Effects of High Potassium and Low Temperature on the Growth and Magnesium Nutrition of Different Tomato Cultivars

Huixia Li, Zhujun Chen, Ting Zhou, Yan Liu, Sajjad Raza, and Jianbin Zhou¹

College of Natural Resources and Environment, Northwest A&F University, Yangling 712100, China; and Key Laboratory of Plant Nutrition and the Agri-environment in Northwest China, Ministry of Agriculture, Yangling 712100, China

Additional index words. *Solanum lycopersicum*, Mg deficiency, temperature stress, K–Mg competition

Abstract. The interaction between potassium (K) and magnesium (Mg) in plants has been intensively studied. However, the responses of different tomato (*Solanum lycopersicum* L.) cultivars to high K levels at low temperatures remained unclear. Herein, a complete randomized hydroponic experiment was conducted to evaluate the effects of temperature (25 °C day/18 °C night vs. 15 °C day/8 °C night) and K concentrations (156 mg·L⁻¹ vs. 468 mg·L⁻¹) on the growth and Mg nutrition of tomato cultivars Gailiangmaofen (MF) and Jinpeng No. 1 (JP). Compared with the control temperature (25 °C day/18 °C night), the low temperature decreased total biomass, shoot biomass, and Mg uptake in shoot by 17.3%, 24.1%, and 11.8%, respectively; however, the root/shoot ratio was increased. High K had no significant effect on plant growth or biomass compared with the control K concentration (156 mg·L⁻¹); however, Mg concentrations and uptake in shoot were significantly lower under high-K treatment. Significant difference was observed for K uptake, but not for Mg uptake, between the two cultivars. There was no significant interaction between temperature and high K on Mg uptake of tomato, so a combined stress of low temperature and high K further inhibited Mg uptake and transport. Low temperature and high K increased the risk of Mg deficiency in tomato.

Magnesium is an essential mineral element for plant. It is the most abundant divalent cation in the cytosol of plant cells and plays a critical role in many physiological processes and reactions, such as photosynthesis, photophosphorylation, protein synthesis, and chlorophyll formation (Davies and Winsor, 2010; Li et al., 2001). Mg deficiency is common in acidic soil, particularly in highly leached humus acid soil or sandy soil with a heavy dressing of lime (Cakmak and Yazici, 2010; Gransee and Führs, 2013; Mengel and Kirkby, 2001). By contrast, Mg deficiency is uncommon in calcareous soil because of abundant Mg in the parent materials (Broadley and White, 2010; Gransee and Führs, 2013). Cation competition between Mg²⁺ and other ions, such as K⁺, Ca²⁺, H⁺, NH₄⁺, and Al³⁺, is another reason for crop Mg deficiency (Mengel and Kirkby, 2001; Shaul, 2002), with high levels of K tending to inhibit Mg uptake in forage wheat (*Triticum*

aestivum L.) (Ohno and Grunes, 1985), rice (*Oryza sativa* L.) (Ding et al., 2006), and safflower (*Carthamus tinctorius* L.) (Farhat et al., 2013).

Many studies have examined Mg nutrition of forests, grasses, and arable crops (Cakmak, 2013; Gerendás and Führs, 2013; Guo et al., 2016). Compared with the crops mentioned previously, vegetables such as tomato (*S. lycopersicum* L.) require more K and Mg to form the same biomass (Hao and Papadopoulos, 2004); however, little is known about the interaction between K and Mg in vegetable crops. Recently, Mg deficiency is frequently observed in tomato grown in calcareous soil in solar greenhouses in North China regions, such as Shaanxi and Shandong provinces, with worsening symptoms in winter months, as a result, tomato yield and quality are significantly reduced (Yan et al., 2016). The calcareous soils in North China are developed from loess or loess-like materials, which are usually rich in K bearing minerals (Huang et al., 2012). Farmers usually apply high rates of K fertilizer as they believe that K is important for tomato (Wang et al., 2015). Available K in greenhouse soil can be as high as 600 mg·kg⁻¹ (Chen et al., 2017), which is significantly increasing the K/Mg ratio, and is one of the reasons for tomato Mg deficiency in calcareous greenhouse soil

in North China (Chen et al., 2013; Chen et al., 2017).

Numerous reports have shown a close relationship between nutrient uptake and root-zone temperature (Clarke et al., 2015; Hwang et al., 2016). In general, uptake of mineral nutrients by plants increases with increasing temperatures within the temperature range of 6–38 °C (Marschner, 2012); however, the optimum temperature range differs among crop species from 20–30 °C in rice (Zia et al., 1994) to 15–25 °C in barley (*Hordeum Vulgare* L.) (Pettersson, 1995). Extensive studies have documented Mg uptake in various plant species at low temperatures. At the same low root-zone temperature, Mg uptake was almost constant in pumpkin (*Cucurbita pepo* L.), whereas in cucumber (*Cucumis sativus* L.) leaves a significant decrease in Mg was observed (Tachibana, 1988). Furthermore, although Mg concentration and total uptake in calceolaria (*Calendula officinalis* L.) (White and Biernbaum, 1984) and snapdragon (*Antirrhinum majus* L.) (Hood and Mills, 1994) were found to be lower at a low root-zone temperature, an increase was observed in pepper (*Capsicum annuum* L.) (Gosselin and Trudel, 1986). Thus, the effect of low temperature on Mg uptake depends on the plant species. The response of different cultivars of tomato to low temperatures remains largely unknown.

