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A TRANSPORT KINETIC CONCEPT OF ION UPTAKE FROM SOIL BY PLANTS

II. THE CONCEPT AND SOME THEORETIC CONSIDERATIONS

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SUMMARY

By means of a transport kinetic concept the uptake of a given ion by plants can be expressed as a function of the concentration of the ion in soil solution, isolated from the soil *in situ* in the soil–plant system at any given time during the growth period without disturbance to growing plants.

The kinetic model rests on the assumption that the rate determining step in ion absorption at concentrations of 1 m*M* or less, is located in the tissues between epidermis and xylem and in all probability in the plasmalemma of the cortical cells.

As the rate of ion transport through the cell membrane may be expressed by a kinetics, analogous to that proposed by Michaelis and Menten for enzyme-catalyzed reactions, the rate of uptake (v) of ion M at any time may be expressed by the differential equation

$$v \rightarrow v_{t_a} = V_{t_a} \left[\frac{(M)}{(M) + Km}\right]_{t_a} \quad \text{for } t \rightarrow t_a$$

The uptake by plants of M during a time interval t_0 — t_n is expressed by the integral of above equation.

One solution is submitted and experimental conditions, necessary for a verification of the proposed kinetic concept, are discussed.

INTRODUCTION

The transport of nutrient elements to roots, the absorption by and translocation in plants are complicated processes. Results of studies of specific parts of the overall ion transport have elucidated the nature of the processes and added to the understanding of some of the mechanisms involved. Most of the studies on factors which influence the movement of plant nutrient elements in soils have been carried out in the absence of plants, and almost all detailed investigations on absorption and translocation of nutrient elements in plants were conducted as short-term experiments in water cultures with plant organs and /or intact plants.

However, there still remain many unknown details in respect of values and variation in values of various factors governing ion absorption by plants growing in soil. This is due not least to the difficulties of determining the actual concentrations or activities of nutrient elements in soil solution near ion absorbing roots.

However, the method developed by the author [20], of isolating the soil solution *in situ* during the growth period without disturbance of the growing plant, has opened up new possibilities of studying the absorption of nutrient elements.

In the present work a transport kinetic concept of the absorption of nutrient elements from the soil by plants is submitted. Verification of this, based on the results of chemical analyses of isolated soil solution and plants, is to be presented in a subsequent publication.

UNDERLYING ASSUMPTION IN THE TRANSPORT KINETIC CONCEPT.

The absorption of an ion by plants in a given soil–plant system gives rise to and generally equals the net flow (sum of convective and diffusive flow) of the ion to the root (for further details see [24]).

It is well established that ion absorption, when the concentration of the considered ion in the nutrient solution is 1 m*M* or less, depends on carbohydrate supply to the root from aerial plant organs, is sensitive to inhibition of the metabolism of the root cells, and is almost uninfluenced by variation in the transpiration of the plant [3 17 19 30]. This supports the assumption that the rate determining step in ion absorption at the above concentrations is located in the tissues between the epidermis and xylem in the root. The present transport kinetic model for ion absorption is based on this assumption.

If the premise proves tenable, it is possible to express the rate (v) of the absorption by the plant of a given ion M as a function of (a) the concentration [M] in the nutrient solution at the active root surface, (b) the area (A) of the active root surface, and (c) the conductivity (k′) of the active root surface for M.

The establishing of a transport kinetics, thus includes both defining the circumstances under which the rate of transfer through the active root surface is the rate determining step for ion uptake, and deducting equations which express the rate and changes in rate of transport in the rate determining step as a function of [M], A, and k′ or analogous factors.

Epstein and Hagen [5] were able to express the rate of ion accumulation in excised barley roots as a function of ion concentration in the nutrient solution by a kinetics, analogous with that of Michaelis and Menten for enzyme catalyzed processes.

