

# RELATIONS BETWEEN MN CONCENTRATION AND YIELD, NUTRIENT, WATER STATUS, AND GAS EXCHANGE PARAMETERS OF TOMATO

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Nutrition is one of the most important factors influencing quantitative and qualitative plant yield. This study examined the effect of manganese (Mn) in nutrient solution on photosynthetic activity parameters, and the relations between photosynthetic activity parameters, yield and plant nutrient status in tomato (*Solanum lycopersicum* L.). Mn supplementation significantly modified the nutrient content of leaves. Macronutrient content varied less than micronutrient content. The optimal Mn concentration differed between the studied cultivars. Both Mn deficit and Mn excess caused a decrease of tomato yield. Gas exchange parameters, relative water content (RWC) and specific leaf area (SLA) were measured in fully expanded tomato leaves. Certain levels of Mn were found to be needed for proper plant function and future yield, and toxic effects of excess Mn were noted. Changes in  $P_N$  (net photosynthetic rate) were found to be the first signal of plant response to higher Mn supply, while yield was as for optimal Mn concentrations. Under Mn treatment, uptake of some nutrients increased. A higher level of absorbed Mg led to a higher photosynthesis rate and increased stomatal opening.  $P_N$  and  $g_s$  (stomatal conductance) also increased, while  $C_i$  (intercellular  $CO_2$  concentration) decreased, indicating proper  $CO_2$  consumption during the assimilation process.

**Key words:** Macroelement, microelement, *Solanum lycopersicum* L., photosynthetic activity, manganese stress.

## INTRODUCTION

Manganese (Mn) is a metallic micronutrient and also a heavy metal (atomic mass 54.93). Mn plays important roles in plant physiology as a building block of photosynthetic proteins, lignins, flavonoids and several enzymes (Lidon et al., 2004; Ducic and Polle, 2005; Humphries et al., 2007). Mn significantly influences photosynthesis. A deficit of it disturbs photosystem II (PSII) activity but an excess may damage the photosynthetic apparatus, significantly reducing chlorophyll content in leaves (Millaleo et al., 2010; Lee et al., 2011). An imbalance of Mn can disturb the uptake of other nutrients such as calcium, magnesium, iron, zinc (Foy et al., 1981; Fleming, 1989; Kazda and Znacek, 1989; Shenker et al., 2004; Lee et al., 2011), phosphorus, potassium and sodium (Kasraei et al., 1996). Galvez et al. (1989) reported that increased levels of Mn treatment reduced the

uptake of potassium, calcium, magnesium, zinc, copper and silicon. A natural mechanism against Mn stress in plant organisms is to accumulate it at cell sites that are relatively inactive physiologically (Horst, 1988). On the other hand, there was found a positive influence of Mn treatment on the content of phosphorus in plant tissue (Clark, 1982; Galvez et al., 1989). A number of authors have reported that under Mn deficiency in plants, cell metabolism cannot efficiently control the excess formation of various oxygen radicals, leading to oxidative damage (Cakmak and Marschner, 1988, 1992; Tanaka et al., 1995; Yu et al., 1998; Yu and Rengel, 1999). The Mn level also significantly influences plant yield (Shenker et al., 2004; Dragišić Maksimovic et al., 2007; Savvas et al., 2009; Kleiber, 2014).

**Abbreviations:**  $C_i$  – intercellular  $CO_2$  concentration;  $E$  – transpiration rate;  $g_s$  – stomatal conductance;  $P_N$  – net photosynthetic rate; RWC – relative water content; SLA – specific leaf area

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Some effects of Mn on plant functioning are insufficiently studied. Here we examined the effect of various Mn concentrations in nutrient solution on photosynthetic activity parameters, assessed the differences between two tomato cultivars in response to Mn concentrations, and analyzed the relations between photosynthetic activity parameters and tomato yield, as well as macro- and microelement (including Mn) concentrations in leaves.

## MATERIALS AND METHODS

### PLANTS AND CULTIVATION

The experiments were conducted in 2008–2012 (March–September) in a greenhouse of the Department of Plant Nutrition, Poznań University of Life Sciences. The greenhouse has climate control, shading and energy-saving curtain systems. Mn in nutrient solution at concentrations ranging from 0.06 to 19.2 mg·dm<sup>-3</sup> was used to treat two tomato cultivars: *Solanum lycopersicum* L. cv. Alboney F<sub>1</sub> (Enza Zaden) and cv. Emotion F<sub>1</sub> (S&G). The plants were grown in standard rockwool (Grodan; 100 × 15 × 7.5 cm; V 11.25 dm<sup>3</sup>; 60 kg m<sup>-3</sup>), 2.5 plants per m<sup>2</sup>. The experiments used a randomized complete block design in 4 replicates.

Plants were grown using fertigation in a closed system without recirculation of the nutrient solution, which contained (mg dm<sup>-3</sup>): N-NH<sub>4</sub> 2.2, N-NO<sub>3</sub> 230, P 50, K 430, Ca 145, Mg 65, Cl 35, S-SO<sub>4</sub> 120, Fe 2.48, Zn 0.50 and Cu 0.07, pH 5.50, EC 3.00 mS cm<sup>-1</sup>. Solution of manganese sourced from analytical-grade manganese II sulfate monohydrate was prepared and added individually to particular tanks in the following treatments (mg Mn dm<sup>-3</sup>, concentrations on the day of dilution of nutrient solution for the main tank): 0.06 – without Mn addition; 0.3, 0.6, 1.2 (2008–2011, Experiment I); 2.4, 4.8, 9.6, 19.2 (2012, Experiment II). The respective treatments are denoted Mn-0/Control, Mn-0.3, Mn-0.6, Mn-1.2, Mn-2.4, Mn-4.8, Mn-9.6 and Mn-19.2. The fertigation system was computer-controlled. During intensive growth and yield (June–August), daily consumption of nutrient solution was 3.0–3.5 dm<sup>3</sup> daily per plant, in 10–20 single doses applying a 20–30% drip of excess nutrient solution from the beds.

