

A THEORETICAL STUDY OF THE DISTRIBUTION
OF SUBSTANCES AROUND ROOTS RESULTING
FROM SIMULTANEOUS DIFFUSION AND
MASS FLOW

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Nutrients and other soluble substances move to roots by diffusion and by mass flow induced by the transpiration stream. Our aim is to relate the concentration of solute to its distance from the root surface and the absorption time, in terms of the diffusion characteristics of the solute in the soil, the movement of the solvent, and the absorbing power of the root.

Roots move through the soil at rates of the order of 1 cm per day; and an element of root absorbs for many days after it is produced. Diffusion through the soil occurs over distances of a few mm per day at most, and high transpiration rates may induce water to move around 1 mm per day near the root surface. Hence we shall regard the direction of movement as normal to the root surface.

Nye and Spiers⁹ expressed the variation of concentration around unit length of root with time and radial distance in terms of a second order partial differential equation, which they did not solve; though they did discuss the variation of concentration with radial distance in the special case when a steady state was attained after long times. Nye⁷ has also given an analytical solution for the corresponding problem of absorption at a planar surface, which gives an insight into the complexities of the cylindrical case. We give here computer solutions of the Nye and Spiers equation, and include a more comprehensive boundary condition.

THEORETICAL CONSIDERATIONS

Mathematical formulation

Consider 1 cm of root cylinder in soil.

- Let C = total conc. of diffusible solute (g.cm^{-3} of soil)
 C_1 = conc. in soil soln. (g.cm^{-3} of soln.)
 C_{11} = initial uniform conc. in soil soln. (g.cm^{-3} of soln.)
 C_{1_0} = conc. in soil soln. at r_0 (g cm^{-3} soln.)
 v, v_0 = inward flux of water at radius r, r_0 ($\text{cc/cm}^2/\text{sec}$)
 D = differential diffusion coefficient of solute in soil ($\text{cm}^2 \text{sec}^{-1}$)
 b = differential buffer power (defined as dC/dC_1)
 F = inward radial flux of diffusible solute ($\text{g sec}^{-1} \text{cm}^{-2}$)
 r = radial distance from the root axis (cm)
 r_0 = radius of the root (cm)
 k = root absorbing power at low C_1 (cm sec^{-1}) (defined by $F = kC_{1_0}$)

Consider the balance of solute in a small annular element, thickness δr , over time, δt . For conservation of solute we have

$$\frac{\delta 2\pi r F}{\delta r} = 2\pi r \frac{\delta C}{\delta t} \quad (1)$$

also

$$F = D \frac{\delta C}{\delta r} + v C_1 \quad (2)$$

also, for conservation of water,

$$2\pi r v = 2\pi r_0 v_0 \quad (3)$$

Hence from (1), (2) and (3) and $b = dC/dC_1$ we obtain

$$\frac{1}{r} \frac{\partial}{\partial r} \left(r D \frac{\partial C_1}{\partial r} + \frac{v_0 r_0 C_1}{b} \right) = \frac{\partial C_1}{\partial t} \quad (4)$$

Choice of boundary conditions

For the solution of Equation (4) two boundary conditions are required. The first is:

$$t = 0 \quad r > r_0 \quad C_1 = C_{11}$$

The second relates the flux to the concentration at the root surface. Many uptake studies in stirred nutrient culture show the flux across the surface follows the Michaelis type equation

$$F = \frac{kC_{1_0}}{1 + kC_{1_0}/F_{\max}} \quad (5)$$

At low values of C_{1_0} , $F = kC_{1_0}$.

At high values of C_{1_0} , $F = F_{\max}$, a constant.

Since we include solutions in which C_{1_0} rises to high values at the root surface, we have used Equation (5), and investigated the effects of both F_{\max} and k .

