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DIFFUSION AND ABSORPTION OF IONS IN PLANT TISSUE
III. THE ROLE OF THE ROOT CORTEX CELLS IN ION ABSORPTION[1]

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SUMMARY

The theoretical aspects of diffusion of Rb^+ ions in the free space of young barley roots and their concomitant absorption by the epidermal and cortical cells were studied on the basis of a simplified geometrical model.

It is concluded that participation of the cortical cells in the process of Rb^+ uptake is irreconcilable with the kinetic features of this process as determined experimentally.

Limitation of uptake to the root surface is considered to pertain to other macronutrient ions and other objects as well.

1. INTRODUCTION

In the application of carrier kinetics to experimental data on ion absorption by plant roots, the absence of appreciable diffusion resistances between the outward solution and the absorbing cell surfaces is usually implied. On the other hand, solutes are known to be able to penetrate into the cell walls and water-injected intercellular spaces of roots by free diffusion. More specifically, therefore, – ignoring effects of unstirred layers at the root surface – the tacit assumption is either that the diffusion resistance in the free space is too low to appreciably reduce the ion concentrations at the cell surfaces lining this space or, alternatively, that somehow these surfaces do not participate in the absorption process. Such an exclusion could occur if the diffusion resistance in the free space were too high to allow for effective penetration of the substance absorbed to the internal cell surfaces but could equally well be due to a lack of absorption capacity of the surfaces involved.

These problems do not seem to have been studied in any detail, and there does not seem to be any real consensus about these matters. For instance, in his 1969 review LATIES expresses doubt as to a considerable reduction of the ion concentration in the free space by absorbing cortex cells, to which he ascribes a "gathering" function. This opinion is endorsed by EPSTEIN (1972). BOWLING & ANSARI (1972) also assign the cortical cells a role in ion absorption. But VAKHMISTROV (1967), basing himself on the results of short-term experiments on

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free space depletion, holds the view that the epidermis is the only actively absorbing part of the root, the salt solution in the free space representing in a sense a ballast volume.

The divergence of these opinions justifies an analysis of the theoretical aspects of the problem. It should be kept in mind that in this study we will consider the entrance of ions into the root free space to proceed exclusively by free diffusion from the outside solution. An alternative possibility would be a radial polarity of the epidermal and cortical cells such that uptake of ions from the free space predominates at the side facing outward and release of ions into the free space at the side facing inward. For justification of this view, we may refer to the published evidence on symplasmatic transport of ions in parenchymatous tissues (cf. ARISZ 1960; KLEPPER & GREENWAY 1968).

Young barley roots served as test-material, but the conclusions drawn are deemed to have a wider bearing.

2. SIMPLIFICATION OF THE FREE SPACE GEOMETRY

For a quantitative treatment of diffusion in the root free space the complicated geometry of this space must be caught in a simplified model without loss of any essential features.

We started with transverse and longitudinal sections of a barley root (specimens are illustrated in *fig. 1, A* and *B*) grown in the usual way (cf. BANGE &

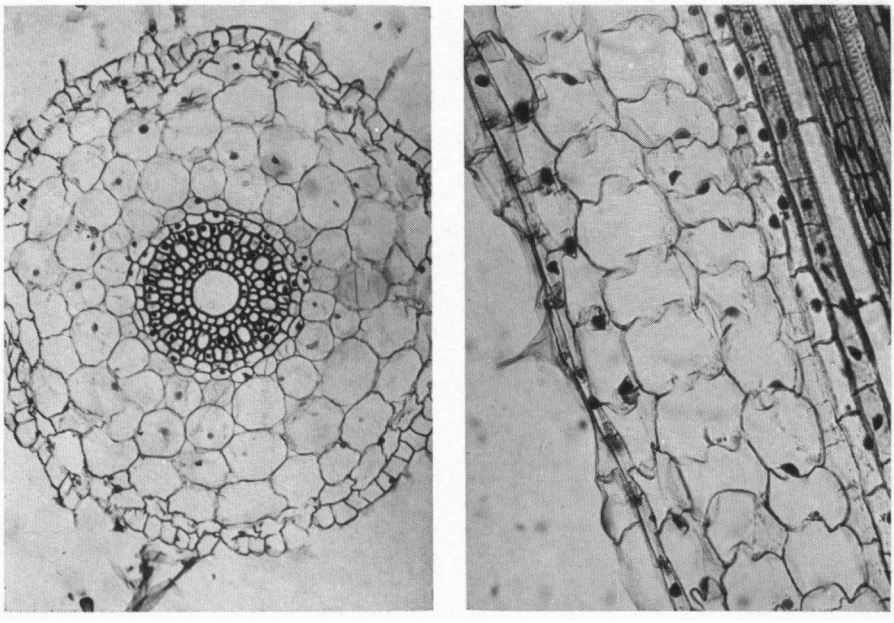

Fig. 1. Cross-section (A) and longitudinal section (B) from the mature zone of a young barley root.

