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EFFECT OF CALCIUM ON MAGNESIUM UPTAKE IN PLANTS

(Part 1) The Apparent Accelerative Effect of Calcium on Magnesium Uptake*

Masumi MORITSUGU and Toshio KAWASAKI

It has been generally reported that calcium depressed uptake and translocation of magnesium in plants (1-9). However, in the course of our investigations of the calcium effect on uptake of monovalent cations by plant roots (10, 11), it was shown that the corn roots grown in high calcium levels contained more magnesium than grown in low calcium levels. This accelerative effect of calcium on magnesium uptake in corn roots cannot be explained by the repressive effect which was generally observed between both divalent cations.

The present investigation was undertaken to clarify the details of the phenomenon, and solution culture experiments were carried out. First, the accelerative effect of calcium on magnesium uptake was examined with several species of plants. Then, it was investigated whether the accelerative effect of magnesium on calcium uptake was observed or not. In addition, to explain a mechanism of the calcium effect on magnesium uptake, the release rate of magnesium from corn roots was studied with several kinds of dilute acids.

MATERIALS AND METHODS

Materials and Methods in Solution Culture Experiments

In the solution culture experiments, plant species used were as follows: corn (cv. Nagano 1), sorghum (cv. Mini Milo 54 BR), barley (cv. Akashinriki), kidney bean (cv. Masterpiece), and lowland rice (cv. Akebono).

Culture vessels were a/5000 pots. Seedlings were transplanted and grown for 3 to 4 weeks. The density of plant cultured was 2 plants per pot (in rice plants, 2 seedlings in each hole, and 2 holes in a plastic cover fitted on a pot). The experiments were carried out in the duplicate or triplicate system in a green house, the temperature of which was roughly controlled. To avoid the excessive rise of solution temperature, culture pots were cooled with running tap water in the daytime throughout the summer season.

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The composition of nutrient solutions used are shown in Table 1. Deionized water was used for the preparation of nutrient solution. The nutrient solution was renewed at weekly intervals. Adjustment of the solution pH and addition of iron compounds were usually made every other day throughout the experimental period. Concentrations of calcium or magnesium in the nutrient solution were 3 to 6 levels between 0.1 and 10.0 mM.

TABLE 1
Composition of nutrient solutions

For upland field crops		For lowland rice	
KNO_3	4 mM	$(NH_4)_2SO_4$	2 mM
$NH_4H_2PO_4$	1	KNO_3	1
$CaCl_2$*1	1	KH_2PO_4	1
$MgSO_4$*2	1	$CaCl_2$*1	1
		$MgSO_4$*2	1
		SiO_2*3	2
Fe*4	1.0 or 3.0 ppm	B	0.5 ppm
Mn	0.5	Zn	0.05
Cu	0.02	Mo	0.01

*1 When Ca concentration was varied 0.1 to 10.0 mM, Mg concentration of every solution was 1.0 mM.
*2 When Mg concentration was varied 0.1 to 10.0 mM, Ca concentration of every solution was 1.0 mM.
*3 It was prepared from Na_2SiO_3 solution through column of H^+-form cation exchange resin.
*4 Iron was added every other day as EDTA salt or citrate.

Bubbling pieces were handmade using pieces of polyurethane foam rubber and soft polyvinyl chloride tubes, because calcium ions are leaked from the commercial bubbling equipment " air stone " which is usually made of limestone.

At the end of the growth period, plants were harvested, divided into tops and roots, and washed by tap water and deionized water successively. Dry matter was weighed after oven-drying at 100°C for several hours. Dried materials were roughly ground and mixed uniformly by a pulverizer for laboratory use, and mineral elements were determined with the ground samples.

A modified method of Fiskel and Brams (12) was used for desorption experiments. In these experiments, corn plants were cultured under conditions of 0.25 or 2.5 mM of calcium in nutrient solutions for 16 days (July, 1970). At the end of the growth period, roots were excised, and dipped in 500 m*l* of 0.1 N hydrochloric acid, 0.1 N acetic acid, or deionized water. After shaking for 5 minutes, the roots were rinsed rapidly with deionized water and blotted with filter papers. Then, the roots were dried, weighed and ground in preparation for mineral determination. To obtain higher accuracy, the quadruplicate system was used for the experiment. Mineral elements were determined with both roots and solutions after the desorption treatment.