### CHEMICAL ANALYSES OF LEAVES

In the course of the experiments, samples of index parts (8<sup>th</sup>–9<sup>th</sup> fully expanded leaves counting from the apex) were collected at monthly intervals (June 15, July 15, August 16). Plant material was dried at 45–50°C and then ground. For assays of total N, P, K, Ca and Mg the plant material was mineralized in concentrated sulfuric acid (IUNG, 1972). After min-

eralization of the plant samples, chemical analyses were performed using the following methods: total N according to Kjeldahl in a Parnas-Wagner distillation apparatus, P by colorimetry with ammonium molybdate, and K, Ca and Mg by AAS with a Carl Zeiss Jena spectrometer (Thornwood, NY, USA). For determinations of total Fe, Mn, Zn and Cu the plant material was mineralized in a mixture of dioxonitric and tetraoxochloric acids (3:1 v/v) and then analyzed by AAS.

### GAS EXCHANGE MEASUREMENTS

A CI 340aa handheld photosynthesis system (CID BIOSCIENCE Inc., Camas, USA) was used to measure net photosynthetic rate ( $P_N$ ), stomatal conductance ( $g_s$ ), transpiration rate ( $E$ ) and intercellular CO<sub>2</sub> ( $C_i$ ) concentration, under the following constant conditions in the leaf chamber: CO<sub>2</sub> inflow concentration [390 μmol (CO<sub>2</sub>) mol<sup>-1</sup>], photosynthetic photon flux density (PPFD) 1000 μmol (photon) m<sup>-2</sup> s<sup>-1</sup>, chamber temperature 25°C, and relative humidity 40±3%. Analyses were performed on fully expanded leaves (9<sup>th</sup> one from the plant apex) showing no mechanical injury, during the full generative stage. Five plants were used for these analyses.

Specific leaf area (SLA) is a parameter indicating leaf thickness. It is the ratio of leaf area to leaf dry weight:

$$\text{SLA} = \text{leaf area/leaf dry matter content} \\ [\text{cm}^2 \text{mg}^{-1} \text{d.m.}]$$

If the leaf is thicker the value is lower. Leaf material was taken at the required times: minimum 2–3 h after sunrise and maximum 3–4 h before sunset (Garnier et al., 2001).

Relative water content was calculated as follows:

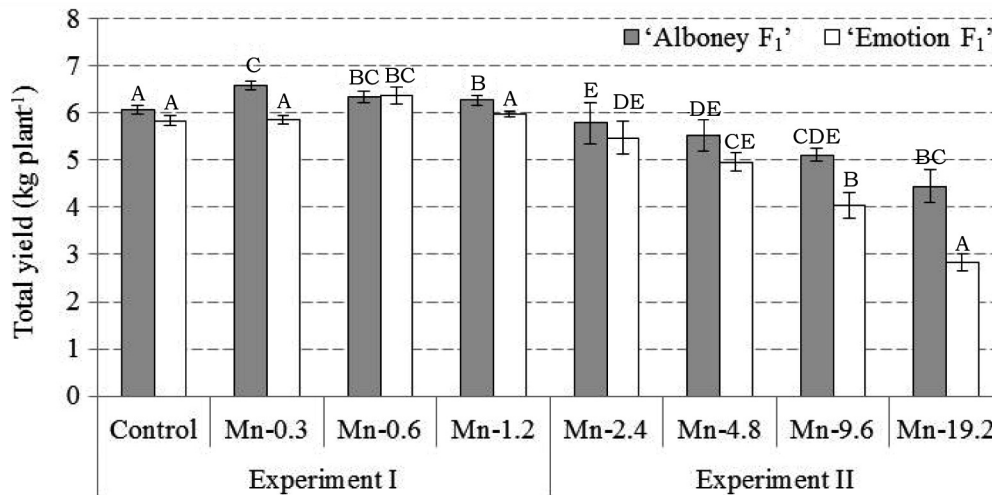
$$\text{RWC} = (\text{FW}-\text{DW})/(\text{TW}-\text{DW}) \times 100 [\%]$$

where: FW – fresh weight [g]; TW – full saturation weight [g]; DW – dry weight [g] (González and González-Vilar, 2001).

### STATISTICAL ANALYSIS

The data were analyzed using STATISTICA 9.1. The results were analyzed by factorial ANOVA with Mn level in nutrient solution and tomato cultivar as fixed factors. Tukey's test was employed to analyze differences between measured parameters.

Principal component analysis (PCA) was used to analyze the relations between gas exchange parameters, micro- and macronutrient concentrations in leaves, Mn level in nutrient solution, and tomato fruit field. This analysis employed orthogonal transformation of the observed variables to a new set of non-correlated variables (components).



**Fig. 1.** Effect of manganese nutrition on total tomato yield. Letters denote significant differences between means at  $p=0.05$ .

The macro- and microelement content of tomato leaves was analyzed using canonical multivariate analysis (Lejeune and Caliński, 2000). As in principal component analysis, it entails transformation of the original set of variables into a set of new variables carrying similar information but distributed in a multivariate Euclidean space (Kayzer et al., 2009; Budka et al., 2011). In this case, canonical multivariate analysis is based on a matrix including differences between the mean values of macro- and microelement content in tomato leaves at the various manganese concentrations and the means of macro- and microelement content for all treatments in the experiment.

