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Article

Influence of Calcium Supply on the Growth, Calcium and Oxalate Contents, Mineral Nutrients and Ca-oxalate Crystal Formation of Cucumber

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Although the roles of calcium in plant are widely known, little is known about on an antagonistic effect of macro elements, oxalate biosynthesis and main shape of crystal in cucumber plant organs. Seeds of cucumber (*Cucumis sativus* cv. Ijoeunbackdadagi) were germinated in perlite tray supplied with distilled-deionized water. Seedlings were transplanted into aerated containers with a half strength of Ross nutrient solution. Ca levels treated in media were as follows; No-Ca, $Ca(NO_3)_2$ 0.25, 1.25 and 2.5 mmol L^{-1}, and $Ca(NO_3)_2$ 2.5 mmol L^{-1} + $CaCl_2$10, 25 and 50 mmol L^{-1}. Ca-deficient and -excessive conditions severely reduced cucumber growth, as compared to the control, and adversely affected an accumulation of macro elements (N, P, K, and Mg). Calcium favorably induced oxalate (acid-soluble) synthesis in leaves and roots of cucumber plant, but not in stem. Acid-soluble oxalate contents in leaves proportionally increased with Ca supply levels (0.91, $P<0.001$), however, this pattern was not observed in stem and roots. Ca-oxalate crystal formation and compositional analysis were examined using SEM-EDS technique in cucumber leaves. The main type of crystal revealed a prismatic crystal and main components were Ca, Na and Cl.

Key words: Cucumber, Calcium, Oxalate, Ca-oxalate, Mineral nutrient

Introduction

Calcium (Ca) in its ionic form, Ca^{2+}, performs critical functions in metabolism and as a signaling agent in cells (Sanders et al., 2002; White and Broadley, 2003). However, to be effectively used as a signaling molecule, cytoplasmic Ca^{2+} concentrations must be <1 μM. Since Ca is generally very abundant in the environment and the driving force for entry of Ca^{2+} into the plant cell is large (up to 10,000-fold more Ca^{2+}in the apoplast than the cytoplasm), Ca accumulates within tissues of plants that do not strictly limit uptake at the root (Kirby and Pilbeam, 1984). Organic acids have a potential role as metabolically active solutes for the osmotic adjustment and the balance of cation excess. Oxalate-producing plants, which include many crop plants, accumulate crystals in the range of 3-80% (w/w) of their dry weight (Libert and Franceschi, 1987). A number of pathways for oxalate biosynthesis have been proposed (Hodgkinson, 1977). These pathways include the cleavage of isocitrate, hydrolysis of oxaloacetate, glycolate/glyoxylate oxidation, and/or oxidative cleavage of L-ascorbic acid. Current evidence suggests that oxalate is derived primarily from the cleavage of ascorbic acid (Li and Franceschi, 1990; Keates et al., 2000; Kostman et al., 2001). The formation of Ca oxalate is an essential process in many species, and more than 90% of tissue Ca can be tied up as this compound (Gallaher et al., 1975; Gallaher and Jones, 1976). Ca oxalate crystals often occur within the vacuole of crystal idioblasts (Foster, 1956), specialized cells that generally encompass less than 1% to 2% of the total cells of the Ca-accumulating tissue. Because Ca oxalate formation is the end result of a mechanism for controlling Ca at the tissue and organ levels in the plant (Borchert, 1985; DeSilva et al., 1996; Franceschi, 2001; Volk et al., 2002), cells producing the crystals are considered to be high capacity Ca sinks. They are categorized into several morphological types: rapides, druses, styloids, prisms and cystal sand (Franceschi and Horner, 1980). Calcium is one of essential macro elements for plant growth, and it is well known that Ca taken into plants is quickly immobilized with Ca-oxalate crystal and so is considered as a hard element to move upper parts of plant. The objectives of

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this study are to know 1) how calcium and oxalate are distributed into plant parts under various calcium levels, 2) an antagonism between Ca and other macro elements and the relationship between Ca and oxalate, and 3) main type of Ca-oxalate crystal in cucumber plants.

