

THE ROLE OF POTASSIUM IN ALLEVIATING BORON TOXICITY AND COMBINED EFFECTS ON NUTRIENT CONTENTS IN PEPPER (*CAPSICUM ANNUUM* L.)

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Abstract

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As regards the interaction between boron (B) and potassium (K), there is limited our knowledge, and the nature of this complex interaction is still clearly unknown. The present study was based on the hypothesis that K might alleviate the detrimental effects of excess B. For this purpose, the effects of three levels of K (0, 200, and 400 mg kg⁻¹) and four levels of B (0, 5, 10, and 20 mg kg⁻¹) on the growth and mineral nutrient contents of pepper (*Capsicum annuum* L.) were investigated in greenhouse natural light conditions. Plant growth was dramatically restrained by excess B, while added K partially attenuated the inhibitory effect of excess B on plant growth. However, this effect was seen more in the shoots than in the roots. Along with increasing levels of B, additions of K decreased the B content of the pepper shoots. Added B increased the shoot contents of phosphorus (P), magnesium (Mg), calcium (Ca), manganese (Mn), iron (Fe), copper (Cu), and sodium (Na), while added K decreased the shoot contents of P, Mg, Ca, and Na. It was concluded that addition of K to the growing media can be beneficial in alleviating plant growth reduction and mineral imbalances caused by excess B.

Key words: *Capsicum annuum* L., boron toxicity, potassium, alleviation, nutrient content

Introduction

Boron (B), an essential nutrient for higher plants, is primarily absorbed by roots in the form of boric acid and, in connection with the transpiration rate, quickly relocates to the growing points (Brown and Shelp, 1997). The B uptake of plants is related to the B concentrations in the soil and the water consumption of the plant (Hu and Brown, 1997). It plays a vital role within the metabolism of nucleic acid, carbohydrate and protein, IAA, RNA and phenol (Loomis and Durst, 1992; Tanaka and Fujiwara, 2008). Furthermore, B is involved in membrane function, through complex formations with glycoprotein (Goldbach and Wimmer, 2007), and in the transport of sugar (Steven and Moreland, 1981). The range between B toxicity and B deficiency is very narrow, and both cause significant crop losses. Boron toxicity in arable lands has been

attributed to over-fertilization with B, B-contaminated irrigation water, surface mining, and formation of soil on marine sediment (Nable et al., 1997). Much enzyme activity is affected negatively by a toxic level of B in plants (Shkolnik, 1974), causing enhancement of membrane permeability and degradation of membrane integrity and membrane structure (Karabal et al., 2003).

Potassium (K) is called a non-constitutive element as it does not form components/ compounds in the plant system, but acts as a plant nutrient with a vital role in metabolism, including protein synthesis, plant water balance maintenance (Marschner, 2012), and transportation of water and nutrients. Potassium is absorbed by the roots in the form of K⁺ ions and exists as a free or absorptive-bound cation that can be displaced quite easily in plants (Lindhauer, 1985). Plants need K to regulate some vital activities such as enzyme activation, photosyn-

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thesis, osmo-regulation, stomatal movement, energy transfer, phloem transport, cation-anion balance and stress resistance (Marschner, 2012). Moreover, K essential functions as a transmitter of electrical charge in the plant cell and activate over 60 enzymes in the plant system as catalysts for many of the enzymatic processes in the plant (Mengel and Kirkby, 2001).

Boron affects other nutrient elements as well, specifically K, calcium (Ca), magnesium (Mg), and sodium (Na) (Mozafer, 1989). Due to the overlapping roles played by K and B in plant physiology, the effects of these two plant nutrients on plant development are significant. Both K and B serve as buffers and are necessary for the maintenance of conducting tissues (Mengel and Kirkby, 2001). Schon et al. (1990) reported that an optimal level of B increases K permeability in the cell membrane. Previous studies have investigated the relationship between K and toxic levels of B. Ismail (2003) emphasized the fact that B and K contents for both maize and sorghum increased with excess B treatments. Furthermore, excess B treatment increased B and K contents in radish (Tariq and Mott, 2006) and in rice (Kumar et al., 1981). Additionally, it was noted that B and K concentration of tomato fruit increased when increasing K treatments were applied to the soil together with foliar B (Huang and Snapp, 2009). The shoot and root growth of bean (Samet et al., 2013) and cucumber (Çikılı et al., 2013) were impressed by excess B, but added K to the growth media mitigated the detrimental effect of excess B. In the present study, the role of K on the alleviation of B toxicity was investigated in pepper, as a B-sensitive plant.

