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# A Model of Diffusion and Mass Flow of Water in Cylindrical Membrane Systems with Application to Plant Roots

M.G.T. Shone, B.O. Bartlett, and Ann V. Flood

Agricultural Research Council Letcombe Laboratory, Wantage, Oxfordshire OX12 9JT, United Kingdom

**Summary.** Measurements of the radial diffusion of tritiated water, combined with axial and radial flow in an artificial cylindrical membrane, are examined with the aid of a mathematical model. The results are used to assess how far measurement of diffusion of labeled water in plant roots may throw light on pathways of movement of water and on barriers to flow.

Diffusion of water labeled with deuterium or tritium has been examined in many biological systems to throw light on membrane permeability and structure. These investigations have included studies on plant roots to elucidate the pathways of radial movement of water and the location of the tissues presenting major resistance (Ordin & Gairon, 1961; Woolley, 1965; Raney & Vaadia, 1965; Ginsburg & Ginzburg, 1970*a*). Radial diffusion across the roots of intact plants to or from the conducting tissues is difficult to study since the xylem is not directly accessible to measurements; this consideration has prompted the use of detached roots or preparations derived from them (e.g. Anderson & House, 1967; Jarvis & House, 1967; Ginsburg & Ginzburg, 1970*a*; Clarkson, et al., 1978), in which pathways of water movement may differ from those in intact transpiring plants.

We began the present study primarily to help interpret experiments on the diffusion of labeled water in roots of intact barley roots (Shone & Wood, 1977; Shone & Flood, *in preparation*). In these experiments, labeled water was supplied to apical zones of the roots, and the quantities released by diffusion to unlabeled solution surrounding the basal zones were measured; there was evidence that a large proportion of the labeled water had been translocated between the two zones via the xylem vessels. This implies a concentration gradient of labeled water along the longitudinal axis of the xylem conducting tissues within that portion of the roots in the unlabeled solution, accompanied by a net uptake of the unlabeled water across the radial axis of the roots. To assess the experimental results it was necessary to calculate the rate of radial diffusion of the labeled water across the root from the xylem to the outer medium, but standard mathematical solutions for the conditions outlined above seemed not to be available in the literature (e.g., Crank, 1964). We have accordingly derived an equation for the radial diffusion of labeled water from a longitudinal cylindrical source of varying concentration when there is net radial movement of water (Fig. 1). The equation was tested

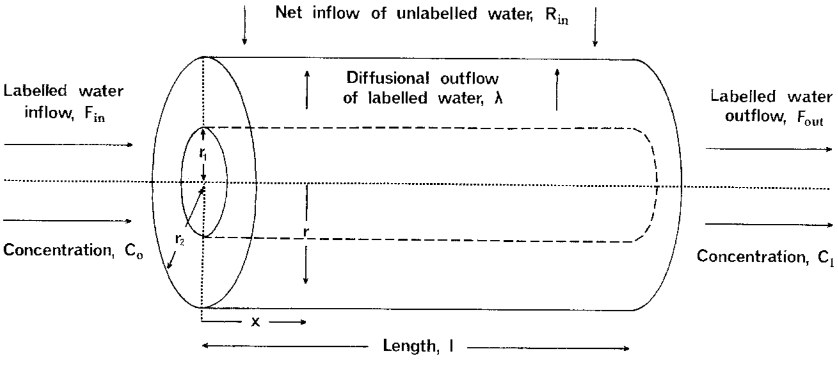

**Fig. 1.** Radial diffusion ($\lambda$) of tritiated water which has entered the lumen of a cylindrical membrane (external and internal radii $r_2$ and $r_1$, respectively) at a rate of flow $F_{\text{in}}$ and tritium concentration $C_0$. Unlabeled water passes radially into the membrane with a flow $R_{\text{in}}$ resulting in a decrease in the concentration of tritium along the length $l$ of the membrane. In the Appendix, the longitudinal ($F_{\text{in}}$) and radial ($R_{\text{in}}$) flows are defined per unit area as $F_0$ and $(-R_0)$ respectively

