/RT),
\]

(A3)

where *C_\text{x}*- is the solute concentration of the xylem sap. Equating eqns (A2) and (A3) and solving for *\Pi^s* then gives

\[
\Pi^s = \frac{RTQ^s_\text{x} + [(1 - \gamma)(1 - \sigma)Q_v + 2\pi \rho \omega R T]\Pi^u(a)}{Q_v[1 - \gamma(1 - \sigma)] + 2\pi \rho \omega RT}.
\]

(A4)

To obtain an expression for *\Pi^u(a)* we assume the following diffusion equation applies within the unstirred layer:

\[
Q_\text{s} = 2\pi r \rho x D_s (dC^s_\text{eq}/dr) + C^s_\text{o}Q_v.
\]

(A5)

Separating variables and integrating gives

\[
C^s_\text{o}(a) = [C^s_\text{o}(b) - (Q_v/Q_v)]e^{AQ} + Q_v/Q_v,
\]

(A6)
where \( k \) is given by eqn (7). Or, from eqns (A1) and (A3):

\[
\Pi^o(a) = (\Pi^o(b) - \Pi^x)e^{kQ} + \Pi^x. \tag{A7}
\]

Substituting into eqn (A4) yields an expression for \( \Pi^x \) in terms of the measurable quantity \( \Pi^o(b) \):

\[
\Pi^x = \frac{\Pi^o(b)[(1 - \gamma)(1 - \sigma)Q_v + 2\pi\alpha L P + RTQ^*_v e^{-kQ}]}{Q_v[(1 - \gamma)(1 - \sigma) + \sigma e^{-kQ} - 1]} + 2\pi\alpha L P. \tag{A8}
\]

Similarly, eliminating \( \Pi^x \) between eqns (A4) and (A7) we get

\[
\Pi^o(a) = \frac{\Pi^o(b)[(1 - \gamma)(1 - \sigma)Q_v + 2\pi\alpha L P + RTQ^*_v e^{-kQ}]}{Q_v[(1 - \gamma)(1 - \sigma) + \sigma e^{-kQ} - 1]} + 2\pi\alpha L P. \tag{A9}
\]

Substituting eqn (4) into eqn (1) and solving for \( \Delta P \) gives

\[
\Delta P = Q_v/2\pi\alpha L P + \sigma(\Pi^o(a) - \Pi^x). \tag{A10}
\]

Substituting for \( \Pi^x \) and \( \Pi^o(a) \) from eqns (A8) and (A9) then gives eqn (6).

**Appendix B**

*Analysis of Miller’s Model When \( \gamma = 0 \)*

As \( Q_v \to \infty \), diffusional transport within the symplastic compartment becomes negligible at the outer membrane (cf. the two-compartment case). And since diffusional transport is also negligible within the xylem, we have

\[
\lim_{Q_v \to \infty} Q_s = Q_v \lim_{Q_v \to \infty} C^i_{s1} = Q_v \lim_{Q_v \to \infty} C^i_s. \tag{B1}
\]

Now for \( \gamma = 0 \), Miller’s (unnumbered) expression for \( Q_s \) (outer membrane) becomes

\[
Q_s = (1 - \sigma)C^o_s Q_v + K_1(S_{\infty} - C^i_{s1}), \tag{B2}
\]

where \( K_1 \) and \( S_{\infty} \) are constants (see Miller, 1985). Then from eqns (A1), (B1) and (B2) we obtain eqn (15). Equations (15) and (B3) then give inequality (16), which seems improbable (see text). Furthermore, from Miller’s eqn (6), together with eqns (15) and (16) we get

\[
\Delta P_0 = 2\sigma^2 \Pi^o, \tag{B5}
\]

from which we again conclude that \( \Delta P_0 \leq 2\Pi^o \), which is inconsistent with experimental observation (e.g. Fig. 1).

**Appendix C**

*Analysis of the Ginsburg–Newman Three-Compartment Model*

Let \( A_1 \) and \( A_2 \) be the surface areas of membranes 1 and 2, respectively. Then assuming a steady state of volume transport we have

\[
Q_v = A_1 L P_1[P^o - P^i - (\Pi^o_i - \Pi^x_i) - \sigma_{j1}(\Pi^o_j - \Pi^x_j)]
= A_2 L P_2[P^i - P^x - (\Pi^x_i - \sigma_{j2}(\Pi^x_j - \Pi^*^x_j)], \tag{C1}
\]
from which we obtain
\[ \Delta P = P^\infty - P^x = [(A_1L_p_1)^{-1} + (A_2L_p_2)^{-1}]Q_v + \Pi_i^o + \sigma_{j1}\Pi_j^o + (\sigma_{j2} - \sigma_{j1})\Pi_j - \sigma_{j2}\Pi_j. \]  
(C2)