Nutrient uptake at different temperatures also depends on the presence of different ions (Marschner, 2012). Mineral ions absorbed by an active pathway such as NO₃⁻ and H₂PO₄⁻ decrease significantly with a decreasing root-zone temperature (Polat et al., 2012), whereas a weaker effect is observed in ions absorbed by a passive pathway, such as K⁺ and Ca²⁺ (Broadley and White, 2010). Mineral ions absorbed by a passive pathway are affected by extreme low temperatures (Marschner, 2012). Meanwhile, the dominant pathway of Mg²⁺ uptake remains controversial (Gransee and Führs, 2013; Nathalie and Christian, 2013).

The aim of this study was to determine the effects of low temperature and high K on Mg uptake of two tomato cultivars. Our hypothesis was that low temperature and high K would inhibit Mg uptake and translocation by tomato.

Materials and Methods

Plant materials. Two tomato cultivars were selected, *S. lycopersicum* L. cv. Gailiangmaofen and *S. lycopersicum* L. cv. Jinpeng No. 1, both are dominant cultivars in calcareous soil in North China. Both MF and JP are cold- and drought-tolerant cultivars, which are suitable for cultivation during autumn and winter in North China. These two cultivars are indeterminate and have single vines, with matured fruits being pink in color. JP has a hard sarcocarp, whereas MF has a soft one. They are different in genetic traits and planting habits (Yu et al., 2005).

Seeds of the two tomato cultivars were provided by the seed breeding center of the

Received for publication 13 Feb. 2018. Accepted for publication 10 Mar. 2018.

This work was supported by the National Key Research and Development Program of China (2017YFD0200106) and the National Natural Science Foundation of China (41671295).

¹Corresponding author. E-mail: jbzhou@nwsuaf.edu.cn.

Horticulture College, Northwest A&F University (Yangling, Shaanxi Province, China), disinfected with 0.1% HgCl₂ then soaked in water for 15 min before sowing into hole trays. Seedling substrate was a mixture of cattle manure, maize straw, peat, vermiculite, and humic acid at the ratio of 5:1:2:1.95:0.05 (w/w). The properties of the substrate were suitable for the growth of tomato seedlings (pH 5.5–6.5; bulk density 0.39 g·cm⁻³; total porosity 75.8%). All the materials were offered by Yujing Agriculture Co., Ltd, Shandong Province, China. When the fifth leaf was fully expanded (40 d after emergence), seedling roots were washed; and plants were transplanted into a hydroponic culture system.

Experimental design. A complete randomized design was used to study the effects of temperature (25 °C day/18 °C night vs. 15 °C day/8 °C night) and K concentration (156 mg·L⁻¹ vs. 468 mg·L⁻¹) on the growth and Mg nutrition of different tomato cultivars (MF and JP) under hydroponic conditions. The experiment included eight treatments and each had eight replications. Two plants were planted for each replication in a pot, and all replications were placed randomly in an incubation chamber.

Mg ions were provided by MgSO₄·7H₂O (for sufficient Mg of 24 mg·L⁻¹) and K ions by KNO₃ (for optimum K of 156 mg·L⁻¹), and high K (468 mg·L⁻¹) was obtained using KNO₃ for the first 156 mg·L⁻¹ K and K₂SO₄ for the remaining amount of K. Concentrations of Mg, K, and other ions were formulated based on Yamazaki (1981) nutrient solution, prepared by dissolving analytical reagents in deionized water containing (in mg·L⁻¹) the following: Ca(NO₃)₂·4H₂O: 354, NH₄H₂PO₄: 76, Na₂Fe-EDTA: 16, H₃BO₃: 1.2, MnCl₂·4H₂O: 0.72, ZnSO₄·7H₂O: 0.09, CuSO₄·5H₂O: 0.04, and (NH₄)₆Mo₇O₁₂: 0.01. The nutrient solution was replaced every 5 d. The average pH was adjusted daily with 0.01 M NaOH and maintained at 6.5 ± 0.1, and the electrical conductivity of the solution was also monitored regularly to meet the requirement of the hydroponic culture.

Transplanted plants were grown in opaque plastic pots (15 cm in height × 35 cm in length × 15 cm in width, Yujing Agriculture Co., Ltd.) containing 7 L of nutrient solution at different K concentrations and covered with an opaque bubble plate. Two plants of each replication within the pot were planted 20 cm apart from each other. The pots were placed in an artificial growth chamber at an air temperature of 25 °C day/18 °C night (root-zone temperature: 21–22 °C) or 15 °C day/8 °C night (10–11 °C), with temperatures changed every 12 h. Humidity was maintained at 60% to 65% and photosynthetic photon flux density was controlled at 270 μmol·m⁻²·s⁻¹ for 12 h every day. Temperature and light were changed simultaneously. The nutrient solution was aerated using an oxygen pump for 4 h each day.

