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Influence of different manganese concentrations on eggplant (*Solanum melongena* L.) grown in a hydroponic system

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Abstract
The study aimed to evaluate the effect of three different manganese (Mn) concentrations on the plant growth, leaf chlorophyll, carotenoid content, photosynthetic activity, and root morphological development in eggplant (*Solanum melongena* L. 'Adana cv. Dolmalık' and 'Köksal cv. F1'). Plants were grown continuously in aerated nutrient solution by using a deep-water culture (DWC) technique in a fully automated climate room. A randomized block design with three replications was used. Both excessive (400 µM) and insufficient (0.4 µM) Mn concentrations in the root zone reduced the shoot fresh and dry matter, branch number, leaf area, and leaf chlorophyll content in both examined genotypes in comparison with optimal Mn concentrations (200 µM). Köksal cv. F1 produced higher shoot and root biomasses, root:shoot ratio, total leaf number, leaf total chlorophyll and carotenoid content, total leaf area, and average root diameter at the low concentration of Mn. Conversely, Adana cv. Dolmalık produced significantly higher stem length, shoot and root biomasses, total root length and root volume at high Mn concentrations. Overall, both deficit and excess Mn nutrition could induce disorders in the growth and development of eggplant which may reduce crop yield.

Keywords
Photosynthesis, Mn^{2+}, Deficiency, SPAD, Root morphology

Introduction
Eggplant (*Solanum melongena* L.), also known as the aubergine, guinea squash or brinjal, is an economically important vegetable crop in tropical and subtropical regions of the world. After tomato, watermelon, onion, cabbage, and cucumber, it is the world's sixth most important vegetable. It is widely cultivated in Asia and to a lesser extent in the Mediterranean basin, including Turkey. The approximate total world production for eggplants in 2019 was 52.309.119 metric tons, up by 2.2% from 51.192.811 tons. China was by far the largest producer of eggplants, accounting for over 62% of global production (FAO, 2019). It is highly valued for its taste, nutritional and health benefits (Adamczewska-Sowinska and Kotota, 2010), as it contains 1.4 g protein, 0.30 g fat, 0.30 g minerals, 0.30 g fiber, 4.0 g carbohydrates, 18.0 mg calcium (Ca), 18.0 mg oxalic acid, 47.0 mg phosphorus (P), 2.0 mg potassium (K), 124 I.U vitamin A, 0.11 mg riboflavin and 12.0 mg vitamin C per 100 g of edible portion as well as dietary fiber (Sánchez-Castillo et al., 1999). In addition, Eggplant fruits have shown high hydrophilic oxygen radical absorbance capacity (ORAC) (Cao et al., 1996), which has been correlated to phenolic compounds presence, including delphinidin as a major component in peel (Koponen et al., 2007) and chlorogenic acid in flesh (Whitaker and Stommel, 2003). The young and almost mature fruits are used as vegetable. Since it is able to absorb large amounts of sauces and cooking fats, it is used in preparing very rich dishes, while in Indonesia

and Malaysia they are also eaten raw (Sutarno et al., 1993). Anthocyanins had proven to be abundant in eggplant, Delphinidin glucosides are the type of anthocyanins which contribute to the purple dark color of eggplant (Gürbüz et al., 2018). Eggplant has some properties such as antibacterial, anti-inflammatory, antibacterial, antiallergic and anticarcinogenic which are useful to human health (Martínez-Ispizua et al., 2021).