Results of later investigations [4 7 8 11] showed that there are at least two systems – a double mechanism – involved in ion accumulation in roots: System I, which operates at low concentrations (1 m*M* or less) of the ion in the nutrient solution, and System II operating at concentrations between 1 and 50 m*M*. The importance of this double mechanism for ion accumulation in excised roots was further illustrated by Torrii and Laties [28] with results suggesting that System I operated in the plasmalemma and System II in the tonoplast of the root cells.

If the transfer of an ion through plasmalemma into the symplast (System I) governs the transport of the ion to the aerial parts of the plant, the rate of this transport may be expressed by the same kinetics as for System I, as shown by Lüttge and Laties [15 16], who also showed that the sensitivity to metabolic inhibitors differs for System I and System II, whereas ion transport both to the top and into the symplast (System I) were affected to the same degree by inhibitors, when the concentration in the nutrient solution was 1 m*M* or less (for details see Lüttge [17]).

The findings support the view that at low concentrations (1 m*M* or less) the transfer of an ion through the plasmalemma of cortical cells determines the rate both of the uptake and of the transport to the aerial part of the plant of the ion.

THE KINETICS FOR ION TRANSPORT THROUGH PLASMALEMMA

Key to main symbols.

A	area of the active root surface (cm^2 $plant^{-1}$).
k′	conductance of active root surface (cm $time^{-1}$).
k	(with subscript): rate constant.
Km	concentration of the ion M at the active root surface required for half-maximal uptake rate (mol $litre^{-1}$).
[M]	concentration of the ion M at the active root surface (mol $litre^{-1}$).

$[M]_b$	concentration of the ion M in bulk-solution (mol litre^{-1}).
ΣR	total number per plant of effective 'carriers' in plasmalemma of cortical cells.
r_o	radial distance between the centre axis of the root to the root surface (cm).
r_b	radial distance between the centre axis of the root and the bulk-solution (cm).
t	time (sec, min, hour or day).
v	rate of ion uptake (mol time^{-1}plant^{-1}).
v_m	mean rate of ion uptake in the time interval Δt (mol time^{-1} plant^{-1}).
V	maximal rate of ion uptake (mol time^{-1} plant^{-1}).
V_m	mean maximal rate of ion uptake in the time interval Δt (mol time^{-1} plant^{-1}).
x	fraction of absorbed ion translocated to the aerial part of the plant.
$1-x$	fraction of absorbed ion remaining in the root.

Of the numerous hypotheses put forward as models for the transport of ions through cell membranes, the mobile carrier models, according to Stein [27], represent the most acceptable hypothesis although details of the mechanisms involved are still not fully known [25 26 37].

The carrier model used below can be illustrated by the following reaction steps:

I	$M + R \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} MR$	Establishing of the ion-carrier-complex on the outside of the plasmalemma.
II	$MR \underset{k_{-2}}{\overset{k_2}{\rightleftharpoons}} R + M$	Transport of ion-carrier-complex through the membrane and dissociation of the complex on the internal side of the plasmalemma.
III	$M \underset{k_{-3}}{\overset{k_3}{\rightleftharpoons}} \begin{cases} xM \\ \\ (1-x)M \end{cases}$	Fraction of total absorbed M translocated to the aerial part of the plant. Fraction of total absorbed M remaining in the root.

where k with index denote rate constants for the respective reactions, and M and R are, respectively, the ion and the 'carrier'.

The carrier model is in accordance with observations that following some fast transport processes in 'water-' and 'Donnan-free space' the rate (v) of ion absorption in plants remains constant for several hours, and that v asymtotic approaches the maximum rate (V) as the concentration of M in the nutrient solution increases. As shown by Epstein and Hagen [5] this relationship can be expressed by

$$v = V \frac{[M]}{[M] + Km} \qquad [1]$$

where the value of Km (analogous with the Michaelis-Menten constant) is the same as [M] at which $v = V/2$.