Accordingly, the second boundary condition is:

$$t > 0 \quad r = r_0 \quad Db \frac{\partial C_1}{\partial r} + v_0 C_{1_0} = \frac{kC_{1_0}}{1 + kC_{1_0}/F_{\max}} \quad (6)$$

Further assumptions

We have assumed that F_{\max} and k are independent of v_0 . It is generally found that at low concentrations of a nutrient culture solution, and with plants of low salt status, uptake of nutrients is little affected by the rate of transpiration. At high concentrations of the solution, the rate of uptake may be increased by increasing the rate of transpiration, though the effect depends greatly on the nature of the nutrient, the plant species, and the conditions of the experiment (see Russell and Barber ¹⁴, for a review). We do not pursue these possibilities in detail. However, should it seem desirable to test their effects further, only a trivial change in the computer programme is required to take account of the fact that k and F_{\max} are some known function of v_0 .

Equation (4) assumes that D is independent of v . It is known that on a microscale flow through porous materials is irregular, and tends to disperse solutes, so increasing the apparent value of D . Nielsen and Biggar ⁵ have found that in Aitken clay loam the apparent diffusion coefficient of Cl was $2.5 \times 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$ when v was $16 \times 10^{-6} \text{ cm sec}^{-1}$, and $9.4 \times 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$ when v was $950 \times 10^{-6} \text{ cm sec}^{-1}$. The true diffusion coefficient is $2.0 \times 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$. These velocities are very much higher than the maximum likely to be found near roots (v of the order $10^{-6} \text{ cm sec}^{-1}$), and there

is no data for lower velocities. Hence, on present evidence, it seems reasonable to assume that D will be unaffected over the range of v considered here.

The possible presence of root hairs is a complication. If they are closely spaced, it has been argued (Passioura,¹² Nye⁶) that the effective radius of the root is the radius of the cylinder joining their tips. The solute within this cylinder will certainly contribute to the plant's uptake, and it has been calculated (Nye⁶) that the relative contribution from this source will be large when the diffusion coefficient and absorption time are small. However, we are here concerned with the dependence of the concentration outside the cylinder, on radial distance and time. This should not be affected, provided it is understood that k , r_0 , F_{\max} , v_0 refer to the surface of the cylinder.

We take no account of a third 'root interception' process proposed by Oliver and Barber¹¹. The roots in passing through the soil push out of their way portions of the soil solid and liquid, but solutes in them still have to move to the root surface before they can be adsorbed. They are not engorged by the advancing roots, for it is most unlikely that the root cap is an efficient absorbing surface.

We have assumed that b and D are independent of concentration; which implies that there is a linear relation between C and C_1 over the range of interest. If this is not so, the values assigned to b and D in the examples given should be regarded as averages between the concentration limits calculated (Nye⁶).

We have assumed that the root radius is constant. Except for a very short length near the tip this is often true. In the examples given it will be shown that the relative concentration at the root surface C_{1_0}/C_H approaches v_0/k , so that the effect of any increase in the root radius may be judged from its likely effect on this ratio.

We have not allowed for a possible decline in k and v_0 with the age of the root element. In diffusion experiments with onion roots in soil Drew, Vaidyanathan and Nye (unpublished) found the absorbing power to be effectively constant for at least 16 days. When more experimental information about these parameters is available, their effects on the relative concentration in the root zone could be roughly assessed by inspection from Figs. 1 and 2 in this paper.

COMPUTATION OF THE RESULTS

The numerical solutions were calculated by the Crank-Nicolson method (Crank ², p. 189). In this technique, the first and second differentials at each point in time and space are replaced by first and second differences between the concentration values at points of a closely spaced lattice. The problem can then be reduced to that of solving a set of simultaneous equations.

Suppose for each time-step C_1 is estimated at $N + 1$ points at distances from the axis of the cylinder increasing by steps of h . The concentration C_1 ranges from a distant value C_{1_N} to the surface value C_{1_0} , and an additional value $C_{1_{-1}}$ included for computational purposes. The last point lies inside the cylindrical root; the computed value of $C_{1_{-1}}$ has no physical meaning, but is used in calculating the differences corresponding to $\frac{\delta C}{\delta r}$ and $\frac{\delta^2 C}{\delta r^2}$ at the surface. Now if the values of C_1 are known at time t , it is possible to set up simultaneous equations for the values C_1' at time $t + g$, where g is a small time-step. Each equation will involve three successive values of C_1 and the corresponding values of C_1' ; the first equation relates $C_{1_{-1}}'$, C_{1_0}' and C_{1_1}' to $C_{1_{-1}}$, C_{1_0} and C_{1_1} , and so on. There are thus $N - 1$ equations in the $N + 1$ unknowns. Two additional conditions are required; first, C_{1_N} , the concentration at the most remote point, is supposed to remain constant, and secondly the surface flux is governed by the equation

