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Water Movement Through Root Systems

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Water movement through root systems

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The root system provides a considerable resistance to water flow through it. This resistance is important because it influences the water deficits which can build up in the above-ground parts of the plant even when the roots are in moist soil. The permeability of roots per unit surface area varies between species, and between different parts of the same root (depending on age). It is sensitive to environmental conditions such as temperature, oxygen and salinity; this suggests that a major part of the resistance lies in living material in the 'radial-flow pathway', i.e. between the root surface and entry to the xylem. It is uncertain which is the main pathway of radial flow. Possible alternatives are: (1) the vacuolar pathway, crossing the cortex and other tissues by passing from vacuole to vacuole; (2) the free-space/endodermis pathway, water moving in the cell walls except at the endodermis where it enters the protoplasm; or (3) the symplasm pathway, water moving in the protoplasm and passing from cell to cell by plasmodesmata. Calculations are presented, based on the primary root of maize whose cell dimensions and root permeability are known, to show what permeabilities of membranes, wall material and plasmodesmata would be necessary to allow each of the three pathways to predominate. These calculations predict the symplasm as the most likely pathway. The free-space/endodermis pathway is unlikely because the permeability of cell wall material is too low. Several pieces of experimental evidence also favour the symplasm pathway.

There are large variations between species in the permeability of roots for longitudinal flow in the xylem. Usually this xylem flow will present much less resistance than the radial flow pathway. However, there is no adequate evidence on whether the resistance may be greatly increased by bubble formation in vessels under water stress.

Introduction

One of the functions of a root system is extracting water from soil and transporting it to the above-ground parts of the plant. It is convenient to consider this as two steps, (1) the movement of water through the soil to the root surface, and (2) the movement of water from the root surface through the root up to the stem. Stage (1) was the subject of the last paper; stage (2) is considered here.

Water will move through the root system only if there is a driving force to move it, in other words a difference in water potential between the root surface and the upper parts of the plant. For this reason plants can suffer a water deficit in their above-ground parts even when their roots are surrounded by moist soil. The magnitude of this deficit depends on (1) the transpiration rate, which determines the rate of water movement through the plant; and (2) the resistance to water flow within the plant. A considerable part of the plant's resistance to water flow lies in its roots, and it is thus clear that the magnitude of the root's resistance to water flow is very important to the plant. This paper is concerned with root resistance. It first surveys briefly some of the known variation of root resistance, between species, within a single plant, and in response to environmental factors. Much of the remainder of the paper is concerned with the question, where within the root do the main sites of resistance to water flow lie? This is an

old question, but the answer is still uncertain. I believe that only when we know the answer will we have a sound scientific basis for understanding all the features of the root system as an organ of water uptake.

Water taken up by the root first moves radially inwards across the root until it reaches the xylem. Then it moves along the xylem, up into the stem and ultimately the leaves. The distance between the root surface and the xylem is usually less than 1 mm, but the tissues do not provide an easy pathway for water movement, and evidence will be presented later that there is in fact considerable resistance to water movement across this short distance.

Once in the xylem the water flows mainly in vessels, relatively large tubes with few cross walls, so that the resistance to flow is small. However, the distances to be covered to reach the stem and leaves are usually many centimetres and often some metres, so that significant resistance to flow may perhaps be located in this pathway also. After the initial brief survey of variations in root permeability, this paper considers separately each of these two main parts of the pathway in the root system.

Factors influencing root permeability

The permeability of a root system (which is the reciprocal of its resistance) can be determined after the stem has been cut off below the lowest leaves. One method is to apply a steady, known suction to the cut stump, and determine the rate at which water is exuded from the cut end. Alternatively the root system may be enclosed in a pressure vessel, with the cut stump protruding, and pressure applied to force water through it. In other methods the root system is not under suction or pressure, and the water is taken up into the xylem by osmosis (root pressure exudation). The osmotic potential of the exuding xylem sap must be determined, which can be done either directly on collected samples, or indirectly by changing the osmotic potential of the solution surrounding the roots and determining how the rate of exudation is altered (Arisz, Helder & van Nie 1951). These methods give the permeability per root system. If the root surface area is also determined, permeability can be expressed per unit surface area, but unfortunately this has rather rarely been done.

Table 1. Permeability per unit surface area of whole root systems of five species grown under the same conditions. (From Newman 1973)

	permeability / nm s^{-1} MPa^{-1}	standard error
broad bean (*Vicia faba*)	5.4	0.5
dwarf bean (*Phaseolus vulgaris*)	5.6	0.2
sunflower (*Helianthus annuus*)	7.1	0.6
maize (*Zea mays*)	22	2.7
tomato (*Lycopersicon esculentum*)	61	15

Table 1 shows the permeability per unit surface area of the root systems of five species, which had been grown under the same standardized conditions in a growth room. There are large and statistically significant differences between species. When permeability is expressed per unit root length or per unit volume large differences still remain. The cause of these differences, in terms of root anatomy or physiology, is not known.

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These values are mean permeabilities over the whole root system. It is known, however, that permeability can vary with root age, which means in effect distance from the root tip. Figure 1*a* shows the rate of water uptake at different distances from the tip, by roots of two species. The roots were attached to the intact plants, which were transpiring normally. In marrow the rate of uptake declined markedly beyond about 8 cm from the tip, in the region where the endodermis was becoming suberized (i.e. suberin was being deposited on the inner surface of the cell walls). A low uptake rate was maintained beyond 12 cm, back at least to 26 cm. Maize, in contrast, showed at first a rise with increasing distance from the tip, and then a plateau of high uptake. (The slight decline from 10 to 14 cm was not statistically significant.) There might, of course, have been a marked decline in uptake beyond 14 cm, but no measurements were made there.