Materials and Methods

Plant culture and treatments This study was conducted in a glass house at NAAS, RDA in 2009. Seeds of cucumber (*Cucumis sativus* cv. Ijoeunbackdadagi) were germinated in perlite tray supplied with distilled-deionized water. Seedlings were transplanted into aerated containers with a half strength of Ross nutrient solution ($Ca(NO_3)_2$•$4H_2O$, 2.5 mmol L^{-1} KNO_3, 2.5 mmol L^{-1} $MgSO_4$•$7H_2O$, 1.0 mmol L^{-1} KH_2PO_4, 0.5 mmol L^{-1} Fe-EDTA, 0.5 mmol L^{-1} H_3BO_3, 0.5 mmol L^{-1} $MnCl_2$•$4H_2O$, 0.5 mmol L^{-1} $ZnSO_4$•$7H_2O$, 0.5 mmol L^{-1} $CuSO_4$•$5H_2O$, 0.5 mmol L^{-1} H_2MoO•$4H_2O$, 0.5 mmol L^{-1}). Ca levels treated in media were as follows; No-Ca, $Ca(NO_3)_2$ 0.25, 1.25 and 2.5 mmol L^{-1}, and $Ca(NO_3)_2$ 2.5 mmol L^{-1} + $CaCl_2$ 10, 25 and 50 mmol L^{-1}. Five week-old cucumber plants were subjected in 12 holes-aerated 20L capacity containers with different Ca levels. Plants were constantly exposed for 2 weeks with average day temperature between 25 and 30°C and night temperature between 16 and 20°C. Mid-day photosynthetic photon flux density was 900-1,000 μmol m^{-2} s^{-1}. The nutrient solution was replaced every 3 days. Plants were harvested between 13:00 and 14:00 at 7 and 14 days after treatment, immediately separated into leaves, stem and roots, and used for further analysis.

Dry weight determinations and chemical analysis The extraction and measurement of macro-nutrients were determined according to Walinga method (1989). Five randomly selected per treatment were divided into leaves, stem, and roots, and dried in an oven at 70 °C for 2 days to determine dry weights and elemental concentrations. Chemical analyses were carried out on dry weight basis with three repeats. The absorbance of N and Pwas measured at 660 and 880 nm, respectively, using UV-spectrophotometer, and K, Ca, and Mg were measured with ICP-OES (INTEGRA XMP, GBC, Australia).

Acid-soluble oxalate determination Acid-soluble oxalate was analyzed according to Libert (1981) and Yu et al. (2002) methods. Fresh samples (0.5g) of leaves, stem and roots were homogenized in 4ml of 0.5 N HCl. The homogenate was heated at 80 °Cfor 10 min with intermittent shaking. To the homogenate was added distilled water up to a volume of 25 ml. Three ml of the solution was taken and centrifuged at 12,000 g for 10 min. One milliliter of supernatant was passed through a filter (0.45 μm) before HPLC analysis. Sunfire C18 column (5 μm, 4.6 mm 250 mm) equipped Waters 2487 (Waters, MA, USA) was used as the static phase and the mobile phase was a solution containing 0.5% KH_2PO_4 and 0.5 mM TBA buffered at pH 2.2 with *o*-phosphoric acid. Flow rate was 1 ml min^{-1} and detection wavelength was at 220 nm.

SEM-EDS For observation with SEM (scanning electron microscope), leaf tissues fixed with Karnovsky's solution (2% *p*-formaldehyde and 2% glutaraldegyde in 0.05M sodium phosphate buffer (pH 7.2)) for overnight were washed three times in carcodylate buffer (CB, pH 7.2), post-fixed for 2 hr in 2% osmium tetraoxide in CB at room temperature, re-washed in CB. Dehydration was done with an ascending series of 50-100% ethyl alcohol in seven steps for 30 min each. The dehydrated samples were soaked in amyl acetate for 30 min and then dried under liquid carbon dioxide condition. The dried samples were mounted on stub and gold-coated. The Ca-oxalate crystals were observed using scanning electron microscope (HITACHI S-3500N, Japan), and the compositional analysis was studied by EDS (energy dispersive spectrophotometer) technique(Horiba EX-200, Japan).