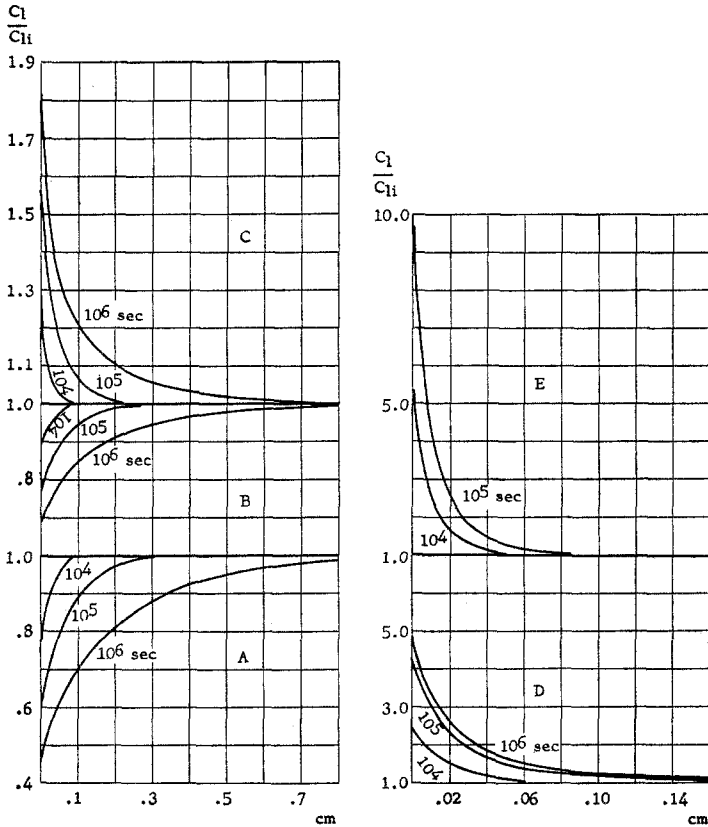
$$\left(\frac{\delta C_1}{\delta r}\right)_0 = \frac{C_{1_0}}{Db} \left(\frac{k}{1 + kC_{1_0}/F_{max}} - v_0\right) \text{ (see Eqn. (6)),}$$

which is replaced by the corresponding difference equation. The equations are now easily solved by a condensation procedure.

If an initial constant value of C_1 is assumed at every point at $t = 0$, it is thus possible to build up the values of C_1 at any subsequent time by proceeding in small time-steps and solving a set of simultaneous equations at each step. The computations were carried out on an Elliott 803 computer, and the programme, in Elliott ALGOL, is available in the library of the Department of Agriculture, Oxford.

The only difficulties in the computation arise in choosing the size and number of the time and space steps. If the differences are to approximate well to the corresponding differentials, g and h must be fairly small, especially where the curves are steep. On the other hand, unnecessarily small steps can greatly increase the amount of calculation, and this is particularly important on a relatively slow computer.

The initial rate of change of C_1 at the surface is very rapid in many cases, and a very short time-step is needed. There is, in fact, a discontinuity in $\delta C_1/\delta t$ at $t = 0$, and this introduces some distortion into the finite-difference approximation. Fortunately, this presents no great problem: since only the first differential is involved, the time-step can be varied without difficulty. In practice, the equations were calculated at steps of g up to $10g$, then by steps of $10g$ up to $100g$, and so on. The first one or two sets of values may be



inaccurate, but the irregularities soon even out, and any inaccuracy carried forward appears only as a small error on the time scale.

The space step is more difficult to deal with, because it is harder to change the step when second differentials are involved. The condition that C_{1N} is constant replaces the theoretical condition that C_1 is constant at infinity. This change affects the solution at infinite time; in particular, the computation always reaches limiting values, even when the theoretical solution diverges. It is thus important to take C_{1N} at a point remote enough to ensure that the wave of disturbance does not reach it within the period for which the computation is required – otherwise, the solution will be distorted.

