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ROOTS AND WATER

Transport of water to plant roots in soil

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The theory of water uptake by a single root is reviewed, including infinite and finite systems, and constant and variable diffusivity. This theory predicts the water potential and content at the root surface will depend upon soil and root parameters, most of which are readily determinable, but the uptake rate of water per unit length of root is uncertain. Uptake rates averaged over whole root systems will usually be small, suggesting only very small gradients of water content around roots, but it is likely that local rates may, on occasion, be much larger than the averages, and the possibility of large gradients cannot then be dismissed.

Certain special effects may alter these conclusions, particularly salt accumulation around roots and no contact or partial contact of roots with soil. Both demand a fast uptake rate of water before they become important, and salt accumulation is unlikely to be important except in saline soils.

Methods of dealing with whole root systems are briefly considered. Differing root density can be dealt with by subdividing the root volume into compartments, or by regarding the problem as one of dispersion pattern. Further advance requires better information about local boundary conditions imposed by roots on the surrounding soil.

1. Introduction

The supply of water from soil to plant is of fundamental importance to the growth of all species except those with an aquatic habitat. The debate over the 'availability' of water held in the soil has continued for many decades, often shifting ground or terminology, but always concerned with the central problem of identifying the factors which determine for how long a plant can survive and grow without restraint on the soil water reserves. Concepts such as field capacity, permanent wilting point and available water are of considerable use in field work, but it has long been clear that the fundamental questions concern the rate at which water can be delivered to the root surface and the suction which the plant has to exert to obtain it. The soil component of the system is now fairly well understood in outline, but is not simple, firstly because the physics of soil water movement is still being developed, secondly because the irregular geometry of soil and root systems make the application of accurate and detailed theory very difficult, and thirdly because the uncertainties which still persist in our understanding of the physiology of water uptake make it difficult to define adequate boundary conditions.

2. Water movement in soil

The physics of soil water is based upon the definition of soil water potential (Slatyer & Taylor 1964). Recently this has been modified (I.S.S.S. 1974), so that it is more 'operational' in character, and refers directly to the measurement of water by a tensiometer. This distinction may appear somewhat academic, but the exact definition of potential is of practical importance, because the reduction in water potential can arise from several physical mechanisms, and not all these forms of potential affect water movement equally. Osmotic potential causes water movement only in a limited set of circumstances, and the new definition distinguishes between this and the other forms of potential which may be measured by a tensiometer, including 'overburden potential'. For simplicity, I shall assume in this paper that the term 'potential' (Ψ) applies to the appropriate driving force for water movement; it therefore excludes osmotic potential in the normal soil situation, but includes it when we consider movement across a semipermeable barrier, such as a root surface or an air-water interface. Water transport theory is built on two equations, which are here given for movement in one dimension only

Darcy's law:

$$F = -K\frac{\mathrm{d}\Psi}{\mathrm{d}x} = -D_{\mathrm{w}}\frac{\mathrm{d}\theta}{\mathrm{d}x}; \tag{1}$$

differential equation for unsaturated flow:

$$\left(\frac{\mathrm{d}\theta}{\mathrm{d}t}\right)_x = \frac{\mathrm{d}}{\mathrm{d}x}\left[K\frac{\mathrm{d}\Psi}{\mathrm{d}x}\right] = \frac{\mathrm{d}}{\mathrm{d}x}\left[D_{\mathrm{w}}\frac{\mathrm{d}\theta}{\mathrm{d}x}\right] \tag{2}$$

or, in three dimensions

$$\frac{\partial\theta}{\partial t} = \nabla(D_{\mathrm{w}}\nabla(\theta)) \tag{3}$$

where F is water flux density, K the hydraulic (saturated) or capillary (unsaturated) conductivity, D_{w} the water diffusivity, Ψ the water potential, θ the volumetric water content, and x and t are distance and time respectively.

The equation for unsaturated flow, in the second formulation, is similar to the diffusion equation. This is mathematically highly convenient, since it allows the use of published solutions of the latter, but it should be quite clear that it is not physically correct. Water in soil is not transferred by diffusion, which is independent of pore radius, but by bulk or mass flow, which is dependent on pore radius. The conductivity, K, is therefore the true measure of ease of transport of water.

Both K and D_{w} vary sharply with water content in the soil. The problems caused by variable D_{w} are precisely analogous to those found with concentration-dependent diffusion coefficients (Crank 1957) in diffusion theory. In addition, K and D_{w} both show hysteresis, and their values can be greatly different at the same value of θ, depending upon whether the soil is wetting or drying, or indeed upon its recent wetting-drying history (e.g. Staple 1964). In this paper D_{w} refers to the value for a drying soil, since plant roots extract water.

3. WATER FLOW TO A SINGLE ROOT

(a) *Basic theory*

Early detailed approaches to uptake of water by single roots were made by Philip (1957) and by Gardner (1960), and though the details have been improved and elaborated, the latter still stands as one of the simplest and clearest treatments. This started from the equation for unsaturated flow for a radial (cylindrical) systems, with water moving in towards the root from the surrounding soil

$$\left(\frac{\partial\theta}{\partial t}\right)_r = \frac{1}{r}\frac{\partial}{\partial r}\left(rD_{\mathrm{w}}\frac{\partial\theta}{\partial r}\right). \tag{4}$$

For boundary conditions given by (*a*) a constant rate (I_{w}) of uptake per unit length of root where $I_{\mathrm{w}} = -2\pi a K \mathrm{d}\Psi/\mathrm{d}r$ at $r = a$, and (*b*) an infinite soil volume, the solution is

$$\Psi_{\mathrm{s}} - \Psi_{\mathrm{a}} = \frac{I_{\mathrm{w}}}{4\pi K}\left[\ln\frac{4D_{\mathrm{w}}\,t}{a^2} - 0.577\right], \tag{5}$$

when Ψ_a and Ψ_s are respectively the water potentials at the root surface and in the bulk soil, and a is the root radius. Gardner used this to investigate whether an important decrease in water potential could occur at the root surface during water uptake, i.e. whether a 'dry zone' forms round an absorbing root (Macklon & Weatherley 1965). Using data for 3 soils, he found that a serious potential drop could occur if the bulk soil were moderately dry (see figure 1); if the soil were moist, the potential decrease at the root surface must always be trivial.

