preceding or following irrigations. No reduction in the rate of photosynthesis was detected as soil moisture was extracted, until the approximate time the first visible signs of wilting appeared. As the severity of wilting increased, the photosynthetic rate declined rapidly. When the plants were distinctly wilted, photosynthetic activity had been reduced to approximately 75 % of its maximum value. Severely wilted plants irrigated one day after the permanent wilting percentage had been reached showed 40 to 50 % increases in rate of photosynthesis within 6 hours. Experiments carried out under continuous light supported the above conclusion.

The respiration rate of the aerial portions of the ladino clover plant tended to increase slightly as wilting appeared. These increases were relatively much smaller than accompanying changes in photosynthesis.

Results of these studies are in accord with those of Allmendinger et al on apple trees and of Loustalot on pecan trees, but differ in degree from those of Schneider and Childers on apple trees.

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A STUDY OF THE ROLE OF THE HYDROGEN ION IN THE MECHANISM OF POTASSIUM ABSORPTION BY EXCISED BARLEY ROOTS[1]

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The hydrogen ion has an important place in many theories of cation accumulation by plants including those of Brooks (3), Osterhout (13), Briggs (2), Lundegårdh (10), and Jacobson, Overstreet, et al (9). All of these workers postulated that the absorption of cations takes place by means of an exchange of the cation for a hydrogen ion from the root, and this hypothesis is supported by experimental evidence. Perhaps the most convincing evidence on this point is the physiological acidity which develops when plant

roots are placed in a salt solution, such as K_2SO_4, containing a rapidly accumulated cation and slowly accumulated anion (8).

Of the above-mentioned hypotheses, all except that of Jacobson, Overstreet, et al have in common the postulation that the driving force for accumulation of cations against a concentration gradient is a hydrogen ion concentration gradient in the opposite direction. Hoagland and Broyer (8) conducted experiments designed to ascertain whether such a gradient in hydrogen ion concentration was necessary for cation absorption. These workers concluded that cations could be accumulated against a gradient in their concentration even though the pH in the exter-

nal solution was lower than that of the expressed root sap.

Overstreet and Jacobson (14) adopted the absorption model of Rosenberg in proposing, as a working hypothesis, the following mechanism for mineral absorption by plant roots. A membrane or region exists in the cytoplasm of root cells which is impermeable to free ions, but permeable to complexes formed by the reaction of ions with compounds designated as HR and R'OH. The compounds HR and R'OH are produced at the external interface of this region where they can combine with anions and cations forming complexes as follows:

(a) $M^+ + HR \rightleftarrows MR + H^+$
(b) $A^- + R'OH \rightleftarrows R'A + OH^-$
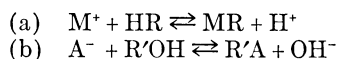
where M^+ represents a cation, A^- an anion.

The complexes MR and R'A then diffuse across this region and at the inner boundary are chemically altered in such a way that the R's can no longer serve as carriers, M^+ and A^- being secreted to the region beyond the inner boundary. An inward diffusion gradient of MR and R'A in the membrane region is maintained by the production of HR and R'OH at the external boundary and the alterations of MR and R'A at the internal boundary. Thus, the production and alteration of these compounds by metabolic chemical reactions is the driving force for the accumulation of ions against their concentration gradient, not the difference in hydrogen ion concentration between external solution and interior of the root.

The purpose of the present investigation was to obtain experimental data useful in testing the above hypothetical absorption mechanism.

Jacobson, Overstreet, et al (9) performed experiments designed to provide information on the reversibility of reaction (a), the cation-binding reaction. They placed excised barley roots in HCl solutions ranging in pH from 1 to 6.5 and measured the loss of K from the roots. However, the loss of K from the roots as a function of pH rather closely paralleled the loss of various other constituents such as inorganic phosphate, soluble organic phosphate, soluble nitrogen, etc. This casts doubt on the interpretation that the loss of K from the roots was merely a reversal of the K-binding reaction. In all probability, a more general disruption of the system occurred causing changes in permeability characteristics of the membranes and a resultant outward diffusion or leakage of cell constituents. This interpretation is supported by the fact that the dry weight of the roots decreased by approximately 25 % at a pH below 3. Also, roots that were treated with 0.005 N HCl solution exhibited a marked reduction in ability to absorb K from KCl solution subsequent to this treatment. These facts illustrate a basic difficulty in studying the effect of hydrogen ion on the absorption mechanism, namely, the difficulty in distinguishing between hydrogen ion effects on the actual absorption mechanism and other effects such as a general injury to the tissue. The possibility of injury to the root tissue has been excluded as rigorously as possible from data used to elucidate the reaction mechanism in the present study. Also, rates of ion accumulation have been investigated, rather than changes in the composition of the root material resulting from treatments of arbitrary duration, in order to rule out secondary effects and to provide data which can be interpreted in terms of the kinetics of the ion absorption mechanism.