And assuming a steady state of solute transport
\[ Q_j = (1 - \sigma_{j1})C_{j1}Q_v + A_1\omega_{j1}(\Pi_j - \Pi_j^o) + Q_j^o. \]  
(C3)

where
\[ C_{j1} = C_j^\infty - \gamma_{j1}(C_j^\infty - C_j^o), \]  
(C4)
\[ C_{j2} = C_j^\infty - \gamma_{j2}(C_j^\infty - C_j^o). \]  
(C5)

Substituting eqns (A1), (A3), (C4) and (C5) into eqn (C3) we can solve for \( \Pi_j^o \) and \( \Pi_j^x \):
\[ \Pi_j^o = \frac{a(Q_v/RT)^2 + b(Q_v/RT) + c}{d(Q_v/RT)^2 + e(Q_v/RT) + f}, \]  
(C6)
\[ \Pi_j^x = \frac{Q_j^o + [(1 - \gamma_{j2})(1 - \sigma_{j2})(Q_v/RT) + A_2\omega_{j2}]\Pi_j^o}{A_2\omega_{j2} + [1 - \gamma_{j2}(1 - \sigma_{j2})](Q_v/RT)}, \]  
(C7)

where
\[ a = \Pi_j^o(1 - \gamma_{j1})(1 - \sigma_{j1})[1 - \gamma_{j2}(1 - \sigma_{j2})], \]  
(C8)
\[ b = \Pi_j^o(1 - \gamma_{j1})(1 - \sigma_{j1})A_2\omega_{j2} + \gamma_{j2}\sigma_{j2}A_1\omega_{j1} \]  
\[ + \gamma_{j2}\sigma_{j2}Q_j^o - Q_j^o, \]  
(C9)
\[ c = A_2\omega_{j2}[Q_j^o + A_1\omega_{j1}\Pi_j^o], \]  
(C10)
\[ d = [\gamma_{j1}(1 - \sigma_{j1}) - 1][\gamma_{j2}(1 - \sigma_{j2}) - 1] - \sigma_{j2}, \]  
(C11)
\[ e = A_1\omega_{j1}[1 - \gamma_{j2}(1 - \sigma_{j2})] + A_2\omega_{j2}[1 - \gamma_{j1}(1 - \sigma_{j1})], \]  
(C12)
\[ f = A_1\omega_{j1}A_2\omega_{j2}, \]  
(C13)

In general, \( \Pi_j^o \to \pm \infty \) as
\[ \frac{Q_v}{RT} \to -e \pm \sqrt{e^2 - 4df}. \]  
(C14)

This asymptotic behavior is not acceptable for \( Q_v \geq 0 \), but we will allow it for \( Q_v < 0 \), since the models considered here are generally not applicable when \( Q_v < 0 \) [see Murphy (1999) for a two-compartment analysis of this “exosmotic” case].

It can be shown from eqns (C2), (C6) and (C7) that \( \Delta P(Q_v) \) approaches a linear function as \( Q_v \to \infty \), provided that \( \gamma_{j1} \) and \( \gamma_{j2} \) approach constant values. The interpretation of the intercept \( (\Delta P_0) \) on the \( AP \) axis depends on whether one chooses the low- or high-flow approximations for \( \gamma_{j1} \) and \( \gamma_{j2} \) (we assume the same approximation applies to both).

**Low-flow approximation:** \( \gamma_{j1} = \gamma_{j2} = 0.5 \):

From eqns (C6)–(C8) and (C11)
\[ \Pi_j^o(\infty) = \lim_{Q_v \to \infty} \Pi_j^o = \frac{\Pi_j^o(1 - \sigma_{j1})(1 + \sigma_{j2})}{(1 + \sigma_{j1})(1 + \sigma_{j2}) - 4\sigma_{j2}}, \]  
(C15)
\[ \Pi_j^x(\infty) = \lim_{Q_v \to \infty} \Pi_j^x = \frac{\Pi_j^x(1 - \sigma_{j1})(1 - \sigma_{j2})}{(1 + \sigma_{j1})(1 + \sigma_{j2}) - 4\sigma_{j2}}. \]  
(C16)

By observation, \( \Pi_j^x(\infty) < \Pi_j^o \). It can then be shown from eqn (C16) that
\[ \sigma_{j1} > \sigma_{j2}. \]  
(C17)