MEIJER 1966) and measured in them all the essential dimensions except for the thickness of the cell walls, which was derived from electron micrographs of the same material. A transverse section of the model used is shown in *fig. 2.* "Cells" are taken as having unlimited extension in longitudinal direction. *Table 1* compares the quantitative geometrical characteristics of the root and the model.

The most salient difference between them is that in the model the thickness of the epidermal + cortical layer is reduced from 188 to 158 μm. This reduction is connected with the fact that the natural curved layer was replaced by a non-

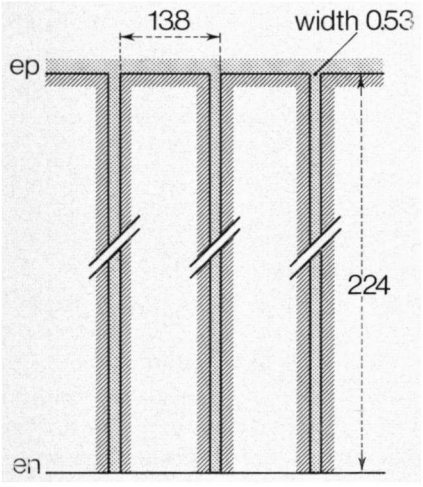

Fig. 2. Model of the diffusion volume (dotted) and absorbing surfaces (hatched) in the root cortex + epidermis; dimensions are in μm; ep = epidermis, en = endodermis.

Table 1. Comparison of the geometrical characteristics of the root and the model. Areas and volumes are given per kg fresh weight of roots.

	Root	Model
Diameter (total)	540 μm	–
Diameter of stele	165 μm	–
Thickness of epidermal + cortical layer	187.5 μm	158 (224+) μm
Thickness of cell wall	0.50 μm++	0.53 μm
Total volume of internal cell walls of epidermis + cortex	36.2×10^{12} μm³	38.3×10^{12} μm³
Total volume of intercellular spaces (lining cell walls excluded)	28.9×10^{12} μm³	0
Total area of internal surfaces of epidermis + cortex	145×10^{12} μm²	145×10^{12} μm²
Percentage of total volume of epidermis + cortex occupied by:		
cell walls (total)	3.99	4.22
intercellular spaces (lining cell walls excluded)	3.19	0
free space	7.18	4.22

+ = after multiplication by a labyrinth factor of $2^{1/2}$
++ = average value

curved layer in the model. This was done because mathematical treatment of the diffusion-absorption interaction in a curved layer is very complicated. The effect of the curvature is to reduce the average distance of the cells from the root surface as compared with a non-curved layer of the same thickness. We therefore computed an equivalent thickness for a non-curved layer (see *Appendix, 1*) and multiplied it by a labyrinth factor equal to $2^{1/2}$ to take into account the meandering shape of the diffusion path in the root cell walls. In this way we arrived at a final thickness of 225 μm for the "cortical" layer of the model.

Another point of difference is that in the model the natural system of relatively wide intercellular spaces and narrow cell walls was replaced by a "cell wall" of uniform but slightly greater thickness chosen so as to give the same diffusion resistance as in the original system. At the same time, the total diffusion volume decreased from 7.18 to 4.22%. To clarify this important point, let us represent the network of cell walls and intercellular spaces in the root by a system consisting of pieces of flat cell wall alternating with "intercellular spaces" in the shape of parallel square tubes oriented perpendicular to the direction of diffusion (*fig. 3*). The small extension of the intercellular spaces in the direction of the diffusion path (radial-tangential) justifies this representation (cf. *fig. 1*). The dimensions indicated in *fig. 3* approximate the actual mean dimensions and volume ratio of both free space components. The diffusion resistance in this system is approximately proportional to (146/0.50) + (8.7/8.7) = 293 at a volume of $146 \times 0.50 + 8.7^2 = \pm 149$ μm³. If the cell wall did not widen into intercellular spaces, the diffusion resistance of the system at equal total length would be proportional to $(146 + 8.7)/0.50 = \pm 309$. Therefore, as far as the diffusion resistance is concerned, the system of intercellular spaces and cell walls in the root may be replaced by an equivalent cell wall of equal total length but slightly larger thickness, viz. $(309/293) \times 0.50 = \pm 0.53$ μm, occupying a volume of only $(146 + 8.7) \times 0.53 = \pm 82$ μm³. Thus, despite their relatively large volume, the intercellular spaces do not effectively reduce the resistance to radial diffusive penetration into the root.