Methods of Analysis

About 2.5 g (for EDTA titration method) or 1.0 g (for atomic absorption spectrophotometry) of dried and ground samples were placed in ceramic crucibles. Accurate dry weights were evaluated after redrying. Then, the samples were ignited at 500°C for about 6 hours by an electric muffle furnace in which the temperature was regulated automatically. The ash was dissolved in about 3 m*l* of 1 : 1 hydrochloric acid, and mixed with deionized water to fill 50 m*l* measuring flasks.

Calcium and magnesium contents were determined by the EDTA titration method, after the separation of interfering ions with a column of cation exchange resin (13), or by atomic absorption spectrophotometry. Potassium was determined by flame photometry or atomic absorption spectrophotometry. Phosphorus and iron were determined by the molybdovanadophosphate method and atomic absorption spectrophotometry respectively.

RESULTS

Effect of Calcium on Magnesium Uptake

Corn, sorghum, bean, barley and rice plants were used in this experiment. Plants were grown in nutrient solutions at 3 to 6 levels of calcium concentrations ranging 0.10 to 10.0 mM. The magnesium concentration was at the 1.0 mM level in all solutions. After the growth period, the plants were harvested. Dry matter was weighed, and calcium and magnesium contents were determined. The results are shown in Fig. 1 (A~E).

In the plant tops except rice, calcium content increased and magnesium content decreased with increasing concentrations of calcium in nutrient solutions within a similar yield range. In rice plants, the calcium content of the plant tops increased with increasing calcium concentrations in the nutrient solutions, but magnesium content was not affected by calcium concentrations.

In the roots of corn, sorghum and barley plants, the magnesium content increased with increasing concentrations of calcium in the nu-