## RESULTS

### TOTAL TOMATO FRUIT YIELD

Manganese nutrition significantly influenced total yield (Fig. 1). There were significant differences between cultivars. 'Alboney F<sub>1</sub>' produced high yield in the 0.3–0.6 mg Mn dm<sup>-3</sup> treatments, and 'Emotion F<sub>1</sub>' in the 0.6 mg Mn dm<sup>-3</sup> treatment. Both deficient and excess/toxic Mn nutrition reduced total plant yield.

### RELATIONS BETWEEN MACRO- AND MICRONUTRIENT CONTENT

Experiment I. Table 1 presents the macro- and micronutrient content of leaves of the two tomato cultivars in the Mn treatments ranging up to 1.2 mg Mn dm<sup>-3</sup>. There were significant differences in

macro- and micronutrient levels between cultivars and Mn treatments. Mn levels were low in both cultivars in the treatments without manganese sulfate, and high in plants fertigated with nutrient solution containing 0.6 and 1.2 mg Mn dm<sup>-3</sup>. The levels of the other analyzed metallic microelements (Fe, Zn, Cu) were highest for Mn-0 and lowest for Mn-1.2.

Figure 2 presents the micro- and macronutrient content of tomato leaves graphically in the canonical variate space (Fig. 2). The direction and location of the points due to the first canonical coordinate (explaining 93% of variability) correspond to increasing Mn and decreasing iron in leaves. Variation was highest for Mn-0.3.

The concentrations of P, K and Ca in leaves of both cultivars were low in the control (without Mn nutrition) and high in the 0.6 and 1.2 mg Mn dm<sup>-3</sup> treatments. Magnesium content in leaves was highest for 'Alboney F<sub>1</sub>' at Mn-0.6 and for 'Emotion F<sub>1</sub>' at Mn-0.3 (Tab. 1).

There were no differences in nitrogen concentrations between cultivars except for 'Alboney F<sub>1</sub>' at Mn-0.3. Determining the location of macronutrient content near the beginning of the coordinate system indicate slower variability of these elements.

Experiment II. Table 2 presents the macro- and micronutrient content of leaves of the two tomato cultivars in the Mn treatments ranging from 2.4 to 19.2 mg Mn dm<sup>-3</sup>. As in Experiment I, the cultivars and Mn treatments differed significantly in their levels of macro- and micronutrients. 'Emotion F<sub>1</sub>' showed high Mn content under the highest Mn treatment and the lowest Mn content in the Mn-2.4 treatment. 'Alboney F<sub>1</sub>' also showed the lowest Mn con-

TABLE 1. Differences in macro- and micronutrient content of tomato leaves of two tomato cultivars grown with different concentrations of manganese in nutrient solution, and means of all treatments, in Experiment I

Combination mg dm <sup>-3</sup> Mn	Mn	N	P	K	Ca	Mg	Fe	Zn	Cu
A-0.0	-145.6**	0.024	-0.141**	-0.968**	-0.526**	-0.048*	31.76**	8.775**	7.299**
A-0.3	-33.2**	0.352**	-0.046	-0.180	-0.138	0.017	16.18**	5.025**	0.939
A-0.6	52.3**	-0.020	0.019	0.270**	0.242**	0.119**	-8.29**	-3.600**	-3.411**
A-1.2	82.4**	-0.128	0.222**	0.632**	0.359**	-0.003	-40.04**	-5.025**	-4.986**
E-0.0	-137.4**	-0.226	-0.223**	-0.743**	-0.251**	-0.126**	56.48**	9.925**	6.214**
E-0.3	21.3**	0.092	0.034	-0.313**	-0.026	0.052*	3.96	2.675*	-0.736
E-0.6	55.3**	0.062	0.047	0.468**	0.207**	0.029	-14.59**	-8.100**	-2.211**
E-1.2	104.8**	-0.156	0.089**	0.835**	0.132	-0.041	-45.44**	-9.675**	-3.111**

A – 'Alboney F<sub>1</sub>'; E – 'Emotion F<sub>1</sub>'; significance level – \* 0.05, \*\* 0.01

TABLE 2. Differences in macro- and micronutrient content of tomato leaves of two tomato cultivars grown with different concentrations of manganese in nutrient solution, and means of all treatments, in Experiment II

Combination mg dm <sup>-3</sup> Mn	Mn	N	P	K	Ca	Mg	Fe	Zn	Cu
A-2.4	-37.59**	0.201**	0.027	0.903**	0.002	0.091**	7.78**	8.494**	1.003**
A-4.8	2.78	0.001	-0.018	0.653**	0.125	0.053*	6.86**	1.444	0.403
A-9.6	10.41	0.111	-0.026	-0.324**	0.552**	-0.002	7.56**	0.894	0.853**
A-19.2	9.81	-0.144*	0.064*	-0.434**	-0.020	-0.094**	-12.14**	-5.206**	-4.572**
E-2.4	-15.44**	0.258**	-0.146**	0.841**	-0.120	0.086**	7.63**	5.344**	2.178**
E-4.8	-2.17	0.138**	-0.081**	-0.382**	-0.038	0.064**	4.48**	-0.806	2.153**
E-9.6	4.28	-0.144*	0.054*	-0.604**	-0.218**	-0.052*	-5.99**	-2.631**	-0.297
E-19.2	27.91**	-0.419**	0.127**	-0.654**	-0.283**	-0.147**	-16.19**	-7.531**	-1.722**

A – 'Alboney F<sub>1</sub>'; E – 'Emotion F<sub>1</sub>'; significance level – \* 0.05, \*\* 0.01

tent in the Mn-2.4 treatment but did not show the highest Mn content in the highest Mn treatment.

