Journal of Experimental Botany, Vol. 35, No. 161, pp. 1723-1732, December 1984

Dual Pattern of Potassium Transport in Plant Cells: A Physical Artifact of a Single Uptake Mechanism

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Received 12 August 1983

ABSTRACT

Analysis of potassium transport in plant root cells shows two rate-influencing regions: an unstirred boundary layer adjacent to the cell wall acts as a rate-limiting region and the negatively charged cell wall acts as a rate-enhancing region. The rate-enhancing region gives rise to a pseudo 'dual mechanism'. These two regions act in concert to influence significantly the characteristics of the concentration-dependent potassium uptake process. The anomalous ion uptake behaviour found in the literature is explained on the basis of a single active uptake mechanism operating under the influence of these two regions. The most critical property in support of the concept of a 'dual mechanism' for cation uptake in plant roots is explained on this basis. It is unnecessary to invoke separate groups of enzymes, each one of which is active over different concentration ranges. One mechanism operating over the entire concentration range is sufficient.

Key words: Potassium transport; Rate-limiting region; Rate-enhancing region.

INTRODUCTION

Short distance transport and accumulation of salts in plant roots is understood in terms of relatively simple experiments which measure the concentration dependence of ion uptake rates by excised plant roots. This type of experiment gives a collective property of root cells different from the property of cells of a mature transpiring intact plant. Nevertheless, fundamental information concerning uptake mechanisms is thought to be obtained.

The similarity between the Michaelis-Menten theory for enzyme catalyzed reactions and the experimentally observed ion uptake rates led investigators to interpret the results of such experiments as evidence of enzyme or carrier mediated ion uptake (Epstein and Hagen, 1952; Epstein, 1960). Thorough experimentation eventually led to the concept of a dual-uptake mechanism operating within the plant cell (Epstein and Rains, 1965; Epstein, 1966; Osmond and Laties, 1968). Epstein (1976) points out that a general and persistent phenomenon is always observed, the general features of which are shown in Fig. 1. He summarizes these observations by pointing out that when a continuous plot of the ion uptake rates over the entire range of bulk solution concentrations is made, then almost always a so-called 'dual pattern' is observed. It is delineated by two ranges of bulk solution concentration (C) ($C \ll 1{\cdot}0$ mol m^{-3}, high affinity mechanism 1, and $C \gg 1{\cdot}0$ mol m^{-3}, low affinity mechanism 2) over which the rate of uptake dramatically increases with increasing concentration. These regions are separated by a plateau over which no increase takes place. It is further held that separate uptake mechanisms are operating in each concentration range.

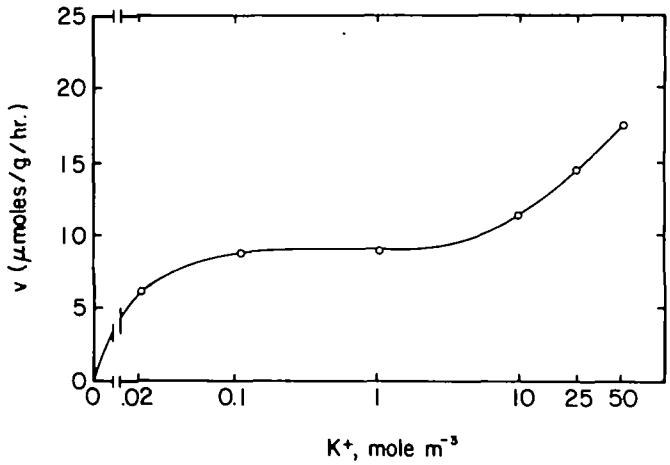

FIG. 1. Concentration dependence of potassium uptake rate in excised barley roots: taken from Epstein (1976).

By analysing available uptake data from the literature, Nissen (1973) interpreted the uptake mechanism to be a single, but multiphasic mechanism. Borstlap (1981) then argued that this multiphasic interpretation was a misconception due to inadequate statistical tests and to the assumption that the concentration-dependent uptake rate does not contain a linear term. Theuvenet and Borst-Pauwels (1976) considered uptake in the presence of competing ions. Using phenomenological rate equations describing the competition, they performed a simulation study of the effect of a membrane surface potential on the concentration-dependent ion uptake velocities. According to their model 'general deviations from Michaelis-Menton kinetics may be expected', including an 'apparent dual mechanism'. Their analysis omits any possible effect of an unstirred layer or negatively charged cell wall on the experimentally observed uptake pattern. Diffusion to the uptake site is never considered and their results are not quantitatively compared to any experimental observations.