Sample collection and analysis of growth parameters. After 30 d of culture, tomato seedlings were harvested. Three replication

samples per measurement of each root parameter and five replication samples for determination of shoot growth (height, stem diameter, petiole number, and internode height) and nutrient concentration (K and Mg) were made. Roots of all plant replication samples were washed with deionized water and surface-dried with filter paper repeatedly. Plant height and internode height were measured with a ruler, stem diameter measured with a vernier caliper, and root volume determined according to the water displacement method (Gao, 2006).

Measurement of total and active absorption areas of roots. The method of Gao (2006) and Mu et al. (2006) was used to measure total and active absorption areas of roots. Briefly, the volumes of fresh root samples were measured firstly. Then, the roots were poured in three beakers (marked as 1, 2, and 3, and volumes were recorded as V_1 , V_2 , and V_3 , respectively) containing methylene blue solution (C) (Sinopharm Chemical Reagent Co., Ltd, Beijing, China). Then, the root samples were stained orderly with methylene blue solution for 90 s. After staining, the volume loss of the solution in the beakers was refilled with distilled water. The concentration of methylene blue solutions (C_1 , C_2 , and C_3) was measured at 660 nm using an ultraviolet-1200 spectrophotometer (Mapada Instruments, Shanghai, China).

The total absorption area (m²) was calculated as follows:

$$[(C - C_1) \times V_1 + (C - C_2) \times V_2] \times 1.1.$$

The active absorption area (m²) was calculated as follows:

$$[(C - C_3) \times V_3] \times 1.1,$$

where, C is the initial concentration (mg·mL⁻¹); C_1 , C_2 , and C_3 are the final concentration of methylene blue solution after soaking roots in three beakers (1, 2, and 3, respectively); V_1 , V_2 , and V_3 are the volume of methylene blue solution in the three beakers before soaking roots.

Specific surface area (m²·m⁻³) was calculated as the total absorption area/root volume.

Remaining plant samples were divided into shoots and roots. Each sample was deactivated at 105 °C in an oven for 30 min and then dried at 70 °C for 48 h to constant weight to determine the dry weight. Dry samples were crushed, passed through an 80-mesh sieve, and stored in sample vials until use.

K and Mg analysis. The shoot and root samples (0.5 g dry sample) were weighed in a crucible and then carbonized in an electric stove at a low heat. The crucible was then placed into a muffle furnace for 6 h of ashing at 550 °C. The ash was dissolved in nitric acid (1:1, v/v) and LaCl₃ added as a masking agent. Total Mg was analyzed by atomic absorption spectrophotometry (AAS, Z-2000; Hitachi High-Technologies Corporation, Shanghai, China) at a burner height of 7.5 mm and a wavelength of 285.2 nm and total K was determined by flame photometry. Total uptake of K (or Mg) was calculated as the sum of the dry biomass × nutrient

concentration of the shoots and roots, respectively.

Statistical analyses. Data were subjected to three-way analysis of variance (ANOVA) for main effects (T , temperature; K , K concentration; and C , cultivar), three first-order interactions ($T \times K$, $K \times C$, and $T \times C$), and one second-order interaction ($T \times K \times C$). Multiple comparisons of means were performed by Duncan's test at the 5% level following three-way ANOVA. Statistical analyses were carried out using SAS 8.1 (SAS Institute Inc., Cary, NC).

Results

Growth of shoot. Temperature significantly affected the growth of tomato (Tables 1 and 2). Compared with the control temperature (25/18 °C), plant height, petiole number, and internode height were significantly decreased by 25.2%, 26.2%, and 21.9%, respectively, under low temperature conditions (15/8 °C). Moreover, under a high K level, a decrease of 12.06%, 1.02%, and 8.0% and an increase of 14.62%, 11.76%, and 9.05% was observed under the control (25/18 °C) and low temperatures (15/8 °C), respectively, compared with control K treatment. These findings suggest that high K inhibits shoot growth at normal temperatures and facilitates growth at low temperatures. The mutual interaction of $T \times K \times C$ significantly affected the petiole number (Table 1). Overall, the effects of low temperature and high K on the shoot parameters were higher in JP than MF.

Absorption of root parameters. At low temperature, the total and the specific surface areas of roots increased by 32.2% and 23.7%, respectively, compared with the control temperature (Table 2). Meanwhile, no differences in root parameters were observed between K concentrations. Significant $T \times K$ interaction was observed on root volume and specific surface area (Table 1). Root volume and the specific surface area also differed significantly between the two cultivars, with significantly larger root volume and smaller specific surface area recorded in JP than MF.

Biomass. Compared with the control temperature, a significant decrease in total biomass (17.3%) and shoot biomass (24.1%) was observed under low temperature (Table 2), with a subsequent increase in root biomass. The root/shoot ratio was also significantly higher under low temperature compared with control temperature. By contrast, there were no significant differences in total biomass or the root/shoot ratio between K concentrations. Significant $T \times C$ interaction effects were observed on shoot biomass, with a subsequent influence on total biomass and root/shoot biomass ratio. Under a low temperature and high K, a decrease in biomass of 16.4% and 30.8% was observed in MF and JP, respectively.

