Kinetic Studies of Anion Absorption by Potato Slices at 0 C [1, 2]

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Generally speaking, the time course of ion uptake by plant tissue is characterised by two distinct phases, a relatively short initial period of rapid uptake followed by a less rapid but prolonged period of absorption. Frequently this basic absorption pattern still holds after discounting the ions present in the water free space (WFS), i.e., that part of the apparent free space (AFS) which is in effect an extension of the medium. The term, AFS, refers to the fraction of the tissue volume into which the external solution appears to diffuse readily and equals the sum of the WFS, in which both ions of a permeating salt are freely diffusible, and the DFS in which ions (mostly cations) are held in exchangeable form by the fixed charges of the tissue. With cation uptake the absorption shoulder can be attributed to adsorption exchange on fixed negative groups (mainly free carboxyl groups) on the cell wall (See Laties, 8). A two-component anion absorption pattern is less readily observed and is more difficult to interpret. Since the cell wall with its associated DFS is predominantly negatively charged, anion adsorption to exchange surfaces is thought to be negligible, i.e. when using mobile anions the DFS assumes a zero value. Even so an anion absorption shoulder has been observed in wheat roots and potato disks by Lundegardh (10, 11, 12), who attributed the initial rapid uptake to anion adsorption sites, and in potato disks by Laties (9), who suggested that the shoulder represented latent carrier potential attending the transfer of potato slices from room temperature to 0 C. The rationale offered was that the concentration of carrier (using the term in an operational sense) present in the tissue at any given moment is a function of temperature, and that the carrier level characteristic of the steady state at 25 C is measureably higher than that at 0 C, so that on transferring tissue from 25 C to 0 C there is a transistory excess of carrier for the 0 C steady state which leads to a more rapid absorption initially.

The absorption shoulder reported by Lundegardh (10, 11, 12) is ambiguous in nature. In some experiments the technique involved a switch to a lower temperature, but it may well be that for the most part his absorption shoulders are attributable to the fact that uptake was measured by determining the salt concentration remaining in the experimental solution, and, therefore, his absorption values would include free space uptake, since a pre-absorption rinse with the test solution of only seconds duration (10) would not fill the free space. That his absorption shoulders were not under metabolic control would seem to be borne out by the fact that they varied in magnitude almost linearly with concentration yielding values unreasonably high and independent both of temperature and ion species. Only the cyanide results reported would seem to be at variance with this interpretation and their significance cannot be assessed without a clearer understanding of the separate effects of cyanide on AFS penetration and phase I uptake. The absorption shoulder observed by Laties (9), however, is directly related to a lowering of the temperature and, thus, represents a special phenomenon of particular interest since it may conceivably illumine an aspect relating to the mechanism or geometry of absorption not readily detectable otherwise.

This study was an attempt to characterise further the anion absorption shoulder in potato tissue and to determine in particular whether the carrier potential as manifested by the shoulder is specific with respect to a given ion or whether ions presumed to be transported by different carriers utilize the latent transport capacity in a mutually exclusive manner.

Materials & Methods

Russet Burbank potato tubers were cut into blocks which were pierced with a cork borer, and slices 1.0 mm thick removed with a hand microtome to yield disks 9 mm in diameter. The slices were washed under running distilled water for about 20 minutes until all cell debris had been removed. Disks used without further treatment are designated as fresh. Usually 10 g of disks were aged in a liter erlenmeyer flask containing 150 ml 0.1 mM $CaSO_4$ in which they were gently swirled at approximately 25 C on a New Brunswick Gyrotary Shaker for 24 hours.

Anion absorption was followed by introducing 7 disks (0.5 g fr wt) at zero time into 10 ml salt solution containing a labelled anion (21 disks added to 20 ml gave identical values) in 50 ml erlenmeyer flasks which were agitated in a reciprocal shaker in a temperature controlled water bath throughout the experimental period. For absorption studies at 0 C the

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bath was refrigerated and chipped ice was added so that ice was continually present. At the end of the absorption period the contents of a flask were poured into a Buchner funnel fitted with a Whatman No. 1 filter paper. The disks were then given a 10 minute wash under suction with distilled water at room temperature. As will be seen below (fig 1) this was more than adequate to remove all free space salt. The washed disks from Cl^{36} experiments were surface dried by light blotting and arranged on a 30 mm planchet spread with 0.2 ml of 3.6 % polyvinyl alcohol (Elvanol, grade 51.05, Dupont). The disks as spread on the planchet were dried on a hot plate, the planchets were fed into an automatic sample changer (Nuclear Chicago) and the radioactivity determined with a gas-flow micromil window detector. Washed disks from Br^{82} experiments were counted in a scintillation well counter (Nuclear Chicago).