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in a model system consisting of a hollow cylindrical ultrafiltration membrane (Amicon, Diafiber H1 P10) of approximately the same external diameter as the seminal axis of a barley root, but with a single central lumen, as opposed to the multiple xylem vessels in the root. This membrane had a nominal molecular weight cut-off of $10^4$. Data published by the manufacturers and microscopical examination suggest that the effective ultra-filtration "skin" on the internal surface of the membrane is about 1 µm thick and that this is surrounded by a spongy layer of the same material about 85 µm thick, with much wider pores. The material is, therefore, inhomogeneous and, by analogy with a root, comprises a "free space", with wide pores surrounding a thin "endodermis." Experiments on this physical model lead to some conclusions as to how far effects associated with unstirred layers must be taken into account in comparable studies on plant roots; the importance of allowing for these effects with rapidly diffusing solutes has been clearly discussed in reviews by Dainty (1963, 1976). Using earlier measurements as data (Shone & Wood, 1977), we estimate apparent diffusion coefficients of labeled water in roots in intact, transpiring barley plants and examine the relevance of measurements of tracer diffusion to elucidating pathways of water movement. A major difficulty in interpreting such measurements lies in the composite nature of many membranes and tissues, including those in the present study. Apparent diffusion coefficients derived from measurements of overall permeabilities may not provide information on the permeabilities of the individual components of the tissue.

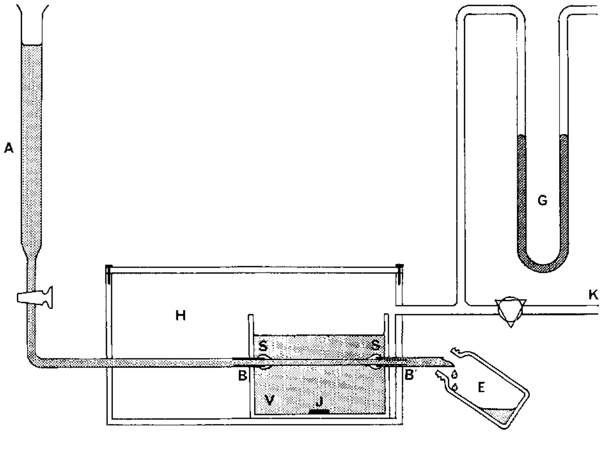

**Fig. 2.** Apparatus for measuring radial diffusion of tritiated water and net flow of unlabeled water in a Diafiber cylindrical membrane. *A*, burette containing tritiated water; *B*–*B'*, membrane; *E*, vessel collecting outflow from membrane; *G*, manometer; *H*, Perspex chamber; *J*, magnetic stirrer; *K*, air line for applying pressure or suction to *H*; *S*, seals; *V*, Polythene vessel containing unlabelled water

## Materials and Methods

Diafiber (Amicon) membranes (mean external and internal diameter 0.039 and 0.022 cm, respectively, and length $l$) were mounted in the apparatus (Clarkson et al., 1978 and Fig. 2). Measured volumes of water labeled with tritium (THO, 1.5 µCi $\mathrm{ml}^{-1}$) were passed from the burette *A* through the membrane *B*–*B'* which was sealed (*S*) into polythene tubing and mounted in a polythene vessel *V* holding 50 ml of unlabeled water; in some experiments this was vigorously stirred with a magnetic stirrer *J*, 12 mm long and 5 mm diameter, rotating at $2 \times 10^3$ rpm. Some experiments were also made with labeled water in the vessel *V* and unlabeled water passing through the membrane. Labeled water emerging from the membrane was collected at *E* and the radioactivity measured by liquid scintillation counting. The tubing between the membrane and *E* was made as short as practicable to minimize dead-space effects. The apparatus was mounted in a Perspex chamber *H*, and a net radial flow of water through the membrane was induced by applying pressure or suction through tube *K*; pressure differences were measured with the manometer *G*. In most experiments, about 1 $\mathrm{cm}^3$ water, representing about 500 times the volume of the membrane lumen, was passed longitudinally through the membrane. At the end of each experimental run, a sample of the water in vessel *V* was counted to find the tritium content.

Let $F_{\mathrm{in}}$ = rate of volume flow of labeled water entering lumen of membrane at *B* ($\mathrm{cm}^3\ \mathrm{sec}^{-1}$)

$C_o$ = specific activity of labeled water entering at *B* (µCi $\mathrm{cm}^{-3}$)

$R_{\mathrm{in}}$ = net radial volume inflow of unlabeled water from *V* ($\mathrm{cm}^3\ \mathrm{sec}^{-1}$)

$\lambda$ = rate of loss of THO to *V* per unit specific activity $C_o$ ($\mathrm{cm}^3\ \mathrm{sec}^{-1}$)

$C_l$ = specific activity of labeled water emerging at *E* (µCi $\mathrm{cm}^{-3}$)

