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

by P. H. NYE

Soil Science Laboratory, Dept. of Agriculture, University of Oxford

Many have tried to relate the uptake of plant nutrients, especially phosphate and potassium, to their quantity or intensity values in the soil, or to some combination of both (see Williams [22] for a review). For example, Mattingly *et al.*[11] have found in pot experiments that uptake of phosphate by ryegrass in the early stages of growth is closely related to the calcium monophosphate potential, but in the later stages is much more closely related to the labile phosphate; Blanchet [3] found the index "rapidly exchangeable P × concentration of P in the soil solution" gave the best prediction of the yields of hay on a series of P-deficient soils; and Nye [13] has argued that one should measure an intensity value, which should be related to the immediate rate of uptake, and a buffering power value, which should reflect the soil's ability to maintain this intensity as the nutrient is depleted. Since it is now clear that diffusion is usually the dominant way by which phosphorus and potassium reach root surfaces (Barber *et al.*[1]), the relation between their uptake and their quantity and intensity values that is provided by a diffusion model seem worth exploring.

Since diffusion is initiated by depletion at the root surface, the influence of plant factors and their interaction with the soil factors must be considered. Of these, the inherent absorbing power of a root, and its geometry, including its root hairs, are clearly important, and their effects can be calculated theoretically. Possible rhizosphere effects such as production of CO_2 and chelates are not

List of symbols

C	total concentration of mobile ions (g.cm^{-3}).
C'	total concentration of mobile ions (origin transposed) (g.cm^{-3}).
C_l	concentration of nutrient in the soil solution (g.cm^{-3}).
C_{l_1}	initial concentration of nutrient in the soil solution (g.cm^{-3}).
$\Delta C/\Delta C_l$	buffering power of the soil.
M_t	amount of nutrient absorbed per unit area of root surface after time (t) since the surface was produced (g.cm^{-2}).
α	root absorbing power (cm.sec^{-1}).
$\dot{\alpha}$	$\alpha \Delta C_l / \Delta C$ (cm.sec^{-1}).
γ	radial distance from the centre of the root cylinder (cm).
a	radius of root (cm).
t	time (sec).
D	diffusion coefficient of mobile ions (cm^2.sec^{-1}).
v_l	fraction of total volume occupied by soil solution.
f_l	impedance factor.
D_l	diffusion coefficient of the nutrient in free soil solution (cm^2.sec^{-1}).
$\overline{C_l/C_{l_1}}$	average concentration ratio at the root surface.
l	average length of root hair (cm).
a_h	radius of root hair (cm).
n	no. of hairs per unit length of root (cm^{-1}).
a_r	radius of central root cylinder (cm).
a_e	radius of the equivalent root hair cylinder (cm).
$\overline{F}_h$	average flux to root hairs (g.cm^{-2}.sec^{-1}).
$\overline{F}_r$	average flux to root cylinder (g.cm^{-2}.sec^{-1}).
$\overline{F}_e$	average flux to the equivalent root hair cylinder (g.cm^{-2}.sec^{-1}).

$$G_h, G_r, G_e = \frac{a\overline{F}_h}{DC}, \quad \frac{a\overline{F}_r}{DC}, \quad \frac{a\overline{F}_e}{DC}.$$

included in this treatment though it should be possible to allow for them later when more experimental data is available. The treatment concentrates on a single root, the complications introduced by multiple rooting being postponed for a later paper. Experimental data on single roots in soil, obtained by M. C. Drew, will also be presented separately. The approach used here has been developed from Bouldin's [4] treatment of duffusion to a root. The work of Olsen et al.[16] on phosphate diffusion to plant roots has also been useful, particularly because of its recognition of the buffer power factor.

The conclusions reached here must be modified if mass flow contributes significantly in bringing ions to the root surface. The combined effects of diffusion and mass flow have been discussed by Passioura [17] and Nye and Spiers.[15] Fortunately, from a knowledge of the concentration of an ion in the soil solution, the amount of the ion taken up by a crop, and the water transpired, it is possible to calculate that mass flow will contribute only about one tenth of the potassium and one hundredth of the phosphorus taken up by a crop of maize under median conditions, as examined by Barber et al.[1]. For nitrogen, calcium, and magnesium mass flow usually makes a much more important contribution.

Let us consider a newly-formed portion of root that has just entered a uniform zone of soil. The portion will be treated as an absorbing cylindrical surface, and the complication caused by root hairs will be ignored for the present. The rate of absorption will be determined primarily by the absorbing power of the root and the nutrient concentration at its surface; and this concentration will depend on the rate of removal by the root on the one hand and the rate of supply by diffusion on the other. We have to find the relation between uptake and the characteristics of the soil and the root.

For an actively growing plant creating a continuing demand for a nutrient, it is reasonable to assume, for example, from the results of Russell et al.[19], that below a threshold the rate of uptake is directly proportional to the concentration of nutrient in the soil solution at the surface, i.e.

$$\frac{\mathrm{d}M_t}{\mathrm{d}t} = \alpha(C_l) \text{ surface} \qquad (1)$$

where

C_l = concentration of nutrient in the soil solution

M_t = amount of nutrient absorbed per unit area of root surface after time (t) since the surface was produced

α = root absorbing power – an inherent characteristic of the root under the prevailing conditions.

As Bouldin [4] has pointed out, even if Equation (1) is not strictly obeyed, for instance at high concentrations, the initial concentration at the root surface rapidly falls to a lower level from which it declines only slowly, so that there is small error in using a value of α appropriate to this lower concentration. The value of α is taken to

include effects on the root due to levels of other ions in the soil. It is also assumed to remain constant with time, so this treatment does not take account of ageing in the root. Experiments with onion roots – to be published – have in fact given little evidence of ageing over a 12-day period. The effect of a possible change in α with time can be shown qualitatively on graphs, as will discussed. The boundary condition chosen here, besides seeming the most likely, has the advantage that it enables the interplay of soil and plant factors to be examined in a unified manner. Other boundary conditions – flux to a constant concentration at the root surface, and constant flux at the root surface – have been used by Olsen et al.[16], and their limitations discussed.

Diffusion of a substance from an infinite uniform medium (the soil) to a cylindrical absorbing sink (the root) with the boundary condition given by Equation (1) has been treated by Crank[6] (Section 5.5, ii) following Carslaw and Jaeger[5] (p. 336). The diffusion equation to be solved is

$$\frac{\partial C}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left(rD \frac{\partial C}{\partial r} \right) \tag{2}$$
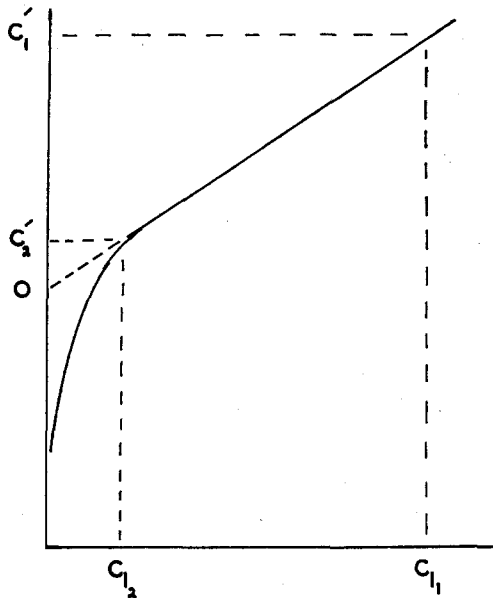

Fig. 1. Relation between total concentration of mobile nutrient and soil solution concentration [C_1].

where r is the radial distance from the centre of the root cylinder, t is time, D is the diffusion coefficient of the mobile ions and C is the concentration of mobile ions.