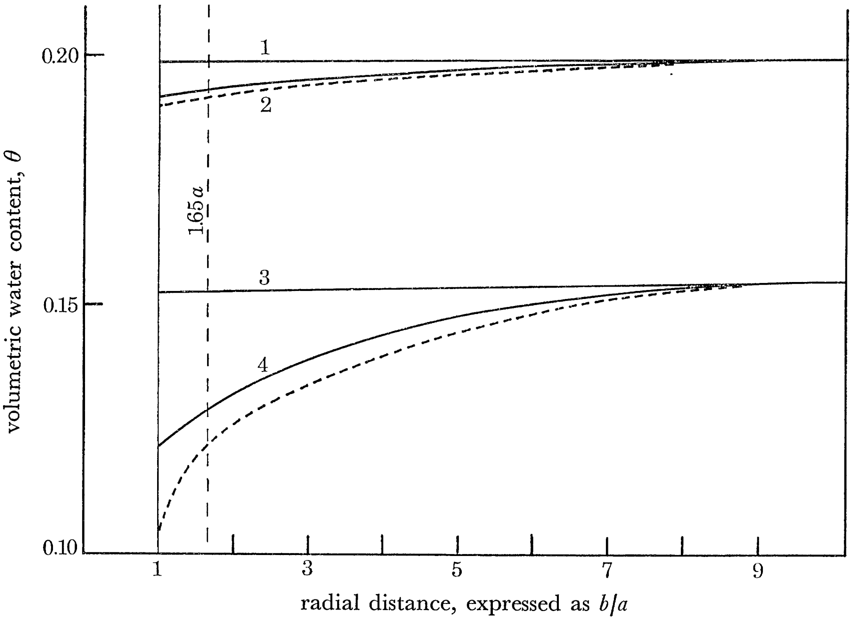

FIGURE 1. Water gradients in the equivalent cylinder, for Yolo light clay ($D_0 = 0.47$ cm, $\beta = 25.8$, $\theta_0 = 0.1$); $b/a = 10$.

(1) $\theta_b = 0.20$, $I_{\mathrm{w}} = 0.01\ \mathrm{cm^2\,d^{-1}}$
(2) $\theta_b = 0.20$, $I_{\mathrm{w}} = 0.15\ \mathrm{cm^2\,d^{-1}}$
(3) $\theta_b = 0.155$, $I_{\mathrm{w}} = 0.01\ \mathrm{cm^2\,d^{-1}}$
(4) $\theta_b = 0.155$, $I_{\mathrm{w}} = 0.15\ \mathrm{cm^2\,d^{-1}}$

Full lines are 'steady rate', dotted lines 'steady state'. $\theta_a = 0$ when $\theta_b = 0.155$ and $I_{\mathrm{w}} = 0.25\ \mathrm{cm^2\,d^{-1}}$.

This treatment appears to give clear and unambiguous results. Most of the remainder of this paper is concerned with the various assumptions and simplifications built into this model, and whether these are such as to render the general conclusions incorrect.

(*b*) *Limited soil volume*

The above discussion has assumed that each root absorbs from an infinite amount of soil, and that there is always more soil, at a steadily increasing distance, which can be drawn upon. In real root-soil systems this is not correct, since roots compete, and each root can be assumed to have a limited amount of soil for its sole exploitation. The root surface water potential will therefore fall faster than predicted above, and the mean water content and potential of the soil volume will decrease steadily.

The simplest way of dealing with this situation is to assign an equal 'equivalent cylinder' of soil to each root, and to assume that all water entering the root originates in this cylinder. This is nearly equivalent to saying that roots are organized in equally spaced parallel array. There are no analytical solutions of the diffusion equation sufficiently simple to be of general use for this case (see Youngs & Gardner 1968), and numerical solutions or approximations have to be employed. The latter are most useful for discussing the general features of the system.

Passioura & Cowan (1969) have discussed the two usual methods, the 'steady state' and 'steady rate' approximations. For a steady *state*, it is assumed that all the water is injected into the system at the periphery of the equivalent cylinder, and the appropriate equation is for the steady state flow in a cylinder:

$$\Psi_{\mathrm{b}} - \Psi_{\mathrm{a}} = \frac{I_{\mathrm{W}}}{2\pi K} \ln \frac{b}{a} \tag{6}$$

or

$$\theta_{\mathrm{b}} - \theta_{\mathrm{a}} = \frac{I_{\mathrm{W}}}{2\pi D_{\mathrm{W}}} \ln \frac{b}{a}, \tag{7}$$

where b is the radius of the equivalent cylinder. Water is in fact being removed from the equivalent cylinder all the time, and this is allowed for by calculating the water loss after some convenient time interval Δt $(I_{\mathrm{W}}\, \Delta t = \pi\, (r_{\mathrm{b}}^2 - r_{\mathrm{a}}^2)\, \Delta\theta)$, and recalculating with the new values of Ψ_{b}, K or D_{W} to allow for the change in θ.

The steady *rate* approximation (Cowan 1965) is rather more realistic, since it embodies the assumption that water is being supplied uniformly from within the soil cylinder to maintain the constant flow (figure 1). The equation for this system is

$$I_{\mathrm{W}} \frac{(b^2 - r^2)}{(b^2 - a^2)} = 2\pi r\, D_{\mathrm{W}} \frac{\partial\theta}{\partial r}. \tag{8}$$

This yields

$$\theta_{\mathrm{b}} - \theta_{\mathrm{a}} = \frac{I_{\mathrm{W}}}{2\pi D} \left[\frac{b^2}{b^2 - a^2} \ln \frac{b}{a} - \frac{1}{2}\right]. \tag{9}$$

In practice, $b^2 \gg a^2$, and the equation may be simplified to

$$\theta_{\mathrm{b}} - \theta_{\mathrm{a}} \approx \frac{I_{\mathrm{W}}}{2\pi D_{\mathrm{W}}} \left[\ln \frac{b}{a} - \frac{1}{2}\right] = \frac{I_{\mathrm{W}}}{2\pi D_{\mathrm{W}}} \ln \frac{b}{1.65a}. \tag{10}$$

The solutions are therefore closely similar, but the steady rate equation predicts a value of θ_{a} (for constant θ_{b}) which is identical to that of θ with the steady state equation at $r = 1.65\, a$.