Manganese (Mn) is an essential micronutrient necessary for plant growth and metabolism. Mn has a profound influence on three physiological processes in plants: (i) it participates in the structure of the water-splitting system of photosystem II (PSII), which provides the necessary electrons for photosynthesis (Graham, 2018). Mild Mn deficiency harms the stability and functionality of PSII, causing reduced photosynthetic CO_2 assimilation (Schmidt et al., 2020), (ii) is required for N metabolism, it functions in nitrate reduction, by acting as an activator for the enzymes nitrite reductase and hydroxylamine reductase, and (iii) it is essential for the biosynthesis of aromatic amino acids (tyrosine) and secondary products like lignin and flavonoids (Buchanan et al., 2000). Mn is a crucial constituent of Mn-superoxide dismutase, a major antioxidant enzyme (Lidon et al., 2004). It also participates in carbohydrate and lipid biosynthesis. Mn also performs as a cofactor of many enzymes, like Mn-catalase, Mn-peroxidases, TCA cycle decarboxylases, RNA polymerases and numerous glycosyltransferases (Lidon et al., 2004). Mn deficiency appears as interveinal chlorosis (yellow leaves with green veins) of the young leaves, sometimes with tan, sunken spots in the chlorotic areas between the veins as well as plants reduced growth and stunted in size (Heine et al., 2011). Despite lack of visual symptoms, latent Mn deficiency in early growth stages can cause a substantial reduction of crop yields (Schmidt et al., 2019). On the other hand, the high concentration of Mn causes brown spots on leaves, followed by chlorosis, necrosis and leaf shedding, reduced growth of plants (Mou et al., 2011); interrupts essential metabolic and reproductive processes, such as absorption, translocation, and utilization of other mineral elements in plants, stimulates the phenolic metabolism, affects the energy metabolism, decreases respiration rates, and causes oxidative stress (Shanahan et al., 2007).

Mn accumulates significantly in shoots by in roots; thus, the shoot is more affected from Mn toxicity than roots (Millaleo et al., 2010). Furthermore, excess Mn is stored in vacuoles and in cell walls in plant tissues. It negatively impacts photosynthesis by reducing biosynthesis of chlorophylls and carotenoids, preventing electron transport activity in light reaction of photosynthesis, modifying the activity of Rubisco, etc. (Millaleo et al., 2010; Parashar et al., 2014). Mn-excess in plants inhibits the functioning of PSII and oxidized form of Mn and different phenolic compounds accumulate in the leaf apoplast (Marschner, 2012). Cell homeostasis gets interrupted in Mn-treated plants. Mn binds to the outer thylakoid membranes of the chloroplasts (Rajpoot et al., 2018). Generally, Mn-tolerant genotypes employ a serial detoxifying strategy to detoxify excess Mn, such as sequestration and translocation of Mn into the vacuole and endoplasmic reticulum, chelation in the cytosol and evoking the induction of antioxidant enzymes (Boojar and Goodarzi, 2008). Phytotoxicity in growth media occurs due to low pH and also high Mn dose. The bark is used as a substitute for peat media and mostly used when peat media is scarce to find. The bark is effective in preventing phytotoxicity (Sabatino, 2020). Growth media with low pH could be adjusted by applying lime (Savvas and Gruda, 2018).

In higher plants, Mn stress caused by deficiency or toxicity experiments, which involve good control over the root environment, is generally carried out in solution culture experiments rather than soils. While solution culture disregards significant impacts of the soil and rhizosphere, it allows control of element content and pH of the nutrient solution, which are crucial factors in controlling microelements uptake and regulating of microelements methods in plant metabolism. Several nutrient solution compositions have traditionally been employed in hydroponic culture (Shenker et al., 2004). Hydroponic screening has been extensively applied to evaluate genotypic variation for Mn tolerance and accumulation ability (Khabaz-Saberi et al.,2010). Genotypic differences in Mn tolerance and accumulation have been studied in different crops such as durum wheat (Khabaz-Saberi et al.,2010), bread wheat (Sadana et al., 2002), barley (Hebbern et al., 2005), rice (Wang et al., 2002), rapeseed (Moroni et al., 2003), and other woody plants (Kitao et al., 2001; Ducĭć et al., 2006; Yao et al., 2012).

However, to date, and our knowledge, Mn tolerance and accumulation inhibiting plant biomass, photosynthesis, accumulation of reactive oxygen species (ROS) and crop yield in eggplant genotypes are poorly understood. Therefore, this study aimed to evaluate the response of two different eggplant genotypes to Mn tolerance and accumulation in a hydroponic system.