K and Mg concentrations. At low temperatures, a significant increase in both Mg and K concentrations was observed in the shoots and roots (Table 3). Mg increased by 14.2%

Table 1. Results of three-way ANOVA for independent variables, including temperature (*T*), K concentration (*K*), and cultivar (*C*), and their interactions.

Parameter	<i>T</i>	<i>K</i>	<i>C</i>	<i>T</i> × <i>K</i>	<i>K</i> × <i>C</i>	<i>T</i> × <i>C</i>	<i>T</i> × <i>K</i> × <i>C</i>
Shoot growth							
Plant height	55.5**	0.09	6.98*	16.7**	0.34	3.24	0.66
Stem diameter	5.22	2.82	11.6**	0.84	0.24	11.0**	0.13
Petiole number	89.0**	1.68	2.77	2.77	0.03	1.68	7.70**
Internode height	29.9**	0.11	3.45	3.1	0.65	2.77	1.42
Root parameters							
Total absorption area	8.92**	0.36	0.12	0.77	0.56	0.02	0.14
Active absorption area	0.4	0.02	0.14	0.01	1.30	0.13	0.46
Volume	0.94	0.19	7.65	12.3**	1.10	0.31	0.24
Specific surface area	11.4**	2.19	12.5**	16.5**	0.02	0.41	0.08
Biomass							
Shoots	60.9**	0.19	3.35	3.8	0.00	8.84**	2.63
Roots	36.9**	3.77	2.08	0.66	1.42	0.04	1.13
Total	34.7**	0.01	4.03	3.92	0.09	6.97**	3.01
Root/shoot ratio	131.9**	3.31	0.63	0.12	1.56	5.17*	0.47
Nutrient concentrations and their ratio							
Mg in shoots	24.3**	5.13*	26.9**	1.53	1.14	8.59**	0.01
Mg in roots	37.2**	36.1**	0.85	5.18*	2.33	0.21	12.6**
K in shoots	119**	143**	6.25*	79.2**	1.37	0.22	3.55
K in roots	57.7**	47.2**	2.4	2.09	0.82	3.22	11.9**
K/Mg ratio in shoots	32.6**	95.2**	18.9**	43.8**	0.08	0.81	1.22
K/Mg ratio roots	23.5**	72.2**	4.80*	3.65	3.91	1.67	3.11
Nutrition uptake							
Mg in shoots	9.51**	4.29*	3.86	2.3	0.13	0.08	3.07
Mg in roots	71.7**	1.25	0.65	0.37	0.00	0.00	7.58*
Total Mg uptake	2.39	4.84*	3.13	1.87	0.12	0.08	4.70
K in shoots	12.7**	78.0**	6.39*	51.8**	1.20	4.11	7.65**
K in roots	150.9**	73.8**	6.68*	9.48**	2.17	1.90	14.8**
Total K uptake	25.3**	90.9**	7.53*	52.4**	0.71	4.45*	9.88**

* $P < 0.05$ and ** $P < 0.01$. MF = Gailiangmaofen; JP = Jinpeng No. 1; T_C = temperature at 25 °C day/18 °C night; T_L = temperature at 15 °C day/8 °C night; K_{156} = K concentration of 156 mg·L⁻¹; K_{468} = K concentration of 468 mg·L⁻¹; $T \times K$ = interaction between temperature and K concentration; $T \times C$ = interaction between temperature and cultivar; $K \times C$ = interaction between K concentration and cultivar; $T \times K \times C$ = interaction among temperature, K concentration, and cultivar.

Table 2. Effects of low temperature and high K concentration on growth and biomass of two tomato cultivars after 30 d of incubation.

Parameter	<i>T</i> (temperature)		<i>K</i> (K concn)		<i>C</i> (cultivar)	
	T_C (25/18 °C)	T_L (15/8 °C)	K_{156}	K_{468}	MF	JP
Shoot growth parameters						
Plant height (cm)	31.5 ± 1.07 a	23.6 ± 0.79 b	27.4 ± 1.64	27.7 ± 0.86	26.1 ± 1.22 b	29.0 ± 1.32 a
Stem diameter (cm)	0.514 ± 0.01 b	0.542 ± 0.01 a	0.517 ± 0.01	0.538 ± 0.01	0.549 ± 0.01 a	0.506 ± 0.04 b
Petiole number (no.)	9.75 ± 0.23 a	7.20 ± 0.20 b	8.30 ± 1.40	8.65 ± 0.32	8.70 ± 0.35	8.25 ± 0.37
Internode height (cm)	2.64 ± 0.09 a	2.07 ± 0.07 b	2.37 ± 0.12	2.34 ± 0.09	2.25 ± 0.12	2.45 ± 0.07
Root parameters						
Total absorption area (m ²)	2.36 ± 0.14 b	3.12 ± 0.17 a	2.81 ± 0.19	2.66 ± 0.19	2.69 ± 0.18	2.78 ± 0.20
Volume (cm ³)	6.30 ± 0.53	6.91 ± 0.62	6.47 ± 0.46	6.74 ± 0.69	5.73 ± 0.43 b	7.48 ± 0.61 a
Specific surface area (m ² ·m ⁻³)	0.38 ± 0.03 b	0.47 ± 0.03 a	0.45 ± 0.04	0.41 ± 0.02	0.47 ± 0.03 a	0.38 ± 0.03 b
Biomass (g dw)						
Total	2.48 ± 0.07 a	2.06 ± 0.05 b	2.27 ± 0.09	2.26 ± 0.07	2.19 ± 0.05	2.34 ± 0.09
Shoots	2.17 ± 0.07 a	1.65 ± 0.04 b	1.93 ± 0.09	1.89 ± 0.07	1.85 ± 0.06	1.97 ± 0.10
Roots	0.31 ± 0.01 b	0.41 ± 0.02 a	0.34 ± 0.01	0.37 ± 0.02	0.35 ± 0.01	0.37 ± 0.02
Root/shoot ratio	0.14 ± 0.01 b	0.25 ± 0.01 a	0.19 ± 0.01	0.20 ± 0.01	0.19 ± 0.01	0.20 ± 0.02