Cl^{36} was supplied by Oak Ridge as 1.92 N HCl with a specific activity of 0.520 mc/g Cl. This was diluted to a suitable activity with stable chloride added as the salt desired, and the pH adjusted to 6.0

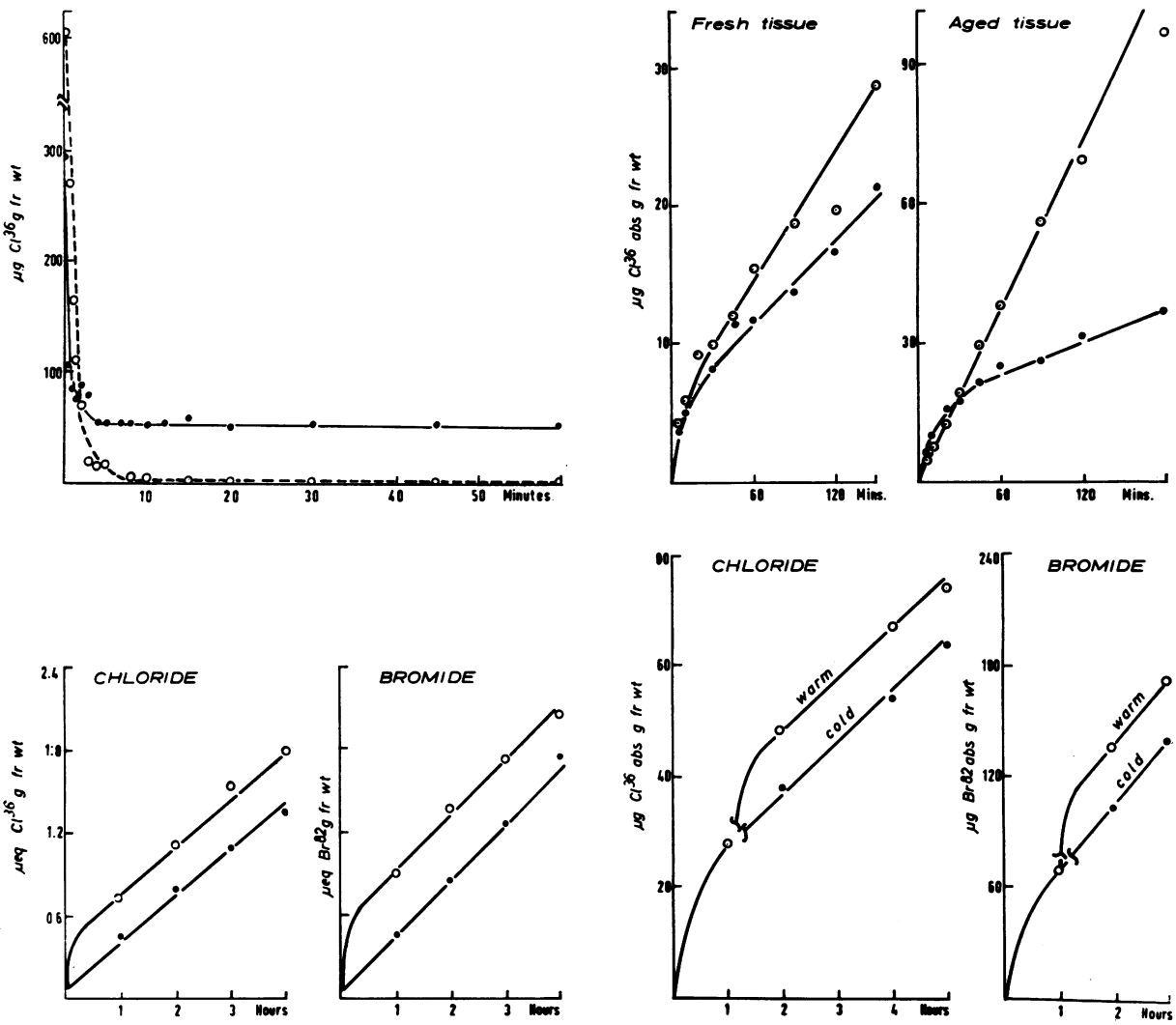

Fig. 1 (*upper left*). The time course of Cl^{36} efflux in water from disks after 3 hours absorption in 0.04 M KCl^{36}. ● control disks; ○ ethyl acetate treated disks.

