Interactions Between Potassium and Calcium in Their Absorption by Intact Barley Plants. I. Effects of Potassium on Calcium Absorption

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Abstract. Increasing concentrations of K (20, 200, 2000 μM) in the nutrient solution depressed Ca content and concentration in barley plants growing in nutrient solutions of low Ca concentrations (250 and 2500 μM). Increasing K from 20 to 200 μM depressed Ca absorption more than increasing K from 200 to 2000 μM K.

The strong depression of Ca absorption by low concentrations of K must involve a different process from that studied by other workers at high concentrations of K. Since the depression in net absorption of Ca was as great at 250 as at 2500 μM Ca the results fail to support previous suggestions that a specific mechanism for Ca absorption operates at low Ca concentrations. It is suggested that, at the low concentrations of K and Ca likely to be found at the root surface in many soil solutions, the above mentioned effect of K in inhibiting Ca absorption may be important in the Ca nutrition of plants.

Increasing concentrations of K generally depress Ca content of plants (4, 9, 11, 13, 16, 17, 22). Lazarooff and Pitman (13) found the depressive effect of monovalent cations on Ca content to be confined to the tops of barley plants and to occur only at high concentrations of monovalent cations (5000–60,000 μM Na + K). This depressive effect of monovalent cations was attributed (13) to reduced transpiration at high monovalent ion concentrations with a consequent reduction in Ca transport to tops. There was no depression of Ca content in tops at lower concentrations (2000 to 5000 μM Na + K).

Studies with Atriplex spongiosa (17) showed that increasing K concentrations only had depressive effects on leaf Ca contents at high levels of Ca in solution (50,000 μM) with no effect of K at low Ca levels (500 and 5000 μM). Two independent mechanisms of Ca absorption were proposed (17)—a highly specific, K insensitive mechanism at low Ca concentrations and a non-specific, K sensitive mechanism at higher Ca concentrations. Such dual absorption mechanisms have been suggested for other nutrient ions (6).

We have examined the effects of K on Ca absorption into barley plants growing in solutions maintained at Ca and K concentrations lower than those previously studied and approximating those found in soil solution extracts (1,3). Three other species (Lolium perenne L.; Trifolium subterraneum L. cv Mt. Barker; Medicago truncatula Gaertn. cv Cyprus) were also studied and gave essentially similar results. Results for barley only are presented in this paper.

Materials and Methods

Plant Culture. Barley seeds, Hordeum vulgare L. cv Beecher, were soaked in aerated flasks of deionized water for 1 day before transferring to cheesecloth-covered wire screens in plastic buckets containing 4 liters of aerated nutrient solution. The composition of these solutions was the same as that of the basal solution of the main experiment, except for the addition of 19 μM NH₄H₂PO₄, 250 μM Ca(NO₃)₂, and 20 μM KNO₃. The temperature of the nutrient solutions was maintained at 20 ± 1° and the pH at 5.5 ± 0.3. The nutrient solutions in the buckets were renewed after 3 days.

After 5 days, seedlings were transferred to 6 recirculating solution culture units (2). In each unit a total volume of 2800 liters of nutrient solution continuously recirculated through 32 pots in parallel at a flow rate of 1300 to 1400 liters/pot/day. Filtered air was bubbled through the solution in each pot and the solutions were maintained at 20 ± 0.5°. The pH was maintained at 6.0 ± 0.3 by titration with 0.15 N NH₄OH.

Six treatments were imposed in a simple 3 × 2 factorial: K as KNO₃ at 20, 200, 2000 μM and Ca at 250 [Ca(NO₃)₂] and 2500 μM [250 μM Ca(NO₃)₂ + 2250 μM CaSO₄].

The Ca concentrations were chosen to approximate soil solution concentrations from soils of low and high Ca status (3). The K concentrations were chosen with specific reference to the dual mechanisms of K absorption (6, 7). These K con-
centrations also encompass the range commonly encountered in solutions extracted from soils of low to high K status (1, 3). In choosing the lowest concentrations of K and Ca, extreme values which would have induced severe deficiencies (1, 15) were avoided.