The equations are most useful in the relation to the mean water content $\bar{\theta}$, rather than θ_{b}, and then give (Passioura & Cowan 1968)

steady state

$$\bar{\theta} - \theta_{\mathrm{a}} = \frac{I_{\mathrm{W}}}{2\pi D} \left(\frac{b^2}{b^2 - a^2} \ln \frac{b}{a} - \frac{1}{2}\right) \approx \frac{I_{\mathrm{W}}}{2\pi D} \ln \frac{b}{1.65a} \tag{11}$$

steady rate

$$\bar{\theta} - \theta_{\mathrm{a}} = \frac{I_{\mathrm{W}}}{2\pi D_{\mathrm{W}}(b^2 - a^2)} \left[\left(\frac{b^4}{b^2 - a^2} \ln \frac{b}{a}\right) - \left(\frac{3b^2 - a^2}{4}\right)\right] \approx \frac{I_{\mathrm{W}}}{2\pi D_{\mathrm{W}}} \ln \frac{b}{2.1\, a}. \tag{12}$$

Again, the values of $\bar{\theta}$, D_{W} or K have to be recalculated at intervals. Passioura & Cowan (1968) compared both approximate methods with a numerical solution, and found fair agreement, particularly for the steady rate method. It therefore appears to the author that the pursuit of exact solutions at considerable effort is hardly warranted in a situation where our understanding of the detailed processes is so incomplete, and that these approximations are acceptable. It will be noted that in neither case is the total size of the gradient closely dependent upon b, i.e. upon the total size of the equivalent cylinder; the latter quantity exerts its effect in the new time-step recalculation of $\bar{\theta}$, and the final equation for the steady rate would be

$$\bar{\theta}_i - \theta_a = I_w \left[\frac{t}{\pi(b^2 - a^2)} + \frac{\ln(b/2.1\,a)}{2\pi D_w}\right] \tag{13}$$

where $\bar{\theta}_i$ is the initial water content of the soil.

(c) *Variable diffusivity*

Gardner assumed constant values of D_w and K, which is reasonable if θ varies little. This assumption renders the numerical results for decrease in Ψ_a in dry soils quite incorrect, but it should not affect the conclusion that Ψ_a differs little from Ψ_s in moist soil.

Several more elaborate treatments have considered this point. Whisler, Klute & Millington (1970) and Lang & Gardner (1970) pointed out that the variation of D_w with θ implied that a maximum value of I_w is reached quite rapidly, as Ψ_a decreases and the soil dries out around the root. Further decreases in Ψ_a then simply reduce K and D_w so much that no increase in water inflow occurs (figure 1). This maximum I_w will of course depend upon the original water content in the soil, and upon how D_w varies with θ. In the results of Whisler *et al.* for Chino clay, I_w reached a maximum of below 0.1 $\text{cm}^3\,\text{cm}^{-1}\,\text{d}^{-1}$ with Ψ_b at -0.3 MPa and Ψ_a at -0.9 MPa (-3 and -9 bar) respectively.

It has frequently been assumed that D_w and θ are exponentially related (a 'Gardner' soil) (Cowan 1965; Williams 1974), so that

$$D_w = D_{w0} \exp[\beta(\theta - \theta_0)].$$

Using the steady rate approximation, it is then simple to derive

$$\theta_a - \theta_0 \sim \frac{1}{\beta} \ln\left[\exp[\beta(\theta_b - \theta_0)] - \frac{\beta I_w}{2\pi D_{w0}} \ln\frac{b}{1.65\,a}\right]. \tag{14}$$

The results of this equation agree well with those of the basically similar method of Cowan (1965).

(d) *Numerical value of chosen parameters*

It is well known that good models may yield any desired result so long as the parameter values are chosen appropriately. In this case, the crucial values in equation (14) are β, I_w and D_0; b and a matter less since they occur in a logarithmic term. D_w seems unlikely to be seriously in error, though its accurate measurement in soil is difficult, and these treatments do assume that a quantity measured in bulk soil (assumed to be homogeneous) will still apply over distances comparable to the particle size of the soil. Gardner (1972) makes the point that values of D_w are strongly dependent upon soil structure (and therefore on preparative treatment) for large θ, but are much less sensitive at low θ. The value of β lies in the range 15–25. It is noteworthy that the popular Yolo light clay (Cowan 1965; Williams 1974) has a rather large value of β, and relatively large gradients are therefore easily predicted. Other soils which have been considered in this type of work (Gardner 1960) appear to give smaller gradients.

There is much more uncertainty over appropriate values of I_w. Newman (1969) has argued that the values used by Gardner and by Cowan are unrealistically large, and that $\Psi_s - \Psi_a$ is therefore overestimated. This conclusion was based upon the mean transpiration rate of a complete crop cover, and the total root length below unit land surface, from which $\overline{I_w}$ (inflow averaged over time and whole root length) is found. Root density varies greatly between genera and species, being extremely large in the Gramineae (Welbank, Gibb, Taylor & Williams 1974) for which $\overline{I_w}$ appears to be of the order of 0.001 $cm^3\ cm^{-1}\ d^{-1}$ or less. The maximum value of $\overline{I_w}$ for ryegrass found by Hansen (1974) was 0.005 and by Lawlor (1972) 0.0007 $cm^3\ cm^{-1}\ d^{-1}$.

If these values are correct, then it is obvious that local drying out of soil around roots is unlikely in the field, even if it can be induced in the laboratory. It is unlikely that transpiration ever greatly exceeds 0.5–1 cm d^{-1}, unless there is a considerable supply of advective energy, when it may rise to 1.5–2 cm d^{-1} in arid climates (Davenport & Hudson 1967). The short-term rate in the middle of the day may well be at least twice the daily mean, but we are concerned with orders of magnitude rather than factors of two in this question. There is also the possibility of water storage within the plant, so that $\overline{I_w}$ does not follow the immediate rate of transpiration exactly.

The assumption of a uniform distribution of water entry velocity over the total root surface is much more doubtful. It is likely that all root, even that which is suberized, is able to absorb water (Kramer & Bullock 1966), but the entry velocity will vary greatly (Newman, this volume, p. 465). Thus Graham, Clarkson & Sanderson (1974) found that uptake rate declined by a factor of about 8 during the ageing of a single piece of marrow root from 0 to 90 h, contemporary with suberin deposition in the endodermis. The largest rate found was nearly 0.1 $cm^3\ cm^{-1}\ d^{-1}$. The question is further complicated by the finding of Brouwer (1964) that water uptake varies with suction in the xylem in quite different ways, depending upon distance from the root tip. In his experiments, the uptake rate in broad bean roots 10 cm behind the apex reached a maximum of about 0.2 $cm^3\ cm^{-1}\ d^{-1}$.