Fig. 2 (*upper right*). The time course of Cl^{36} absorption from 0.04 M KCl^{36} by fresh and aged tissue at 0 C and 25 C. ● absorption at 0 C; ○ absorption at 25 C.

Fig. 3 (*lower left*). The time course at 0 C of Cl^{36} and Br^{82} absorption by aged disks from 0.04 M KCl^{36} and 0.04 M KBr^{82}, respectively, showing the effect of 1 hour pretreatment in water at 0 C and 25 C, respectively. ● pretreatment at 0 C; ○ pretreatment at 25 C.

Fig. 4 (*lower right*). The time course at 0 C of Cl^{36} and Br^{82} absorption by aged disks from 0.04 M KCl and 0.04 M KBr^{82}, respectively, showing the regeneration of the absorption shoulder by 1 hour treatment in water at 25 C (warm treatment) following the initial uptake period. Cold treatment represents 1 hour treatment in water at 0 C.

with the hydroxide of the appropriate cation. KBr was supplied with a specific activity of 33.035 mc/g Br and handled similarly to the chloride.

Experimental Results

The adequacy of the washing procedure for removing all free space Cl^{36} was established by determining the residual activity in disks washed for varying lengths of time. At the end of a 3 hour absorption period in 0.04 M KCl^{36} at 0 C the disks were tipped into a Buchner funnel where they were subjected to continuous washing with distilled water; samples were taken at minute intervals for the first 10 minutes and thereafter at intervals up to 1 hour. Cl^{36} was lost rapidly from the tissue during the first 3 minutes of washing, but between 4 minutes and 60 minutes there was no further loss of Cl^{36} (fig 1). An identical experiment was run with disks which had first been treated with ethyl acetate at 0 C for 30 minutes and washed free of the latter for a further 30 minutes before introduction to KCl^{36}. Due to the impairment of metabolism and the destruction of the semi-permeability of the membranes by this treatment these disks would not be expected to retain any activity upon washing. They were almost completely washed free of Cl^{36} within 6 minutes (fig 1), this increase in washing-out time over that observed with healthy disks being entirely consistent with the increase in WFS created by the treatment.

Figure 2 illustrates the time course for Cl^{36} uptake from 0.04 M KCl^{36}. The pattern for uptake by fresh disks at 0 C and 25 C can be compared with the uptake curves for aged tissue (24 hr) at these temperatures. It is clear that while aged tissue at 0 C shows the fullest development of the shoulder, a shoulder is also shown by fresh tissue both at 0 C and at 25 C. In aged tissue the shoulder at 25 C is barely discernible and is of no more than 5 minutes duration compared with 45 minutes at 0 C. This effect, although small, is consistently reproducible. A surprising feature which is consistently shown under the experimental conditions is that the Cl^{36} uptake by aged tissue at 0 C exceeds that at 25 C for the first 20 minutes or so. This has also been noticed in wheat roots (10).

Laties (9) established the presence of a shoulder for chloride uptake at 0 C and showed that it could be wiped out by pretreatment of the tissue in water at 0 C. Figure 3 confirms this finding and establishes the fact that the characteristics of Br^{82} uptake are similar. Disks aged 24 hours were introduced into the absorption flasks and shaken for 1 hour in water at 0 C or 25 C, following which the KCl^{36} or KBr^{82} was added directly to the flasks to give a final concentration of 0.04 M. This ensured that the disks pretreated at 0 C were not even momentarily exposed to an elevated temperature prior to absorption since even brief exposure to room temperature can induce a shoulder. Figure 3 shows that for both Cl^{36} and Br^{82} uptake, pretreatment at 0 C all but wiped out the absorption shoulder at 0 C without affecting the steady-state absorption.

The absorption shoulder for both bromide and chloride uptake can be regenerated very simply by exposing the tissue to room temperature. Figure 4 shows the pattern resulting from subjecting slices which had been absorbing for 1 hour at 0 C to an hour in water at 0 C or 25 C before absorption was resumed at 0 C. For both Cl^{36} and Br^{82} uptake the characteristics are the same. A shoulder is regenerated at 25 C but not at 0 C, and in both cases the steady-state remains the same as that of tissue in which absorption had not been interrupted by treatment in water at either temperature.