An uncertainty is introduced by the unknown value of the diffusion coefficient

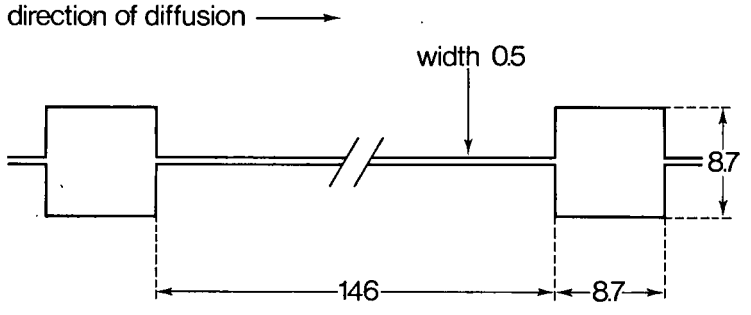

Fig. 3. Simplified model of a cell wall with intercellular spaces (cross-section); dimensions are in μm.

of RbCl in cell wall material. Reduction of the water volume and a labyrinth factor will tend to lower this value with respect to free water. Therefore, we started from a value slightly lower than in water (1.5×10^{-5} cm^2.sec^{-1} instead of 1.9×10^{-5} cm^2.sec^{-1} at 25°C) and investigated the effect of deviating values.

3. MATHEMATICAL PROCEDURE

The following symbols will be used;

a, b	parameters (cm.sec^{-1} and mmoles.cm^{-2}.sec^{-1}, respectively)
a_1, b_1	parameters valid within the concentration interval from c_1 to c_2
c	concentration (mmoles.cm^{-3})
D	diffusion coefficient in water (cm^2.sec^{-1})
D′	diffusion coefficient in cell wall material (cm^2.sec^{-1})
D_a	apparent diffusion coefficient in the tissue (cm^2.sec^{-1})
K_m	Michaelis-Menten constant (mmoles.cm^{-3})
l	total length of diffusion path in the model (cm)
m	thickness of cell wall in the model (cm)
O_c	total cross-sectional area of cell walls in the model (cm^2.kg^{-1})
O_e	total area external surface of the root (cm^2.kg^{-1})
p	concentration expressed in terms of K_m (dimensionless)
q	proportionality factor (sec.cm^{-3})
r_o	radius of root (cm)
r_i	radius of stele (cm)
v	absorption rate per unit area of absorbing surface (mmoles.cm^{-2}.sec^{-1})
V_m	the value of v at saturation (mmoles.cm^{-2}.sec^{-1})
V'_m	maximal absorption rate per cm^3 of tissue (mmoles.cm^{-3}.sec^{-1})
v_t	over-all absorption rate of the root (mmoles.kg^{-1}.h^{-1})
x	distance from inner boundary

Subscripts indicate the following:

i	at inner boundary (endodermis)
o	at outer boundary (root surface)
x	at distance x form inner boundary
1, 2	at distance x_1, x_2 from inner boundary
s	at saturation
h	at half saturation

A detailed discussion of the diffusion of a substance into and its concomitant absorption by a layer of plant tissue has been given by BRIGGS & ROBERTSON (1948). The basic equation for the steady state (dc/dt = 0) is

$$d^2c/dx^2 = q.v. \qquad (1)$$

In general, v will be a function of c. For our special case we suppose that a Michaelis-Menten relation exists between c and v. In other words, in the absence of any diffusive restraints the relation between rate of ion absorption by the cell surface and ion concentration is assumed to be given by

$$v = V_m.c/(K_m + c). \qquad (2)$$

This assumption seems justified because, within a limited range of concentrations, over-all root absorption shows saturation kinetics and consequently the basic relation must also show this behaviour. Furthermore, this type of relation is characteristic for a great number of absorption processes in all sorts of material.

Thus, we have

$$d^2c/dx^2 = q.V_m.c/(K_m + c), \quad (3)$$

the value of q in the model being given by

$$q = 2/(D'.m). \quad (4)$$

Equation (4) implies that no diffusion gradients are assumed to exist in a direction perpendicular to the cell wall plane.

Integration of equation (3) between the limits $(dc/dx)_x$, $(dc/dx)_i = O$, c_x and c_i yields

$$(dc/dx)^2_x = 4V_m.[c_x - c_i - K_m.\log(K_m + c_x)/(K_m + c_i)]/(D'.m). \quad (5)$$

Further integration at constant value of c_i would give a relation between c_x and x from which, with the aid of the known length of the total diffusion path, the corresponding value of c_o could be calculated. Over-all internal absorption being proportional to $(dc/dx)_o$ could then be computed with the aid of equation (5).