Materials and Methods

Plant Material, and Experimental Design

This study was carried out in the summer season of 2018 in the Plant Nutritional Physiology Laboratory of Erciyes University, Faculty of Agriculture, Department of Soil Science and Plant Nutrition, in Kayseri, Turkey. Two eggplant genotypes, ('Adana cv. Dolmalık' and 'Köksal cv. F1') were used as plant materials in this study. Plants were grown continuously in aerated nutrient solution by using a deep water culture (DWC) technique in a fully automated climate room. The eggplant seeds were sown in 77-cell multipots with a mixture of peat (pH: 6.0 – 6.5) and perlite (2v:1v). For the vegetation period, the average day/night temperatures were maintained at 25/22 °C, and the relative humidity was 60-80%. The supplied photon flux in the growth chamber was 350 µmol m^{-2} S^{-1} with a photoperiod of 16/8 h (light/dark). When the seedlings produced 3-4 leaves, they were transplanted to plastic pots for six weeks, after roots were washed. Each vessel was filled with an 8 L modified composition of Hoagland solution. Sufficient dissolved oxygen was supplied into the solution with the aid of an air pump. Due to transplanting small seedlings, the solutions were

entirely changed in the first two weeks and subsequently every 7th day.

Three different (Mn) concentrations: (low Mn: 0.4 µM, optimal: 200 µM, and high: 400 µM) were supplied. $MnSO_4$ was used as Mn source. The nutrient solution had the following composition (µM): $(NH4)_2SO_4$ (500); $Ca(NO_3)_2$ (1500); K_2SO_4 (500); KH_2PO_4 (250); $CaSO_4$ (1000); $MgSO_4$ (325); NaCl (50); H_3BO_3 (8); $ZnSO_4$ (0.4); $CuSO_4$ (0.4); $MoNa_2O_4$ (0.4); Fe-EDDHA (80). A randomized complete block design with three replications was used.

Harvest, Shoot, and Root Dry Weight and Main Stem Length Measurements

For the fresh weight determination, plant organs were fractioned into the leaf, stem and roots and then weighted (g/plant) at the final harvest. Plant dry matter was determined by drying the plant tissues at 70 °C for 72 h in a forced-air oven first and then by weighing them on an electronic digital scale. Total shoot dry matter was determined by adding each aerial vegetative plant parts (leaves + stems) separately. To calculate the shoot/root ratio, the sum of leaf and stem dry weights was divided by the total root dry weight. With the aid of a ruler main stem length (cm) of each plant was measured.

Leaf Area, Total Leaf Number, Branch Number and Photosynthetic Activity Measurements

The leaf-level CO_2 gas exchange (µmol CO_2 m^{-2} s^{-1}) was measured nondestructively by using a portable photosynthesis system device (LI-6400XT; LI-COR Inc., Lincoln, NE, USA). The measurement was performed by using an artificial light source (photosynthetically active radiation (PAR) = 1000 µmol m^{-2} s^{-1}) and artificial CO_2 (400 µmol mol^{-1}) tube of the device. The photosynthesis was measured in the third and fifth weeks of the growth period on the youngest fully expanded leaves, using four replicate leaves per treatment. The total leaf area of the plants was measured destructively during the harvesting process by using a portable leaf-area meter (LI-3100, LI-COR. Inc., Lincoln, NE, USA). Total leaf area was recorded as cm^2. Each fully developed leaf was counted and recorded as leaf number per plant (LN/plant). The branch number (BN) was counted and recorded as BN/plant. SPAD readings were taken with the Minolta SPAD-502 chlorophyll meter for each experimental treatment. During the growth period, two series of SPAD 502 chlorophyll meter readings were performed at the center of the leaves on the fully expanded youngest leaf for each treatment.

