Radial Exchange of Labeled Water in Intact Maize Roots[1]

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Little is known either of the path taken by water as it moves from the outside of the root to the xylem elements of the stele, or of the barriers which might impede the movement of water. Valuable clues concerning the possible pathways of movement and barriers to the movement of water can be obtained by study of the time course of equilibration of roots immersed in tritiated water, under conditions which prevent transpiration. This equilibration may be diffusional or may be accelerated by protoplasmic streaming, but does not involve a net transfer of water.

Philip (2), in his figure 3, gave theoretical curves for the equilibration (by diffusion) of a uniform, isotropic sheet, cylinder, or sphere with an external medium of constant concentration. He also gave an exponential curve for the single cell. Figure 1 shows Philip's curves, modified by being plotted to a linear scale. The single cell curve describes the equilibration for a cell or tissue, regardless of shape, if the only significant limitation of movement of the material in question is the diffusion of this material across the external boundary of the cell or tissue. (The mechanism of movement need not be restricted to diffusion, provided that the kinetics of the movement are the same as those of diffusion). We can therefore determine whether the epidermis, for instance, acts as a barrier limiting the diffusion of water into the root. If the time course of equilibration of the root with tritiated water fits Philip's cylinder curve, the tissue can be said to be uniform in resistance to flow, and an apparent diffusion coefficient can be calculated. If, on the other hand, the time course of equilibration fits the single cell curve, special surface resistance is indicated. In this latter case no apparent diffusion coefficient can be calculated without further assumptions or measurements of the thickness of the resistant surface layer.

This method of locating resistant layers in the root becomes insensitive as the layer in question is farther removed from the surface. In fact, an especially resistant endodermis in a maize root tends to cause an equilibration curve more like that of a sphere than that of a cylinder or single cell because such an endodermis slows the later (stelar) stages of equilibration without greatly affecting the initial (cortical) rate. The endodermis must have a very high resistance if it is to cause a measurable change in the shape of the equilibration curve. A more powerful tool for the detection of a relatively impermeable endodermis is the separation of the stele from the cortex after exposure to tritiated water, and comparison of the equilibration of the stele with that of the cortex. A curve (figure 2) showing the theoretical stelar equilibration versus the cortical equilibration for a uniformly permeable root of given dimensions can be calculated from Philip's (2) figure 2b or Carslaw and Jaeger's (1) figure 19. A resistant endodermis should cause the stelar equilibration to be less than the theoretical shown by this curve.

If specific preferred paths for the flow of water across the cortex existed in an otherwise uniform root, the stele would receive its material, not from the average of the cortical tissue, but from the special paths. The concentration in these paths would be much higher than the concentration in the average of the cortex. Therefore, if such paths were sufficiently preferred, the equilibration of the stele could be found to have progressed farther at a certain moment than would be indicated by the theoretical curve of figure 2. The stelar equilibration might even be greater than the average cortical equilibration.

In assessing water movement by the use of tritiated water, it is desirable to estimate the effect of cyclosis. If a significant portion of the water movement is through the cytoplasm, cyclosis will accelerate the equilibration of the root with tritiated water. Inhibition of cyclosis could decrease the rate of equilibration even though there might be no permeability change. Observations were therefore made of the effects of metabolic inhibitors on both equilibration curves and rates of cyclosis.

Methods

Maize (*Zea mays* L. WF-9 × M-14) seeds were germinated on paper towels moistened with 10^{-4} M $CaCl_2$ at 31° in glass baking dishes. Each baking dish was covered with plastic film to retard evaporation, with a few slits in the plastic film to provide aeration. Three days after planting, when the radicle was about 12 cm long, the roots other than the radicle were removed, and a thin film of petrolatum was applied by hand to the seed, root stumps, and shoot of each plant, to retard transpiration. The radicle was immersed for 1 hour (except as otherwise