Since chloride and bromide uptake at 0 C have similar characteristics it is pertinent to know whether these ions compete with one another as regards both the shoulder and steady-state uptake. Figure 5 illustrates the results of an experiment to determine the extent of competition between chloride and bromide. It will be seen by comparing the uptake of Cl^{36} from 0.04 M KCl^{36} with that from a solution of 0.04 M KCl^{36} + 0.04 M KBr that bromide interferes with Cl^{36} uptake, diminishing both the shoulder (taken as the intercept derived by regressing the line of the steady state to the ordinate) and to a lesser extent the steady-state uptake. However, the presence of additional K^+ ions in the mixed solution where the K^+ concentration is in effect 0.08 M has a stimulatory effect on Cl^{36} uptake, so that the full effect of the bromide inhibition is obscured. A truer estimate is obtained if Cl^{36} uptake from the KCl^{36} + KBr solution is compared with that from a 0.04 M KCl^{36} solution to which K_2SO_4 is added to bring the total K^+ concentration to 0.08 M. Such a comparison increases the discernible inhibitory effect of bromide on the steady-state uptake of Cl^{36}. Conversely, chloride inhibits Br^{82} uptake both with respect to the shoulder and the steady state, but the inhibition is less marked. Indeed upon addition of KCl the stimulatory effect of additional K^+ ions on Br^{82} uptake is greater than the inhibitory effect of the chloride ions and the inhibition only becomes apparent when K_2SO_4 is added to the control in compensatory concentration (fig 5).

It is apparent, therefore, that bromide and chloride compete with one another in the absorption process. On the other hand, sulfate does not appear to interfere with halide uptake (fig 5), nor does phosphate (fig 6). Figure 6 again shows the stimulatory effect of additional K^+ ions on Cl^{36} uptake, and it should be noted that the magnitude of the effect is virtually independent of whether the associated anion is $SO_4^=$ or $PO_4^=$. An absorption shoulder can be demonstrated for phosphate too, and in figure 7 it can be seen that chloride neither competes for the phosphate shoulder nor affects the steady-state uptake of phosphate.

The possibility remains that since additional K^+ may stimulate chloride uptake such that inhibition by bromide is obscured (fig 5), so additional K^+ may

do the same in the case of K_2SO_4, with the result that an inhibitory effect of SO_4 on Cl^- would be obscured by the K^+ stimulation. However, since potassium phosphate and potassium sulphate stimulate Cl^{36} uptake to the same extent (fig 6) there is a strong probability that neither of these anions interferes with chloride uptake. In addition, evidence is also on hand (Laties, MacDonald, & Dainty, in preparation), that K saturation is approached at the High K concentrations and in that event the absence of apparent inhibition by $SO_4^=$ and $PO_4^=$ is unambiguously meaningful.

These results, therefore, are consistent with the widely held view that sulfate and phosphate are non-competitive with chloride. However, nitrate is another ion (in addition to bromide) thought by some to compete in the absorptive process with chloride. In determining the extent of interference between nitrate and chloride, cognizance must again be taken of the influence of the cation provided with NO_3^- on

