https://doi.org/10.17221/473/2024-PSE

Magnesium deficiency or excess hinders tomato growth, potassium and calcium uptake

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Citation: Li H.X., Liu F., Zhang X.K., Gao J.B., Chen P. (2024): Magnesium deficiency or excess hinders tomato growth, potassium and calcium uptake. Plant Soil Environ., 70: 719–730.

Abstract: Despite accumulating evidence for the adverse effects of magnesium (Mg) deficiency or excess on grain crops, how Mg imbalance affects plant growth and potassium (K) and calcium (Ca) nutrition in vegetable crops is still unclear. The aim of this study was to ascertain the response of plant growth, nutrient uptake and Mg-K-Ca interactions in tomato (*Solanum lycopersicum* L.) to various levels of Mg supply. The growth parameters and nutrient contents of hydroponic plants were measured under the Mg levels of 0, 0.5, 1.0, 1.5 and 3.0 mmol/L Mg^{2+} from seedling to fruit ripening stage. Results showed that both Mg deficiency (0 mmol/L Mg^{2+}) and excess (3.0 mmol/L Mg^{2+}) negatively affected shoot and root growth, leading to a noticeable decrease in total plant biomass across different stages (41.2–52.8% and 17.7–38.3%, respectively). Mg imbalance additionally altered leaf morphology and disrupted chloroplast structure. As a consequence of increased Mg levels, the Mg contents in various plant organs increased, whereas the Ca contents decreased substantially. The trend of K contents under different Mg levels was dependent on the plant growth stage. Although Mg levels did not prominently affect plant K contents during the early growth stage, they were significantly negatively correlated in the leaves and positively correlated in the fruit during the late growth stage. When translocated from roots to aboveground organs, Mg and Ca were mainly distributed in the leaves, with K preferentially distributed in the fruit. The findings of this study underscore that the symptoms of Mg imbalance generally develop from middle leaves in vegetable crops, exemplified by tomato, which is different from the pattern in common grain crops. Vegetable production necessitates nutrient supply for the middle and upper parts of Mg-deficient plants, and attention should be paid to the nutritional imbalance of Ca and K in plants under excessive Mg supply.

Keywords: magnesium imbalance; micronutrient; ion uptake; Mg application; nutrient interactions

Magnesium (Mg) – one of the essential nutrients in higher plants – is required to stabilise the structure of biological macromolecules (for example, nucleic acids and proteins) and cell membranes. Mg additionally participates in the maintenance of various enzyme activities, the balance of reactive oxygen species metabolism and the regulation of cellular osmotic pressure (Cakmak and Yazici 2010, Guo et al. 2016, Tian et al. 2020). More importantly, Mg plays a major role in the stabilisation of chloroplast structure, as optimal Mg concentrations support the stacking of thylakoid membranes, leading to a tighter combination of thylakoids and a more prominent separation of grana and stroma lamellae. This allows higher production of starch and sucrose through photosynthesis, thereby promoting plant growth (Hao and Papadopoulos 2004, Jezek et al. 2015, Ye et al. 2019, He et al. 2020).

Supported by the National Natural Science Foundation of China, Project No. 31960628.

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At an appropriate ratio of potassium (K) to Mg, plants can translocate photosynthetic products from the source leaves in a timely manner, which enables coordinated growth above and below ground (Nathalie and Christian 2013, Kasinath et al. 2015, Li et al. 2018). In the case of nutritional imbalance, leaf chlorosis occurs in Mg-deficient crop plants, which present spot-, stripe- and network-like symptoms depending on the pattern of leaf veins. The entire leaves may wither due to serious Mg deficiency (Lasa et al. 2000, Hermans et al. 2004, 2013). When excessive Mg accumulates in crop plants, Mg poisoning is manifested by bronze stripes or necrotic spots on the edge of affected leaves. Even though such symptoms are barely visible in mild poisoning cases, the plants still experience noticeable physiological and biochemical changes, such as a decrease in leaf peroxidase and catalase activities (Lasa et al. 2000, Yang et al. 2018).

Like Mg^{2+}, K^+ and calcium ion (Ca^{2+}) are cations, yet their ionic properties and plant uptake patterns differ considerably (Broadley and White 2010). The charge carried by ions and their hydration radius determine the pathway and rate of ion uptake by the roots. While Mg^{2+} and K^+ are mainly taken up by the symplast pathway, Ca^{2+} is taken up by the apoplast pathway (Karley and White 2009, Horie et al. 2011, Wang and Wu 2013). The symplast-dependent transmembrane transport of Mg^{2+} and K^+ may be achieved through transporters or ion channels in which the ions interact with each other (Mao et al. 2014, Chen et al. 2017, Yan et al. 2018, Xie et al. 2020). Many studies have shown that at low concentrations, K^+ and Mg^{2+} synergise with each other, allowing rapid uptake by crop plants. At high concentrations, a strong antagonistic effect emerges between K^+ and Mg^{2+}, which hinders nutrient uptake (Dechen et al. 2016, Li et al. 2018, Koch et al. 2019). According to Omar and Kobbia (1966), this antagonism arises from a unidirectional effect of K to Mg. A high concentration of K limits Mg uptake and transport in crop plants, whereas the changes in Mg concentration have minimal or no effect on the K contents in plant roots and aboveground organs in sugarcane, rice, and safflower (Ding et al. 2006, Farhat et al. 2013, Rhodes et al. 2018).

Some other studies have shown that the changes in Mg concentration affect K uptake by crop plants. For instance, K uptake increased remarkably in sunflower, onion, and banana plants under low Mg conditions (Tomasz et al. 2012, Lasa et al. 2000, He et al. 2020). In practical production, it was also observed that Mg imbalance did not prominently affect tomato plants' growth and K contents at the seedling stage. Nevertheless, the effects of Mg supply on plant K contents gradually increased with the progression of vegetable growth. The antagonistic relationship between K and Mg is most likely related to crop type and/or growth stage, but little is known about this relationship in vegetables during the fruit ripening stage.

