

TRANSPORT PROCESSES IN THE SOIL AS FACTORS OF POTASSIUM AVAILABILITY

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ABSTRACT

Potassium can only be absorbed by roots after it has been transported to the root surface. These processes can conveniently be considered in terms of transport within the profile on a macroscopic scale, and transport within the rhizosphere up to the root or root hair surface.

The physical processes involved in transport of potassium in soil are briefly reviewed, with the factors which determine the transport coefficients. Potassium is of intermediate mobility in the soil, and is particularly complicated to deal with because the mobility depends upon the arbitrary and varying concentration of anions in the soil solution.

The uptake by single roots and root systems, and the depletion of the whole soil, are considered. There is now evidence that the required fluxes of potassium to the roots of rapidly growing plants are such that transport may be a rate-limiting step, though many further measurements are needed.

The movement within the profile is usually fairly rapid, and leads to sufficient distribution, but the possibility of low mobility and restrictions on distribution in zero-cultivation systems are discussed. High rainfall, low buffer capacity and high anion concentration lead to excessive mobility, and leaching losses from the profile.

INTRODUCTION

Virtually all nutrient ions must be transported in the soil before their uptake by plant roots, because the amount of material which is literally in

contact with the root or root hair surface, subsequent to the growth of these, is exceedingly small. In addition, ions are constantly being moved within the soil profile due to physical and biological processes. The soil profile is not a uniform medium, but a highly heterogeneous mass, within which transport processes are a continual and essential part of its normal state.

The fact that a process is essential does not, however, prove that it is rate-limiting. The purpose of this paper is to review the latest evidence on the transport of potassium up to root surfaces, and otherwise within the soil profile, and to assess the likelihood that these processes are rate-limiting to plant growth. This demands that our present theory of the transport processes is essentially correct, and also that we know the speed of other processes involved in plant growth, because in a series of linked processes, it is the slowest which is the most rate-limiting.

Ion transport studies in soil have a relatively short history, with little published work before 1962. Previous concepts of potassium availability have been stated most clearly in terms of quantity and intensity factors, and these can be absorbed into a general view of availability, as measured by transport rate to roots, which we can now define with fair precision. However, in contrast to most earlier ideas of 'availability', this view necessarily involves plant properties also. Transport rates can only be defined in terms of specified root systems, or for arbitrary special cases. For this reason the approach cannot give a clear-cut single value, as can the analytical methods which set out to determine 'available' potassium, and it is unlikely to supersede the latter as a practical tool to aid agronomy. However, it should help us to understand the results of these simple analytical techniques better, and to use them more effectively.

PRINCIPLES OF POTASSIUM TRANSPORT IN SOIL

These principles are by now fairly well agreed¹, though there are still differences in nomenclature and definition. Only a very brief summary will be given here.

All transport occurs by mass flow or diffusion. The former is defined by the equation

$$F = VC_1 \quad (1)$$

where F is ion flux, V volumetric solution flow rate and C_1 solution concentration. Diffusion is defined in general by

$$F = -D \frac{dC}{dx} \quad (2)$$

where D is the diffusion coefficient, C the total concentration of the diffusible ion in the soil, and x the distance. For non-adsorbed solutes we can define the flux by

$$F = -D_1 \Theta f_1 \frac{dC_1}{dx} \quad (3)$$

where D_1 is the diffusion coefficient in solution, Θ is the volumetric water content in the soil, and f_1 is the tortuosity factor which expresses the irregular and indirect pathway of diffusion in the pores of the soil.

Potassium ions, and many other solutes, do adsorb on the soil medium. It greatly simplifies the treatment of these if we may assume that ions are only mobile when in solution, and not when on the exchange complex². Then

$$D = D_1 \Theta f_1 \frac{dC_1}{dC} = D_1 \Theta f_1 \frac{1}{b} \quad (4)$$

where b is the buffer power of the soil for that ion. For small percentage saturation with potassium, it is permissible in many soils to assume that

$$\frac{dC_1}{dC} \sim \frac{C_1}{C}$$

The general equations for flux may then be stated as

$$F = VC_1 - D_1 \Theta f_1 \frac{dC_1}{dx} \quad (5)$$

and for concentration changes with time and position as

$$b \frac{dC_1}{dt} = D_1 \Theta f_1 \frac{d^2C_1}{dx^2} - V \frac{dC_1}{dx} \quad (6)$$

Equation (6) defines conditions in 'linear transient state systems'. Equivalent equations for cylindrical systems are also available.