Treatment concentrations in each nutrient solution were maintained within the limits indicated in Table I by additions after analysis for K (daily) and Ca (every 3 days). K was determined on a Unicam SP 900 flame photometer by the method of Dean (5). Ca was determined by atomic absorption spectroscopy after addition of strontium to 0.2% (w/v) to prevent interference from other elements (21).

Basal nutrient concentrations were (µM): Mg 100; N (as NH₄⁺) 101; N (as NO₃⁻) 100; S 100; P 1; Na 10; Cl 10; Fe (as sequestrene 138) 10; B 2; Mn 0.3; Zn 0.1; Cu 0.1; Co 0.04; Mo 0.02.

Phosphate concentrations were determined every 3 or 4 days by the method of Truog and Meyer (19), and additions made to maintain 1 µM P. Excessive depletion of other nutrients was avoided by draining one quarter of the total solution volume of each unit after each 7 days and refilling with fresh solution.

Harvest and Chemical Analysis. At planting (Day 0), 24 five-day old seedlings were placed in each pot of 4 pairs of pots in each unit. Each pair of pots was treated as a single replicate which was harvested 4 times at successive 3 day intervals from planting. At each harvest equal numbers of plants were taken from each pot of a pair and bulked to give a single sample. At the first harvest (Day 5) 24 plants were taken per replicate. At the 3 remaining harvests (Day 10, Day 15, Day 20) 8 plants per replicate were taken.

At each harvest the plants were divided into tops and roots. The shoots were dried in a ventilated drying room at 25°C and the dry weight of the shoots was determined. The roots were washed, blotted dry, and weighed. The above results are presented as average weights for each harvest, that is, the means of the 24 plants in each replicate. All weights are given in milligrams per plant.

Table I. Concentration of Ca and K in Nutrient Solutions

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ca₂₅₀K₂₀</th>
<th>Ca₂₅₀K₂₀₀</th>
<th>Ca₂₅₀K₂₀₀₀</th>
<th>Ca₂₀₀₀K₂₀</th>
<th>Ca₂₀₀₀K₂₀₀</th>
<th>Ca₂₀₀₀K₂₀₀₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>µM Ca</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>256 ± 7</td>
<td>256 ± 7</td>
<td>256 ± 7</td>
<td>2557 ± 57</td>
<td>2547 ± 67</td>
<td>2532 ± 90</td>
<td></td>
</tr>
<tr>
<td>19.0 ± 1.0</td>
<td>195 ± 10</td>
<td>1956 ± 25</td>
<td>19.4 ± 1.0</td>
<td>199 ± 12</td>
<td>1970 ± 20</td>
<td></td>
</tr>
</tbody>
</table>

Table II. Effect of Ca and K Concentrations in Nutrient Solution on Fresh Weights, Ca Content and Ca Absorption Rates of Barley Plants

Means of 4 replications.