This inequality ensures that \( d > 0 \) [eqn (C11)]. And since \( e > 0 \) and \( f > 0 \) [eqns (C12) and (C13)], it follows that asymptotes in \( \Pi_j^o \) occur only for \( Q_v < 0 \) [eqn (C14)], which is acceptable. However, it can be shown from eqn (C15) that inequality (C17) also implies \( \Pi_j^x(\infty) < \Pi_j^o \), which seems unlikely. Furthermore, on substituting eqns (C15)
and (C16) into eqn (C2) we get
\[
\Delta P_0 = \Pi^o + \Pi^a_j(1 - \sigma_{j1}) \\
\left(\frac{(\sigma_{j2} - \sigma_{j1})(1 + \sigma_{j2}) - \sigma_{j2}(1 - \sigma_{j2})}{(1 + \sigma_{j1})(1 + \sigma_{j2}) - 4\sigma_{j2}} - 1\right),
\] (C18)
where \(\Pi^o = \Pi^a_1 + \Pi^a_2\) is the total external osmotic pressure. It then follows from inequality (C17)

\[
\Pi^a_j = \left[\Pi^a_j + (J^a_j/\omega^a_j)\right]\left\{[(A^s\omega^s_j/A^c\omega^c_j) + \gamma_j][1 - (1 - \sigma^c_j)\gamma_j,y] + (A^s\omega^s_j/A^c\omega^c_j)\gamma_j,y\right\}/a + by + cy^2,
\]
(D3)
\[
\Pi^o_j = \left[\Pi^o_j + (J^o_j/\omega^o_j)\right]\left\{[(A^s\omega^s_j/A^c\omega^c_j) + \gamma_j][1 - (1 - \sigma^c_j)(1 - \gamma_j)y\right\}/a + by + cy^2,
\]
(D4)
\[
\Pi^a_j = \left[\Pi^a_j + (J^a_j/\omega^a_j)\right][A^s\omega^s_j/A^c\omega^c_j][1 - (1 - \sigma^c_j)(1 - \gamma_j)y\right\}/a + by + cy^2,
\]
(D5)

that \(\Delta P_0 < \Pi^o\). Accordingly, the low-flow approximation must be rejected.

**High-flow approximation:** \(\gamma_{j1} = \gamma_{j2} = 0\).

From eqn (C11), \(d = (1 - \sigma_{j2}) > 0\), and so there are no asymptotes in \(\Pi^a_j\) for \(Q_v > 0\) [eqn (C14)], and from eqns (C6)–(C8) and (C11)

\[
\Pi^a_j(\infty) = \Pi^a_j\left(\frac{1 - \sigma_{j1}}{1 - \sigma_{j2}}\right),
\]
(C19)
\[
\Pi^a_j(\infty) = \Pi^a_j(1 - \sigma_{j1}).
\]
(C20)

Hence, consistent with observation, \(\Pi^a_j(\infty) < \Pi^o_j\) [eqn (C20)]. If we also require that \(\Pi^a_j(\infty) > \Pi^a_j\), then eqn (C19) implies inequality (18). Substituting eqns (C19) and (C20) into eqn (C2) gives eqn (19).

**Appendix D**

**Analysis of the Four-Compartment Model**

Remembering eqns (A1) and (27), eqn (31) can be written as

\[
Q^i = [(1 - \gamma_j)(1 - \sigma^c_j)(Q_v/RT) + A^s\omega^s_j]\Pi^a_j
\]
\[
+ [\gamma_j(1 - \sigma^c_j)(Q_v/RT) - A^s\omega^s_j]\Pi^a_j.
\]
(D1)

In the steady state

\[
Q^i = Q^s_j = C^j_vQ_v = \Pi^a_j(Q_v/RT).
\]
(D2)

Remembering eqn (34), substituting eqn (D2) into eqns (28), (29) and (D1) then gives three equations in \(\Pi^o_j, \Pi^a_j\) and \(\Pi^a_j\). These may be solved in terms of \(y\) to give

\[
Q^i = (1 - \sigma^c_j)\Pi^a_j(Q_v/RT) + A^s\omega^s_j\Delta \Pi^o_j,
\]
(D9)

where

\[
a = A^s\omega^s_j/A^c\omega^c_j,
\]
(D6)
\[
b = 1 + \left(\frac{A^s\omega^s_j}{A^c\omega^c_j}\right)[1 - (1 - \sigma^c_j)\gamma_j] + \frac{A^s\omega^s_j}{A^c\omega^c_j},
\]
(D7)
\[
c = [(1 - \gamma_j)(A^s\omega^s_j/A^c\omega^c_j) - \gamma_j](1 - \sigma^c_j),
\]
(D8)

