Interrelations of Calcium and Rubidium Absorption by Excised Roots of Barley and Plantain[1]

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ABSTRACT

The uptake rates of Rb and Ca, applied alone or together, by excised barley and plantain roots were compared. The barley roots absorbed Rb at a faster rate than Ca, whereas the reverse was true for plantain roots. The presence of Ca increased the rate of Rb uptake by barley roots, but the presence of Rb had very little effect upon the Ca uptake. The uptake rate of either ion by plantain was reduced by the presence of the other ion.

Calculations indicate that the depressing effect of one ion on the uptake of the other by plantain was due predominantly to ionic competition when the ions were present in the concentration range of $10^{-2}N$, but factors in addition to competition were responsible in the concentration range of $10^{-4}N$. The significance of the differences in response of the two species is discussed.

COLLANDER (3) GREW DIFFERENT species of plants in solutions containing equivalent amounts of K and Ca and found that oats accumulate much more K than Ca while *Plantago lanceolata* accumulates K and Ca in about equal amounts. This difference in cation selectivity between plant species, which has been confirmed by de Wit and Dijkshoorn (unpublished) for *Dactylis glomerata* and *P. lanceolata*, may be associated with the utilization of the ions during growth or related to the cation uptake mechanism by the roots. With the assumption that the uptake of cations by exised roots is affected to only a small extent by cation utilization, the interrelations between Ca and Rb uptake by excised roots of barley *(Hordeum vulgare)* and plantain *(P. lanceolata)* were compared.

Competitive Relations

The n equations

$$r_i = \frac{b_i C_i}{b_1 C_1 + \text{--} \ b_i C_i + \text{--} + b_n C_n + 1} \ R_i \ (i = 1, 2, \text{--}n) \quad [1]$$

with proper designations for the symbols are widely used to describe competitive phenomena in physical and chemical engineering, physical chemistry, biochemistry, plant ecology, and animal ecology.

In the case of ionic uptake $C_1, -C_i, -C_n$ represent concentrations of ions of the same sign in the root medium and r_i, the absorption, adsorption, or sorption of the ionic species by roots, and b_i and R_i are constants for each ionic species. R_i is the value of r_i for infinite concentration of C_i. Epstein and Hagen (6), Fried and Noggle (7), and others used these equations to evaluate whether two ions affect each other competitively.

If one of the ions, in a n-ion system, is varied and the others are kept constant, equation [1] reduces to

$$r_i = \frac{(b_1/K) \ C_i}{(b_1/K) \ C_i + 1} \ R_i \quad [2]$$

in which

$$K = 1 + \sum_{i=2}^{n} b_i C_i = \text{constant},$$

Fried and Noggle (7) tested the validity of this equation over a wide concentration range and found that for barley roots the results can be described with two equations [2], one being predominant at concentrations in the order of 10^{-4} equivalents (eq.) per liter and the other at concentrations around 10^{-2} eq. per liter. Bear (1), Dijkshoorn (5), Sutcliffe (10), and Said (9) used replacement series to study the effect of one ion on the other. These are series of treatments in which the total cation content of the solution is constant but the ratios of the cations vary.

For a replacement series of the ions 1 and 2, equation [1] can be simplified by substituting the identity

$$K = K\, \frac{C_1 + C_2}{C_1 + C_2} = K\, \frac{C_1 + C_2}{a}\ \text{for}\ K = 1 + \sum_{i=3}^{n} b_i\, C_i = \text{constant}$$

in equation [1].
This gives

$$r_1 = \frac{k_{12} C_1}{k_{12} C_1 + C_2}\, R_1{}'$$

and

$$r_2 = \frac{C_2}{k_{12} C_1 + C_2}\, R_2{}' \qquad [3]$$

with

$$k_{12} = \frac{b_1/K + (1/a)}{b_2/K + (1/a)},\ R_1{}' = \frac{b_1/K}{b_1/K + (1/a)}\, R_1 \ \text{and}\ R_2{}' = \frac{b_2/K}{b_2/K + (1/a)}\, R_2.$$

Hence a competitive relation as described by equation [1] may exist if for any concentration ratio within a replacement series, the sum $r_1/R_1{}' + r_2/R_2{}' = 1$, that is, if the curves $r_1/R_1{}'$ vs. C_1 and $r_2/R_2{}'$ vs. C_2 are both curved to the same extent but in opposite directions. A detailed discussion of the interrelations for this type of competition was given by De Wit (4). A more critical test of the applicability of equation [1] involves calculation of the constants b/K and R for both ions by matching equation [2] to the observations from a concentration series and checking whether substituting these values into equations [3] will yield curves to fit the observed data of the replacement series.