The underlying theory is thus well established, but a number of practical problems remain:

- (a) The theory is for a completely homogeneous medium. In many

cases we consider transport over distances which are small compared with the aggregate size of the soil, and the effects are not known. Virtually all measurements so far have been made in sieved, uniform soils, and data for structured field soils are necessary.

(b) f_1 is not easy to measure accurately, especially in dry soils, where its value is very small and where diffusion is most likely to be rate-limiting.

(c) The definition and measurement of the buffer power, $\frac{dC}{dC_1}$, may be difficult. For cations, such as potassium, it is affected by two special factors. Firstly, exchangeable cations are replaced by other cations, and the identity of the replacing ion determines the relative binding strengths. Replacement is usually by Ca, but in acid soils it may be Al³⁺ and in saline soils Na. Secondly, the electrolyte concentration in the soil solution has a major effect, as can be seen from the Q/I relationship⁶. If the activity ratio $\frac{(K)}{\sqrt{(Ca+Mg)_{ex}}}$ is constant

for a given value of the exchangeable potassium K_{ex} , then (K) will vary with $(Ca+Mg)$, which normally is close to the total soil solution molarity. In our notation, $K_{ex} + \Theta(K) = C \sim K_{ex}$ and $(K) = C_1$. Hence

$$\frac{1}{b} = \frac{dC_1}{dC} \sim \frac{C_1}{C} \sim \frac{(K)}{K_{ex}} = G \frac{\sqrt{(Ca+Mg)}}{(Ca+Mg)_{ex}} \sim G \frac{\sqrt{\text{soil solution molarity}}}{\text{Exchange capacity}} \quad (7)$$

where G is Gapon's constant. Hence b can never be a 'constant' for a given soil but has to be assessed in each situation. In addition, potassium may have a concentration-dependent diffusion coefficient, if the slope of the Q/I curve (and hence $\frac{dC_1}{dC}$) changes, as it usually does at low values of the activity ratio. This can however be dealt with by averaging D or by using computer modeling techniques.

TABLE 1. Transport of potassium

Situation	Mechanism	Speed cm day ⁻¹
In profile	Mainly mass flow	Up to 10
Around fertilizer source	Mass flow and diffusion	ca 0.1
Around root	Mainly diffusion	0.01-0.1
Out of clay interlayers	Diffusion	10 ⁻⁷

TRANSPORT IN THE IMMEDIATE VICINITY OF ROOTS

A variety of models have been prepared for the transport of ions to roots¹, differing mainly in whether a limited or infinite system is assumed, and in the boundary conditions ascribed to the absorbing root surface. The practical questions to which these models should be applied, concern the position of the rate-limiting step in potassium uptake⁶, and can be stated as (a) Is the concentration of potassium at the surface of the root appreciably reduced by transport processes? (b) If so, does this restrict the uptake rate of potassium by the plant as a whole? For the purposes of this discussion we use the 'steady state' model of Baldwin *et al.*⁷, because of its simplicity, and because it allows for root competition. This gives

$$\frac{C_{1a}}{\bar{C}_1} \sim \frac{1 + \frac{V_a a}{Db} \ln \frac{x}{1.65a}}{1 + \frac{\alpha a}{Db} \ln \frac{x}{1.65a}} \sim \frac{1}{1 + \frac{\alpha a}{Db} \ln \frac{x}{1.65a}} \quad (8)$$

where \bar{C}_1 is the mean liquid phase potassium concentration in the soil, C_{1a} the liquid phase potassium concentration at the root surface, V_a the water flux at the root surface, a the root radius, α the root absorbing power and x the mean half-distance between roots. Note that $Db = D \frac{dC}{dC_1} = D_0 \theta f_1$, from equation (4).

