

THE SUPPLY OF NUTRIENT IONS BY DIFFUSION TO PLANT ROOTS IN SOIL

II. THE EFFECT OF ROOT HAIRS ON THE UPTAKE OF POTASSIUM BY ROOTS OF RYE GRASS (*LOLIUM MULTIFLORUM*)

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Young roots of many soil grown plants are densely covered in living root hairs. Because the presence of root hairs increases the surface area of the root from 5 to 18 times (Miller¹¹; Weaver and Clements²¹; Dittmer⁴) it has long been assumed that root hairs aid ion uptake by the root. Recently, calculations based on diffusion theory indicate more precisely how root hairs could contribute to the absorbing efficiency of the root when nutrient supply occurs by diffusion in soil (Bouldin²; Nye¹²).

This paper gives experimental data on the absorption of potassium by rye grass growing in two soils with different diffusion characteristics, and at a range of concentrations of solution and labile soil potassium. The significance of root hairs in potassium absorption is examined.

THEORETICAL CONSIDERATIONS

Diffusion model for root with root hairs

Quantitative diffusion models applicable to studies of nutrient absorption by roots with root hairs are described by Nye¹². The root is considered as a cylinder from which hairs project densely and more or less normal to the surface, an arrangement observed in soil grown roots of rye grass as will be described. Rigorous mathematical treatment of diffusion to this composite structure is not available,

List of symbols and abbreviations	
UGS	Upper Greensand Soil
CRC A0, CRC A2	Coral Rag Clay. A0 and A2 are initial and potassium-enriched subsamples
C	concentration of labile potassium (= solution + exchangeable) in g/cc soil
$C_0 - C_1$	depletion or net decrease in concentration in g/cc soil, where C_0 is uniform initial concentration and C_1 is concentration maintained constant at a root surface
C_1	concentration of potassium in soil solution in g/ml liquid
C_{i_0}	uniform initial solution concentration on equilibrium with C_0
\bar{C}_1	average solution concentration at root surface during absorption time
(D)	effective diffusion coefficient for concentration range ($C_0 - C_1$) in cm^2/sec
M_t	g absorbed per cm length of root in t secs
F	flux across root surface in $\text{g}/\text{cm}^2/\text{sec}$
r	radial distance from centre of root in cm
a, a_e	radius of root, root hair cylinder in cm
α , α_e	absorbing power per cm^2 of root surface for the central root (α) or the root hair cylinder (α_e) in cm/sec
μg	10^{-6} g
μ	10^{-4} cm

but approximate methods can be applied since the volume of soil occupied by root hairs forms a regular cylinder with an imaginary boundary or 'equivalent cylinder' located near the root hair tips. Concentration gradients created by individual root hairs will tend to overlap after short absorption times and depletion within the volume of soil trapped between root hairs is assumed to be uniform at a given time. Uptake will be supplied from two sources: (i) net depletion within the equivalent cylinder by diffusion to root and hairs, and (ii) simultaneous diffusion from the bulk soil to the surface of the equivalent cylinder under the concentration gradient imposed by (i). The relation between (i) and (ii) is illustrated in Figure 5.

Net diffusion to the root plus root hair system is therefore considered to occur by radial diffusion from a semi-infinite medium to

a simple cylinder. Little error should be introduced for the uptake periods used here by assuming the change in concentration within the equivalent cylinder occurs in a single step at zero time, so that the boundary condition to be applied at the surface of the equivalent cylinder of radius a_e cm becomes

$t = 0, r \geq a_e, C = C_0 =$ uniform initial concentration in soil

$t > 0, r = a_e, C = C_1 =$ constant concentration at the boundary between equivalent cylinder and bulk soil.

Calculations

The immediate aim is to determine the value of C_1 at the surface of the equivalent cylinder. The approach consists of calculating the amount that has diffused to unit length of the equivalent cylinder and the amount removed from within the equivalent cylinder. Details of diffusion equations are described in paper I⁵.

Source (i) – the amount supplied from inside the root hair or equivalent cylinder is $\pi a_e^2 (C_0 - C_1)$, neglecting the volume of soil occupied by the root and hairs (only 3.3 per cent). A value for a_e was determined by measurement of soil grown root hairs.

Source (ii) – the theoretical uptake after a given absorption time is calculated for a fixed value of a_e and a series of values of (D) and $(C_0 - C_1)$. Allowance is made for the dependence of (D) on $(C_0 - C_1)$ which was determined experimentally¹⁹.

The total theoretical uptake, M , (Source i + ii) after 4 days absorption is shown in figure 3 and 4 as a function of $(C_0 - C_1)$. If the total uptake is measured experimentally the value of the unknown, C_1 , can thus be determined.

Lewis and Quirk^{8 10} have applied cylindrical flux equations to the root and individual root hairs separately, and have added the two contributions (Ref.¹⁰, table 2). This approach assumes absorbing surfaces do not compete for nutrient, a condition certainly not obeyed for the root hair densities and diffusion coefficients in this work even after short times. It should be noted that our model does not imply that uptake by a root *with* root hairs is necessarily much greater than by a root *without* although this is implied if no allowance is made for competition.