On the other hand, the concentration gradient near the surface in the steady state may be very steep. It involves a term in $r^{-\nu\sigma r_0/Db}$, and the exponent may be as large as 50. In this case, a very small value of h is needed to get a satisfactory approximation to the limiting form.

Fig. 1. The effect of the rate of soil solution flow on the relative concentration near a root surface. ($k = 2 \times 10^{-7}$ cm sec $^{-1}$; $D = 10^{-7}$ cm 2 sec $^{-1}$; $b = 0.2$; F_{\max} high; $r_0 = .05$ cm).

- 1A $v_0 = 0$ cm sec $^{-1}$, *i.e.* diffusion alone. C_i/C_{II} continues to drop at the root surface and the zone of depletion to spread outwards at 10^6 secs.
- 1B $v_0 = 10^{-7}$ cm sec $^{-1}$. C_{I_0}/C_{II} has not reached the limiting value $v_0/k = 0.5$ after 10^6 secs.
- 1C $v_0 = 4 \times 10^{-7}$ cm sec $^{-1}$. C_{I_0}/C_{II} has nearly reached the limiting value $v_0/k = 2$ after 10^6 secs, but the zone of accumulation continues to spread outwards since $\frac{r_0 v_0}{Db} = 1$

For a steady state $\frac{r_0 v_0}{Db}$ must exceed 2.

- 1D $v_0 = 10^{-6}$ cm sec $^{-1}$. $\frac{r_0 v_0}{Db} = 2.5$. After 10^6 secs C_{I_0}/C_{II} has almost reached the steady state value $v_0/k = 5$, and the zone of accumulation has ceased to spread outwards.
- 1E $v_0 = 2 \times 10^{-6}$ cm sec $^{-1}$. $\frac{r_0 v_0}{Db} = 5$. Both C_{I_0}/C_{II} and the zone of accumulation have nearly attained the steady state after only 10^5 secs. C_{I_0}/C_{II} is increased to $v_0/k = 10$ but the zone of accumulation is compressed.

Fortunately, these difficulties do not arise together. If the concentration gradient is very steep in the steady state, the spread of the wave of disturbance is correspondingly small. It is usually possible to get a satisfactory approximation with a reasonable number of steps, but the value of h must be chosen rather carefully. In this study, values of N ranged up to 200. The complete programme, involving about 40 values of t , then ran for about $1\frac{1}{2}$ hours on the Elliott 803.

An alternative approach to the computation problem would be to replace r by $z = \log_e r$, and solve the differential equation

$$e^{-2z} \frac{\delta}{\delta z} \left(D \frac{\delta C}{\delta z} + \frac{v_0 r_0}{b} C \right) = \frac{\delta C}{\delta t} \quad (\text{Eyres } et al.^3) \quad (7)$$

in which D depends on z . This method was not used in the present study.

Values for the concentration at the root surface when $v = 0$, obtained by the numerical solutions, agree well with those calculated from the analytical solution of this particular case by Carslaw and Jaeger¹ (p. 336).