All experiments so far have supported the early prediction of Barber⁸ that mass flow would not be very important for potassium. This must be particularly true under deficiency conditions, when C_1 must be small. Hence we can ignore the terms containing V_a in equation (8). All models then predict a lowering of C_{1a} below C_1 , and the factors which determine this are best seen by re-writing (8) in terms of I, the inflow or rate of uptake of potassium per unit length of root. αa is defined by

$$I = 2a \alpha a C_{1a} \quad (9)$$

$$\text{Hence} \quad \frac{\bar{C}_1 - C_{1a}}{\bar{C}_1} = \frac{I \ln \frac{x}{1.65a}}{2a Db \bar{C}_1} \quad (10)$$

The relative lowering of the concentration at the root surface thus depends directly upon I, and inversely upon Db and \bar{C}_1 . The root size and distance between roots have, in the first instance, less effect because they occur in logarithmic terms. Taking the reasonable values $I=10^{-12}$ mole cm⁻¹ s⁻¹,

$x = 0.28$ cm, $a = 0.02$ cm, $D_b = 10^{-6}$ cm² s⁻¹ and $C_1 = 10^{-3}$ M, there will be a 34% reduction in concentration at the root surface. Table 2 lists published experiments which have mostly found decreases larger than this. A recent published model of potassium uptake⁹ does not give sufficient data to allow this calculation and has therefore not been included. If root-soil contact is poor, or part of the root system is ineffective, then the real I values and depletion at the root surface will be still larger than estimated.

TABLE 2. Reported uptake parameters for plant experiments with potassium

Species	State	I mol cm s ⁻¹ × 10 ⁻¹³	$\frac{C_1 - \bar{C}_{1a}}{100 C_1}$	$\frac{\alpha a}{D_b}$ Cm ² s ⁻¹ × 10 ⁻⁶	References
Onion	Laboratory	10-40	21-53	0.5-1.5	15
Onion	Laboratory	0.02-0.03*	92-99	0.3-0.6*	12
Onion	Laboratory	10-50	20-100 ⁺	—	16
Rape	Laboratory	4-20	80	2	17
Ryegrass	Laboratory	1-10	1.47 ⁺	0.1-3	10
Leek	Field	10-15 ^o	60-86	1.4	18
Maize	Field	0.2-50 ^o	—	—	19
Oil palms	Field	3	30	0.3	20

^odepending upon age.

⁺depending upon soil.

*calculated from root plane data to single root basis by assuming $a = 0.03$ cm.

It is uncertain at present how plant roots react to such a decrease. At low concentrations the well-known Michaelis-Menten type uptake equation approximates closely to the first-order conditions implied by equation (9). In this case I will be reduced proportionately to C_{1a} , but there is much evidence that plants can adapt to low-nutrient conditions, and that αa will increase when the plant is stressed by low soil potassium levels. The value of any such adaptation is however strictly limited, because the restriction on supply to the root by diffusion becomes more and more dominant as the term $\frac{\alpha a}{D_b}$ becomes larger, and in the limit further increases in αa , have no effect. Thus in the example given above, that value of inflow requires a concentration difference ($\bar{C}_1 - C_{1a}$) of 0.34×10^{-3} M, and if \bar{C}_1 falls below this value, I cannot be maintained by any change in αa , because C_{1a} cannot be less than zero.

In such cases the plant must respond by having a lower internal potassium concentration, by growing more slowly (i.e. suffering a yield decrease due to potassium deficiency), producing a greater length of root per unit plant weight, and/or by producing root hairs. The last is generally supposed to aid phosphorus uptake greatly, by absorbing outside the depleted zone around the root, but this zone is so much larger for potassium that the benefits would be fairly small with root hairs of average length (ca 1 mm)¹⁰. Mycorrhizal hyphae probably absorb and translocate potassium to the host plant¹¹, but there is as yet no good evidence that they can prevent deficiencies.

The data in Table 2 show that there is normally a sharp decline in concentration at the root surface. Far more data are however required from field investigations, especially on sites known to be deficient. The most difficult part in such work is to estimate how local I values are distributed over the total root surface. It is relatively easy to measure the mean I over the whole root system, but the concentration depletion depends upon the local value of I. In homogeneous soil it may be argued that I is reasonably constant, but this is most unlikely in field soil profiles with varying water and potassium contents. Methods for dealing with such situations are urgently needed.