It is often supposed that the first step in ionic uptake is an exchange reaction. This being the case, it may be that the competitive interrelations between a monovalent ion and a divalent ion are more complicated than indicated by equation [1]. For resin systems this has been analyzed by Heald et al. (8). Their treatment and data show that experiments must be executed rather accurately over a wide concentration range to show these complications. Neither the accuracy nor the range of concentrations used in the present study permit the use of an equation other than [1].

EXPERIMENTAL TECHNIQUES

Barley roots were obtained from 7-day-old seedlings grown in a solution of 4×10^{-4} eq. $CaSO_4$ per liter, as described by Epstein and Hagen (6). About 24 hours before the beginning of an experiment, the $CaSO_4$ solution was replaced by demineralized water.

Plantain was removed from the field and the roots and tops were clipped. The plants were allowed to regrow for 3 to 4 weeks in a half-strength Hoagland nutrient solution with micro-nutrients and iron chelate as developed by Said (9). About 48 hours before beginning the experiment, the nutrient solution was replaced by demineralized water in order to remove Ca from the surface of the roots. After removal of the roots the tops were clipped and the plants were returned to the nutrient solution for regrowth and use in subsequent experiments.

The roots were excised shortly before the beginning of an experiment and washed in demineralized water. Samples of an estimated 0.5 g. were transferred to the treatment solutions at the beginning of the sorption period. The treatment solution was decanted at the end of the sorption period and adhering solution was removed by washing one minute with demineralized water. The adhering water was removed by blotting the roots with tissue paper before determining the fresh weight. Roots containing Ca^{45} were ashed at 400°C. before Ca^{45} was determined.

Chloride salts of Ca and Rb were used in all cases. When both Ca and Rb uptake were to be determined from a mixture of the two ions, sufficient solution was prepared and divided

into two portions. One portion was tagged with Rb^{86} and the other with Ca^{45}. Solution volume to root ratios were sufficiently large to limit exhaustion to within 25%.

Fried and Noggle (7) showed that Rb and K are practically indistinguishable by excised barley roots in short-time sorption studies so that within rather narrow limits it is allowed to read K uptake for Rb uptake.

RESULTS AND DISCUSSIONS

Time Series

The uptake of Rb by barley from a solution with 10^{-4} eq. RbCl per liter in the absence and presence of 10^{-3} eq. $CaCl_2$ per liter is given in figure 1, left; figure 1, right, represents the data during the first 40 minutes of sorption plotted on a larger scale. The uptake rate in the presence of Ca does not change appreciably during the 3 hours, but in the absence of Ca a much smaller rate is established after 50 minutes. Although the amount of Rb associated with the roots is lower during the first 40 minutes, the rate of uptake (slope of line) between 5 and 180 minutes is higher in the presence than in the absence of Ca. The uptake of Rb by plantain roots from a solution with 10^{-4} eq. RbCl per liter in the absence and presence of 10^{-4} eq. $CaCl_2$ per liter during 3 hours is given in figure 2, left. A steady uptake rate is reached after half an hour. Calcium appears to depress the uptake of Rb during the entire 3-hour period.

The uptake of Ca from a solution with 10^{-4} eq. $CaCl_2$ per liter by plantain is given in figure 2, right. After 40 minutes a steady uptake rate is established which is small compared with the sorption before that time. The sorption of Ca by barley roots before 40 minutes is often so high, compared with the sorption between 40 and 180 minutes, that it is difficult to establish an uptake rate after 40 minutes.
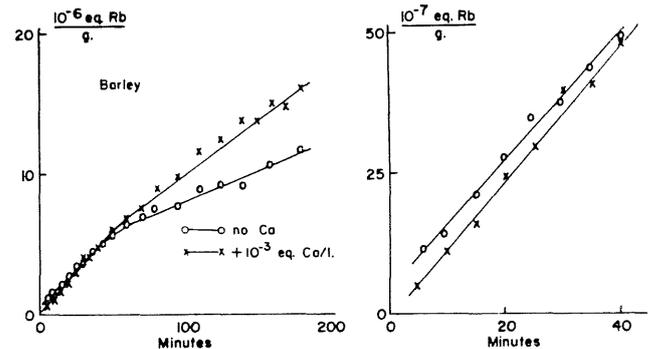