Unfortunately, further integration of equation (5) is impossible, so an approximation has to be used. For that purpose we represented the Michaelis-Menten relation by a system of five straight lines, each valid within a definite concentration interval (see *fig. 4*, *A* and *B*, and *table 2*).

The basic equation then becomes

$$d^2c/dx^2 = q.(a.c + b). \quad (6)$$

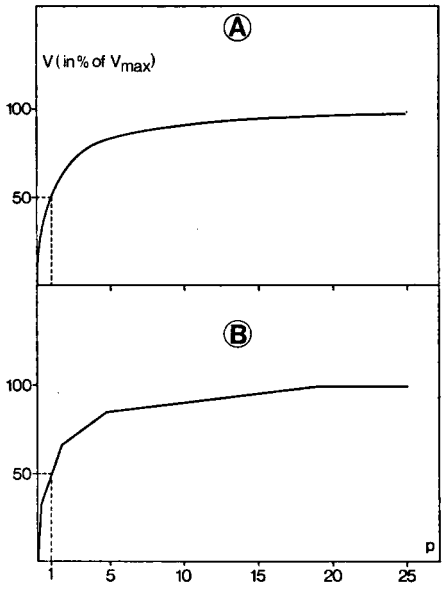

Fig. 4. The Michaelis-Menten relation (A) and the approximation used (B); concentration plotted as multiples of K_m.

Table 2. Parameters of the straight lines used to approximate the Michaelis-Menten relation and their p and v intervals.

Line number	a	b	p and v intervals	
1	V_m/K_m	0	$p = 0$	$p = 1/3$
			$v = 0$	$v = V_m/3$
2	$V_m/4K_m$	$V_m/4$	$p = 1/3$	$p = 5/3$
			$v = V_m/3$	$v = 2V_m/3$
3	$V_m/16K_m$	$9V_m/16$	$p = 5/3$	$p = 33/7$
			$v = 2V_m/3$	$v = 6V_m/7$
4	$V_m/100K_m$	$81V_m/100$	$p = 33/7$	$p = 19$
			$v = 6V_m/7$	$v = V_m$
5	0	V_m	$p = 19$	$p = \infty$
			$v = V_m$	$v = V_m$

By integration between the limits $(dc/dx)_1$, $(dc/dx)_2$, c_1, c_2, x_1 and x_2 we obtain

$$(dc/dx)_2 = [a_1.q.(c_2^2 - c_1^2) + 2b_1.q.(c_2 - c_1) + (dc/dx)_1^2]^{1/2} \quad (7)$$

and

$$x_2 - x_1 = (a_1.q)^{-1/2}.\log\{[a_1^2.(c_2^2 - c_1^2) + 2a_1.b_1.(c_2 - c_1) + a_1.(dc/dx)_1^2/q]^{1/2} + a_1.c_2 + b_1\} - (a_1.q)^{-1/2}.\log[(a_1/q)^{1/2}.(dc/dx)_1 + a_1.c_1 + b_1]. \quad (8)$$

For simplicity, it is convenient to express all concentrations in terms of K_m according to

$$c = p.K_m. \quad (9)$$

The further procedure is as follows. For any arbitrarily chosen value of p_1, with the aid of equations (7) and (8), the distance from the inner boundary can be calculated at which the concentration attains the lower limit of the next concentration interval. With new values for a and b the procedure is repeated so that for each concentration interval a value for the corresponding interval on the diffusion pathway is obtained. The length of the last interval is calculated by subtracting the sum of the lengths of all preceding intervals from the total length of the pathway. Substitution of this value in equation (8) gives the value of p_o corresponding to the chosen value of p_1.

The over-all rate of root absorption is then expressed by the equation

$$v_t = 3600.[D'.O_c.(dc/dx)_o + O_e.V_m.c_o/(K_m + c_o)]. \quad (10)$$

4. RESULTS AND DISCUSSION

The rate of Rb^+ absorption by low-salt excised barley roots in the initial rapid phase lasting about 2 hours has a saturation level of approximately 8.5 mmoles. $kg^{-1}.h^{-1}$ (BANGE & MEIJER 1966), which is attained at an external concentration of about 0.15 mM. When it is assumed that this absorption capacity is distributed uniformly over the whole external and internal surface of the epidermal and cortical cells, the maximal absorption rate per unit area of absorbing surface ($= V_m$) can be calculated to equal 0.163×10^{-8} mmoles.$cm^{-2}.sec^{-1}$. For any chosen value of K_m the relation between external concentration and

over-all absorption rate can then be calculated. *Fig. 5 A* shows the relation for a K_m value of 0.0002 mM and *fig. 5 B* for the 25-times higher value of 0.005 mM. The corresponding values of c_i are also given.