The basic concept of a dual mechanism for ion uptake still persists and is used as a basis for interpreting fundamental experiments on ion uptake in plant roots. This paper develops an alternative theory based upon known physical phenomena, which does not require a 'dual mechanism' to explain the observed concentration-dependent uptake pattern. The theory is demonstrated for the uptake of potassium in the absence of other competing ions.

THEORY

It is assumed that enzyme mediated ion transport across lipid bilayers in plant cell membranes requires that the ion–enzyme complex form on the outer surface of the membrane. The enzyme is considered membrane bound. For the purposes of this analysis, the plasmalemma is assumed to be the site of ion complexation and irreversible absorption (Fig. 2). Since the pressure difference across the membrane is assumed to be zero, there is no convective contribution to the ion flux (Dalton, Raats, and Gardner, 1975). The steady state ion uptake rate is dependent upon the cation concentration at the plasmalemma, C_p, and is assumed to be approximated by the Michaelis-Menten equation,

$$V = \frac{V_m C_p}{C_p + K_m}, \qquad [1]$$

where V is the velocity of ion uptake and K_m is the ion concentration at which the ion uptake velocity is one-half the maximum uptake velocity, V_m.

The active uptake site is separated from the bulk solution by two distinct regions (Fig. 2): the cell wall and the stagnant boundary layer of the substrate solution. The cell wall pectin is a source of negative fixed charges. For the purposes of this analysis the density of these charges, σ, is assumed to be uniformly distributed throughout a region of thickness d. The boundary layer thickness, δ, is a constant for a given experiment but does depend upon the rate of stirring. The dimensions d and δ are well documented, while σ is left as an adjustable parameter.

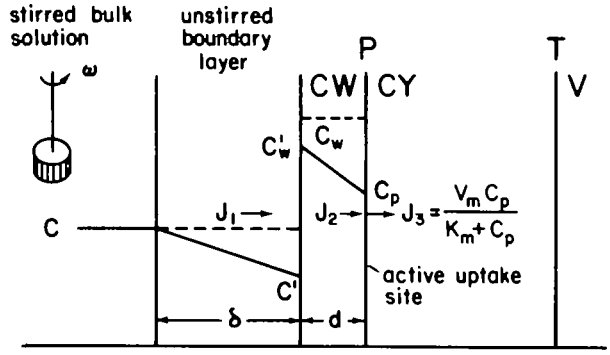

FIG. 2. Schematic diagram of plant root cell in contact with test solution of cation concentration C: CW = cell wall, P = plasmalemma, CY = cytoplasm, T = tonoplast, V = vacuole. Concentration profiles are indicated by dashed lines (---) for static, and solid lines(——) for dynamic conditions.

The initial and boundary conditions for this transport system are established by considering the experimental procedure that is used to determine the concentration-dependent, steady-state ion-uptake rates. Replicate samples of roots from 6 week old seedlings are placed in solutions of varying ion concentration. After a time interval of about 15 min the roots are removed and analytic procedures are used to determine the amount of irreversibly absorbed ions (Epstein, Rains, and Elzam, 1963). For the purposes of this analysis, the initial ion flux across the plasmalemma is assumed to be zero, in which case a static equilibrium would be established between the cation concentration in the cell wall C_w, and the cation concentration of the bulk solution, C (Fig. 2, dashed lines). As the uptake process begins, the rate is determined by the response of the active uptake mechanism to the ion concentration at the cell wall-plasmalemma interface. As ions are depleted from the interface and the concentration is reduced, there is a corresponding decrease in active uptake as described by equation 1. Similarly, there is a reduction in ion concentration at the stagnant layer-cell wall interface as ions are removed from the stagnant layer region to replenish those removed from the cell wall. The steady-state uptake rate occurs when the cation concentration at the cell wall-plasmalemma interface, C_p, is reduced to a value such that the resulting active transport velocity V is equal to the diffusional flux across both the cell wall and stagnant layer. The resulting steady-state cation gradients across the regions are indicated by solid lines in Fig. 2. C' is the reduced interfacial cation concentration in the stagnant layer solution. C'_w is the new interfacial cation concentration of the cell wall which is in equilibrium with C'.