As the efflux from the roots of M, at concentrations of 1 m*M* or less, is very small in balanced nutrient solutions [1] [2], k_{-2} in reaction step II may be neglected. It follows from the carrier hypothesis and reaction steps I and II that

$$V = k_2 \Sigma R \text{ and } Km = \frac{k_2}{k_1} + \frac{k_{-1}}{k_1}$$

where ΣR is the total number of effective 'carriers' in the plasmalemma of cortical cells in the root; k_2/k_1 and k_{-1}/k_1 are respectively the kinetic constant of the reaction and the complexicity constant of the presumed ion-carrier complex.

A TRANSPORT KINETICS FOR ION ABSORPTION BY PLANTS AT VARYING VALUES OF V AND [M] DURING THE EXPERIMENTAL PERIOD.

Using the above carrier hypothesis and Equation [1] on results from numerous ion uptake experiments, it has been possible to express the rate of ion absorption by intact plants or excised roots, and to explain interactions between ions during absorption [6] [12] [13] [14]. As earlier mentioned most of the kinetic studies of ion absorption have been restricted to short time (hours) experiments, generally with excised roots. In such experiments the assumption that V and Km remain constant is justified. Further, if the concentration of the ion M in the nutrient solution remains constant during the experiment, the rate (v) of ion uptake can be expressed by Equation [1] and values of Km and V calculated.

However, in transport kinetic studies during periods of several weeks, changes in V and [M] must be expected and taken into account. This necessitates equations which express rate of ion absorption during an interval of time, $\Delta t = t_{n_2} - t_{n_1}$, in which V, [M] and possibly Km may vary.

If Equation [1] is considered as a differential equation of the time (t), so that $v \rightarrow v_{t_a}$ for $t \rightarrow t_a$, it follows

$$v_{t_a} = V_{t_a}\left[\frac{[M]}{[M] + Km}\right]_{t_a} \quad \text{for } t \rightarrow t_a \tag{2}$$

where t_a is any one time in the time interval Δt.

Considering a restricted soil–plant system with y plants during the time interval from t_0—t_n, in which t_0 denotes the beginning of the growth period, where vt_0 approaches zero, and t_n indicates any one time in the growth period, the accumulated amount of the ion M in y plants up to t_n can be expressed by the integral of Equation [2].

$$\left.\begin{array}{l}\text{Accumulation of the}\\ \text{ion M in y plants at}\\ \text{the time } t_n\end{array}\right\} = \int_{t_0}^{t_n} v\,dt = \int_{t_0}^{t_n} V \frac{[M]}{[M] + Km}\,dt \tag{3}$$

$$\int_{t_0}^{t_n} v\,dt = \int_{[M]t_0}^{[M]t_n} V \frac{dt}{d[M]}\,\frac{[M]}{[M] + Km}\,d[M] \tag{3a}$$

Equation [3a] can be solved when $dt/d[M]$ remains constant during the time interval, because V and variation in value of V are independent of [M] in the considered range of concentration.

Applying the Mean Value Theorems to Integrals in solving Equation [3a] leads to Equation [4], when $[M]_{t_n} \neq [M]_{t_0}$, and to Equation [5], when $d[M]/dt = 0$ during the time interval.

Accumulation of the ion M in y plants at the time t_n

$$= v_m \Delta t = V_m \Delta t \left[1 + \frac{2.303\ Km}{[M]_{t_n} - [M]_{t_0}} \log \frac{Km + [M]_{t_0}}{Km + [M]_{t_n}}\right] \tag{4}$$

$$[M]_{tn} \neq [M]_{t_0}$$

where

$$\left.\begin{array}{l}\text{Mean rate during}\\ \text{time interval } \Delta t\end{array}\right\} = v_m = \frac{1}{t_n - t_0}\int_{t_0}^{t_n} v\,dt \tag{4a}$$

$$\left.\begin{array}{l}\text{Mean maximum rate}\\ \text{during time interval}\\ \Delta t.\end{array}\right\} = V_m = \frac{1}{t_n - t_0}\int_{0}^{t_n} V\,dt \tag{4b}$$