It is therefore not possible to state what the local flow rate at any point over an entire root system will be. However, a speculative calculation is possible; for example the work of Graham *et al.* (1974) indicates that there is a low-resistance zone in the first 8 cm of the barley root. From the data of Hackett (1967), we can calculate that about 90% of the total root length of his barley plants was within this distance of an apex, if we assume constant length of individual roots. It is therefore possible that I_w does not vary much over the root system for actively growing plants. However, root systems often cease to extend near maturity, and the mean age and degree of suberization of roots could then increase rapidly. Including diurnal and spatial variations, it seems possible that I_w might rise locally to $10\ \overline{I_w}$, which could materially alter our conclusions.

(*e*) *Differential uptake in soil layers*

The above discussion has assumed that water is equally available at all points in the root system, but in practice this must often be untrue. The surface soil horizon will almost always dry out more rapidly than lower layers of soil, because drainage is completed there first, because evaporation into the atmosphere can occur, and because there is usually a relatively dense root distribution leading to rapid water uptake. Even if root properties were, on average, equal over the whole root system, the mean flow would thus vary with position in the soil. The work of Ogata, Richards & Gardner (1960) showed clearly that the water depletion shifted down the profile during the growth of the plants. Similar results of Reicosky, Millington, Klute & Peters

(1972) showed this effect even more markedly, and roots near a water table absorbed up to 0.67 $\mathrm{cm^{-3}\,cm^{-1}\,s^{-1}}$, 1000 times the rate of roots in dry soil higher up. However, this argument indicates the largest rate of uptake in the wettest soil, where the possibility of localized dry zones is at a minimum. We cannot therefore simply take mean $\overline{I_\mathrm{W}}$ values and apply them in dry parts of the rooting volume.

It is obvious that our knowledge is least certain in relation to the value of I_W. Entirely different conclusions can be reached on the basis of different assumptions, and direct measurements of local I_W values seem an urgent need.

(*f*) *Practical test of theoretical predictions*

It may appear surprising that there have been so few direct tests of these theoretical conclusions. The detection of small changes in water content or potential close up to a single root surface is technically extremely difficult, and I am aware of only two such attempts. Campbell (1968) measured the water content of soil slices in contact with roots by γ-ray densitometry and was able to show that water gradients existed. However, they could not be measured sufficiently exactly to allow detailed comparison with theory, and no certain conclusions could be drawn.

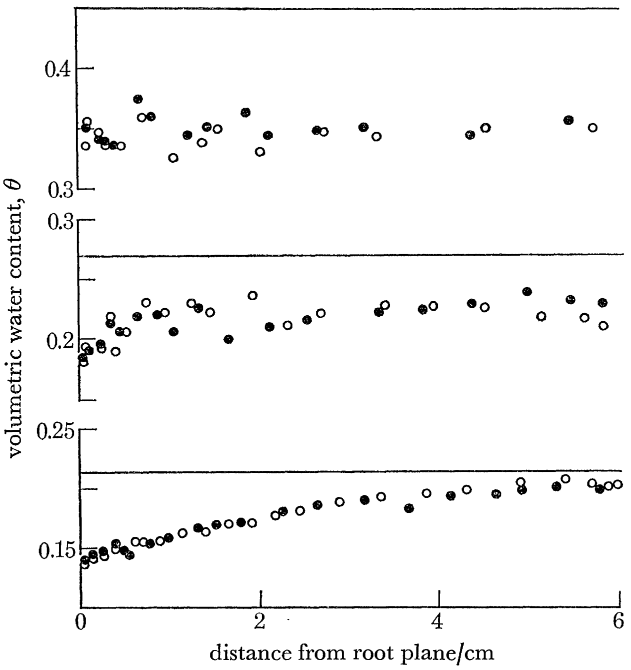

FIGURE 2. Water content gradients developed in soil near a sheet of parallel onion roots. Initial water contents shown as full horizontal line. Circles and dots indicate results from the two sides of the root plane. (From Dunham & Nye 1972.)

Dunham & Nye (1973) used a direct method in which a block of soil was placed against a layer of onion roots for several days, after which the block was frozen and sectioned on a freezing microtome. The water gradients were considerable in dry soil (figure 2), even though the transpiration rate decreased sharply with the original water content of the soil, and the gradients would presumably have been much steeper if the largest transpiration rate had been maintained. These results fitted theory reasonably well, and confirmed that the gradients in moist soil were very small. This gives some confidence in the theoretical treatments, though further practical tests would be very desirable, using other plant species, root types and soils.

Several experiments (e.g. Fiscus 1972) have attempted to determine the water potential at the root surface by measurements on a piece of bare root at some distance from the part in contact with soil. In view of the uncertainty of the site of resistance to flow in the root, it seems hazardous to assume that the root surface potential in these two parts will be the same.

4. Disturbances at the root–soil interface

It is implicitly assumed in the 'classical' theory that soil properties, with the sole exception of water content, remain constant from the bulk soil right up to the root surface. This is unlikely to be true.

(a) *Salt accumulation*

Soluble or adsorbed cations and anions can in principle increase or decrease in concentration near the root surface, in response to its uptake behaviour. Our concern here is with the possibility that soluble salts in the soil solution are drawn in, with the transpiration stream, at such a rate that they accumulate near the root. This topic has been the subject of several theoretical studies (Marriott & Nye 1968; Tinker 1969; Passioura & Frere 1967), but little quantitative practical work. The existence of such accumulations of sulphate has been shown by Barber, Walker & Vasey (1963) by autoradiography, and Riley & Barber (1969) have separated 'rhizosphere soil' and shown that it contained a higher salt concentration than the original soil. If this does occur, quite large osmotic stresses may develop at the root surface during transpiration, which would gradually disappear if transpiration ceased.