The relationship for the equilibrium interfacial concentrations for static and dynamic conditions is obtained following Helferich (1962). By assuming equilibrium between ions in the unstirred layer and ions adsorbed in the cell wall and making use of the Poisson-Boltzman distribution law for cations, the relation between interfacial concentrations can be written

$$C/C_w = C'/C'_w. \qquad [2]$$

The steady-state ion flux across the two outer regions is approximated by integrating Fick's law of diffusion, $J = -\int D\frac{\partial c}{\partial x}$ across each region to give

$$J_1 = \frac{D}{\partial}(C - C') \quad [3]$$

and

$$J_2 = \frac{D_w}{d}(C'_w - C_p) \quad [4]$$

where J_1 is the flux through the unstirred layer and J_2 is the flux through the cell wall. D and D_w are the ionic diffusion coefficients in the stagnant layer and cell wall, respectively. Flux across the plasmalemma, is denoted by J_3, and is equal to the uptake velocity V given by equation 1. At steady state all fluxes are equal,

$$J_1 = J_2 = J_3 = J. \quad [5]$$

By substituting C_p from equation 1 into equation 4, substituting C'_w from equation 2 into equation 4, using C' from equation 3 and then making use of equation 5, one then solves for J and expresses the ion flux in terms of the bulk solution concentration C, and the static equilibrium concentration of the cell wall C_w. Considering only positive values of J and positive values of C' one obtains,

$$J = \frac{-B - (B^2 - 4AF)^{\frac{1}{2}}}{2A} \quad [6]$$

where

$$A = 1 + \frac{D_w C_w \delta}{DCd} \quad [7]$$

$$B = \left(K_m D_w + V_m + D_w C_w + \frac{V_m D_w C_w \delta}{DCd}\right) \quad [8]$$

$$F = \frac{D_w C_w V_m}{d}. \quad [9]$$

To complete the analysis, a relation between C and C_w is required. For the purposes of this analysis, it is assumed to be given by a Donnan distribution law for electrolytes in equilibrium with a medium containing fixed charges. By equating the electrochemical potential of the ions in the bulk solution phase with the electrochemical potential of the ions in the charged medium (i.e., the cell wall) and making use of the electroneutrality conditions of both phases, the equilibrium condition is obtained (Helferich, 1962). For a monovalent electrolyte such as KCl, the relation between C_w and C is

$$C_w = \left(\frac{\sigma^2}{4} + C^2\right)^{\frac{1}{2}} + \frac{\sigma}{2}. \quad [10]$$

Since C_w is now defined in terms of C, its insertion into equations 7, 8, and 9 gives the desired relationship for the dependence of the cation flux, J, on the bulk solution ion concentration, C.

ANALYSIS OF RESULTS

The parameters that make up these equations are divided into two categories: fixed parameters and adjustable parameters. The fixed parameters are those parameters whose order of magnitude value (OMV) are known from other independent measurements or are determined by experimental constraints. These include the diffusion coefficients, D and D_w; the unstirred layer and cell wall dimensions, δ and d; and the bulk solution ion concentration, C. The adjustable parameters are those parameters whose values are not known from independent experimental measurements. In this instance the adjustable parameters are the

effective fixed charge density, σ; the disassociation constant, K_m; the maximum uptake rate of the enzyme system, V_m and the effective root area, α, which contributes to the irreversible ion absorption.

The order of magnitude values (OMV) for the fixed parameters come from well documented experimental measurements. The bulk solution diffusion coefficient, D, for potassium varies slightly with concentration (Robinson and Stokes, 1959). A nominal value of 2×10^{-9} m^2 s^{-1} is used here. The diffusion coefficient of K^+ in the cell wall will be less than the diffusion coefficient in the bulk solution due to tortuosity, viscosity and electrostatic interactions. While there are no specific data available for this reduced diffusion coefficient an OMV can be obtained from other sources. The effects of tortuosity, viscosity and electrostatic interactions on the self diffusion coefficient of K^+ has been determined in a 3% clay suspension (Gast, 1963). A reduction of 50% from the bulk diffusion coefficient was observed and the same reduction is assumed for the diffusion coefficient of the cell wall. This order of magnitude of reduction in diffusion coefficient for chloride in the apparent free space of roots was also observed by Bernstein and Nieman (1960). Thus, $D_w \approx 1 \times 10^{-9}$ m^2 s^{-1}.

The unstirred boundary layer thickness depends upon the fluid velocity relative to the fixed surface of the root. Polle and Jenny (1971) reported values as low as $2{\cdot}8 \times 10^{-5}$ m for beet discs and noted that for cylindrical roots the film will be thinner than with discs. Here a nominal value of 2×10^{-5} m is used. Numerous electron micrographs of cell wall thickness have been made and while there is some variability, Bange (1973) gives an OMV of 1×10^{-7} m and this value is used here.