Material and Methods

Growth Conditions and Treatments: A pot culture experiment was conducted under natural light in greenhouse conditions in the summer of 2011. Pepper (*Capsicum annuum* L., cv. 'Yalova Çorbacı-12') seeds were germinated in a seedling viol filled with peat. Three-week-old seedlings were transplanted, one plant per pot containing 2 kg of air-dried soil. The properties of the soil used in the experiment were as follows: loam texture (sand: clay; 36: 22, by dry weight), pH (1:2.5 soil/water) 7.34, saturation extract of 0.51 dS/m EC, CaCO₃ 17.29 g/kg, organic carbon 6.25 g kg⁻¹ and total nitrogen 0.86 g kg⁻¹. The concentrations of NH₄OAc-extractable K, Na, Mg, and Ca were 100, 64, 124, and 2151 mg kg⁻¹, respectively. The NaHCO₃-available P concentration was 12.43 mg kg⁻¹ and hot water extractable-B was 1.64 mg kg⁻¹. The concentrations of DTPA-extractable Fe, Mn, Zn, and Cu were 24.28, 65.27, 2.09, and 1.17 mg kg⁻¹, respectively. The soil characteristics were determined according to methods detailed in Page et al. (1982).

Boron was applied as H₃BO₃ at levels of 0, 5, 10, and 20 mg kg⁻¹, and potassium as K₂SO₄ was added at levels of 0, 200, and 400 mg kg⁻¹. The treatments were replicated three times in a completely randomized factorial design. For basal fertilization, N and P, as NH₄NO₃ and NH₄H₂PO₄, were applied at 150 and 75 mg kg⁻¹, respectively, and mixed properly before planting out the seedlings. During the experimental period, the soil was watered with tap water and kept at approximately 70% of the field capacity.

Chemical Analyses: After six weeks, the shoots were carefully harvested, washed with running tap water, and then rinsed three times with de-ionized water. Similarly, the roots were carefully removed, cleaned and washed. All shoots and roots were oven dried at 70 °C for at least three days, and the dry weight (DW) was immediately measured. All materials were ground separately and kept for B, K and the other nutrient ion analyses. The samples were digested by using the dry-ash method for extraction. These nutrient ions were determined by ICP-OES (Perkin Elmer Optima 2100 DV).

The total uptakes in the shoots were calculated using the following formulation:

$$\text{Total K or B uptake} = DW_{\text{shoot}} \times [K \text{ or } B]_{\text{shoot}}$$

Statistical Analyses: The design structure was completely randomized. Obtained data were analyzed by ANOVA and the differences were compared by the LSD test ($P < 0.05$) and performed by using the MINITAB package program.

Results and Discussion

Plant Growth and Dry Weights: The combined effect of K and B on shoot and root dry weights and the membrane permeability of pepper are shown in Table 1. The effects of B ($P < 0.001$), K ($P < 0.001$) and their interaction ($P < 0.01$) on the DW in the shoots and roots were found to be statistically significant. The shoot dry weights were dramatically decreased with increasing B applications. However, with the application of 200 mg kg⁻¹ K to the soil, the shoot dry weights at all B levels were found to be more than two times higher than the control. Compared to the control, the average shoot DW increases for added 200 and 400 mg kg⁻¹ K to the soil were 116.4% and 62.3%, respectively. Similarly, decreases in root dry weights with added B levels were ameliorated by increasing K applications. According to the average of the K, the roots were influenced less from B toxicity than the shoots. This indicated that B transports rapidly to the upper organs and accumulates there (Camacho-Cristobal et al., 2008). The reduction of B toxicity effects on shoot and root growth has been studied in cultivated plants such as pepper (Yermiyahu et al., 2008), tomato and cucumber (Alpaslan and Gunes, 2001). Potassium

amelioration on shoot and root growth of plants under B-toxic conditions was also reported previously for cucumber (Cikili et al., 2013) and bean (Samet et al., 2013).

Boron and Potassium Contents and Uptakes of Plants:

The combined effect of K and B applications on the K and B contents of the shoot and their uptakes are given in Figure 1, and the high correlation between the applications and the contents is clearly visible. The accumulation of B in the leaves of the plant depends only on the B levels in the root media (Salinas et al., 1986). The shoot B content linearly increased depending on the increasing B levels, but dramatically decreased with increasing supplementations of K (Figure 1a). This might be explained as a protective effect resulting from the essential role of K in the physiological process, i.e., the maintenance of conducting tissues or cation-anion balances. Therefore, supplied K seemed to alleviate the toxic effects of B. The shoot K content of pepper was markedly increased by K applications, but with B applications, the shoot K contents did not follow a discernible trend (Figure 1b). In K-untreated plants and in the highest K-treated (400 mg kg⁻¹ K) plants, the shoot K contents significantly decreased with increasing B application, but increased at the level of 200 mg kg⁻¹ added K. Irrespective of the level of K treatment, however, supplied B significantly reduced the shoot K content of the plants. This effect might have been caused by K efflux out of the roots due to the detrimental effect of B toxicity on plasmalemma permeability. Similar findings have been reported in plants such as hot pepper in saline conditions (Supanjani, 2006), to-