Despite the appreciable disparity of the underlying K_m values, the quantitative differences between both lines appear to be very small. Their shape deviates considerably from the Michaelis-Menten type of curve, especially with respect to a rather abrupt transition to saturation, which is due to the limited depth of the absorbing layer. This effect is the more pronounced the lower the K_m value

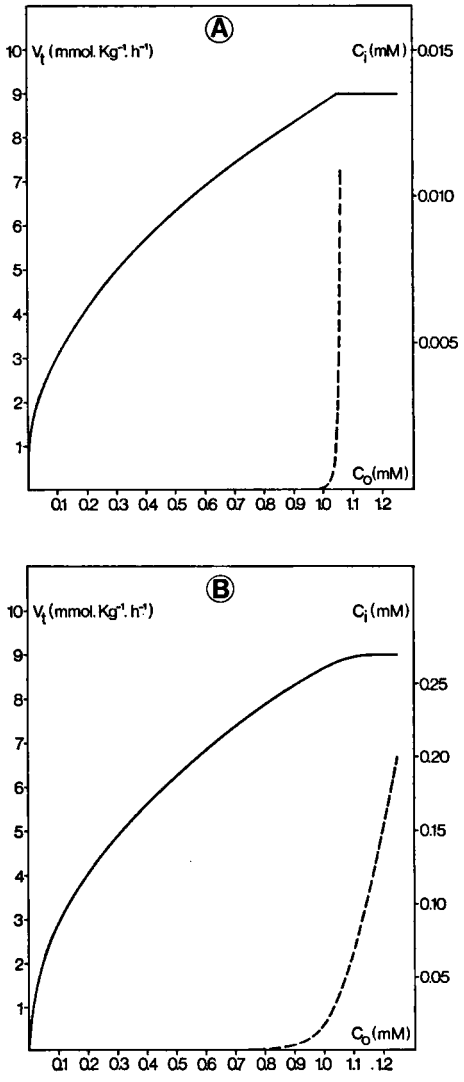

Fig. 5. Theoretical relation between the over-all rate of Rb^+ absorption (= v_t) and external concentration (= c_o) for the case that the absorption capacity observed at 0.15 mM (BANGE & MEIJER 1966) is distributed uniformly over the surface of all epidermal and cortical cells and is characterized by a K_m value of 0.0002 mM (A) or 0.005 mM (B), respectively; the dashed line represents the concentration at the inner boundary (= c_i; ordinate on the right).

chosen and reflects the abrupt increase of the concentration at the inner boundary to saturating levels when the outside concentration attains a certain value (cf. *fig. 5*). The lower the K_m value chosen, the smaller in general the outside concentration at which over-all absorption saturates. Nevertheless, it can be shown easily (see *Appendix, 2*) that however low the value of K_m, over-all absorption in the system described will not saturate below a limiting external concentration of 1.04 mM Rb^+. This value is 7 times higher than the actual saturating concentration of about 0.15 mM Rb^+. By the same token the half-value for over-all internal absorption can be shown (see *Appendix, 2*) to have a limiting lower value of about 0.25 mMRb^+ or about 20 times higher than the value actually observed.

Both these minimal values are proportional to $l^2/D'.m$. So only if the value of this factor were 7 or 20 times lower, respectively, than assumed, could theory and experiment be brought into line. Underestimation of the part played by the intercellular spaces may lead to a value that is too high, but in view of the considerations in Chapter 2 (cf. *fig. 3*) it would seem extremely unlikely that the error would be so large.

If considerable accumulation of the cation in the Donnan-phase of the cell wall occurs, diffusion will be enhanced as a result of steeper gradients. In the example chosen, 5 mM $CaSO_4$ was present in the solution. Even so, calculation shows that there is sufficient accumulation of the monovalent cation in the DFS to enhance diffusion appreciably. On the other hand, Rb^+ absorption at 0.1 mM is almost insensitive to a 50-fold excess of Ca^{++} (BANGE & HOOYMANS 1967), so apparently diffusion in a Donnan-phase is not at all involved in the process of Rb^+ uptake by excised barley roots.

Therefore, it must be concluded that a uniform distribution of the observed absorption capacity over the external and internal surfaces of all epidermal and cortical cells would result in a kinetic pattern deviating irreconcilably from the actual findings, and must consequently be rejected.