Accurate treatments require numerical solution methods, but Marriott & Nye showed that an approximate treatment originally due to Passioura (1963) was reasonably dependable in general, though it seriously underestimated the effect if large salt accumulations were occurring. The correct statement of the linear situation is given by

$$\theta \frac{\partial C_1}{\partial t} = \frac{\partial (\nu C_1)}{\partial x} + D_{\mathrm{p}} \frac{\partial^2 C_1}{\partial x^2}, \tag{15}$$

where C_1 is the concentration of the salt in the solution, D_{p} is the porous system diffusion coefficient, ν the flux density of water, x distance and t time. The approximate treatment for the cylindrical situation states that

$$I_{\mathrm{w}} C_1 - I = 2\pi D_{\mathrm{p}} \, (C_{1,\mathrm{i}} - C_{1,a}) \, g, \tag{16}$$

where I is the inflow of the salt into the root, and g is a complex term dependent upon Dt/a^2, when a is the root radius. The approximation lies in assuming that C_1 in the term $I_{\mathrm{w}} C_1$ is equal to the original soil solution concentration $C_{1,\mathrm{i}}$, whereas it in fact varies with position and time. Such accumulations seem most likely in a saline soil, and if we assume $C_{1,\mathrm{i}} = 0.05$ M NaCl, $I_{\mathrm{w}} = 0.1$ cm^3 cm^{-1} d^{-1} and reasonable values for other terms, the root surface concentration would increase by about 0.026 M, or about 0.11 MPa, after 12 h. A steady state approximation for the problem was suggested by Gardner (1965; see Newman 1974) as

$$C_{1,a} = C_{1,b} \, (b/a)^{I_{\mathrm{w}}/2\pi D_{\mathrm{p}}} \tag{17}$$

but this assumes no root uptake, and takes no account of time changes, which may be important.

The alternative 'steady rate' assumption for water movement can easily be applied, and this yields

$$C_{1,a} = C_{1,b} \exp\left[\frac{I_{\mathrm{w}}}{2\pi D_{\mathrm{p}}(b^2-a^2)}\left\{b^2 \ln\frac{b}{a} - \tfrac{1}{2}(b^2-a^2)\right\}\right]. \tag{18}$$

Since D_{p} varies with θ, the true situation can be dealt with only by computer simulation methods, but the approximations should be adequate to indicate where the effect is of any magnitude.

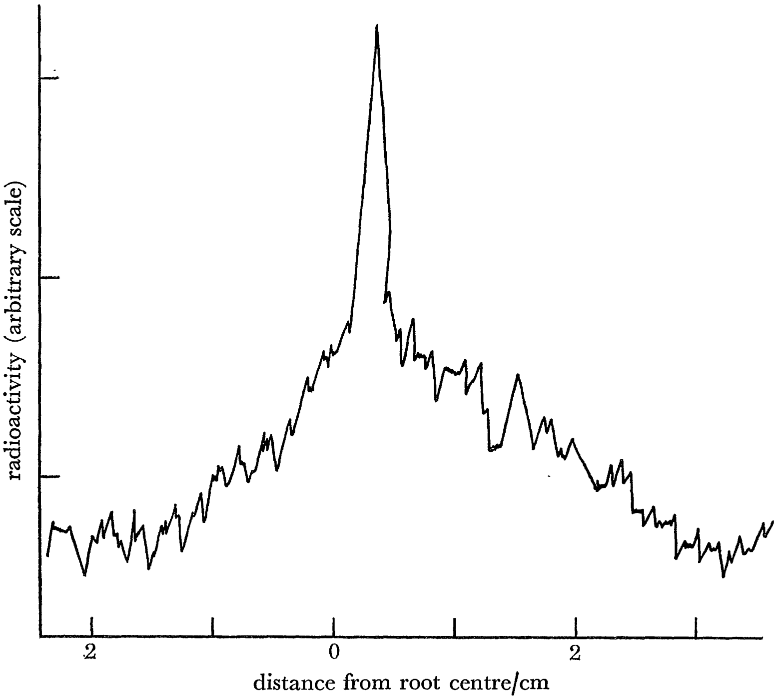

FIGURE 3. ^{35}S concentrations in soil near a root of a transpiring onion plant, obtained by β-ray scanner. Water entry velocity *ca.* 0.1 cm^3 cm^{-1} d^{-1}. Central spike probably indicates Ca_2SO_4 precipitation. (From Wrag 1970.)

Theoretical predictions of Nye (1966*a*) were tested by Wray (1970) and Wray & Tinker (1969, and unpublished) in a linear system, in which a single onion root was embedded in a thin layer of soil. Labelled sulphate solution was supplied to the soil, and the sulphate concentration in the soil determined by a β-ray scanner. Over fivefold accumulations were detected at the root surface (figure 3) and the sulphate distribution was found to fit the theory for such a system (figure 4), which predicts that the concentration at the root surface should rise with the dimensionless term v^2t/b^2D, where b is the soil buffer power. This emphasizes the importance of the flow speed of water, and the time effect on the accumulation. It therefore appears that theoretical predictions are reasonably reliable, but the effect is unlikely to be important in practice unless there are fairly large local rates of water uptake, and a concentrated soil solution, such as is found in arid-zone agriculture or in greenhouse culture.

(*b*) *Root–soil contact*

The assumption of a homogeneous soil which is continuous up to the root surface implies that the fraction of the root surface in contact with solid, water or air should be equal to the volume fraction of these components of the soil adjacent to the root. It is also implicitly assumed

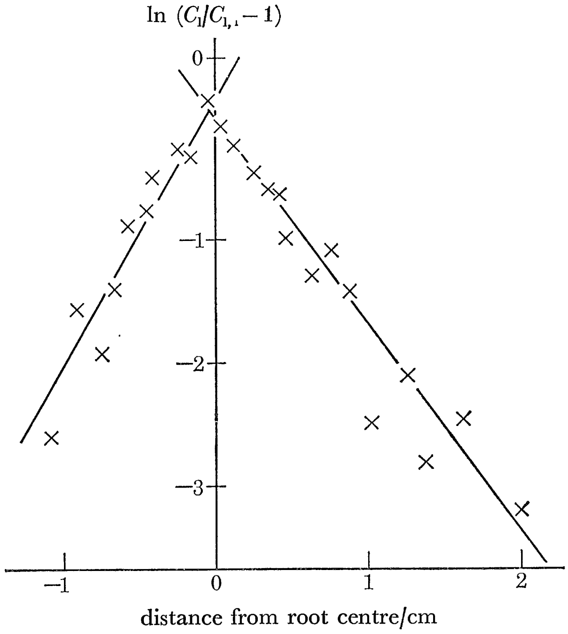

FIGURE 4. Distribution of sulphate concentration with distance from root. Theory indicates a straight line relation of x and ln $(C_l/C_{l,i}-1)$; points are experimental results. (From Wray 1970.)