Then the rate of mass flow of water emerging at *E* $(F_{\mathrm{out}}) = F_{\mathrm{in}} + R_{\mathrm{in}}$ and from the balance of inflow and outflow of tritium

$$F_{\mathrm{in}}\, C_o = \lambda C_o + C_l (F_{\mathrm{in}} + R_{\mathrm{in}})$$

or

$$C_l/C_o = (1 - \lambda/F_{\mathrm{in}})/(1 + R_{\mathrm{in}}/F_{\mathrm{in}}). \tag{1}$$

From the model described in the Appendix, a relationship between the apparent diffusion coefficient of THO, $D$, $R_{\mathrm{in}}$ and $\lambda$ can be derived as follows:

$$D = \frac{R_{\mathrm{in}} \ln(r_2/r_1)}{2\pi l \ln\left\{1 - \dfrac{\ln(1 + R_{\mathrm{in}}/F_{\mathrm{in}})}{\ln(1 - \lambda/F_{\mathrm{in}})}\right\}} \tag{2}$$

where $l$, $r_1$ and $r_2$ are, respectively, the length, and the internal and overall radii of the cylindrical membrane (Fig. 1). In the derivation, it is assumed that the specific activity in the medium surrounding the membrane is negligible by comparison with that in the membrane lumen; this condition was fulfilled in practice under our experimental conditions.

## Results and Discussion

### *Estimates of Diffusional Permeabilities in the Model System*

Constant values of $D$ were obtained in preliminary experiments when $l$ and $F_{in}$ were varied in the absence of stirring, both when the labeled water was passed through the lumen of the fiber membrane and when it was supplied externally. However, when $R_{in}$ was increased by applying pressure to the system at $K$, there was a corresponding increase in $D$; this was further accentuated when the water in the vessel $V$ was stirred (Fig. 3). This observation seemed consistent with the presence of an unstirred layer of water around the membrane acting in the absence of stirring or net uptake of water as a resistance to diffusion of labeled water in series with the membrane itself. The increase in $D$ at larger values of $R_{in}$ seemed consistent with the progressive disruption of the unstirred layer, or its displacement closer to the surface of the membrane.

Stirring seems unlikely to have resulted in any appreciable mixing of the solution within the "free space" of the membrane, which constitutes the major fraction of the total length of the radial pathway across the membrane and therefore may govern the magnitude of $D$ in the membrane as a whole. For values of $R_{in}$ greater than zero, when $F_{in}$ ranged from $2.1 \times 10^{-3}$ to $0.8 \times 10^{-3}$ cm$^3$ sec$^{-1}$, $D$ increased only marginally and seemed to tend towards a value of about $8 \times 10^{-6}$ cm$^2$ sec$^{-1}$ under stirred conditions, or about one-third of the self-diffusion coefficient of THO in water ($24 \times 10^{-6}$ cm$^2$ sec$^{-1}$, Dick, 1966). Hays (1968) investigated diffusion of THO across cellulose acetate membranes, of structure and thickness comparable with the Diafiber material, composed of a thin ultrafiltration skin supported by a much thicker porous layer. He showed that removal of the skin had little effect on the magnitude of $D$ which was about 25% of that in water. He accordingly concluded that diffusion was rate-limited by the thick porous layer and that about one-fourth of the area of this layer was open to diffusion. It was not possible to remove the ultrafiltration skin of the Diafiber membranes but the similarity to Hays' material suggests that the thick supporting layer again offered the main resistance to diffusion.

Neglecting any residual unstirred layer, the corresponding value of the membrane permeability ($P_m$) may be calculated from the relationship (Ginsburg & Ginzburg, 1970*b*)

$$P = D/[r_2 \ln(r_2/r_1)] \qquad (3)$$

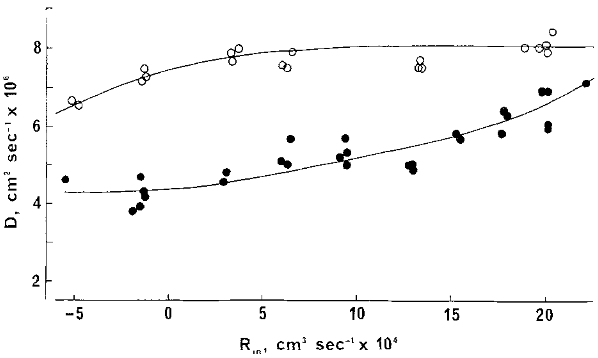

**Fig. 3.** Relationship between apparent diffusion coefficient ($D$) of tritiated water in Diafiber membrane and net radial flow ($R_{in}$) of unlabeled water. Open and closed circles represent, respectively, stirred and unstirred conditions

whence

$P_m = 7.1 \times 10^{-4}$ cm sec$^{-1}$.

