THE EFFECT OF CALCIUM ON THE ABSORPTION OF POTASSIUM BY BARLEY ROOTS[1]

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(WITH SIX FIGURES)

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Introduction

In a recent investigation (**3**) the absorption of potassium by excised barley roots was studied. It was proposed that, as a working hypothesis, the absorption of ions depended upon the presence of metabolically produced binding compounds. According to this idea, the absorption of a cation may be expressed as: $M^+ + HR = MR + H^+$, where HR is the metabolically produced binding compound.

Studies of the absorption of potassium in the presence of H^+ and other monovalent cations appeared to be consistent with the above hypothesis; that is, H^+ caused what appeared to be a reversal of the absorption reaction and pronounced competitive effects were noted between potassium and the other cations. On the other hand, in accordance with the observations of VIETS (**5**), it was shown that the presence of calcium exerted a stimulating effect on potassium absorption. Since this calcium effect is in apparent conflict with the above hypothesis, a special study was made of the calcium-potassium relationship in absorption. The purpose of the present paper is to show that certain extensions of the theory of cation absorption appear necessary to explain adequately the behavior of calcium.

Experimental methods

The experimental material used was excised barley roots, cultured and prepared as described in the previous article (**3**). In general, the absorption experiments were performed using one gram of root tissue per liter of solution in order to minimize concentration changes during the course of the experiment. Usually 15 grams of roots were placed in 15 liters of solution. The root suspensions were continuously aerated throughout the experimental period, and with the exception of the isotopic exchange determinations, investigations were carried out at 26° C. Potassium was determined as the cobaltinitrite and calcium as the oxalate.

Results

In order to ascertain the rates of absorption of K^+ and Ca^{++} from pure salt solutions, absorption experiments were conducted using KCl solutions and $CaCl_2$ solutions. The observed absorption of the cations plotted as a

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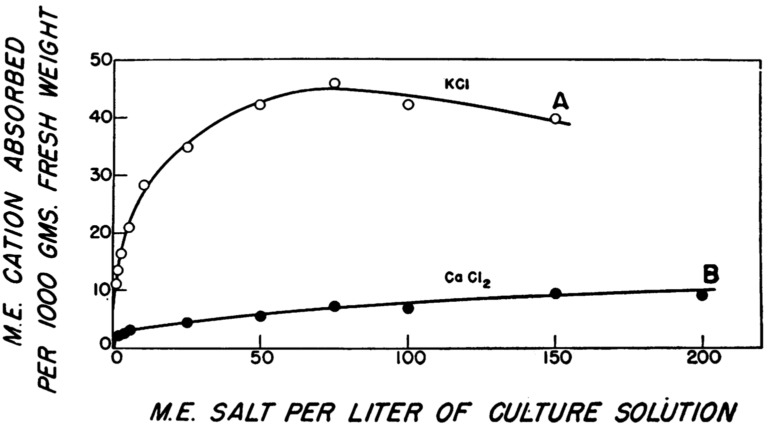

FIG. 1. A. Absorption by barley roots of potassium from a pure solution of KCl. B. Absorption by barley roots of calcium from a pure solution of $CaCl_2$.

function of salt concentration is presented in figure 1. The absorption period was three hours.

The effect of potassium on the absorption of calcium was determined by adding increasing amounts of KCl to 0.005 N $CaCl_2$ solutions and measuring the resulting calcium absorption (fig. 2). The reciprocal effect, the effect of calcium on potassium absorption, was determined in the following manner: A series of experiments was set up in which the calcium content was maintained constant for a given set and the potassium permitted to vary. Several levels of calcium concentration were employed. In this way,