and \(J^a_j = \gamma_j/A^c\omega^c_j\) is the active solute flux across membrane oc. For \(\gamma_j = 0.5\) (low-flow approximation), the denominator in eqns (D3)–(D5) can be zero for \(y > 0\), and \(\Pi^a_j\) can be negative [eqn (D3)]. This behavior is unacceptable, so we choose the high-flow approximation (\(\gamma_j = 0\)), which ensures that asymptotes do not occur for \(y > 0\) (since \(b > 0, c > 0\), and also that \(\Pi^a_j \geq 0\). Nonetheless, eqn (D3) shows that with \(\gamma_j = 0\), \(\Pi^a_j \to 0\) as \(y \to \infty\). Clearly, \(y\) must be restricted so that \(\Pi^a_j\) maintains reasonable values. Assuming the high-flow approximation applies also to solute \(i\) we have

\[
Q^i = (1 - \sigma^c_j)\Pi^a_j(Q_v/RT) + A^s\omega^s_j\Delta \Pi^o_j,
\]
(D9)

whence

\[
\Delta \Pi^o_j = (J^a_j/A^c\omega^c_j) - (1 - \sigma^c_j)(\omega^s_j/A^c\omega^c_j)\Pi^a_jy,
\]
(D10)
where \( J_{cs}^{\text{eq}} = Q_{cs}^{\text{eq}} / A_{cs} \) is the flux of photoassimilates across the endodermis (i.e., membrane \( cs \)). For simplicity we assume that \( J_{cs}^{\text{eq}} \) and \( P_{ci} \) are constant.

The complexity of the above equations make a general discussion of the four-compartment model difficult. However, some useful insights can be obtained by considering the following simplification. Since solute transport across \( cs \) involves a combination of “solvent drag” and diffusion through plasmodesmata, whereas transport across \( sx \) involves permeation through a cell membrane, it seems reasonable to suppose that \( A_{sx}^{\text{eq}} \omega_{sx}^{\text{eq}} / A_{cs}^{\text{eq}} \omega_{cs}^{\text{eq}} \ll 1 \), whence \( a \ll 1 \) [eqn (D6)]. Now since \( A_{oc}^{\text{eq}} \) presumably includes the surface area of root hairs, and possibly also that of the cortical cells, it seems possible that \( A_{oc}^{\text{eq}} \gg A_{sx}^{\text{eq}} \), and that \( A_{sx}^{\text{eq}} \omega_{sx}^{\text{eq}} / A_{oc}^{\text{eq}} \omega_{oc}^{\text{eq}} \ll 1 \). From these considerations, and remembering that \( \gamma_{j} = 0 \), we conclude that \( b \approx 1 \) [eqn (D7)] and that \( c \ll 1 \) [eqn (D8)]. Hence, there should be some intermediate range of \( y \) values for which the denominator in eqns (D3)–(D5) can be replaced by \( y \), at least to a rough approximation. For example, if \( a \) and \( c \) are both around 0.01, then this simplified model will apply (approximately) for \( 0.1 \leq y \leq 10 \). Then the expression for \( \Pi_{j}^{\text{eq}} \) [eqn (D5)] simplifies to

\[
\Pi_{j}^{\text{eq}} = \left( \Pi_{j}^{\text{eq}} + \frac{J_{j}^{\text{eq}*}}{\omega_{oc}^{\text{eq}}} \right) \left( \frac{A_{sx}^{\text{eq}} \omega_{sx}^{\text{eq}}}{A_{cs}^{\text{eq}} \omega_{cs}^{\text{eq}}} \left( \frac{1}{y} + 1 - \sigma_{cs}^{\text{eq}} \right) \right).
\]

(D11)

Substituting for \( y \) from eqn (34) then gives eqn (35). From eqns (27), (D3) and (D4), \( \Delta \Pi_{j}^{\text{eq}} \) is given by

\[
\Delta \Pi_{j}^{\text{eq}} = \left( \Pi_{j}^{\text{eq}} + \frac{J_{j}^{\text{eq}*}}{\omega_{oc}^{\text{eq}}} \right) \left[ \sigma_{sx}^{\text{eq}} \left( \frac{A_{sx}^{\text{eq}} \omega_{sx}^{\text{eq}}}{A_{cs}^{\text{eq}} \omega_{cs}^{\text{eq}}} \right) - (1 - \sigma_{cs}^{\text{eq}}) y \right].
\]

(D12)

Remembering eqn (34), substituting eqns (D10)–(D12) into eqn (24) gives eqn (36).