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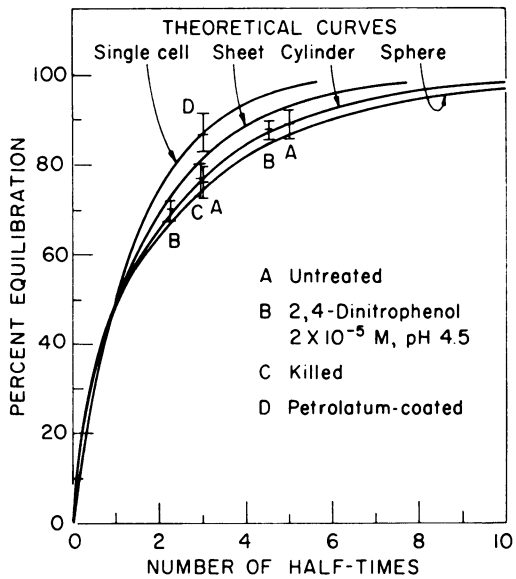

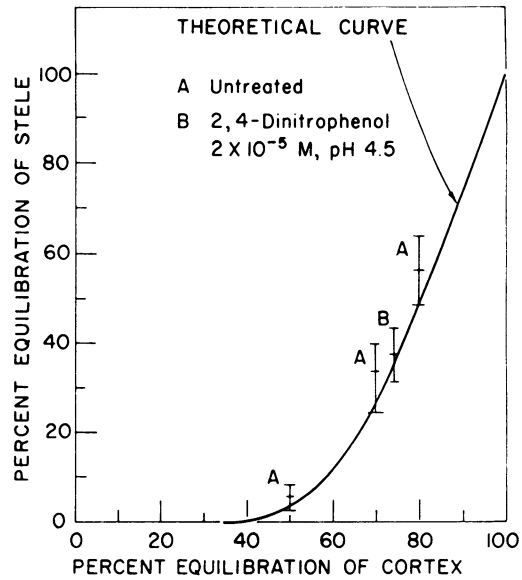

FIG. 1. Theoretical curves for the time course of equilibration of tissues with an external medium of constant concentration [adapted from Philip (3)], and experimental points (with 95% fiducial limits) for the equilibration of maize roots with tritiated water. The letter symbols indicate different root treatments.

FIG. 2. Theoretical curve comparing the equilibration of the stele with that of the cortex for a uniform root having the dimensions of a maize root, and experimental points (with 95% fiducial limits) for maize roots. The letter symbols indicate different root treatments.

Table 1. *Effects of Various Treatments on the Rate of Water Equilibration in Roots and the Rate of Cyclosis in Root Hairs*

All treatments had K phosphate buffer 10^{-2} M, pH 6.1 except as noted.

Treatment	M.E.C.*	Temperature	Half-time seconds	Apparent diffusion coefficient μ^2 sec^{-1}
None (no buffer)		25°	26	490
None		25°	25	500
Carbonyl cyanide *m*-chlorophenylhydrazone	5×10^{-6} M	25°	150	84
2, 4-Dinitrophenol	2×10^{-5} M	25°	150	84
N-Ethylmaleimide	5×10^{-5} M	25°	144	87
KF	10^{-2} M	25°	145	87
K-Iodoacetate	10^{-2} M	25°	149	84
Phenylmercuric acetate	10^{-5} M	25°	97	130
Phenylmercuric acetate (no buffer)	10^{-5} M	25°	97	130
None	†	3°**	480	26
Carbonyl cyanide m-chlorophenylhydrazone, 5×10^{-6} M	†	3°**	840	15
2, 4-Dichlorophenoxyacetic acid, 5×10^{-4} M	††	25°	27	470
Dimethylsulfoxide, 0.1 M	††	25°	26	480
Dimethylsulfoxide, 1.0 M (no buffer)	†	25°	27	470
Roots greased with petrolatum	†	25°	119	
Roots killed by hot water		25°	7	1700
Self-diffusion coefficient of water as measured with tritiated water: †††		25°		2440
		3°		1300

* Minimum effective concentration for both inhibition of water movement and inhibition of cyclosis.
** 100% standard was treated for 5 hours in tritiated solution.
† Treatment not tested on cyclosis.
†† Did not stop cyclosis.
††† From Wang, Robinson, and Edelman (5).