$$\left.\begin{array}{l}\text{Mean value of the coefficient}\\ \text{during the time interval } \Delta t\end{array} \frac{[M]}{[M]+Km}\right\} = \overline{\frac{[M]}{[M]+Km}} \qquad [4c]$$

$$= \frac{1}{[M]_{t_n} - [M]_{t_o}} \int_{[M]t_o}^{[M]t_n} \frac{[M]}{[M]+Km} d[M] =$$

$$= 1 + \frac{2.303\ Km}{[M]_{t_n} - [M]_{t_o}} \log \frac{Km + [M]_{t_o}}{Km + [M]_{t_n}}$$

If $d[M]/dt$ varies during the time interval $\Delta t = t_n - t_0$ this is divided into a series of subdivisions (Δt_i), in which $d[M]/dt$ approaches a constant value. Values for $\overline{\frac{[M]}{[M]+Km}}$ calculated for each Δt_i by means of Equation [4c] are weighted on the basis of the value of the subinterval Δt_i relative to the value of the total interval Δt $(\Delta t_i/\Delta t)$.

The sum of weighted $\overline{\frac{[M]}{[M]+Km}}$ values of all subintervals thus equals $\overline{\frac{[M]}{[M]+Km}}$ of the entire time interval Δt.

If $d[M]/dt = 0$, *i.e.* [M] being constant during the time interval, the solution of Equation [3a] becomes

$$v_m \Delta t = V_m \Delta t \frac{[M]}{[M]+Km} \qquad [5]$$

$$d[M]/dt = 0$$

As equation [4] is difficult to handle for calculating Km and V values, using manual procedure, Equation [6] and [6a] can be used in an approximate determination of Km and V_m.

$$v_m \Delta t = V_m \Delta t \frac{1/\Delta t \sum_1^n ([M]\Delta t)_i}{1/\Delta t \sum_1^n ([M]\Delta t)_i + Km} \qquad [6]$$

$$\frac{1}{v_m \Delta t} = \frac{1}{V_m \Delta t} + \frac{Km}{V_m} \frac{1}{\sum_1^n ([M]\Delta t)_i} \qquad [6a]$$

where $\sum_1^n ([M]\Delta t)_i$ is the sum concentrations in the time interval 1 — n. Equation [6a] is analogous with the Lineveawer and

Burk relationship and allows, thus, the well known graphical determination of Km and V_m.

The formulation of Equation [6] is based on the Law of Proportions in accordance with which

$$\frac{\sum_1^n (v\Delta t)_i}{\sum_1^n (V\Delta t)_i} = \frac{v_m\Delta t}{V_m\Delta t} = \frac{\sum_1^n ([M]\Delta t)_i}{\sum_1^n (([M]\Delta t)_i + Km)} = \frac{\sum_1^n ([M]\Delta t)_i}{\sum_1^n ([M]\Delta t)_i + Km\Delta t} \quad [7]$$

With $[M] < Km$ or $[M] > 8$ Km it would seem justifiable to assume without introducing larger errors, that a direct proportionality exists between $v_m\Delta t$ and $\sum_1^n([M]\Delta t)_i$; as illustrated by *e.g.* the dashed curve in Fig. 4. Under these circumstances and for small changes in [M] during the time interval, $(d[M]/dt \rightarrow 0,)$ it is evident from Equation [7] that determinations of Km and V_m, based on experimentally determined $v_m\Delta t$ and $\sum_1^n([M]\Delta t)_i$ values and Equation [6a], will approximate to values calculated by using Equation [4].

By inserting in Equation [4] values of Km and V_m, representing a range above and below those calculated from Equation [6], it is possible to investigate whether Km and V values can be arrived at, which will give a closer agreement between calculated and experimentally determined $v_m\Delta t$ values than using Km and V_m values derived from Equation [6].