The overall permeability ($P_{total}$) in the absence of stirring, and when $R_{in} = 0$, will be (Eq. (3)) $4.0 \times 10^{-4}$ cm sec$^{-1}$. An estimate of the thickness of the unstirred layer may be made from $P_{total}$ and $P_m$ using the relationship (Dainty, 1963)

$$1/P_{total} = 1/P_m + \delta_1/D_{THO} + \delta_2/D_{THO} \qquad (4)$$

where $\delta_1$ and $\delta_2$ are the thicknesses of the external and internal unstirred layers and $D_{THO}$ the self-diffusion coefficient of THO in water. Unstirred layers in the internal solution are likely to be less important due to the longitudinal flow of water along the lumen of the fibre membrane; this accorded with the finding that $D$ did not vary with $F_{in}$ at constant values of $R_{in}$. Neglecting $\delta_2$ and taking $D_{THO}$ as $2.4 \times 10^{-5}$ cm$^2$ sec$^{-1}$ (Dick, 1966) gives $\delta_1$ as about 0.03 cm.

Although the thickness of the unstirred layer is an equivalent rather than an actual dimension, its significance in both physical (e.g., Bircumshaw & Riddiford, 1952) and biological systems is well documented; depending on the size and shape of the solid phase and on rates of stirring, $\delta$ may vary between 0.002 and 0.05 cm (Dainty, 1963). The value suggested in the present work on a model system of dimensions comparable with a barley root lies in this range; its significance is discussed below.

### *Estimate of Bulk Permeability in the Model System*

Using the diffusion apparatus (Fig. 2) we were able to estimate the bulk (hydraulic) conductivity ($L_p$) of the

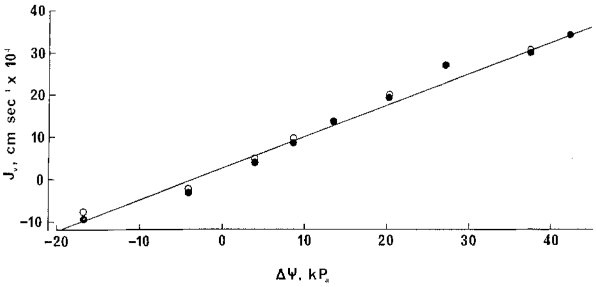

**Fig. 4.** Relationship between net radial influx of water ($J_V$) and applied pressure ($\Delta\psi$) for Diafiber membrane. Open and closed circles represent respectively stirred and unstirred conditions

membrane. In the absence of any difference in osmotic pressure across the membrane, this is given by:

$$J_v = L_p \Delta\psi \tag{5}$$

where: $J_v$ is the bulk flow of water across the membrane per unit area (cm sec$^{-1}$)$= R_{\text{in}}/2\pi r_2\, l$;
$L_p$ is the hydraulic conductivity (cm sec$^{-1}$ kPa$^{-1}$);
$\Delta\psi$ is the hydrostatic pressure difference across the membrane (kPa), and in the present experiments the difference between the applied pressure ($-13$ to 47 kPa) and that attributable to the head of water in the burette $A$ (4 kPa).

The slope of the relationship between $J_v$ and $\Delta\psi$ (Fig. 4) gives $L_p$ as $0.74 \times 10^{-4}$ cm sec$^{-1}$ kPa$^{-1}$; stirring evidently had no effect on this value.

By analogy with other artificial and natural composite membranes (House, 1974; Page, Abramovich & Smith, 1974*a, b*), the magnitude of $L_p$ is probably governed by the pore size of the ultrafiltration skin, whereas that of $P_m$ by the path length and tortuosity of the supporting tissues. This precludes making realistic estimates of pore size from the ratio $L_p/P_m$ such as may be possible in simple membrane systems.