Leaf Total Chlorophyll and Carotenoid Content Measurements

A day before harvesting, 100 mg of fresh leaf samples from each replication of the two treatments was taken to measure the leaf total chlorophyll and carotenoid contents using UV–VIS spectroscopy. The samples were put into 15 mL capped containers where 10 mL of 95% (v/v) ethanol was added. Afterward, to allow for the extraction of the leaf pigments, the samples were held overnight in darkness at room temperature. Measurements were done using a spectrometer (UV/VS T80+, PG Instruments Limited, UK) at 470, 648.6, and 664.2 nm wavelengths. Total chlorophyll (a-Total-Chlo) and total carotenoids (b-TC) were estimated from the spectrometric readings using the formulae described by Lichtenthaler (1987):

a) Total-Chlo (mg/g plant sample) = [5.24 WL664.2 − 22.24 WL648.6 × 8.1]/ weight plant sample (g)

b) TC (mg/g plant sample) = [(4.785 WL470 + 3.657 WL664.2) − 12.76 WL648.6 × 8.1]/ weight plant sample (g).

(Note: WL470, WL648.6, and WL664.2 refer to spectrometric readings at wavelengths 470, 648.6, and 664.2 nm, respectively).

Morphological Root Measurements

The plant root morphological parameters such as total root length (m), total root volume (cm^3) and average root diameter (mm) were measured by using a particular image analysis software program WinRHIZO (Win/Mac RHIZO Pro V. 2002c Regent Instruments Inc., Québec, QC G1V 1V4, Canada) in combination with recording device of Epson Expression 11000XL scanner (Long Beach, CA, USA).

Statistical Analysis

Statistical analysis of the data was performed using the PROC GLM procedure of the SAS Statistical Software (SAS for Windows 9.1, SAS Institute Inc., Cary, NC, USA). A two-factor analysis of variance was performed to study the effects of genotype or Mn-rates and their interactions on the variables analyzed. The levels of significance are represented at $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), or n.s. as not significant (*F*-test and Pearson correlation coefficients). Differences between the treatments were analyzed using Duncan's multiple range test ($p < 0.05$).

Results and Discussions

Changes in Leaf Chlorophyll (a+b) and Carotenoid Content, Photosynthesis and Leaf Chlorophyll Index (SPAD)

The results of the leaf chlorophyll (a+b) content, leaf carotenoid content, photosynthesis and leaf chlorophyll index (SPAD) at the end of the growing cycle of eggplant genotypes grown in different Mn-rates are shown in Figure 1. Leaf chlorophyll (a+b) content, leaf carotenoid content, photosynthesis and leaf chlorophyll index (SPAD) were significantly ($p < 0.001$) affected by genotypes, different Mn rates, and genotype x Mn-rate interaction. However, no differences were observed in carotenoid content by Mn-rate (Figure 1A, 1B, 1C and 1D). Leaf chlorophyll (a+b) content and leaf carotenoid content are the main photosynthetic pigments of higher plants. Low and high Mn-rates decreased the amount of chlorophyll a and b in both eggplant genotypes under hydroponic conditions. Elevated levels of Mn usually have a positive effect on the intensity of photosynthesis and leaf chlorophyll index. Increasing Mn concentration in the nutrient solution increased the intensity of photosynthesis 38.43% and SPAD by almost 3.49% at high Mn-rate than low Mn-rate under hydroponic conditions, though the leaf chlorophyll (a+b) content declined by almost 0.7% and leaf carotenoid content by almost 21.71% at high Mn-rate than low Mn-rate under hydroponic conditions.