The dimensionless relative cation flux, J/V_m, is calculated at specific values of the bulk solution ion concentration using particular values for the fixed parameters, D, δ, D_w and d, and various values for the adjustable parameters, σ, K_m and V_m. Figure 3 shows the result of

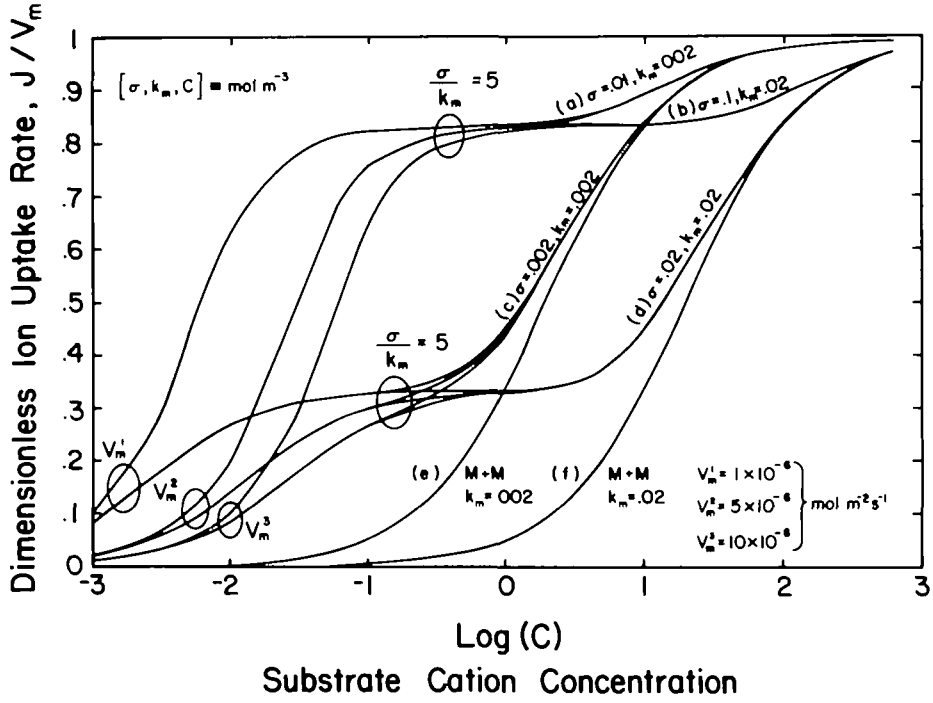

FIG. 3. Concentration dependence of relative potassium uptake rate predicted by equation 6 (curve sets a, b, c, d) and the Michaelis-Menten equation (curves e, f) for various values of σ, K_m and V_m.

these calculations for a five-fold range in bulk solution ion concentration (curve sets a, b, c, d). The relative ion flux given by the Michaelis-Menten equation (equation 1) is also plotted for comparison (curves e, f). These curves represent the possible experimental manifestations of, and deviations from, the fundamental Michaelis-Menten description of ion uptake.

Figure 3 shows that when the bulk solution ion concentration is less than 10^{-3} mol m^{-3}, curves a and b coalesce to one family of curves which are characterized by three different values of the maximum uptake velocity V_m. Curves c and d begin to coalesce at a bulk solution ion concentration of approximately 10^{-4} mol m^{-3}. In both of these concentration regions it is seen that the relative ion flux depends only on the maximum uptake velocity V_m and the ratio of the fixed charge density to the disassociation constant, σ/K_m. At higher concentrations, σ/K_m is no longer a scaling factor, and the relative ion flux depends upon the specific values of σ and K_m. At these higher concentrations, the relative ion flux approaches that of the assumed real uptake mechanism (curves e, f) and also becomes independent of the maximum uptake velocity, V_m.