EXPERIMENTAL

Italian rye grass (*Lolium multiflorum Lam.*) was chosen for experiment because soil grown roots were cylindrical (over lengths of at least 1 cm) and densely covered in root hairs except for the apical zone. Plant uptake was measured from Upper Greensand sandy loam (UGS) and Coral Rag clay (CRC, A0). In CRC a further level of labile potassium (CRC, A2) was established by moist equilibration of the natural soil with added potassium phosphate. Soil samples were brought to a fixed moisture content and bulk density for simultaneous diffusion and plant uptake experiments⁵. Diffusion coefficients of potassium in soil were measured at different concentrations of labile potassium using a cation exchange resin paper method²⁰.

A single root technique was used to measure uptake by a centimeter length of root⁶. Seeds were germinated in the dark at 25°C on moist filter paper and selected for straight radicles 3–4 mm long after 2½ days. The pregerminated seedlings were planted in perspex tubes assembled in three sections. For all three soils a 'soil/sand system' was used, the top section, 1 cm in depth, containing nutrient free sand, the middle section, also 1 cm, the experimental soil and the bottom section, nutrient free sand. Radicles placed in section 1 were allowed to grow rapidly through section 2 into 3. Potassium uptake by the length of root in section 2 was followed by removing replicate plants at different times, up to 5 days, when branching occurred.

In one experiment with UGS a 'soil/soil system' was used in which all three tube sections were filled with soil. To trace potassium absorption from section 2 only, Rb⁸⁶ was used as a tracer, the ratio Rb⁸⁶/K absorbed by rye grass from the same sample being determined in subsidiary experiments. Preparation of soil samples, plant growth conditions and analyses were the same as described previously⁵.

RESULTS AND DISCUSSION

Root hair observations

The diffusion model assumes the presence of a well defined cylinder of root hairs on roots growing in soil. This requires some justification. The majority of observations on root hairs have been made on specimens grown in moist air, water or agar where root hairs attain their full lengths approximately perpendicular to the root surface and a uniform root hair cylinder is clearly developed. Miller¹¹ states, however, that root hairs in soil do not grow straight, but 'retain the irregularities of the objects to which they adhere.' Changes in shape and retardation of growth are also said to occur so that only a fraction of the length obtained in moist air occurs in soil. It was un-

certain therefore whether root hair lengths measured on roots washed from the soil would be representative of the radius of the equivalent cylinder.

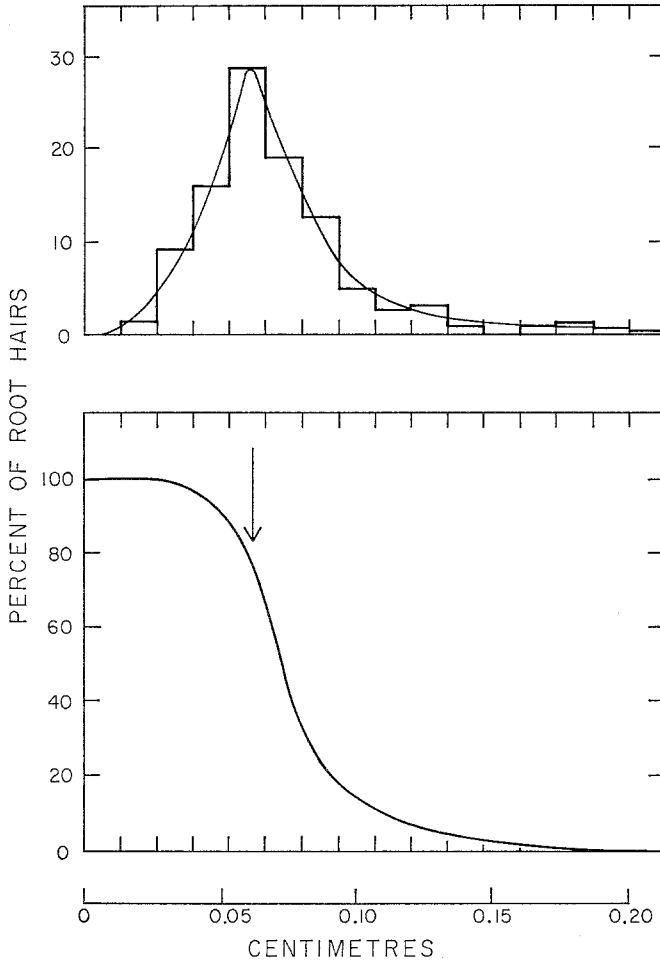


Fig. 1. Root hair lengths.

Upper figure - percentage frequency histogram of root hair lengths. Lengths grouped into classes of 150 microns. Modal length (4.5 units) = 0.675 mm.

Lower figure - cumulative frequency diagram showing percent of root hair length with distance from root surface. *Arrow* indicates modal length.