### *Application of the Model System to Plant Roots*

Simplifying assumptions must be made in using the above model to examine radial diffusion in roots. Thus, in barley, the conducting tissues of the xylem consist of a large central vessel surrounded by seven or eight smaller metaxylem vessels that lie within the endodermis; the latter is often envisaged as a barrier to the free diffusion of water and solutes. In applying the model, estimates of the effective internal radius of the root ($r_1$ in Fig. 1 and Eq. (2)) might therefore be based either on the mean cross-sectional area of the xylem vessels or on the internal radius of the endodermis. The presence on the older zones of the main axes of lateral roots, which may supply water directly to the main xylem vessels, will introduce further uncertainty in applying Eq. (2) to these zones. Results are, however, available from experiments over a 24 hr period (16 hr day-length), on bulk flow of water, axial flow in the xylem, and diffusion of THO out of segments of roots of intact barley plants, about 5 to 8.5 cm from the root tip, and bearing no laterals (Shone & Wood, 1977, Table 8, lines *D* and *E*). From this table, values of $\lambda$, $R_{\text{in}}$ and $F_{\text{in}}$ for pairs of root segments, each 3.5 cm long ($l = 7$ cm), were, respectively, 0.164, 0.115 and 0.183 cm$^3$ day$^{-1}$. Measurements on transverse sections of the roots gave $r_2$ as 250 μm and $r_1$ as 85 μm (radius of endodermis) or 39 μm (effective radius of xylem vessels). In these experiments, the calculated minimum concentration of tritium in the xylem vessels ($C_l$, Eq. (1)) was ten times that in the medium surrounding the roots into which the labeled water was diffusing; $C_0$ was greater by a factor of over 100. On the basis that the external concentration was small in relation to that in the xylem, values for $D$ were calculated from Eq. (2) (Table 1). $L_p$ was calculated from $R_{\text{in}}$ and $\Delta\psi$ (Eq. (5)), using data from separate measurements of leaf water potential ($\Delta\psi = 0.6$ MPa). We also compared values for these quantities in other root systems and in the Diafiber membrane (Table 1).

On the basis of Eq. (4), the effect on tracer permeability of an external unstirred layer 0.03 cm thick around roots of radius about 0.02 cm (as in barley) would be only about 1% if the apparent diffusion coefficient were less than $0.3 \times 10^{-6}$ cm$^2$ sec$^{-1}$; this accords with the observation (Shone & Wood, 1977) that gentle stirring by aeration had no significant effect on the rate of loss of labeled water by these roots. The tracer permeabilities ($P$) calculated from Eq. (3) were 6.0 or $6.5 \times 10^{-6}$ cm sec$^{-1}$ based respectively on the stelar and effective xylem radii.

The values for the apparent diffusion coefficient in segments of roots of intact, transpiring barley plants are considerably smaller than those reported for detached roots and preparations derived from them, and for roots of plants where transpiration had been eliminated; the hydraulic conductivity, $L_p$, was, however, within the range quoted for whole root systems of various plant species and markedly less than those in root preparations (Table 1). In applying Eq. (2) to roots, the small value found for $D$ is unlikely to result from experimental errors in determining the variables in the equation. Thus, a fivefold increase in $R_{\text{in}}$, with the remaining variables constant, would only double the value of $D$. Even if $\lambda = 0.99\, F_{\text{in}}$, the value of $D$ would be increased by a factor of less than 2. In our experiments with barley, although some of the la-

**Table 1.** Comparisons between estimates of apparent diffusion coefficients ($D$) and hydraulic conductivities ($L_p$) in plant roots and an artificial cylindrical membrane

| Material/reference | $D$ cm$^2$ sec$^{-1}$ $\times 10^6$ | $L_p$ nm sec$^{-1}$ MPa$^{-1}$ |
|---|---|---|
| *Vicia faba* root segments (Ordin & Gairon, 1961) | 1.8 | – |
| *Zea mays* roots intact plants; transpiration eliminated (Woolley, 1965) | 5.0 | – |
| *Zea mays* detached roots (House & Jarvis, 1968) | 1.9 | – |
| *Zea mays* roots: cortical sleeve preparations (Ginsburg & Ginzburg, 1970*a*) | 1.2$^a$ | 89 |
| *Allium cepa* roots: nonliving epidermal/hypodermal sleeve preparations (Clarkson et al., 1978) | 2.0$^{a,b}$ | 6–10 × 10$^3$ |
| Various plant species, whole root systems (Newman, 1976) | – | 5.4–61 |
| Roots of intact transpiring barley plants, 5–8.5 cm from root apex (Shone & Wood, 1977) | 0.17–0.29$^{a,b,c}$ | 20$^d$ |
| Artificial Diafiber membrane (present work) | 8.0$^a$ | 74 × 10$^4$ |
| Self-diffusion coefficient of THO in water (Dick, 1966) | 24 | – |

[a] Allowance made for effects of unstirred layers.

[b] Calculated from authors' results on tracer permeabilities.