The uptake and transport of Mg and Ca by crop plants share many similarities. Both Mg^{2+} and Ca^{2+} in soil migrate to the roots in a mass flow manner, and they compete for adsorption sites on cell membranes in the free space of roots (Karley and White 2009, Horie et al. 2011). These two ions are mainly transported across the cell membrane through a passive pathway, and their upward transport in xylem vessels is driven by transpirational pull. Despite the same valence, Ca^{2+} has a smaller radius than Mg^{2+} and, consequently, a higher rate of xylem transport. After primary transport, Mg can be circulated in the plant *via* the phloem and thus reused. However, Ca that arrives at the leaves or fruit is difficult to move to other organs. Therefore, Mg-Ca interactions occur in the plant mainly during nutrient uptake and primary transport (Steucek and Koontz 1970, White 2001).

Myriad studies have demonstrated the effects of Mg deficiency or excess on crop plants with respect to physio-biochemical characteristics and K-Mg interactions. In most cases, Mg nutrition at the seedling stage is analysed in grain crops with a relatively simple source-sink relationship of nutrients (Matsuda et al. 2011, Rivera-Amado et al. 2020). In contrast to common grain crops, the majority of vegetable crops (such as tomato, cucumber, and cowpea) feature alternate growth of leaves and fruit, with alternation of leaf development and fruit ripening. As such, the source-sink relationship of nutrients in vegetable crops may be considerably different from that of grain crops. Vegetable crops are an integral part of people's diets, and their mineral nutrient levels are as important to human health as grain crops (Bo and Pisu 2008, Broadley and White 2010, Cakmak 2013). Sustainable vegetable production necessitates a holistic understanding of how vegetable crops respond to deficient or excessive Mg supply.

In the present study, we selected tomatoes as a typical vegetable crop to ascertain the effects of different Mg supply levels on plant growth and nutrient uptake across various growth stages. The aim

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of this study was to unravel how Mg interacts with K and Ca in vegetable crops during plant growth and development. The results of this study could provide empirical evidence for nutrient regulation in vegetable production.

MATERIAL AND METHODS

Experimental conditions and materials. The experiment was conducted between February and November 2021 in a glass greenhouse on the campus of Ningxia University (38°15'N, 106°02'E). The temperature and relative humidity in the greenhouse were controlled in the range of 15–25 °C and 60–70%, respectively. The tomato cultivar used in the experiment was *Solanum lycopersicum* L. cv. Saina – a new pink-fruited F1 hybrid. This cultivar features infinite plant growth, which renders it suitable for cultivation in low- and medium-temperature regions.

Before the experiment, tomato seeds were sown in 96-well trays with Chunrang nursery substrate (Tianliang Agricultural Technology Development Co., Ltd., Liuyang, China). The trays were irrigated with 1/8 Yamazaki (1981) tomato nutrient solution during seedling establishment. When the first four true leaves and one bud developed (40 days after sowing), the roots were washed, and the seedlings were grown hydroponically for subsequent experiments. The Yamazaki tomato nutrient solution contained 354 mg/L $Ca(NO_3)_2 \cdot 4\ H_2O$, 404 mg/L KNO_3, 76 mg/L $NH_4H_2PO_4$, 16 mg/L Na_2Fe-EDTA, 1.2 mg/L H_3BO_3, 0.72 mg/L $MnCl_2 \cdot 4\ H_2O$, 0.09 mg/L $ZnSO_4 \cdot 7\ H_2O$, 0.04 mg/L $CuSO_4 \cdot 7\ H_2O$ and 0.01 mg/L $(NH_4)_6Mo_7O_{12}$. Distilled water (~0.1 mmol/L Mg^{2+}) was used to prepare the nutrient solution.

Experimental setup. Five levels of Mg treatment were used in the experiment based on previous results (Yamazaki 1981, Li et al. 2018) and the reference level of Mg^{2+} in several nutrient solution formulations (1.0 mmol/L). The Yamazaki nutrient solution (containing 0.1 mmol/L Mg^{2+}) was supplemented with 0, 0.5, 1.0, 1.5 and 3.0 mmol/L Mg^{2+} (denoted as Mg0, Mg0.5, Mg1.0, Mg1.5 and Mg3.0, respectively). Mg^{2+} was supplied as anhydrous $MgSO_4$ (analytical reagent, purity 99.9%; Sinopharm Chemical Reagent Co., Ltd., Shanghai, China). Each treatment had nine replications, with a total of 45 pots. Two seedlings were planted in each pot, with a total of 90 seedlings.

The experiment was conducted in 64-cm-long, 22-cm-wide and 18-cm-high hydroponic plastic pots, with 13 L of nutrient solution or distilled water per pot. Seedlings with uniform growth were selected and pre-cultured in distilled water for a week to deplete nutrients. Then, the seedlings were transferred to the 1/8 nutrient solution and cultured for 12 days. Afterwards, the seedlings were changed to the 1/2 nutrient solution for another 12 days and then the complete nutrient solution for 76 days. The solution pH was adjusted between 5.5 and 6.5 using 0.1 mol/L NaOH or HNO_3 during the 100-day experimental period. The nutrient solution was replaced in a timely manner to maintain the electrical conductivity at levels lower than 1.4 mS/cm.

Sample collection and analysis. Plant growth parameters were monitored at the seedling stage (35 days), blooming and fruit setting stage (55 days) and fruit ripening stage (100 days). Plant height and stem diameter were measured with a graduated scale and Vernier calliper. Leaf area was measured using a YMJ-CH intelligent leaf area meter (Topu Yunnong Technology Co., Ltd., Hangzhou, China). Root parameter measurement was completed using a LA-S plant root analyser (Wanshen Testing Technology Co., Ltd., Hangzhou, China). Before measurement, the roots were spread in a flat tray and added with a small amount of water. Completely expanded roots were scanned, and the images were analysed.