This does not imply that the internal cell surfaces show a lack of absorption capacity. There is still the alternative possibility to be examined, that in the range of low Rb^+ concentrations (below 0.5 mM) the observed absorption takes place mainly at the external root surface, although an absorption density (= absorption capacity per cm^2) similar to that of the external surface extends over all internal epidermal and cortical surfaces as well. The area of the external root surface being about 5% of the area of the internal surfaces, the value of V_m will be about 20 times higher in this case than under the assumption elaborated above, and equal to 3.38 $mmoles.cm^{-2}.sec^{-1}$.

In this situation the contribution to over-all absorption by the external relative to the internal surface will be much higher in the range of low concentrations than under the previous hypothesis, because, unlike external absorption, internal uptake at a given value of c_o increases proportionally not to V_m but to $V_m^{1/2}$ (equation 5). Consequently, the over-all concentration-isotherm in this range may be expected to deviate less from the basic relation between concentration and uptake as expressed by equation (2). This feature is demonstrated

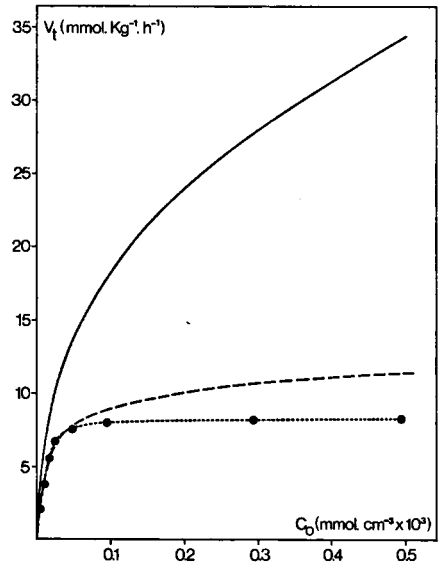

Fig. 6. Theoretical relation between the over-all rate of Rb^+ absorption ($= v_t$) and external concentration ($= c_o$) for the case that the absorption capacity observed at 0.15 mM (BANGE & MEIJER 1966) is located at the external root surface and is characterized by the half-value found experimentally, viz. 0.012 mM; the dashed line represents the same relation for a diffusion resistance 100 times larger; the dotted line is based on the absorption data embodied in fig. 2 A of the work cited above.

by the curve in *fig. 6*, which was calculated for a K_m value of 0.012 mM (cf. fig. 2 A in BANGE & MEIJER 1966). In this case equation (5) could be used, the concentration at the inner boundary being negligible in the range of concentrations studied (cf. *fig. 5*).

Despite this shift in the relative contributions of the external and internal component to over-all absorption, it appears from *fig. 6* that in comparison with the empirical relation the theoretical curve remains far from saturation. It can be shown that its rise continues until the outward concentration attains a value of about 24 mM and internal absorption exceeds external uptake by a factor of 20.

This discrepancy could be due to an overestimation of the value of the diffusion coefficient for RbCl in the cell wall material. However, internal absorption being proportional to $D'^{1/2}$, even in the unlikely case that the value of D' were 100 times smaller, the theoretical and empirical curve would not coincide (*fig. 6*).

In the case of Cs^+ absorption by the same material the discrepancy is even larger. Using the absorption data of BANGE & OVERSTREET (1960), we worked out the theoretical curves for Cs^+ absorption (*fig. 7*) to be expected under the prevailing assumption in the same way as for Rb^+ absorption in *fig. 6*. For Cs^+ absorption, the concentration-saturated region extends from 0.1 to 2 mM. Hence, even if the diffusion resistance were as much as 900 times larger than assumed in Chapter 2, theory and experiment would not be reconciled in this case (*fig. 7*).

Still, it may be argued that a secondary rise in the concentration-isotherm is more rule than exception in ion uptake by roots. But it is equally true that quite frequently such a rise sets in sharply as the concentration is increased, the re-

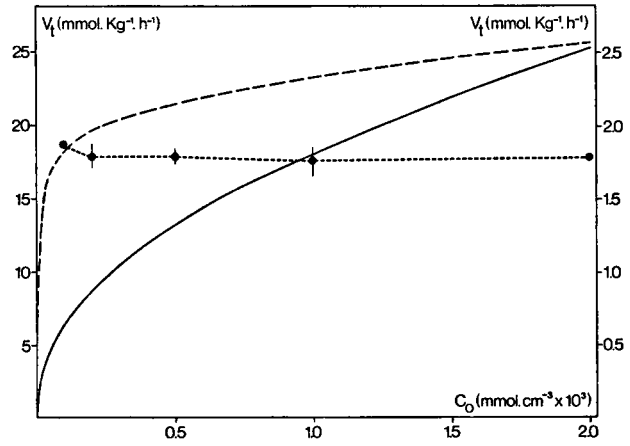

Fig. 7. Theoretical relation between the over-all rate of Cs^+ absorption (= v_t) and external concentration (= c_o) for the case that the absorption capacity observed at 0.1 mM (BANGE & OVERSTREET 1960) is located at the external root surface and is characterized by the half-value found experimentally, viz. 0.008 mM; the dashed line (ordinate on the right) represents the same relation for a diffusion resistance 900 times larger; the dotted line (ordinate on the right) is drawn through the experimental points found by the authors cited above.