that all air-filled space bordering on the root is composed of separate voids so small that water readily moves to all parts of the root surface in the water film on it. In practice, neither is true, and the simplest inspection of root chambers or peds dug out of the soil, shows that much of the root surface must be in contact with air, and that these parts of the root can be quite extensive. These gaps between root and soil can arise either because the root grows through a pre-existing void (caused by soil cracking, soil fauna or an earlier root), or because either or both the soil and the root shrink on drying. The shrinkage and cracking of a clay soil is obvious,

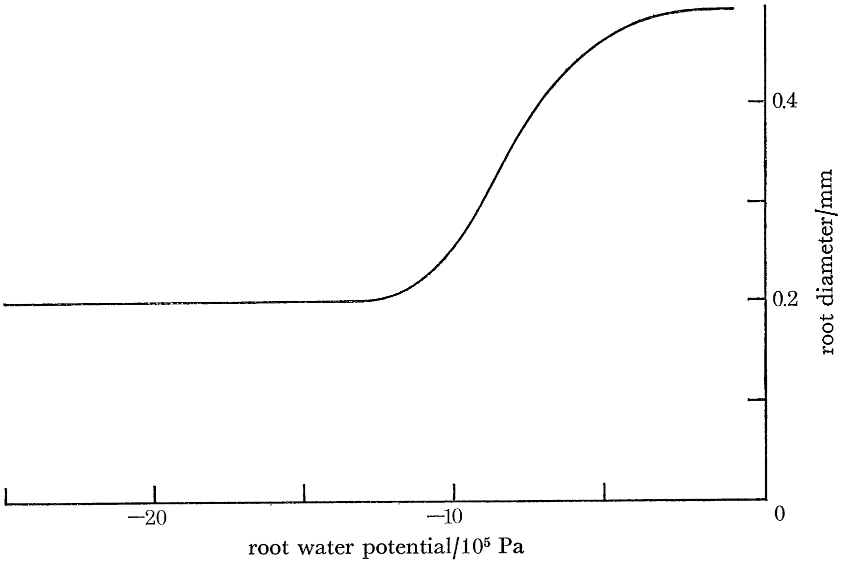

FIGURE 5. Shrinkage of excised maize roots on drying (from Cole & Alston 1974).

and may be up to 10^4 and 10^5 Pa. If cracking occurs, it will normally do so along pre-existing planes of weakness between soil structural units, and it is precisely here that roots are most likely to penetrate. Roots normally shrink when dried, and Cole & Alston (1974) found that this occurred mainly between 0.5 and 1 MPa (5 and 10 bar) suction in excised roots (figure 5). Huck *et al.* (1970) reported a shrinkage of 25% in diameter of a root in a soil void, while the rest of the soil volume was between 0.2 and 0.5 MPa (2 and 5 bar) suction. In this case there was no evidence whether roots actually in contact with soil shrank, and the pictures in this paper give the impression that the shrinkage may have been local. However, if shrinkage of either or both roots and soil occur, this implies that comparatively large gaps, of 10 μm or more, may open up around the root.

If so, several points require comment, since this could be an important effect, and Weatherley (1974) has suggested that the root–soil interface resistance could account for the observed changes in leaf water potential in his experiments.

(i) 'Mucigel' is the name applied to the rather ill-defined organic gel found around the root. It is often assumed that this material, apart from lubricating the root tip in its progress through the soil, also helps to maintain contact between the root surface and the water in soil pores. I am not aware of any but the most qualitative studies on this material. It is not clear whether it is elastic and how much it shrinks when a water stress is applied, or whether it has a large resistance to water transfer. Such information is clearly needed.

(ii) Root hairs will certainly bridge any gap that is formed. The most usual – in fact the only practicable – theoretical method of dealing with ion or water uptake by roots with root hairs is to regard it as a much thicker root, whose epidermis lies at the extremities of the root hairs, and to add a correction for any uptake from soil between the true root surface and this hypothetical surface (Nye 1966*b*). This correction is unlikely to be large for water unless the root hairs are appreciably longer than 1 mm, and the effect of a change in root radius on the water potential at the root surface, for constant I_{w}, is not very great, according to equation (14). It has been shown by direct potometry that root hairs absorb water at quite high rates (Rosene 1943). It appears from this argument that they may not be of much value for water uptake by a root in complete contact with the soil, but they could be exceedingly useful to a root which otherwise would have little or no contact with the soil, since the hypothetical 'root surface' at the root hair tips would be almost unchanged. Any consideration of the possibility of poor root contact in any particular plant and situation will thus require a study of the fraction of the root bearing root hairs. Newman (1974) has calculated a rather low conductivity for root hair transport of water, in comparison with that of soil around the root, but his estimate implies an I_{w} of 0.07 $\mathrm{cm^3\,cm^{-1}\,d^{-1}}$ for a potential difference along the length of the hairs of 0.1 MPa, which is quite sufficient for most situations. The root hairs would therefore appear to be a perfectly adequate uptake mechanism if the root cylinder itself is not in contact with soil.

(iii) Cowan & Milthorpe (1968) have made the very interesting suggestion that gaps between root and soil are of small importance, since vapour phase transport can carry a sufficient flux density of water. It is normal to assume (Rose 1963; Philip & de Vries 1957) that vapour phase transport is of negligible importance until soils become very dry – certainly too dry to support reasonable plant growth. Cowan & Milthorpe's conclusion rests on assuming a fairly small I_{w} (0.007 $\mathrm{cm^3\,cm^{-1}\,d^{-1}}$) and a moderate gap of 40 μm. The potential difference required across the air gap is 0.5 MPa (5 bar). The important point seems to be, not so much whether the gap is an absolute barrier to water transfer or not, but whether the gradient across the gap is much greater than would otherwise be found in a similar thickness of soil in normal contact with the root. Since it seems that the gradient will usually be much greater with the air gaps, water transport must be more or less hindered by this increased impedance.

