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POTASSIUM INHIBITION OF CALCIUM AND MAGNESIUM ACCUMULATION IN ROOTS OF INTACT MAIZE SEEDLINGS

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ABSTRACT: The effects of solution potassium (K) on the accumulation of magnesium (Mg) and calcium (Ca) in roots was assessed with 7-day-old corn (*Zea mays* L.) seedlings. Root accumulation of Ca and Mg was studied in replacement type experiments, *i.e.* the ratio of Ca to Mg was altered but the concentration of Ca plus Mg was kept constant at 2 mM. Concentrations of Ca in the tissue after 12 h exceeded that of Mg, except when Mg comprised over 85% of the divalent cations in the uptake solution. The addition of 0.1 mM K to the llptake solutions significantly altered the accumulation of Ca and Mg. The concentration of Mg was affected more than that of Ca. The relative effects of solution K on Mg and Ca accumulation in roots could be explained by comparing the relative acid-base characteristics of the metals.

INTRODUCTION

It has been recognized for almost 20 years that Ca and Mg are mutual competitors for absorption by plant roots (1,2,3,4,5,6). In general, Mg uptake is more sensitive to inhibition by Ca than the reverse. Such results indicate that at least part of the Mg is absorbed via a mechanism similar to that of Ca. Our knowledge of the biochemical basis for Mg transport is almost unknown. Understanding of Ca transport has increased recently due to the suspected role of this cation in regulating cellular responses to environmental and developmental changes (7). There is growing evidence that the normally low concentration of Ca in the cytoplasm is maintained by Ca antiporters and Ca-translocating ATPases which extrude Ca into either the extracellular space or the vacuole (8). Calcium influx is more poorly understood. However, there is growing evidence that influx may be mediated by a dihydropyridine-sensitive Ca channel similar to those found in mammalian tissue (9).

The basis for the inhibition of Mg uptake by Ca and the reverse is poorly understood. Mutual competition between two ions for a transport site on a carrier protein is commonly used to account for decreases in uptake. This concept of mutual competition was introduced to plant nutrition over 20 years ago by Epstein (10) to explain the interaction between K and Na and it has been expanded over the years. Binding of ions to a site, such as a transport site on a carrier protein, can be accounted for by considering the ionic radius and the free energy of hydration of the binding ions (11). This theory can adequately describe the interaction between series of monovalent and divalent ions. However, this theory has difficulties in describing the interactions between ions of different valence, such as the observed inhibition of Mg uptake by plant roots by the presence of K. The relative acid-base characteristics of metals may be useful to describe the interaction between ions (12). In this study, the competition between K, Ca, and Mg for uptake by roots of corn seedlings was examined and the relative acid-base characteristics were found to be useful in describing the effects of K on the interaction between Ca and Mg uptake.

MATERIALS AND METHODS

Corn Seedling Experiments: One-week-old maize seedlings (cv. WF9 x Mo17) were grown in 0.2 mM calcium sulfate ($CaSO_4$) solution as has been described previously (13). Roots at the start of experiments contained approximately 40, 180, and 200 meq/kg dry weight of Mg, Ca, and K, respectively. Uptake experiments were started at the beginning of the light phase of the diurnal cycle and lights remained on throughout the experinient. Plants were placed in uptake solutions typically containing various concentrations of K, Ca, and Mg as sulfate salts adjusted to pH 6.0 by the addition of sulfuric acid (H_2SO_4). Samples of the nutrient solutions before and after the uptake period were collected and analyzed by atomic absorption spectrophotometry to insure that solution depletion did not exceed 10% of initial values. Uptake was terminated by rinsing the roots in one 1 min change of distilled water followed by a 5 min desorption in 1 mM strontium chloride ($SrCl_2$). Roots were then excised with 1 cm of the cotyledonary and dried at 65°C. Fifty to 100 mg portions were digested in a 9:1 (v/v) nitric-perchloric acid (HNO_3-$HClO_4$) mixture. The acids were removed with heat and the residue was resuspended in 1N hydrochloric acid (HCl) containing 2 g $SrCl_2$/L. Potassium, Ca, and Mg concentration of the resuspended residue was determined by atomic absorption spectrophotometry using an air-acetylene flame. Typically, data from three to four sets of plants containing four seedlings each were averaged per treatment. Data are expressed on a dry weight basis. Results from each experiment were verified by duplicate investigations. The standard error of the mean is presented as a bar where the variation exceeds the size of the data symbol.