It will be noted that this equation is expressed in terms of the total concentration, in solution and on the solid, of the mobile ions $[C]$, while the boundary condition is in terms of their concentration in solution $[C_l]$. In soil the mobile ions are the exchangeable ions. For potassium and phosphorus particularly, it is rarely true that C is directly proportional to C_l: they are usually related by an iso-therm like the one shown in Fig. 1. However, if the initial concen-tration in solution is C_{l_1}, and we restrict our interest to a range of depletion between C_{l_1} and C_{l_2}, we can make progress by assuming that the isotherm is roughly linear over this range. As will be shown, the solution obtained is approximately true even with a curved isotherm. In fact many soils do have this linear portion till low concentration in solution, as shown by Beckett [2] for potassium on all of 14 soils tested, and stated by Olsen et al.[16] to be true for phosphate in calcareous soils they have tested.

If the total concentration lying above the point O in Fig. 1 is now called C', then

$$\frac{C'}{C_l} = \frac{C'_1 - C'_2}{C_{l_1} - C_{l_2}} = \frac{\Delta C}{\Delta C_l}$$

where $\Delta C/\Delta C_l$ is the buffering power of the soil over this range, and

$$\frac{\mathrm{d}M_t}{\mathrm{d}t} = \alpha \frac{\Delta C_l}{\Delta C} C' = \alpha' C' \tag{3}$$

where $\alpha' = \alpha (\Delta C_l/\Delta C)$

Equation (2) may now be solved to show how C_l at the root surface, where $r = a$, varies with C_{l_1}, D, t, a, α and $\Delta C/\Delta C_l$. Since the flux at the root surface varies as C_l, the total uptake to time t may be obtained by integration.

The procedure is as follows: Carslaw and Jaeger [5] (p. 338) give the solution to Equation (2), written with C' instead of C, with the boundary condition of Equation (3) in the form of a series of curves of $(C'/C_1)_{\text{surface}}$ plotted against Dt/a^2 for various values of $a\alpha'/D$. The terms have been transposed to conform with this paper. By

graphical integration a series of curves of

$$\int_0^{Dt/a^2} \left(\frac{C'}{C_1'}\right)_{\text{surface}} \mathrm{d}\left(\frac{Dt}{a^2}\right) \text{ are obtained.}$$

The product

$$\frac{1}{Dt/a^2} \int_0^{Dt/a^2} \left(\frac{C'}{C_{l_1}'}\right)_{\text{surface}} \mathrm{d}(Dt/a^2) = \frac{1}{t} \int_0^t \left(\frac{C'}{C_{l_1}'}\right)_{\text{surface}} \mathrm{d}t,$$

and is the average value of $C'/C_{1\text{surface}}'$ and hence $C_l C_{l_1\text{surface}}$ to time t. This concentration ratio will be represented by $\overline{C_l/C_{l_1}}$, and it is plotted against Dt/a^2 for various values of $a\alpha'/D$ in Fig. 2. The
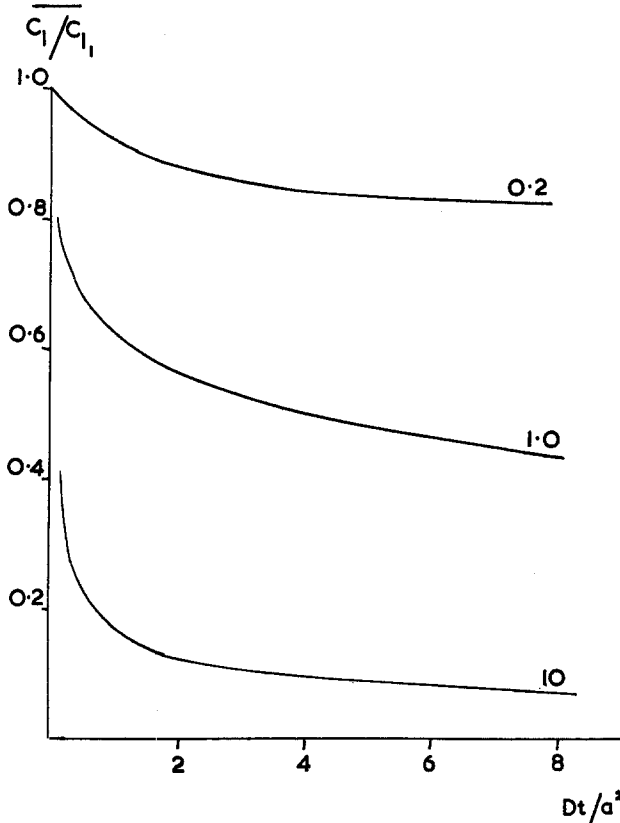

Fig. 2. Variation of the average concentration ratio at the root surface with Dt/a^2. Numbers on curves are values of $a\alpha'/D$.

treatment is no longer strictly valid if C_l falls below the linear part of the isotherm.

The uptake may be readily determined from this figure, since

$$M_t = \alpha t C_{l_1} \frac{\overline{C_l}}{C_{l_1}} \tag{4}$$

The form of the curve relating uptake per unit concentration with time for fixed values of other variables is shown in Fig. 3.

The parameter $a\alpha(\Delta C_l/\Delta C)/D$ assigned to each of the curves in Fig. 2 may often be simplified. There is now evidence that move-

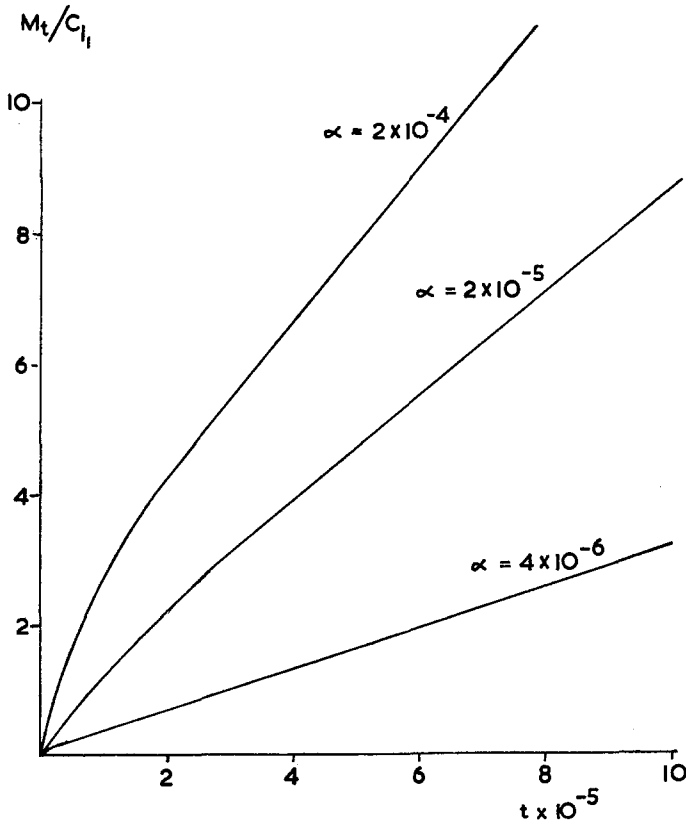Fig. 3. Variation of uptake per unit concentration in solution with time
$$a = .05 \text{ cm}$$
$$D = 2.5 \times 10^{-8} \text{ cm}^2 \text{ sec}^{-1}$$
$$\Delta C_l/\Delta C = 2.5 \times 10^{-2}$$