To observe root hair development in the soil environment, rye grass seedlings were grown in thin-walled glass tubes containing UGS at the same moisture and compaction as in uptake experiments. Tubes were sloped so that vertically elongating roots passed close to the wall and could be observed in situ under the microscope. Plate 1 is a photomicrograph showing the morphology of a 5- 6-day-old root. Hairs project normal to the root surface and pass through soil aggregates or voids forming a root hair cylinder resembling the type seen in moist air or water. Plate 2 at higher magnification, shows that hairs penetrate, and presumably derive nutrients, inside soil aggregates.

Measurement of the equivalent cylinder radius was therefore based on root hair lengths of specimens grown in soil. Five- to six-day-old roots were washed free from soil and mounted under the microscope. To avoid bias in the measurement of root hair lengths, the side of the root was sharply focussed and the actual length of a number of hairs in sequence along the root were measured, irrespective of length or contortion, using a calibrated eyepiece graticule. On average there were 98 hairs per millimeter length of root. Hairs were $10\ \mu$ in diameter. Data on 300 measurements is shown in Fig. 1. Root hair lengths are grouped into classes of 1 micrometer unit (0.015 cm) and plotted as a percentage frequency histogram. The lengths follow a skew distribution with a clear mode at 4.5 units (= 0.0675 cm) indicating a well defined root hair cylinder. The cumulative frequency plot of the same data is shown in Figure 1. This plot gives the percentage of root hair length present at a given distance from the root surface and shows that 80 per cent of the total length attains the modal length. This length was taken as representative and added to the average root radius to give the limits of the equivalent cylinder for the diffusion model (0.082 cm).

Potassium uptake with time

In order to justify the boundary conditions used for later calculation and to check the absorptive activity of the centimeter length of rye grass root, uptake was measured with time in UGS and CRC, A2 (Fig. 2). Roots continue to absorb potassium over the experimental period, the increase in rate of uptake after 5 days coinciding with the rapid elongation of lateral roots into the soil. Zero time is the time at which roots, from their known rate of elongation (about

1.0 cm per 16 h) were half-way through section 2. Theoretical curves have been constructed to pass through the 4-day uptakes, these being the largest and most reliable values before lateral root proliferation. Experimental uptakes at earlier times are generally less than predicted by the diffusion model which, by assuming the establishment of a root hair cylinder at zero time, does not take account of root hair elongation. In fact root hairs required about 10 h from the time they were initiated as minute papillae behind the root apex until they reached their full length. Uptakes at early times would therefore be expected to be less than predicted.

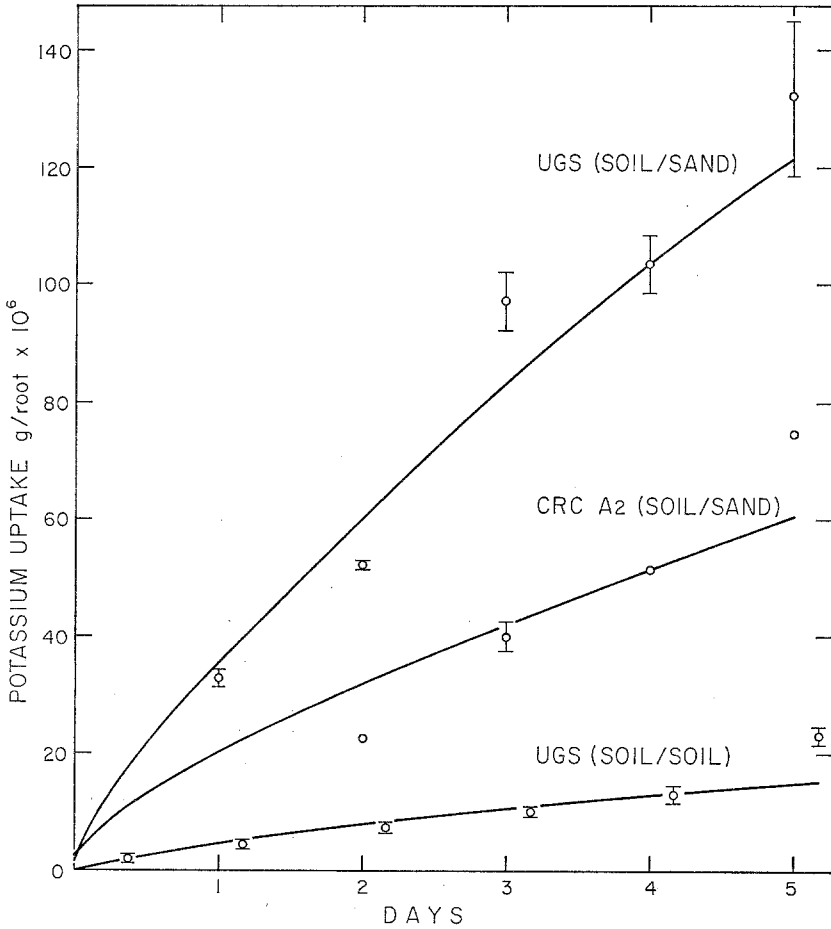


Fig. 2. Experimental uptake of potassium from Upper Greensand soil and from Coral Rag Clay, A2 by a cm length of rye-grass root with time. Limits show standard error of means.