[c] Calculated respectively on the basis of the internal radius of the endodermis and the effective radius of the xylem vessels.

[d] Based on separate measurements of water potential difference between leaves and solution of 0.6 MPa.

beled water may have moved longitudinally through the cortex, the major proportion had probably diffused radially from the xylem vessels to the external medium (Shone & Wood, 1977). This contrasts with some earlier work (Ordin & Gairon, 1961; Woolley, 1965; Raney & Vaadia, 1965), where rates of diffusion into the tissues as a whole were estimated by immersing the roots in labeled water or by measuring efflux from previously labeled roots (Jarvis & House, 1967; House & Jarvis, 1968). These experiments would presumably have provided a measure of rates of influx and efflux of THO into the cortical vacuoles. By contrast, experiments with detached roots in which THO concentrations in the root tissues were compared with those in the xylem sap exuding from the cut end of the root (Hodges & Vaadia, 1964; Anderson & House, 1967) suggest markedly slower rates of exchange of water with the sap than with the cortical cells. In other work the central elements of the root had been removed to give a sleeve of tissue about 10 (Ginsburg & Ginzburg, 1970*a*) and 2 (Clarkson et al., 1978) cells thick. Note that in the experiments of Ginsburg and Ginzburg (1970*a*) with cortical sleeves of maize, there was no significant difference between the rates of radial influx and efflux of labeled water.

The pathways of movement of water may differ in intact roots and may also vary with environmental conditions. Raney and Vaadia (1965) found that when roots of sunflower plants were immersed in tritiated water, the THO content of the roots approached equilibrium with that in the ambient medium considerably more rapidly with detached roots, or with roots of shaded plants, than with those of transpiring plants in the light. They conjectured that in the latter case most of the bulk flow of water might be occurring via the cell walls ("free space") and that equilibration of THO was tending to take place with this fraction of the water in the roots rather than with the total volume, which would include water within the cells. Restricted diffusion of water across the cortex, which comprises the major portion of the root tissue, could thus account for the low value of $D$. Diffusion would then be rate limited by the path length and available area as with the composite cellulose acetate membranes of Hays (1968) and, by analogy, the Diafiber membrane. However, over the root zone examined in the present experiments, there is a progressive deposition of suberin lamellae in the endodermis which appears to coincide with a decline in the permeability of the root to mass flow of water (Graham, Clarkson & Sanderson, 1974). Under conditions where the resistance of the cortex remains constant, a comparison of $D$ for younger and older zones of the root, before and after these developmental changes in the endodermis, could indicate whether the latter presents a high resistance to diffusion. We are currently investigating this question.

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## Appendix

Mathematical model of volume flow and diffusion of water in cylindrical membrane.

In Fig. 1, let

$x$ = distance along axis, $l$ = total length
$r$ = radial distance from central axis

$r_1$ = radius of lumen
$r_2$ = effective outer radius of membrane, which may include an unstirred layer
$F(x)$ = longitudinal flux of THO along lumen
$= F_o$ when $x=0$
$R(r)$ = radial flux of THO within membrane, measured in the direction of $r$
$= R_o$ when $r = r_2$
For a net inflow, $R$ will be negative.
$C(x,r)$ = specific activity of THO, $= C_o$ when $x=0$, $r=0$
$D$ = apparent diffusion coefficient of THO in membrane.

### Radial Movement

Consider a cross-section of the membrane of thickness $dx$. Assuming a steady state, let $L(x)$ = rate of loss of THO per unit area across the outer surface of the membrane. Total volume flow of THO must be constant for all $r$ so that

$$2\pi r\,dx\,R(r) = 2\pi r_2\,dx\,R_o,$$

i.e., flux

$$R(r) = \frac{r_2 R_o}{r}. \tag{A1}$$

Total diffusion flow of THO in the cross-section at distance $r$ from the center

$$= -2\pi r\,dx\,D\frac{\partial C(x,r)}{\partial r}$$

and, using Eq. (A1), total flow of THO

$$= 2\pi r_2\,dx\,R_o\,C(x,r).$$

For a steady state

$$-2\pi r\,dx\,D\frac{\partial C(x,r)}{\partial r} + 2\pi r_2\,dx\,R_o\,C(x,r)$$

$$= 2\pi r_2\,dx\,L(x)$$

or

$$\frac{\partial C(x,r)}{\partial r} - \frac{r_2 R_o}{rD}C(x,r) = -\frac{r_2 L(x)}{rD}.$$