The levels of the other metallic microelements (Fe, Zn, Cu) were highest for Mn-2.4 and lowest for Mn-19.2 in both cultivars. Figure 2 presents the results in the canonical variate space. The cultivars differed in macro- and micronutrient content in particular treatments. N, K and Mg content declined with increasing Mn nutrition. Ca was lowest for Mn-9.6 and Mn-19.2 for the 'Emotion F<sub>1</sub>' cultivar (Tab. 2). That cultivar showed low levels of P for Mn-4.8 and Mn-9.6, and high levels of P levels for Mn-19.2.

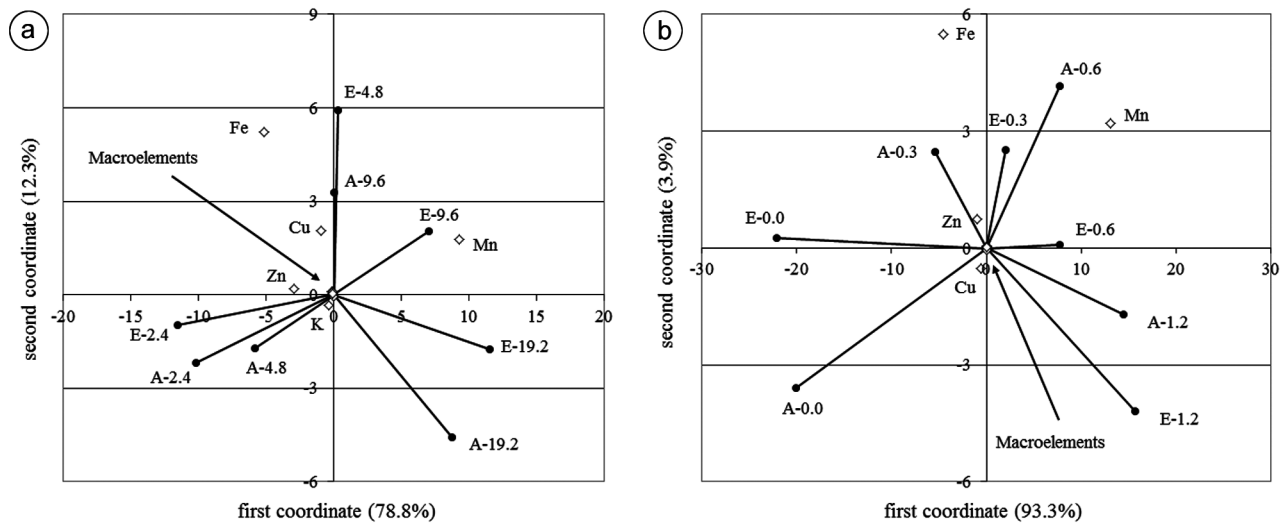
#### PHOTOSYNTHETIC ACTIVITY AND ITS RELATIONS TO OTHER PARAMETERS

Gas exchange parameters were analyzed for both experiments together. Two-way ANOVA showed highly significant differences in photosynthetic activity parameters between Mn treatments. Cultivar did not significantly affect the level of stomatal conductance (Tab. 3). In 'Alboney F<sub>1</sub>' it was highest for

Mn-0.3 and for 'Emotion F<sub>1</sub>' it was highest for Mn-0.6.  $P_N$  level significantly decreased at Mn-1.2 in both cultivars, and thereafter the net photosynthesis rate decreased with increasing Mn (Fig. 3). In the 0–0.6 Mn treatment range, stomatal conductance trended similarly to  $P_N$  in both cultivars. Above that range 'Alboney F<sub>1</sub>' showed no decrease of  $g_s$  at Mn-1.2 but a significant decline at Mn-2.4. In both cultivars  $g_s$  declined and reached the lowest values at Mn-19.2 (Fig. 3). The transpiration rate trended similarly to  $P_N$  in 'Alboney F<sub>1</sub>'; in 'Emotion F<sub>1</sub>' there was no decrease of E in treatments exceeding Mn-2.4 (Fig. 3). Intercellular CO<sub>2</sub> concentration was inversely related to  $P_N$  and  $g_s$ , and a highly significant increase was recorded at Mn-1.2 (Fig. 3).

Principal component analysis was performed for each cultivar separately to determine the relations between particular parameters. This system of coordinates explains ~80% ('Emotion F<sub>1</sub>') and ~90% ('Alboney F<sub>1</sub>') of all variation. Linear relations for both cultivars were recorded for  $P_N$ ,  $g_s$  and E, together with some nutrients (Mg, K, N, Cu, Zn, Fe) and total yield. These parameters showed positive





**Fig. 2.** Position of selected experimental objects for Experiment I (a) and Experiment II (b) differing in level of macro- and micronutrient content in tomato leaves in the space of the first two canonical variates, and spacing of the nutrients in the dual space of canonical variates; values of canonical coordinates multiplied by 2 (Experiment I) and by 5 (Experiment II)

relations to low Mn in nutrient solution (0–1.2) but negative relations with  $C_i$ , SLA, Ca, P and Mn under high Mn in the nutrient solution (2.4–19.2). Both cultivars responded similarly except in regard to relative water content; ‘Alboney  $F_1$ ’ showed a linear relation of RWC with lower Mn dose, while ‘Emotion  $F_1$ ’ showed no clear tendency (Fig. 4).