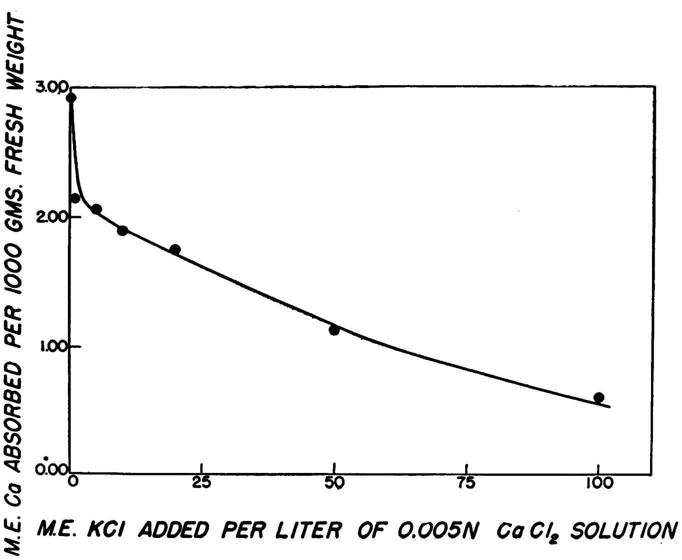

FIG. 2. Calcium absorption from 0.005 N $CaCl_2$ as affected by increasing concentrations of KCl.

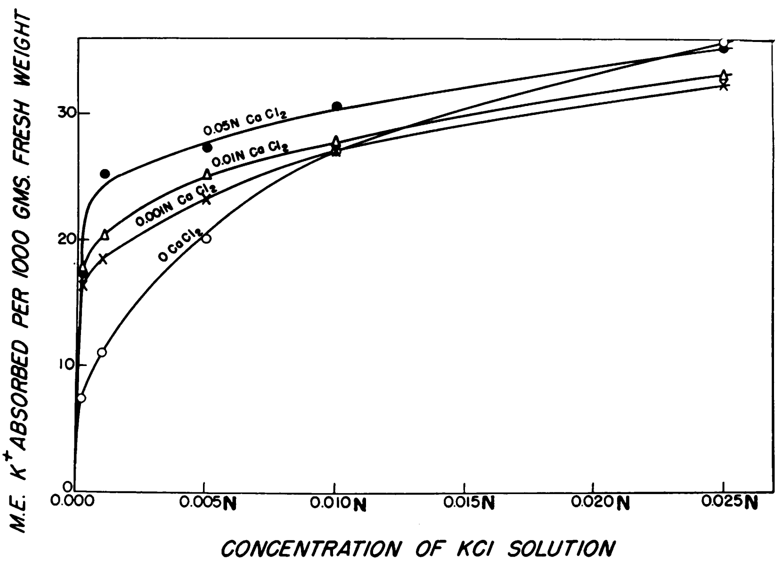

FIG. 3. Effect of different concentrations of $CaCl_2$ on the absorption of potassium from increasing concentrations of KCl.

the effect of the concentrations of both KCl and $CaCl_2$ on the absorption of potassium from the mixtures was observed. The results are summarized in figure 3. In this series of experiments, as well as in the preceding experiment, the absorption period was three hours.

Since the data of figure 3 indicated a marked dependency of the stimulating effect of calcium on the concentration of KCl, the following experiment was performed: A series of solutions was prepared in which the $CaCl_2$

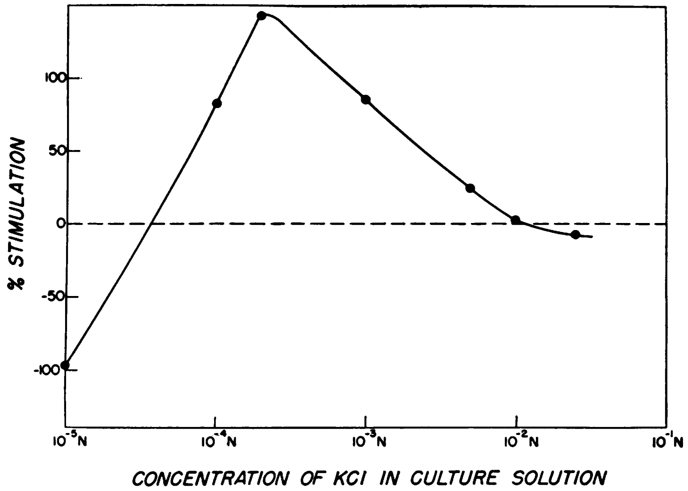

FIG. 4. Stimulating effect of 0.01 N $CaCl_2$ on the absorption of potassium from different concentrations of KCl.