noted) in nontritiated pretreatment solution and was then transferred to the tritiated treatment solution for the desired length of time. The composition of the pretreatment solution was always the same as that of the corresponding treatment solution except that the latter contained tritiated water. The compositions of the pretreatment and treatment solutions are listed in table I. The pretreatment solutions and the treatment solutions were stirred and aerated by a constant stream of air bubbles in intimate contact with the roots. Stirring was considered to be adequate because pilot experiments had showed no change in equilibration half-time of untreated roots when the bubbling rate was reduced to about one-fourth of normal. Finally the root was removed, blotted, and cut into segments. The segments were immediately put into vials containing 17 ml of scintillation fluid (55 mg 2, 5-diphenyloxazole, 9.2 ml toluene, 7.8 ml ethanol). Each seedling was handled individually. The blotting took about 5 seconds, cutting took about 10, and placing the segments in the vials took about 15 seconds. Tests showed that no significant amount of water evaporated from the roots during this time. Routinely, 2 segments were taken, the tip cm and the next 3-cm piece. The data reported are for the 3-cm segment. Table II shows that in a pilot experiment the rate of equilibration was about the same at all parts of this 3-cm segment.

In some experiments the stele was separated from the outer tissues of the root (here called the cortex), in the following manner. As soon as the root had been blotted it was bent sharply about 7 cm from the tip, so that the cortex was cracked transversely. A gentle pull with the fingers then caused the stele to stretch slightly throughout its length and finally break at a point between 0.5 and 1 cm from the root tip, the endodermis shearing so that the external tissues could be pulled from the stele with no obvious crushing or other distortion. Figure 3 shows cross sections of the separated stele and cortex compared with a cross section of an intact root. Removal of the stele took about 10 seconds. The stele was pulled through a small heap of petrolatum, and petrolatum was applied to the cortex by hand to retard evaporation. The desired segments were cut and placed in the scintillation fluid. Data reported are for the tip 3.2-cm segment of the stele (the extra 0.2 cm to compensate for the stretching as the stele was removed) and the approximately corresponding cortical segment, the 3-cm piece starting 1 cm from the root tip. Other segments, taken occasionally, did not differ markedly from the reported segments. Eight segments were placed in each vial. The water of the roots dissolved completely in the scintillation fluid within a few minutes, but for convenience the root segments were left in the vials while the tritium was counted by a refrigerated scintillation spectrometer. The standard for the determination of the percentage of equilibration of a given sample was a similar sample which had been left in the tritiated treatment solution for at least 20 half-times (the half-time being the time necessary for the tissue to become 50 % equilibrated), usually a total of either 60 or 90 minutes. The tritium count of a given sample was divided by the count of the standard, and the result expressed as a percentage to give the percent equilibration of the sample. The validity of this standard was tested in 2 ways. First, pilot experiments showed the same amount of tritium in roots after 180 minutes as was found after 30 minutes in the tritiated water. Second, counting of the tritium combined with weighing of root segments before and after drying at 80° showed that the root water had the same specific activity as the external solution after 30 minutes.

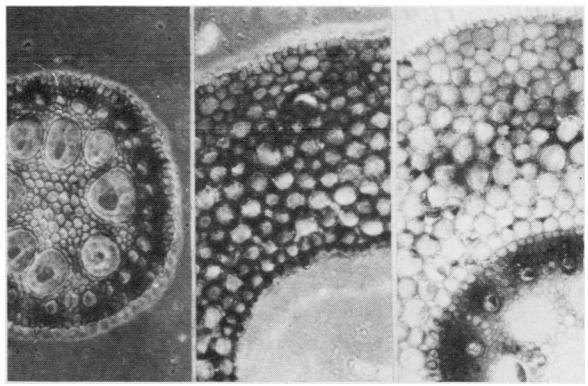

FIG. 3. Cross sections of separated stele and cortex compared with cross section of intact root.

To obtain the statistical accuracy needed to show which curve of figure 1 was followed by roots having a given treatment, large numbers of samples were needed. Each of the points in figure 1 indicates the results of 6 separate experiments involving 8 individual roots for each time involved. One treatment time was calculated (on a basis of results from preliminary experiments) to be close to the half-time for that particular treatment. From the percent of equilibration for this treatment time, the true half-time was determined with the theoretical curves of figure 1, all of which are close together near 1 half-time. Then the remaining treatment times, expressed in multiples of the half-time, were plotted with their percentages of equilibration and 95 % fiducial limits. Thus, for the 2 points of untreated root data shown in figure 1, 4 different treatment times were used

Table II. *Degree of Equilibration of Root Segments after 30 Seconds in Tritiated Water*
Data are means for 32 individual roots.