Fully expanded upper leaves were collected to observe chloroplast structure at fruit ripening (90 days). As previously reported, sample embedding and section preparation were performed (Ma et al. 2021). Briefly, leaf samples were cut into 1 mm × 2 mm blocks and fixed in 5% glutaraldehyde (prepared in 0.1 mol/L phosphate buffer, pH 7.4). Then, the samples were post-fixed in 1% osmium acid (prepared in 0.1 mol/L phosphate buffer, pH 7.4) for 5 h at 20 °C. After three washes with 0.1 mol/L phosphate buffer, the samples were dehydrated with gradient ethanol, transmitted with acetone and embedded with epoxy resin Epon812 (McGahee Reagent, Micxy Chemical Co., Ltd., Chengdu, China). The embedded samples were sectioned using an EM UC7 ultramicrotome (Leica, Wetzlar, Germany), followed by staining with uranyl acetate and lead citrate. The section samples were observed and photographed under a Hitachi transmission electron microscope (Hitachi, Tokyo, Japan).

Fully expanded upper leaves, root stems, and fruit samples (the second cluster) were collected at the seedling (35 days) and fruit ripping (100 days) stages. There were only leaves but no fruit clusters at 35 days, and the leaves were sampled at the apical

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end of the second fruit cluster from the bottom up at 100 days. After weighing, fresh samples were deactivated in an oven at 105 °C for 30 min and then dried at 65 °C to constant weight. Dry samples were ground, passed through a 0.25-mm sieve and stored in bottles. Approximately 0.5 g of each sample was carbonised and then incinerated in a 550 °C muffle furnace (TM, Yingan Meicheng Scientific Instrument Co., Ltd., Beijing, China) for 4 h. After cooling, the sample was transferred to a 100-mL volumetric flask by repeatedly washing with diluted nitric acid (nitric acid:water = 1:9, *v*/*v*; 20 mL each). Distilled water was used to wash the crucible two to three times, and the washing solution was transferred to the same volumetric flask. The sample solution was adjusted to constant volume with distilled water and then diluted appropriately. The K, Ca and Mg concentrations in the sample solution were measured using a Z-2000 atomic absorption spectrophotometer (AAS, Z-2000, Shanghai, China).

Statistical analysis. Excel 2010 (Microsoft Corp., Redmond, USA) was used to process data and draw graphs. SPSS 20.0 (IBM Corp., Armonk, USA) was used for all statistical analyses. Means were compared using a one-way analysis of variance followed by the least significant difference test for multiple comparisons. The relationship of Mg supply, nutrient uptake and plant biomass was analysed using binary logistic regression and Spearman correlation analyses. A *P*-value of less than 0.05 was considered statistically significant.

RESULTS

Effects of Mg supply level on plant growth

Shoot growth. With increasing levels of Mg supply, plant height increased first and reached a peak value in the Mg1.0 treatment across various growth stages (Figure 1). The plant height of the Mg1.0 treatment was significantly higher than that of other treatments at each stage, and a further increase in Mg level resulted in lower plant height. Stem diameter exhibited a similar pattern as plant height in response to increased Mg level, with the highest value in the Mg1.0 treatment. Compared with the Mg1.0 treatment, both plant height and stem diameter decreased more prominently under lower Mg levels than under higher Mg levels. The results indicate that 1.0 mmol/L Mg^{2+} was the optimal level of Mg supply for the shoot growth of the tomato. Either lower or higher Mg supply hindered shoot growth, and the adverse effect of Mg deficiency was greater than that of Mg excess (Figure 1).

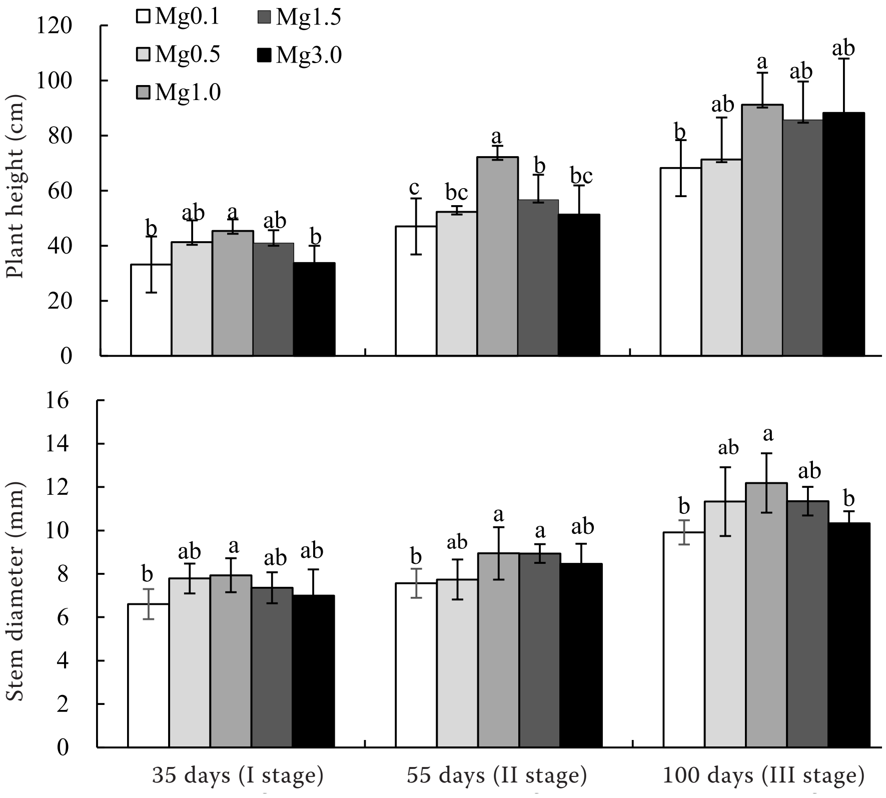

Figure 1. Shoot growth of tomato plants under different levels of magnesium (Mg) supply. Mg0.1 to Mg3.0 indicate Mg supply at the level of 0.1 to 3.0 mmol/L Mg^{2+}. I, II and III stage represent seedling, blooming and fruit setting and fruit ripening of tomato, respectively. Different letters above the error bars indicate significant differences in group means among the treatments at the same growth stage by the *LSD* (least significant difference) method at the 5% level

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Table 1. Root parameters of tomato plants under different levels of magnesium (Mg) supply at fruit ripening (100 days)