ment of potassium and phosphate ions through the solid part of the
soil contributes little to their diffusive flux compared with move-
ment through the liquid. (Vaidyanatham and Nye (unpublished);
Lewis and Quirk [10]. The diffusion coefficient in the range C_{l_1} to C_{l_2}
is then given by (Nye [14])

$$D = v_l f_l \frac{\Delta C_l}{\Delta C} D_l \tag{5}$$

where
D_l = diffusion coefficient of the nutrient in free soil solution
v_l = fraction of the total volume occupied by the soil solution
f_l = impedance factor
The parameter may therefore be written as $a\alpha/D_l v_l f_l$ and becomes
independent of the buffering power.

   The uptake derived from the curves in Fig. 2 will be approxi-
mately correct even if the isotherm is not linear over the range of
interest, as in Fig. 4. As may be seen from Fig. 2, the concentration
at the surface falls – rapidly at first, to C_l say, and thereafter only
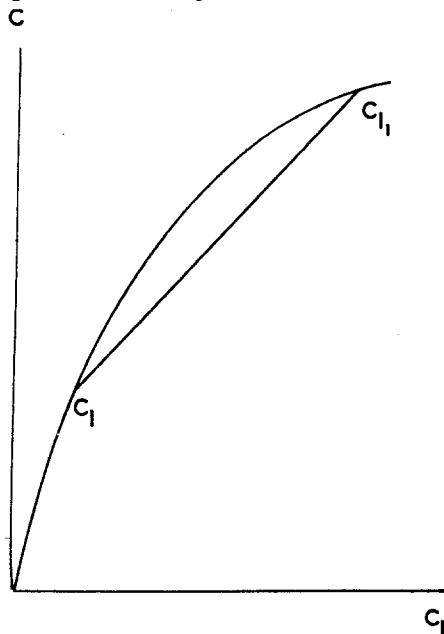slowly. The slope of the straight line drawn from C_{l_1} to the con-

Fig. 4. Relation between total concentration of mobile nutrient and soil
solution concentration – Non-linear approximation.

centration C_l on the isotherm (Fig. 4) gives the average buffering power $\Delta C/\Delta C_l$ over the range C_{l_1} to C_l. If uptake is now calculated from Equation (4), the assumption made is equivalent to supposing the course of depletion follows the straight line C_{l_1} to C_l instead of the curve C_{l_1} to C_l. This should usually make little difference to the conclusions of this paper. It will be noted that the substitution for D given in Equation (5) is still valid. D will now depend on concentration, and the integral diffusion coeffcient between C_{l_1} and C_l must be used. This is given by

$$\bar{D} = \frac{1}{\Delta C} \int_{C}^{C_1} D dC = \frac{1}{\Delta C} \int_{C_l}^{C_{l_1}} v_l f_l D_l dC_l = v_l f_l \frac{\Delta C_l}{\Delta C} D_l$$

which is the same expression as that given in Equation (5).

The effects of the individual variables

The value of $\overline{C_l/C_{l_1}}$ is basic to understanding the relation between soil supply and plant demand. A low value implies that diffusion is limiting the supply of nutrient to the surface. A high value, approaching unity, implies that the soil is able to meet the plant's demands so that uptake depends mainly on inherent plant factors.

Let us now fix the plant characteristics, α and a, and the time, t, and examine the influence of the soil characteristics on the uptake, M_t, in Equation (4). It may be helpful to recall that D_l for $K^+ \simeq 2.0 \times 10^{-5}$, and for $H_2PO_4' \simeq 0.9 \times 10^{-5}$; and that in many soils near field capacity the order of magnitude of D for $K^+ \simeq 10^{-7}$ and for $H_2PO_4' \simeq 10^{-9}$. C.g.s. units are used throughout this paper.

We note:

(a) *Soil solution concentration*

Uptake depends directly on the soil solution concentration C_{l_1}. The term $\overline{C_l/C_{l_1}}$ depends on the buffer power $\Delta C/\Delta C_l$ because D depends on this by Equation (5), but it does not depend on C_{l_1} itself.

(b) *Diffusion coefficient*

If the soil solution concentration is fixed, and the parameter, $a\alpha/D_l v_l f_l$, which designates each curve in Fig. 2, is also fixed for a given nutrient by considering a given moisture level and compaction, then the uptake declines as the diffusion coefficient for the soil, D, increases. This is shown by the fall in $\overline{C_l/C_{l_1}}$ on any of the curves in Fig. 2 as Dt/a^2 increases on the x-axis. This apparently curious

result is explained because D varies inversely as $\Delta C/\Delta C_l$, as shown by Equation (5); *i.e.* a high value of D (at constant moisture level and compaction) implies a low buffering power. Thus uptake decreases as buffering power decreases – the expected result. This effect may now be examined in greater detail.

(c) *Buffering power*

There is no simple relation between uptake and buffering power when C_l, D_l, v_l and f_l are fixed. In Fig. 5 curves derived from Fig. 2
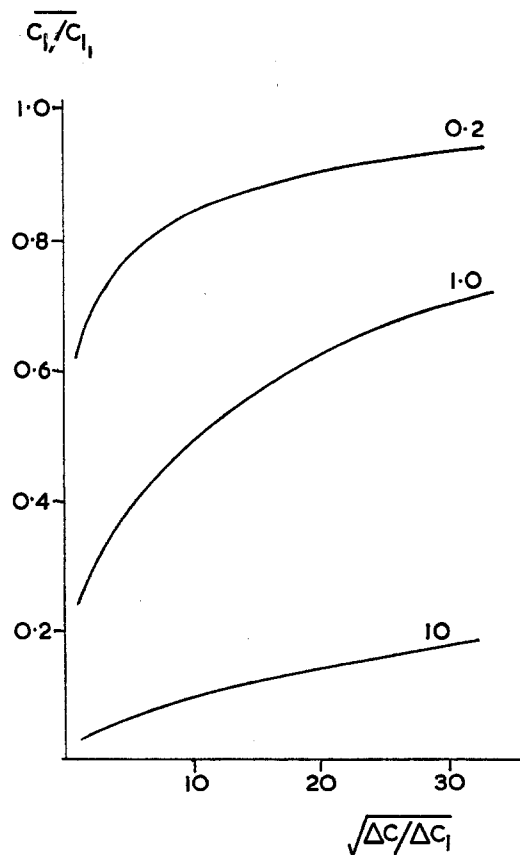

Fig. 5. Variation of average concentration ratio at the root surface with $\sqrt{\text{buffering power}}$