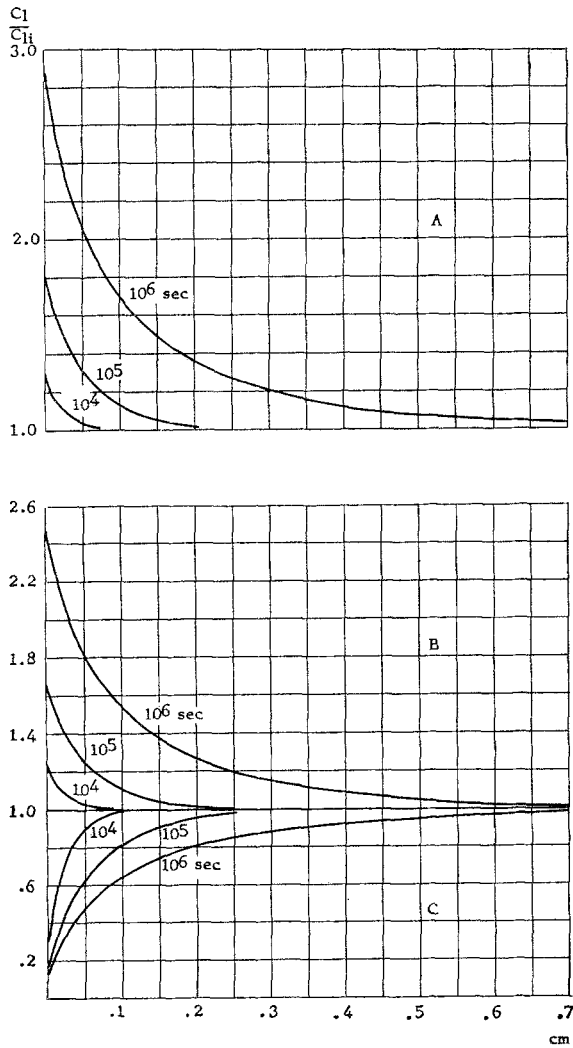


Fig. 2. The effect of the root absorbing power on the relative concentration near the root surface. ($v_0 = 2 \times 10^{-6}$ cm sec $^{-1}$; $D = 10^{-7}$ cm 2 sec $^{-1}$; $b = 2$; F_{\max} high; $r_0 = .05$ cm).

- 2A $k = 0$, *i.e.* no absorption by the root. C_{10}/C_{1i} continues to increase and the zone of accumulation to spread outwards.
- 2B $k = 2 \times 10^{-7}$. The limiting value of $C_{10}/C_{1i} = 10$ is approached very slowly.
- 2C $k = 2 \times 10^{-8}$ cm sec $^{-1}$. The limiting value of C_{10}/C_{1i} ($v_0/k = 0.1$) is rapidly approached at this high value of k , but the rate at which the zone of disturbance spreads outwards is little affected.

RESULTS

The effects of variation in turn of v , k , D and b when F_{\max} is high are shown first. The effect of variable F_{\max} is then discussed. v and k are controlled by the plant, unless soil moisture limits v , while D and b are controlled by the soil. r_0 is given the value 0.05 cm throughout.

Variable v

In Fig. 1 the effects of a change in v_0 from 0 to 2×10^{-6} are shown. $k = 2 \times 10^{-7}$, $D = 10^{-7}$, $b = 0.2$, F_{\max} is high. Values of the fixed parameters might be found for absorption of SO_4'' from a weakly anion adsorbing soil at a low moisture level. The maximum value of v_0 chosen is such that $r_0v_0 = 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$. The transpiration rate of lucerne measured by Ogata *et al.*¹⁰ yields a maximum value of $r_0v_0 = 3.7 \times 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$ when an evaporating pan was losing 1 cm per day.

It will be noted that:

1) C_I/C_{II} approaches the value v_0/k at the surface more rapidly, the greater is v_0 .

2) The zone of disturbance is closer to the surface, the greater is v_0 . If a steady state is reached Nye and Spiers⁹ showed, by solving

equation (4) with $\frac{\partial C}{\partial t} = 0$, that

$$\frac{C_I}{C_{II}} = 1 + \frac{v_0 - k}{k} \left(\frac{r}{r_0} \right)^{-r_0v_0/bD} \quad (8)$$

The steady state is only attained if $\frac{r_0v_0}{bD} > 2$. It will be seen that

curves for $v = 10^{-6}$, 2×10^{-6} $\left(\frac{r_0v_0}{bD} = 2.5, 5 \right)$ have nearly attained the theoretical steady state after 10^6 secs. When $v_0 = 0$, 10^{-7} , 4×10^{-7} $\left(\frac{r_0v_0}{bD} = 0, .25, 1 \right)$ no steady state is reached: the concentration at the root boundary still approaches v_0/k , but the zone of disturbance continues to spread outwards.

The effect of increase in v on the uptake of solutes has been further discussed by Passioura¹², and by Marriott and Nye⁴.

Variable k

Figure 2 shows the effect of an increase in root absorbing power when the transpiration rate is high. $v_0 = 2 \times 10^{-6}$, $D = 10^{-7}$, $b = 2$, F_{\max} is high. Since $\frac{rv}{Db} = 0.5$ in all cases no steady state is reached. The limiting value v_0/k is approached more rapidly as k is increased. However, the rate at which the zone of disturbance spreads outwards is little affected by k . The same conclusions were reached in the planar case.