Data analysis Statistical analysis of data was carriedout using ANOVA. To determine the significance of the difference between the means of treatments, least significant difference (LSD) was computed at the 5 % probability level (SAS 9.1), and *Pearson's* correlation coefficient analysis was performed to know the relationship between Ca and Mg, and between Ca and oxalate.

Results

Dry matter production was used to assess the effect of deficient- or excessive-Ca on cucumber growth (Fig. 1). Dry weight did not showed statistically significant difference in all the Ca supply conditions at 7 days, however decreased compared to the control at 14 days, when less $Ca(NO_3)_2$ than 0.25 mM or supplementary $CaCl_2$ was supplied. The reduction rate in plant growth by

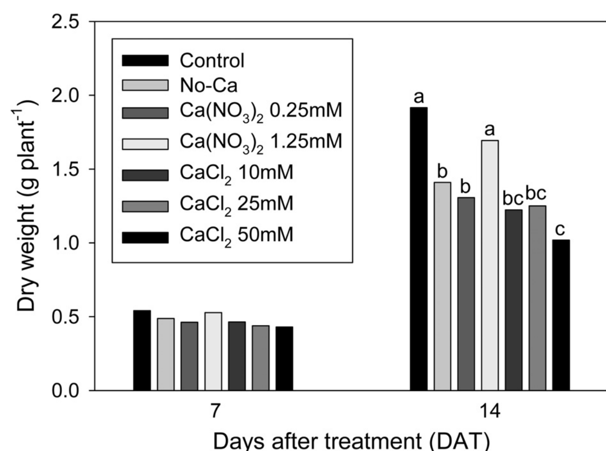

Fig. 1. Temporal changes in shoot growth of cucumber grown under different Ca levels in media. The control means 2.5 mM of $Ca(NO_3)_2$, which is 50% of Ross nutrient solution, in media, and $CaCl_2$ treatments include 2.5 mM of $Ca(NO_3)_2$. The same letter means not statistically significant difference as determined by LSD (*p*<0.05, n=5).

the deficiency or excess of Ca was ranged from 25 to 45%.

To determine whether Ca-deficient and -excessive supply conditions affected the accumulation and partitioning of Ca, Ca concentration in plant organs, leaves, stem and roots, was measured (Fig. 2). It was highest in leaves followed by stem and roots. Calcium concentration was strongly dependent upon calcium supply levels, and showed statistically significant difference (*P*<0.05). The concentration in leaves, stem and roots by Ca supply conditions was ranged from 1.29 to 7.42, from 0.63 to 5.27 and from 0.51 to 2.98 %, respectively.

Acid-soluble oxalate levels were measured in plant organs (Fig. 3), highest content in roots followed by leaves and stem, and were significantly dependent upon Ca supply. The range of oxalate in leaves and roots was from 39 to 155 and from 227 to 486 $\mu g\ g^{-1}$, respectively, which showed that roots had 3.3-fold higher oxalate than leaves, and oxalate was not detected in stem except for the treatment of 50 mM of $CaCl_2$ (17 $\mu g\ g^{-1}$).

The relationship between Ca and Mg and between Ca and acid-soluble oxalate in cucumber leaves exposed to different calcium supply conditions (Fig. 4). Correlation coefficient between Ca and Mg was -0.85 (*P*<0.001), and between Ca and acid-soluble oxalate 0.91 (*P*<0.001). This presented that Ca and Mg was in competition and oxalate biosynthesis was closely engaged with Ca concentration in plant cells.