Means ± SE with different lowercase letters within a row of the same factor are significant differences by Duncan's multiple range tests following three-way ANOVA at the 5% level.

dw = dry weight; MF = Gailiangmaofen; JP = Jinpeng No. 1; T_C = temperature at 25 °C day/18 °C night; T_L = temperature at 15 °C day/8 °C night; K_{156} = K concentration of 156 mg·L⁻¹; K_{468} = K concentration of 468 mg·L⁻¹.

and 14.6% in the shoots and roots, respectively, whereas K increased by 57.1% and 49.4%, respectively. High K treatment caused an increase in K concentration in the shoots and roots but a decrease in Mg concentration of 5.92% and 12.4%, respectively; thus, a significant increase in K/Mg ratio was observed in the shoots and roots. In addition, a significant $T \times C$ interaction affected Mg concentration in shoots, with an increase in shoot Mg of 2.07% and 14.2% in MF and JP, respectively.

Mg and K uptake and translocation. K and Mg uptake was significantly affected by low temperature (Table 3). Compared with the control temperature, K uptake by

whole plant and the shoots increased by 19.8% and 26.9% under low temperatures, respectively. By contrast, Mg uptake increased by 48.6% in roots but decreased by 11.8% in shoots. Moreover, translocation of Mg from the roots to shoots decreased from 89.6% to 83.6%. High K caused a significant increase in K uptake by the whole plant but a decrease of 8.09% in Mg uptake by the shoots. Significant difference was observed for K uptake, but not for Mg uptake, between the two cultivars. There was a significant $T \times K$ interaction on K uptake, and Mg uptake in roots was significantly affected by $T \times K \times C$ interaction (Table 1).

Discussion

Effect of low temperature on tomato growth and Mg uptake. This study revealed that low temperature caused an increase in the shoot diameter, root absorption area, and specific surface area (Tables 1 and 2). This might be because of the adaptability mechanisms of tomato plants to avoid chilling injury, which include expansion of the root absorption area and slowing of respiration and decreasing water content in plant (Hund et al., 2007). Moreover, low temperature also caused a significant increase in K uptake in our study (Tables 1 and 3). Because K plays an incredible role in enabling plants

Table 3. Effects of low temperature and high K concentration on K and Mg concentrations and uptake of two tomato cultivars after 30 d of incubation.

Parameter	T (temperature)		K (K concn)		C (cultivar)	
	T _C (25/18 °C)	T _L (15/8 °C)	K ₁₅₆	K ₄₆₈	MF	JP
Nutrient concentration (mg·g ⁻¹ dw)						
Mg in shoots	7.19 b	8.21 a	7.93 a	7.46 b	8.23 a	7.16 b
Mg in roots	5.70 b	6.52 a	6.52 a	5.70 b	6.17	6.05
K in shoots	32.4 b	50.9 a	31.5 b	51.7 a	39.5 b	43.7 a
K in roots	23.1 b	34.5 a	23.7 b	33.9 a	27.7	29.9
K/Mg ratio in shoots	4.65 b	6.36 a	4.04 b	6.96 a	4.84 b	6.15 a
K/Mg ratio in roots	4.09 b	5.41 a	3.59 b	5.91 a	4.46 b	5.05 a
Nutrition uptake (mg/plant dw)						
Mg in shoots	15.3 a	13.5 b	15.3 a	13.0 b	15.2	13.9
Mg in roots	1.77 b	2.63 a	2.26	2.14	2.16	2.24
Total Mg uptake	17.1	16.2	17.6 a	15.2 b	17.17	16.1
K in shoots	70.6 b	84.6 a	60.2 b	95.0 a	72.6 b	82.6 a
K in roots	7.26 b	14.1 a	8.30 b	13.1 a	9.98 b	11.4 a
Total K uptake	77.8 b	98.7 a	68.5 b	108 a	82.6 b	94.0 a

Means with different lowercase letters within a row of the same factor are significant differences by Duncan's multiple range tests following three-way ANOVA at the 5% level.

dw = dry weight; MF = Gailiangmaofen; JP = Jinpeng No. 1; T_C = temperature at 25 °C day/18 °C night; T_L = temperature at 15 °C day/8 °C night; K₁₅₆ = K concentration of 156 mg·L⁻¹; K₄₆₈ = K concentration of 468 mg·L⁻¹.

to withstand low temperature stress, it further contributes to root vigor and the thickness of xylem vessel. K also improves the contents of starch and soluble proteins in plants (Marschner, 2012). Significant decrease in plant biomass and Mg uptake was observed in tomato plants exposed to low temperature for a long time (Tables 1–3). This was possibly due to the slowing down of metabolism and enzyme activities related to plant respiration because the respiration is mainly regulated by enzymatic reactions that are highly sensitive to temperature (Atkin and Tjoelker, 2003).