Distance from root tip, cm	0–0.5	0.5–1.0	1.0–2.0	2.0–3.0	3.0–4.0	4.0–5.0
Percent equilibration	64	56	54	56	53	55

in each experiment: 36 seconds (to approximate the half-time), 108 seconds, 180 seconds, and 1 and one-half hours (for the fully-equilibrated standard).

Apparent diffusion coefficients were calculated from the formula (derived from Philip's figure 1b):

$$D = \frac{0.062\ b^2}{t_{1/2}} \qquad \text{I}$$

where D is the apparent diffusion coefficient in $cm^2\ sec^{-1}$, b is the root radius in cm, and $t_{1/2}$ is the half-time in seconds. The average root diameter was found to be 0.09 cm, giving

$$D = \frac{1.255 \times 10^{-4}\ cm^2}{t_{1/2}}. \qquad \text{II}$$

As an example of the method of calculation, the 360-second carbonyl cyanide *m*-chlorophenylhydrazone treatment at 3° gave 30.3 % equilibration. From the cylinder curve of figure 1 this 30.3 % was found to represent 0.43 half-times, so the actual half-time was 838 seconds, giving an apparent diffusion coefficient of $1.5 \times 10^{-7}\ cm^2\ sec^{-1}$.

All experiments were at 25° except as is noted.

For the viewing of cyclosis the tip 4-cm portions of roots were placed in water on microscope slides. Cyclosis was observed in the root hairs with a phase-contrast microscope, the microscope light being used only during observations. The water was replaced with various treatment solutions (table I) and the effects of these solutions were observed. Cyclosis within the epidermis or cortex, while probably occurring, could not be observed in unsectioned material. Hand sectioning usually damaged the tissue, so that only occasionally could cyclosis be seen in other cells than root hairs. Reported observations are for root hairs only.

Results

No evidence was found that the epidermis offered any special resistance to the entrance of water in normal roots, in roots which had been treated with 2, 4-dinitrophenol [Woolley's (6) statement to the contrary is erroneous], or roots which had been killed by immersion in hot water. Although these treatments gave widely different half-times for equilibration (table I) with tritiated water, the uptake for each fitted the cylinder curve (figure 1). As a test of the method, some roots were coated with petrolatum by hand before being placed in the tritiated treatment solution. These roots followed the single cell curve with a half-time of 119 sec, about 3 times that of the untreated roots. The permeability of the petrolatum-coated surface layer was 1.3×10^{-4} cm sec^{-1}.

The stele did not take up tritiated water more slowly, compared to the cortex, than indicated by the theoretical curve of figure 2, so the endodermis was probably not especially resistant to passage of water. Actually, the average values for the stelar equilibration shown in figure 2 are all slightly higher than would be expected theoretically. This could be interpreted as evidence for specific preferred paths of water movement in the cortex, or possibly a slight passage of tritiated water from the cortex to the stele during the removal of the stele from the root. The tritiated water concentration in the stele never exceeded that in the cortex.

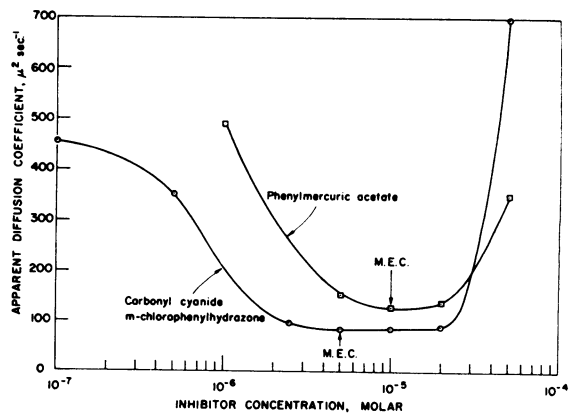

FIG. 4. Dependence of apparent diffusion coefficient upon concentration of phenylmercuric acetate and carbonyl cyanide *m*-chlorophenylhydrazone, both in 10^{-2} M K phosphate buffer at pH 6.2. M.E.C. denotes minimum effective concentration (see text).