EXPERIMENTAL METHODS

The experimental material used was excised roots of *Hordeum vulgare*, var. Atlas 46, cultured and prepared as described by Jacobson et al (9), except that the H_2O_2 treatment was eliminated because it proved to be injurious to Atlas 46 barley. On the sixth day following the initial soaking of the seed, the roots were excised just below the seed, cut into segments 1 to 2 cm in length, rinsed thoroughly in distilled water, and centrifuged for 5 minutes at 670 RPM with 13 cm centrifugal radius to remove the water adhering to their surfaces. Samples of root material were then weighed out and placed in various salt solutions, generally 3 gms of roots in 3 liters of solution. Since a root to solution ratio of 1 gm/l was used, the salt concentration of the solutions remained essentially constant throughout the absorption period. None of the solutions were buffered as it was considered desirable to avoid indirect effects of buffering ions on absorption. All solutions were aerated and maintained at 26° C.

Ion absorption was determined by chemical analysis of the root material before and after it was placed in a solution and was expressed as meq ion/1000 gm fresh root material. All solutions were aerated and maintained at 26° C. Potassium was determined as the cobaltinitrite, Br by a modified version of Van der Meulen's iodometric method (17) and Na by use of a flame photometer. Values of absorption from a given solution using root samples from one batch of material or from batches of root material produced on different dates varied less than 5 %.

RESULTS

Potassium absorption from KBr solutions at several concentrations at pH 4 and 6 was determined for periods of time ranging from ½ to 6 hours. A series of identical KBr solutions was prepared at each concentration and pH, and samples of root material were placed in each solution for the specified period of time. The pH 4 solutions were adjusted in pH with HBr. The amount of K absorbed in each case is related to time in figure 1 at pH 6 and 4, respectively. The rate of absorption at any point in time is, therefore, obtained by the slope of the curve in each case. All of the curves in figure 1 are linear between the ½- and 3-hour points indicating a constant rate of absorption. Data on Br absorption from KBr solutions in the pH range from 4 to 6 obtained in the same manner as those in figure 1 show that Br absorption also remains constant during the first 3-hr period except during the initial half hour.