SOME ASPECTS OF THE EXPERIMENTAL CONDITIONS NECESSARY FOR DETERMINING V_m AND Km

Equations [4] and [5] derived by solving Equation [3a] allow determination of value and variation in value of Km and V_m during the growth period of plants growing in soil or water culture solution.

From Equations [4], [5] and [6] it is evident that the calculation of Km and V_m, based on experimental estimations of $v_m\Delta t$ and $\sum_1^n([M]\Delta t)_i$, necessitates having a range of treatments for which $v_m\Delta t$ increases due to increases in $\sum_1^n([M]\Delta t)_i$. For the calculation of Km and V_m values it is further imperative that the variations in V during a time interval remain unaltered by treatments.

Some considerations on the experimental conditions necessary for the verification of the above transport kinetics are illustrated by the following hypothetical experiments: Two pot experiments are carried out, in which all experimental conditions are identical with the exception of varying addition of a trace element M. In Experiment 1, a mg *M*/pot is applied to all pots. In Experiment 2 increasing amounts, 0 — c (c > a) mg *M*/pot are added. Except for standard deviation, the cumulative dry matter production in Experiment 1 will be the same in all pots, because they received identical treatment. The relationship between cumulative dry matter production and time is shown schematically in Fig. 1. In Fig. 2 which depicts the relationship (Exp. 2) between increasing application of

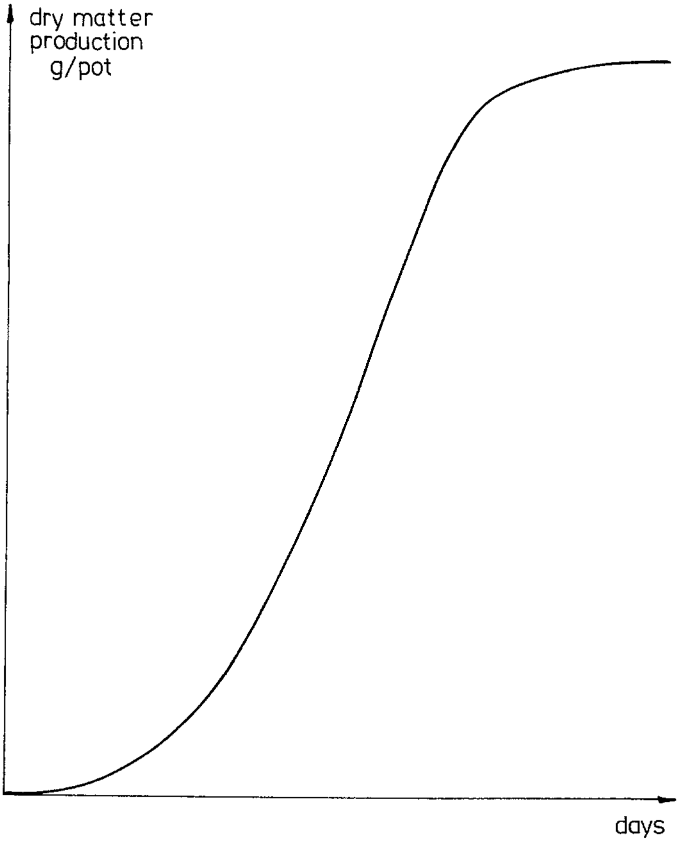

Fig. 1. Graphical representation of the cumulative dry matter production in aerial parts of plants as function of time.