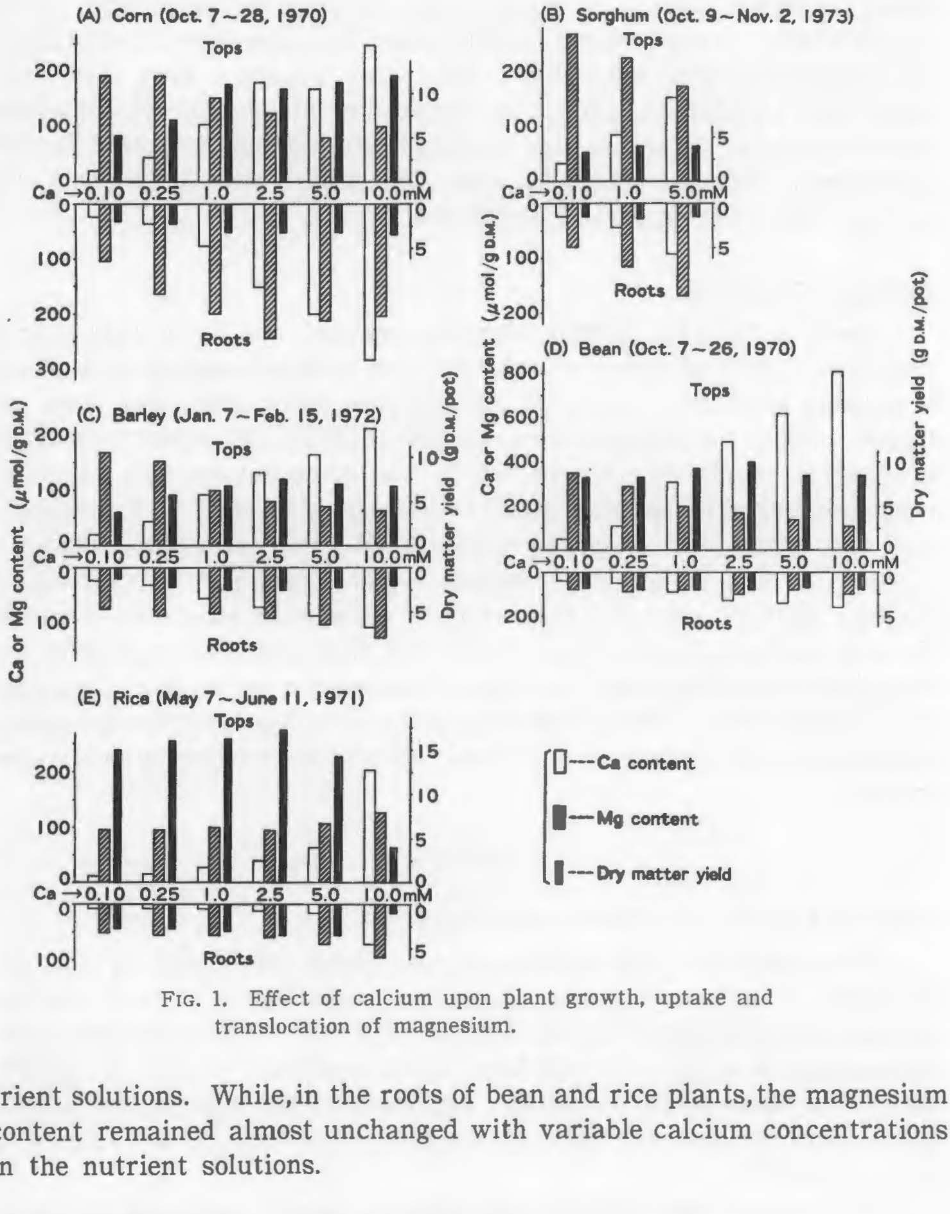

FIG. 1. Effect of calcium upon plant growth, uptake and translocation of magnesium.

trient solutions. While, in the roots of bean and rice plants, the magnesium content remained almost unchanged with variable calcium concentrations in the nutrient solutions.

Effect of Magnesium on Calcium Uptake

Corn, barley, bean and rice plants were used in this experiment. Plants were grown by solution cultures at 6 levels of magnesium concentrations ranging 0.10 to 10.0 mM in the nutrient solutions. The calcium concentration was held at the 1.0 mM level in all solutions. After 3 to 4 weeks of plant growth, plants were harvested and calcium and magnesium contents were determined. The results are shown in

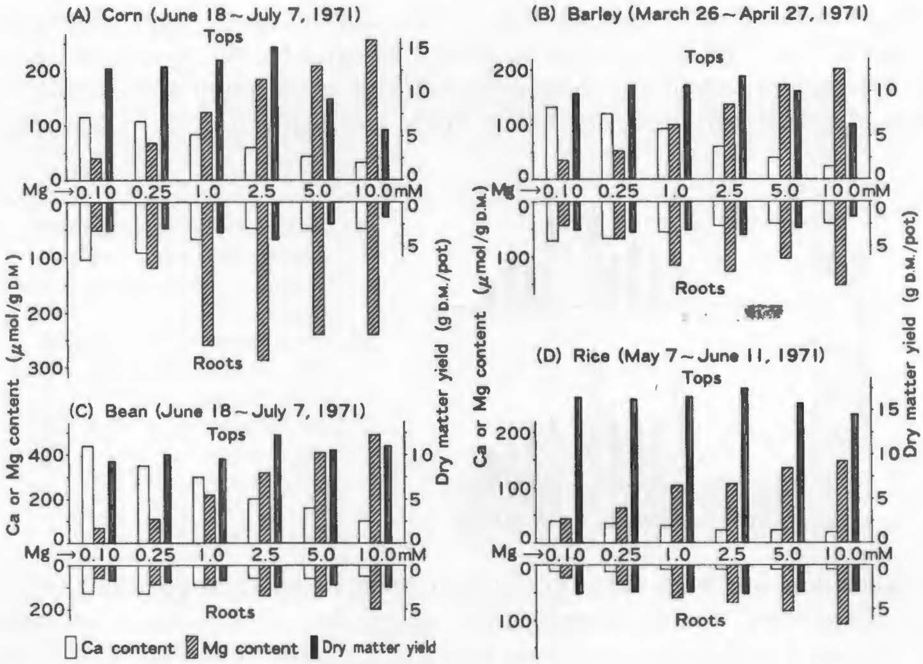

FIG. 2. Effect of magnesium upon plant growth, uptake and translocation of calcium.

Fig. 2 (A~D). In corn, barley and bean plants, calcium contents of tops and roots decreased with increasing magnesium concentrations in the nutrient solutions, while in rice plants, the calcium content was not affected.