Since the rate of K and Br absorption from KBr

solutions remains constant between ½ hour and 3 hours of contact, the effects of pH on absorption were determined after periods of 3 hours. In figure 2 the amounts of K and Br absorbed during a 3-hr period
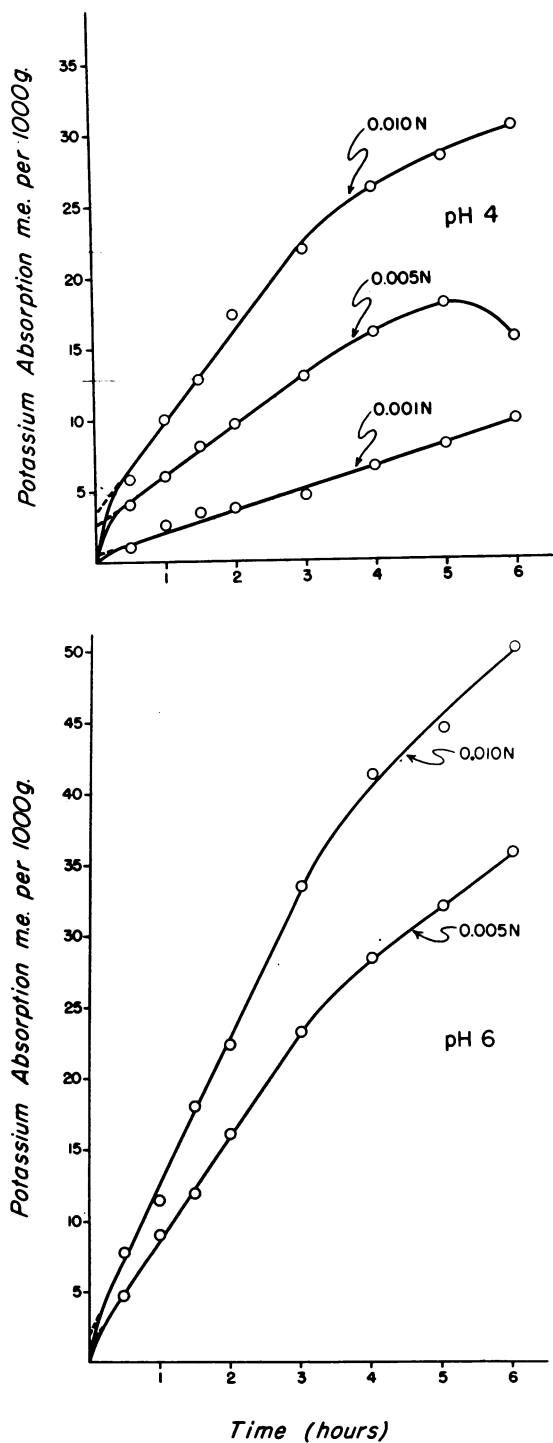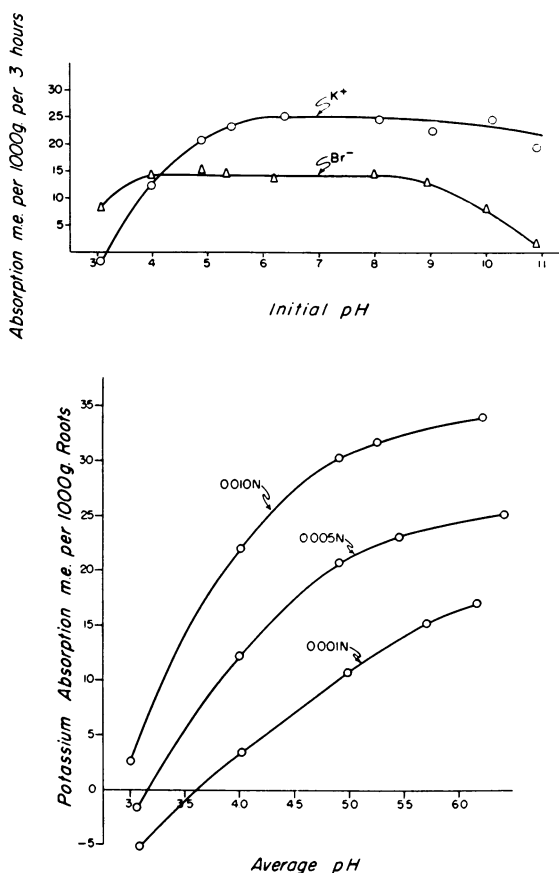

Fig. 2 (*above*). Absorption of K and Br from 0.005 N KBr solution as a function of pH.

Fig. 3 (*below*). Absorption of K as a function of pH from 0.001, 0.005 and 0.010 N KBr solutions; 3-hr absorption period.

from 0.005 N KBr are plotted as functions of the initial pH of the solutions. Solutions used for determination of K absorption had a constant K concentration at 0.005 N, and those used for the determination of Br absorption had a constant Br concentration also at 0.005 N.

In the above-mentioned solutions, the hydrogen ion concentration increased only slightly during the 3-hr absorption period in the case of the solutions more acid than pH 6.5. For example, the pH of the solution initially at 6.5 was 6.3 at the end of the 3-hr absorption period. However, in the case of the basic solutions, the changes in pH during the absorption period were much greater. The final pH of the solution initially at pH 10.1 was 7.5, for example. Hence, the absorption data of figure 2 for the solutions at pH higher than 6.5 must be considered only as approximations indicative of a trend.

Because of the large variations in pH in the higher pH range, primary attention was directed toward the pH range below pH 6.5. In figure 3, the amounts of K absorbed from 0.001, 0.005, and 0.010 N

Fig. 1. Absorption of K from KBr solutions as a function of time at pH 4 (*above*) and pH 6 (*below*).

KBr solutions is related to the average of the initial and final pH of these solutions. The pH of the solutions was adjusted with HBr. Negative values of absorption indicate loss of K from the root tissue.