<table>
<thead>
<tr>
<th>µM Ca</th>
<th>Day 0</th>
<th>Day 5</th>
<th>Day 10</th>
<th>Day 15</th>
<th>Day 20</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>µM K</td>
<td>µM K</td>
<td>µM K</td>
<td>µM K</td>
<td>µM K</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>200</td>
<td>2000</td>
<td>20</td>
<td>200</td>
</tr>
<tr>
<td>250</td>
<td>310</td>
<td>350</td>
<td>350</td>
<td>620</td>
<td>710</td>
</tr>
<tr>
<td>2500</td>
<td>340</td>
<td>360</td>
<td>360</td>
<td>790</td>
<td>780</td>
</tr>
<tr>
<td>P = 0.05</td>
<td>24</td>
<td>80</td>
<td>167</td>
<td>450</td>
<td></td>
</tr>
<tr>
<td>250</td>
<td>190</td>
<td>180</td>
<td>170</td>
<td>480</td>
<td>430</td>
</tr>
<tr>
<td>2500</td>
<td>190</td>
<td>180</td>
<td>170</td>
<td>480</td>
<td>430</td>
</tr>
<tr>
<td>P = 0.05</td>
<td>14</td>
<td>66</td>
<td>202</td>
<td>421</td>
<td></td>
</tr>
<tr>
<td>250</td>
<td>4.4</td>
<td>3.5</td>
<td>3.4</td>
<td>2.8</td>
<td>7.5</td>
</tr>
<tr>
<td>2500</td>
<td>8.1</td>
<td>6.8</td>
<td>6.0</td>
<td>18.8</td>
<td>15.3</td>
</tr>
<tr>
<td>P = 0.05</td>
<td>0.4</td>
<td>1.7</td>
<td>2.6</td>
<td>8.3</td>
<td></td>
</tr>
<tr>
<td>250</td>
<td>0.38</td>
<td>0.35</td>
<td>0.30</td>
<td>0.88</td>
<td>0.90</td>
</tr>
<tr>
<td>2500</td>
<td>0.55</td>
<td>0.43</td>
<td>0.38</td>
<td>1.03</td>
<td>1.03</td>
</tr>
<tr>
<td>P = 0.05</td>
<td>0.05</td>
<td>0.15</td>
<td>0.31</td>
<td>0.46</td>
<td></td>
</tr>
<tr>
<td>250</td>
<td>0.15</td>
<td>0.13</td>
<td>0.35</td>
<td>0.35</td>
<td>0.43</td>
</tr>
<tr>
<td>2500</td>
<td>0.25</td>
<td>0.20</td>
<td>0.23</td>
<td>0.55</td>
<td>0.55</td>
</tr>
<tr>
<td>P = 0.05</td>
<td>0.03</td>
<td>0.05</td>
<td>0.22</td>
<td>0.31</td>
<td></td>
</tr>
</tbody>
</table>

1 Including seed reserves.
2 Calculated by equation I.

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and roots (and seed reserve at the first harvest), blotted, and weighed. The roots were rinsed in deionized water and desorbed in 0.01 M MgSO₄ solutions at 5° for 1 hr. Desorbing solutions were analyzed for K and Ca. After desorption, the roots were rinsed in deionized water and, together with the tops, oven dried for 48 hr at 70°.

After weighing, the dried material was digested in a nitric-perchloric acid mixture (12) and analyzed for Ca by atomic absorption spectroscopy after addition of strontium to 0.2 % (w/v) to prevent interference from other elements (21).

Results

Growth. Treatments had relatively small or no effect on fresh weights of plants at any harvest (table II). Dry weights reflected fresh weights as treatments had no effect on dry matter content. Values for dry matter content at successive harvests were 10.7, 8.8, 9.3, 9.4 respectively for tops and 6.2, 5.1, 5.0, 3.9 % respectively for roots. Increasing K tended to increase plant growth by a small amount at both concentrations of Ca and increasing Ca had little effect except at K₅₀. At each harvest, the growth of barley plants at Ca₅₀K₅₀ was slightly less than that in the other 5 treatments (P < 0.05): the cause of this effect is not known.

In all treatments plants grew vigorously and relative growth rates at all times exceeded 15g/100g fr wt/day.

Effect of K on Ca Content. Increasing K concentrations in solution generally decreased Ca concentrations of both tops and roots of barley plants at both Ca₅₀ and Ca₂₅₀ (fig 1 shows results for Day 10). The effect of K in decreasing Ca concentrations of plants was not due to dilution from the small increases in plant weight since total Ca contents of plants (table II) also decreased with increasing K treatment.

The concentrations and contents of Ca in tops reflect those of whole plants since tops always contained more than 90 % of the plant's Ca. The effect of increasing solution K in decreasing the Ca content and concentration of barley tops tended to be more marked than its effects on roots (table II). The depression of Ca in tops and whole plants was evident in early harvests over the whole range of K concentrations in solution: it was most marked at low concentrations (from K₅₀ to K₉₀). The substantial effects of increasing K in solution from K₅₀ to K₉₀ persisted throughout all harvests whereas the smaller effects from K₉₀ to K₂₀₀ tended to diminish with time.

Increasing K tended to decrease Ca content and concentration of tops at Ca₅₀ by nearly the same amount as at Ca₂₅₀. Hence the relative effect on tops and whole plants was very much greater at Ca₅₀. Therefore solution K decreased the absorption of Ca by barley plants proportionately more at low concentrations of both K and Ca in solution.