Calcium oxalate crystals observed using SEM in cucumber leaves typically formed regular prismatic

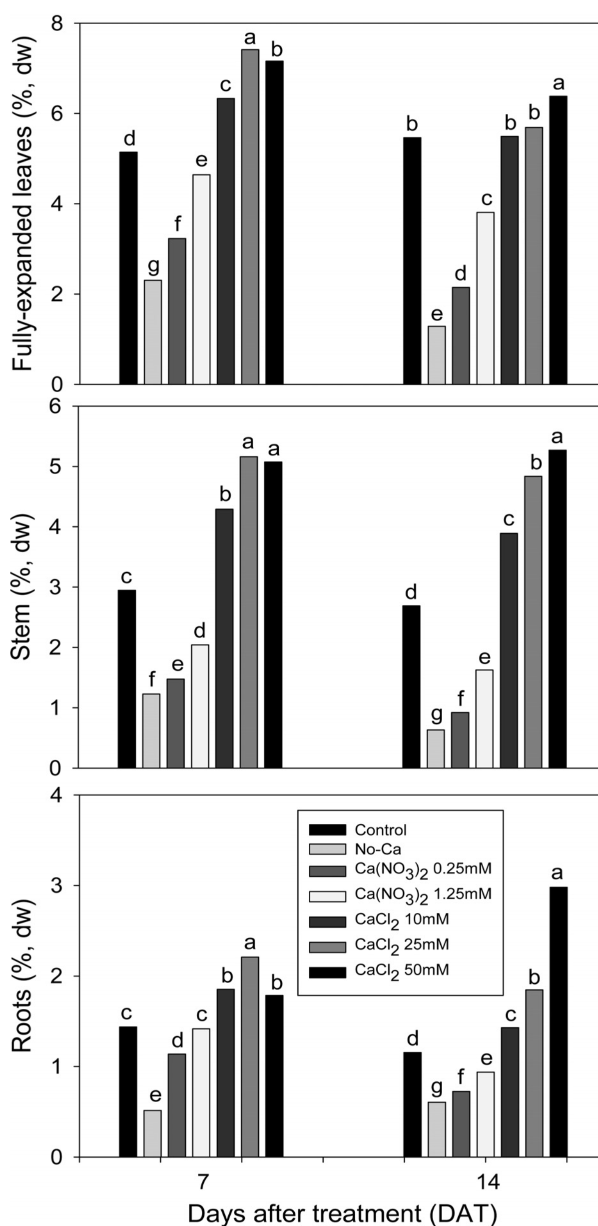

Fig. 2. Temporal changes in Ca contents in leaves, stem and roots of cucumber grown under different Ca levels in media. The control means 2.5 mM of $Ca(NO_3)_2$, which is 50% of Ross nutrient solution, in media, and $CaCl_2$ treatments include 2.5 mM of $Ca(NO_3)_2$. The same letter means not statistically significant difference as determined by LSD (*p*<0.05, n=3).

shapes (Fig. 5), and were much more synthesized in high Ca condition ($Ca(NO_3)_2$ 2.5 mM + $CaCl_2$ 50 mM) compared tothe control ($Ca(NO_3)_2$ 2.5 mM). The compositional analysis of isolated crystals was done by the EDS technique. All intensities from the EDS-profiles showed a chemical composition typically obtained for Ca oxalate crystal: Ca, Na and Cl.

Macro-elements in leaves, stem and roots were analyzed in order to know the effect of Ca on the uptake and