To verify that the hydrogen ion was not per se injurious in the pH range from 4 to 6, barley root material was placed in dilute HBr solutions at pH 4, 4.5, and 6 for a 3-hr period, and subsequent to this treatment, K absorption from $0.005\,N$ KBr was determined as a function of time. Twenty-five gm samples of root material were placed in 15 liters of each solution for a 3-hr period, removed, washed with distilled water, and re-centrifuged in the standard manner. The fresh weight and K content of this material was determined and 3-gm samples were weighed out, placed for varying time periods in 3-l volumes of $0.005\,N$ KBr solution at pH 6, and analyzed. The K absorption data were similar to those of figure 1 in that the curves were curvo-linear up to the ½-hour point and linear beyond this point. However, the curves deviated from linearity beyond the 2-hr point which might be expected since at this point the root material had been in the pre-treatment solutions and the KBr solution for a total of 5 hours. The rates of K absorption were identical in the case of the root material pre-treated at pH 4.5 and 6, while the rate of K absorption by the root material pretreated at pH 4.0 was somewhat lower.

Earlier work with barley and other root tissue has demonstrated that Ca and other polyvalent cations
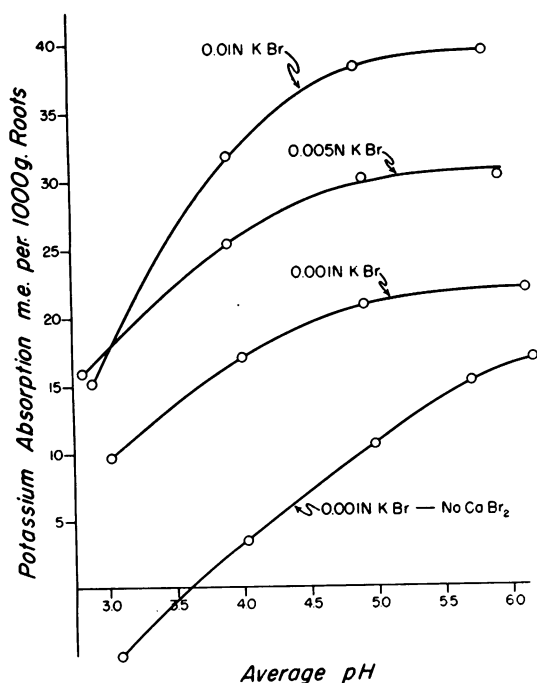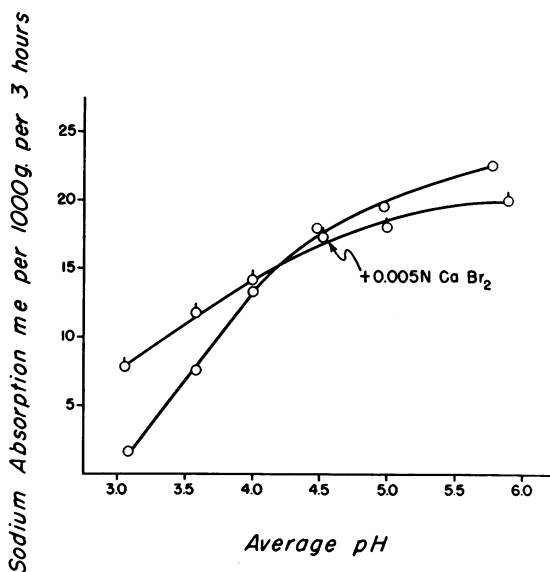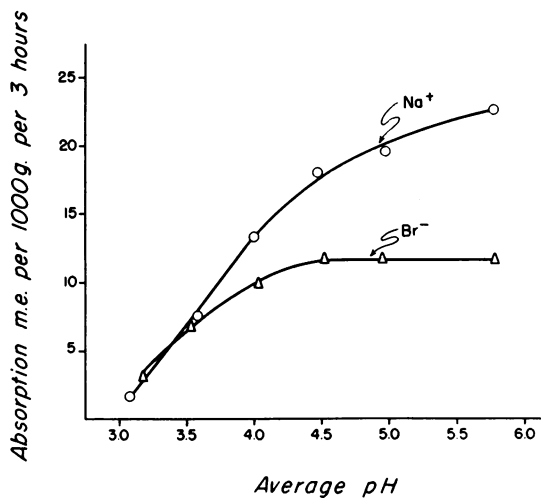

FIG. 5 (above). Absorption of Na and Br from $0.005\,N$ NaBr as a function of pH.