mato (Alvarez-Tinaut et al., 1979), and maize (Leece, 1978). Furthermore, Wuding et al. (1987) noted that there was no difference in the K content of cotton leaves with B application. But, there are some evidence related to positive effects of excess B on K content of bean (Samet et al., 2013), cucumber (Cikili et al., 2013), tomato, pepper and cucumber (Dursun et al., 2010), Brussels sprouts (Turan et al., 2009), *Brassica rapa* (Tariq and Mott, 2006) and sunflower (Schon et al., 1990).

The effects of K and B interaction were significant for the K uptake ($P < 0.001$), but not significant for the B uptake of pepper. The B uptake in the shoots increased significantly with supplied K and B, except at the highest level of added B (Figure 1c). Carr et al. (2011) indicated that there was a linear relationship between B application and uptake. The B uptake in radish was enhanced with increased applications of B, as reported by Tariq and Mott (2006). The shoot uptake of K increased expectedly with additions of K, while it decreased significantly with additions of B (Figure 1d). The increment in the K uptake of the plants was greater at a low level of K (200 mg kg⁻¹) than at a high K (400 mg kg⁻¹) level. This reduction of growth might be due to an ion imbalance arising from an excess amount of K in the growing medium. Davis et al. (2003) studied the effects of B in tomato and reported that the addition of B increased growth and the uptake of K and B.

Mineral Nutrient Contents of Plants: The contents of phosphorus P, Ca, Mg, and Na in the pepper shoots were influenced by the increasing of both B and K (Figure 2). The

Table 1
The combined effects of B and K on shoot and root dry weight of pepper

Added K, mg kg ⁻¹	Added B, mg kg ⁻¹				Mean
	0	5	10	20	
Shoot dry weight, g plant⁻¹					
0	1.15 ±0.13	0.67 ±0.03	0.59 ±0.09	0.03 ±0.00	0.61 ±0.08
200	2.40 ±0.08	1.58 ±0.17	1.17 ±0.05	0.12 ±0.01	1.32 ±0.08
400	1.52 ±0.16	1.35 ±0.23	1.00 ±0.07	0.10 ±0.03	0.99 ±0.12
Mean	1.69 ±0.20	1.20 ±0.16	0.92 ±0.09	0.08 ±0.02	
ANOVA	B***	K***	BxK**		
LSD _{0.05}	B: 0.188	K: 0.163	BxK: 0.326		
Root dry weight, g plant⁻¹					
0	0.48 ±0.01	0.33 ±0.02	0.21 ±0.02	0.18 ±0.02	0.30 ±0.08
200	0.92 ±0.11	0.52 ±0.05	0.32 ±0.01	0.03 ±0.00	0.45 ±0.10
400	0.46 ±0.03	0.41 ±0.05	0.30 ±0.01	0.06 ±0.01	0.31 ±0.05
Mean	0.62 ±0.08	0.42 ±0.03	0.27 ±0.02	0.09 ±0.01	
ANOVA	B***	K***	BxK**		
LSD _{0.05}	B: 0.066	K: 0.057	BxK: 0.114		

Values are means of three replicates (Mean ±SE, $n = 3$). LSD_{0.05} indicates significant differences according to Duncan's Multiple Range Test ($P < 0.05$). ANOVA shows significant difference at: *** $P < 0.001$ and ** $P < 0.01$.

interaction of B and K had a significant effect on the shoot P and Mg contents ($P < 0.01$) and the shoot Na content ($P < 0.001$), but not on the shoot Ca content. The shoot P and Mg contents with increases of both B and K varied from 2.06 - 3.10 mg g⁻¹ and 2.81 - 4.83 mg/g, respectively (Figure 2a and 2c). The shoot P and Mg contents increased dramatically with supplied B, but decreased with supplied K. These changes in shoot nutrient contents might have occurred as nutrient absorption increased due to the detrimental effect of excess B on plasmalemma permeability. These results agree with the previous findings of Sotiropoulos et al. (2006), who reported that the P, Ca and Mg concentrations of apple were increased by increasing B concentration of the culture medium from 0.1 to 6 mM B. Furthermore, Huang and Snapp (2009) observed that both foliar-applied B and increasing soil K levels enhanced the K content and also slightly increased the tissue P, Ca, and Mg concentration in tomato. Moreover, Dursun et al. (2010) reported that B application increased the tissue P and K concentration of tomato, pepper, and cucumber, but decreased the tissue Ca and Mg.