Treatment	Total length (cm)	Projected area (cm^2)	Superficial area (cm^2)	Volume (cm^3)	Mean diameter (mm)
Mg0.1	976 ± 106^b	201 ± 21.2^b	632 ± 66.5^b	146 ± 29.3^b	0.58 ± 0.05^c
Mg0.5	1 415 ± 152^{ab}	241 ± 63.6^b	759 ± 200^b	199 ± 118^{ab}	1.55 ± 0.07^b
Mg1.0	1 818 ± 720^a	356 ± 66.1^a	1 117 ± 208^a	297 ± 69.4^a	2.01 ± 0.14^a
Mg1.5	1 585 ± 207^a	330 ± 25.4^a	1 036 ± 79.7^a	263 ± 38.8^a	1.51 ± 0.07^b
Mg3.0	1 078 ± 171^b	194 ± 74.4^b	609 ± 234^b	141 ± 121^b	1.53 ± 0.15^b

Mg0.1 to Mg3.0 indicate Mg supply at the level of 0.1 to 3.0 mmol/L Mg^{2+}. Values with different letters in a column indicate significant differences in group means among the treatments. The same applies to the following tables

Root development. During each growth stage, various root parameters showed consistent responses to different levels of Mg supply (Table 1). In particular, the parameter values were significantly higher in the Mg1.0 and Mg1.5 treatments than in the other treatments. For example, at fruit ripening, the root total length, projected area, superficial area, volume and diameter of Mg1.0 treatment increased by 46.3, 43.5, 43.4, 50.8 and 71.1% compared with those of Mg0 treatment, respectively. The respective increase in the root parameters of Mg1.0 treatment relative to Mg3.0 treatment was 40.7, 45.5, 45.5, 52.5 and 23.9%, respectively. These results signify that Mg supply between the levels of 1.0–1.5 mmol/L was favourable for root development of tomato. Lower Mg supply had a more profound effect on root diameter than higher Mg supply.

Effects of Mg supply level on leaf chloroplast structure

Different levels of Mg supply strongly affected chloroplast ultrastructure in tomato leaves (Figure 2). In the Mg1.5 treatment with optimal Mg supply, chloroplasts were well-developed and structurally intact in a regular fusiform shape. They were located close to the cell wall, with clear grana and stroma lamellae. Numerous stroma thylakoids were stacked and densely arranged. The chloroplasts contained abundant large starch granules and a few plastoglobuli. In the Mg0 treatment with deficient Mg supply, the chloroplasts were irregularly shaped and remarkably decreased in number, with blurred stroma lamellae, wrinkled starch granules and many plastoglobuli. In the Mg3.0

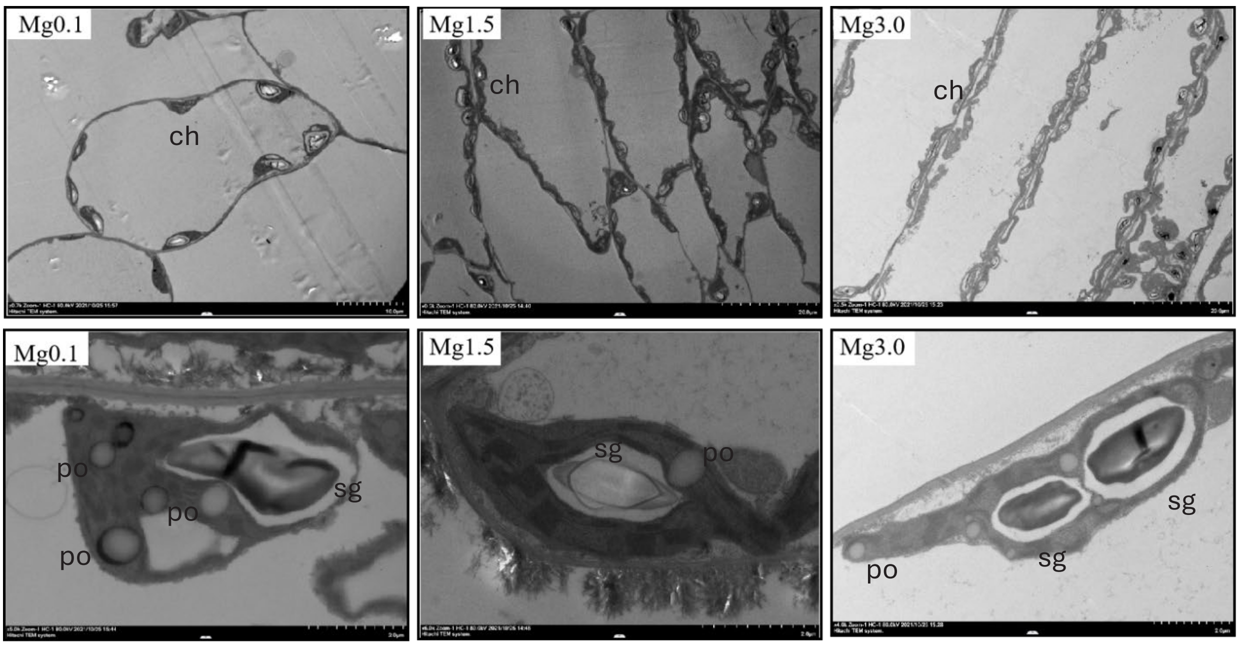

Figure 2. Leaf chloroplast ultrastructure of tomato plants under different levels of magnesium (Mg) supply. The samples shown were middle-upper leaves collected at the fruit ripening stage (100 days). ch – chloroplast; sg – starch grain; po – plastoglobulus; Mg0.1 to Mg3.0 indicate Mg supply at the level of 0.1 to 3.0 mmol/L Mg^{2+}

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treatment with excessive Mg supply, the chloroplasts were elongated in shape and contained an increased number of wrinkled starch granules. There were also some plastoglobuli in the chloroplasts, and grana lamellae displayed a denser stacking pattern. The results reflect that deficient or excessive Mg supply influenced chloroplast structure in tomato leaves and starch conversion in chloroplasts. Low Mg levels mainly affected chloroplast number, whereas high Mg levels altered chloroplast shape.