Rates of Ca Absorption. Since treatments had only small effects on plant growth and did not change root-weight ratios (the proportion of root to whole plant), the total amount of Ca in plants permitted a reasonable comparison of the rates of Ca absorption at any given harvest (table II). However, comparisons of absorption rates between successive harvests involve plants with different quantities of roots. These comparisons may be made by expressing rates of absorption per unit weight of roots. Since root weights changed during each absorption period, Williams' (20) formula has been used for calculation of mean rates of calcium absorption per unit weight of root (v) using fresh weights rather than dry weights of roots (14):

$$v = \frac{(\log W_{x_2} - \log W_{x_1}) (M_x - M_1)}{(t_2 - t_1) (W_{x_2} - W_{x_1})}$$

where $W_{x_1}$ and $W_{x_2}$ are the fresh weights of roots, $M_1$ and $M_2$ are the total quantities of mineral nutrient in the plant at the start ($t_1$) and completion ($t_2$) of the absorption period.

The effects of treatments on rates of Ca absorption per gram fresh weight of roots paralleled their effects on Ca content and concentration (table II). Since the rates of Ca absorption per gram fresh weight of roots remained approximately constant in each treatment over successive 5 day periods (table II) the depression of Ca absorption by increasing solution K from 20 to 200 μm persisted throughout the experiment. When taken over the whole 20 day period, increasing K from 20 to 2000 μM depressed the rate of Ca absorption per gram fresh weight of roots by approximately 20 to 25 % at both Ca levels.

Discussion

The strong depression of Ca absorption by low concentrations of K (20-200 μM) observed in the
present experiment appears to involve a process different from that studied by other workers. However, the minimal effects of K on Ca absorption over the 200 to 2000 μM K range correspond with Lazaroff and Pitman's work (13) in which there was no effect of monovalent cations at lower concentration ranges (2000-5000 μM with K:Na in ratio 1:3) on Ca absorption by barley plants.

Lazaroff and Pitman (13) only observed a depression of Ca content in plant tops at high concentrations of monovalent ions and suggested that the mechanism involved was a reduction in transpiration at these high ion concentrations. In fact, most other studies showing depressions of Ca absorption by increasing K concentrations (4, 9, 11, 16, 22) have involved concentrations of both Ca and K in solution which are sufficiently high to be explained by Lazaroff and Pitman's transpiration theory. For example, since transpiration can influence Ca absorption from high concentrations of Ca in solution (15,000 μM) but not from low concentrations (500 μM Ca) (13) this mechanism might explain the contrasting effects of high K concentrations in inhibiting Ca absorption by Atriplex spongiosa from solutions of high Ca concentrations while having no effect at lower Ca concentrations (17). However, transpirational effects cannot account for the results presented in this paper which show a very marked effect of K on Ca absorption when solution concentrations of both ions are very low. Some other phenomenon must be involved.

The results of the present experiment do not support the operation of a Ca-specific, K-insensitive mechanism of Ca absorption in barley plants such as has been postulated to operate at Ca concentrations below 5000 μM in Atriplex (17). Instead, Ca absorption from nutrient solution containing 250 μM Ca was inhibited by increasing K to the same extent as Ca absorption from solutions of 2500 μM Ca. However, since increasing K could inhibit net Ca absorption by influencing mechanisms of either Ca influx or Ca efflux (18) the present results do not exclude the operation of a Ca-specific, K-insensitive mechanism of Ca influx into barley plants.

Since the average concentrations of K and Ca in solutions extracted from soils are generally quite low [e.g. Barber (3) cites common values for Ca as 200 to 2000 μM and for K as 80 to 1500 μM], it is possible that the suppression of Ca absorption by K may influence the development of Ca deficiency in plants growing on soils of low nutrient status. Such an effect is particularly likely to occur if, as suggested (3), the K concentration at the root surface is considerably lower than it is in the average soil solution. This possibly explains why application of K to soils increases Ca deficiency in cotton roots (10) and the severity of blossom-end rot in tomatoes (8).

Literature Cited