The shoot Ca content with the increasing of both B and K ranged from 9.01 - 16.51 mg g⁻¹, respectively. Regardless

of each separate level of application, the Ca content declined with supplied K, while it accrued with supplied B (Figure 2a). As K, Ca, and Mg compete with each other, the addition of any one of them in the growth medium will reduce the uptake rate of the other two (Mengel and Kirkby 2001). Tanaka (1967) reported that the uptakes of Ca and B were decreased when K was increased in growth media. Additionally, Alvarez-Tinaut et al. (1979) explained that the uptake and translocation of P, K, and Ca was significantly stimulated by excess B in hydroponically-grown tomato. The shoot Na content varied from 280 - 1450 µg g⁻¹ with the increasing of both B and K. Although the Na content followed no discernible pattern, it was remarkably reduced with added K, while added B increased the shoot Na content (Figure 2d). The reductions of the Na content with added K might result from the antagonistic relationship between K and Na, as El-Kholi (1961) observed that, with levels of excess B, an antagonism existed between Na and K. The increment in P, K and Na contents with applied B was noted in barley (Singh and Singh, 1984). Moreover, celery and lettuce plants in a sand culture accumulated more K with supplied B, but less Ca, Mg and Na, as reported by Francois (1988).

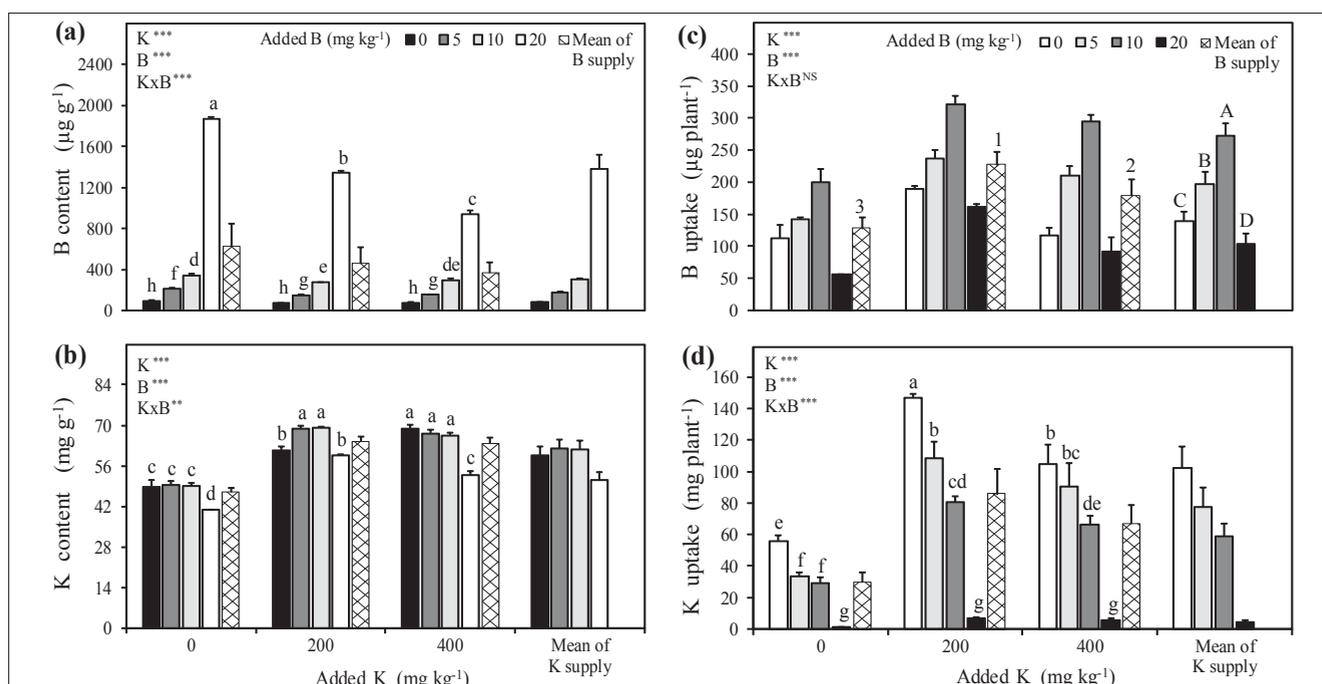


Fig. 1. The combined effects of potassium and boron on the contents and uptakes of B and K in pepper shoots