Effects of Mg supply level on plant biomass

Various levels of Mg supply showed significant effects on the different organ biomass of tomato plants during various growth stages (Figure 3). At the seedling stage, the plants of Mg0.5 and Mg1.0 treatments produced significantly higher root and leaf biomass compared with other treatments. Compared with these two treatments, the mean values of total biomass in the Mg0 and Mg3.0 treatments decreased by 41.2% and 27.8%, respectively (Figure 3A). At the blooming and fruit setting stage, the different organ biomass peaked in the Mg1.0 treatment; total biomass decreased by 50.1% and 38.3% in the Mg0 and Mg3.0 treatments, respectively (Figure 3B). At the fruit ripening stage, the highest different organ biomass was observed in the M1.0 and Mg1.5 treatments. Compared with the M1.0 treatment, the total biomass of the Mg0 and Mg3.0 treatments decreased by 52.8% and 17.7%, respectively (Figure 3C). The results signify that low or high Mg supply inhibited different organ biomass formation, and the production of more biomass called for increased levels of Mg supply with the progression of plant growth. Maintaining Mg supply between levels of 0.5–1.5 mmol/L throughout the growth period of tomato contributed to the formation of more dry matter in various plant organs.

Effects of Mg supply level on nutrient contents in various plant organs

Seedling stage. The Mg contents in various plant organs increased as a consequence of increased Mg supply, and there was a significant positive correlation between these two factors (Figure 4). In the Mg3.0 treatment, the Mg contents of root, stem and leaf samples were 1.82, 2.49 and 3.58 times those of the Mg0 treatment (leaves > roots > stems). In contrast, no significant changes occurred in the K contents of various organs

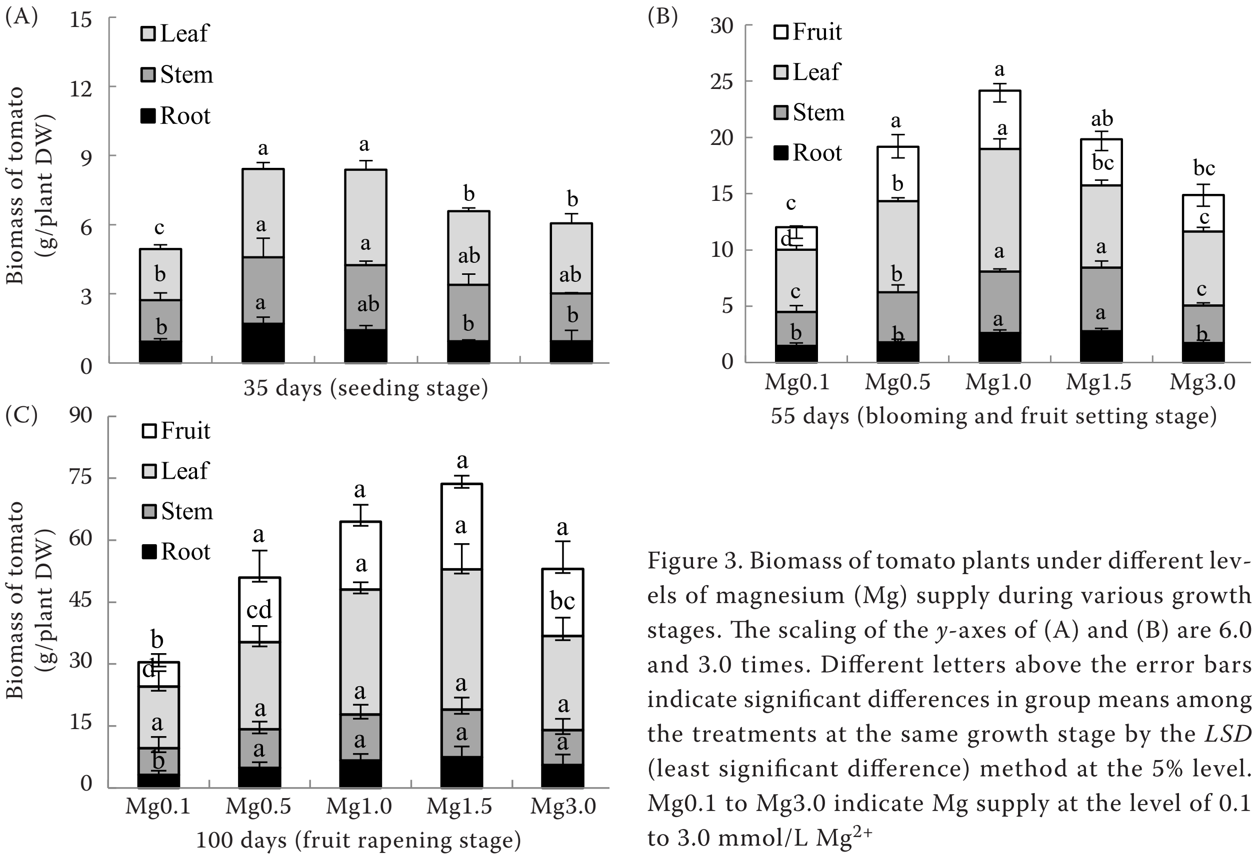

Figure 3. Biomass of tomato plants under different levels of magnesium (Mg) supply during various growth stages. The scaling of the *y*-axes of (A) and (B) are 6.0 and 3.0 times. Different letters above the error bars indicate significant differences in group means among the treatments at the same growth stage by the *LSD* (least significant difference) method at the 5% level. Mg0.1 to Mg3.0 indicate Mg supply at the level of 0.1 to 3.0 mmol/L Mg^{2+}