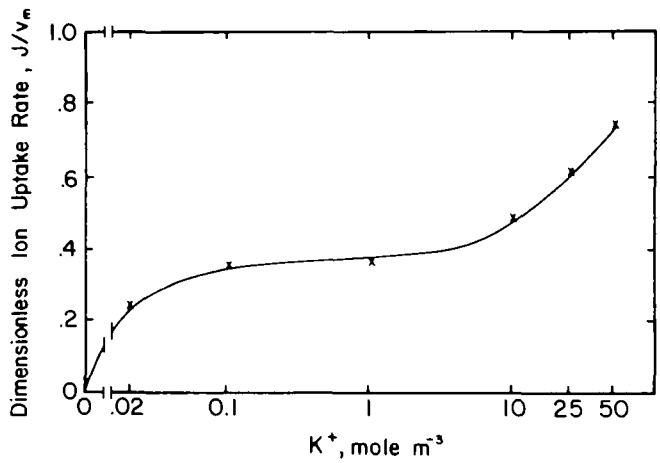

FIG. 4. Relative potassium uptake rate from equation 6, Table 1 (solid line) and experimentally determined relative uptake rate from Fig. 1 (x).

Comparing curve sets b to d and a to c shows the effects of the fixed charge density on the calculated results. Comparing curve sets a to d shows the effects of the disassociation constant on the calculated results and the effects of changing both σ and K_m are shown by comparing curves c and d.

The marked similarity between these curves and the experimental data shown in Fig. 1 is obvious. In Fig. 3, just as in Fig. 1, it is seen that after an initial increase in the relative ion flux with increasing bulk solution ion concentration, a plateau develops where the ion flux no longer increases with increasing substrate concentration (curves a, b, d). The height of the plateau increases as the ratio σ/K_m increases. The value of the bulk solution ion concentration at which this plateau begins is determined by the value of the maximum enzyme mediated ion uptake rate, V_m (see V_1, V_2, V_3 of curves a, b, c and d). Experimentally, this plateau is interpreted to be the saturation kinetics of the 'high affinity' mechanism one.

The fixed charge density, σ, affects the concentration range where the second increase in ion uptake rate occurs (compare curve sets a to c) and this second rate increase corresponds to the beginning of the so called 'low affinity' system, mechanism two.

In order to compare this theory quantitatively to the experimental data of Fig. 1, it is necessary to express the experimentally measured uptake rates in the same dimensionless

TABLE 1. *Fixed and adjustable parameters used in equations 7 and 12*

	Symbol	Units	OMV
Fixed parameters			
Bulk solution diffusion coefficient	D	$m^2\ s^{-1}$	2×10^{-9}
Cell wall diffusion coefficient	D_w	$m^2\ s^{-1}$	1×10^{-9}
Unstirred boundary layer thickness	δ	m	2×10^{-5}
Cell wall thickness	d	m	1×10^{-7}
Bulk solution concentration	C	$mol\ m^{-3}$	0 to 50
Adjustable parameters			
Maximum uptake velocity	V_m	$mol\ m^{-2}\ s^{-1}$	$4{\cdot}5 \times 10^{-6}$
Dissociation constant	K_m	$mol\ m^{-3}$	23
Effective fixed charge density	σ	$mol\ m^{-3}$	13

form as the theory. Let the superscript e represent experimentally determined ion uptake rates. Then the concentration dependence of J^e/V_m^e is compared with J/V_m. A Lineweaver–Burke analysis of the high concentration range data of Fig. 1 yields a value for V_m^e of 5·94 nmol g^{-1} fr. wt. s^{-1}. The data in Fig. 1 can now be expressed in the dimensionless form J^e/V_m^e which then becomes comparable to the relative ion flux, J/V_m, predicted by use of equations 6 and 10. The results of such a comparison are shown in Fig. 4 and the values used for the fixed and adjustable parameters are listed in Table 1. This comparison shows that to within the validity of the values used for the three adjustable parameters σ, V_m and K_m, the anomalous uptake behaviour is explained on the basis of one active uptake mechanism operating over the entire range of substrate concentrations.

Comparing theory and experiment in this way implicitly defines the effective surface area for transport per gram fresh weight of roots. Since $J^e = (V_m^e/V_m)J$, where the units of J^e are mol g^{-1} fr. wt. s^{-1} and the units of J are mol $m^{-2}\ s^{-1}$, then it follows that the effective surface area per gram fresh weight of roots is given by V_m^e/V_m, and in this case is equal to $0{\cdot}13 \times 10^{-2}$ $m^2\ g^{-1}$ fr. wt.