With this evidence that the root was fairly uniform, calculation of apparent diffusion coefficients for these conditions was considered to be valid. Several other treatments were applied and apparent diffusion coefficients were calculated, on the assumption that the root remained uniform under these treatments, too. The half-times and corresponding apparent diffusion coefficients are listed in table I.

The typical effect of concentration of metabolic inhibitors is shown by the concentration curve of carbonyl cyanide *m*-chlorophenylhydrazone in figure 4. Generally, increasing concentrations of a given inhibitor cause decreases in the apparent diffusion coefficient, up to a certain point, above which there is no further change in apparent diffusion coefficient over a range of inhibitor concentrations. At even higher inhibitor concentration the apparent diffusion coefficient increases drastically as the inhibitor kills the root. The minimum concentration producing the lowest apparent diffusion coefficient will be referred to as the minimum effective concentration (M.E.C. in figure 4).

Inhibition of cyclosis is difficult to evaluate quantitatively. The movement dies down gradually and erratically after the inhibitor is applied. Nevertheless, with every inhibitor used, the minimum effective concentration for decreasing the equilibration rate was the same as the minimum concentration that would completely stop cyclosis in all root hairs within 20 minutes. Normal cyclosis in root hairs was often

seen to be as fast as 2×10^{-3} cm sec^{-1}. This would be fast enough to have considerable effect on the equilibration time if cyclosis occurred at this rate throughout the root.

Discussion

How impermeable would the epidermis have to be in order for this resistance to be detected by the method used here? I do not know how to calculate the answer to this question accurately, but I can place an extreme lower limit on the permeability of the epidermis. To do this it is merely necessary to accept the experimentally-determined half-time for the root and then calculate the epidermal permeability that would give this half-time if all of the resistance to diffusion resided in the epidermis. This can be done by using Philip's equation II for the single cell,

$$t_{1/2} = \frac{0.693\ V}{K_s A} \qquad \text{III}$$

where $t_{1/2}$ is the half-time in seconds, V is the volume of a unit length of root in cm^3, A is the area of the external surface in cm^2, and K_s is the permeability of the cell surface in cm sec^{-1}. Solving for K_s and using 25 sec as the half-time and 0.045 cm as the root radius,

$$K_s = \frac{0.693\ V}{t_{1/2}\ A} = 6.25 \times 10^{-4} \text{ cm sec}^{-1}. \qquad \text{IV}$$

If the epidermis is 1.2×10^{-3} cm thick, the apparent diffusion coefficient in the epidermis would be 7.5×10^{-7} cm^2 sec^{-1}, which is about one-seventh of the apparent diffusion coefficient found for the root when it was treated as a uniform cylinder. Since the root uptake follows the cylinder curve, rather than the single cell curve, we know that the epidermal resistance cannot be as much as 7 times the resistance, per unit thickness, of the bulk tissue. This is an extreme value. The epidermal resistance is probably no greater than 3 times the resistance of the remainder of the tissue.

A similar calculation should be possible in order to determine the possible limits of resistance that the endodermis could have. It seems reasonable to suppose that the stelar equilibration would have been significantly below the theoretical curve of figure 2 if the half-time for the stele had been twice as long as the half-time for the root as a whole. Treating the stele as a cylinder with all of the resistance in the endodermis, with a radius of 0.015 cm and with a half-time of 50 seconds, we obtain a permeability of 10^{-4} cm sec^{-1}. If the endodermis were 10^{-3} cm thick, the apparent diffusion coefficient in the endodermis would be 10^{-7} cm^2 sec^{-1}. This is about one-fiftieth of the diffusion coefficient found for the bulk of the tissue.

The obvious morphological location for a special path for movement of water in the cortex would be through the cell walls, with cytoplasm and vacuoles excluded, or possibly through cell walls and cytoplasm, with vacuoles excluded. In either case, in order for the special path to be detected, the half-time for the excluded portions would have to be about as long as the half-time for the root. Treating the average cortical cell as a cylinder having a radius of 10^{-3} cm and a half-time of 25 seconds, with all of the resistance to diffusion near the surface, we find a permeability of 1.4×10^{-5} cm sec^{-1}. It is difficult to decide whether this is a reasonable value, but it can be compared with the value for the greased surface of a root, 1.3×10^{-4} cm sec^{-1}.