Values are means of three replicates (Mean ±SE, $n = 3$) and the bars represent their standard errors. Different letters above each column represent significant differences based on Duncan's Multiple Range Test ($P < 0.05$). It indicates that small letters for the combined effects of supplied B and K, capital letters for mean of B supply, and numbers for mean of K supply are the statistical differences. Significant difference is shown at: ** $P < 0.01$, *** $P < 0.001$, ^{NS} not significant

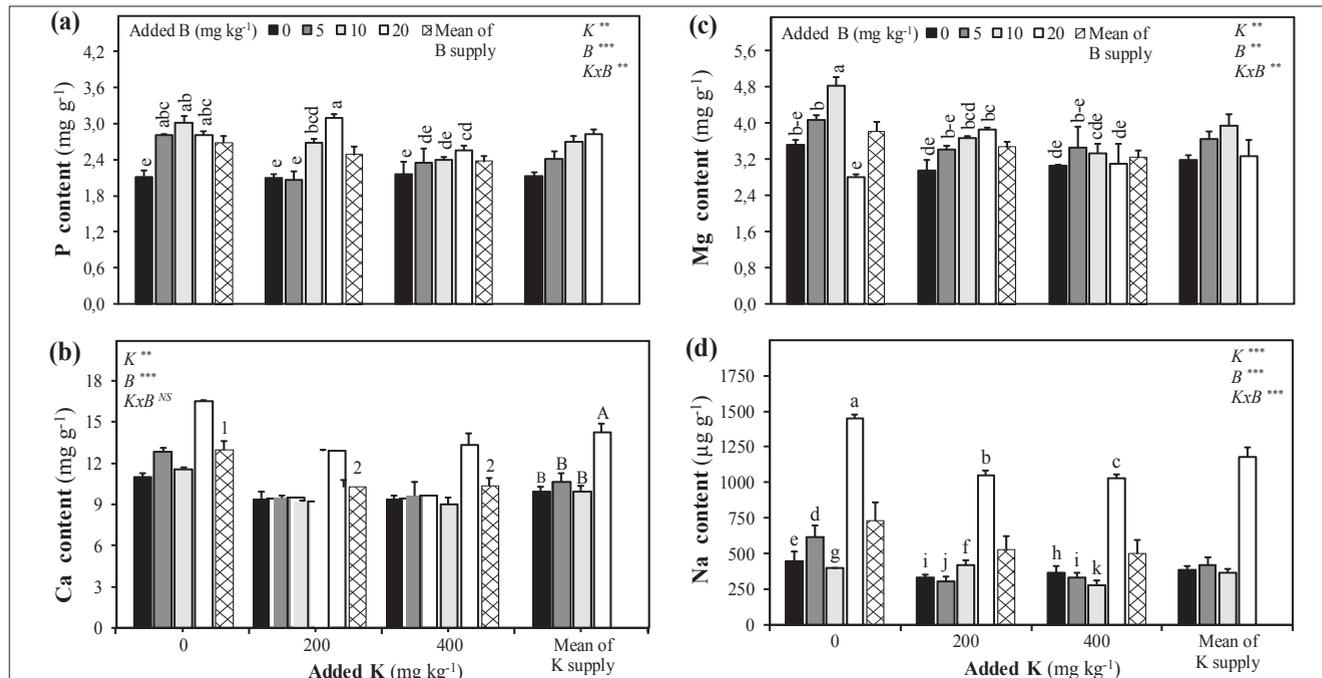


Fig. 2. The combined effects of potassium and boron on P, Ca, Mg and Na contents of pepper shoots

Values are means of three replicates (Mean \pm SE, $n = 3$) and the bars represent their standard errors. Different letters above each column represent significant differences based on Duncan's Multiple Range Test ($P < 0.05$). It indicates that small letters for the combined effects of supplied B and K, capital letters for mean of B supply, and numbers for mean of K supply are the statistical differences. Significant difference is shown at: ** $P < 0.01$, *** $P < 0.001$, ^{NS} not significant