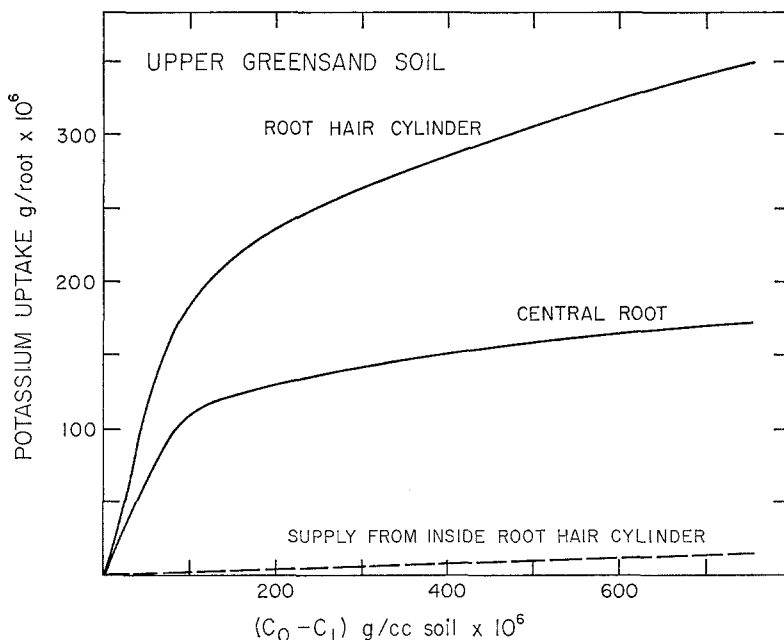


Fig. 3. Upper Greensand soil.

Figs. 3 and 4. Theoretical relation between the uptake by a cm. length of root after 4 days absorption and the depletion of labile potassium ($C_0 - C_1$) at the root/soil boundary.

Dotted lines indicate amount supplied from inside root hair cylinder - source (i) Figures are calculated from measurements of the diffusion coefficients of potassium in soil and the root dimensions.

Potassium depletion within the root hair zone

The theoretical uptake from each soil by a centimeter length of root after 4 days, calculated for different depletions ($C_0 - C_1$) within the root hair zone is shown in Figures 3 and 4. Amounts that would be absorbed by the root hair cylinder (source i and ii) and by the central root alone, as if root hairs were inactive, are compared. The potential advantage of root hairs is apparent, for by providing a larger effective surface area per cm length of root, amounts diffusing across the equivalent cylinder are greater than across the central root for equal depletions at the root surface. Amounts supplied by net depletion within the root hair cylinder, $\pi a_e^2 (C_0 - C_1)$, - source i - are small compared with diffusion to central root or root hair cylinder.



Plate 1. Photomicrograph demonstrating root hair cylinder in soil. 5 to 6-day-old root in Upper Greensand soil. Scale = 1 mm.

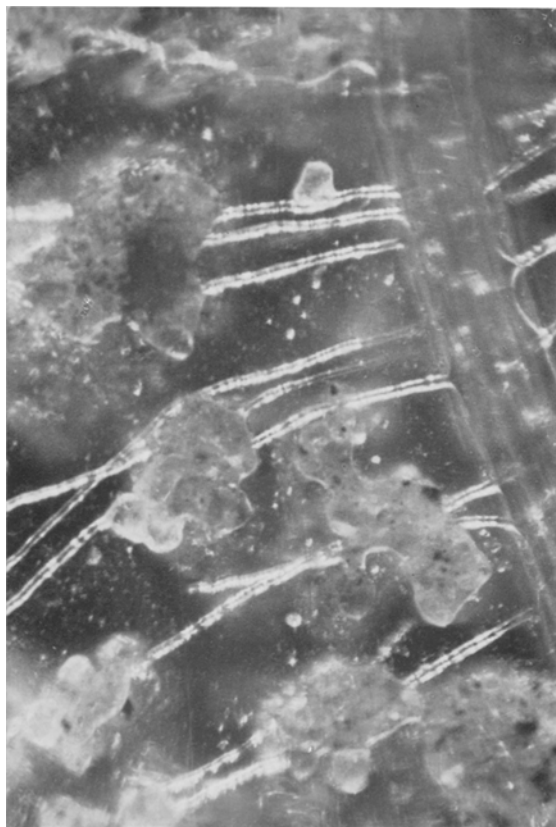


Plate 2. Photomicrograph showing penetration of soil aggregates by root hairs. Scale = 0.5mm.