Numbers on curves are values of $a\alpha/D_1 v_1 f_1$

$a = 0.05 \text{ cm}$
$t = 10^6 \text{ sec}$
$v_1 f_1 = 0.1$
$D_1 = 10^{-5} \text{ cm}^2 \text{ sec}^{-1}$

are drawn to show the relation between $\overline{C_l/C_{l_1}}$ and the buffering power, plotted, for convenience of range and to make a theoretical point later, as the square root, when $a = 0.05$ cm, $t = 10^6$ sec (11.6 days), $D_l = 10^{-5}$ and $v_l/l = 0.1$. It will be seen that $\overline{C_l/C_{l_1}}$ increases only slowly with the buffering power. For phosphorus and potassium in most soils the value of $\Delta C/\Delta C_l$ lies between 1 and 1000, so for reasonable absorption times the uptake should be insensitive to changes in the buffering power. If t/a^2 is very small and the buffering power is very large $\overline{C_l/C_{l_1}}$ approaches 1, – the commonsense result, since the soil will then be able to maintain the initial concentration C_{l_1} at the absorbing surface.

The relatively small importance of the buffering power arises from the cylindrical geometry of the system. As uptake proceeds, each new radial cylindrical element $[dr]$ exploited provides an increasing amount of diffusing ion $[2\pi r C_1 dr]$, and this tends to reduce the importance of the buffering power term. The situation may be compared with uptake at an infinite plane sheet where no such effect occurs. Crank [6] (p. 36) gives a graph of $M_t \alpha'/DC'$ against α', the symbols being those in this paper. When $\alpha'\sqrt{t}/\sqrt{D}$ is large, a condition reached after the initial rapid drop in surface concentration, $M_t \propto C'_1 \sqrt{Dt}$

Thus, by substituting Equation (5) for D

$$M_t \propto C'_1 \sqrt{\frac{\Delta C_l}{\Delta C}} \propto C'_1 \frac{\Delta C_l}{\Delta C} \sqrt{\frac{\Delta C}{\Delta C_l}}$$

and since

$$\frac{\Delta C_l}{\Delta C} = \frac{C_{l_1}}{C'_1}$$

$$M_t \propto C_{l_1} \sqrt{\frac{\Delta C}{\Delta C_l}}$$

i.e. the uptake varies with the solution concentration and the square root of the buffering power.

The conclusion that uptake should depend mainly on C_l and only slightly on buffering power, when roots are not competing, agrees with the findings of Mattingly *et al.*[11] previously quoted. Of course, when roots do compete, the uptake may be expected to depend more on the buffering power.

(d) *Soil moisture*

In Equation (4), soil moisture may influence uptake through its effect on $v_l f_l$, C_l and $\Delta C/\Delta C_l$. As soil moisture decreases in a given soil, the diffusion coefficient decreases through the product of v_l and f_l both of which decrease (Porter *et al* [18]). Thus, in Fig. 2, the parameter Dt/a^2 on the x-axis is reduced; but the term $a\alpha/D_l v_l f_l$, identifying each curve, is raised and this proves to be the most important effect. Values of $\overline{C_l/C_{l_1}}$ are plotted against time for different values of $v_l f_l$ in Fig. 6. In order to isolate the effect of $v_l f_l$, fixed values have been assigned to a, D_l, α and $\Delta C_l/\Delta C$ as indicated in Fig. 6.
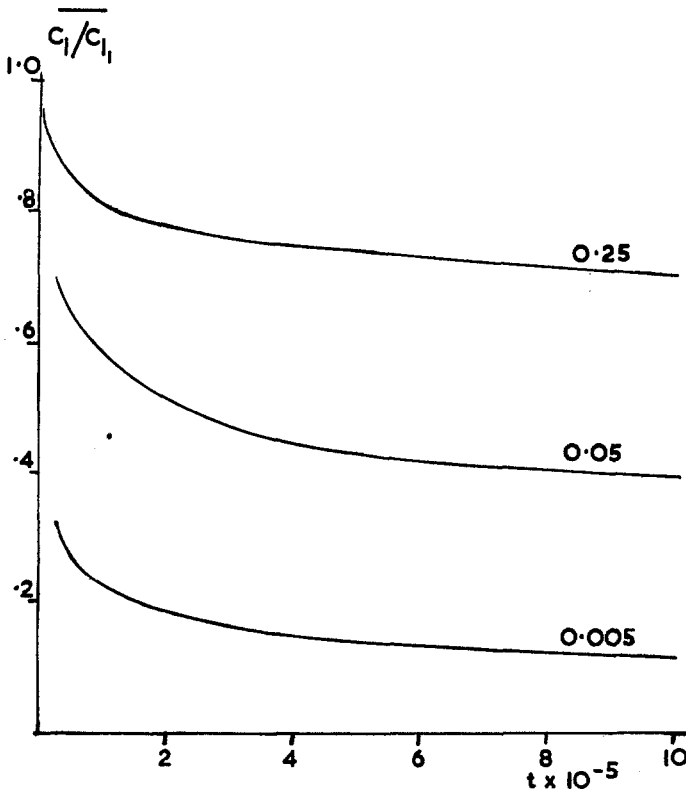

Fig. 6. Variation of the average concentration ratio at the root surface with
time for different soil moisture levels

$a = .05$ cm   Numbers on curves are values of $v_l f_l$
$D_l = 10^{-5}$ cm^2 sec^{-1}
$\alpha = 10^{-5}$ cm sec^{-1}
$\Delta C_l/\Delta C = 10^{-1}$

A decrease in moisture may also cause an increase in C_l and a decrease in $\Delta C / \Delta C_l$ for potassium, as shown by Fig. 7. Though these effects counteract one another, the effect of the increase of C_l will predominate. If the reduced activity ratio

$$\frac{a_K}{\sqrt{a_{Ca} + a_{Mg}}}$$

in solution remains constant over the field moisture range, and Moss [12] has verified this on three soils, the concentration of K should increase by about 40 per cent if the moisture content is halved.

In the present state of knowledge, it is unsafe to predict the effect of decreasing moisture on the concentration of phosphate in solution over the field moisture range.
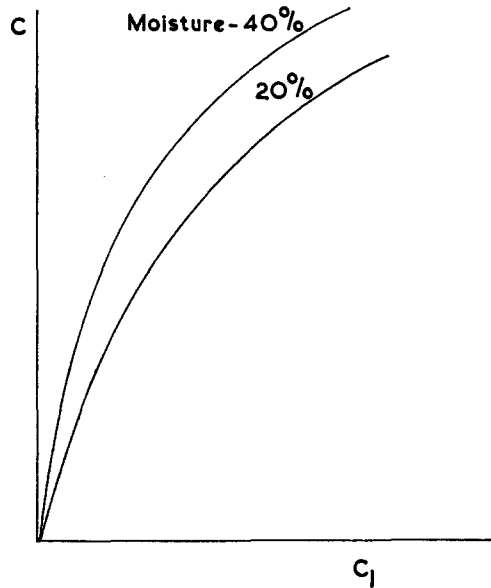

Fig. 7. Sketch of the effect of moisture level on the absorption isotherm for soil potassium

Since roots are normally absorbing moisture as well as nutrients, it is worth considering whether the decrease in moisture towards the root surface is sufficient to affect the diffusion coefficient of the nutrients in this crucial zone. Gardner [8] has calculated the distribution of water around absorbing roots. He shows, in Fig. 2

of his paper, that for both a sandy loam and a clay in the field moisture range at reasonable transpiration rates, the decrease in moisture towards the root surface is small, and can be neglected for the present purpose.