content was kept constant at 0.01 N and the KCl content varied from 10^{-5} N to 2.5×10^{-2} N. The absorption from these solutions was compared with the absorption from solutions of pure KCl. From the data obtained, the quantity:

$$\% \text{ stimulation} = \frac{(\text{absorption from KCl+CaCl}_2) - (\text{absorption from KCl})}{(\text{absorption from KCl})} \times 100$$

was calculated for the various KCl concentrations. Therefore, in figure 4 a value of –100% indicates that $CaCl_2$ completely prevented absorption of potassium, a value of 0% stimulation indicates no effect of $CaCl_2$ on potassium absorption and +100% means the absorption of potassium was doubled by the presence of $CaCl_2$.

In another experiment, the effect of calcium on the uptake of potassium at the carrier-free level was determined. The potassium was prepared and isolated by a method previously described (**4**). The concentration of radio-potassium was calculated to be approximately 10^{-14} N. The solutions contained no inactive potassium other than that due to impurities in the water, reagents, etc. The uptake of radio-potassium at constant potassium concentration and varying $CaCl_2$ concentration is given in figure 5.

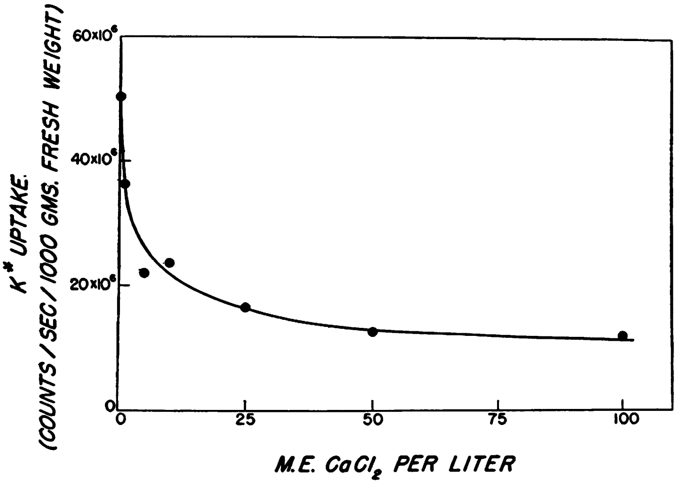

FIG. 5. The uptake of radio-potassium from a carrier-free solution of radio-potassium as affected by increasing concentrations of $CaCl_2$.

In order to determine the rate of isotopic exchange of potassium absorbed in the presence and absence of $CaCl_2$, the following experiment was conducted: The roots were divided into two batches and one batch was permitted to absorb potassium from 0.001 N KCl; the other batch absorbed potassium from 0.001 N KCl plus 0.01 N $CaCl_2$. In both cases, the KCl was labeled with radioactive potassium. After an absorption period of three hours, each batch of roots was removed from the solution, washed and centrifuged and further divided into two portions. One of these portions was then placed in 0.005 N KCl and the other in 0.005 N KCl plus 0.01 N