RESULTS AND DISCUSSION

The time course of the accumulation of Ca and Mg in roots of corn seedlings from solutions containing 2 mM Ca or Mg followed a similar time course (Fig. 1). The rate of uptake was linear over the first 2 h of incubation. The rate of accumulation declined as the incubation period was increased beyond 2 h, approaching a steady-state concentration after 8 to 12 h. This characteristic rise in Ca and Mg accumulations over a fairly long time period indicated that these cations were being accumulated within an intracellular locations, as opposed to binding to the cell walls which would have reached steady-state levels after a few minutes (3). The time course of Ca and Mg accumulation in roots was independent of the composition of the uptake solution (data not shown).

The relative selectivity of root accumulation for Ca versus Mg was determined by a replacement experiment, *i.e.* the total concentration of Ca plus Mg was maintained at a constant of 2.0 mM, while the molar fraction was altered from 0.0 to 1.0. In the absence of Mg, *i.e.* [Mg]/([Mg+Ca]) ratio of 0.0, root Ca accumulation attained a steady-state concentration of 265 meq/kg of roots after 12 h of incubation (Fig. 2). As the molar fraction of Mg in solution was increased, the amount of Ca in the tissue decreased in a biphasic pattern. A sharp decline in Ca concentration was observed as the molar fraction of solution Mg was increased from 0.0 to 0.2. A nearly constant concentration of Ca was found until the fraction exceeded 0.8.

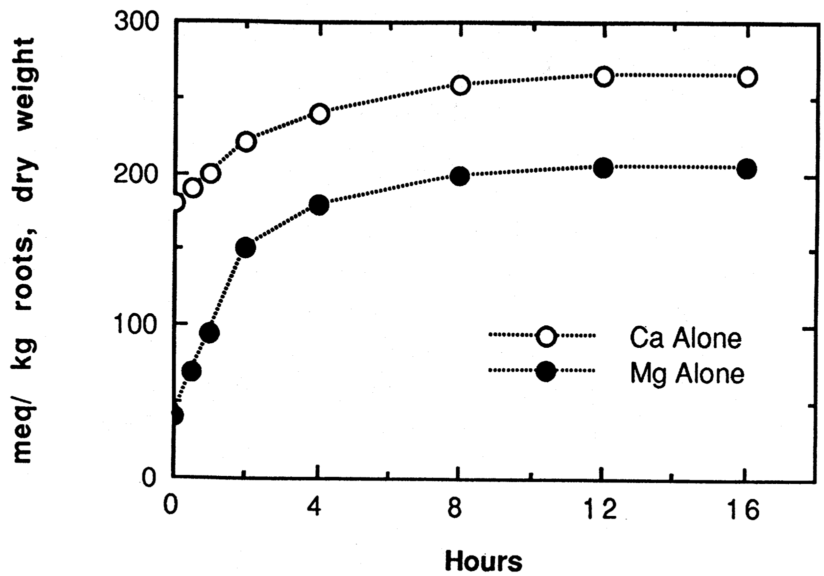

FIGURE 1. Time course of Ca and Mg accumulation in roots. Roots of intact maize seedlings were placed in an uptake solution containing either 2 mM $CaSO_4$ or 2 mM $MgSO_4$ for 0.5 to 16 h and then analyzed for either Ca (o) or Mg (•) content.

Decreases in tissue levels of Ca were accompanied by an increase in the Mg concentration. In the absence of Mg, tissue levels of Mg averaged 60±6 meq/kg of roots, which was comparable to the level of 50±11 meq/kg of roots at the start of the experiment. Magnesium concentration increased rapidly to 145 meq/kg of roots at a molar fraction of 0.2 Mg. There was only a slight change in Mg concentration until the molar fraction was increased above 0.8. Only at molar fractions above 0.9 Mg did the steady-state concentration of Mg in the tissue exceed that of Ca. Such results imply that the uptake by the corn seedlings had a preference for Ca over Mg. Such a conclusion is supported by the observation that the roots contained more Ca than Mg at molar fractions near 0.5.

The K concentration of the root tissue was rather independent of the molar fraction of Mg in solution, averaging 180±11 meq/kg of roots after 12 h of