The effect of temperature on mineral nutrient uptake depends on the nutrient pathway. Active pathway is a temperature-dependent process, whereas passive pathway is less affected by temperature (Marschner, 2012). The pathway of Mg uptake remains controversial (Karley and White, 2009), with Mg entering the cytoplasm across the cytomembrane dependent on transporter protein (Verbruggen and Hermans, 2013), enzymatic activity of which is closely related to temperature (Peterson et al., 2007). This is perhaps one reason for the significant reduction in Mg uptake under low temperature.

In North China, the solar greenhouses are commonly not heated with additional energy, such as light or fossil fuel, during winter when temperature is very low. From November to December, winter tomato tends to be at the fruit enlargement stage, during which it requires abundant nutrients (Georgieva et al., 1980). Temperatures of 15 °C in the day and 8 °C or lower at night are common in solar greenhouses in the study region and could, therefore, be an important cause of Mg deficiency in tomato in this region.

Effect of high K on tomato growth and Mg uptake. Our results also showed that high K had no significant effect on tomato biomass at low temperatures (Tables 1 and 2). By contrast, high K caused a significant increase in K concentration and uptake but a significant decrease in Mg concentration in the shoots and roots (Tables 1 and 3). These findings are also consistent with other studies; for example, excessive K⁺ was found to

significantly inhibit Mg uptake in rice (Ding et al., 2006; Ding and Xu, 2011), maize (*Zea mays* L.) (Sadana, 2008), safflower (Farhat et al., 2013), apple trees (*Malus pumila* Mill.) (Vangpetersen, 1980), and green bean (*Pisum sativum* Linn.) (Huda et al., 2010). Competition between K and Mg uptake occurs because of the similar chemical properties of K⁺ and Mg²⁺ ions (Gransee and Führes, 2013), causing competition for uptake sites on the cell membrane (Marschner, 2012). Because K⁺ ions have a smaller hydraulic diameter, they occupy more adsorption sites, inhibiting Mg²⁺ absorption. Competition between K and Mg is, therefore, thought to occur largely in the roots (Ohno and Grunes, 1985).

Competition between K⁺ and Mg²⁺ also occurs during ion transport from the roots to shoots (Hannaway et al., 1982). In the present study, the K/Mg ratio in the shoots increased significantly under high K and was higher than that of the roots, suggesting that high K also inhibits the root to shoot transport of Mg in tomato. Although K and Mg are both highly mobile, they behave differently during xylem and phloem transport (Karley and White, 2009). Compared with K⁺, Mg²⁺ is more easily absorbed by parenchymal cells because of its high valence. When the K/Mg ratio becomes imbalanced because of high K concentrations, the transport rate of K⁺ may be far higher than that of Mg (Tromp and Vuure, 2010). Our study suggests, therefore, that competition between K and Mg occurs both during uptake by the roots and subsequent transport from the roots to shoots.

The Mg concentration in calcareous soil is high in solar greenhouse tomato production in North China. However, heavy K input in the form of manure and chemical fertilizer results in a significant increase in soil-available K to more than 600 mg·kg⁻¹, higher than the optimum concentration of available K in the soil (240–300 mg·kg⁻¹) (Chen et al., 2017; Gao et al., 2012). High K levels in the soil significantly alter the balance between K and Mg ions in greenhouse soil, resulting in a marked increase in the K/Mg ratio and a decrease in soil Mg activity (Chen et al.,

2013). It is possible; therefore, that excessive K input in solar greenhouses is another reason for Mg deficiency in tomato in calcareous soils. To mitigate the effects of Mg deficiency in tomato, we therefore recommend controlling K application rates in solar greenhouse.

Responses of different tomato cultivars to low temperatures and high K. Although growth, biomass, and Mg concentrations of the two tomato cultivars showed similar responses to low temperature and high K, the difference between the two was significant (Tables 1–3). Low temperature and high K treatment caused a decrease in biomass of MF and JP, whereas Mg concentrations increased. The growth of JP was more easily depressed, but it showed higher potential for Mg uptake than MF under double stress condition and is, therefore, at a lower risk of Mg deficiency (Tables 1–3). These findings highlight the importance of proper cultivar selection in reducing the occurrence of Mg deficiency in vegetables.

Effects of multifactor interactions on tomato Mg uptake. Low temperature had a significant negative effect on tomato growth and biomass, whereas high K and cultivar had no such effects. However, high K had a negative effect on both Mg concentration and Mg uptake (Tables 1–3). Under the double stress of low temperature and high K, no significant interactive effects were observed on Mg uptake; nonetheless, each had a superposed negative effect (Table 1). The extent of Mg deficiency is, therefore, enhanced as a result of the double stress of low temperature and high K during tomato production.