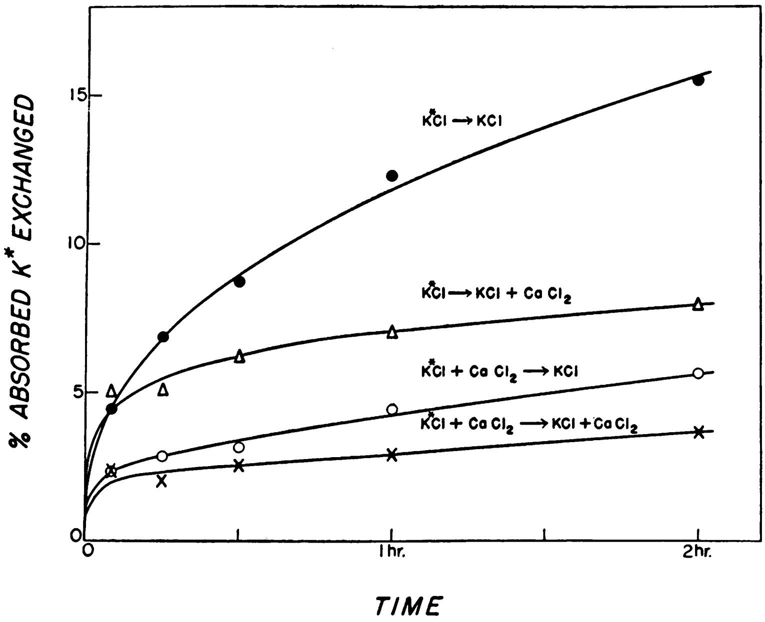

FIG. 6. Isotopic exchange of radio-potassium absorbed from 0.001 N K*Cl and from 0.001 N K*Cl + 0.01 N $CaCl_2$ and exchanged in solutions of 0.005 N KCl and 0.005 N KCl + 0.01 N $CaCl_2$. Absorptions carried out at 26° C and exchange reactions at 0° C.

$CaCl_2$. The other batch of roots was treated in the same manner. The exchanging solutions were kept at 0° C and the course of isotopic exchange followed by sampling the solutions for radioactivity at definite time intervals. The data for these experiments are given in figure 6.

Discussion

As may be seen from figure 1, the curves for absorption at increasing concentrations of potassium and calcium are markedly different. Aside from an initial rapid rise at low concentrations, the rate of calcium absorption is linear up to at least 0.200 N $CaCl_2$ concentration. In contrast to this, the absorption rate of potassium rises to a maximum at 0.080 N KCl and then falls. The character of the potassium absorption curve is markedly different from that observed in the low-salt barley roots of HOAGLAND and BROYER (**2**). In this latter type of material, the absorption rate rises to a maximum between 0.001 N and 0.005 N KCl and then remains virtually constant, *i.e.*, the absorption is independent of the concentration (**1**). The fall in absorption rate above 0.080 N KCl observed with the material used in these experiments deserves comment. It is doubtful that the decline is the result of osmotic effects since no corresponding behavior was noted with equivalent concentrations of $CaCl_2$. Thus far no adequate explanation for this decline has been found. Another significant difference between the uptake of potassium and calcium is the considerably greater uptake of potassium.

The competitive effect of potassium on calcium uptake is clearly shown in figure 2. As the potassium concentration is increased, there is an initial rapid drop in the uptake of calcium and then a considerably slower falling off in the rate of uptake. This curve seems best interpreted as indicating that calcium is taken up both in the absorbed and the adsorbed form and potassium has a pronounced inhibiting effect on that fraction of the calcium which is absorbed and a considerably smaller inhibiting effect on the adsorbed fraction. In figure 1, the initial rapid rate of uptake also suggests that two fractions of calcium are involved.

However, the reciprocal effect, *i.e.*, the effect of calcium on potassium absorption, cannot be explained on so simple a basis. In this case, the absorption of potassium is markedly stimulated by the presence of calcium as is shown in figure 3. The data show that the effect is related to both the calcium and potassium concentrations in the external media. Even relatively small concentrations of calcium exert a stimulating effect, which increases as the calcium concentration increases. A study of figure 3 shows that for a given calcium concentration the effect diminishes as the KCl concentration increases. As the KCl concentration decreases, calcium has an increasingly stimulating effect down to a concentration of $2 \times 10^{-4}\,N$ KCl (fig. 4). Below this value the stimulating effect diminishes and eventually the calcium depresses the absorption of potassium at very low concentrations of KCl.