## DISCUSSION

Manganese is an essential micronutrient for plants, required for proper functioning of amino acid synthesis, some enzyme activation processes and chlorophyll formation (McLaughlin et al., 1999). Hence a deficiency of it is usually observed as chlorosis. On the other hand, too high a concentration can have phytotoxic effects (Pitman, 2005) and visible symptoms such as brown spotting of leaves, petioles and stem (McCain and Markley, 1989; Wu, 1994; Kleiber, 2014). Mn supply has been linked to yield improvement in many species, including cotton, pumpkin and tomato (Foy et al., 1981; Orhue and Nwaoguala, 2010; Kleiber, 2014). Certain levels of it seem to be needed for proper tomato biomass production as well. Tomato yield in ‘Alboney  $F_1$ ’ was lower in the control (Mn-0) than at Mn-0.3, and in ‘Emotion  $F_1$ ’ it was lower in the control than at Mn-0.6. We noted a possible negative effect of excessive Mn on tomato yield above the Mn-2.4 level. At both Mn-0 (deficit) and  $\geq$ Mn-4.8 (toxicity), tomato plants showed visible symptoms (Kleiber, 2014). Reporting a similar effect, Savvas et al. (2009) stat-

**TABLE 3.** Two-way ANOVA of net photosynthesis rate ( $P_N$ ), stomatal conductance ( $g_s$ ), intercellular  $CO_2$  concentration ( $C_i$ ) and transpiration rate ( $E$ ) in two tomato cultivars cultivated with different concentrations of manganese in nutrient solution

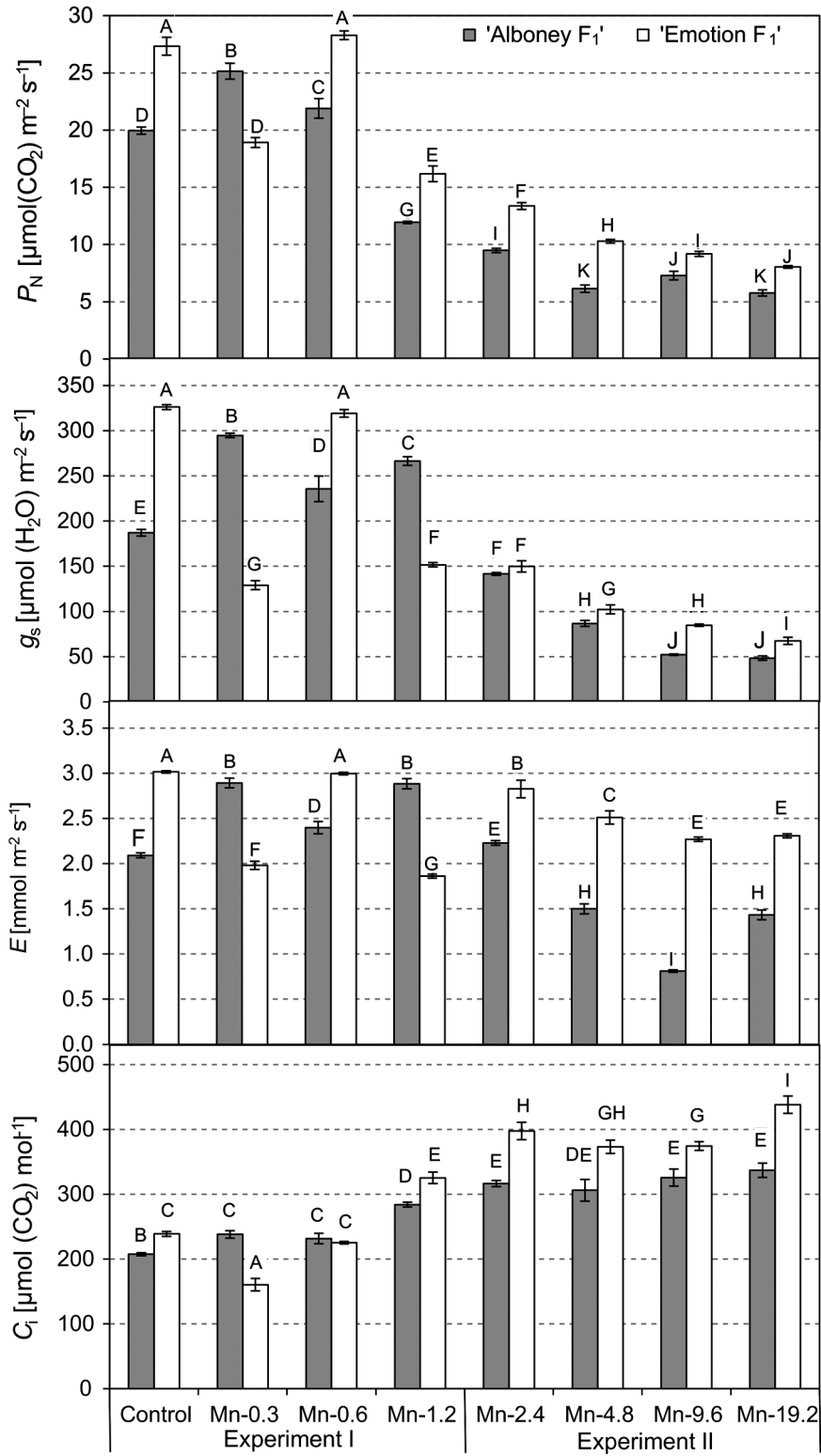
Parameter	Mn level	Cultivar	Interaction
$P_N$	587.98**	189.79**	43.17**
$g_s$	641.97**	0.67ns	206.50**
$E$	92.57**	225.48**	118.21**
$C_i$	83.16**	46.27**	13.51**