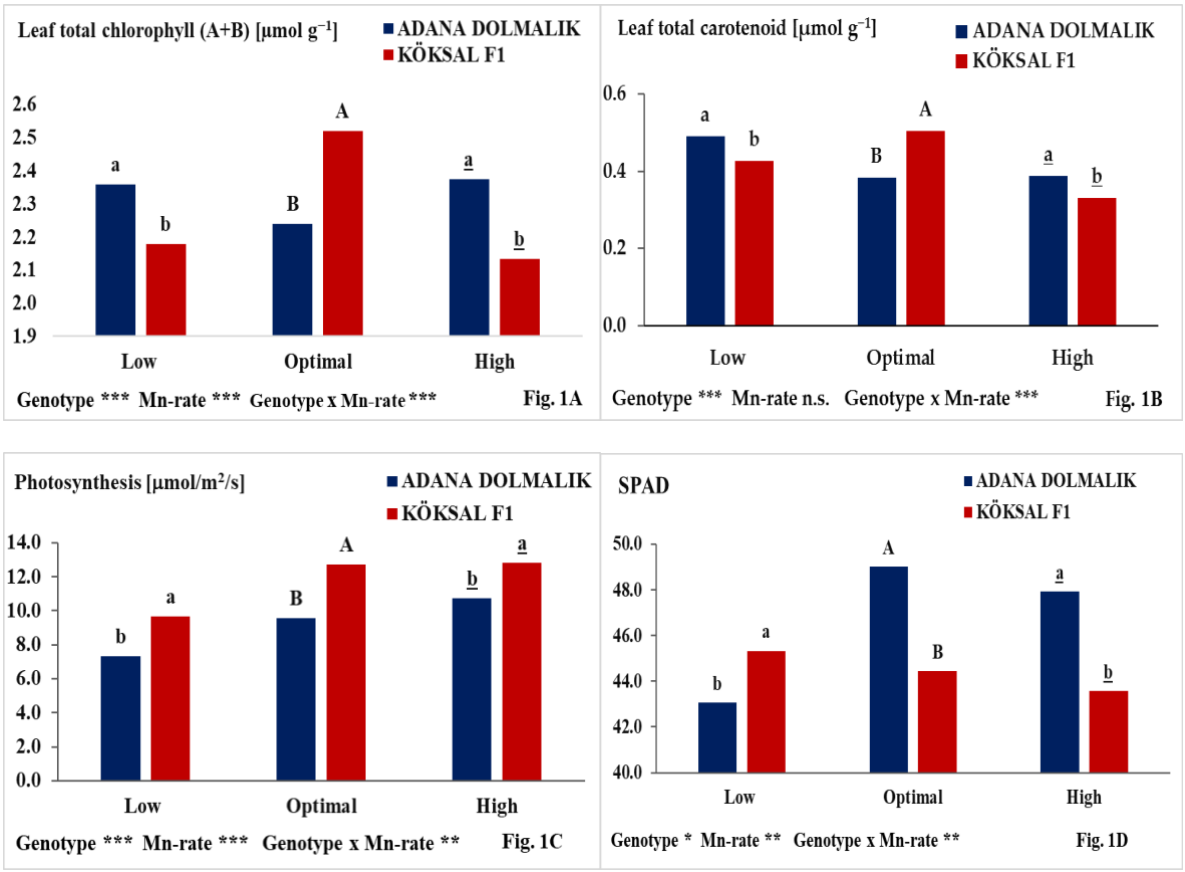

Figure 1. Leaf chlorophyll (a+b) (1A), carotenoid content (1B), photosynthesis (1C), and leaf chlorophyll index (SPAD) (1D) of eggplant genotypes (Adana cv. Dolmalık and Köksal cv. F1) grown under low, upper, and underlined case letters for low, optimal and high Mn supply, respectively) are significantly different between genotypes within columns. Significance of main and interaction effects *F* values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