sulting inflection point being preceded by a region in which the rise is negligible as in the case of Cs^+ absorption quoted above (cf. BANGE & OVERSTREET 1960). It seems inconceivable that an interplay between diffusion and absorption as visualized here could bring about such a discontinuous behaviour. Besides, a comparable secondary rise has also been described for a unicellular organism (KANNAN 1971).

These considerations seem to rule out the possibility that a latent absorption density as high as calculated for the external root surface extends over all internal epidermal and cortical surfaces as well.

Therefore, our arguments admit of no other final conclusion than that the cell surfaces lining the root free space show a lack of absorption capacity for Rb^+ ions and, presumably, for other macronutrient ions as well. It is not only extremely unlikely that the internal surfaces would discriminate between ion species in a completely different way than the outer root surface, but also argumentation similar to that presented above, albeit quantitatively somewhat different, can be given for other macronutrient ions.

The margin of the theoretical considerations on which this conclusion is based, is sufficiently ample to allow for any imperfections in the geometry of the model and uncertainties as to the true value of the diffusion resistance in the cell wall. Nor will it be of any consequence whether, in the basic relation between rate of absorption and concentration, saturation is attained in strict accordance with Michaelis-Menten kinetics or, for instance, after a sigmoid initial part of the curve. For as the external concentration rises, the contribution to over-all

uptake by cells absorbing at non-saturating concentrations becomes less and less important.

5. CONCLUDING REMARKS

In Part I of this series VAN DEN HONERT & HOOYMANS (1961) described striking differences in the relation between NH_4^+ uptake and external NH_4^+ concentration in maize roots on the one hand and potato discs on the other. Their suggestion that the difference might be due to a restriction of the absorptive capacity to the root surface is borne out by the present study provided a generalization of our inferences to other types of roots is not too bold.

Thus, the divergent behaviour of these two types of tissue reflects not a quantitative difference in diffusion-absorption relations but a more fundamental qualitative distinction. The development of an absorption capacity in discs of storage tissue is a phenomenon closely linked to the abandonment of a dormant state and as such may be expected to extend over the whole surface of the reactivated cells. On the other hand, a root is an organ adapted to water and salt absorption and therefore it would not be surprising if the absorption capacity were concentrated in the region where it can be used most effectively, viz. the outer surface. One compelling reason fur such a concentration could be the fact that under natural conditions the soil solution may be very dilute and consequently its diffusion pressure low. Expansion of this surface by root hairs would also seem to have more effect when the absorption capacity at the root surface is high than when its contribution represents only a small percentage of the overall absorption capacity.

Nevertheless, even though our conclusion can be understood from this teleological point of view, there is still the theoretical possibility that the lack of absorption capacity of the internal surfaces is due not to the absence of an absorbing mechanism but to some kind of repression of the activity of such a mechanism. At any rate it is noteworthy that the cortical cells are able to accumulate considerable amounts of ions in their vacuoles, as shown by the direct measurements of DUNLOP & BOWLING (1971) and BOWLING (1972). So apparently in these cells transport at the tonoplast can occur quite independently of transport at the plasmalemma.

As to the role of the root free space in the absorption of macronutrient ions, this study endorses the statement by Vakhmistrov referred to in the introduction, i.e. that it represents just a ballast volume without further significance.

APPENDIX

1. *Calculation of the equivalent thickness of a non-curved cortical layer.*

The amount of salt diffusing through a cylindrical plane of radius $= r_i + x$ and unit length between the outer and inner boundary is given by

$$D_a.2\pi.(r_i + x).dc/dx.$$

In the steady state this amount equals the amount of salt absorbed by the part

of the tissue between this plane and the stele. Thus, when uptake is independent of concentration and equals V'_m, we have

$$D_a.2\pi.(r_i + x).dc/dx = \pi.[(r_i + x)^2 - r^2_i].V'_m,$$

from which

$$c_o - c_i = (V'_m/4D_a).[r^2_o - r^2_i - 2r^2_i.\log(r_o/r_i)].$$

For a non-curved layer of thickness = y and width = b, we have under the same conditions

$$D_a.b.dc/dx = b.x.V'_m,$$

from which follows

$$c_o - c_i = (V'_m/4D_a).\,2y^2.$$

In order for c_i to be identical in both cases at equal c_o, we must have

$$2y^2 = r^2_o - r^2_i - 2r^2_i.\log(r_o/r_i),$$

from which for our case a value of y = 158 μm can be calculated.