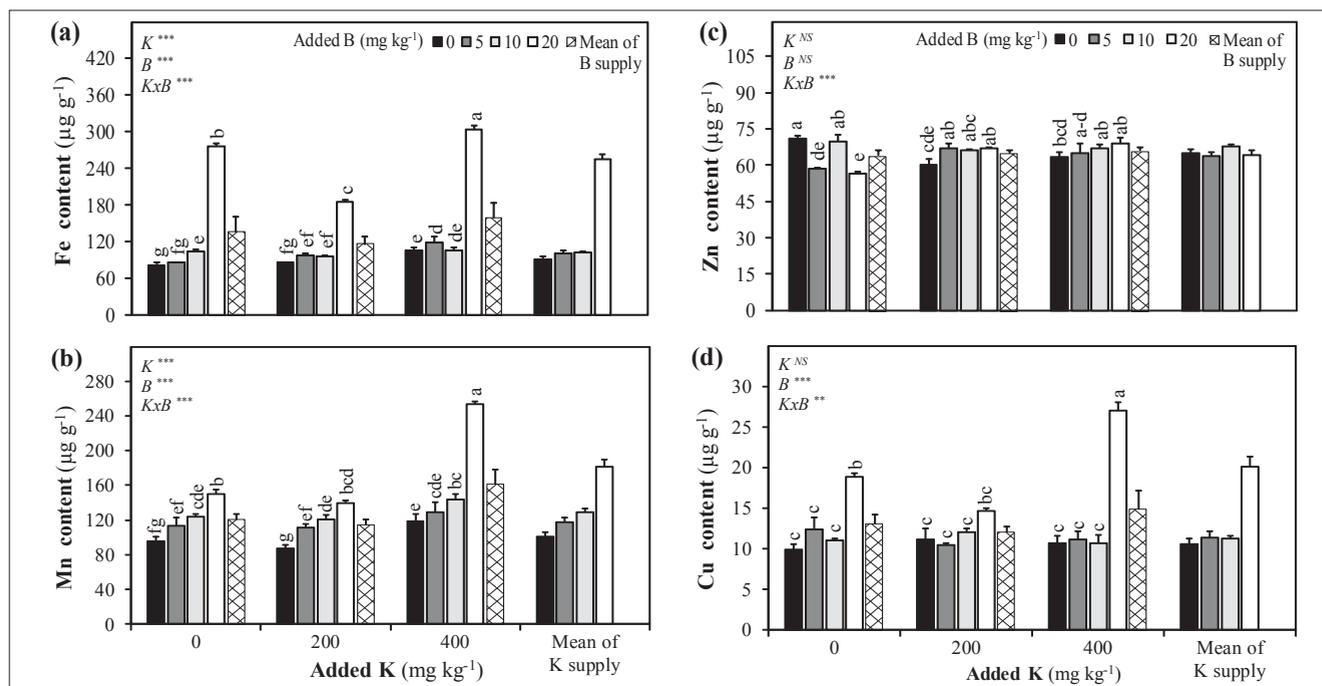


Fig. 3. The combined effects of potassium and boron on Fe, Mn, Zn, and Cu contents of pepper shoots

Values are means of three replicates (Mean \pm SE, $n = 3$) and the bars represent their standard errors. Different letters above each column represent significant differences based on Duncan's Multiple Range Test ($P < 0.05$). It indicates that small letters for the combined effects of supplied B and K. Significant difference is shown at: ** $P < 0.01$, *** $P < 0.001$, ^{NS} not significant

The contents of iron (Fe), manganese (Mn), zinc (Zn), and copper (Cu) in the pepper shoots were influenced by the increasing of both B and K (Figure 3). The interaction of B and K had a significant effect on the shoot contents of Fe, Mn, Zn ($P < 0.001$), and Cu ($P < 0.01$). The shoot Fe and Cu contents ranged from 81.5 - 304.2 $\mu\text{g g}^{-1}$ (Figure 3a), and 9.9 - 27.0 $\mu\text{g g}^{-1}$ (Figure 3d), respectively, with increasing levels of both B and K. Added B significantly enhanced the Fe and Cu contents. This might be an accumulative effect due to the reduction of plant growth resulting from B toxicity. Increments in concentrations of Fe and Cu with the increasing of B have been observed previously in kiwifruit (Sotiropoulos et al., 1999) and groundnut (Patel and Golakiya, 1986); however, regardless of the levels of supplied B, no discernible trend was observed with added K.

The Mn content of the plant shoots was significantly enhanced with increasing levels of both B and K and varied from 86.8 - 253.8 $\mu\text{g g}^{-1}$ (Figure 3b). The shoot Zn content ranged from 56.3 - 71.1 $\mu\text{g g}^{-1}$ with the increasing of both B and K (Figure 3c). In K-untreated plants, the shoot Zn content decreased with additions of B, but without any notable pattern of decline (Figure 3c). In K-treated plants, however, slight increases were observed in the Zn content. In agreement with these findings, similar results were achieved by Sotiropoulos et al. (1999), who reported that the concentrations of Zn and Cu increased with increasing B in kiwifruit. Turan et al. (2009) mentioned increases in the tissue Fe, Mn, Zn, and Cu contents of Brussels sprouts resulting from B application. Tariq and Mott (2006) also found increments in Zn and Cu concentrations, but decreases in Fe and Mn concentrations in radish. They also found that low and high levels of added B had interactive effects on the concentration and total uptake of micronutrients.