We may now turn to the plant variables and relax the condition of constant α and a. We note:

(e) *Root absorbing power*

As long as $\overline{C_l/C_{l_1}}$ remains near unity, *i.e.* the soil is well able to satisfy the plant's demands, then M_t, by Equation (4), is directly proportional to the root absorbing power $[\alpha]$. Otherwise an increase in α leads to a fall in $\overline{C_l/C_{l_1}}$. The net result on uptake is shown in Fig. 3 where M_t is plotted against t for different values of α. M_t approaches a limit as α is increased, which corresponds to the
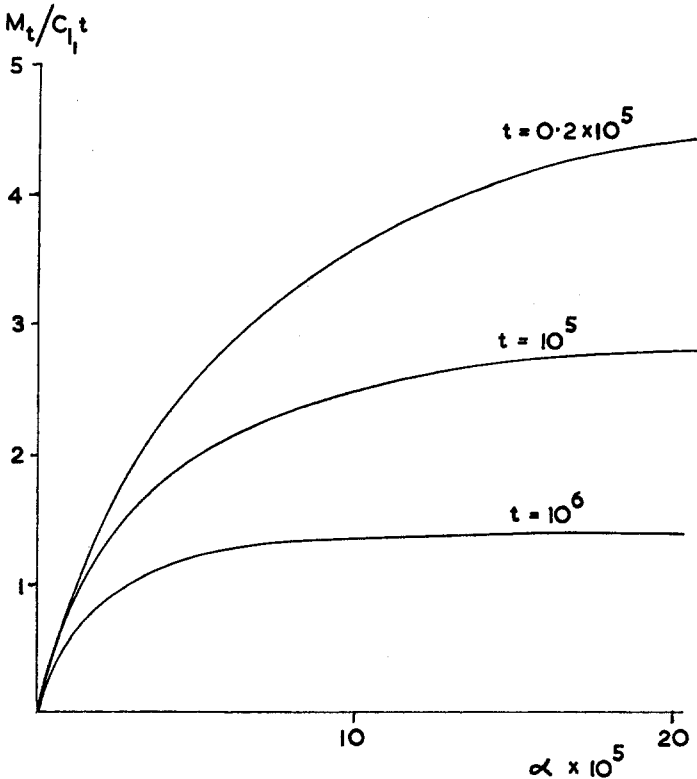

Fig. 8. Variation of the average flux per unit concentration $[Mt/C_{l_1} t]$ with root absorbing power $[\alpha]$.

amount of nutrient arriving at a surface maintained at a very low solution concentration. Supply is then independent of the plant absorbing power. This effect is shown in Fig. 8, in which the average flux per unit concentration $M_t/C_{l_1}t$ is plotted against α for various values of t. Bouldin [4] has stated that increases in α may lead to a decrease in flux, but this conclusion appears to be due to a mis-calculation in his Fig. 4 of the curve marked $D = 10^{-7}$ when $a = 5 \times 10^{-2}$ cm.

If α should fall in time due to physiological ageing of the root, the effect may readily be seen from Fig. 3. If, for example, after 4 days α dropped from 2×10^{-5} to 4×10^{-6} the uptake curve would fall below that corresponding to 2×10^{-5}, and still maintaining a positive gradient, would gradually approach that corresponding to 4×10^{-6}. If depletion has been severe, so that M_t has approached the limit discussed above, a substantial fall in α will have little effect – as shown in Fig. 8.

(f) *The radius of the root*

When $Dt/a^2 < 0.1$ the root cylinder behaves as a plane surface and uptake per unit surface area is independent of the radius [a]. However, in most instances when uptake proceeds for days $Dt/a^2 > 0.1$, and the smaller the radius, the more effective the absorption per unit surface area, since in Fig. 2 the influence of a lower value of a in the parameter $a\alpha/D_lv_lf_l$ in raising $\overline{C_l/C_{l_1}}$ outweigths its influence through Dt/a^2 in lowering $\overline{C_l/C_{l_1}}$. The net result of these effects is illustrated in Fig. 9 where $\overline{C_l/C_{l_1}}$ is plotted against t for roots of 10^{-1} and 10^{-2} cm. radius and fixed values of other variables. The uptake per unit *length* of root varies as $2\pi a \, \overline{(C_l/C_l)}_1$ and it may be seen by inspection of Fig. 9 that this will increase with a. It is here assumed that α does not change with the root radius.

(g) *Root hairs*

The function of root hairs is obscure. The hairs are protuberances in epidermal cells and may be assumed to absorb nutrients through their walls like the rest of the epidermal cells (Scott [20]). The factors controlling the frequency and length of hairs are little understood and their incidence has usually been studied systematic-ally only in moist air and culture solution and not in soil. Estimates of the greatly increased absorbing area of roots due to the root hairs
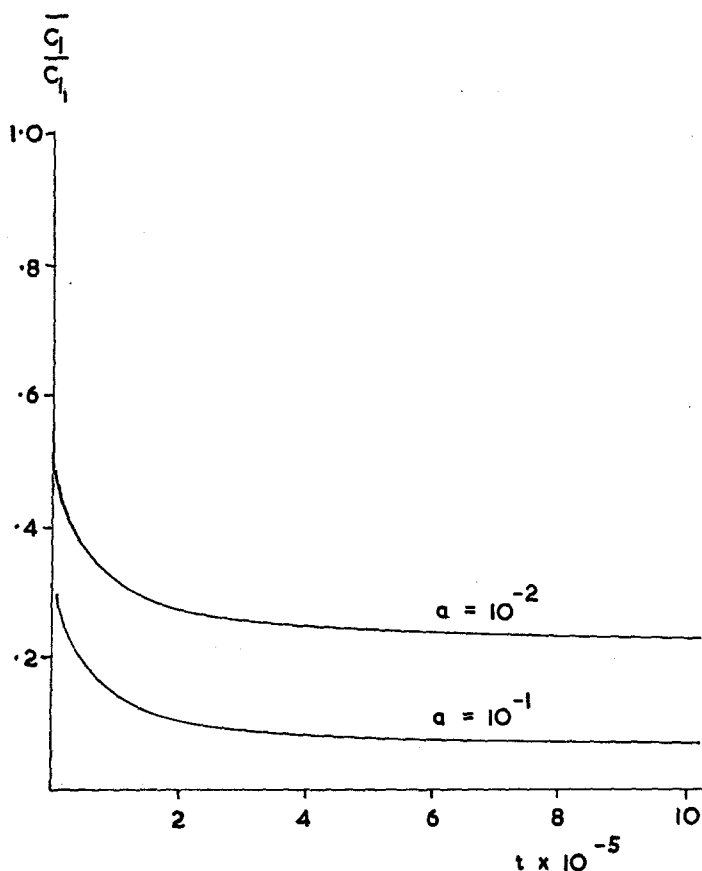
Fig. 9. Effect of root radius on the average concentration ratio at the root surface

$$D = 10^{-7} \text{ cm}^2 \text{ sec}^{-1}$$
$$\alpha = 10^{-5} \text{ cm sec}^{-1}$$

have been made by Dittmer [7]. Bouldin [4], having observed root and root hair dimensions of unspecified "greenhouse cultures", calculates that the total flux across root hair surfaces may be 3 to 10 times greater than the flux across the surface of the central root cylinder. Observations such as these must clearly not be taken to imply, as numerous workers have done, that the hairs are in general responsible for an increased uptake of this order. They may be in the very early stages of absorption, but they are normally so crowded together that they very soon interfere with each other's uptake.