FIG. 6 (below). Absorption of Na from $0.005\,N$ NaBr and from $0.005\,N$ NaBr $+ 0.005\,N$ CaBr₂ as a function of pH.

FIG. 4. Potassium absorption as a function of pH from KBr $+ 0.005\,N$ CaBr₂. Also, K absorption from $0.001\,N$ KBr without CaBr₂ as a function of pH; 3-hr absorption period.

have an ameliorating effect on injury to the tissue resulting from hydrogen ions (1, 6, 9). It was considered desirable, therefore, to investigate the hydrogen ion effect on K absorption in the presence of Ca ion. In figure 4, the amount of K absorbed in a 3-hr period from 0.001, 0.005 and $0.010\,N$ KBr solutions all $0.005\,N$ in CaBr₂ is plotted as a function of average pH of the solution. HBr was used to obtain the pH indicated. Data of K absorption from $0.001\,N$ KBr alone is included for comparison.

To verify that rates of K absorption from mixtures of KBr and CaBr₂ are constant during the initial 3 hrs of contact, K absorption was determined as a function of time from the $0.005\,N$ KBr $+ 0.005\,N$

CaBr$_2$ mixture at pH 6 and 4. This was done in the manner as indicated above for the experimental results presented in figure 1. The curves were linear throughout the initial 3-hr period indicating constant rates of absorption.

Sodium and Br absorption from 0.005 N NaBr solutions of varying pH were determined in order to compare the H-Na interaction with that of H-K. Also, Na absorption from 0.005 N NaBr + 0.005 N CaBr$_2$ mixtures at several pH's was determined. A series of 0.005 N NaBr and 0.005 N NaBr + 0.005 N CaBr$_2$ solutions were prepared and adjusted to varying pH with HBr. Samples of root material were placed in each solution for a 3-hr period and the Na and Br absorptions were determined. In figure 5, the Na and Br absorption from 0.005 N NaBr is plotted as a function of the pH of the solution. In figure 6, Na absorption from 0.005 N NaBr and from the 0.005 N CaBr$_2$ mixture is plotted as a function of the pH of the solution.

DISCUSSION

Data have been presented showing the effect of hydrogen ion concentration of solution on K and Br absorption by barley roots. The interpretation of these data in terms of a direct hydrogen ion effect on the absorption mechanisms requires the establishment of a lower pH limit above which injurious effects of hydrogen ion can be excluded. One line of evidence useful for this purpose is the similarity in shape of the curves of figure 1. The curves at both pH 4 and pH 6 show a constant rate of K absorption between the ½- and 3-hr points. If hydrogen ion injury to the tissue were of any consequence at pH 4, one would expect a progressive decrease in rate of absorption as the root material remained in the solution for increasing periods of time. Since no such decrease in absorption rate occurs, in the case of either K or Br absorption, one must conclude either that hydrogen ion injury at pH 4 is unimportant and that the effect of the hydrogen ion concentration in decreasing the rate of K absorption is a direct effect on the K absorption mechanism, or that a peculiar sort of hydrogen ion injury is operative, namely, one that affects the root material almost instantaneously when roots are placed in a solution and has no further effect. The latter possibility is highly unlikely.

A further criterion of hydrogen ion injury is the effect of treatments of root material at various hydrogen ion concentrations on the subsequent ability of the material to absorb ions. The data showing rates of K absorption subsequent to treatments of root material at pH 4, 4.5, and 6 (mentioned above) indicated that both the pH 4.5 and 6 treatments had the same effect on subsequent K absorption. However, the subsequent rate of K absorption by the root tissue treated at pH 4 was somewhat lower. This indicates an injurious effect of hydrogen ion under the conditions of this experiment.

Other experiments with barley root tissue (6, 9) have indicated that the presence of salt in solution mitigates to a considerable extent the injurious effect of hydrogen ion. This must be taken into consideration in making inferences from the above data on hydrogen ion injury in the absence of salt applicable to those in the presence of KBr (figs 1, 2, and 3). Considering both of the above-mentioned criteria of hydrogen ion injury, one must conclude that hydrogen ion injury, can be ruled out in interpreting the data of figures 2 and 3, certainly between pH 4.5 and 6 and very probably between pH 4 and 6. Moreover, since the data in figure 1 demonstrate that the rates of K absorption remain constant during the initial 3 hrs of contact except for a slightly higher rate immediately after the roots are placed in the solution, the amounts of K absorbed given in figures 2 and 3 are measures of these constant rates of absorption. The same is true of the amounts of Br absorbed given in figure 2.