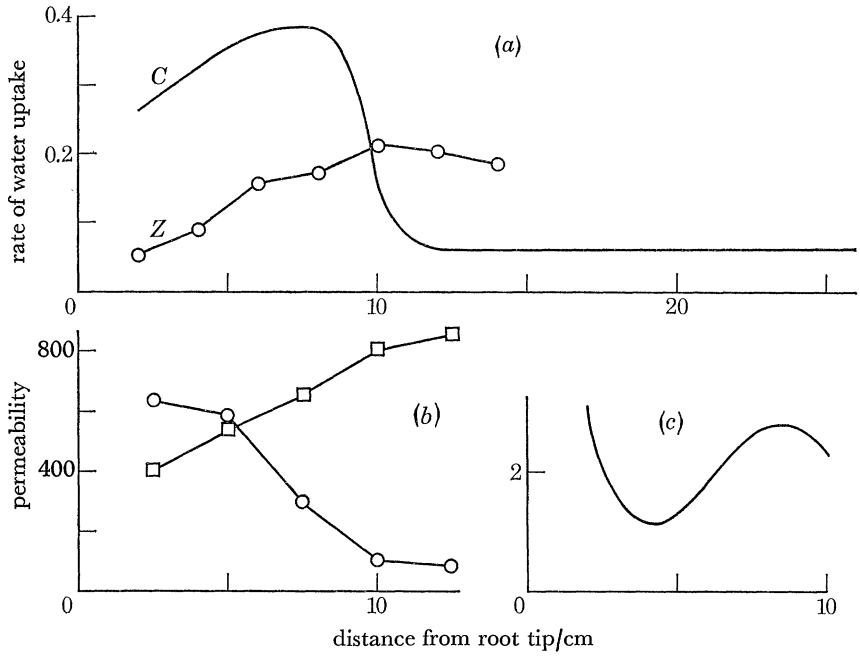

FIGURE 1. Water uptake or permeability of roots to water at different distances from the tip. (*a*) Rate of water uptake. *C*: *Cucurbita pepo* (marrow), data of Graham, Clarkson & Sanderson (1974). *Z*: *Zea mays* (maize), data of Hayward, Blair & Skaling (1942). Units of uptake: for *C*, $mm^3\ mm^{-1}\ h^{-1}$; for *Z*, $mm^3\ mm^{-2}\ h^{-1}$. (*b*) Permeability of *Vicia faba* (broad bean), data of Brouwer (1953). ○, all plant roots in water; □, all roots except test root in solution of salts, thus increasing uptake rate of test root. (*c*) Permeability of detached roots of *Zea mays*, data of Anderson, Aikman & Meiri (1970).
Units of permeability: (*b*) $\mu m^2\ s^{-1}\ MPa^{-1}$; (*c*) $cm^2\ s^{-1}\ osmol^{-1}$.

These uptake data do not conclusively prove a change in permeability, since the xylem water potential is not known. Brouwer (1953), working with broad bean, went one step further, by determining xylem water potential at one point along the root. Assuming the potential was the same all along the xylem (an assumption supported by preliminary tests), he calculated the permeabilities shown in figure 1*b*. This shows permeability highest in the younger parts of the root when rate of uptake is slow, but highest in the older parts when uptake is rapid. The change in permeability of the older parts is an example of the phenomenon discussed by Weatherley (p. 440), that root permeability increases with increasing pressure difference or rate of water flow across the root. In this species apparently only the older parts of the root

show this change. The difference between maize and barley in the relation of uptake to age (figure 1*a*) could be due to differences in transpiration rate.

Ideally, xylem water potential should be determined at various points along the root, not just one, but this has rarely been done. Anderson, Aikman & Meiri (1970) obtained results from single detached roots of maize of various lengths, which allow the xylem osmotic potential to be estimated. Their calculation of the variation of permeability along the root is shown in figure 1*c*. Maize roots grown under similar conditions had their endodermis well suberized by 8 cm from the tip (Anderson & House 1967); apparently this was not accompanied by any reduction in permeability.

The results in figure 1 illustrate how variable is the relation between permeability and root age. Beyond the statement that permeability does often change with age, no generalization seems justified.

Root permeability is sensitive to many environmental factors. An increase of temperature leads to an increase in permeability (Kuiper 1964). Since the Q_{10} is usually 2 or over, this is evidently not due merely to a change in the viscosity of water. Low oxygen levels and high CO_2 levels in the medium surrounding the root lead to reduced permeability (Kramer 1949). Metabolic inhibitors, too, lead to reduced permeability; this is shown, for example by sodium azide (Lopushinsky 1964). These reductions occur provided the roots are not permanently damaged by the treatment. If roots are killed their permeability increases (Kramer 1933). NaCl can also reduce permeability. For example, O'Leary (1969) found that if kidney beans (*Phaseolus vulgaris*) were grown in nutrient solution with sufficient NaCl added to lower the osmotic potential by 0.2 MPa, the root permeability was markedly reduced compared with controls grown in nutrient solution only. Root systems can also show an autonomous rhythm of permeability (Parsons & Kramer 1974). If the plants have been grown in a normal 24 h cycle of dark and light, and the shoots are then cut off and the roots removed to constant conditions, the permeability may continue to show a diurnal cycle for several days. Permeability may be several-fold higher by day than by night.

