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

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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 Galiaiagmoaafen and Jimpeng 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 Fuhrs, 2013; Mengel and Kirby, 2001). By contrast, Mg deficiency is uncommon in calcareous soil because of abundant Mg in the parent materials (Broadley and White, 2010; Gransee and Fuhrs, 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 Kirby, 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 Fuhrs, 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 (Yu et al., 2005). 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 calcioarlia (Calendula officinalis L.) (White and Birnbaum, 1984) and snapdragon (Antirrhinium 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 Fuhrs, 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. Gailiaangmaaofen and S. lycopersicum L. cv. Jimpeng 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
Horticult 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. The mixture was stored in a muffle furnace for 6 h of ashing, then dried at 70 °C for 48 h to constant weight and ground. The ash was stored in sample vials until use.

**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 × K × 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 × 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 × 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%
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 × 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 the 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 × K interaction on K uptake, and Mg uptake in roots was significantly affected by T × C × K 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                  | $T_c$ (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 b   | 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 Mg uptake            | 77.8             | 100.0           | 68.5 b   | 149.0 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; $K_{156} =$ K concentration of 156 mg·L$^{-1}$; $K_{468} =$ 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, excess 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.) (Vang Petersen, 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 Mg$^{2+}$ (Gransee and Führs, 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 Mg$^{2+}$ absorption. Competition between K and Mg is, therefore, thought to occur largely in the roots (Ohno and Grunes, 1985).

Competition between K$^+$ and Mg$^{2+}$ 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$^+$, Mg$^{2+}$ 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. 8:343–349.

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. Yacizi. 2010. Magnesium: A forgotten element in crop production. Better Crops Plant Food 94:23–25.

Chen, Z.J., W.Y. Zhao, and X.M. Zhang. 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. Elbehairi, M. Eldesuki, M.O. Bakry, and A.F. Abouhadid. 2010. Response of green bean to fertilization with potassium and magnesium. Int. 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. Kim, and K-J. Choi. 2016. Effect of active nutrient uptake on heading under low temperature in rice. Korean J. Crop Sci. 61:163–170.

Kamyab, M., and S.M. Liu. 2016. The relationships between magnesium deficiency of tomato and cations and magnesium nutrition and their interactions in ‘cox’s orange’ apple trees. Scientia Hort. 212:151–163.

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).

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.