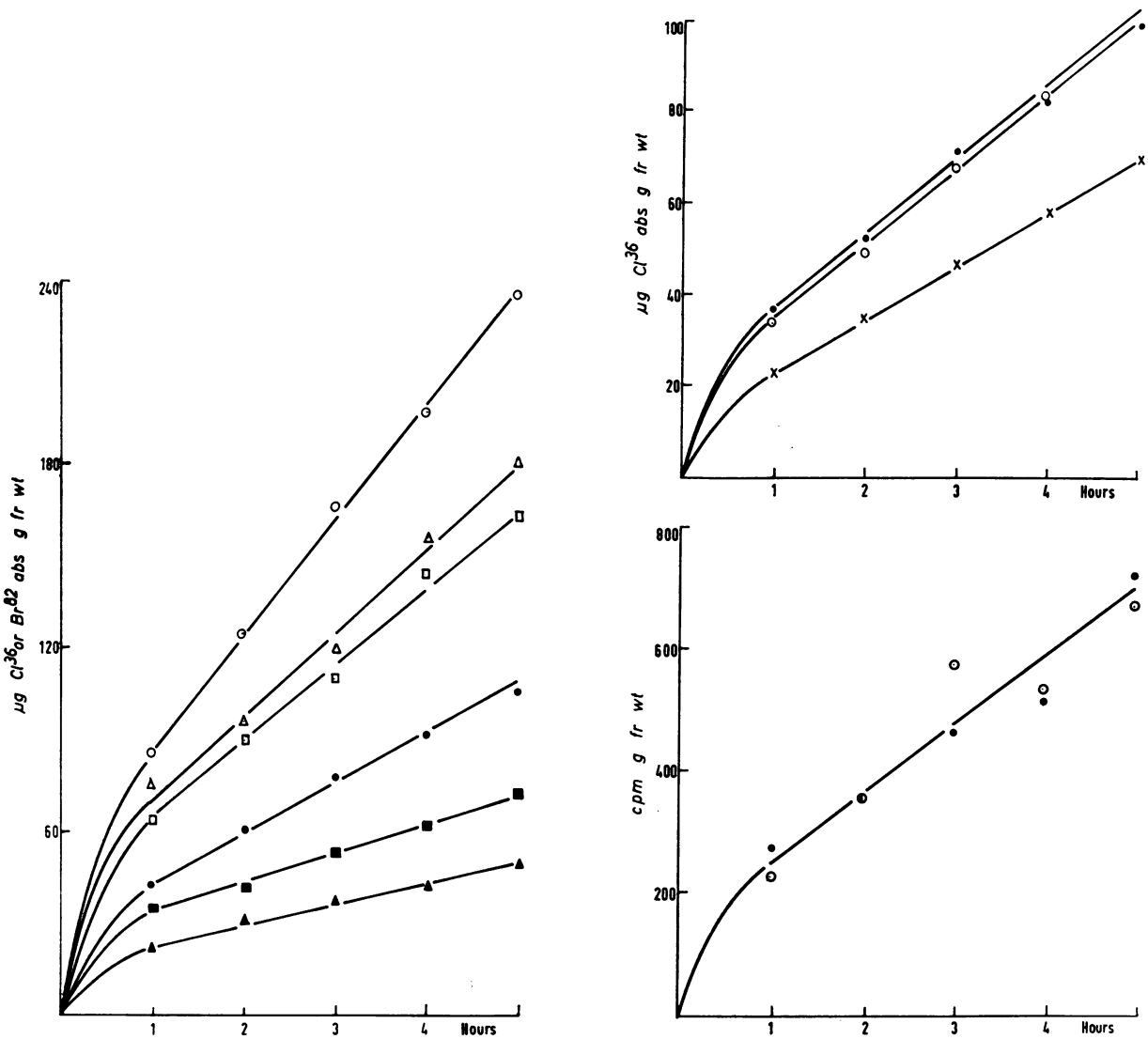

Fig. 5 (*left*). The time course at 0 C of Cl^{36} and Br^{82} absorption by aged disks showing the interaction of chloride and bromide on the shoulder and steady state. ○ Br^{82} uptake from 0.04 M KBr^{82} + 0.02 M K_2SO_4. △ Br^{82} uptake from 0.04 M KBr^{82} + 0.04 M KCl. □ Br^{82} uptake from 0.04 M KBr^{82}. ● Cl^{36} uptake from 0.04 M KCl^{36} + 0.02 M K_2SO_4. ▲ Cl^{36} uptake from 0.04 M KCl^{36} + 0.04 M KBr. ■ Cl^{36} uptake from 0.04 M KCl^{36}.

Fig. 6 (*upper right*). The time course at 0 C of Cl^{36} absorption from 0.04 M KCl by aged disks showing the effect of 0.02 M K_2SO_4 and 0.04 M KH_2PO_4 on the shoulder and steady-state absorption. × 0.04 M KCl^{36}. ○ 0.04 M KCl^{36} + 0.04 M KH_2PO_4. ● 0.04 M KCl^{36} + 0.02 M K_2SO_4.

Fig. 7 (*lower right*). The time course of P^{32} absorption by aged disks at 0 C from 0.04 M KH_2PO_4 and $K_2HPO_4 \cdot 3H_2O$ (pH 6.0) with and without 0.04 M KCl. ○ control. ● plus chloride.

the absorption of Cl^{36}. The addition of 0.02 M $CaSO_4$ reduces Cl^{36} uptake while 0.02 M Na_2SO_4 and 0.02 M K_2SO_4 increase uptake; the effects are related to the cation in each case. Nitrate salts of these cations inhibit Cl^{36} uptake, but the extent of the inhibition depends upon the effect of the associated cation (fig 8); that is to say, after correcting for the cation effect on Cl^{36} uptake, the inhibitory effect of nitrate remains substantially constant irrespective of the salt. These particular cation effects seem peculiar to low temperature uptake, and relate to the absorption isotherm characteristics which will be treated in greater detail elsewhere (Laties, MacDonald, & Dainty, in preparation).