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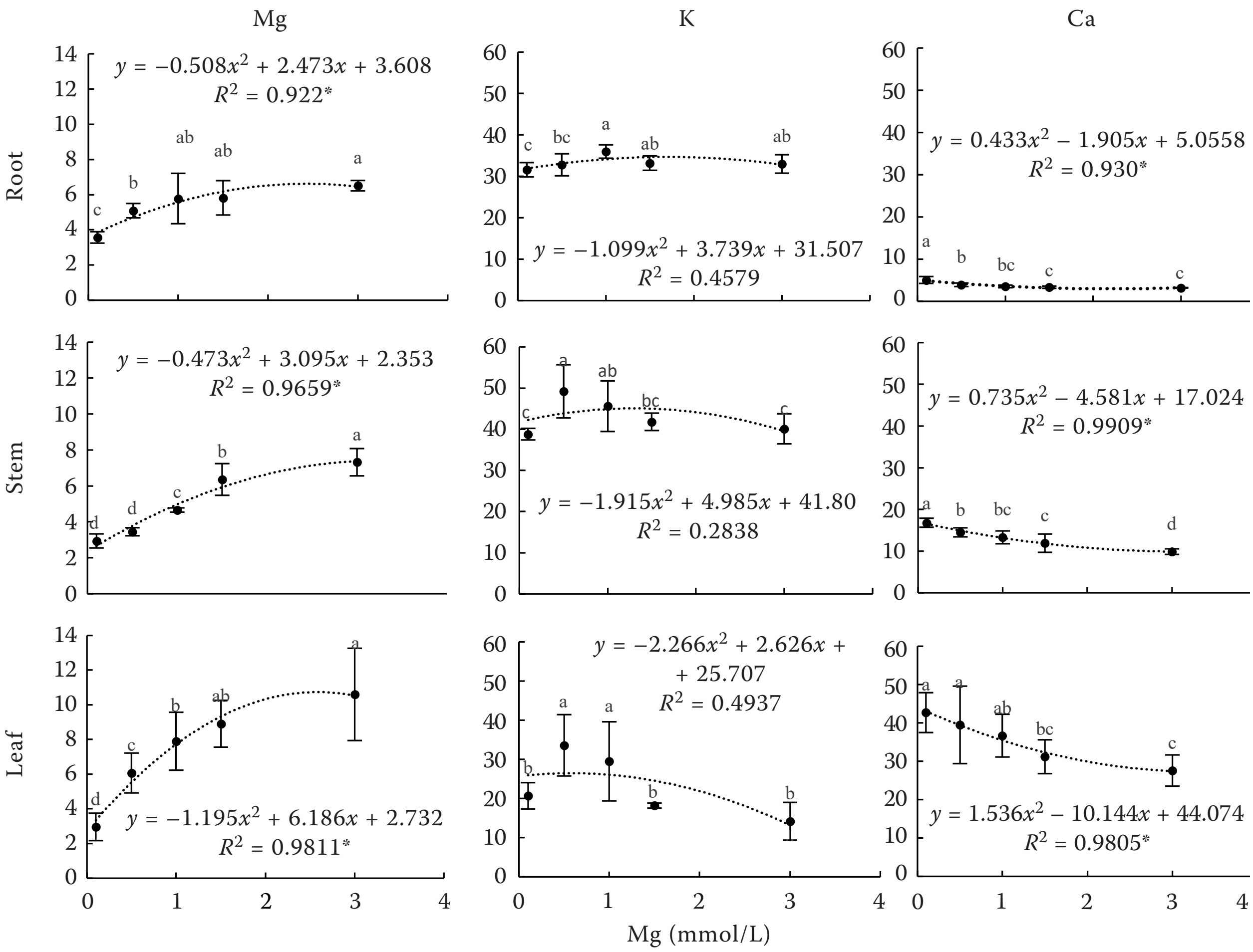

Figure 4. Relationship between magnesium (Mg) supply and nutrient contents (g/kg) in various organs of tomato plants at the seedling stage (35 days). Different letters above the line bars indicate significant differences in group means among the treatments by *LSD* (least significant difference) method at the 5% level

(stems > roots > leaves). The Ca contents in various organs exhibited a significant downward trend with increasing levels of Mg supply, and a significant negative correlation emerged between them. Compared with the Mg0 treatment, the Ca contents of root, stem and leaf samples from the Mg3.0 treatment decreased by 36.6, 41.3 and 35.4%, respectively (leaves > stems > roots). The results indicate that the Mg supply level exerted a noticeable effect on the uptake and translocation of Mg and Ca, but not K, in tomato plants during the early growth stage, with distinct antagonism between Mg and Ca.

Fruit ripening stage. At fruit ripening, the patterns of Mg and Ca contents in tomato roots stems, and leaves mirrored those observed at the seedling stage. However, root K contents first increased and then decreased with increasing Mg levels, accompanied by a remarkable decrease in leaf K contents and a substantial increase in fruit K contents (Figure 5). These results indicate that the Mg supply level still had a considerable effect on Mg and Ca uptake and allocation to various organs of tomato plants during the late growth stage, with distinct antagonism between these two elements. There was a synergistic effect between K and Mg under relatively low Mg levels, which was reversed to a remarkable antagonistic effect under higher Mg levels. Higher Mg levels hindered K translocation to the leaves while promoting K translocation to the fruit.

DISCUSSION

Plant growth and development in relation to Mg supply

As essential nutrients for plants, Mg, K and Ca perform a range of vital physiological functions to support plant growth and development. Our results