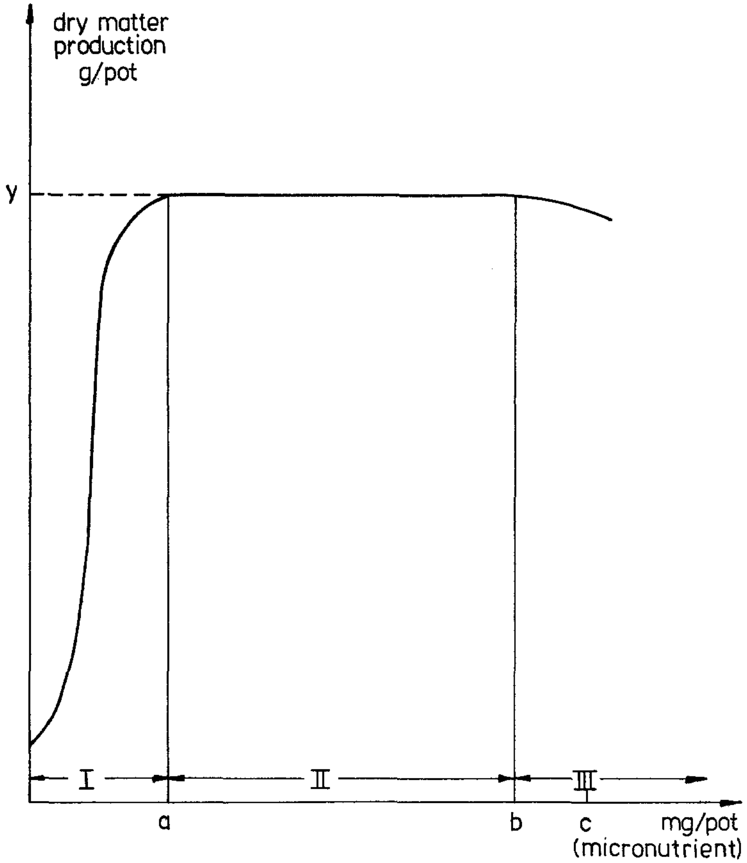

Fig. 2. Graphical representation of the relationship between dry matter production in aerial parts of plants and increasing application to soil of a micronutrient element M.

M and yield at any one time in the experimental period the results of Experiment I are represented by a single point (with the coordinates (y; a)).

From the identical cumulative dry matter production in all pots (Exp. 1) it follows that the plants are uniform and that V_m and variations of V and Km for M remain the same. This implies that any deviation from the above cumulative dry matter production must be associated with changes in V and presumably also in Km.

In Experiment 2 the uptake of M by the plants will increase due to treatment, and the relationship between dry matter production and increasing application of M can be illustrated graphically as shown in Fig. 2. The second section of the curve includes results from pots receiving M in amounts between a and b. In this section dry matter production remains constant and the cumulative dry matter production is the same for the corresponding pots, although application of M to the soil and absorption of M by the plant increases from pot to pot. Further, the same statement in regard to V_m and variations of V and of Km as made for results of Experiment I applies to this section, because the plants presumably are uniform; otherwise it would be expected that the cumulative dry matter production would differ. If the statement is correct, it should be possible, under the above experimental conditions, to obtain values of V_m and Km from determining $v_m\Delta t$, the concentration [M] in the soil solution at the active root surface, and by using Equations [4], [5] and [6].

DETERMINATION OF THE CONCENTRATION OF THE ION M IN SOLUTION AT THE ACTIVE ROOT SURFACE FROM THE CONCENTRATION IN THE BULK SOLUTION.

For some years, Nye and co-workers [18 21 22 23] have studied the variations in ion concentration in solution surrounding ion absorbing roots. The results have shown, as illustrated schematically in Fig. 3, that [M] in soil solution at the root surface can be less (curve A), the same (curve B) or larger (curve C) than the concentration ($[M]_b$) in the bulk solution, depending on whether the rate of uptake of M by the root is larger, the same or less than mass flow of M to the root due to transpiration. It is therefore only under special circumstances that $[M]_b$ equals [M] at the active root surface (curve B). The same holds for soil solutions isolated from soils carrying growing plants [20].