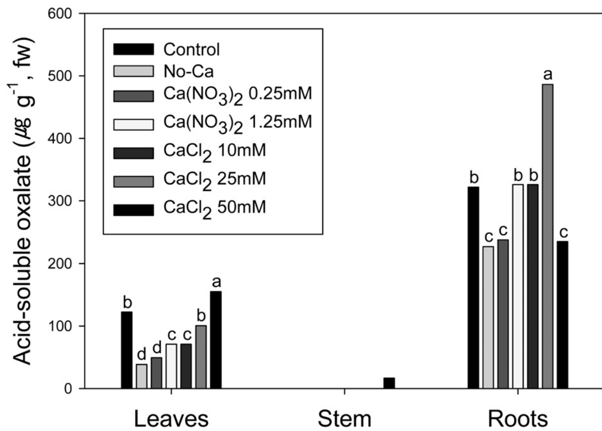

Fig. 3. Contents of acid-soluble oxalate in leaves, stem and roots of different Ca-treated cucumber measured at 14 days after treatment. The data from the stem is below detection limit except the treatment of $CaCl_2$ 50 mM. The control means 2.5 mM of $Ca(NO_3)_2$, which is 50% of Ross nutrient solution, in media, and $CaCl_2$ treatments include 2.5 mM of $Ca(NO_3)_2$. The same letter means not statistically significant difference as determined by LSD (*p*<0.05, n=3).

accumulation of other nutrients (Table 1). N, P and K presented the pattern of gradual decrease with an increase or decrease of Ca supply however P and K of roots under those conditions revealed highest concentrations. The accumulation of Ca positively responded to Ca supply conditions, in contrast, Mg showed negative response.

Discussion

Suppression of plant growth under stress conditions is a common phenomenon, but such suppression occurs differently depending on plant species, age and organs. In the present study, shoot dry weight was greatly affected at 14 days of various Ca supply conditions (from deficiency to surplus) (Fig. 1), and the extreme deficiency or excess condition of Ca also induced leaf senescence (data not shown).

Cucumber organs accumulated Ca in proportion to Ca supply conditions (Fig. 2). Calcium concentration in Ca-deficient and -excessive conditions was slightly decreased at 14 days compared to 7 days, and the decrease seemed to be come from low mobility toward growing parts and Ca-induced stress. Some reports presented that plants under different Ca levels took Cain proportion to calcium supply (Zindler-Frank, 1975; Borchert, 1986; Zindler-Frank et al., 2001), and, in addition, Ca concentration was higher in older parts than in younger ones in both high and low calcium conditions (Zindler-Frank et al., 2001).

Calcium enhancing the oxalate contents of plants varies according to the species (Franceschi and Horner, 1982; Kinzel, 1989). The oxalate is synthesized to deal with elevated levels of tissue calcium by forming the osmotically and physiologically inert calcium oxalate crystal (Franceschi, 1989). Different Ca supply conditions seemed to significantly influence acid-soluble oxalate biosynthesis in at least leaves and roots (Fig. 3), and an increase in Ca supply stimulated the increased oxalate production in leaves in accordance with the result of previous study (Zindler-Frank et al., 2001) (Fig. 4). However, it was expected that Ca played different roles depending on plant parts considering no detection of oxalate in stem and highest levelsin roots, and it was needed to analyze insoluble oxalate to correctly interpret the relationship between Ca and oxalate.

Calcium initiation is fastest in the young, just unfolded leaf, number and size of crystals then steadily rise during