Thus root permeability can vary between species or within a single root; it can vary in response to environmental factors or to internal plant rhythms. We cannot adequately explain these variations, in terms of root anatomy or physiology, and our understanding of water flow through the root system thus lacks a coherent scientific basis. The primary reason for this is that we do not know where the main resistance to water flow lies.

When water passes through cell wall material and along xylem vessels, the resistance to flow is provided by an essentially non-living frame-work. Since the root permeability is so sensitive to environmental factors, this suggests that the main resistance does not lie in the cell walls or the xylem vessels, but in some part of the root whose state is closely linked to metabolism. This must lie in the 'radial-flow pathway', i.e. in passing from the root surface to the xylem.

Pathway of radial movement

Figure 2 shows a semi-diagrammatic transverse section of a maize root. Water entering the root must cross the epidermis, cortex, endodermis and pericycle before it can reach the xylem. To reach the innermost xylem, the large metaxylem vessels, it must also cross some stelar parenchyma cells, though in most dicotyledonous species this would not be necessary since the xylem forms a single block of tissue. The questions which arise are: (*a*) what is the pathway of

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water movement across these tissues, and (*b*) where does the main resistance lie? The possible pathways are shown diagrammatically in figure 3. The vacuolar pathway (1) involves the water entering the vacuoles of the epidermal cells by crossing the plasmalemma and tonoplast; then passing to the vacuoles of neighbouring cortex cells which involves crossing two more pairs of membranes; and so passing from vacuole to vacuole until it reaches the pericycle or stelar parenchyma, and thence the xylem vessels. In this pathway the membranes of all the cells would presumably provide the main resistance. Pathway (2) is the free-space/endodermis pathway. The water passes through the wall material of the epidermis and cortex. At the

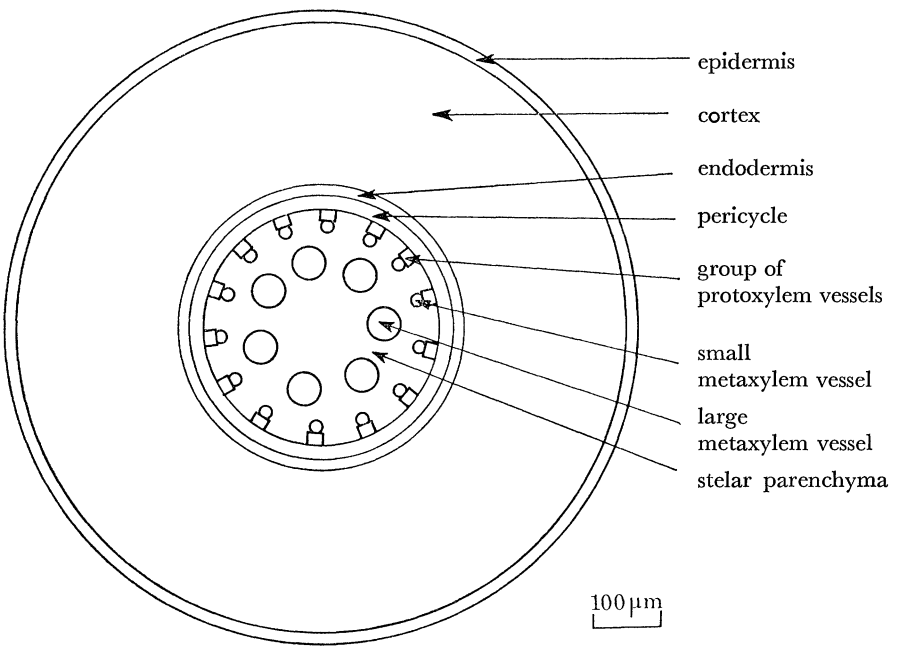

FIGURE 2. Semidiagrammatic transverse section of primary root of maize (*Zea mays*). The dimensions of the various parts are approximately to scale.

endodermis the radial walls are impermeable at the Casparian strip, so there the water must pass across the plasmalemma to enter the protoplasm. It passes out again by the inner surface of the endodermal cells, and by further cell wall movement reaches the vessels. By this pathway the plasmalemmas of the endodermal cells would provide the main resistance. Pathway (3) is the symplasm pathway. Water enters the protoplasm of epidermal or cortical cells, and once inside passes from cell to cell by the plasmodesmata. Somewhere inside the endodermis the water leaves the symplasm again and reaches the vessels. If this is the pathway, there are several alternative sites of the main resistance. If the wall and the symplasm both provide low-resistance pathways, the membranes crossed when entering and leaving the symplasm would be the main resistance. Water entry would be expected to distribute itself fairly evenly over the cortex and epidermis, and water exit over the pericycle and stelar parenchyma. If, on the contrary, the wall is a high-resistance pathway, then most water will enter the symplasm at the epidermis and leave by cells near the xylem vessels. The main resistance could still be in the membranes, or it could be in the symplasm itself, probably mainly in the plasmodesmata.