Significance level – \*\*0.01; ns – not significant

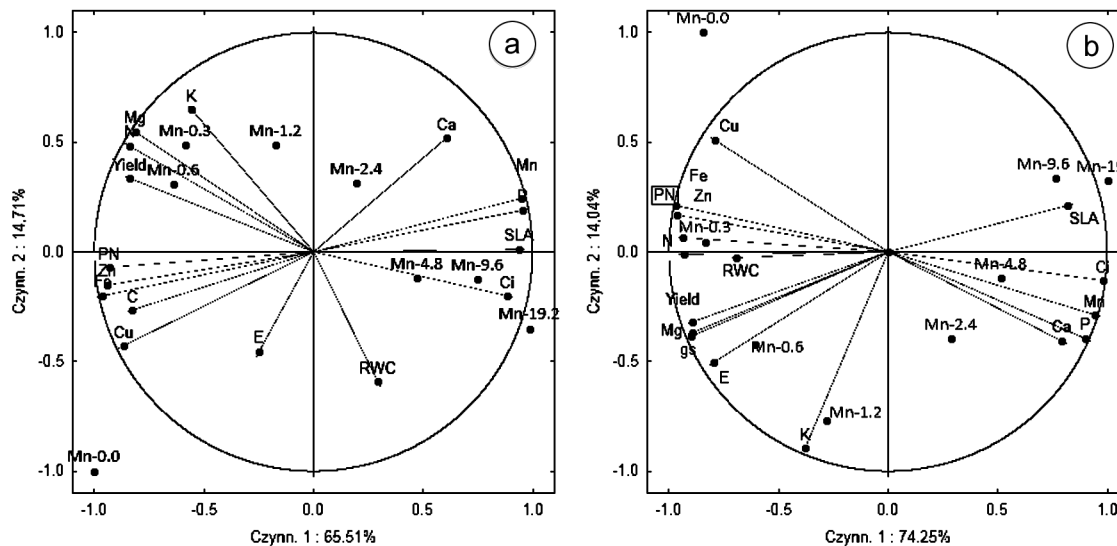
ed that excessively high Mn levels in the root environment of tomato reduced yield by decreasing the number of fruits per plant but had no effect on mean fruit weight.

Mn was also found to affect the uptake of other elements, including those important for proper plant functioning. Positive effects on Mg, K and Zn uptake have been found in maize and common bean (Fageria et al., 2002). Excessive Mn can affect the uptake of Ca, Mg, Fe and P (Clark, 1982; Lei et al., 2007).

Manganese fertilization increases crop yield and quality, due to improved plant nutrition and increased photosynthesis in plants (Hiller, 1995; Kelling and Speth, 2001; Crosier et al., 2004; Mousavi et al., 2007). Mn plays an important role in photosynthesis by aiding chlorophyll synthesis; hence, a deficiency appears as chlorosis. Decreased chlorophyll content under Mn deficit has been found



**Fig. 3.** Means  $\pm$ SE of net photosynthesis rate ( $P_N$ ), stomatal conductance ( $g_s$ ), transpiration rate ( $E$ ) and intercellular  $\text{CO}_2$  concentration ( $C_i$ ) in two tomato cultivars cultivated with different manganese concentrations in nutrient solution. Letters denote significant differences between means at  $p=0.05$ .



**Fig. 4.** Principal component analysis of selected photosynthetic activity parameters ( $P_N$ ,  $g_s$ ,  $E$ ,  $C_i$ ), macro- and microelement content of leaves and tomato yield for 'Alboney  $F_1$ ' (a) and 'Emotion  $F_1$ ' cultivars (b).

in tomato (Moshe et al., 2004), barley (Alam et al., 2006) and kidney bean (Gonzalez et al., 1998). Mn also serves as a means of electron storage and delivery to chlorophyll reaction centers (Diedrick, 2010; Millaleo et al., 2010). In our experiment the net photosynthesis rate was related to yield up to the Mn-0.6 level. There was an evident decrease in the net photosynthesis rate beginning at Mn-1.2 but no corresponding visually obvious effect on fruit yield; detailed measurements showed a statistically significant decline in fruit yield, however.

Stomatal opening declined with the decrease of  $P_N$ . In a study of three common bean species differing in Mn tolerance, Gonzales and Lynch (1997) observed a decrease of  $g_s$  only in leaves showing visible symptoms of Mn excess, such as necrosis and chlorosis, but did not find a relation between transpiration and stomatal conductance in leaves without visible symptoms. Our analyses used leaves without visible symptoms and noted physiological responses before the appearance of Mn toxicity symptoms. Similar effects of excess Mn were reported by Li et al. (2010) in citrus plants and by Mortley (1993) in sweet potato. Li et al. (2010) concluded that Mn excess impaired the whole photosynthetic electron transport chain from the donor side of PSII up to the reduction of end acceptors of PSI, limiting the production of reducing equivalents and hence the rate of  $CO_2$  assimilation. In Chinese cabbage, Lee et al. (2011) found significantly lower chlorophyll content under excess Mn, with a simultaneous decrease of fresh and dry root weight. Wei et al. (2004) found a highly positive effect of manganese on  $P_N$ ,  $g_s$  and water use efficiency (WUE) in drought-

treated maize plants, suggesting that application of manganese fertilizer alleviated the drought-caused inhibition of maize photosynthesis. In our work, relative water content had an effect on the transpiration rate; the unusual response of transpiration rate to Mn treatment in 'Emotion  $F_1$ ' was related to RWC but not to other parameters.