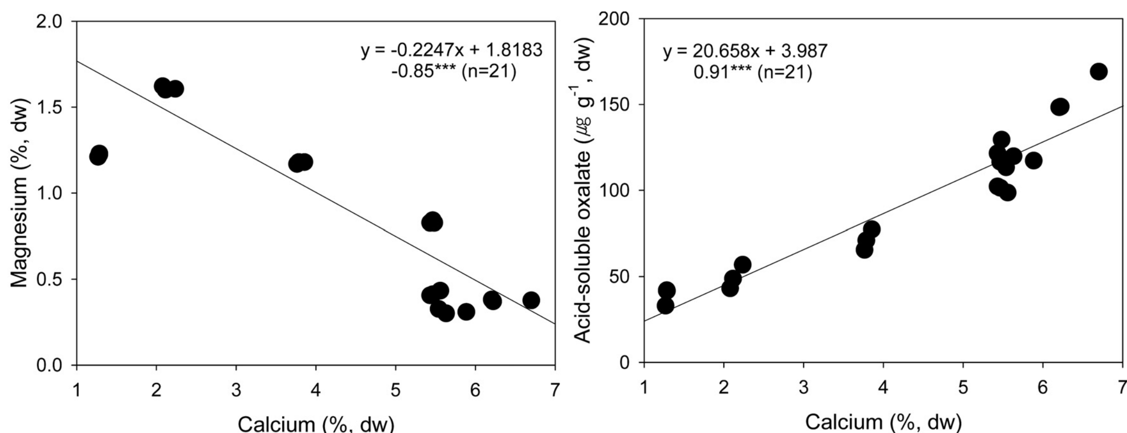

Fig. 4. Pearson correlation coefficient (n=21) between Ca and Mg and between Ca and acid-soluble oxalate in cucumber leaves exposed for 14 days under different Ca levels in media.

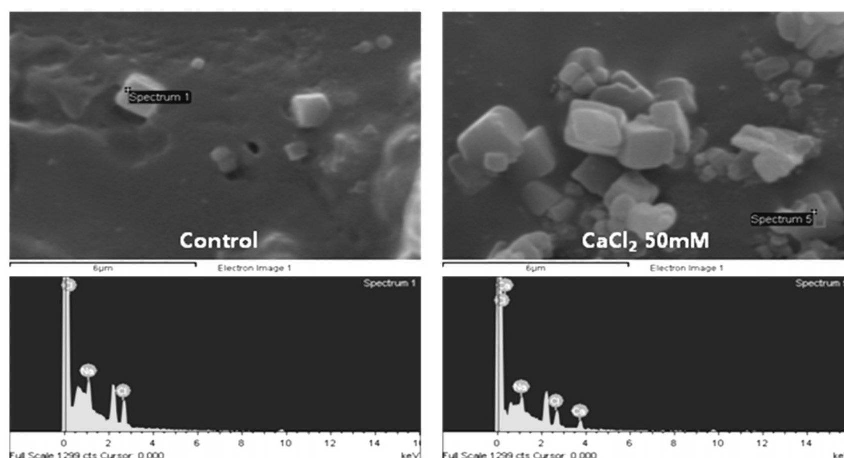

Fig. 5. SEM-EDS structural characterization of calcium oxalate crystals in cucumber leaves between control ($Ca(NO_3)_2$ 2.5 mM) and $CaCl_2$ 50 mM. $CaCl_2$ treatments include 2.5 mM of $Ca(NO_3)_2$.

Table 1. Macro-nutrients in leaves, stem and roots of cucumber at 14 days after Ca treatments.

Organ	Treatment	N	P	K	Ca	Mg
		------------------------		%, dw		------------------------
Leaves	Control	4.36a	0.99a	2.01a	5.47b	0.83d
	No-Calcium	1.94f	0.93ab	1.37d	1.29e	1.22b
	$Ca(NO_3)_2$ 0.25 mM	2.34e	0.89b	1.91b	2.15d	1.61a
	$Ca(NO_3)_2$ 1.25 mM	4.45a	0.91ab	1.92b	3.81c	1.17c
	$CaCl_2$ 10 mM	3.09d	0.87b	1.78c	5.49b	0.41e
	$CaCl_2$ 25 mM	3.93b	0.75c	1.80c	5.69b	0.31g
	$CaCl_2$ 50 mM	3.63c	0.95ab	1.37d	6.38a	0.37f
Stem	Control	3.23a	0.97bc	6.11a	2.69e	0.40c
	No-Calcium	1.88c	1.00b	4.17f	0.63g	0.58a
	$Ca(NO_3)_2$ 0.25 mM	2.38bc	0.94c	6.11a	0.92f	0.58a
	$Ca(NO_3)_2$ 1.25 mM	3.62a	0.80e	5.37c	1.63e	0.45b
	$CaCl_2$ 10 mM	2.58b	0.87d	5.54b	3.89c	0.28e
	$CaCl_2$ 25 mM	2.32bc	0.82e	5.26d	4.83b	0.28e
	$CaCl_2$ 50 mM	1.89c	1.46a	4.33e	5.27a	0.33d
Roots	Control	3.71a	1.00d	2.76d	1.15d	0.29a
	No-Calcium	1.97c	1.43b	3.35b	0.61g	0.27ab
	$Ca(NO_3)_2$ 0.25 mM	2.83b	0.95d	2.50e	0.72f	0.25bc
	$Ca(NO_3)_2$ 1.25 mM	3.02b	1.10cd	2.82d	0.94e	0.26bc
	$CaCl_2$ 10 mM	2.17c	1.16c	3.00c	1.43c	0.25c
	$CaCl_2$ 25 mM	1.92c	1.04cd	3.30b	1.85b	0.25c
	$CaCl_2$ 50 mM	1.16d	1.97a	4.79a	2.98a	0.26bc