Figure 1—The uptake of Rb by barley roots from a solution with 1×10^{-4} eq. Rb/liter.
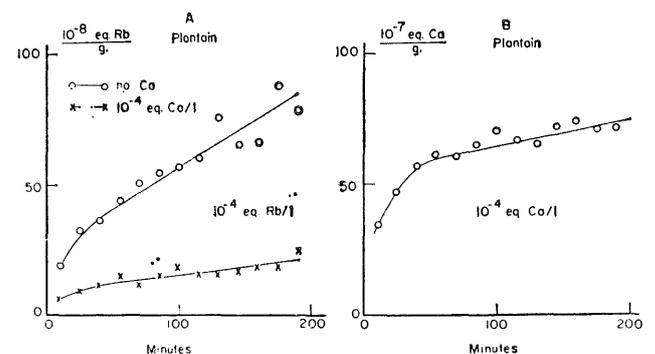

Figure 2—The uptake of Rb (left) and Ca (right) by plantain roots from a solution with 1×10^{-4} eq./liter.

Table 1—Concentrations of RbCl and CaCl$_2$ used
in uptake rate studies.

Concentration series		Replacement series	
RbCl	CaCl$_2$	RbCl	CaCl$_2$
	10^{-4} eq./liter		
0.33	0.00	1.00	0.00
0.67	0.00	0.67	0.33
1.00	0.00	0.33	0.67
0.00	1.00	0.00	1.00
0.00	0.67		
0.00	0.33		

These time studies show a steady rate of Rb and Ca uptake between 40 and 180 minutes. Therefore, in subsequent experiments the sorption of Rb and Ca per gram of fresh roots was determined in duplicate after 40 and 180 minutes. The value for the rate of uptake, expressed as equivalents per gram fresh root per 140 minutes, was obtained by subtracting the sorption for 40 minutes from the sorption for 180 minutes.

Experiments at Concentrations Around 10^{-4} eq. per liter

The uptake of Rb and Ca was studied at the concentrations and combinations as shown in table 1. It should be noted that only one cation, either Rb or Ca, is present in a solution of the concentration series, but both Rb and Ca may be present in the same solution of a replacement series. The sum of Rb and Ca is constant in all solutions of a replacement.

The uptake rates for Rb and Ca by barley are presented in figure 3 and by plantain in figure 4. The concentrations of Rb and Ca, expressed in a scale from 0 to 1 $\times$ 10^{-4} eq. per liter, are given along the abscissa in opposite directions. Increasing Ca concentrations are plotted from right to left on the concentration series so that the uptake rates are more easily compared with the uptake rates of the replacement series.
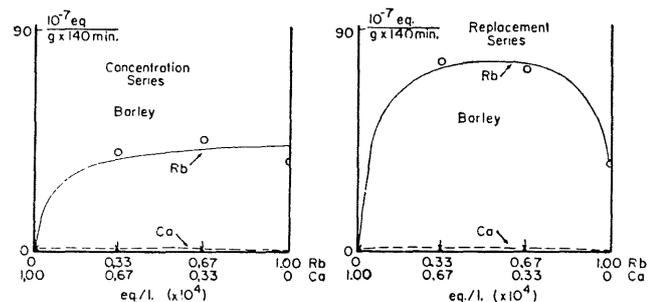
The uptake rate of Ca by barley roots is negligible compared with the uptake rate of Rb, figure 3, left. The rate of Rb uptake appears to double in the presence of CaCl$_2$, figure 3, right. It has been suggested by Briggs, Hope, and Robertson (2) that the enhancement effect of Ca on the uptake of Rb is due to the uptake of the anion which is associated with the Ca. The Cl concentration is constant in the replacement series which eliminates any effect that the anion might have on the uptake of the Rb. The uptake rate of Rb from solutions of 0.33 and 0.67 $\times$ 10^{-4} eq. Rb per liter in the presence of Ca is higher than the uptake rate from a solution of 1 $\times$ 10^{-4} eq. Rb per liter in the absence of Ca while the Cl concentration is constant in the three solutions. This agrees with the results of Viets (11) who found the effect by adding CaSO$_4$, while the uptake rate of SO$_4$ is slow compared to Cl. It is useless trying to recognize competition in these data because of the enhancement effect of Ca on Rb uptake.