From figure 2, it is evident that in the range of pH from 4 to 6 the rates of Br absorption is independent of hydrogen ion concentration while the rate of K absorption decreases markedly as the hydrogen ion concentration increases. Since it has been established that hydrogen ion is not injurious in this pH range, the differential effect of hydrogen on K and Br absorption must be attributed to a direct effect of hydrogen ion concentration on the K absorption mechanism.

The data of figure 3 show that the magnitude of the reduction in rate of K absorption at a given hydrogen ion concentration varies with KBr concentration of the solution. For example, the rates of K absorption at pH 4 are 65.3, 53.4, and 20.0 % of the rates at pH 6 in the 0.010, 0.005, and 0.001 N KBr solutions, respectively.

Olsen (12) in his studies of ion absorption by intact rye plants, arrived at conclusions similar to those mentioned in the preceding two paragraphs concerning the influence of hydrogen ion concentration on K absorption. One important difference in behavior viz ion absorption between the intact rye plants used by Olsen and the root material used in this study is that absorption rates with the rye plants were reported to be independent of concentration at solution concentrations greater than 0.003 M, while in the case of excised barley roots the amounts of K absorbed increased with increasing concentration up to 0.075 M.

According to the ion absorption hypothesis of Jacobson et al (9), the initial step of the cation absorption mechanism is reaction (2), the cation-binding reaction. For the case of K absorption, the reaction would be

$$(c) \quad K^+ + HR \rightleftharpoons KR + H^+$$

Moreover, since the methods used in this investigation for measuring ion absorption do not distinguish between ions bound as KR or R'Br and free ions liberated to the region beyond the membrane, the measured rates of absorption must be equal to the rates of the ion-binding reactions, assuming that the ion absorption hypothesis is correct. Overstreet et al

(15) concluded that the rate-determining factors in this reaction are the concentrations of K^+, HR, KR, and H^+ at the reaction site. The overall rate of reaction (c) would be the difference between the rate of the forward and reverse reactions. It would be expected, therefore, that increased concentrations of K^+ and HR at the site of the cation-binding reaction would increase the rate of K absorption; while increased KR and H^+ concentrations at this site would decrease this rate. If the assumption is made that the concentrations of K^+ and H^+ at the reaction site are direct functions of the bulk solution phase concentrations of these ions, the absorption rate should increase with increasing concentration of K and decrease with increasing concentration of hydrogen in the external solution.

The data of figure 3 are in agreement with the Jacobson-Overstreet hypothesis for the ion absorption mechanism and the assumption as stated above. Moreover, considering also the anion absorption hypothesis, one would expect that cation absorption would be depressed by an increase in hydrogen ion concentration and anion absorption by an increase in hydroxyl ion concentration. The differential effect on cation and anion absorption both in the lower and higher pH ranges is illustrated in figure 2.

The effect of Ca ion on the K-H ion interaction is illustrated in figure 4. The effect of Ca ion is to decrease considerably the magnitude of the depressing effect of the hydrogen ion on K absorption in the pH 4 to 6 range.

The increase in rate of K absorption caused by Ca (and other polyvalent ions (6, 16), the Viets effect (16)), is illustrated by the K absorption data from $0.001 N$ KBr and the $0.001 N$ KBr $+ 0.005 N$ $CaBr_2$ mixture (fig 4). These data also illustrate the marked pH-dependence of the Viets effect.

Overstreet et al (15) concluded that Ca ion in the solution increased the rate of K absorption in the concentration range where it stimulated K absorption because of its function as a cofactor in the utilization of the K complex KR. Thus, the concentration of KR at the site of the ion binding reaction, the external membrane interface, would be reduced in the presence of Ca ion, and consequently the rate of the reverse reaction in equation (c) would be decreased. The question which arises concerning the data of figure 4 is whether or not the role of Ca assumed by Overstreet et al will explain, at least qualitatively, the Ca ion effect on the H-K interaction.

With a reduced concentration of KR because of Ca ion, changes in the rate of the reverse reaction brought about by changes in hydrogen ion concentration would be expected to be reduced in magnitude since the rate of the reverse reaction depends on the concentrations of both KR and H^+. This would produce a smaller change in the rate of the over-all reaction, the difference in the rates of the forward and reverse reactions, as shown by figure 4. Hence, one can conclude that these data are consistent with the Overstreet et al hypothesis.