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Calculated permeabilities

Water will follow the path of least resistance, and one way to determine the main pathway is to calculate the resistances of the various alternative pathways, from their dimensions and the permeabilities of membranes, wall material and plasmodesmata. There have been attempts in the past to do this, and different people have come to different conclusions about which pathway would provide the lowest resistance. The main reason for this disagreement is uncertainty about what values to take for the permeabilities of membranes, wall material and plasmodesmata. Table 2 summarizes values reported in the literature. Membrane permeabilities reported for vascular plants are generally lower than those for algae, which are mostly determined on giant cells of Characeae. It is not certain whether this difference is genuine or is due to technical problems with the smaller cells of vascular plants. The permeability (per

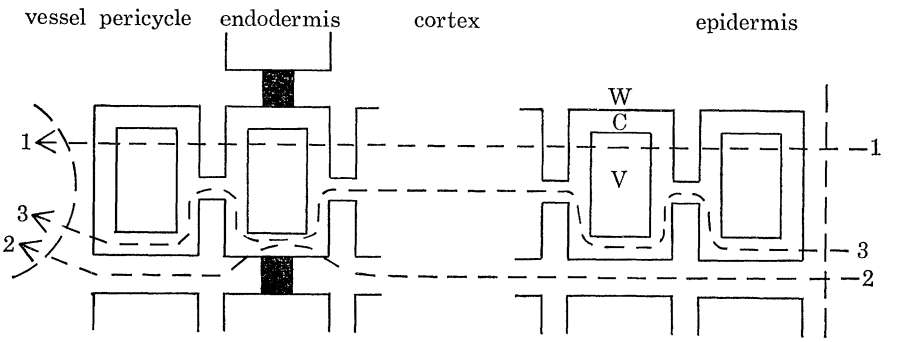

FIGURE 3. Diagram of part of transverse section of root, showing possible pathways for water movement. C, cytoplasm; V, vacuole; W, wall.

TABLE 2. PERMEABILITIES OF CELL MEMBRANES, CELL WALL MATERIAL AND PLASMODESMATA

(*a*) Permeability of cell membranes (plasmalemma + cytoplasm + tonoplast). Each source cited is itself summarizing results of several workers

permeability/(nm s^{-1} MPa^{-1})		
vascular plants	algae	source of data
2–180	180–3000	Bennet-Clark (1959)
5–200	1000–2000	Slatyer (1967)
—	18–3000	House (1974)

(*b*) Permeability of cell wall material

material	permeability μm^2 s^{-1} MPa^{-1}	source of data
cell wall of *Nitella* (alga)	50	Kamiya, Tazawa & Takata (1962)
	140	Tyree (1969)
artificial cellulose membrane	280	Russell & Woolley (1961)
xylem of *Pinus*	560	Briggs (1967)

(*c*) Summary of possible ranges of permeability

membrane/(nm s^{-1} MPa^{-1}):	
vascular plants	2–200
algae	20–3000
wall/(μm^2 s^{-1} MPa^{-1})	50–500
plasmodesmata, per unit area of wall /(nm s^{-1} MPa^{-1})	0–16000

unit area of wall) for movement through plasmodesmata is even more uncertain. Plasmodesma structure is still uncertain. They may be blocked by membranes or other structures so that they allow virtually no water flow. On the other hand, it is also possible that they are open tubes. The value of 1600 given in part (*c*) for plasmodesmatal permeability is calculated from the Poiseuille-Hagen equation assuming 0.5 plasmodesmata per square micrometre of wall (Clarkson 1974), each plasmodesma an open tube 0.3 μm long, 15 nm in radius with contents of viscosity 2×10^{-2} g cm^{-1} s^{-1}. This represents a maximum permeability; it seems likely that the tube is at least partly blocked.

TABLE 3. DIMENSIONS (μm) OF MAIZE ROOT ASSUMED IN CALCULATIONS OF PERMEABILITIES OF ALTERNATIVE PATHWAYS

root radius (centre to outer wall of epidermis) 475
stele radius (centre to outer wall of pericycle) 195

		cell dimensions		wall
		radial	tangential	thickness
epidermis		17	17	0.3
cortex		15	17	0.3
9 layers of cells		rising to		
		35	39	0.3
endodermis		12	15	0.3
pericycle		17	14	2
stelar parenchyma		10	10	0.3
vessels				
protoxylem	56†	9	9	
small metaxylem	14†	25	25	
large metaxylem	7†	60	60	

† Number of vessels in transverse section of root.

Because there is such a wide range of permeabilities possible for membranes, wall material and plasmodesmata, it is possible, by suitable choice of values, to make any one of the three pathways in figure 3 the one of lowest resistance. I shall adopt a slightly different approach, by starting from the two sets of relevant facts which are definitely known, namely the dimensions of the cells and the permeability of the whole root. I use the primary root of maize (*Zea mays*) for all my calculations. I have chosen it because it has been more investigated than any other root. The dimensions I use are shown in table 3. They are based on my own measurements on hand-cut sections, but they agree well with published photographs. Wall thickness in many cells is too thin to be easily measured by a light microscope, and the values are mostly taken from published electron micrographs, making some allowance for contraction during preparation.

Several sets of measurements have been made of the permeability of maize primary roots, and the values range from 18–68 nm s^{-1} MPa^{-1}, expressed on a root surface area basis (see Newman 1973, Table 1). This figure agrees with the value of 22 nm s^{-1} MPa^{-1} for whole root systems of maize (table 1), suggesting that the primary root is quite typical of the whole root system. Further, there is evidence that in the field too the root permeability is of about this magnitude. Data of Mengel & Barber (1974) for a maize field in Indiana showed root lengths of about 100 cm/cm^2 ground surface. By using the permeability per unit length derived from table 1 (24 μm^2 s^{-1} MPa^{-1}), at a rapid transpiration rate of 0.5 mm/h the predicted water

potential drop across the root would be 0.6 MPa. Allowing for resistance in the root xylem, the stem and the leaves, maize plants growing in moist soil should have, on a sunny day, leaf water potentials somewhat below −0.6 MPa (−6 bar). Turner & Begg (1973) found that under those conditions in Connecticut the lower leaves of maize were at −0.8 to −1.0 MPa near noon. This suggests that the value for root permeability is about right. I shall use the permeability value 40 nm s^{-1} MPa^{-1}, since this is at about the mid-point of the range reported.