Desorption Pattern of Magnesium in Corn Roots

In corn roots, chemical characteristics of magnesium increased with ambient calcium were examined by desorption experiments. Corn plants were grown in the nutrient solution at 0.25 or 2.5 mM calcium. After the growth period, excised roots were washed with dilute hydrochloric acid, acetic acid or deionized water as a control. The ratio of released parts to total content of each element was calculated from respective analytical data of roots and solutions after the treatments.

As shown in Fig. 3, the ratio of released parts to total content of magnesium was compared with that of other elements: calcium, potassium, phosphorus and iron. Standard deviations are indicated as vertical bars in Fig. 3.

Several elements tested were only slightly released in deionized water. With dilute hydrochloric acid, the desorption of magnesium from corn roots was less than that of calcium or iron, and almost equal to that of potassium or phosphorus. With dilute acetic acid, desorption ratios of iron and phosphorus decreased as expected due to the character of the solvent, while the desorption ratio of magnesium was similar to that of potassium and also that in dilute hydrochloric acid. Comparison

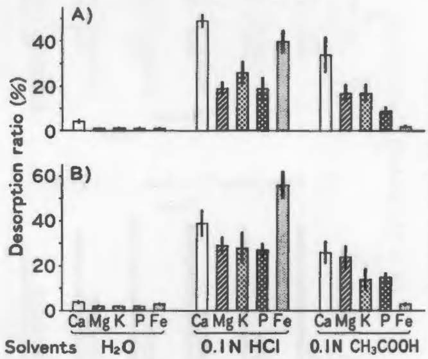

FIG. 3. Desorption ratio of magnesium and other mineral elements contained in corn roots.
A) Pre-cultured in 0.25 m*M* Ca (Mg content of roots 164 μmol/g D. M.)
B) Pre-cultured in 2.5 m*M* Ca (Mg content of roots 227 μmol/g D. M.)

between low and high calcium concentrations in nutrient solutions during the pre-culture period showed that magnesium desorption from roots pre-cultured with 2.5 mM calcium was slightly more than that of 0.25 mM calcium.

DISCUSSION

Many reports (1–9, 14) have been published on the mutual interference between divalent cations in the uptake and translocation processes of plants. However, there are no reports with respect to the accelerative effect of a divalent cation on the uptake of another divalent cation.

In these experiments, it was emphasized that the magnesium content in plant roots, especially in corn and sorghum, increased with increasing calcium concentrations in nutrient solutions. The results are quite similar to those of previous papers (10, 11). This phenomenon cannot be explained by the repressive effects which are generally observed between divalent cations. But, even in corn and sorghum plants, the total uptake of magnesium was depressed by ambient calcium as shown in Fig. 4.

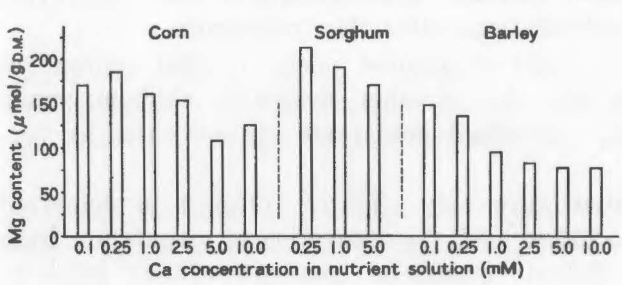

FIG. 4. Effect of calcium in nutrient solution upon magnesium content in total plants.

Accordingly, it can be said that the phenomenon of increasing magnesium content in plant roots with increasing concentrations of ambient calcium is only apparent acceleration, because it is observed only in the roots. Therefore, the cause of this phenomenon may be explained as follows. In corn, sorghum and barley plants, magnesium uptake in roots is not affected much by ambient calcium, but the translocation from roots to shoots is clearly depressed by calcium. To examine the above explanation, the ratio of plant top to total plant magnesium content was calculated as shown in Table 2. From the table, it was clarified that

TABLE 2
Effect of calcium in nutrient solution on translocation ratio of magnesium in plants

Ca conc. in nutrient solution	Translocation ratio of Mg (Mg TOP/Mg TOTAL)				
	Corn	Sorghum	Barley	Bean	Rice
0.10 mM	0.84		0.88	0.95	0.91
0.25	0.77	0.89	0.83	0.93	0.91
1.0	0.73	0.81	0.77	0.91	0.90
2.5	0.63		0.73	0.91	0.89
5.0	0.57	0.72	0.68	0.89	0.86
10.0	0.63		0.61	0.83	0.83

the translocation ratio of magnesium (Mg TOP/Mg TOTAL) was lowered with increasing calcium concentrations in the nutrient solution, especially in corn, sorghum and barley plants.