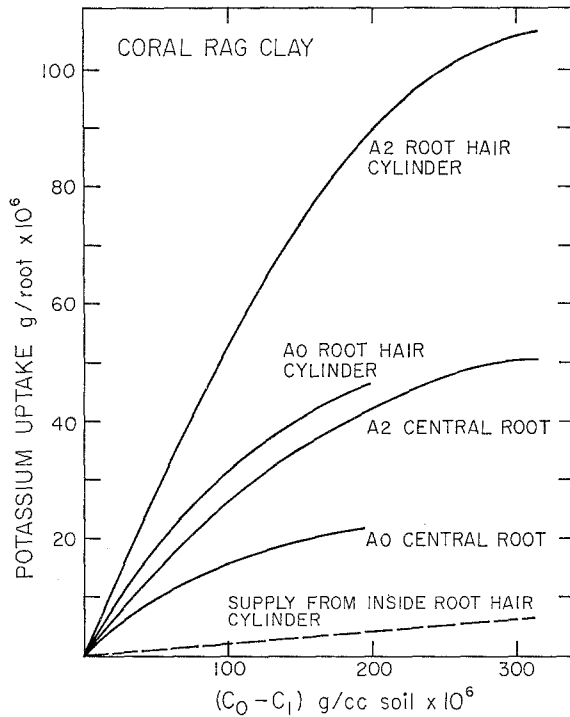


Fig. 4. Coral Rag Clay.

Depletion within the root hair zone corresponding to experimental uptakes, using Figures 3 and 4, are summarized in Table 1. Values calculated for UGS are bracketed in tables 1 and 2 because estimates of (D) may be inaccurate⁵. Potassium uptake from UGS (soil/soil system) is accounted for by a minute decrease in concentration within the root hair zone, 0.7 per cent of the initial labile potassium. The net amount removed from within the root hair cylinder is only 0.1 μg (see Table 2) and the remainder is supplied by diffusion from the soil outside the zone occupied by hairs. Uptake in this experiment could also be readily explained by diffusion to the central root (as Fig. 3 shows) as if root hairs were non-absorptive, the depletion still being small.

To see whether higher depletions could be obtained the soil/sand system was used. The rate of uptake from UGS was increased 8-fold and a 6 per cent depletion within the root hair zone was calculated, although it is again possible to account for this uptake by diffusion

TABLE 1

Potassium uptake by rye-grass: summary of soil and plant factors, experimental and calculated							
Experiment	<i>r</i> M 4 days	<i>2</i> C ₀	<i>3</i> $\frac{(C_0 - C_1)}{C_0}$	<i>4</i> α	<i>5</i> C ₁ /C ₀	<i>6</i> M/M _{max} 4 days	<i>7</i> M root hairs M root
	UGS (Soil/Soil)	13	754	(0.007)	(10)	(0.98)	(0.04)
UGS (Soil/Sand)	104	754	(0.06)	(104)	(0.71)	(0.29)	(1.13)
CRC, A0 (Soil/Sand)	30.1	194	0.47	200	0.60	0.66	1.77
CRC, A2 (Soil/Sand)	51.4	313	0.31	160	0.59	0.48	1.46

Column

- 1 Experimental absorption after 4 days ($g \times 10^{-6}$)
- 2 Initial concentration of labile potassium ($g/cc \text{ soil} \times 10^6$)
- 3 Depletion or lowering of concentration of labile K in root hair cylinder, as fraction of initial concentration
- 4 Root absorbing power at the central root ($cm/sec \times 10^{-6}$)
- 5 Average concentration of potassium in soil solution in root hair cylinder as a fraction of the initial concentration
- 6 Experimental absorption after 4 days as a fraction of the maximum possible uptake by the root hair cylinder (sources i and ii)
- 7 Uptake by root with hairs as fraction of calculated uptake by root without hairs

to the central root alone. The increased uptake in this experiment may also have been partly due to a higher growth rate, the average increase in fresh weight per plant being .0096 g in the soil/soil system and .0186 g in the soil/sand system.

It was anticipated that root hairs would become more important in supply at lower concentrations of labile potassium and experiments were therefore continued in CRC A0 and CRC A2. Evidence was obtained for the participation of root hairs in nutrient supply. Uptake from sample A0 was measured after 3 days only, the mean value 25.3 μg being extrapolated to a 4 day value of 30.1 μg for the purpose of comparison in Table 1. Table 1 shows that depletion in the root hair zone was high, 47 per cent in A0 and 31 per cent in A2. Diffusion to the central root in A2 could supply a theoretical maximum of 50.1 μg in 4 days which would approximately account for the experimental uptake of 51.4 μg . This is not the case in A0, where the maximum supply to the central root (14.6 μg in 3 days) is less than the experimental uptake (25.3 μg). The difference is considered to be outside experimental error and appears to demonstrate a real absorption of potassium by root hairs.

Utilization of soil potassium by the root

Many workers ^{1 18 22} have attempted to estimate the distance in the soil nutrients move to root surfaces during absorption. Direct information is difficult to obtain because of the short distances involved in diffusion. Wiersum ²² considers that the quantity of exchangeable potassium initially held within the volume of soil occupied by root hairs is sufficient to account for uptake by the root system, assuming diffusion over larger distances is insignificant.