Now I propose to take each possible pathway in turn and to calculate what permeabilities of membranes (per unit area), of wall material, of plasmodesmata would be required to give the observed root permeability. These required values will then be compared with the actual ranges of values summarized in table 2. The calculations were performed for each concentric layer of cells, and then summed to arrive at the total resistance for the pathway. The calculations have involved some geometric simplifications. The cells are all considered as cuboids, with two faces radial longitudinal, two radial transverse and two tangential. Since in reality the cells have more sides than this, the true pathway for movement in the wall would be more irregular and longer. To compensate for this, the transverse walls were ignored as pathways for wall movement, the calculation being based on movement only in the radial longitudinal walls. When membrane and plasmodesmatal permeabilities are being considered, intercellular spaces are allowed for by reducing the area of contact between one layer of cells and the next by an amount ranging from 30% in the inner cortex to zero in the outer cortex and other tissues. Normally the calculations are for water movement from the outer surface of the epidermis to the inner surface of the pericycle. This ignores the complications presented by root hairs and by movement to individual vessels.

Considering first the case where all the water moves by the vacuolar pathway, the permeability required for the membranes is 1.87 μm s^{-1} MPa^{-1}, to give a root permeability of 40 nm s^{-1} MPa^{-1}. This is for delivery of water to the inner boundary of the pericycle. To reach the large metaxylem, which would involve crossing stelar parenchyma, would require a higher membrane permeability. Thus the required membrane permeability is higher than any reported for vascular plants by about a factor of 10, and is near the high end of the range for algae.

If the free-space/endodermis pathway operates, most of the resistance must be in the plasmalemmas of the endodermis, since, as explained earlier, it must be in living material. If we assume that two plasmalemmas (one for entry to endodermis, one for exit) provide the same resistance as one plasmalemma plus one tonoplast, then if all the resistance were at the endodermis the required membrane permeability would be 90 nm s^{-1} MPa^{-1}, which is near the middle of the range of reported values for vascular plants (table 2). If the wall material is to provide $\frac{1}{4}$ or less of the root resistance, wall material must have a permeability of at least 7300 μm^2 s^{-1} MPa^{-1}, which is more than 10 times the highest reported value. Therefore the free-space/endodermis pathway seems to be impossible, since wall material is not permeable enough.

If, as just concluded, the wall provides too high a resistance to be a major pathway, then the symplasm pathway (if it operates) must involve entry mainly at the epidermis. According to Anderson & House (1967) in maize there are no plasmodesmata between stelar parenchyma cells, though there are many in the cortex. I therefore base my calculations on symplasm movement from the epidermis to the outermost layer of stelar parenchyma. If 80% of the total resistance is in the plasmodesmata and 20% in the membranes at entering and leaving the

symplasm, the required permeabilities would be: membrane 200 nm s^{-1} MPa^{-1}, plasmodesmata (per unit area of wall) 1.9 μm s^{-1} MPa^{-1}. If on the other hand, only 20% of the resistance were in the plasmodesmata and 80% in the membranes, the values would be 50 and 7.6. All of these are within the reported ranges.

The conclusion from these calculations is that the free-space/endodermis pathway is impossible; the vacuolar pathway is possible only if maize root cells have membranes as permeable as giant algae; and the symplasm pathway is possible. These conclusions rest upon the assumption that the true values for permeability must lie within the ranges shown in table 2, which may not be so. In fact the data for cell wall permeability (table 2*b*) are scanty and none is for higher plant parenchyma. Furthermore, they are all for movement *across* the wall; whether permeability longitudinally in the wall is higher is not known. The possibility that wall permeability in root cortex is much higher than the range shown in table 2 cannot be entirely excluded. Measurements of membrane permeability for higher plants are also fairly scanty, and may not represent the possible range of values. Finally, for the symplasm pathway to operate the plasmodesmatal permeability must be not lower than about 1.9 μm s^{-1} MPa^{-1}; while this is possible on available evidence, there is no definite proof that it is so. These calculations, therefore, favour the symplasm pathway, but cannot be considered as by any means conclusive evidence.

One other possible site of resistance may be considered. There are reports (Higinbotham, Davis, Mertz & Shumway 1973) that in maize the xylem vessels retain their protoplasm and membranes for some distance behind the tip. This would make little difference to the conclusions from my calculations, since at most it provides one extra set of membranes to be crossed. But it does provide a possible explanation for the apparent increase in root permeability when transpiration rate increases. Observations by Higinbotham *et al.* (1973) suggest that living contents are lost first from the protoxylem vessels, and are retained longest in the large metaxylem. Consider the region of the root where the large metaxylem vessels have living contents while the other vessels do not. Suppose, as has been suggested (Higinbotham *et al.* 1973), that the living xylem cells are much more active in ion accumulation than the dead ones. Suppose also that there is considerably greater resistance to water entering the large metaxylem than the small metaxylem and the protoxylem; this could be either because of the membranes themselves or because of the intervening stelar parenchyma. Then, when there was no suction applied to the xylem, uptake being by root pressure exudation would be mainly via the large metaxylem. But as suction was increased the smaller vessels would come increasingly into play, and since the resistance to water reaching them was less, the root permeability would appear to increase. This mechanism would operate only in that part of the root where some xylem vessels are dead and some alive. This could explain the results for broad bean (figure 1*b*): permeability failed to rise in the youngest part, where perhaps all xylem vessels still had membranes. Scott (1949) reported that in broad bean roots some vessels retained living contents to at least 8 cm from the tip.