(iv) The idea that shrunken roots remain suspended in the geometrical centre of the root channels formed by them in the soil seems unlikely. In practice, it seems probable that such roots will remain in contact with soil over a limited part of their periphery, i.e. they will touch one side of the root channel only (figure 6). The problem, then, is only partly to decide how I_w is increased in those parts of the root system maintaining a normal degree of contact. In addition, the effect of partial contact must also be considered. If this occurs, and I_w is to be maintained, the flux density of water in the small part of the soil which remains in contact with the root will be increased, and the water potential and water content gradients must become greater. The simple theory given above will then not apply.

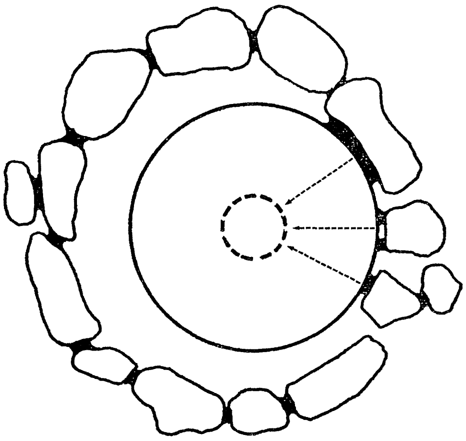

FIGURE 6. Partial contact between root and soil.

An analogous problem has been briefly investigated by Sanders (1971), who studied the effect of partial contact of roots on uptake of nutrients using an electrical analogue (Sanders, Tinker & Nye 1971; Baldwin, Tinker & Nye 1972). This analogue is simply a large resistance-capacity two dimensional network, representing a slice of soil. The effect of inserting 'roots' – represented by resistors connected to earth – in different positions and with different uptake properties can then be tested. The contact problem was investigated by cutting out a circular section of the network, to represent the position of a root in cross-section. The earthed resistors could then be connected to varying fractions of the periphery of this hole, representing varying contact of the soil with the root. This of course represents a limited system, and the analogue can be regarded as a cross section of an 'equivalent cylinder'. The major drawback of this method lies in the need to assume a constant diffusion coefficient. In the nutrient study, a first-order boundary condition for the root's uptake was assumed, but in water uptake it is more realistic to assume a constant flow of water to the root, with varying degrees of contact, and to investigate how this determines the water potential and water content of the soil at the root surface.

The operation of this analogue raises the question of whether partial external contact alters the root resistance to uptake of water (for the equivalent discussion for nutrient uptake, see Sanders 1971). If the root epidermis and cortex can be regarded as a low-impedance pathway of movement for water, and most of the resistance is considered to reside in the endodermis, then poor contact would not be expected to alter the root impedance to uptake. If a substantial part of the resistance does reside in the cortex than a correction should be made (Newman 1974).

Results were obtained with the analogue by using a variable resistance as the 'root'. The current was monitored, and the resistance varied to keep the current constant. The results of several runs are in figure 7. The time scale is given as the dimensionless term $4D_{\mathrm{w}}t/\pi a^2$; the value of θ is relative to the initial value. The relation between current i and I_{w} is given by $i = EI_{\mathrm{w}}/D_{\mathrm{w}}\,\theta_{\mathrm{i}}$ where E is the electrical potential at the start of a run. Hence

$$E/i = R_{\mathrm{s}} = D_{\mathrm{w}}\,\theta_{\mathrm{i}}/I_{\mathrm{w}},$$

with R_{s} the value of the sink resistor at the start of the run. R_{s} values of 1 MΩ and 20 MΩ were used in these runs; for $\theta_{\mathrm{i}} = 0.15$, and $D_{\mathrm{w}} = 2\ \mathrm{cm^2\,d^{-1}}$, this would give I_{w} values of 0.3 and 0.015 $\mathrm{cm^3\,cm^{-1}\,d^{-1}}$. As before, the size of I_{w} is crucial: with a small value the degree of contact is of little importance, but if I_{w} is large, then the potential at the surface is critically dependent upon contact. These results understate the true effect, in that D_{w} would of course decrease with reduction in θ_a caused by poor contact, but as earlier, they are probably reliable where they indicate only small effects.

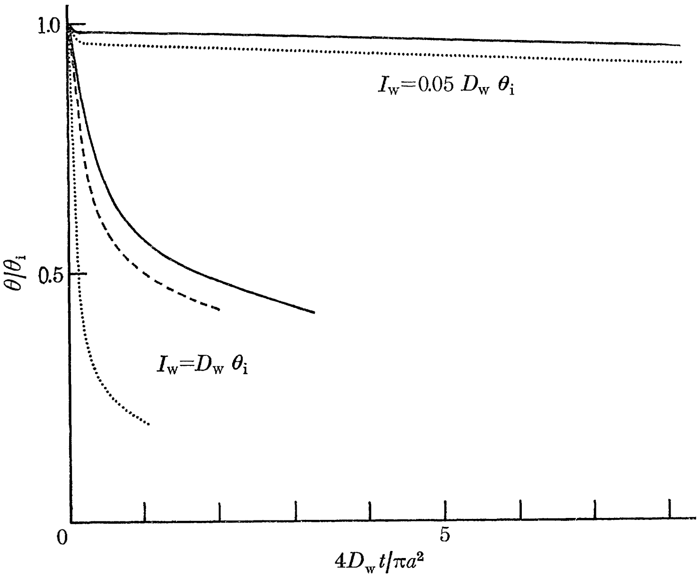

FIGURE 7. Effect of partial contact of root and soil on the water content at the root surface with constant I_{w} and D_{w}. Time given as $4D_{\mathrm{w}}t/\pi a^2$. Full lines, 100 % contact; dashed line 50 %; dotted lines 12.5 %.

$$I_{\mathrm{w}} = (R/R_{\mathrm{s}})\,D_{\mathrm{w}}\,\theta_{\mathrm{i}},$$

where R is the analogue resistance parameter, R_{s} the initial value of the sink resistor, and θ_{i} the simulated initial water content.

Sanders (1971) made visual observations on apple roots in the root laboratory at East Malling Research Station, and concluded that 40 % of the root was not in contact with the soil at all, and a further large percentage in only incomplete contact. The situation at the surface of a root chamber is not representative of the bulk soil, but such observations suggest that no or incomplete contact may be frequent.

5. Complete root systems

The earlier parts of this paper have discussed the various uncertainties surrounding our understanding of water uptake by single roots. It is hardly surprising that it is not possible to present any very exact model of water uptake by a complete root system, but some published methods, and unsolved problems, are indicated here.