The effect of 0.1 mM 2,4-dinitrophenol (DNP) on chloride uptake is exerted primarily on the steady state if the DNP is presented concomitantly with the salt. DNP strongly inhibits steady-state uptake of Cl^{36} from a mixed solution of KCl^{36} and K_2SO_4 without affecting the shoulder (fig 9). When introduced along with KBr, which itself reduces both the shoulder and steady-state uptake of Cl^{36}, DNP further affects only the steady-state uptake. However, a very substantial reduction in the shoulder results from pretreating the tissue in 0.1 mM DNP for 20 minutes at room temperature before introducing the salt solution, and a further small reduction in the shoulder is recorded if following DNP pretreatment bromide is introduced along with the Cl^{36} (fig 9).

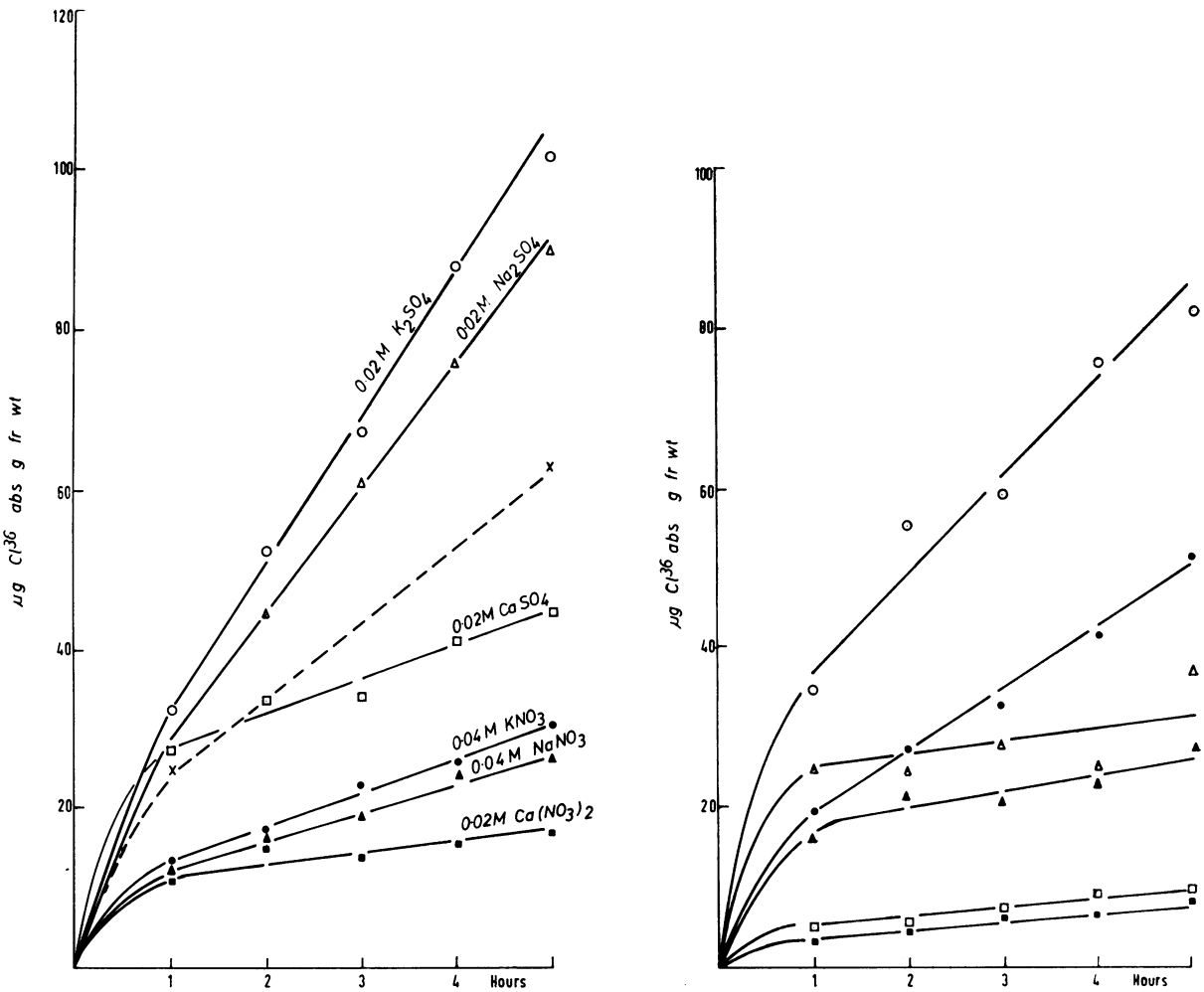

Fig. 8 (*left*). The time course at 0 C of Cl^{36} absorption by aged disks from 0.04 M KCl^{36} showing the effect of different nitrate salts on the shoulder and steady-state uptake. 0.04 M KCl^{36} is present in all treatments. The second salt present is indicated on each curve. KCl alone is indicated by the broken line.