Experimental evidence

Much use has been made of tracers to study the pathway of water movement. The roots of an intact plant are immersed in a solution of a dye (Scott & Priestley 1928, Huisinga & Knijff 1974) or of some substance which can be made visible to the electron microscope (Tanton & Crowdy 1972, Nagahashi, Thomson & Leonard 1974). Later the roots are sectioned and the position of the tracer is determined by light or electron microscopy. The tracer is found in all

the walls of the epidermal and cortical cells. In some experiments it is also found at points within the endodermis, in other cases it is not. I find it difficult to draw any useful conclusions from these experiments. The presence of tracer in the cortex walls is no proof of a major water flow by that pathway: the tracer could get there by diffusion. Equally the failure of some tracers (though not all) to penetrate beyond the endodermis is no proof of a barrier to water flow at that point. The penetration of THO into roots has also been studied (Woolley 1965), though its location within the root has not been determined. The problem here is that diffusion of THO over these short distances is so rapid that the rate and pathway of its movement is probably unaffected by mass flow water movement.

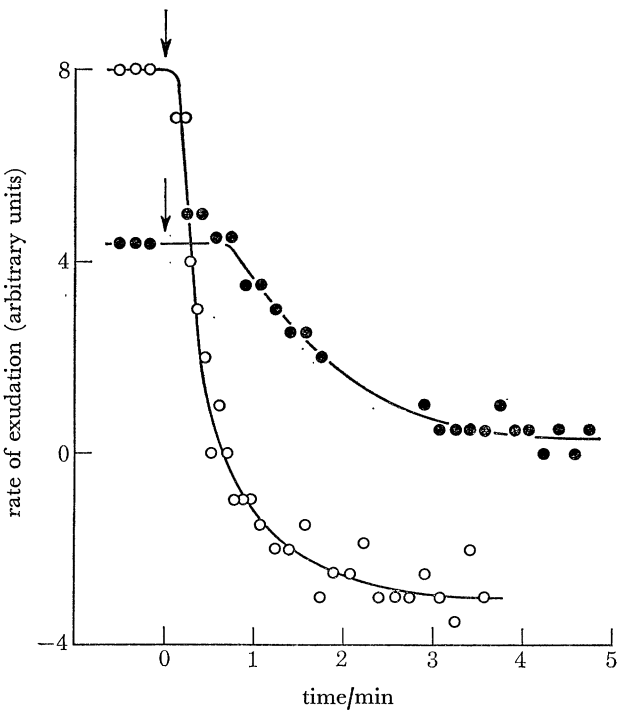

FIGURE 4. Rate of exudation from cut end of a detached primary root of maize. At time 0 (arrows), 0.15 M mannitol was added to the solution surrounding the root. ○, untreated root; ●, same root after treatment with 3×10^{-3} M sodium azide.

In many species the endodermis of fairly old roots becomes suberized; often this is followed by deposition of a thick layer of cellulose. It seems extremely probable that this makes the endodermis impermeable to water. If, therefore, all water passes by the vacuolar or free-space/endodermis pathways, suberized roots should be unable to take up water. In fact suberized roots of several species do continue to take up water. Graham, Clarkson & Sanderson (1974) have shown that in barley and marrow water uptake continues, although at a reduced rate (see figure 1*a*), when all endodermal cells are suberized. In maize, permeability to water remains high at 10 cm from the tip, when endodermal suberization of roots grown under the same conditions is well advanced by 8 cm (figure 1*c*). Robards, Jackson, Clarkson & Sanderson (1973) showed that in barley there were still many plasmodesmata in the inner wall of the endodermis after it had become suberized and thickened. These plasmodesmata thus joined the lumina of the endodermal cells to those of the pericycle, and seem the most likely pathway for water

movement in these roots. This, therefore, is indirect evidence that water can move from cell to cell via plasmodesmata.

House & Findlay (1966) studied the way in which the exudation rate from single detached maize roots is altered when the osmotic potential of the external solution is suddenly changed. S. C. Manning, working in this department, has performed similar experiments with an improved technique which allows exudation rate to be measured over a much shorter period. An example of his results is shown in figure 4. When an osmoticum (here mannitol) is added to the external solution the rate of exudation drops, but there is a lag before a new minimum rate is reached. House & Findlay (1966) explained this lag as being due to the time taken for the osmoticum to diffuse through the free-space of the root to an osmotic barrier (e.g. the endodermis). This might seem to be evidence for the free-space/endodermis pathway. However, the lag could also be caused by the time taken for some 'middle compartment' in the root (e.g. the cortex), through which the water has to pass, to adjust its water potential. One piece of evidence against House & Findlay's explanation is the speed of adjustment in Manning's experiments: the half-time was usually about 25 s, whereas Ehwald, Sammler & Göring (1973) found a half-time for melibiose equilibration in the free-space of maize roots of $2\frac{1}{2}$ min. Other evidence comes from experiments by Manning with sodium azide. Diffusion of an osmoticum through the free-space should be unaffected by a metabolic inhibitor, whereas the rate of water entry to a 'middle compartment' would be slowed down. Figure 4 shows that pre-treatment with azide did slow down the rate of adjustment. Hence the lag appears not to be due to diffusion in the free-space, and the results would be in agreement with water moving by the vacuolar or symplasm pathways.