Of all the experiments in Table 2, only that by Dunham and Nye¹² has actually measured, rather than inferred, a concentration decrease. However, the fair agreement found by these workers between theory and measurement, supported by the autoradiographic measurements of Place and Barber¹³ suggest that the theory is reliable, and that these decreases do actually occur.

Very recently the results of Baligar and Barber¹⁴ have raised doubts over some of the assumptions on which the theory rests. They measured the Rb/K ratio of ions absorbed into plants, in the soil solution, and on the exchange complex of the soil in which the plants grew. They reasoned that if plants absorb directly from the soil solution—as is assumed in this theory—then the ratios in both should be similar because there is little plant selectivity between these ions. In fact it was similar for wheat and onions, but for maize, the ratio in the plant was much closer to the ratio in the exchange complex than to that in solution. It is suggested that this indicated diffusion of exchangeable ions directly into the plant root. If this result is confirmed as contradicting current theory, new interpretations will be urgently required. The explanation could lie in excretion of hydrogen ions by the root, which would tend to reduce the exchange capacity of the soil, and

thereby displace a large fraction of the exchangeable cations locally around the root. However, the root density of maize was far larger than for the other two crops, and it is possible that the degree of exploitation was so great that the total supply of ions was more important than the solution concentration. The theory outlined above requires development when uptake continues over a long period from a limited soil system, because \bar{C}_1 then itself alters. This development of equation (8)⁷ gives

$$\frac{M_t}{M_\alpha} = 1 - \exp\left(\frac{-2\pi\alpha a L_v t}{b\left(1 + \frac{\alpha a}{Db} \ln \frac{x}{1.65a}\right)}\right) \quad (11)$$

where M_t and M_α are plant uptakes at respectively times t and infinity, and L_v is the root density. In this case b is much more important, because it represents the size of the total reserve present. It is simple to show from this that for two ions (K and Rb) with the same α , absorbed by the same root system,

$$\frac{\ln(1 - M_t^{Rb}/M_\alpha^{Rb})}{\ln(1 - M_t^K/M_\alpha^K)} = b^K/b^{Rb} \quad (12)$$

and experiments to test this equation are required.

Equation (11) shows how existing methods of characterizing availability are included within this theory. M_α is the total amount of available, or exchangeable, potassium present per unit amount of soil, and the close relationship between b and the Q/I diagram has been explained above. To these are now added the plant parameters αa , L_v and x , and the transport properties of the soil which are described by Db . The equation thus includes all aspects of ion uptake by a uniform, regularly spaced root system growing in homogeneous soil.

TRANSPORT FROM FERTILIZER INTO SOIL AND WITHIN THE PROFILE

Superficially transport from fertilizers is a very simple problem. Potassium fertilizers are almost all highly soluble, and simple salt diffusion could carry them out from granules into soil, or mass flow caused by rain could distribute them even more widely. This undoubtedly occurs, but the dissolution of salts in soil is by no means simple. Gradients of water vapour are set up in the soil, and a saturated salt solution forms from condensed water; this then moves out into the soil by mass flow, and the direction

may be preferentially downwards because of its high density. For this reason fertilizer salts distribute themselves more rapidly in the soil than simple diffusion theory would indicate.²¹

Initial distribution is thus rapid. The soluble anion (e.g. chloride) continues to diffuse outwards rapidly, but potassium will exchange with other cations, and it will in effect soon be left behind by the chloride front. Further movement of potassium is then progressively slower as the soil solution becomes more dilute, and enriched soil pockets can persist for long periods.

Our practical interest is that potassium shall be sufficiently mobile to be adequately distributed, but not so much that it is readily lost. With cultivated arable soils, there is good distribution of applied potassium fertilizers, but this is less certain when it is applied only on the surface, as in orchards, grassland and in zero-cultivation systems. In these systems there is a sharp concentration gradient near the surface²² (Table 3). A steady-state system is established, in which potassium application at the surface balances plant removal, leaching and diffusion downwards. P. Robinson (personal communication) also found an exponential distribution of exchangeable potassium with depth under barley where zero cultivation had been practised for six years, with constant values below 10 cm. Diffusion appeared to be the most important transport process, and biological agencies such as earthworms were of little importance. It appears that potassium applied in this way will be adequately available to the plant in humid climates, but it might not be so in drought periods or semi-arid areas.