Variable D and b (D × b constant)

It may be inferred from Equation (4) and the boundary conditions that if Db is kept constant, the effect of a change in D (or b) should appear only as a change on the time scale in figs. 1–3. Thus if D is reduced tenfold and b is increased tenfold, the times are increased tenfold.

Variable D × b

The product Db is related to the moisture level of the soil. If a solute is relatively immobile when adsorbed on the soil solid, which is true for important nutrient ions (Nye⁸),

$$D \simeq D_1 v_1 f_1 \frac{dC_1}{dC} \quad (9)$$

or

$$Db \simeq D_1 v_1 f_1 \quad (10)$$

where D_1 is the diffusion coefficient of the solute in water

v_1 is the volume fraction of solution in the soil

f_1 is an impedance factor.

$D_1 = 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$ within a factor of 2 for the simple inorganic nutrient ions. But since f_1 falls sharply as v_1 falls the product Db depends sensitively on the moisture content.

In a sandy loam soil, Rowell *et al.*¹³ found that $v_1 f_1$ changed from 0.2 at pF 2 to 7×10^{-4} at pF 4.2. The corresponding range for $D_1 v_1 f_1 = Db$ would be about 2×10^{-6} to 7×10^{-9} . Curves for $Db = 2 \times 10^{-9}$, 2×10^{-8} , 2×10^{-7} are shown in Fig. 3. $v_0 = 2 \times 10^{-6}$, $k = 2 \times 10^{-7}$, $b = 2$, F_{\max} is high. In moist soil, when $Db = 2 \times 10^{-7}$, giving $rv/Db = 0.5$, the approach to the

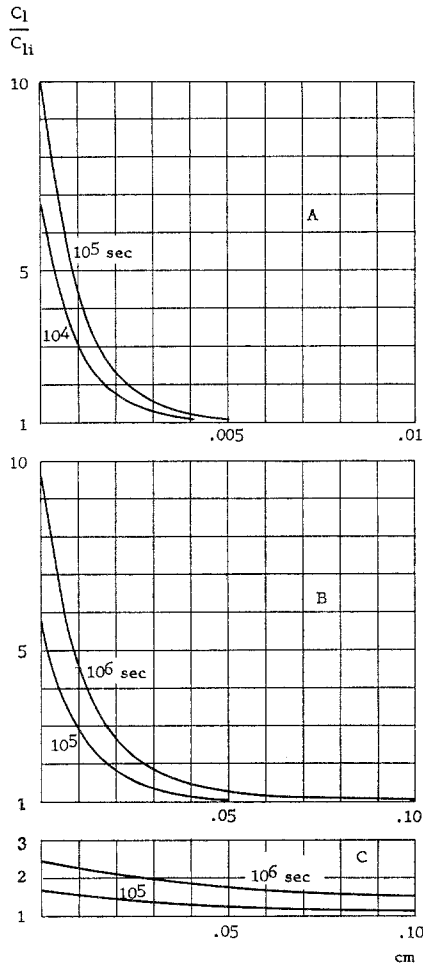


Fig. 3. The effect of Db on the relative concentration near the root surface. Db increases as the moisture level in the soil increases. ($v_0 = 2 \times 10^{-6}$ cm sec^{-1} ; $k = 2 \times 10^{-7}$ cm sec^{-1} ; $b = 2$; F_{max} high; $r_0 = .05$ cm).

- 3A $Db = 2 \times 10^{-9}$, corresponding to a very dry soil. C_{1_0}/C_{1i} at the root surface rapidly attains its limiting value, and the zone of disturbance is very compressed.
- 3B $Db = 2 \times 10^{-8}$ corresponding to a moderately dry soil. C_{1_0}/C_{1i} has attained its limiting value after 10^6 secs, and the zone of accumulation is less compressed.
- 3C $Db = 2 \times 10^{-7}$, corresponding to a moist soil. C_{1_0}/C_{1i} increases very slowly, and the zone of disturbance spreads outwards more rapidly than in 3B. No steady state will be reached because $\frac{r_0 v_0}{Db} = 0.5$.

limiting value of 10 at the root surface is very slow. As the soil is dried, the limiting value is attained more rapidly and the zone of disturbance is more compressed.