Ginsburg & Ginzburg (1970) conducted experiments with cortical sleeves of maize. These are made from segments of primary roots by separating the stele from the cortex; the break occurs at the endodermis, which ruptures. By sealing a tube to the end of the central cavity of the sleeve (where the stele had been), they could study water and ion movement across the sleeve. In several respects the sleeves behaved very like intact roots. They acted as efficient osmometers, with a reflexion coefficient near 1. The permeability was similar to that of intact maize roots, and was reduced by metabolic inhibitors. If the free-space/endodermis pathway normally operates, one would have expected much leakage of solutes through the ruptured endodermis of the sleeves, and also a much reduced permeability of the remaining endodermal membranes because the metabolism of the endodermal cells was drastically upset. Hence osmotic water movement to the root centre should have been greatly reduced, but in fact it was not. The results would be best explained if in the intact root there is very little water flow in the wall and most water passes either by the vacuolar or symplasm pathways. It should be noted, however, that some workers have failed to get cortical sleeves to act as osmometers (Anderson 1973, p. 563). Ginsburg & Ginzburg (1970) left their sleeves for 9 h after preparation before starting the actual experiments, and it is conceivable that repair of endodermal membranes occurred during this period.

Thus both calculations of permeabilities and experimental evidence are against the free-space/endodermis pathway, and on balance the symplasm pathway is most favoured. However, I think that more conclusive evidence is needed before we can decide definitely, particularly in view of the uncertainty about plasmodesma structure. The maximum value for plasmodesma permeability in table 2 assumed the plasmodesma to be an open tube, which is not in agreement with most modern electron microscope studies (Robards 1971, Clarkson 1974). If

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water does move mainly in the symplasm it raises several interesting questions. (1) Can a turgor pressure difference be maintained between neighbouring cells? (2) When a change in metabolic rate alters root permeability, how is it acting? It might be by effects on membranes, or on the state of protoplasm in the plasmodesmata, or even on the rate of protoplasmic streaming, if this accelerates water movement.

Root hairs

So far I have ignored root hairs. These are generally assumed to enhance water uptake. There is no doubt that root hairs can take up water, but this has been demonstrated only with roots under highly artificial conditions (Rosene 1943, Cailloux 1972). When a root is growing in soil the root hairs and the soil provide two alternative radial pathways to the root itself, and the question is, which of these is the path of least resistance? The soil provides by far the greater area for radial flow: even at the root surface only about 1 % or less of the surface area is occupied by hairs. The resistances for entry to a hair and flow along it are not known, but elsewhere (Newman 1974, p. 413) I have made estimates which suggest that even when the soil is quite dry most water will move radially in the soil rather than the root hairs.

Movement in xylem

If the diameters of the xylem vessels are known, the permeability for longitudinal flow in a root can be calculated by the Poiseuille–Hagen equation. A suitable form for our purposes is

$$P_x = 12.5 \times 10^7 \, \pi \Sigma \, r^4$$

where P_x is the longitudinal permeability per root (units $cm^4 \, s^{-1} \, MPa^{-1}$), and r is the radius of each individual xylem vessel (in cm). The viscosity of water is assumed to be 10^{-2} g $cm^{-1} \, s^{-1}$, its value at 20 °C. Permeability can also be measured, by determining the rate at which water moves through a length of detached root under an applied pressure gradient. Some values obtained by these two methods are shown in table 4. There is evidently considerable variation between species. It is unfortunate that more data of this kind are not available.

Table 4. Longitudinal permeability of single roots, measured by pressure flow or calculated from Poiseuille–Hagen equation

(Units 10^{-2} $cm^4 \, s^{-1} \, MPa^{-1}$, i.e. mm^3/s flowing under a pressure gradient of 0.1 MPa/cm.)

	measured	calculated	source
Zea mays (maize)			
adventitious root	150	—	Kozinka & Luxova 1971
primary root	—	24	data of table 3
Triticum aestivum (wheat) seminal root	—	1.5	Passioura 1972
grasses			
Phleum pratense	1.4	—	Emerson 1954
Lolium perenne	0.6	—	
Dactylis glomerata	0.06	—	

It would be very desirable to know the relative magnitudes of radial-flow and xylem resistances in plants. The fact that the root permeability is so sensitive to metabolism suggests that radial flow provides the major resistance. However, most experiments on root permeability have been conducted on small plants with only short distances from the root tips to the stem base. In field situations xylem resistance may be greater.

In order to answer this question for any species, one would need to know how both radial-flow and xylem permeabilities vary between main roots, primary laterals and secondary laterals, and along each of these types; also the lengths and frequencies of each root type. Such information is unfortunately not available for any species. The simpler sort of question which can be answered is this. Suppose that the soil above depth D were so dry that water uptake could occur only below that depth. What would be the magnitude of (*a*) the radial-flow resistance in the roots below D and (*b*) the resistance for xylem transport in the main root from depth D to the surface? We can answer this approximately for maize, using permeability data from tables 1 and 4, plus data of Mengel & Barber (1974) on root distribution under a maize crop in the field in Indiana. They reported little root penetration below 75 cm, so let us suppose all water uptake is confined to the 60–75 cm depth. The root length below 60 cm was 18.2 cm/cm^2 ground surface area. If radial-flow permeability per unit length was 24 $\mu m^2\ s^{-1}\ MPa^{-1}$, then for radial-flow and xylem resistances to be equal, the number of main roots penetrating to 60 cm depth would need to be 1.75/m^2 ground area. Since there were about 5 plants/m^2, this is only one root per three plants, and in practice many more roots would probably reach 60 cm. So this calculation suggests that even in this extreme case radial-flow resistance will be much greater than xylem resistance.