TABLE 3. Distribution of potassium, with ploughed and direct-drilled soil carrying barley (after Drew & Saker²³)

Depth cm	Potassium ($\mu\text{g g}^{-1}$) in soil	
	Ploughed	Direct-drilled
0-2.5	374	638
2.5-5	411	648
5-7.5	379	473
7.5-10	378	416
10-20	350	345
20-30	262	304
30-40	237	282
40-50	215	236

The theory of leaching is well developed, and can best be described as a combination of the transport theory outlined above with the concepts of chromatography. In the simplest case the solute follows the uniform water flow, and the only effect leading to dispersion or 'band-spreading' during downward movement is diffusion. If the solute is adsorbed, it will be slower than a non-adsorbed solute by the factor θ/b , which is the fraction of the solute actually in solution at any time. From the earlier discussion (equation (7)) it is clear that b for a cation depends on the exchange capacity, and rapid leaching in sandy soil is thus to be expected.

Leaching will also be increased by a high water flux, a high electrolyte concentration in the soil solution and a high percentage saturation of the exchange complex with potassium. Unnecessary additions of soluble anions such as chloride will therefore promote leaching losses. However, if a given quantity of soluble anions has to be leached out, then the loss of potassium is least if they are leached out in a small, concentrated volume, rather than in larger and more dilute volumes, due to the square

root term in the activity ratio $\frac{K}{\sqrt{Ca+Mg}}$. Thus Terman and Allen²³ found that the cumulative leaching losses were largest where potassium chloride was applied in split instead of single dressings.

This approach is almost certainly sufficient for rough prediction in most soils, but it is not adequate for accurate work on structured soils. Some degree of hydrodynamic dispersion in the direction of flow always occurs²⁴, which tends to eliminate any concentration gradients, and can be taken into account by using a 'dispersion coefficient' instead of the diffusion coefficient. In strongly structured and fissured soils this effect may be very marked, and much attention has been given to it in relation to nitrate leaching e.g.²⁵. However, such soils are almost always fine-textured, and leaching of potassium is therefore likely to be small. It seems probable that most cases of practical importance can be dealt with by the simple theory.

TRANSPORT OF POTASSIUM OUT OF MINERALS

Potassium is supplied to the soil solution, if it is sufficiently dilute, from micaceous clays, feldspars and other soil minerals. If this occurs by total dissolution of the mineral surface, it is essentially not a transport phenomenon, though the transport of the solution products away from the surface may possibly be a rate-limiting step.

However, the loss of potassium from micaceous clays involves transport in the interlayer space before it can be exchanged out into the solution and this has been treated as a diffusion process by several authors. Chute and Quirk²⁶ used a planar model for mica, and Talibudeen *et al.*²⁷, considered diffusion-controlled release from a planar 'periphery' and a spherical 'matrix' phase. Both obtained diffusion coefficients of the order of 10^{-10} cm² s⁻¹. However, de Haan *et al.*²⁸ found the much smaller value of 10^{-23} cm² s⁻¹ for *self* diffusion, in which there is no net loss of potassium from the clay. It is therefore questionable whether this release can be properly regarded as a simple diffusion process in the long term. When potassium is lost, the clay laminae separate at the edge, hence the state of the clay alters. It may be more reasonable to view the process as the slow penetration of a zone of alteration into the mineral, though diffusion models may be appropriate for short-term studies.

CONCLUSION

Present results suggest that transport of potassium to roots in soil can be rate-limiting to uptake, especially when a plant is becoming deficient. However, the number of experiments is small, and the interpretation relies heavily on diffusion theory. Further work seems called for, and this should be done under conditions as near to those in the field as possible.

The transport processes in the profile can undoubtedly decrease availability of potassium, by excessive leaching or by insufficient penetration from above, and the processes are well understood in principle.

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