Using the integrating factor $r^{-\frac{r_2 R_o}{D}}$ gives

$$C(x) = \frac{L(x)}{R_o} + A(x)\,r^{\frac{r_2 R_o}{D}}$$

or, assuming (*see* page 172) that $C=0$ when $r=r_2$ for all $x$,

$$C(x,r) = \frac{L(x)}{R_o}\left\{1 - \left(\frac{r}{r_2}\right)^{\frac{r_2 R_o}{D}}\right\}. \tag{A2}$$

### Movement along Lumen

Now consider an element of the lumen of length $dx$. Assuming the lumen is sufficiently narrow for any radial non-uniformity to be negligible, the specific activity in it

$$C(x) = \frac{L(x)}{R_o}\left\{1 - \left(\frac{r_1}{r_2}\right)^{\frac{r_2 R_o}{D}}\right\}. \tag{A3}$$

Total volume flow of THO into lumen over length $x$

$$= \pi r_1^2 F_o - 2\pi r_2 R_o x, \text{ using Eq. (A1)}$$

and flow out

$$= \pi r_1^2\,F(x)$$

so that

$$F(x) = F_o - \frac{2 r_2 R_o X}{r_1^2}. \tag{A4}$$

Total flow of THO into element along lumen

$$= \pi r_1^2\,F(x)\,C(x). \tag{A4a}$$

Total flow in from membrane

$$= -2\pi r_2\,R_o\,C(x)\,dx, \text{ using Eq. (A1)}. \tag{A4b}$$

Total diffusion flow out to membrane

$$= -2\pi r_1\,dx\,D\left\{\frac{\partial C(x,r)}{\partial r}\right\}_{r=r_1}$$

$$= -2\pi r_1\,dx\,D - \frac{L(x)}{D}\left(\frac{r_1}{r_2}\right)^{\frac{r_2 R_o}{D}-1}$$

$$= 2\pi r_2\left(\frac{r_1}{r_2}\right)^{\frac{r_2 R_o}{D}} L(x)\,dx. \tag{A4c}$$

Total flow out of element along lumen

$$= \pi r_1^2\,F(x+dx)\;C(x+dx)$$

$$\simeq \pi r_1^2\,F(x)\,C(x) + \pi r_1^2\,F(x)\frac{dC(x)}{dx}dx$$

$$-2\pi r_2\,R_o\,C(x)\,dx, \text{ using Eq. (A4)}. \tag{A4d}$$

For a steady state, equating $(a)+(b)$ to $(c)+(d)$

$$\pi r_1^2 F(x)\frac{\mathrm{d}C(x)}{\mathrm{d}x}\mathrm{d}x+2\pi r_2\left(\frac{r_1}{r_2}\right)^{\frac{r_2R_o}{D}}L(x)\,\mathrm{d}x=0$$

or, substituting for $F(x)$ from Eq. (A4) and $L(x)$ from (A3) and rearranging

$$\left\{\left(\frac{r_2}{r_1}\right)^{\frac{r_2R_o}{D}}-1\right\}\frac{\mathrm{d}C(x)}{C(x)}+\frac{2r_2R_o\,\mathrm{d}x}{r_1^2F_o-2r_2R_ox}=0.$$

Integrating, and putting $C=C_o$ when $x=0$

$$C(x)=C_o\left(1-\frac{2r_2R_ox}{r_1^2F_o}\right)^{\frac{1}{\left(\frac{r_2}{r_1}\right)^{\frac{r_2R_o}{D}}-1}} \tag{A5}$$

From Eqs. (A2), (A3) and (A5), a general expression for the concentration of THO at any point in the membrane may be written

$$C(x,r)=C_o\frac{1-\left(\frac{r}{r_2}\right)^{\frac{r_2R_o}{D}}}{1-\left(\frac{r_1}{r_2}\right)^{\frac{r_2R_o}{D}}}\left(1-\frac{2r_2R_ox}{r_1^2F_o}\right)^{\frac{1}{\left(\frac{r_2}{r_1}\right)^{\frac{r_2R_o}{D}}-1}} \tag{A6}$$

*Derivation of* Eq. (2), p. 172

Total flow of THO into lumen (at $x=0$)

$$=\pi r_1^2F_o\,C_o$$

and flow out (at $x=l$) $=\pi r_1^2\,F(l)\,C(l)$

$$=\pi r_1^2F_o\,C_o\left(1-\frac{2r_2R_ol}{r_1^2F_o}\right)^{\frac{1}{1-\left(\frac{r_1}{r_2}\right)^{\frac{r_2R_o}{D}}}},$$

using Eqs. (A4), (A5) and rearranging so that volume rate of loss of THO from outer surface of membrane per unit $C_o$ is

$$\lambda=\pi r_1^2F_o\left\{1-\left(1-\frac{2r_2R_ol}{r_1^2F_o}\right)^{\frac{1}{1-\left(\frac{r_1}{r_2}\right)^{\frac{r_2R_o}{D}}}}\right\}.$$