Fig. 9 (*right*). The time course at 0 C of Cl^{36} absorption by aged disks from 0.04 M KCl^{36} showing the effect of 0.1 mM DNP on the shoulder and steady-state uptake both in the presence and absence of a competing anion (Br^-). ○ 0.04 M KCl^{36} + 0.02 M K_2SO_4. △ 0.04 M KCl^{36} + 0.02 M K_2SO_4 + 0.1 mM DNP. □ as in open triangles but with pretreatment in 0.1 mM DNP. ● 0.04 M KCl^{36} + 0.04 M KBr. ▲ 0.04 M KCl^{36} + 0.04 M KBr + 0.01 mM DNP. ■ as in closed triangles but with pretreatment in 0.01 mM DNP.

Discussion

Potato disks transferred from room temperature to 0 C display a two-phase anion absorption pattern. The compelling question arising from this observation concerns the meaning of the initial rapid phase of anionic uptake. The experimental procedure excludes the WFS as a contributory factor, and since post-absorptive washing in a non-radioactive salt solution is no more effective than water rinsing in reducing the phase I uptake [a phenomenon also reported for sulfate in barley roots, (7)] it would seem that adsorption exchange in the DFS must also be excluded. Lundegardh (10, 11) reported anion absorption shoulders in wheat roots and potato slices and while favoring adsorption or ion exchange as chiefly responsible for phase I uptake, noted that in respect to the initially absorbed fraction, Cl^- is more firmly bound than $H_2PO_4^-$. Butler (5), in a study of the relative importance of exchange-adsorption phenomena in wheat roots concluded that adsorption sites for $SO_4^=$ binding were present at an extremely low level of the order of 10^{-6} M. The all but complete extinction of the shoulder by pretreatment at 0 C (fig 3) suggests that the shoulder is a property of the living cell in contradistinction to the cation exchange capacity for which closely similar values can be obtained from fresh, dried, or ether-killed roots at 0 C and 20 C. The treatment with ethyl acetate (fig 1) indicates that the shoulder cannot be attributed to the cell wall. The possibility remains that it may be associated with cytoplasmic components which may be considered altered under the ethyl acetate treatment, but although changes in cell characteristics as a function of temperature are too complex for simple analyses the destruction of the shoulder at 0 C (fig 3) does not encourage the view that it results from ionic bonding to anion exchange sites.

The earlier report by Laties (9) that the shoulder represented carrier potential left unanswered the question whether the shoulder is specific with respect to a given ion or whether ions presumed to be transported by different carriers utilize the latent transport capacity (i.e., the shoulder) in a mutually exclusive manner. The results presented in figures 5 to 9 now characterize the shoulder as being specific rather than generic. After making allowance for the stimulatory effect of additional K^+ ions on halide uptake at 0 C it is clear that bromide ions do interfere with Cl^{36} uptake, reducing both the initial uptake and steady state proportionately (fig 5). Conversely, the presence of chloride ions reduces the uptake of Br^{82} both with respect to the shoulder and the steady-state when the K^+ concentration is equalized (fig 5). The magnitude of the shoulder as measured by regressing the line of the steady-state uptake in figure 3 amounts to approximately 0.44 μeq/g fr wt for Cl^{36} and 0.46 μeq/g fr wt for Br^{82}. In figure 4 the Cl^{36} shoulder amounts to 0.72 μeq/g fr wt, while the Cl^{36} shoulder in the presence of bromide amounts to 0.40 μeq/g fr wt. When to this is added a value for the Br^{82} shoulder in the presence of chloride of 0.38 μeq/g fr wt, the total of the Cl^{36} + Br^{82} values 0.78 μeq/g fr wt approximates that of the Cl^{36} shoulder alone.