The data of figure 5 indicate a depressing effect of calcium on radiopotassium uptake at extremely low potassium concentration ($10^{-14}\,N$ plus reagent and glassware contamination). However, it should be noted that the depression in this case is not as extreme as at the higher concentration of $10^{-5}\,N$. When roots are placed in a solution of potassium salt, both absorption and isotopic exchange occurs. At very low levels of potassium, *i.e.*, carrier-free radioactive solutions, isotopic exchange predominates. At higher levels, absorption predominates. For this reason, it is believed that figure 5 essentially shows the effect of calcium on exchange rather than on actual absorption.

In order to explain the interrelationships between calcium and potassium reported thus far, it is desirable to re-examine the mechanism proposed for ion absorption, namely, for potassium: $HR + K^+ = KR + H^+$. In this reaction, there are four rate determining factors, that is, the concentrations of the substances HR, K^+, KR and H^+. It can be expected that an increase in the amount of HR would lead to an increased rate of potassium absorption. Since HR is a metabolically produced substance, its amount would be dependent on temperature. The rate of absorption as a function of temperature has long been recognized and studied in root tissue (**2**). In the experiments described here, the temperature was constant and the root tissue metabolically uniform; hence, any variations in the quantity of HR must be attributed to other factors. Likewise, an increase in K^+ should lead to an increased absorption rate. If the assumption is made that the concentration of K^+ at the reaction site is proportional to the external concentration, then the absorption rate should increase with increasing concentration of potassium in the external solution. That this is so is indicated by the data of figure 1 which show that the absorption rate rises with increasing potassium concentration until some other factor becomes limiting, possibly the amount of HR.

A decrease in the concentrations of KR and H^+ should also result in increased potassium absorption. In the experiments described, the concentration of the H^+ in the external solution was maintained at a constant value. However, considerable variations in H^+ concentration may occur at the site of the reaction. The level of KR is determined by the difference between its rate of formation and its rate of utilization. It is reasonable that in high potassium roots, the level of KR is higher than in low potassium roots; and hence the latter plants should absorb potassium more rapidly than the former. The more rapid absorption by low potassium roots has been observed experimentally (**2**).

On the basis of the foregoing considerations, the stimulating effect of calcium on potassium absorption would best be explained either as an enhancement of the rate of formation of HR or an increased rate of utilization of KR. In other words, calcium may act as a co-factor in the formation of HR or it may accelerate the removal of KR from the site of the absorption reaction by either chemical alteration or physical means. A corollary of the postulated absorption reaction is that exchange for absorbed potassium must occur through the mediation of KR. If the KR level is reduced through the agency of calcium, then the rate of the following isotopic exchange reaction should decrease: $K^*R + K^+ = KR + K^{*+}$. The data of figure **6** show that this is indeed the case. Had the calcium functioned as stimulating the production of HR, then the level of KR would have remained constant or increased and therefore we should not obtain a decrease in the exchange rate. On the basis of the isotopic exchange curves, it appears that calcium affects the level of KR rather than the production of HR.

To summarize, the interrelationships between calcium and potassium in absorption may be explained in terms of two simultaneous processes. The first of these is a competition between calcium and potassium for HR. The second is a depressing effect of calcium on the level of KR and a resulting stimulating effect on the absorption of potassium. Since potassium has a much greater affinity for HR than calcium (fig. 1), the competitive effect of calcium on potassium absorption becomes important only when the concentration of potassium is very low when compared to that of calcium. As the concentration of potassium increases, the competitive effect of calcium decreases and the stimulating effect becomes important. At still higher concentrations of potassium, unknown factors become limiting and the stimulating effect diminishes (fig. 4).

Summary

The interrelationships between potassium and calcium in absorption by barley roots have been investigated. It has been demonstrated that a given concentration of calcium exerts both a depressing and a stimulating effect on the absorption of potassium and that the effects are related to the concentration of potassium in the external media. The depressing effect has been interpreted as the result of a competition for a metabolically produced binding compound. In order to explain the stimulating effect, it is necessary to postulate that calcium functions as a cofactor in the utilization of the potassium complex produced during absorption.

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