The effect of variable F_{max}

If conditions are such that the concentration at the root surface rises so that the flux approaches its maximum value, the root is no longer so efficient in absorbing the solute swept towards it, and the relative concentration at the root surface may rise considerably above v_0/k .

A limiting value of C_{10}/C_{11} at the surface will be attained if the

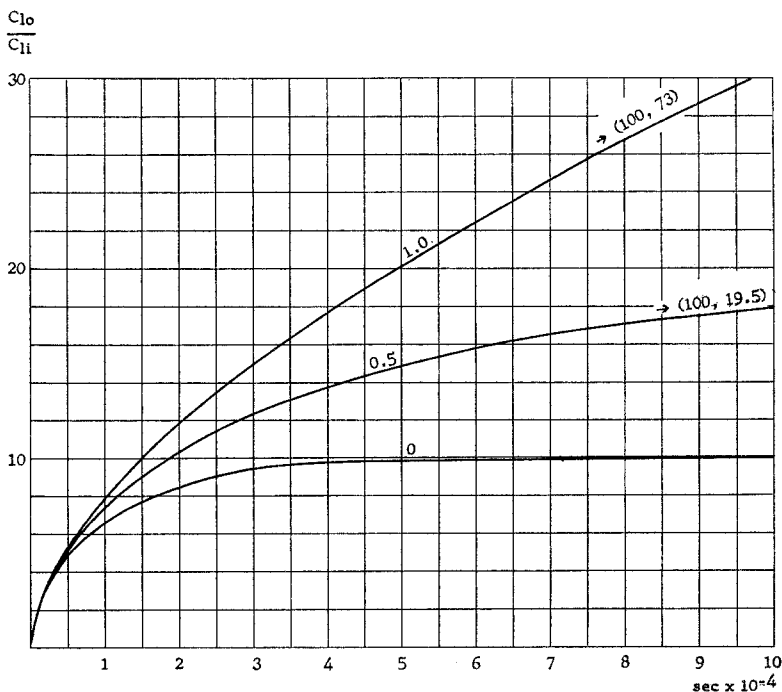


Fig. 4. The effect of F_{max} , the maximum flux at the root surface, on the change of relative concentration at the root surface with time. ($k = 2 \times 10^{-7}$ cm sec $^{-1}$; $v_0 = 2 \times 10^{-6}$ cm sec $^{-1}$; $D = 10^{-9}$ cm 2 sec $^{-1}$; $b = 2$; $C_{11} = .001$ g cm $^{-3}$). C_{10}/C_{11} at the root surface approaches a limiting value with time
 F_{max} is $> 2 \times 10^{-9}$ g sec $^{-1}$ cm $^{-2}$.

Figures on curves are values of $\frac{v_0 C_{11}}{F_{max}}$.

amount of solute being brought into the zone of disturbance in a given time equals the amount absorbed by the root, *i.e.*

$$2\pi vrC_{1i} = 2\pi r_0 \frac{kC_{1_0}}{1 + kC_{1_0}/F_{\max}} \tag{11}$$

which leads to

$$C_{1_0}/C_{1i} = \frac{v_0}{k} \left(\frac{1}{1 - v_0C_{1i}/F_{\max}} \right) \tag{12}$$

When $v_0C_{1i} \ll F_{\max}$, $C_{1_0}/C_{1i} = \frac{v_0}{k}$. However, when v_0C_{1i} approaches F_{\max} , C_{1_0}/C_{1i} may reach high limiting values; and when $v_0C_{1i} > F_{\max}$ no limiting value is attained. It will be seen intuitively that the condition $v_0C_{1i} > F_{\max}$ implies that solute is being swept towards the root faster than the maximum rate at which it can be absorbed.

Figure 4 shows the effect of F_{\max} on the increase in concentration at the root surface. Values of $\frac{v_0C_{1i}}{F_{\max}}$ are 0, 0.5 and 1; and $v_0/k = 10$. It will be seen that when $\frac{v_0C_{1_0}}{F_{\max}} = 0.5$, C_1/C_{1_0} approaches the limiting value of 20, but when $\frac{v_0C_{1_0}}{F_{\max}} = 1.0$, no limit is reached, while the assumptions of the model used hold good.