Phenylmercuric acetate was found by Zelitch (7) to be more effective than carbonyl cyanide *m*-chlorophenylhydrazone in causing closure of stomata, yet the carbonyl cyanide *m*-chlorophenylhydrazone was much more effective than the phenylmercuric acetate in increasing the root equilibration time. This hints that the stomate-closing action is more than a simple change of permeability. Further, carbonyl cyanide *m*-chlorophenylhydrazone, which was found by Stoner (4) to be more effective than 2, 4-dinitrophenol, at about one one-thousandth of the concentration required of the 2, 4-dinitrophenol, in uncoupling the respiration of maize mitochondria, increased the equilibration time of maize roots to about the same degree as did the 2, 4-dinitrophenol, but at one-fourth the molar concentration.

The apparent diffusion coefficient of tritiated water in the normal root (ca. 500 μ^2 sec^{-1}) is about one-fifth of the diffusion coefficient of tritiated water in water. If all water movement were confined to the cell walls, these walls would have to occupy something over 20 % of the root volume in order for such rapid diffusion to occur, yet the cell walls actually occupy between 3 and 6 % of the root volume, estimated microscopically on hand-cut sections. Thus at least 70 % of the water movement must involve the cytoplasm in some way. This conclusion is strengthened by the fact that metabolic inhibitors would be unlikely to affect the movement of water unless this movement involved protoplasm, yet the rate of movement decreases drastically when inhibitors are applied. It is not obvious how much of the inhibitor-induced change is caused by actual permeability changes and how much is caused by cessation of cyclosis. A partial solution to this problem is provided by phenylmercuric acetate, which stops cyclosis in root hairs, but does not reduce the apparent diffusion coefficient to the same degree as do several other inhibitors. The difference between the action of phenylmercuric acetate and that of other inhibitors seems not to be in the degree of inhibition of cyclosis, so this difference should be attributed to a change in permeability. One might suspect from the phenylmercuric acetate concentration curve (figure 4) that the phenylmercuric acetate kills some of the cells before the entire tissue becomes

inhibited, so that the apparent diffusion coefficient never reaches the minimum induced by other inhibitors. That this is not true is shown by the fact that even double the minimum effective concentration of phenylmercuric acetate, when combined with the minimum effective concentration of carbonyl cyanide *m*-chlorophenylhydrazone, still allows an apparent diffusion coefficient in the neighborhood of 85 μ^2 sec^{-1}.

The uniformity of the apparent diffusion coefficient in roots treated with several different inhibitors is striking. The minimum effective concentrations of 2, 4-dinitrophenol, carbonyl cyanide *m*-chlorophenylhydrazone, N-ethyl maleimide, KF, and iodoacetate all reduce the apparent diffusion coefficient to the same extent. These inhibitors do not all act at the same point in metabolism, and widely different concentrations are required for the different inhibitors. Therefore it seems reasonable to suppose that the apparent diffusion coefficient in inhibited roots indicates the apparent diffusion coefficient when the cytoplasm is essentially eliminated as a possible route for water movement. That is, the apparent diffusion coefficient for water movement confined to the cell walls may be 85 μ^2 sec^{-1}, or about 17 % of the 500 μ^2 sec^{-1} for the untreated root. This 17 % may be a fair estimate of the fraction of the movement which does not involve the protoplasm in the normal root. The 85 μ^2 sec^{-1} is 3.5 % of the diffusion coefficient in free water, so it could represent movement in the cell walls if the cell walls occupied slightly more than 3.5 % of the root volume and if the diffusion coefficient in the cell walls were a substantial fraction of that in free water. Such a high permeability of the cell walls seems probable, in view of the high diffusion coefficient observed in roots killed by hot water (table I).