In pot experiments with soil where the rate of uptake of M by the plant may be expressed by the above transport kinetics, variations in ion concentration in soil solution, as exemplified in curve A of Fig. 3, are to be expected. The concentration [M] of the active root surface can under those conditions be expressed by

$$[M] = [M]_b - \Delta[M] \qquad [8]$$

where $\Delta[M] = [M]_b - [M]$ (see Fig. 3) theoretically can be regarded as an expression of the concentration gradient of the ion flux by diffusion through the radial distance ($\Delta r = r_b - r_0$) from the root surface.

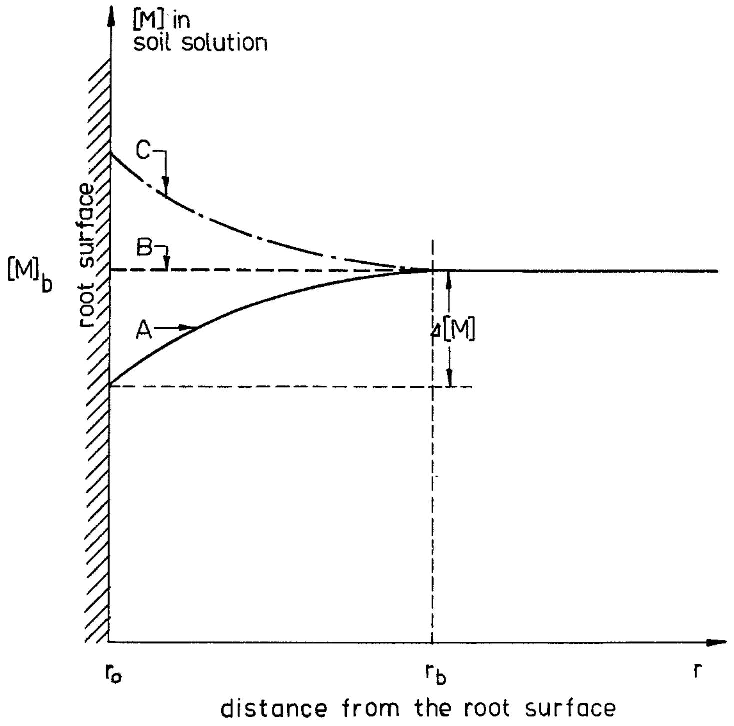

Fig. 3. Graphical representation of the relationship between the distance (r) from the centre axis of absorbing root and [M] in soil solution near root surface. $[M]_b$ greater (curve A), equal to (curve B) or less (curve C) than the concentration of M at the root surface.

From the foregoing it follows that the relationship between $v_m\Delta t$ and $\sum\limits_1^n([M]_b\Delta t)_i$ may be graphically represented as in Fig. 4. If the solid curve is extrapolated to the abscissa, the distance (a) between the zero point of the coordinate system and the point of intersection signifies the product of the apparent difference ($\Delta[M]$) between $[M]_b$ and [M] (Equation [8]) and Δt, so that $a = \Delta[M]\Delta t$. If the value of a is subtracted from $\sum\limits_1^n ([M]_b\Delta t)_i$ we obtain:

$$\sum_1^n([M]\Delta t)_i \geqq \sum_1^n([M]_b\Delta t)_i - a \qquad [9]$$

in which the equal sign approximately holds for all values of $\sum\limits_1^n([M]\Delta t)_i \leqq Km\Delta t$. Calculation of $\sum\limits_1^n([M]\Delta t)_i$ by Equation [9]