Passioura (1972) described experiments with wheat in which xylem resistance was probably significant. Wheat plants were grown in columns of soil 90 cm tall. In some containers only one seminal root per plant was allowed to penetrate the soil, whereas all roots of the control plants could do so. At the start the soil was thoroughly moist, but no further water was added, so that the plants had to depend entirely on stored water. The unexpected result was that the grain yield by the single-rooted plants was higher than that of the controls. This was because during the period 3–5 weeks after germination the single-rooted plants used less water, and thus had more available later on, during grain development. This much seems indisputable. The question which now arises is, why did the single-rooted plants take up less water at 3–5 weeks of age? Passioura concluded that it was due entirely to the large resistance to flow along the xylem of the single main root. There is no doubt from his calculations that xylem resistance would be large in the single-rooted plants. The calculated permeability is shown in table 4. He predicted that for a peak mid-day transpiration rate, a pressure gradient of 0.12 MPa/cm would be required to drive the water along the xylem at the required rate, so that even a 10 cm distance of travel would require the leaf water potential to be lowered by 1.2 MPa. But we can still ask whether the radial-flow resistance may not have been larger still. Passioura totally ignored its existence. Direct measurements of radial-flow permeability have not been made for wheat, but an approximate value can be obtained from data of Andrews & Newman (1969). These give the permeability of whole wheat plants, on a root length basis, as 3.6 $\mu m^2\ s^{-1}\ MPa^{-1}$. If half of the resistance was in xylem and leaves, the radial-flow permeability would be 7 $\mu m^2\ s^{-1}\ MPa^{-1}$; this is likely to be correct within a factor of 2. If all the roots on Passioura's 3-weeks-old single-rooted plants were operative and had this permeability, the radial-flow permeability per plant would be 0.24 $mm^3\ s^{-1}\ MPa^{-1}$. The xylem permeability for the full 90 cm of depth (using Passioura's own estimate of permeability per centimetre) would be higher, 0.36 $mm^3\ s^{-1}\ MPa^{-1}$. So even in this very unusual case radial-flow resistance was probably significant, perhaps of the same order of magnitude as xylem resistance. This does not in itself disprove Passioura's claim that the only significant difference between single-rooted and control plants was in xylem resistance. This will depend on whether the plants differed in root surface area as well as

number of main roots, and his results on this are equivocal. This experiment is interesting in illustrating an extreme case where xylem resistance was almost certainly of some significance, though perhaps not as overwhelmingly as Passioura assumed.

The data of table 4 on xylem permeability have a serious weakness: they were determined or calculated under conditions where all vessels were filled with water. In the intact plant it is possible that bubbles develop in some vessels when the water is under tension, and these vessels would then be blocked. There is evidence for stems and petioles that bubbles do form in xylem (Haines 1935, Milburn & Johnson 1966, Milburn 1966, 1973), but so far evidence for roots is lacking. If bubbles start at randomly located points they would be commonest in the widest vessels. There is in addition the claim that water in narrower vessels is intrinsically less prone to cavitate (Salisbury & Ross 1969, p. 128). For either reason we may expect the largest vessels to become blocked first, and these are the ones which provide the easiest flow. According to calculations by the Poiseuille–Hagen equation for the maize root of table 3, if the large metaxylem vessels became blocked, flow would drop to 6% of its former rate (under a given pressure gradient); and if the small metaxylem was also blocked, flow would be only 0.4% of that through all vessels.

Unfortunately no data are available on xylem permeabilities when the water is under tension. One source of indirect evidence is available, however. Suppose an extensive root system, attached to the plant, is surrounded by soil of uniform moisture content. Then if the xylem resistance is negligible, water uptake should be controlled by radial-flow permeability and uptake per unit amount of root should be unrelated to distance from the stem base. On the other hand, if xylem resistance is significant, uptake should be faster nearer to the stem base. Davis (1940) carried out such an experiment with maize, growing in a box of soil 1.2 m long. The roots appeared, by observation through the glass side of the box, to be evenly distributed. Soil moisture was also uniform, yet uptake was initially fastest near the base of the stem, and the zone of rapid uptake gradually extended along the box. Taylor & Klepper (1971) found the opposite result with cotton growing outdoors: water uptake per cm of root was uniform throughout the 2 m of soil depth studied, provided soil moisture content was uniform. Davis's results appear to conflict with my previous predictions that in maize xylem resistance will not be significant, and they raise the possibility that the larger vessels can become blocked by bubbles. In his experiment the plants had suffered a drying cycle before the uniform wetting of the soil, and bubbles could have formed at that time.

Conclusion

This paper has shown that we are still unable to answer unequivocally the key questions about water flow through root systems: what is the pathway of water movement between root surface and xylem? Where in this region does the main resistance lie? How significant is xylem resistance? To answer these questions would be a major advance in understanding plant water relations.

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