## CONCLUSIONS

Some amount of manganese is necessary for higher tomato fruit yield and improved photosynthesis. The level of Mn in nutrient solution was related to tomato cultivar yield. Photosynthetic activity was the first parameter to reflect Mn toxicity at Mn-1.2, while tomato yield was not yet affected at that level. Stomatal conductance responded similarly to net photosynthesis rate, while transpiration rate reacted similarly to  $P_N$  and  $g_s$  in one of the cultivars but not in the other. Yield and relative water content also trended similarly. In both cultivars, Mn, P and K levels were directly proportional to Mn concentration in nutrient solution (Experiment I), while Fe, Zn and Cu were inversely proportional to Mn concentration in the nutrient solution (Experiment I and II). The micronutrient concentrations varied more than the macronutrient concentrations. Gas exchange parameters were related to total yield and macro- and micronutrient concentrations. These experiments supply strong evidence for the graded effects of Mn on physiology and yield in tomato. Further work should shed more light on the relations between photosynthesis parameters, macro- and

micronutrients, and other elements (e.g., silicon or selenium, which may alleviate manganese stress). Studies should be extended to new tomato cultivars, other plant species and other parameters.

## AUTHORS' CONTRIBUTIONS

TK design and performance of experiments, plant material analyses; KB gas exchange measurements; AB, DK, KB, TK analyses of experimental data and preparation of the paper.

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## REFERENCES

- ALAM S, RYUSHI K, FUMIHITO A, KAMEI S and KAWAI S. 2006. Alleviation of manganese phytotoxicity in barley with calcium. *Journal of Plant Nutrition* 29: 59–74.
- BUDKA A, BOROWIAK K, ZBIERSKA J, KAYZER D and KRZESIŃSKI W. 2001. Application of a multidimensional linear model to compare degrees of tobacco leaf injury caused by tropospheric ozone at rural and urban exposure sites. *Fresenius Environmental Bulletin* 4: 969–975.
- CAKMAK I, and MARSCHNER H. 1988. Enhanced superoxide radical production in roots of Zn deficient plants. *Journal of Experimental Botany* 39: 1449–1460.
- CAKMAK I, and MARSCHNER H. 1992. Magnesium deficiency and high light intensity enhance activities of superoxide dismutase, ascorbate peroxidase, and glutathion reductase in bean leaves. *Plant Physiology* 98: 1222–1227.
- CLARK RB. 1982. Plant response to mineral element toxicity and deficiency. In: Christiansen MN, Lewis CF [eds.], *Breeding Plants for Less Favorable Environments*, 71–142. John Wiley & Sons, New York.
- CROSIER CR, CREAMER NG, and CUBETA MA. 2010. Soil facts. Soil fertility management for Irish potato production in eastern North Carolina. North Carolina Cooperative Extension.
- DIEDRICK K. 2010. Manganese fertility in soybean production. Crop Insights. Pioneer Hi-Bred Int., Inc., Johnston, IA. [Online] <https://www.pioneer.com/home/site/us/agronomy/library/template.CONTENT/guid.6693CDF7-8169-DE29-F6B2-52A7C87A6E80>
- DRAGIŠIĆ MAKSIMOVIC J, BOGDANOVIC J, MAKSIMOVIC V, and NIKOLIC M. 2007. Silicon modulates the metabolism and utilization of phenolic compounds in cucumber (*Cucumis sativus* L.) grown at excess manganese. *Journal of Plant Nutrition and Soil Science* 170: 739–744.
- DUCIC T, and POLLE A. 2005 Transport and detoxification of manganese and copper in plants. *Brazilian Journal of Plant Physiology* 17: 103–112.
- FAGERIA N, BALIGAR V, and CLARK R. 2002. Micronutrients in crop production. *Advances in Agronomy* 77: 185–268.
- FLEMING AL. 1989. Enhanced Mn accumulation by snapbean cultivars under Fe stress. *Journal of Plant Nutrition* 12: 715–731.
- FOY CD, WEBB HW, and JONES JE. 1981. Adaptation of cotton genotypes to an acid, manganese toxic soil. *Agronomy Journal* 73: 107–111.
- GALVEZ L, CLARK RB, GOURLEY LM, and MARANVILLE JW. 1989. Effect of silicon on mineral composition of sorghum growth with excess manganese. *Journal of Plant Nutrition* 12: 547–561.
- GARNIER E, SHIPLEY B, ROUMET C, and LAURENT G. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* 15: 688–695.
- GONZÁLEZ A, and LYNCH JP. 1997. Effects of manganese toxicity on leaf CO<sub>2</sub> assimilation of contrasting common bean genotypes. *Physiologia Plantarum* 101(4): 872–880.
- GONZÁLES L, and GONZÁLES-VILAR M. 2001. Determination of relative water content. In: Reigosa Roger MJ [ed.], *Handbook of Plant Ecophysiology Techniques*, 207–2013. Kluwer Academic Publishers, Netherlands.
- GONZALEZ A, STEFFEN KL, and LYNCH PJ. 1998. Light and excess manganese. Implication for oxidative stress in common bean. *Plant Physiology* 18: 493–504.
- HILLER LK. 1995 Foliar fertilization bumps potato yields in Northwest. *Fluid Journal*. Department of Horticulture and Landscape Architecture at Washington State University.
- HORST WJ. 1988. The physiology of manganese toxicity. In: Graham RD, Hannam RJ, Uren NJ [eds.], *Manganese in Soil and Plants*, 175–188. Kluwer Academic Publishers, Dordrecht, Netherlands.
- HUMPHRIES JM, STANGOULIS JCR, and GRAHAM RD. 2007. Manganese. In: Barker AV, Pilbeam DJ [eds.], *Handbook of Plant Nutrition*, 351–374. Taylor & Francis Group.
- IUNG 1972. *Analytical Methods in Agricultural-Chemistry Stations. Part II. Plant Analyses*. Pulawy, Poland.
- KAYZER D, BOROWIAK K, BUDKA A, and ZBIERSKA J. 2009. Study of interaction in bioindication research on tobacco plant injuries caused by ground level ozone. *Environmetrics* 20: 666–675.
- KELLING KA, and SPETH PE. 2001. Effect of micronutrient on potato tuber yield and quality at Spooner, Department of Soil Science, University of Wisconsin – Madison.
- KLEIBER T. 2014. Wpływ manganu na plonowanie pomidora (*Lycopersicon esculentum* Mill.) uprawianego w wełnie mineralnej. *Nauka Przyroda Technologia* 8, 2, #14.
- KASRAEI R, ROGRÍGUEZ-BARRUECO C, and ARROYO MI. 1996. The effect of Al and Mn on growth and mineral composition of *Casuarina equisetifolia* Forst. *Fertilizers and Environment* 25–29: 75–81.
- KAZDA M, and ZNACEK L. 1989. Aluminum and manganese and their relation to calcium in soil solution and needle in three Norway spruce (*Picea abies* L. Karst.) stands of upper Australia. *Plant Soil* 114: 257–267.