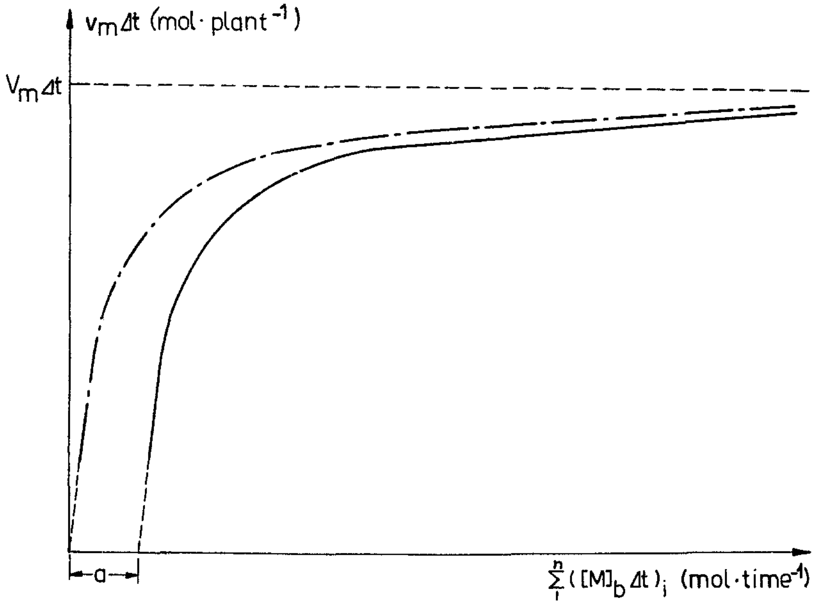

Fig. 4. Graphical representation of the relationship between the sum of the concentrations, $(\sum_1^n([M]_b\Delta t)_i)$, of ion M in soil solution and the corresponding uptake, $v_m\Delta t$ of M in the plant during the time step 1 to n (solid line) and the relationship between $\sum_1^n([M]\Delta t)_i = \sum_1^n([M]_b\Delta t)_i - a$ and $v_m\Delta t$ (dashed line).

allows, thus, a graphic determination of Km and V_m by Equation [6a], based on the relationship between $1/v_m\Delta t$ and $1/\sum_1^n([M]\Delta t)_i$.

DISCUSSION AND CONCLUSIONS

The present transport kinetic concept of ion uptake by plants includes deductions of formulae and submission of a model.

The model is based on the assumption that at low concentrations in soil solution of the given ion M, the rate determining step for absorption is located in the tissues between the epidermis and xylem in the root. This assumption is in accordance with known facts [3 9 10 17 29 30] in regard to anatomy of root and the dependence of ion uptake on the metabolism of root cells.

Irrespective of the precise location of the rate determining step in the tissues between epidermis and xylem the rate (v) is a function of a) the ion concentration in the solution at the active root surface, b) the area (A) of the active root surface, and c) the conductivity (k′) of the active root surface for the ion M.

Assuming that the used carrier model for ion transfer through the cell membrane (plasmalemma) is an acceptable basis for the interpretation of V and Km, it can be shown that $V = k_2 \sum R$. The rate constant (k_2) of the rate governing step may be considered as an expression of the conductivity (k′) of the active root surface for M; and the total area of active root surfaces (A), defined by the part of the plasmalemma of cortex cells absorbing ions either directly from soil solution or from solution in free space, may be indirectly expressed by the total number of effective 'carriers' (ΣR).

In the case of plants growing in soil over a period of several weeks, variations will occur in rate of uptake of M because of changes in [M], and in A and V due to root growth.

By the presented transport kinetics, represented by Equations [2], [4], [5] and [6], it should now be possible to express the uptake ($v_m \Delta t$) of a given ion M by plants as a function of the factors V, Km and [M] even though V and [M] may vary. Further, by indirect estimation of [M] at the active root surface as illustrated in Fig. 4, estimations of values and variations of Km and V_m, during the period of growth, should be possible from experimental determinations of the uptake ($v_m \Delta t$) and concentration of M in soil solution at successive time intervals.

The completed verification of the presented transport kinetics, based on results from a pot experiment with copper applications to barley, will be submitted in the following part.

The transport kinetics would therefore seem to open new possibilities of studying ion uptake and of interpreting the relationship between the chemical composition of plants and that of soil.

As the causes underlying variations in values of Km, V and [M] may differ, investigations on the changes in these factors by varying the plant species, growth medium, combination of applied plant nutrient elements or climatic condition should add to a better understanding of various aspects of plant nutrition.

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