The variation in root resistance with position on the root has been commented upon above, and has been dealt with by other papers in this meeting, as has the uncertainty concerning the potential existing in the root xylem. It would be extremely convenient if the xylem potential could be assumed to be constant throughout the root system, but this appears unlikely. Apart from the varying composition of xylem sap, it is probable that potential gradients exist along roots, which drive the flow in the xylem vessels (see Cowan & Milthorpe 1968).

(*a*) *Root pattern and distribution*

The simplest possible situation is for a set of uniform roots to be placed in a uniform soil at regular intervals, so that all equivalent cylinders are equal. This is most easily visualized as a parallel array of roots, whose intercepts on a plane at right angles form a regular square or triangular pattern. In such a system depletion proceeds uniformly. With this approach, which is essentially that of Cowan (1965), it is possible to determine the degree to which all water in the soil is available to the plant, i.e. if the stomata close at some specified value of Ψ_a, the water remaining in the soil which could have been extracted if the potential of the entire soil mass had been reduced to this value is obtained simply from equation (14). The result is similar in general pattern to the field work data, such as that of Denmead & Shaw (1968). However, in practice, no real root system approaches such a state, for a variety of reasons.

If the soil and roots are uniform, but the root density varies from place to place, local depletion rates vary and potential gradients will be established over distances which are large compared with the inter-root distance. Newman (1969) has discussed this in relation to 'pararhizal' transport of water. This may be approached in two ways:

(i) The soil volume may be subdivided into compartments containing approximately uniform root densities. Each is considered homogeneous, and the rate of water depletion in each is considered separately. The 'pararhizal' transport may be calculated from the water potential difference which appears, and the distance, between compartment centres. This approach lends itself well to simulation techniques. De Wit & van Keulen (1972) have used this type of method to predict salt and water movement in soils. However, the variation in root density may be on a small scale, so that the number of compartments required is quite unacceptable. The inter-compartmental transfer is also somewhat inelegant.

(ii) The alternative approach is to consider root distribution, as a parameter of the system which can be described from the distribution of intercepts on the intercepting plane. This may be described by the normal techniques used in ecology, as nearest neighbour distance or variance/mean ratio (Greig-Smith 1964; Baldwin, Tinker & Nye 1972). A variance/mean ratio of 0 implies regularity (at the specified distance scale), 1 random, and values above 1 increasing degrees of clumping. This approach is useful if the effect of different degrees of regularity and clumping can be established. This was done for nutrient uptake with an electrical analogue by Baldwin *et al.* (1972) who showed that the difference would be relatively small between regular and random arrangements, but that uptake rates were greatly reduced when roots were severely clumped (figure 8). Their results are not directly applicable to water uptake, since a first-order boundary condition was used, but give some indication of what could be expected in a dry soil if soil impedance controlled uptake rate. The establishment of boundary conditions appropriate for water uptake is not easy, especially since the distribution of root water potential within a single root system in soil volumes with different water potentials is by no means clear (see Newman 1974).

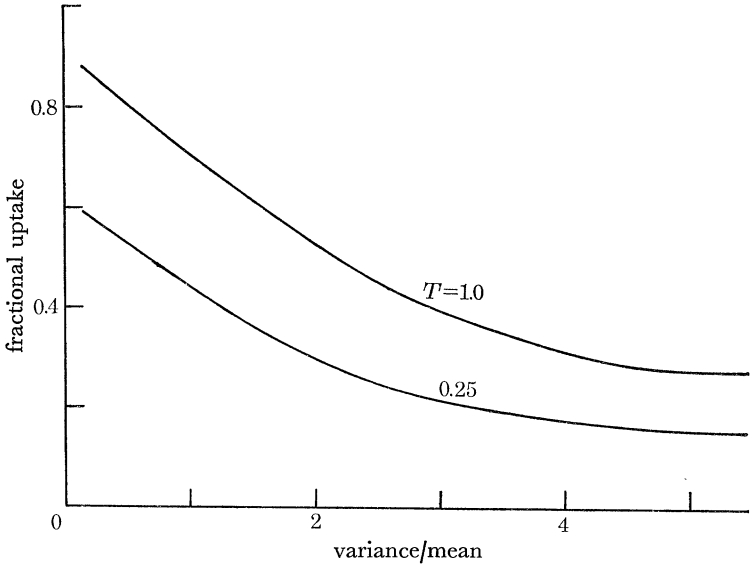

FIGURE 8. Effect of clumping of roots upon the relative speed of uptake for conditions close to 'zero sink' at the root surface. Variance/mean measures clumping in pattern; dimensionless time T given as $D_w t/\pi a^2$. (From Baldwin, Tinker & Nye 1972.)

This latter method is not suitable for situations where the soil properties change appreciably from place to place, as in the different horizons of a profile. It is most appropriate for correcting for small-scale pattern, and may well be combined with the compartmentation method to give a general method of treatment.

(*b*) *Whole profile methods*

A much simpler method was developed by Gardner (1964), who proposed that the 'resistance' to water uptake in the soil could be expressed by $1/BKL$, where B was a constant, and L the length of root per unit volume. Comparison with the equation (14) above shows that this is qualitatively correct. The uptake in unit volume is $I_w L$, and the 'resistance' per unit volume is thus

$$\frac{\Psi_b - \Psi_a}{I_w L} = \frac{\ln(b/1.65a)}{2\pi K L}. \tag{19}$$

The further elaboration to account for uptake throughout a whole soil profile by a crop root system was empirical. Gardner suggested that a total uptake for the whole profile could be obtained by computing the expression $1/BKL$ for each layer, and calculating a weighted average for the total potential. The method has been applied more recently by Lawlor (1972), but it is not clear whether it or later treatments, have predictive value.

6. CONCLUSION

The question was posed at the beginning of this paper whether water potential gradients of any magnitude do develop around roots in soil. No final answer can be given to this until the real local values of I_w are known, but the number of possible mechanisms tending to cause unequal distribution of water uptake rate over a root system indicate that the mean value of I_w is not a real guide to the local situation. There may well be situations where soil resistance is significant, though these are possibly rather unusual. Further research with sparsely rooted crops, with plants at maturity, and with plants growing in soil containing large moisture gradients seems desirable.

It appears to the author that the tools for dealing with the soil aspects of water uptake by crops are available now – the urgent need is for a more exact statement of root system properties, and the solution of some of the root–soil interface problems dealt with here.

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