Conclusion

This study demonstrated that supplied K partially attenuated the inhibitory effect of excess B on plant growth. However, this effect was seen more in the shoots of the plants than in the roots. With increasing levels of B, added K decreased the B content of the shoots. Added B increased the shoot contents of P, Mg, Ca, Mn, Fe, Cu, and Na, while added K decreased the shoot contents of P, Mg, Ca, and Na. Subsequently, addition of K to the growing media can be beneficial in alleviating plant growth reduction and mineral imbalances caused by excess B.

References

- Alpaslan, M. and A. Gunes, 2001. Interactive effects of boron and salinity stress on the growth, membrane permeability, and mineral composition of tomato and cucumber plants. *Plant & Soil*, **236**: 123-128.
- Alvarez-Tinaut, M. C., A. Leal, I. Agui and L. Recalde-Martinez, 1979. Physiological effects of B-Mn interaction in tomato plants. II. The uptake and translocation of macro elements. *Analse de Edafologia y Agrobiologica*, **38**: 991-1012.
- Brown P. H. and B. J. Shelp, 1997. Boron mobility in plants. *Plant and Soil*, **193**: 85-101.
- Camancho-Cristobal, J. J., J. Rexach and A. Gonzales-Fontes, 2008. Boron in plants: Deficiency and toxicity. *Journal of Integrative Plant Biology*, **50** (10): 1247-1255.
- Carr, C.E., W. Lindemann, R. Flynn and R. Steiner, 2011. Boron fertilization of Chile pepper under greenhouse conditions. *Western Nutrient Management Conference*, **9**: 116-121.
- Cikili, Y., H. Samet, and S. Dursun, 2013. Effects of potassium treatment on alleviation of boron toxicity in cucumber plant (*Cucumis sativus* L.). *Soil-Water Journal*, **2**(2-1): 719-726.
- Davis, J. M., D. C. Sanders, P. V. Nelson, L. Lengnick and W. J. Sperry, 2003. Boron improves growth, yield, quality, and nutrient content of tomato. *Journal of the American Society for Horticultural Science*, **128**: 441-446.
- Dursun, A., M. Turan, M. Ekinci, A. Gunes, N. Ataoglu, A. Esringu and E.Yildirim, 2010. Effects of boron fertilizer on tomato, pepper, and cucumber yields and chemical composition. *Communications in Soil Science and Plant Analysis*, **41**: 1576-1593.
- El-Kholi, A. F., 1961. An experimental study of the influence of the microelements on the uptake of macroelements by plants. *Soils & Fertilizer*, **24**: 2642.
- Francois, L. E., 1988. Yield and quality responses of celery and crisp head lettuce to excess boron. *Journal of the American Society for Horticultural Science*, **113**: 538-542.
- Goldbach, H. E. and M. Wimmer, 2007. Boron in plants and animals: Is there a role beyond cell-wall structure? *Journal of Plant Nutrition & Soil Science*, **170**: 39-48.
- Hu, H. and P. H. Brown, 1997. Absorption of boron by plant roots. *Plant & Soil*, **193**: 49-58.
- Huang, J. and S.S. Snapp, 2009. Potassium and boron nutrition enhance fruit quality in Midwest fresh market tomatoes. *Communications in Soil Science & Plant Analysis*, **40**: 1937-1952.
- Ismail, A. M., 2003. Response of maize and sorghum to excess boron and salinity. *Biologia Plantarum*, **47** (2): 313-316.
- Karabal, E., M. Yucel and H. A. Oktem, 2003. Antioxidant responses of tolerant and sensitive barley cultivars to boron toxicity. *Plant Science*, **164**: 925-933.
- Kumar, S., B. R. Arora and H. S. Hundal, 1981. Potassium-boron synergism in the nutrition of rice (*Oryza sativa* L.). *Journal of the Indian Society of Soil Science*, **29**: 563-564.
- Leece, D. R., 1978. Effects of boron on the physiological activity of zinc in maize. *Australian Journal of Agricultural Research*, **29**: 739-749.
- Lindhauer, M. G., 1985. The role of potassium in the plant with emphasis on stress conditions (water, temperature, salinity). In: *Proceedings of the Potassium Symposium*. Department of Agriculture and Water Supply, International Potash Institute and Fertility Society of South Africa. Pretoria, October 1985. p. 95-113.