Even though most of the observed water movement in normal roots involves the protoplasm, the great increase in apparent diffusion coefficient upon the death of the tissue indicates that the protoplasm must offer considerable resistance to water movement. Calculation of the apparent diffusion coefficient within protoplasm is possible from the data presented here, provided that no special qualities are attributed to the tonoplast and plasmalemma, with the diffusion coefficient in the vacuole taken to be 2440 μ^2 sec^{-1}, and with the assumption that the same amount of water moves through the radial cell walls in the normal, the inhibited, and the dead root. The apparent diffusion coefficient so calculated for the protoplasm proper is about 30 μ^2 sec^{-1}. The derivation and actual calculation are not given for this estimate because of the numerous assumptions and because an unknown portion of this apparent diffusion coefficient must be attributed to cyclosis.

Exact computation of permeabilities of specific structures often should involve corrections for tortuosity and for variations in path cross section. No such corrections have been made in the approximate calculations presented here.

A seeming contradiction exists, in that the analysis of the equilibration curve failed to show any special route for water movement, even in the inhibited root, yet the apparent diffusion coefficient data have been interpreted to show that water moves almost exclusively through the cell walls in the inhibited root. The explanation of this contradiction is that the equilibration curve method is not sensitive enough to detect this size of special path. It was previously calculated that a cell permeability of 1.4×10^{-5} cm sec^{-1} or less would be necessary for detection by this method. If the apparent diffusion coefficient within the inhibited protoplasm is taken to be one-tenth (3 μ^2 sec^{-1}) of that estimated for the normal protoplasm, and the thickness of the layer of protoplasm is taken to be 8×10^{-5} cm, the permeability of a layer of protoplasm is found to be 3.8×10^{-4} cm sec^{-1}, a figure small enough to eliminate most of the water movement through the protoplasm, but not small enough to be detected by the equilibration curve method.

The exact relationship of these water measurements to the apparent free space of roots is not clear. The apparent free space concept is defined in terms of salt, rather than water, and the times used in apparent free space measurements are usually longer than the water-equilibration times.

It should be emphasized that the data presented here were obtained in the absence of transpiration. The data are not directly applicable to transpirational water movement for several reasons, but especially because viscous water flow (transpirational flow) does not follow the same mathematical laws as does diffusion. Of these 2 processes in the root of a transpiring plant, diffusion (or diffusion aided by cyclosis) is much faster than transpirational flow. The half-time for equilibration of these roots was about 25 seconds, while a rather fast transpirational flow into the root surface may be 0.01 cm hr^{-1} (3), which would give a half-time of about 4000 seconds for the transpirational replacement of the water of these roots.

Conclusions

The following conclusions are valid for the movement of tritiated water within the portion of a maize root a few centimeters from the root tip, when transpiration is prevented.

The root is fairly uniform in its resistance to water movement, in that A) the apparent diffusion coefficient within the epidermis is no less than one-third of the apparent diffusion coefficient in the root as a whole; B) the apparent diffusion coefficient within the endodermis is no less than one-fiftieth of the coefficient in the root as a whole. In the normal root, at least 70 %, and probably about 83 % of the observed movement involves the protoplasm. In the inhibitor-treated root the water movement is probably confined to the cell walls. The diffusion coefficient in cell walls is probably a

substantial fraction of the diffusion coefficient in free water, regardless of the treatment applied. In the dead root at least 70 % of the root volume is available for water movement. Most metabolic inhibitors reduce the apparent diffusion coefficient in both of 2 ways: A) by inhibiting cyclosis; B) by decreasing the permeability of protoplasm.

Summary

Equilibration of maize (*Zea mays* L.) roots with tritiated water was compared with theoretical curves for the single cell, sheet, cylinder and sphere, and was found to follow the cylinder curve. This was interpreted to indicate that the epidermis does not constitute a barrier to the entrance of water.

The stele was removed from roots after treatment with tritiated water, and the equilibration of the stele was compared with that of the cortex. This equilibration was not greatly different from the theoretical equilibration to be expected of uniform tissue. It was concluded that the endodermis did not constitute a barrier to the diffusion of water.

The apparent diffusion coefficient of tritiated water in a maize root at 25° was 5×10^{-6} cm^2 sec^{-1}. The apparent diffusion coefficient was decreased by metabolic inhibitors, or low-temperature treatment. The apparent diffusion coefficient remained unchanged with treatment by dimethyl sulfoxide or 2, 4-dichlorophenoxyacetic acid. The apparent diffusion coefficient increased about 3-fold when the roots were killed with hot water.

Acknowledgment

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