Conclusions

Low temperature decreased the total biomass and Mg uptake of two different tomato cultivars. On the contrary, low temperature significantly increased K uptake in tomato. At high K concentrations, the total absorption of Mg and its translocation from the roots to shoots were inhibited because of the

competition between K and Mg. A combination of low temperature and high K significantly reduced Mg uptake, and the responses were also dependent on tomato cultivars. Therefore, low temperature and high K may be the two factors inducing Mg deficiency in tomato.

Literature Cited

- Atkin, O.K. and M.G. Tjoelker. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends Plant Sci.* 8:343–351.
- Broadley, M.R. and P.J. White. 2010. Eats roots and leaves. Can edible horticultural crops address dietary calcium, magnesium and potassium deficiencies? *Proc. Nutr. Soc.* 69:601–612.
- Cakmak, I. 2013. Magnesium in crop production, food quality and human health. *Plant Soil* 368:1–4.
- Cakmak, I. and A.M. Yazici. 2010. Magnesium: A forgotten element in crop production. *Better Crops Plant Food* 94:23–25.
- Chen, S., Z. Yan, and Q. Chen. 2017. Estimating the potential to reduce potassium surplus in intensive vegetable fields of China. *Nutr. Cycl Agro.* 107:265–277.
- Chen, Z.J., W.Y. Zhao, and X.M. Zhang. 2013. Relationship of magnesium deficiency of tomato with salt composition and ion activities in greenhouse soil. *Acta Pedologica Sinica* 50:388–395 (in Chinese with English abstract).
- Clarke, S.J., K.J. Lamont, H.Y. Pan, L.A. Barry, A. Hall, and S.Y. Rogiers. 2015. Spring root-zone temperature regulates root growth, nutrient uptake and shoot growth dynamics in grapevines. *Austral. J. Grape Wine Res.* 21:479–489.
- Davies, J.N. and G.W. Winsor. 2010. Effect of nitrogen, phosphorus, potassium, magnesium and liming on the composition of tomato fruit. *J. Sci. Food Agr.* 18:459–466.
- Ding, Y. and G. Xu. 2011. Low magnesium with high potassium supply changes sugar partitioning and root growth pattern prior to visible magnesium deficiency in leaves of rice (*Oryza sativa* L.). *Amer. J. Plant Sci.* 2:601–608.
- Ding, Y., W. Luo, and G. Xu. 2006. Characterisation of magnesium nutrition and interaction of magnesium and potassium in rice. *Ann. Appl. Biol.* 149:111–123.
- Farhat, N., M. Rabhi, H. Falleh, K. Lengliz, A. Smaoui, C. Abdelly, M. Lachaal, and N. Karray-bouraoui. 2013. Interactive effects of excessive potassium and Mg deficiency on safflower. *Acta Physiol.* 35:2737–2745.
- Gao, J.F. 2006. The laboratory procedure for plant physiology, p. 58–62. Higher Education Press, Beijing, China (in Chinese).
- Gao, J.J., X.L. Bai, B. Zhou, and J.B. Zhou. 2012. Soil nutrient content and nutrient balances in newly-built solar greenhouses in northern China. *Nutr. Cycl. Agro.* 94:63–72.
- Georgieva, V., T. Kudrev, S. Genchev, V. Rankov, and G. Dimitrov. 1980. Microelement ration requirements in the nutrient substrate of determinate tomatoes. *Fiziologiya na Rasteniya*. 6:83–88.
- Gerendás, J. and H. Führs. 2013. The significance of magnesium for crop quality. *Plant Soil* 368:101–128.
- Gosselin, A. and M.J. Trudel. 1986. Root-zone temperature effects on pepper. *J. Amer. Soc. Hort. Sci.* 111:220–224.
- Gransee, A. and H. Führs. 2013. Magnesium mobility in soils as a challenge for soil and plant analysis, magnesium fertilization and root uptake under adverse growth conditions. *Plant Soil* 368:5–21.
- Guo, W.L., N. Hussain, Z.S. Liang, and D.F. Yang. 2016. Magnesium deficiency in plants: An urgent problem. *Crop J.* 4:83–91.
- Hannaway, D.B., L.P. Bush, and J.E. Leggett. 1982. Mineral composition of Kenhy tall fescue as affected by nutrient solution concentration of Mg and K. *J. Plant Nutr.* 5:137–151.
- Hao, X.M. and A.P. Papadopoulos. 2004. Effects of calcium and magnesium on plant growth biomass partitioning, and fruit yield of winter greenhouse tomato. *HortScience* 39:512–515.
- Hood, J.M. and H.A. Mills. 1994. Root-zone temperature affects nutrient uptake and growth of snapdragon. *J. Plant Nutr.* 17:279–291.
- Huang, G.B., Z.Z. Luo, L.L. Li, R.Z. Zhang, G.D. Li, L.Q. Cai, and J.H. Xie. 2012. Effects of stubble management on soil fertility and crop yield of rainfed area in western loess plateau, China. *Appl. Environ. Soil Sci.* 2012:1–9.