2. *Calculation of the minimal value of the saturating concentration and of the half-value.*

At sufficiently high values of c_o the rate of internal absorption will saturate up to the inner boundary. In that case equation (3) is reduced to

$$d^2c/dx^2 = q.V_m,$$

from which by integration

$$(dc/dx)_x = (2q.V_m.K_m)^{1/2}.(p_x - p_i)^{1/2}$$

and

$$1 = (D'.m.K_m/V_m)^{1/2}.(p_o - p_i)^{1/2}.$$

Consequently, the saturating concentration is given by

$$c_{os} = 1^2.V_m/(D'.m) + 19K_m,$$

from which follows a minimal value ($K_m \longrightarrow 0$) of 1.04 mM.

By the same token we have at half-saturation

$$\tfrac{1}{2}(dc/dx)_{os} = (\tfrac{1}{2}q.V_m.K_m)^{1/2}.(p_{os} - p_{is})^{1/2} = 1.V_m/(D'.m)$$
$$= (dc/dx)_{oh}$$
$$= (2q.V_m.K_m)^{1/2}.[p_{oh} - p_{ih} - \log(1 + p_{oh})/(1 + p_{ih})]^{1/2}.$$

So for the value of c_{oh} we compute

$$c_{oh} = 1^2.V_m/(4D'.m) + c_{ih} + K_m.\log[(1 + p_{oh})/(1 + p_{ih})].$$

Consequently, the minimal value of c_{oh} ($K_m \longrightarrow 0$) is ¼ times the minimal value of the saturating concentration, or 0.26 mM. For over-all absorption the half-value will be only slightly lower because of the addition of the uptake by the external surface.

REFERENCES

ARISZ, W. H. (1960): Symplasmatischer Salztransport in Vallisneria-Blättern. *Protoplasma* **52**: 309–343.

BANGE, G. G. J. & J. J. M. HOOYMANS (1967): Transport of monovalent cations into, through and out of barley roots: an experimental theory. *Isotopes in Plant Nutrition and Physiology*: 249–263. International Atomic Energy Agency, Vienna.

— & C. L. C. MEIJER (1966): The alkali cation carrier of barley roots: a macromolecular structure? *Acta Bot. Neerl.* **15**: 434–450.

BANGE, G. G J. & R. OVERSTREET (1960): Some observations on absorption of caesium by excised barley roots. *Plant Physiol.* **35**: 605–608.

BOWLING, D. J. F. (1972): Measurement of profiles of potassium activity and electrical potential in the intact root. *Planta* **108**: 147–151.

— & A. Q. ANSARI (1972): Control of sodium transport in sunflower roots. *J. Exp. Bot.* **23**: 241–246.

BRIGGS, G. E. & R. N. ROBERTSON (1948): Diffusion and absorption in disks of plant tissue. *New Phytol.* **47**: 265–283.

DUNLOP, J. & D. J. F. BOWLING (1971): The movement of ions to the xylem exudate of maize roots. I. Profile of membrane potential and vacuolar potassium activity across the root. *J. Exp. Bot.* **22**: 434–444.

EPSTEIN, E. (1972): *Mineral nutrition of plants: principles and perspectives.* J. Wiley and Sons, New York.

HONERT, T. H. VAN DEN & J. J. M. HOOYMANS (1961): Diffusion and absorption of ions in plant tissue. I. Observations on the absorption of ammonium by cut discs of potato tuber as compared to maize roots. *Acta Bot. Neerl.* **10**: 261–273.

KANNAN, S. (1971): Plasmalemma: the seat of dual mechanisms of ion absorption in Chlorella pyrenoidosa. *Science* **173**: 927–929.

KLEPPER, B. & H. GREENWAY (1968): Effects of water stress on phosphorus transport to the xylem. *Planta* **80**: 142–146.

LATIES, G. G. (1969): Dual mechanisms of salt uptake in relation to compartmentation and long-distance transport. *Ann. Rev. Plant Physiol.* **20**: 89–116.

VAKHMISTROV, D. B. (1967): On the function of apparent free space in plant roots. A study of the absorbing power of epidermal and cortical cells in barley roots. *Sov. Plant Physiol.* **14**: 103–107.