Putting $\pi r_1^2F_o=F_{\text{in}}$, $2\pi r_2R_ol=-R_{\text{in}}$ and solving for $D$ gives

$$D=\frac{R_{\text{in}}\ln\left(\frac{r_2}{r_1}\right)}{2\pi l\ln\left\{1-\frac{\ln(1+R_{\text{in}}/F_{\text{in}})}{\ln(1-\lambda/F_{\text{in}})}\right\}}$$

which is Eq. (2), p. 172.

## References

Anderson, W.P., House, C.R. 1967. A correlation between structure and function in the root of *Zea mays*. *J. Exp. Bot.* **56**:544

Bircumshaw, L.L., Riddiford, A.C. 1952. Transport control in heterogeneous reactions. *Q. Rev. Chem. Soc.* **6**:157

Clarkson, D.T., Robards, A.W., Sanderson, J., Peterson, C.A. 1978. Permeability studies on epidermal-hypodermal sleeves isolated from roots of *Allium cepa* (onion). *Can. J. Bot.* **56**:1526

Crank, J. 1964. The mathematics of diffusion. University Press, Oxford

Dainty, J. 1963. Water relations of plant cells. *In:* Advances in Botanical Research. R.D. Preston, editor. Vol. 1, p. 279. Academic Press, London

Dainty, J. 1976. Water relations of plant cells. *In:* Encyclopedia of Plant Physiology, New Series 2A. Transport in Plants II. U. Luttge and M.G. Pitman, editors. p. 12. Springer-Verlag, Berlin

Dick, D.A.T. 1966. Cell water, p. 96. Butterworth, London

Ginsburg, H., Ginzburg, B.Z. 1970*a*. Radial water and solute flows in roots of *Zea mays*. I. Water flow. *J. Exp. Bot.* **21**:580

Ginsburg, H., Ginzburg, B.Z. 1970*b*. Radial water and solute flows in roots of *Zea mays*. II. Ion fluxes across the root cortex. *J. Exp. Bot.* **21**:593

Graham, J., Clarkson, D.T., Sanderson, J. 1974. Water uptake by the roots of marrow and barley plants. *Agric. Res. Coun. (G.B.) Letcombe Lab. Annu. Rep.* (1973), p. 9

Hays, R.M. 1968. A new proposal for the action of vasopressin, based on studies of a complex synthetic membrane. *J. Gen. Physiol.* **51**:385

Hodges, T.K., Vaadia, Y. 1964. Uptake and transport of radiochloride and tritiated water by various zones of onion roots of different chloride status. *Plant Physiol.* **39**:104

House, C.R. 1974. Water Transport in Cells and Tissues. *Monogr. Physiol. Soc.* **24**:144.

House, C.R., Jarvis, P. 1968. Effect of temperature on the radial exchange of labelled water in maize roots. *J. Exp. Bot.* **19**:31

Jarvis, P., House, C.R. 1967. The radial exchange of labelled water in maize roots. *J. Exp. Bot.* **18**:695

Newman, E.I. 1976. Water movement through plant roots. *Philos. Trans. R. Soc. London B* **273**:463

Ordin, L., Gairon, S. 1961. Diffusion of tritiated water into roots as influenced by water status of tissue. *Plant Physiol* **36**:331

Page, K.R., Abramovich, D.R., Smith, M.R. 1974*a*. The diffusion of tritiated water across isolated term human amnion. *J. Membrane Biol.* **18**:39

Page, K.R., Abramovich, D.R., Smith, M.R. 1974*b*. Water transport across isolated term human amnion. *J. Membrane Biol.* **18**:49

Raney, F., Vaadia, Y. 1965. Movement of tritiated water in the root system of *Helianthus annuus* in the presence and absence of transpiration. *Plant Physiol.* **40**:378

Shone, M.G.T., Wood, A.V. 1977. Longitudinal movement and loss of nutrients, pesticides and water in barley roots. *J. Exp. Bot.* **28** 872

Woolley, J.T. 1965. Radial exchange of labelled water in intact maize roots. *Plant Physiol.* **40**:711

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