Drew, in this laboratory, has measured the roots of ryegrass growing in a sandy loam soil, and finds the hairs lie approximately normal to the root surface and are densely clustered within a fairly well defined cylinder. It would seem more profitable, therefore, to regard the hairs as an expansion of the root cylinder to a larger one whose surface is located near their tips. Depletion within this cylinder will occur more or less uniformly, and at the same time, diffusion will occur to its outer surface. Kramer and Coile [9], and Wiersum [21] have treated this cylinder as an effective root volume, and Passioura [17] has treated it as an effective surface for mass flow and diffusion. We shall here consider simultaneous depletion within the cylinder and diffusion to it.

First, to justify the assumption that depletion within the root hair cylinder is effectively uniform, we may calculate the time taken by the hairs to absorb the nutrient in the equivalent hair cylinder, corresponding to a decrease in concentration ΔC within the cylinder, and assuming they do not interfere with one another. This time will be shown to be small. The treatment is equivalent to assigning an 'average' radius to the zone of depletion around each hair, and calculating when the zones overlap.

There will be little error if we assume the drop in concentration ΔC is instantaneous at the hair surface, and apply the equation given by Carslaw and Jaeger [5] (p. 335) for diffusive flux from an infinite uniform medium to a cylinder at constant surface concentration.

Let l = average length of hairs

a_h = hair radius

n = number of hairs per unit length of root

a_r = root radius

The total amount to be taken from unit length of the equivalent cylinder, neglecting the volume of the hairs, is given by

$$\Delta C\pi[(a_r + l)^2 - a_r^2] \tag{6}$$

The total uptake by the hairs, and the central root cylinder, as a function of time is given by

$$(2\pi a_h ln\overline{F}_h + 2\pi a_r \overline{F}_r)t \tag{7}$$

where $\overline{F}_h$ is the average flux to the hairs and $\overline{F}_r$ the average flux to the root over time t.

By equating the Expressions (6) and (7) the value of t may be found. $\bar{F}_h$ and $\bar{F}_r$ are calculated as follows. The parameter $aF/D\varDelta C$ is plotted against Dt/a^2 by Carslaw and Jaeger [5] (p. 338). The average value of $aF/D\varDelta C$ to time t has been obtained from this plot by graphical integration and is shown in Fig. 10. It is given the symbol G_h for the hair and G_r for the central root cylinder. We find, by substituting $D\varDelta CG/a$ for $\bar{F}$ in Equation (7) and equating the amount in the cylinder in Equation (6) with the amount taken up given by Equation (7), that
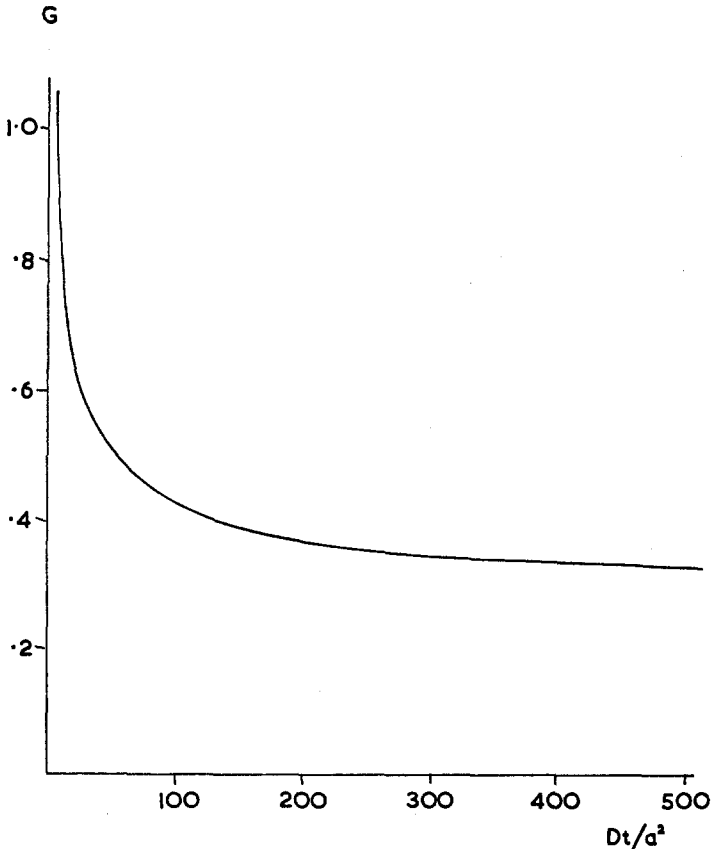
$$2a_r l + l^2 = (2nlDG_h + 2DG_r)t$$

Fig. 10. Variation of "average flux parameter" $[G] = a\bar{F}/D\varDelta C$ with Dt/a^2

If, as is usual, the second term on the right hand side is small compared with the first

$$G_h t = \frac{2a_r + l}{2nD} \qquad (8)$$

A sufficiently accurate value of t can readily be derived by inspection of Fig. 10 and trial and error.

Thus, if $a_r = 0.05$ cm, $l = 0.1$ cm, $a_h = 10^{-3}$ cm, $n = 10^3$ per cm and $D = 10^{-7}$, the value of t is approximately 2.8×10^3 secs (0.8 hours) $(Dt/a_h^2 = 280)$. If D is 10^{-9}, the value of t is approximately 2.8×10^5 secs (78 hours). The value of t is insensitive to the root hair radius, which only appears in Equation (8) because the value of Dta_h^2 is needed to read off G_h.

In practice mutual interference between the hairs will prevent the concentration between them being reduced by a uniform amount of ΔC within time t, for this condition will be reached only at infinite time. Nevertheless, the calculation shows the time taken
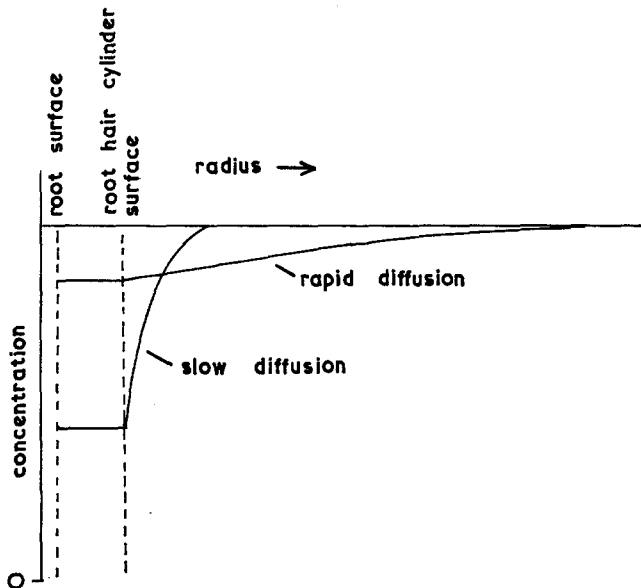

Fig. 11. Nutrient concentration around the root when diffusion is relatively slow – or rapid.

for the zone to become substantially uniform. Even when D is as low as 10^{-9} this time is short, and for most practical purposes it is legitimate to treat the zone as an equivalent cylinder located near the tips of the hairs with a uniform concentration within it.