TABLE 2

Comparison between amount of labile potassium within root hair cylinder and potassium absorbed by rye-grass in 4 days. (Volume of cm length of root hair cylinder = 2.8×10^{-2} cm ³)				
Experiment	Labile Amount initially inside root hair cylinder (g × 10 ⁶)	Amount absorbed in 4 days (g × 10 ⁶)	$\frac{\text{Column 2}}{\text{Column 1}}$	Calculated Amount absorbed from inside root hair cylinder (g × 10 ⁶)
UGS (Soil/Soil)	15.8	12.7	0.80	0.1
UGS (Soil/Sand)	15.8	104	6.6	1.0
CRC, A0 (Soil/Sand)	4.0	30.1	7.5	1.9
CRC, A2 (Soil/Sand)	6.6	51.4	7.8	2.0

However, Table 2 shows that the uptake of potassium by rye grass in 4 days from the CRC samples is more than 7 times greater than the total labile potassium initially present within the root hair cylinder. Supply by diffusion over larger distances is clearly important. When allowance is made for diffusion, the amount of potassium removed from within the root hair cylinder is calculated to supply only 0.8 to 6.3 percent of the total absorbed after 4 days.

The concentration of nutrient with distance from the root can be calculated from diffusion theory, an approach used by Olsen *et al* ¹³ for phosphate. Concentration with distance from the equivalent cylinder is calculated, for a constant diffusion coefficient, from Carslaw and Jaegar ³ equation 7, p. 336. Our calculations are approximate in the sense that a diffusion coefficient averaged over the concentration range for each experiment is used. Figure 5 shows contrasting depletion profiles for rye grass roots in UGS and in CRC, A0 after 4 days absorption. Diffusion distances are little more than

1 cm and the majority of potassium is supplied from within 0.5 cm of the root, although the extent of depletion and the amounts absorbed are very different.

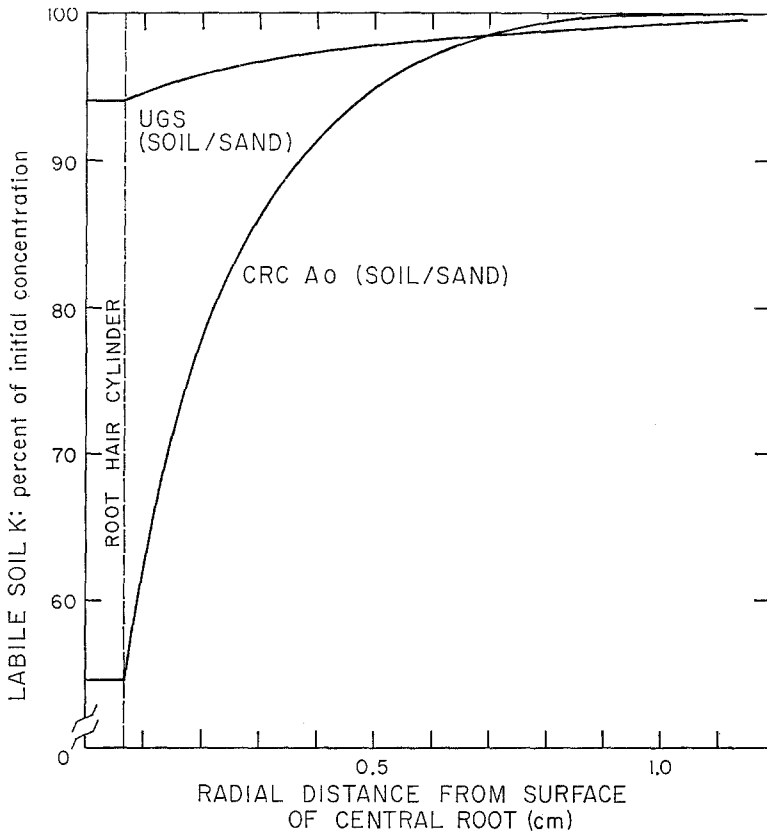


Fig. 5. Calculated concentration of labile potassium with distance from surface of central root after 4 days absorption.
Upper Greensand, soil/soil system.
Coral Ray Clay, sample A0, soil/sand system.

The distance potassium moves to the root depends, in these calculations, on the diffusion coefficient. In the UGS and CRC soils for decreasing values of C_0 , the tendency will be for a greater proportion of potassium to be supplied from the soil close to the root since (D) decreases with decreasing C_0 . In effect the plant 'feeds' from a given soil over shorter distances at lower concentrations of labile potassium.