Like our study Ceballos-Laita et al. (2018) stated that total chlorophyll content in old and young leaves decreased by approximately 50% in plants affected by Mn toxicity in tomato plants. Lidon et al. (2004) did not find any significant changes in the parameters of chlorophyll a fluorescence in plants exposed to increased concentrations of Mn and suggested that the accumulation of photosynthetic electron carriers is a major factor affecting photosynthesis in Mn-excess conditions. In another study, high levels of Mn usually have a positive effect on the chlorophyll content, and this was especially evident in hydroponically grown lettuce (cv. Locarno), in which a significant increase of 24-147% was noted (Przybysz et al., 2017). In contrast to our study, Silber et al. (2009) stated that leaf chlorophyll content was not affected by low Mn concentrations in tomato plants. Chlorophyll a fluorescence measurement of the maximum quantum efficiency of photosystem II (Fv/Fm) has proved useful for characterization of Mn deficiency in barley (Schmidt et al., 2016). This feature reflects the central role of Mn in the water-splitting complex of PSII (Schmidt et al., 2020). In the present work, we observed substantial differences among two eggplant genotypes in PSII quantum efficiency in response to incipient Mn deficiency. Under low and high Mn-rates, the eggplant genotype of Adana cv. Dolmalık produced significantly higher leaf chlorophyll (a+b) content. On the other hand, under optimal Mn-rate Köksal cv. F1 produced significantly higher leaf chlorophyll a and b (Figure 1A). Leaf carotenoid content was decreased under low and high Mn-rates. Under low and high Mn-rates, the higher carotenoid content was observed in Adana cv. Dolmalık, though lower carotenoid content was observed in Köksal cv. F1. Under optimal Mn-rate, significantly higher carotenoid content was produced in Köksal cv. F1 plants (Figure 1B).

Irrespective of the genotype, the addition of Mn increased gas exchange in the examined plants. Regarding the intensity of photosynthesis of the two eggplant genotypes grown in optimal and high Mn-rates, eggplant genotypes produced significantly higher photosynthesis as compared to low Mn-rate. Among the eggplant genotypes, Köksal cv. F1 produced significantly higher photosynthesis under low, optimal and high Mn-rates; on the other hand, Adana cv. Dolmalık produced significantly lower intensity of photosynthesis under low, optimal and high Mn-rates (Figure 1C). The photosynthetic apparatus might also be impaired due to a reduction in the number of chloroplasts and a decrease in the chlorophyll content resulting from excessive Mn accumulation (Demirevska-Kepova et al., 2004), and enhanced production of carotenoids, leading to symptoms similar to those triggered by photo inhibition (Doncheva et al., 2009). Long et al. (2021) documented substantial genotypic differences in maize genotypes in photosynthetic responses to Mn deficiency.

Manganese is taken up by plants as Mn^{2+} cations. Although it is a heavy metal, it may appear in plant tissues in concentrations higher than necessary for the proper functioning of organisms. Manganese is a

nutrient that has many physiological functions, including participation in many enzymes: Mn-catalase, dehydrogenase, decarboxylases, hydroxylases, acid phosphatases, transferases, SOD superoxide. Furthermore, it is present in xylogenesis, flavanols, and PS II complex-protein. Of particular importance is the share of micro-fission reactions of water in the light phase of photosynthesis (Ducic and Polle, 2005; Humphries et al., 2007). Excessive Mn nutrition may interfere with this physiological process and with the nutrient uptake, which could be a reason for worse yielding.

Regarding leaf chlorophyll index (SPAD), plants enhanced SPAD index under optimal and high Mn-rates as compared to low Mn-rate. There were no significant differences stated among eggplant genotypes under low Mn-rate. The eggplant genotype of Adana cv. Dolmalık increased SPAD index under both optimal and high Mn-rates. One of the first signs of the lack of manganese in the growth of plants, chlorophyll formation was collapsed, and the young leaves and branches were not achieving a normal green color. Furthermore, it has been shown by qualitative tests that the starch and sugar content

of the leaves of plants that became chlorotic is much less than the starch and sugar content of similar leaves that were grown during the same time. These facts show that manganese is an important and necessary factor in the synthesis of chlorophyll. Manganese occurs in the largest concentrations in the leaves and the pericarp and germs of seeds of plants (McHargue, 1926). In contrast to our study, Shenker et al. (2004) stated that the extreme Mn levels resulted in a gradual decrease in chlorophyll concentration in 14 days old tomato seedlings.