We may now consider the importance of this root-hair zone. The concentration of nutrient around the roots is sketched in Fig. 11 for relatively rapid, and slow, diffusive flux; and it is clear that if the flux is rapid the presence of the hairs should not make a great difference to the uptake per unit length of the root. If, however, the flux is slow, uptake from the hair zone may well exceed that from the surrounding soil. Their relative contributions to the total uptake may readily be calculated if we assume that the drop in concentration $[\Delta C]$ within the root hair cylinder at time t is the effective boundary condition for the diffusive flux to the equivalent cylinder from $t = 0$ to $t = t$. This will slightly over-emphasize the contribution from outside the equivalent cylinder.

At time t, the uptake from the root hair zone per unit length of root will be $\pi(a_e^2 - a_r^2)\Delta C$, where a_e is the radius of the root hair cylinder. To calculate the amount of nutrient that has moved into the root hair cylinder during that time, we may use as an approximation the equation for flux across the surface of a hollow cylinder with a constant surface concentration, as given by Crank [6] (p. 82):

$$F \simeq \frac{D\Delta C}{a_e} \left[\{\pi(Dt/a_e^2)\}^{-\frac{1}{2}} + \tfrac{1}{2}\right] \tag{9}$$

which is valid for small values of Dt/a_e^2.

By integrating this expression with respect to time between the limits $t = 0$ and $t = t$, and multiplying by $2\pi a_e$, we find the amount of nutrient that has diffused into the cylinder to be

$$2\pi a_e \Delta C \left[\frac{2}{\sqrt{\pi}} \sqrt{Dt} + \frac{Dt}{2a_e}\right]$$

If $a_e \gg a_r$, the total uptake is

$$\pi a_e^2 \Delta C + \pi a_e^2 \Delta C \left[\frac{4}{\sqrt{\pi}} (Dt/a_e^2)^{\frac{1}{2}} + Dt/a_e^2\right] \tag{10}$$

where the first term is the net contribution from within the root hair cylinder and the second term the contribution from outside. Their

relative proportions are shown in Fig. 12. The contributions are equal when $Dt/a_e^2 = 0.14$. Thus, if $D = 10^{-9}$ and $a_e = 0.1$ cm, the contribution from outside the root hair cylinder will not exceed the net contribution from within it, until 0.14×10^7 secs (16 days). On the other hand, if $D = 10^{-7}$ the corresponding value is 0.14×10^5 secs (4 hours).
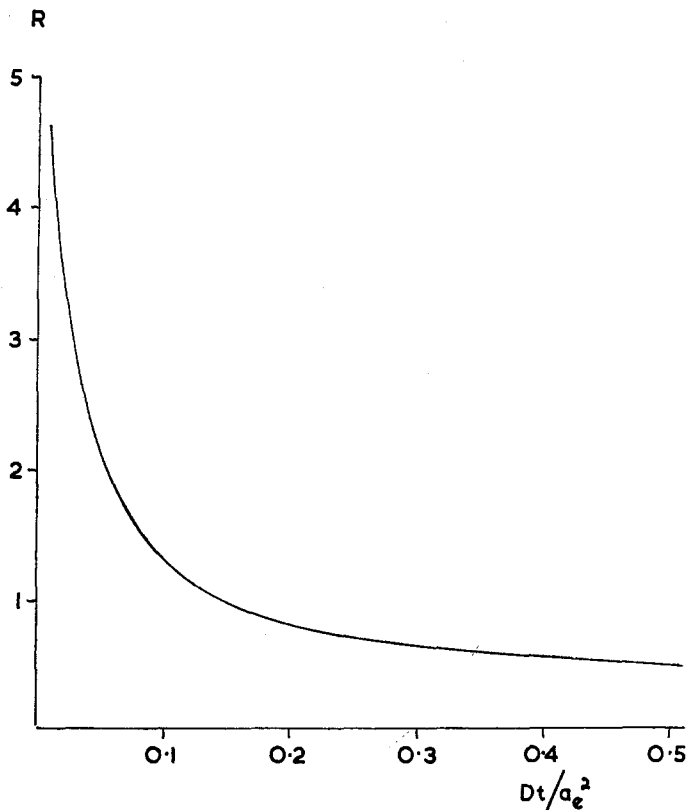

Fig. 12. Ratio [R] of depletion from within and without the root hair cylinder against Dt/a_e^2

We may now attempt to assess the benefit of root hairs by comparing the uptake that a root with root hairs can achieve with the corresponding root without hairs. If the root feeding power is large compared with the diffusive flux, the concentration at the root hair cylinder or at the root surface will be reduced to a low value and it will be possible to treat ΔC as the same in both instances.

The total uptake by the root with hairs is

$$[\pi(a_e^2 - a_r^2)\varDelta C + 2\pi a_e \overline{F}_e t],$$

where $\overline{F}_e$ is the average flux over time t across the surface of the equivalent cylinder, and by the root without hairs is

$$2\pi a_r \overline{F}_r t$$

The values of $\overline{F}_e$ and $\overline{F}_r$ may be obtained from Fig. 10. The ratio between the uptake with hairs and without hairs is

$$\frac{a_e^2 - a_r^2}{2G_r Dt} + \frac{G_e}{G_r} \tag{11}$$

This ratio is plotted against Dt/a_e^2 in Fig. 13, when a_r is 0.02 cm and a_e is 0.1 cm. It will be seen that the effect of the hairs is large when Dt/a_e^2 is less than 10, but levels off to the value of G_e/G_r when Dt/a_e^2 is larger. G_e/G_r has a value of about 2 when $Dt/a_e^2 = 10$ and falls gradually as Dt/a_e^2 increases.
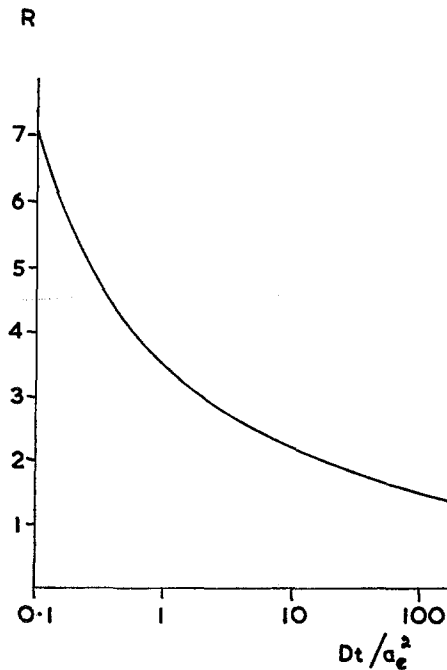