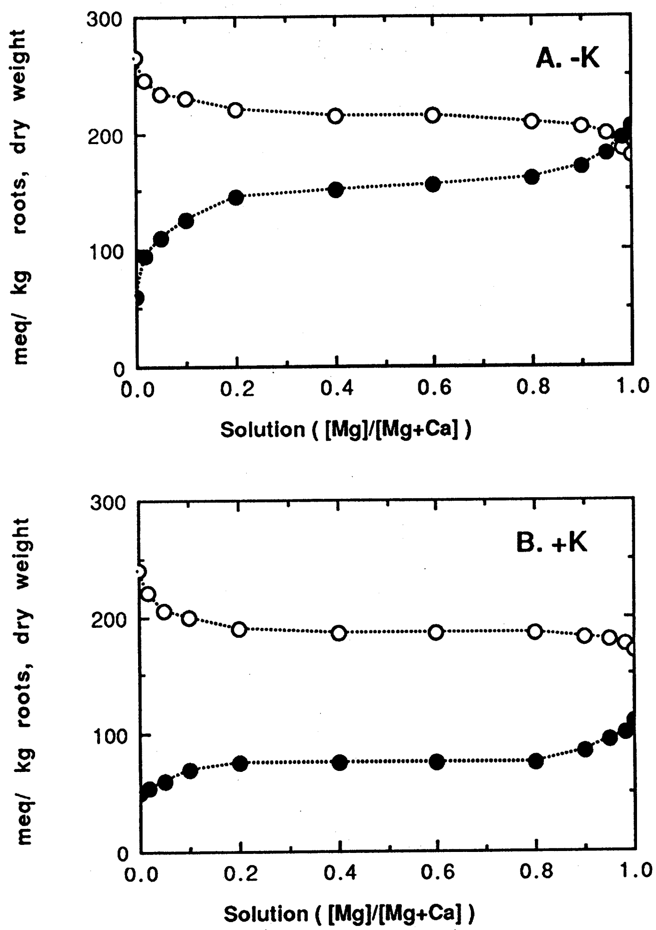

FIGURE 2. Root accumulation of Ca and Mg as affected by the solution ratio of [Mg]/([Mg]+[Ca]) and K. Root tissue was analyzed for Ca (o) and Mg (●) after 12 h of incubation in solution containing 2 mM Ca plus Mg but varying ratios of [Mg]/([Ca]+[Mg]) in the absence (upper panel) and presence (lower panel) of 0.1 mM K.

incubation (data not shown). This concentration was not significantly different from the concentration before the experiment. There was a slight tendency for the roots to have a higher K concentration at lower molar fractions of Mg, 190±9 meq/kg of roots at a molar fraction of 0.0 Mg as compared to 170±11 meq/kg of roots at a molar fraction of 1.0 (data not shown).

The effects of the addition of 0.05 mM potassium sulfate (K_2SO_4) to the uptake solutions on the relative selectivity of root accumulation for Mg and Ca were assessed also by a replacement-type experiment. The addition of the K salt increased the steady state K concentration of the tissue to an average of 334±20 meq/kg of roots after 12 h of incubation (data not shown). There was a slight trend for the K concentration to be less at higher molar fractions of solution Mg. At a molar fraction of 0.0 Mg, the K concentration averaged 345 meq/kg of roots as compared to 320 meq/kg of roots at a molar fraction of 1.0 Mg.

The addition of K to the uptake solutions decreased the concentrations of Ca and Mg in the root tissues (Fig. 2). However, the competition between Ca and Mg for root accumulation persisted. In the absence of Mg, Ca accumulation in root tissue averaged 240 meq/kg of roots, which was slightly less than the 265 meq/kg of roots found in the absence of solution K. Similarly, the level of Ca in roots incubated in solutions containing 0.2 to 0.8 molar fraction of Mg as the divalent cation averaged 185 meq/kg of roots in the presence of solution K as compared to 215 meq/kg of roots in the absence of solution K. Across the 12 molar fractions of solution Mg, the addition of K decreased Ca accumulation by about 11% from an average of 217±24 to 193±20 meq/kg of roots.

The addition of K to the nutrient solution had a more profound effect on Mg accumulation than Ca accumulation. Across the 12 treatments of solution Mg, Mg accumulation in root tissue was decreased by almost 50% by the addition of K to the uptake solutions as compared to an average effect of 11% decrease for Ca mentioned above. In the absence of solution K, Mg accumulation averaged 141±55 meq/kg of roots across the 12 molar fractions of solution Mg as compared to 77±18 meq/kg of roots in the presence of 0.05 mM K_2SO_4. These results demonstrated that sub-millimolar concentrations of solution K have a profound effect on root accumulation of Mg, whereas previous studies have examined only the effects at millimolar concentrations (1,2,3,4,5,6).

ACCUMULATION OF Ca AND Mg IN ROOTS

The relatively greater effect of solution K on Mg accumulation as compared to Ca accumulation can be accounted for by considering the metals' relative acid-base characteristics. Both Ca and Mg are hard acids. However, Mg is considerably harder than Ca with a Misono number of 0.87 as compared to 1.62 for Ca. Potassium is also a hard acid with a Misono number very similar to that of Mg, 0.92. Therefore, K is more similar to that of Mg than Ca on the basis of its relative acid-base characteristic, and one would expect a greater degree of interaction for a binding site to a transport site. In addition, the acid-base theory predicts that the determinant of divalent cation accumulation in roots is a weak base. Root accumulation demonstrated a greater preference for Ca over Mg, thus indicating that weaker acids reacted better. Since weak acids interact best with weak bases, the mechanism responsible for divalent cation accumulation probably contains a weak base.

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