While, in bean and rice plants, magnesium content of the plant roots was rather unaffected by ambient calcium (Fig. 1), in good agreement with the results of Jackson and Evans' investigations of soybean plants (15). Accordingly, a decrease in the translocation ratio of magnesium with increasing calcium in the nutrient solutions was smaller in bean and rice plants (Table 2).

To determine whether the reverse phenomenon may be observed, an effect of magnesium on calcium uptake was investigated with corn, barley, bean and rice plants. The results can be explained by a simple repressive effect in all cases (Fig. 2), as reported by Fageria (16) and Clark (17).

As indicated in Fig. 3, the desorption characteristics of magnesium in corn roots are similar to those of potassium. Generally, potassium is considered to be absorbed into plant tissues by an active process, in contrast to calcium. Accordingly, it may be suggested that process of magnesium absorption in corn roots is rather similar to that of potassium.

Compared with corn roots grown in a low calcium concentration nutrient solution, desorption of magnesium was much higher from corn roots grown in a high calcium concentration (Fig 3). But, this result does not mean that the magnesium fraction increased by ambient calcium is in an easily soluble form alone. Table 3, which was calculated from the data of Fig. 3, shows the easily soluble and almost insoluble fractions of magnesium. As indicated in Table 3, in the increased

TABLE 3

Release of magnesium from corn roots

Solvent	Ca in pre-culture solution (mM)	Total Mg content*1 (μmol/g D. M.)	Easily soluble Mg*2 (μmol/g D. M.)	Insoluble Mg*3 (μmol/g D. M.)
0.1 N	0.25	148.4	28.5	119.9
HCl	2.5	242.2	69.0	173.2
	Mg increased*4	93.8 (100)	40.5 (43)	53.3 (57)
0.1 N	0.25	166.4	27.7	138.7
CH_3COOH	2.5	239.8	59.5	180.3
	Mg increased*4	73.4 (100)	31.8 (43)	41.6 (57)

*1 Sum of easily soluble and insoluble fraction (remained in treated roots).
*2 Mg content in solution after desorption treatment (converted to the basis of μ moles per gram of dry roots).
*3 Mg content in corn roots after desorption treatment.
*4 Difference between Mg content of 2.5 mM Ca pre-cultured roots and 0.25 mM Ca pre-cultured roots.

fraction of magnesium with increasing ambient calcium, the almost insoluble fraction was in higher concentration than the easily soluble fraction. This tendency was quite similar in the cases of both solvents (dilute hydrochloric acid and dilute acetic acid). It may be concluded that about half of the increased fraction of magnesium by higher ambient calcium is actively absorbed like potassium.

SUMMARY

When corn plants were supplied with varying concentrations of calcium in nutrient solutions, a large calcium supply resulted in high magnesium contents in root tissues. This result cannot be explained by the repressive effects generally observed between divalent cations. To establish the details of the phenomenon, solution culture experiments were carried out with corn, sorghum, barley, bean and rice plants. In

addition, desorption experiments with dilute acids were performed for several ions in corn roots. The results were as follows:

1) High magnesium contents in the root tissues of corn, sorghum and barley plants were observed with a large calcium supply, in comparison with a small calcium supply in the nutrient solutions. The accelerative effect of calcium on magnesium uptake was not clear in bean and rice roots.

2) The reverse relationship was not observed for calcium and magnesium in corn and barley roots; i. e. a large magnesium supply did not result in a high calcium content in root tissues.

3) Total magnesium contents in the whole plant decreased with a large calcium supply in nutrient solutions, though the magnesium contents in root tissues increased. Thus, we may conclude that a large calcium supply depressed the translocation of magnesium from roots to shoots. This was emphasized by the rapid decrease in the magnesium translocation ratio (Mg TOP/Mg TOTAL) with an increasing supply of calcium.

4) The results of the desorption experiments showed that the desorption pattern of magnesium from corn roots was similar to that of potassium, but not similar to that of calcium or iron. When a large amount of calcium was present in the nutrient solutions, about half or more of the increased fraction of magnesium in corn roots could not be desorbed easily.

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