Evidence in the literature with regard to competition between chloride ions and nitrate ions is contradictory. Epstein (6), for example, found that nitrate had no affinity for the halide binding sites in barley roots, while Butler (4) found that nitrate antagonized chloride uptake to a high degree in wheat roots, as did Lundegardh (13) in wheat roots and potato slices at high concentrations of nitrate. Better agreement exists regarding the non-interference of phosphate and sulfate on Cl uptake (4, 7). Under our experimental conditions neither phosphate nor sulfate interferes with chloride uptake (fig 6) whereas nitrate markedly reduces both the shoulder and steady-state uptake of chloride (fig 8). In view of the earlier reports that nitrate competes for the halide binding sites, it may be concluded that the shoulder is specific rather than generic. A shoulder is also demonstrable for phosphate uptake and neither the initial uptake nor the steady-state uptake of phosphate is affected by the presence of chloride ions (fig 7). The selectivity, therefore, is not only a characteristic of the steady-state transport but also of the initial uptake. This feature excludes adsorption and diffusive penetration of the free space or cytoplasm as practical explanations of the initial rapid uptake. Experiments with 2,4-dinitrophenol further emphasize that both phases of anion uptake are under metabolic control. If DNP is presented to the disks simultaneously with chloride, the DNP severely inhibits the steady-state uptake without affecting the shoulder (fig 9). However, when bromide is added with the DNP, the shoulder is also reduced. If on the other hand, the tissue is pretreated with DNP at 25 C prior to presentation of KCl, the shoulder as well as the steady state is markedly reduced. If now KBr is added, the shoulder is again reduced. It appears, therefore, that the initial period of rapid uptake represents a consequence of metabolism preceding in time the absorptive act, or as Laties (9) previously postulated provides a measure of the latent-ion-transport capacity for any given ion in the tissue.

It is of interest that Barber and Russell (2), measuring rubidium uptake by carrot disks, obtained basically similar results for cation uptake to those reported here for anion uptake. Having eliminated the exchangeable rubidium, they showed that the time course of Rb^{86} uptake at 25 C was approximately linear, while that at 0.2 C was definitely biphasic. On the assumption that the influence of temperature on uptake is uniform from zero time they calculated the Q_{10} of the phase I uptake to be 1.5, and concluded that diffusion was an important factor controlling the initial influx. However, this assumption may be open to question. If Rb^+ is absorbed as rapidly at 0 C as at 25 C during the first 20 minutes, as in fact is true of Cl^- uptake (fig 2), a low Q_{10} value would

result. The value of the cation shoulder at 0.2 C as determined by regressing the steady-state obtained by Barber and Russell, is of the same order as those reported here for Br^- and Cl^- and may be taken as a measure of the latent-ion-transport capacity for Rb^-.

It is conceivable that the phase I uptake may reflect the filling of the cytoplasm which at room temperature is kept relatively empty by transport into the vacuole. By the same token, pretreatment at 0 C could result in filling the cytoplasm by leakage from the vacuole. Since the tissue is being presented with a radioisotope it might be anticipated that the cytoplasm would be labelled equally irrespective of whether it was full or empty but Briggs (3) has indicated that absolute flux, not only net flux, is diminished when the receptor pool fills up. It must be recognized that penetration into the cytoplasm is metabolically implemented albeit by a different mechanism from that causing movement into the vacuole. This is in keeping with the suggestion by Arisz (1) that movement across the plasmalemma into the cytoplasm and across the tonoplast into the vacuole is in both instances an active process, although the mechanism may not be identical. Arisz found that while cyanide prevented the movement of chloride into the symplasm in Vallisneria leaf, it did not interfere with the passage of chloride into the vacuole. Laties (9) showed that cyanide did not affect the steady-state uptake of Cl^- in potato slices at 0 C, and the obliteration of the phase I uptake by cyanide when presented simultaneously with chloride at 0 C may be due to a reduction in the rate of ion movement into the symplasm so that entry into the symplasm is no faster than entry into the vacuole.

Summary

The time course of chloride, bromide, and phosphate uptake at 0 C by potato disks transferred from 25 C follows a two-component absorption pattern—an initial period of rapid uptake (the absorption shoulder) followed by a period of steady-state uptake.

The absorption shoulder is shown to be specific for a given ion or ionic species. Bromide and chloride compete with one another for the shoulder, and nitrate interferes with halide uptake. Sulfate does not compete with halide nor does phosphate with chloride or vice versa.

The shoulder is clearly a property of the living cell being wiped out by pretreatment at 0 C or by DNP. It is suggested that the shoulder may reflect the filling of absorption sites in the cytoplasm while the steady state is indicative of vacuolar penetration.

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