Root absorbing power

An alternative boundary condition may be applied to the root hair cylinder which allows an examination of the relation between soil supply and plant demand. The amount removed from inside the root hair cylinder has been shown to be small compared with total uptake and for unit length of root the nutrient crossing the surface of the root hair cylinder is nearly equal to nutrient crossing a plane at the surface of the central root, that is,

$$2\pi a_e (F)_{r=a_e} = 2\pi a_r (F)_{r=a} \tag{1}$$

Therefore for unit surface area

$$(F)_{r=a_e} = \alpha_e C_l = \alpha_{a_e}^a C_l \tag{2}$$

where α_e is a proportionality coefficient for flux at the equivalent cylinder, and C_l the concentration in solution at the root/soil boundary. From Equations (1) and (2), uptake after tsecs for unit length of root is

$$\begin{aligned} M_t &= 2\pi a_e \alpha_e \bar{C}_l t \\ &= 2\pi a \alpha \bar{C}_l t \end{aligned} \tag{3}$$

The relation between M_t and α is shown in Figure 6 and was obtained from Equation (3) by the procedure explained in Reference 5: the approach assumes that the desorption isotherm determined on equilibrated soil samples applies in the root vicinity during diffusion. It is seen that uptake by unit length of root at the equivalent cylinder is greater than it would be by the central root alone, for the same root absorbing power. Estimates of α corresponding to experimental uptakes are given in Table 1. For the three experiments using the soil/sand system, α lies between 104×10^{-6} and 200×10^{-6} cm/sec and is uniformly higher than onion roots (25×10^{-6} to 77×10^{-6}) and leek roots (61×10^{-6} to 68×10^{-6}) in the same soils under identical conditions. Presumably α is partly regulated by genetic differences in growth rate and plant mineral composition.

Absorbing power of the cm length is apparently reduced to 10×10^{-6} using the soil/soil system when all lengths of the root are allowed to absorb nutrients. A similar but smaller decrease was noted previously for onion.

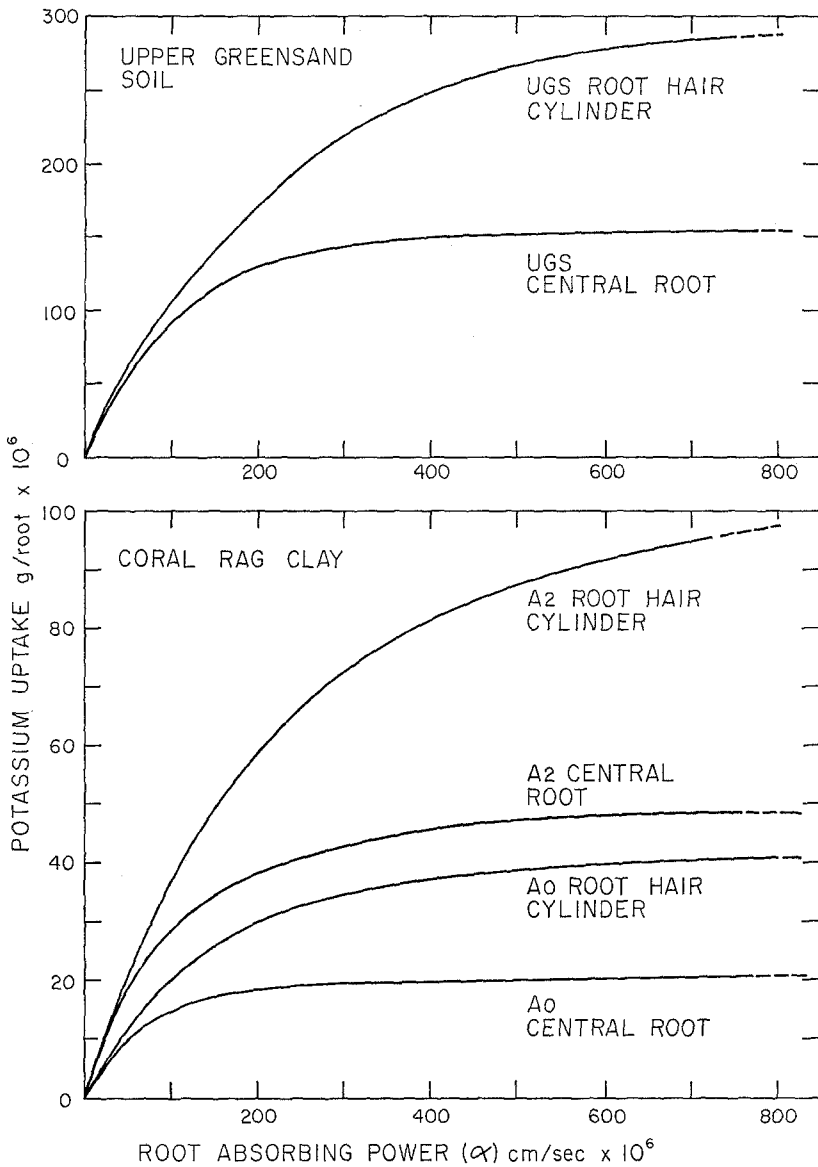


Fig. 6. Theoretical relation between the uptake by a cm length of root after 4 days absorption and the root absorbing power, α .

Figure is calculated from Figures 3 and 4, measurements of the potassium desorption isotherm and the root dimensions.

Upper figure - Upper Greensand soil.

Lower figure - Coral Rag Clay.