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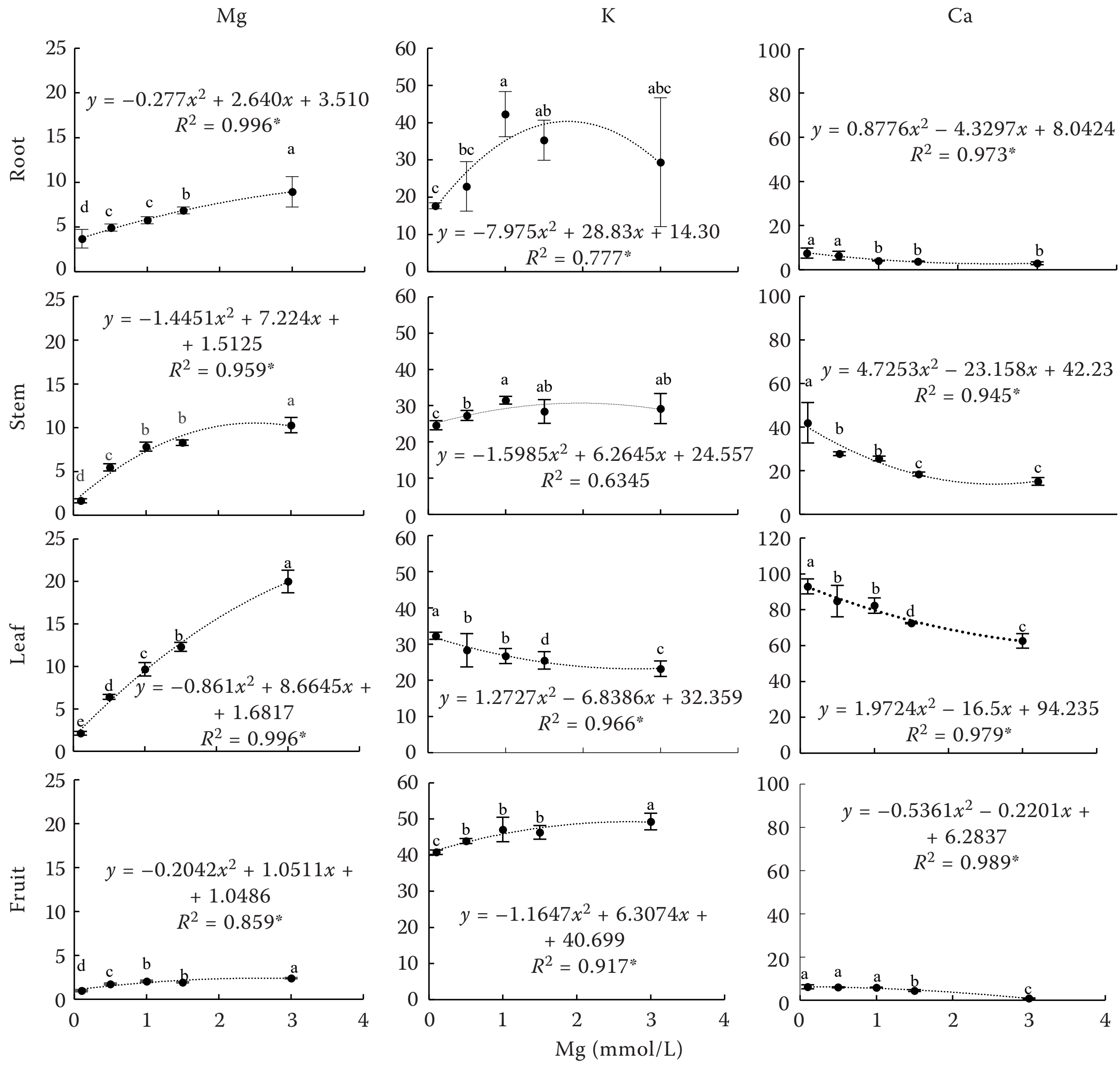

Figure 5. Relationship between magnesium (Mg) supply and nutrient contents (g/kg) in various organs of tomato plants at the fruit ripening state (100 days). Different letters above the line bars indicate significant differences in group means among the treatments by the *LSD* (least significant difference) method at the 5% level

showed that various levels of Mg supply markedly affected biomass formation in tomato plants throughout the growth period. An inhibition of shoot and root growth was observed under deficient Mg supply (Figure 3). Mg deficiency-induced decrease in plant biomass could be attributed to the function of Mg in chloroplasts and ribosomes.

Plants with optimal Mg nutrition allocate ~15% of total Mg in chloroplasts. Since Mg is the central atom of chlorophyll, deficient Mg supply could lead to a decrease of grana lamellae, destruction of the envelope, and a lower number of thylakoids in chloroplasts (Shen et al. 2011). Under different Mg supply conditions, we observed remarkable alterations in the chloroplast ultrastructure of tomato leaves. Low Mg supply resulted in a noticeable decrease in the number of chloroplasts, with blurred grana lamellae and wrinkled starch granules. These alterations are expected to affect the biosynthesis of organic compounds in photosynthesis.

While ~75% of Mg in plants with optimal Mg nutrition is located in ribosomes, cytoplasmic Mg concentration affects the form of ribosomes. Ribosomes encompass separated large and small subunits at

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Mg^{2+} concentrations < 1 mmol, whereas the large and small subunits are bound together, or two ribosomes form a dimer at Mg^{2+} concentrations > 1 mmol (Marschner 2011). The form of ribosomes determines the rate of protein biosynthesis in the plant, thereby influencing biomass formation above and below ground (Marschner 2011). The growth of tomato plants was also inhibited by excessive Mg supply (Figure 3), possibly due to a similar effect on chloroplast structure, which hindered the biosynthesis of photosynthetic products.

We found that various levels of Mg supply led to prominent changes in both K and Ca contents in various organs of tomato plants (Figures 4 and 5). As plants' most abundant metal element, K mainly participates in nutrient transport and facilitates rapid transport of photosynthetic products to sink organs, such as new leaves and roots. A myriad of studies have shown that sufficient K supply can accelerate crop growth and development, as well as improve crop yield and quality (Zengin et al. 2009, Qu et al. 2020, Liu et al. 2021). Ca mainly plays a role in the maintenance of normal metabolic activities in crop plants by stabilising cell walls and membrane structures, which also promotes crop growth (Ehret and Ho 1986, Clarkson 2010). The total biomass of tomato (from seedling to fruit ripening stage) was significantly positively correlated with K and Ca accumulation in plants (Figure 6), indicating that K, Ca and Mg were all in close association with tomato growth (Figure 6). Relationship between nutrient accumulation and biomass formation in tomato plants.

Nutrient use and interactions

This study used constant K^+ and Ca^{2+} concentrations in the nutrient solution, whereas the Mg^{2+} concentration was variable. Under low Mg conditions, there was an evident synergistic effect between Mg and K in tomato plants (Figures 4 and 5). With increasing Mg levels, Mg^{2+} could impede the movement of Ca^{2+} in the free space of roots and compete with K^+ for the adsorption sites on cell membranes. Consequently, a distinct antagonistic effect emerged between Mg and Ca under high Mg levels, and the antagonistic effect between Mg and K enhanced with the progression of tomato growth (Figures 4 and 5).