- Huda, A.I., U.A. Elbehairy, M. Eldesuki, M.O. Bakry, and A.F. Abouhadid. 2010. Response of green bean to fertilization with potassium and magnesium. *Intl. J. Biol. Sci.* 6:834–839.
- Hund, A., W. Richner, A. Soldati, Y. Fracheboud, and P. Stamp. 2007. Root morphology and photosynthetic performance of maize inbred lines at low temperature. *Eur. J. Agron.* 27:52–61.
- Hwang, W-H., J.R. Kang, J-S. Baek, S-H. An, J-H. Jeong, H-Y. Jeong, H-S. Lee, J-T. Yun, G-H. Lee, and K-J. Choi. 2016. Effect of active nutrient uptake on heading under low temperature in rice. *Korean J. Crop Sci.* 61:163–170.
- Karley, A.J. and P.J. White. 2009. Moving cationic minerals to edible tissues: Potassium, magnesium, calcium. *Curr. Opin. Plant Biol.* 12:291–298.
- Li, L., A.F. Tutone, R.S.M. Drummond, R.C. Gardner, and S. Luan. 2001. A novel family of magnesium transport genes in *Arabidopsis*. *Plant Cell* 13:2761–2775.
- Marschner, P. 2012. Marschner's mineral nutrition of higher plants. Elsevier Ltd., Amsterdam, The Netherlands.
- Mengel, K. and E.A. Kirkby. 2001. Principles of plant nutrition. 5th ed., p. 331–342. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Mu, Z., S. Zhang, L. Zhang, A. Liang, and Z. Liang. 2006. Hydraulic conductivity of whole root system is better than hydraulic conductivity of single root in correlation with the leaf water status of maize. *Bot. Stud.* 47:145–151.
- Nathalie, V. and H. Christian. 2013. Physiological and molecular responses to magnesium nutritional imbalance in plants. *Plant Soil* 368:87–99.
- Ohno, T. and D.L. Grunes. 1985. Potassium–magnesium interaction affecting nutrient uptake by wheat forage. *Soil Sci. Soc. Amer.* 49:685–690.
- Peterson, M.E., R.M. Daniel, M.J. Danson, and R. Eiselthal. 2007. The dependence of enzyme activity on temperature: Determination and validation of parameters. *Biochem. J.* 402:331–337.
- Pettersson, S. 1995. Low root zone temperature effects on net mineral nutrient uptake and distribution in barley (*Hordeum vulgare*). *J. Plant Physiol.* 145:459–464.
- Polat, S., Y. Ekmekci, and S. Terzioğlu. 2012. Investigation of antioxidant enzyme activities under low temperatures in wheat plants. *J. Biotechnol.* 161:41–42.
- Sadana, U. 2008. Nutrient influx and growth of maize (*Zea mays* L.) as influenced by interaction of potassium and magnesium. *Environ. Ecol.* 26:347–350.
- Shaul, O. 2002. Magnesium transport and function in plants: The tip of the iceberg. *Biometals* 15:307–321.
- Tachibana, S.C. 1988. Concentrations in roots and root xylem exudate of cucumber and figleaf gourd as affected by root temperature. *J. Jpn. Soc. Hort. Sci.* 56:417–425.
- Tromp, J. and J.V. Vuure. 2010. Accumulation of calcium, potassium and magnesium in apple fruits under various conditions of humidity. *Physiol. Plant.* 89:149–156.
- Vangpetersen, O. 1980. Calcium, potassium and magnesium nutrition and their interactions in 'cox's orange' apple trees. *Scientia Hort.* 12:153–161.
- Verbruggen, N. and C. Hermans. 2013. Physiological and molecular responses to magnesium nutritional imbalance in plants. *Plant Soil* 368:87–99.
- Wang, X., S. Geng, Y. Ma, D. Shi, C. Yang, and H. Wang. 2015. Growth, photosynthesis, solute accumulation, and ion balance of tomato plant under sodium- or potassium-salt stress and alkali stress. *Agron. J.* 65:927–928.
- White, J.W. and J.A. Biernbaum. 1984. Effects of root-zone heating on elemental composition of *Calceolaria*. *J. Amer. Soc. Hort. Sci.* 109:350–355.
- Yamazaki, K. 1981. Status and problems of nutrient solution cultivation in Japan. *Tokyo*. 35: 12–15 (in Japanese).
- Yan, B., T. Zhou, H.M. Wang, Z.J. Chen, J.Y. Cao, and S.M. Liu. 2016. The relationships between magnesium deficiency of tomato and cations balances in solar greenhouse soil. *Scientia Agr. Sinica* 49:3588–3596 (in Chinese with English abstract).
- Yu, G.C., M. Chai, and L.G. Jian. 2005. Study on molecular identification of tomato varieties. *Chin. Agr. Bull.* 21:84–89 (in Chinese with English abstract).
- Zia, M.S., M. Salim, M. Aslam, and M.A. Gill. 1994. Effect of low temperature of irrigation water on rice growth and nutrient uptake. *J. Agron. Crop Sci.* 173:22–31.