[†]The control means 2.5 mM of $Ca(NO_3)_2$, and [††]the treatment of $CaCl_2$ includes 2.5 mM of $Ca(NO_3)_2$.

the whole space of blade expansion. One decisive factor controlling number and size of crystals is the amount of Ca available to the plant (Zindler-Frank et al., 1988). Calcium oxalate crystal observed in plants typically form four main types of crystal morphologies: styloids, raphides, druses and prisms. Visual examination of the leaves, highest Ca level and Control, using SEM-EDS suggested that the increase in Ca and oxalate was most likely attributable to the formation of Ca-oxalate crystal. The prismatic crystal was main type observed in leaves and highest calcium condition produced much more crystal than the control (Fig. 5). Additionally, main components of crystal analyzed

using EDS technique were Ca, Na and Cl. There are many previous results supporting the result of our present study (Horner and Zindler-Frank, 1982a and b; Shouwu et al., 2002; Jáuregui-Zúñiga et al., 2003).

It is known that Ca maintains membrane integrity and controls selectivity of ion uptake and transport (Marschner, 1995). High or low Ca concentrations can reduce the permeability of plasma membrane to other mineral elements, and thus lead to the reduced uptake of elements. In the present study, the abnormal Ca concentrations (deficiency and excess) in media resulted in low uptake of N, P, K and Mg in all the plant organs measured except for P and K in roots (Table 1). In particular, Ca adversely affected Mg uptake due to the antagonism between both ions.

In conclusion, Ca-deficient and -excessive conditions caused a reduction of plant growth and the uptake and accumulation of macro elements. An increased Ca supply stimulated oxalate (acid-soluble form) biosynthesis, and accumulated Ca-oxalate crystal, called a prismatic crystal, in leaf tissue.

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오이생육, 칼슘, 옥살산 및 무기성분 함량 및 칼슘-옥살산염 형성에 대한 칼슘처리 효과

성좌경 · 이수연 · 이예진 · 김록영 · 이주영 · 이종식 · 장병춘*

국립농업과학원 토양비료관리과

식물체 내에서 칼슘의 역할에 대하여 광범위하게 알려져 있지만, 다량원소의 흡수와 축적 및 옥살산 합성에 대한 칼슘의 영향에 대한 연구는 미비한 실정이다. 본 연구는 칼슘 결핍 또는 과잉에 따른 오이생육, 다량원소 흡수, 옥살산 합성 및 칼슘-옥살산 crystal 형성에 대하여 알아보고자 수행하였다. 칼슘의 결핍 또는 과잉조건하의 오이 생육과 다량원소의 흡수는 크게 저해되는 경향을 보였으며, 특히 마그네슘과는 정반대의 흡수패턴을 보였다. 칼슘처리의 증가는 오이 잎과 뿌리 중 옥살산 함량을 증가시켰으며, 오이 엽 중 칼슘과 옥살산과의 상관관계는 매우 높은 것으로 나타났다 (0.91, $P<0.001$). 칼슘-옥살산 crystal의 주요 형태는 prismatic 이었고, crystal은 칼슘 처리량이 증가함에 따라 많이 생성되었다. 또한 crystal의 주요 구성성분은 칼슘, 나트륨 및 염소로 나타났다.