When Mg^{2+}, K^+ and Ca^{2+} are transferred from the root stele to xylem vessels for long-distance transport, their movement rates are substantially different due to the effects of parenchymal cells in vessel walls and the intrinsic ionic properties. The movement rates of the three ions are ranked as $K^+ > Mg^{2+} > Ca^{2+}$, with Ca^{2+} having the lowest movement rate (Karley and White 2009, Horie et al. 2011). When the nutrients in xylem vessels are allocated to the leaves and fruit, a synergistic or antagonistic relationship also emerges between the ions. Interestingly, we found that the Mg supply level did not considerably affect the K contents in various organs of tomato plants during the early growth stage. However, Mg content was significantly negatively correlated with K and Ca in tomato leaves from the blooming and fruit setting stage (Figures 4 and 5). This indicates that when the three ions entered the leaves, Mg^{2+} inhibited the entry of K^+ and Ca^{2+}. Additionally, Mg content was significantly positively correlated with K content and negatively correlated with Ca content in tomato fruit (Figures 4 and 5). This means that when the three ions entered the fruit, Mg^{2+} and K^+ exhibited a synergistic effect, in contrast to an antagonistic effect between Mg^{2+} and Ca^{2+}.

We additionally found that the distribution of Mg and Ca in various organs of tomato plants ranked as leaves > stems > roots > fruit, whereas the K distribution followed the order of fruit > stems > leaves > roots (Figure 5). This suggests that Ca and Mg were

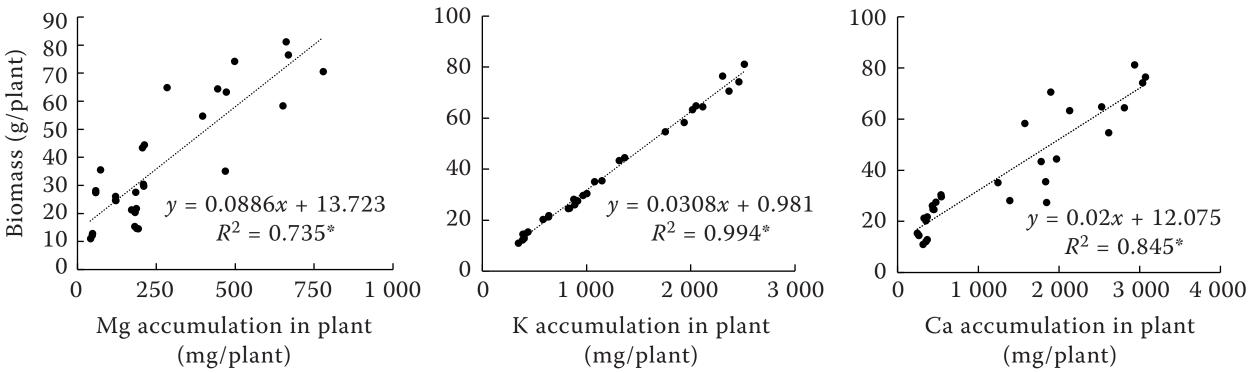

Figure 6. Relationship between nutrient accumulation and biomass formation in tomato plants

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preferentially distributed to tomato leaves, with K preferentially distributed to the fruit (Figures 4 and 5). During the late growth stage, the upper leaves and fruit competed for nutrients, so Mg and Ca were mainly distributed in the leaves and less in the fruit. In vegetable cultivation, Ca and Mg deficiency symptoms often develop from the middle fruit. The collective results allowed us to propose that the application rate of K fertiliser should be controlled at the fruit ripening stage, and attention should be paid to the supply of Ca and Mg nutrients to the fruit of vegetable crops.

The mesophyll of tomato leaves with low Mg supply started to present chlorosis symptoms at 40–45 days of the experiment. With the progression of plant growth, the mesophyll turned yellow, and the veins turned purplish red, which basically mirrors the symptoms in most grain crops under low Mg conditions. However, in grain crops, such symptoms spread upward from the bottom leaves, whereas we observed the spreading of chlorosis symptoms from middle leaves in tomato plants (Gaoqiao et al. 2002, Marschner 2011). Mg deficiency-induced leaf yellowing has also been found to develop upward from the middle or middle-upper parts of cucumber and cowpea plants in vegetable production (Miao 2007).

In most cases, vegetable crops such as tomatoes and cucumbers have alternate leaves, with fruit ripening in stages from the bottom up (Qu et al. 2023). In contrast, the seeds of grain crops are usually formed at the top or middle part of the plant and mature at once. This inconsistency between vegetable and grain crops may lead to a distinct difference in nutrient reuse or source-sink relationship. We found that the Mg contents of middle-upper leaves (mean: 2.02 g/kg) were lower than those of lower leaves (mean: 2.96 g/kg) under low Mg conditions, which contradicts the basic theory of plant nutrition. In principle, Mg is a nutrient with high reuse capacity in plants, and it can be transferred from lower leaves to upper leaves or new tissues in Mg-deficient crops (Martini and Mutters 1985, Karley and White 2009, Reid et al. 2013). This is partially different from our results. The possible reason is that the Mg in tomato leaves was preferentially transferred to the adjacent fruit and hardly transferred upward to other leaves. This mechanism could also account for the difference in Mg imbalance between vegetable and grain crops.

In conclusion, this study demonstrated that Mg supply has a dual relationship with the uptake of K and Ca nutrients in vegetable crops, exemplified by tomatoes. On the one hand, low Mg supply to hydroponic tomato plants resulted in less K uptake, and the deficiencies of K and Mg considerably limited plant growth and development. On the other hand, an excess of Mg hindered both K and Ca uptake by tomato plants, and this effect was particularly manifested in decreased allocation of K to the leaves and Ca to the fruit. The results of this study are partially inconsistent with previous findings on common grain crops since vegetable crops have markedly different growth and development characteristics. Rational Mg application in vegetable cultivation can not only maximise the nutritional function of Mg but also allow it to effectively regulate Ca and K nutrition in vegetable crops.

Acknowledgement. We acknowledge the funding from the National Natural Science Foundation of China, Project No. 31960628.

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Received: November 28, 2023
Accepted: September 4, 2024
Published online: October 7, 2024