The uptake rate of Ca by plantain roots is about 10 times larger than Rb uptake rate (different scales, figure 4, left), but it is apparent that Ca and Rb decrease the sorption of each other, figure 4, right. Using the uptake rates from the concentration curves in figure 4, a value of about 2.3 for k_{CaRb} is calculated. The values for the uptake rate in a replacement series, calculated with this constant and equation [3], are represented by the dotted lines on the replacement series graph of figure 4. The observed depressing effect of each ion on the uptake rate of the other is larger than the calculated effect, and since both measured replacement curves are not bent to the same extent, it must be concluded that although competitive effects may play a role some other effect is also present.

Experiments at Concentrations Around 1 $\times$ 10^{-2} eq. per liter

The experiments of figures 3 and 4 were repeated at 100-times higher concentrations.

The results are represented in figures 5 and 6. With

Figure 3—The uptake rate of Rb and Ca by barley roots from solutions with a concentration around 10^{-4} eq./liter.
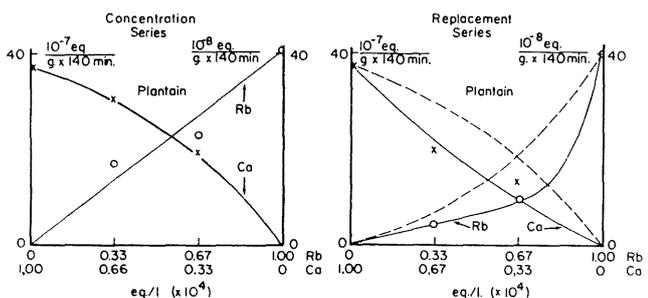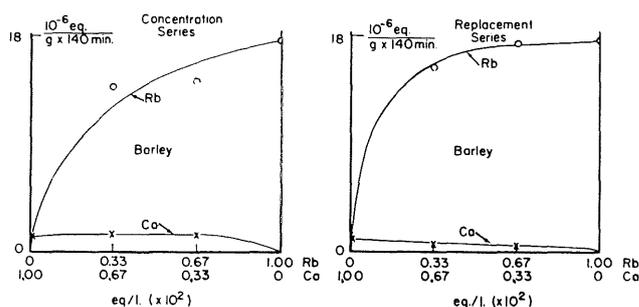

Figure 4—The uptake rate of Rb and Ca by plantain roots from solutions with a concentration around 10^{-4} eq./liter.

Figure 5—The uptake rate of Rb and Ca by barley roots from solutions with a concentration around 10^{-2} eq./liter.
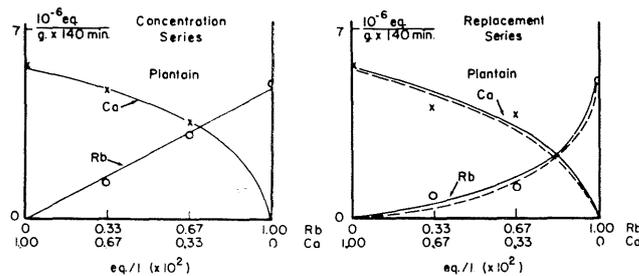