Fig. 13. Ratio [R] of uptake by roots with and without root hairs
$$a_r = 0.02 \text{ cm}$$
$$a_e = 0.1 \text{ cm}$$

The treatment given above is valid when the surface concentration is low. Another approach, which is applicable to any fall in surface concentration as long as Dt/a_e^2 is large, say > 1, treats the root hair zone as an annular region between the root and the soil across which diffusion is very rapid. If the amount of nutrient taken up from the annulus is small compared with the amount crossing it, the amount crossing the central root surface is little greater than the amount crossing the outer surface of the annulus in the same time. Now if the absorbing power of the root is controlled by internal demand, the presence of root hairs should not affect the value of α. Hence the boundary condition at the external annular surface is given by

$$2\pi a_e \left(\frac{dM_t}{dt} \right)_{r=a_e} = 2\pi a_r \left(\frac{dM_t}{dt} \right)_{r=a_r} \tag{12}$$

therefore, by Equation (1),

$$\left(\frac{dM_t}{dt} \right)_{r=a_e} = \alpha_e C_l = \alpha \frac{a_r}{a_e} C_l \tag{13}$$

where α_e is the proportionality constant for flux at the surface of the equivalent cylinder.

The ratio between uptake by a root with hairs and uptake by the same root without hairs may be shown by Equation (4) to be:

$$\frac{2\pi a_e (M_t)_{r=a_e}}{2\pi a_r (M_t)_{r=a_r}} = \frac{\overline{\left(\dfrac{C_l}{C_{l_1}} \right)}_e}{\overline{\left(\dfrac{C_l}{C_{l_1}} \right)}_r} \tag{14}$$

This ratio $\overline{\left(\dfrac{C_l}{C_{l_1}} \right)}_e \Big/ \overline{\left(\dfrac{C_l}{C_{l_1}} \right)}_r$ may be compared on a single curve in Fig. 2, since $a_e \alpha_e$ equals $a_r \alpha_r$, and hence the parameter $a\alpha'/D$ identifying each of the curves is the same for both types of root. By inspection of Fig. 2 we may conclude that root hairs are more important, i.e. $\overline{\left(\dfrac{C_l}{C_{l_1}} \right)}_e \Big/ \overline{\left(\dfrac{C_l}{C_{l_1}} \right)}_r$ is larger, when:

(a) The ratio a_e/a_r is large, for a fixed value of a_r.

(b) The value of a_r is small, for a fixed value of a_e/a_r.

(c) The value of Dt is small.

(d) The average concentration ratio at the root surface is small.

Clearly because of the difference in the value of D, root hairs will usually be more important in the uptake of phosphorus than in the uptake of potassium.

SUMMARY

A portion of a single plant root is treated as an absorbing cylindrical sink to which nutrients move by diffusion. Assuming that the rate of uptake of nutrient is proportional to its concentration at the root surface, and that the nutrient, though reacting with the solid, moves only through the soil solution, standard diffusion equations are used to calculate the effect of soil and plant characteristics on the rate of uptake. The treatment is applicable to phosphorus and potassium. Among soil properties uptake should increase directly with the soil solution concentration. It should also increase, but only slowly, with increasing buffering power. It increases with increasing soil moisture. Among plant characteristics, uptake should increase with the root absorbing power until diffusion through the soil becomes limiting. Absorption by unit surface area of root increases as the root radius decreases. A root hair is shown to interfere quickly with the uptake of adjacent hairs. The hairs increase absorption by the root because they can exploit rapidly the soil between the hairs, and they have the effect of extending the effective root surface to their tips.

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REFERENCES

1 Barber, S. A., Walker, J. M. and Vasey, E. H., Principles of ion movement through the soil to the plant root. Intern. Soil. Conf. New Zealand, 121–124 (1962).

2 Beckett, P. H. T., Studies on soil potassium II. The 'immediate' Q/I relations of labile potassium in the soil. J. Soil Sci. 15, 9–23 (1964).

3 Blanchet, R., Relations entre la vitesse de dilution isotopique du phosphore du sol et l'alimentation phosphatée des plantes. Compt. Rend. 244, 2739–2741 (1957).

4 Bouldin, D. R., Mathematical description of diffusion processes in the soil-plant system. Soil Sci. Soc. Am. Proc. 25, 476–480 (1961).

5 Carslaw, M. S. and Jaeger, J. C., Conduction of Heat in Solids-(2nd Edition) Oxford (1959).

6 Crank, J., The Mathematics of Diffusion, Oxford (1956).

7 Dittmer, H. J., A quantitative study of the subterranean members of soyabean. Soil Cons. 6, 33–34 (1940).

8 Gardner, W. R., Dynamic aspects of water availability to plants. Soil Science **89**, 63–73 (1960).

9 Kramer, P. J. and Coile, T. S., An estimation of the volume of water made available by root extension. Plant Physiol. **15**, 743–747 (1940).

10 Lewis, D. G. and Quirk, J. P., Diffusion of phosphate in soil. Intern. Soil Conf. New Zealand 132–138 (1962).

11 Mattingly, G. E. G., Russell, R. D. and Jephcott, B. M., Experiments on cumulative dressings of fertilizers on calcareous soils in South-West England. II – Phosphorus uptake by Ryegrass in the greenhouse. J. Sci. Food and Agr. **9**, 629–637 (1963).

12 Moss, P., Some aspects of the cation status of soil moisture. Pt. I. The ratio law and moisture content. Plant and Soil **18**, 99–113 (1963).

13 Nye, P. H., Soil analysis and the assessment of fertility in tropical soils. J. Sci. Food and Agr. **14**, 277–280 (1963).

14 Nye, P. H., The measurement snd mechanism of ion diffusion in soils. I. The relation between self-diffusion and bulk diffusion. J. Soil Sci. **17**, 16-23 (1966).

15 Nye, P. H. and Spiers, J. A., Simultaneous diffusion and mass flow to plant roots. Trans. 8th Intern Congr. Soil Sci. Bucharest (1964) (in press).

16 Olsen, S. R., Kemper, W. D. and Jackson, R. D., Phosphate diffusion to plant roots. Soil Sci. Soc. Am. Proc. **26**, 222–227 (1962).

17 Passioura, J. B., A mathematical model for the uptake of ions from the soil solution. Plant and Soil **18**, 225–238 (1963).

18 Porter, L. K., Kemper, W. D., Jackson, R. D. and Stewart, B. A., Chloride diffusion in soils as influenced by moisture content. Soil Sci. Soc. Am. Proc. **24**, 460–463 (1960).

19 Russell, R. S., Martin, R. P. and Bishop, O. N., A study of the absorbtion and utilization of phosphate by young barley plants. III – The relationship between external concentration and the absorbtion of phosphate. J. of Exptl. Botany **5**, 327–342 (1954).

20 Scott, F. M., Root hair zone of soil grown roots. Nature **199**, 1009–1010 (1963).

21 Wiersum, L. K., Utilization of soil by the plant root system. Plant and Soil **15**, 189–191 (1961).

22 Williams, E. G., Chemical soil tests as an aid to increased productivity. Intern. Soil Conf. New Zealand, 820–834 (1962).