In interpreting the Na absorption data of figures 5 and 6 in terms of the Na absorption mechanism, one must assume that the 3-hr absorption values of Na absorption represent close approximations to the rate of absorption as in the case of K absorption. Two reasons for believing that the Na and K absorption processes are similar in the case of barley roots are 1) the amounts of each ion absorbed from NaBr and KBr solutions of equal concentration are similar, and 2) Jacobson et al (9) found marked competition in absorption between Na^+ and K^+ which they interpreted as indicating a single binding compound for these two ions. The curves of figure 5 for Na^+ and Br^- are quite similar to those of figure 2 for K^+ and Br^- absorption. Also, the Ca effect on the Na-H interaction is similar to that of the K-H interaction in that the depressing effect of hydrogen ion on the absorption of both these ions is decreased by Ca ion. However, the Ca ion effect on Na absorption at pH 6 is the opposite of the effect on K absorption, i.e., Ca increases the rate of K absorption and decreases the rate of Na absorption. This finding confirms unpublished data of Handley (7). An explanation for the differences between the Na-Ca and K-Ca interactions is not evident.

In the above discussion, two factors were considered of importance in the quantitative aspects of ion absorption 1) the ionic concentrations at the site of the cation binding reaction and 2) the ion absorption reactions themselves. The first consideration bears some relationships to the ion absorption hypothesis of what may be termed the Swedish school (4, 5, and 11).

This hypothesis apparently implies that the interaction of ions at the plant root surfaces is the only selective step of the ion absorption process, at least for the case of cation absorption. However, the hypothesis fails in the case of the Ca-K interaction of the data presented in figure 6. When Ca^{++} is added to a solution containing K^+, the amount of K^+ absorbed on the surface of plant roots in the solution would be expected to decrease, assuming that the cation adsorptive properties of plant root surfaces are similar to those of more fully understood absorbents such as clay particles or ion exchange resins. Hence, according to the hypothesis, the rate of K^+ absorption should decrease in the presence of Ca^{++}; yet actually it increases.

It is the view of the present authors that factors which affect the ionic distribution at plant root surfaces must be taken into account in the over-all ion accumulation process because of their effect on the ionic concentration at the site of the ion-binding reactions of the Jacobson-Overstreet hypothesis.

SUMMARY

Data were presented showing that changes in hydrogen ion concentration of KBr solutions in the pH range from 4 to 6 had a marked effect on the rate of K absorption from these solutions by excised barley roots. Potassium absorption decreases with

decreasing pH. From measurements of K absorption as a function of time and other data, it was concluded that the effect of hydrogen ion on K absorption could be interpreted as a direct hydrogen ion effect on the K absorption mechanism. The observed hydrogen ion effects on K absorption were consistent with the ion absorption hypothesis of Jacobson and Overstreet.

The presence of Ca ion in solution was found to decrease considerably the depressing effect of hydrogen ion on K absorption. An explanation of this phenomenon in terms of the Jacobson-Overstreet hypothesis was presented.

Increasing hydrogen ion concentrations depressed Na absorption from NaBr solution in a similar manner as K absorption from KBr solution.

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CYTOCHROME OXIDASE CONTENT AND RESPIRATORY RATES OF ETIOLATED WHEAT AND BARLEY SEEDLINGS [1,2]

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Hill and Hartree (10) have reviewed the data which have accumulated during the last several years regarding cytochrome oxidase of plants, and the bulk of the evidence favors the view that this terminal oxidase plays an important role in respiratory oxygen consumption. Also Webster's recent survey (21) stressed the widespread distribution of this enzyme in dicotyledonous plants. Even so, there are several reports that the enzyme is missing from older cereal

tissues. For example, Waygood (20) concluded that the oxidase is not present in extracts of wheat seedlings after the third day of development. Butler (4) reported inability to detect cytochrome oxidase in extracts from 5-day wheat roots, although Lundegårdh (16), using a specially designed spectrophotometer, was able to observe characteristic cytochrome absorption bands in intact roots of older wheat. Albaum and Eichel (1) demonstrated that the oxidase was present in extracts from oat seedlings one or two days old, but did not detect the enzyme in extracts from older seedlings (up to 6 days), and concluded that cytochrome oxidase operated only during the embryonic stages. James (12) detected cytochrome oxidase in barley embryos, but found no evidence for its exist-