- LEE TJ, LUITEL BP, and KANG WH. 2011. Growth and physiological response to manganese toxicity in Chinese cabbage (*Brassica rapa* L. ssp. *campestris*). *Horticulture, Environment, and Biotechnology* 52(3): 252–258.
- LEI Y, KORPELAINEN H, and LI C. 2007. Physiological and biochemical responses to high Mn concentrations in two contrasting *Populus cathayana* populations. *Chemosphere* 68: 686–694.
- LEJEUNE M, and CALIŃSKI T. 2000. Canonical analysis applied to multivariate analysis of variance. *Journal of Multivariate Analysis* 72: 100–119.
- LI Q, CHEN L-S, JIANG H-X, TANG N, YANG L-T, LIN Z-H, LI Y, and YANG G-H. 2010. Effects of manganese-excess on CO<sub>2</sub> assimilation, ribulose-1,5-bisphosphate carboxylase/oxygenase, carbohydrates and photosynthetic electron transport of leaves, and antioxidant systems of leaves and roots in *Citrus grandis* seedlings. *Plant Biology* 10: 42.
- LIDON FC, BARREIRO M, and RAMALHO J. 2004. Manganese accumulation in rice: implications for photosynthetic functioning. *Journal of Plant Physiology* 161: 1235–1244.
- MCCAIN DC, and MARKLEY JL. 1989. More manganese accumulates in maple sun leaves than in shade leaves. *Plant Physiology* 90: 1417–1421.
- MCLAUGHLIN MJ, PARKER DR, and CLARKE JM. 1999. Metals and micronutrients. Food safety issues. *Field Crop Research* 60: 143–163.
- MILLALEO R, REYES-DÍAZ M, IVANOV AG, MORA ML, and ALBERDI M. 2010. Manganese as essential and toxic element for plants: transport, accumulation and resistance mechanisms. *Journal of Plant Nutrition and Soil Science* 10(4): 476–494.
- MORTLEY DG. 1993. Manganese toxicity and tolerance in sweetpotato. *Hortscience* 28(8): 812–813.
- MOSHE S, PLESSNER OE, and TEL-OR E. 2004. Manganese nutrition effects on tomato growth, chlorophyll concentration, and superoxide dismutase activity. *Journal of Plant Physiology* 161: 197–202.
- MOUSAVI SR, GALAVI M, and AHMADVAND G. 2007. Effect of zinc and manganese foliar application on yield, quality and enrichment on potato (*Solanum tuberosum* L.). *Asian Journal of Plant Science* 6: 1256–1260.
- ORHUE ER, and NWAOGUALA CNC. 2010. The effect of manganese on early growth of fluted pumpkin (*Telfairia occidentalis* Hook F) in an ultisol. *Journal of Tropical Agriculture, Food, Environment and Extension* 9(3): 154–160.
- PITMAN JK. 2005. Manganese molecular mechanism of manganese transport and homeostasis. *New Phytologist* 167: 733–742.
- SAVVAS D, PAPASTAVROU D, NTATSI G, ROPOKIS A, and OLYMPIOS C. 2009. Interactive effects of grafting and manganese supply on growth, yield, and nutrient uptake by tomato. *Hortscience* 44(7): 1978–1982.
- SHENKER M, PLESSNER OE, and TEL-OR E. 2004. Manganese nutrition effects on tomato growth, chlorophyll concentration, and superoxide dismutase activity. *Journal of Plant Physiology* 161: 197–202.
- TANAKA K, TAKIO S, and SATOH T. 1995. Inactivation of the cytosolic Cu/Zn superoxide dismutase induced by copper deficiency in suspension cultured cells of *Marchantia paleacea* var. *diptera*. *Journal of Plant Physiology* 146: 361–365.
- WEI X, HAO MD, and QIU L-P. 2004. Effect of manganese fertilizer on maize photosynthetic performance under soil drought condition. *Plant Nutrition and Fertilizer Sciences* 10(3): 255–258.
- WU S. 1994. Effect of manganese excess in the soybean plant cultivated under various growth conditions. *Journal of Plant Nutrition* 17: 993–1003.
- YU Q, OSBORNE LD, and RENGEL Z. 1998. Micronutrient deficiency influences plant growth and activities of superoxide dismutase and ascorbate peroxidase in tobacco plants. *Journal of Plant Nutrition* 21: 1427–1437.
- YU Q, and RENGEL Z. 1999. Micronutrient deficiency influences plant growth and activities of superoxide dismutase and ascorbate peroxidase in narrow leaf lupines. *Annals of Botany* 183: 175–182.