SUMMARY

The change in concentration of a solute in soil, moving near the surface of a root by both mass flow and diffusion, has been calculated by a numerical method with a computer. The effect of change in the plant controlled variables v_0 (the solvent flux at the root surface) and k (the root absorbing power), and the soil variables b (the buffer power) and D (the diffusion coefficient) are described in turn.

The concentration at the root surface, relative to the undisturbed soil solution, approaches a limiting value v_0/k . As v_0 is increased, the limiting value is approached more rapidly, and the zone of disturbance is more compressed. A steady state is reached if $r_0v_0/bD > 2$, but if $r_0v_0/bD < 2$ the disturbance continues to spread outwards even though the concentration at the root surface has nearly attained its limiting value.

As k is increased, other factors being constant, the limiting relative con-

centration at the root surface is approached more rapidly, but the spread of the disturbance away from the root is little affected.

As D_b is decreased, corresponding to a decrease in soil moisture, the concentration at the root surface reaches its limit more rapidly and the zone of disturbance is compressed.

If, because of increase in the concentration at the root surface, the efficiency of root absorption declines, the relative concentration will exceed v_0/k , and may reach no limit – at least until the assumptions of the model used break down.

Received December 19, 1967

REFERENCES

- 1 Carslaw, M. S. and Jaeger, J. C., *Conduction of Heat in Solids*. (2nd Edition) Oxford. (1959).
- 2 Crank, J., *The Mathematics of Diffusion*. Oxford (1956).
- 3 Eyres, N. R., Hartree, D. R., Ingham, J., Jackson, R., Sarjant, R. J., and Wagstaff, J. B., The calculation of variable heat flow in solids. *Phil. Trans. Roy. Soc. A* **240**, 1–57 (1946).
- 4 Marriott, F. H. C. and Nye, P. H., The importance of mass flow in the uptake of ions by roots from soil. *Trans. 9th Intern. Congr. Soil Sci. (Adelaide)*. (*In press*) (1968).
- 5 Nielsen, D. R. and Biggar, J. W., Miscible displacement. III Theoretical considerations. *Soil Sci. Soc. Am. Proc.* **26**, 216–221 (1962).
- 6 Nye, P. H., The effect of the nutrient intensity and buffering power of a soil, and the absorbing power, size and root hairs of a root, on nutrient absorption by diffusion. *Plant and Soil* **25**, 81–105 (1966).
- 7 Nye, P. H., Changes in the concentration of nutrients in the soil near planar absorbing surfaces when simultaneous diffusion and mass flow occur. *Trans. Intern. Soc. Soil Sci. Comm. II and IV, Aberdeen*, 317–328. (1967).
- 8 Nye, P. H., The use of exchange isotherms to determine diffusion coefficients in soil. *Trans. 9th Intern. Congr. Soil Sci. (Adelaide)* (*In press*) (1968).
- 9 Nye, P. H. and Spiers, J. A., Simultaneous diffusion and mass flow to plant roots. *Trans. 8th Intern. Congr. Soil Sci. (Bucharest)* **3**, 535–544. (1964).
- 10 Ogata, G., Richards, L. A. and Gardner, W. R., Transpiration of alfalfa determined from soil water content changes. *Soil Sci.* **89**, 179–182. (1960).
- 11 Oliver, S. and Barber, S. A., An evaluation of the mechanisms governing the supply of Ca, Mg, K and Na to soybean roots (*Glycine max*). *Soil Sci. Soc. Am. Proc.* **30**, 82–86 (1966).
- 12 Passioura, J. B., A mathematical model for the uptake of ions from the soil solution. *Plant and Soil* **18**, 225–238. (1963).
- 13 Rowell, D. L., Martin, M. W. and Nye, P. H., The measurement and mechanism of ion diffusion in soils. III – The effect of moisture content and soil solution concentration on the self-diffusion of ions in soils. *J. Soil Sci.* **18**, 204–222 (1967).
- 14 Russell, R. S. and Barber, D. A., The relationship between salt uptake and the absorption of water by intact plants. *Ann. Rev. Plant Physiol.* **11**, 127–140 (1960).