- Loomis, W.D. and R. W. Durst**, 1992. Chemistry and biology of boron. *Biofactors*, **3**: 229-239.
- Marschner, H.**, 2012. Marschner's Mineral Nutrition of Higher Plants. 3rd edition. *Academic Press, London*. pp. 178-189.
- Mengel, K. and E. A. Kirkby**, 2001. Principles of Plant Nutrition, 5th edition. *Dordrecht: Kluwer Academic Publishers*. 849 pp.
- Mozafar, A.**, 1989. Boron effect on mineral nutrition of maize. *Agronomy Journal*, **81**: 285-290.
- Nable, R.O., G. S. Banuelos and J. G. Paull**, 1997. Boron toxicity. *Plant & Soil*, **193**: 181-198.
- Page, A., R. Miller and D. Keeney**, 1982. Methods of soil analysis. *American Society of Agronomy, Inc., Madison WI, USA*.
- Patel, M. S. and B. A. Golakiya**, 1986. Effect of calcium carbonate and boron application on yield and nutrient uptake by groundnut. *Journal of the Indian Society of Soil Science*, **84**: 815-820.
- Salinas, R., A. Cerda and V. Martinez**, 1986. The interactive effects of boron and macronutrients (P, K, Ca and Mg) on pod yield and chemical composition of pea (*Pisum sativum* L.). *Journal of Horticultural Science & Biotechnology*, **61**: 343-347.
- Samet, H., Y. Cikili, and S. Dursun**, 2013. Interactive effects of boron and potassium on the growth and mineral composition of bean (*Phaseolus vulgaris* L.). *Soil-Water Journal*, **2**(2-1): 690-696.
- Schon, M.K., A. Novacky and D. G. Blevins**, 1990. Boron induces hyperpolarization of sunflower root cell membranes and increases membrane permeability to K⁺. *Plant Physiology*, **93**: 566-571.
- Shkolnik, M.Y.**, 1974. General conception of physiological role of boron in plants. *Plant Physiology*, **21**: 174-186.
- Singh, V. and S. P. Singh**, 1984. Effect of applied boron on nutrients and uptake by barley crop. *Current Agriculture*, **8**: 86-90.
- Sotiropoulos, T. E., A. Molassiotis, D. Almaliotis, G. Mouhtaridou, K. Dimassi, I. Therios and G. Diamantidis**, 2006. Growth, nutritional status, chlorophyll content, and antioxidant responses of the apple rootstock MM 111 shoots cultured under high boron concentrations in vitro. *Journal of Plant Nutrition*, **29** (3): 575-583.
- Sotiropoulos, T. E., N. Ioannis, K. Therios and N. Dimassi**, 1999. Calcium application as a means to improve tolerance of kiwifruit (*Actinidia deliciosa* L.) to boron toxicity. *Scientia Horticulturae*, **81** (4): 443-449.
- Steven, C. H. and D. E. Moreland**, 1981. Co-transport of Potassium and Sugar across the Plasmalemma of Mesophyll Protoplasts. *Plant Physiology*, **67**: 163-169.
- Supanjani, K. D. L.**, 2006. Hot pepper response to interactive effects of salinity and boron. *Plant, Soil & Environment*, **52** (5): 227-233.
- Tanaka, H.**, 1967. Boron absorption by crop plants as affected by other nutrients of the medium. *Soil Science & Plant Nutrition*, **13** (2): 41-44.
- Tanaka, M. and T. Fujiwara**, 2008. Physiological roles and transport mechanisms of boron: Perspectives from plants. *Pflugers Archiv - European Journal of Physiology*, **456**: 671-677.
- Tariq, M. and C. J. B. Mott**, 2006. Effect of applied boron on the accumulation of cations and their ratios to boron in radish (*Raphanus sativus* L.). *Soil & Environment*, **25** (1): 40-47.
- Turan, M., A. Dursun, N. Ataoglu, A. Gunes, M. Ekinci, T. Oztas, Q. M. Ketterings and Y. M. Huang**, 2009. Yield and chemical composition of Brussels sprout (*Brassica oleracea* L. gemmifera) as affected by boron management. *Horticultural Science*, **44** (1): 176-182.
- Wuding, L., P. Meimei and W. Lishu**, 1987. Interaction between boron and potassium in cotton nutrition. *Acta Pedologica Sinica*, **24**: 43-50.
- Yermiyahu, U., A. Ben-Gal, R. Keren and R. J. Reid**, 2008. Combined effect of salinity and excess boron on plant growth and yield. *Plant & Soil*, **304**: 73-87.

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