DISCUSSION

This theory addresses itself to the most critical property of the so called 'dual mechanism': namely the 'high affinity' of mechanism one and the 'low affinity' of mechanism two. The theory at this stage of development is not represented to be a general description of potassium uptake in mixed ionic systems. However, the components of this theory provide new insights into the physical factors affecting the dynamics of ion uptake by plant roots. In this application, a simple Donnan system is used to describe the equilibrium condition between a single monovalent cation–anion system, and is applied to experimental conditions which meet this criteria. Accordingly, one single active uptake system gives the appearance of an additional or pseudo mechanism over the low concentration range: the so-called 'high affinity' mechanism one. The qualitative effect of the fixed negative charge on the cell wall is to increase the cation concentration near the uptake sites above the cation concentration of the substrate itself. The result is an enhanced concentration-dependent uptake rate especially in the concentration range of mechanism 1 (compare curve sets a, b, c, d with e and f, Fig. 3). Therefore an erroneous picture is given of the actual concentration-dependent enzyme reaction.

While the negative fixed charge of the cell wall is responsible for the first plateau, a complete description of the uptake process needs to include the effects of the unstirred layer. In fact in the low concentration range the initial uptake rate is controlled by the physical

constants of the unstirred layer, everything else being equal. Since the unstirred layer constants are fixed by other independent measurements, the effects of different values for these parameters on the uptake kinetics are omitted in the sensitivity analysis shown in Fig. 3. However, they are quite important and provide strong constraints for this analysis. In the high concentration range the cell wall constants are the rate-limiting factor for ion uptake and changes in the unstirred layer have little effect.

According to this model a complete quantitative description of the dual uptake pattern depends on the existence of an unstirred boundary layer and a cell wall with an effective cation exchange capacity. For any given enzyme system the initial uptake rate will be controlled by the unstirred layer while the first plateau that is finally reached depends on the charge density of the cell wall. Evidence that the unstirred boundary layer exists and that it can affect ion uptake rates has been adequately demonstrated (Polle and Jenny, 1971; Winne, 1972, 1977). The existence of a cation exchange capacity of roots has also been shown (Drake, 1965) and Hiatt (1968) qualitatively implied electrostatic association and Donnan phenomena in ion accumulation. The effect is similar to the concentration-dependent fluxes observed in ion exchange resins by Boyd, Adamson, and Myers (1947) and explained by Helferich (1955). Therefore, it becomes unnecessary to invoke two separate groups of enzymes, each one of which is active over two different concentration ranges. One mechanism operating over the entire concentration range is sufficient. This is not to say, however, that this *one* mechanism is not specific for K^+, and that different enzymes cannot vary in their degree of interaction. Therefore, experimental observations of differential ion selectivity and competition as outlined by Epstein (1966) are not, as yet, exclusive to this theory.

The small surface area per gram fresh root weight that was calculated as a consequence of this theory indicates that only the surface layer of cells in the plant root are contributing to the active uptake in these experiments. At higher external solution concentrations, the larger gradients can expose more and more cells of the cortex to the permeating solution and, therefore, become a linear component to the overall uptake process.

As the roots are exposed to changing ionic strengths, the apparent free space is known to be altered (Bernstein and Nieman, 1960). Some of the physical characteristics of the cell wall, D_w, d, and σ will also change, thereby affecting the ion uptake patterns. The possibility for conformational change in the cell wall is also known to be enhanced by a supply of protons and/or a lack of calcium (Soll and Böttger, 1982) and both of these ions are strongly implicated in the overall process of salt uptake by plant roots (Epstein, 1961; Glass, Siddiqi, and Giles, 1981). According to this theory, conformational changes which may occur in the cell wall can have dynamic effects on the ion uptake characteristics of plant roots. This type of phenomena is open to further investigation and may have a strong bearing on the explanation of the varied uptake patterns observed in both the low and the high substrate concentration ranges.

While the plasmalemma was assumed to be the site of complexation in this analysis, it does not rule out the tonoplast as also being an active site for transport. According to this theory, previous arguments against the tonoplast being a site of active transport in the high concentration range (Welch and Epstein, 1969) are inappropriate because they required that the so called first mechanism be independent of, and rate-limiting to, the second mechanism. The arguments for a series or parallel system of enzyme-mediated uptake become inappropriate for the very same reasons.

This approach emphasizes that factors independent of the primary uptake mechanism give rise to anomalous patterns of concentration-dependent uptake rates. These physical factors need to be thoroughly investigated in order to at least reduce the number of phenomena which are postulated to be due solely to *ad hoc* characteristics of transport systems. While the

chemi-osmotic theory of Mitchell (1979) provides an understanding of the fundamental principles of transport mechanisms, the experimental manifestation of this primary mechanism (as measured by concentration dependent ion fluxes) will always be modulated by the physical characteristics of a stagnant boundary layer and the physical interaction of ionic species with the charged matrix of a shrinking and swelling cell wall.

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