Effect of diffusion on uptake

The extent to which diffusion limits the rate of potassium uptake is given by the ratio \bar{C}_l/C_{l_0} ⁵. A value of unity indicates diffusion can keep pace with absorption; a low value indicates that slow movement to the root surface is limiting the concentration and therefore the rate of uptake. In Table 1, \bar{C}_l/C_{l_0} for the three experiments using the soil/sand system (between 0.71 and 0.59) indicates diffusion is significantly limiting uptake. In contrast, in UGS (soil/soil system) the ratio is effectively equal to unity and we conclude that the initial solution concentration and the root absorbing power, but not diffusion, are the factors controlling uptake.

Significance of root hairs in potassium uptake

There is little direct experimental evidence in the literature demonstrating root hairs participate in nutrient absorption either in solution or soil culture. Root hairs would not be expected to enhance uptake from stirred solution since the actual area of epidermal surface is unlikely to be a limiting factor in the rate of absorption. In soil, Place and Barber¹⁴ found Rb⁸⁶ uptake by corn roots with root hairs was 2.7 to 5.0 times greater than roots without hairs, a difference they attributed to root hair activity. Their result could also have been due to differences in experimental method and in the absorbing power of the roots which were from plants of different age and pre-treatment.

We have assumed root hairs are capable of ion absorption from indirect evidence: (i) - a root hair is a thin-walled tubular extension of the outer cell wall and cytoplasm of an epidermal cell. Since epidermal cells are undoubtedly absorptive, the root hair moiety of the same cell should also be involved in ion uptake; (ii) - root hairs of many soil grown roots are living structures. The presence of a nucleus and of a cytoplasm capable of being plasmolysed is evidence of viability^{7 16 17}; (iii) - using a micropotometer technique¹⁵, individual root hairs have been shown to absorb water efficiently, suggesting a similar ability to absorb ions; (iv) - Lewis and Quirk⁹ show autoradiographs of phosphate depletion zones in soil around roots. These are difficult to interpret unless root hairs are actively absorbing.

To what extent do root hairs, assuming they are absorptive, appear to increase potassium uptake in our experiments? As shown in

Figures 3 and 4 and Table 2, the proportion of potassium taken up from within the root hair cylinder is small. The main effect of root hairs arises because they provide a zone around the central root through which potassium passes readily, thus virtually increasing its radius many times. In only one experiment, however, (in CRC, A0) can definite evidence for the participation of root hairs in nutrient absorption be claimed. In the other three experiments, diffusion to the central root alone could still account for the uptake, although in two experiments (CRC A2 and UGS, soil/sand system) the depletion at the root surface and the root absorbing power would need to be substantially greater. In UGS (soil/soil system) the presence of root hairs appears to offer little or no advantage to the root in potassium absorption.

The benefit of root hairs in potassium absorption can be obtained quantitatively from Figure 6. Assuming root absorbing power, being controlled by 'internal demand', does not vary with the presence or absence of root hairs, the theoretical uptake by a root in either condition can be compared for the same value of α . Table 1 shows that for our experiments the presence of root hairs is calculated to have enhanced uptake from between 0 per cent in UGS (soil/soil system) to 77 per cent in CRC, A0.

CONCLUSIONS

In this and the preceding paper we have examined the effects of diffusion on potassium uptake by the roots of intact plants. To answer such questions as, does diffusion limit uptake?, can root hairs aid absorption?, we need to know the interrelation between nutrient demand by the root and the concentration and mobility of the nutrient in the root vicinity. None of these factors are readily obtainable independently and each, as we have shown, may vary for a given soil and plant species. In some experiments, under conditions of high root demand, diffusion supply appears to become a limiting factor in potassium uptake. In these circumstances, the presence of root hairs may be expected to benefit the plant by providing an easy pathway for potassium to move across a cylinder of soil surrounding the central root axis. Except over very short uptake times, this effect is more important than the fact that the

hairs have ready access to the potassium within the cylinder itself, since the proportion of potassium derived from this source is very small. It would be of interest to know the extent to which nutrient demand by seedling roots in these experiments compares with demand by roots of more mature plants under field conditions.

SUMMARY

Observation of soil grown roots of rye-grass shows that an approximately cylindrical volume of soil, the root hair cylinder, is densely occupied by root hairs. Estimates are given of the concentration of labile and solution potassium within the root hair cylinder during experiments measuring potassium uptake from two soils by single roots. Calculations, using a diffusion model, suggest that labile potassium concentrations may be reduced to between 99.3 and 53 per cent of the initial, depending on the diffusion characteristics of the soil and nutrient demand by the root. Of the total potassium absorbed by a root in 4 days, the proportion which is supplied from within the root hair cylinder is small (0.8 to 6.3 per cent) indicating that diffusion to the root from the soil outside the root hair cylinder is of paramount importance. When root demand is high, diffusion appears to limit uptake to between 71 and 59 per cent of that which roots of comparable physiology would be expected to absorb from stirred solution of the same concentration. Nevertheless, the presence of root hairs is calculated to have enhanced uptake by up to 77 per cent compared with roots without hairs because they virtually increase the root diameter. Diffusion does not appear to be a limiting factor when root demand is low and hairs can then add little to the efficiency of the root system in potassium absorption.

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