Figure 6—The uptake rate of Rb and Ca by plantain roots from solutions with a concentration around 10^{-2} eq./liter.
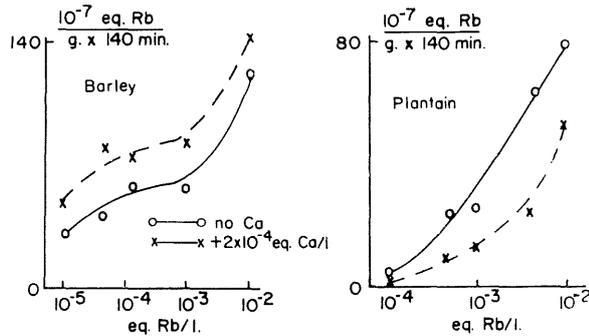
Figure 7—The uptake rate of Rb by barley (left) and plantain (right) from solutions with 2×10^{-4} eq. Ca/liter and varying Rb concentrations.
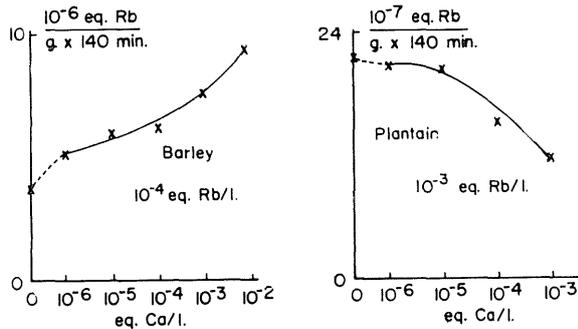

Figure 8—The uptake rate of Rb by barley (left) and plantain (right) from solutions with constant Rb concentrations and varying Ca concentrations.

barley (figure 5), the enhancing effect of Ca is still present, although it is much smaller than at 1×10^{-4} eq. per liter. The data indicate that, although Ca promotes the uptake of Rb, Rb suppresses the uptake of Ca. There are insufficient data to calculate whether this may be a competitive effect.

At concentrations around 1×10^{-4} eq. per liter, the Ca uptake by plantain roots was about 10 times the Rb uptake. At concentrations around 10^{-2} eq. per liter (figure 6), the uptake of both ions are the same order if the ions are given alone. From the concentration curves it is calculated that k_{CaRb} is about 4.9 for the uptake rates, and the replacement curves calculated with this value and equation [3] match very well the measured replacement curves. Hence, competition seems to be the predominate effect at these concentrations.

Experiments at Constant Ca Concentration

Since with both barley and plantain other than competitive phenomena are observed, it is necessary to check whether the effect of Ca can be overcome by increasing Rb concentrations. The graphs in figure 7, with the Rb concentration along the abscissa in logarithmic progression, represent these results. The enhancing effect of 2×10^{-4} eq. Ca per liter on the rate of Rb uptake by barley occurs over a large range of concentrations of Rb. The sigmoid shape of the curves indicates again that at least two equations [2] are needed to describe the relation between concentrations and uptake. Increasing the Rb concentration

did not overcome the effect of 2×10^{-4} eq. Ca per liter on the uptake rate of Rb by plantain roots, although a calculation based on the data of figure 4 ($k_{CaRb} = 2.3$) shows that the depressing effect of 2×10^{-4} eq. Ca per liter due to competition should be negligible at concentrations of 1×10^{-2} eq. Rb per liter. This indicates that something other than competitive effects of Ca may decrease the Rb uptake.

Experiments at Constant Rb Concentrations

The preceding data do not exclude the possibility that beyond a certain minimum concentration the effect of Ca on the Rb sorption is independent of Ca concentration. The graphs in figure 8, with the Ca concentration along the abscissa in logarithmic progression, and the Rb uptake rates from 1×10^{-4} eq. Rb per liter (barley) or 1×10^{-3} eq. Rb per liter (plantain) along the ordinate, show that this is not the case. The enhancing effect of Ca on the Rb uptake by barley and the depressing effect of Ca on the Rb uptake by plantain increases with increasing Ca concentrations up to 1×10^{-2} eq. Ca per liter (barley) and up to 1×10^{-3} eq. Ca per liter (plantain).

CONCLUDING REMARKS

The results of this series of experiments show that the effect of Ca on the uptake of Rb by excised roots of barley and plantain is not consistent. Although competition between Ca and Rb exists with plantain roots, other interactions also occur. These observations place more rigid requirements on any explanation of the interactions of Ca and Rb uptake by excised roots.

The relative uptake rates of Ca and Rb by excised roots of barley and plantain are similar to the relative Ca and K contents of the whole plants. A test of whether Ca increases the uptake of K in growing plants is difficult because plants will not grow in a nutrient medium that does not contain Ca.

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