Biomass Production

Significant differences ($p < 0.001$) were found among genotype, Mn-rate and genotype x Mn-rate interaction in terms of shoot and root fresh matter. Mn is an essential metal (Marschner, 2012). Increasing Mn concentration in the nutrient solution increased the root fresh matter by 34.56% and main stem length %5.40 at high Mn-rate than low Mn-rate. Shoot fresh matter declined by almost 1.29% at a high Mn-rate than low Mn-rate under hydroponic conditions. The significantly higher shoot and root fresh matter were observed at Köksal cv. F1 under low Mn-rate and optimal Mn-rate, while under high Mn-rate significantly lower shoot and root fresh matter were observed at Adana cv. Dolmalık (Table 1). Eggplant "Köksal cv. F1" could be classified as tolerant while "Adana cv. Dolmalık" could be classified as sensitive genotype under Mn deficiency (Table 1). The study of Akinci et al. (2010) claim that in tomato plants root, shoot and leaf growth were generally enhanced at low Mn dose (50 mg L^{-1} Mn) than moderate Mn dose (100 mg L^{-1} Mn) and high Mn dose (200 mg L^{-1} Mn). Similarly, root, shoot and leaf biomass increased in low Mn concentration but decreased with increased Mn from moderate to high Mn concentration. Furthermore, Mou et al. (2011) stated that total plant biomass, shoot biomass and root biomass were significantly decreased under excess Mn concentration which was in line with our studies. With respect to main stem length, there were significant ($p < 0.05$) differences observed at the interaction of genotype x Mn-rate, while there were no significant differences found among genotype and Mn-rate. Increasing Mn concentration in the nutrient solution significantly increased main stem length of the eggplant genotype Adana cv. Dolmalık. However, in eggplant genotype Köksal cv. F1 under optimal Mn-rate recorded higher stem length growth than low and high Mn-rates (Table 1). According to Akinci et al. (2010) shows that increase in Mn-rate of tomato plant significantly decrease its stem length which contrasts with our finding where increasing Mn concentration caused stem length of Adana cv. Dolmalık genotype to decrease.

Table 1. Shoot and root fresh weight and main stem length of eggplant genotypes (Adana cv. Dolmalık and Köksal cv. F1) grown under different concentrations.

Mn rates	Shoot fresh weight (g plant^{-1})		Root fresh weight (g plant^{-1})		Main stem length (cm plant^{-1})	
	Adana D	Köksal F1	Adana D	Köksal F1	Adana D	Köksal F1
Low	117.0 a	115.0 a	19.3 b	33.4 a	16.3 a	15.2 b
Optimal	139.7 A	124.0 B	28.3 B	34.3 A	14.2 B	17.0 A
High	128.0 a	101.0 b	39.2 a	31.7 b	17.8 a	15.4 b
***F*-test**						
Genotype	***		***		ns	
Mn rate	***		***		ns	
Genotype × Mn rate	***		***		*	

[z] Values denoted by different letters (lower, upper and underlined case letters for low, optimal and high Mn supply, respectively) are significantly different between genotypes within columns at $p < 0.05$. Significance of main and interaction effects *F* values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***)

There were significant differences ($p < 0.001$) observed among genotype, Mn-rate, and genotype x Mn-rate interaction in terms of shoot and root dry matter and root:shoot ratio, while no significant differences were stated regarding root:shoot ratio at the interaction of genotype x Mn-rate (Table 2).

Increasing Mn concentration from low to high Mn rate in the nutrient solution recorded a percentage increase of 3.72% in shoot dry matter, 32.89% in root dry matter and 34.47% in root: shoot ratio (Table 2). As compared to optimal Mn-rate, a slight reduction in the biomass accumulation in eggplant was preceded by a decrease in the efficiency of the photosynthetic apparatus, which is in line with the findings of Li et al. (2010) and Lee et al. (2011). The significantly higher shoot and root dry matter and root:shoot ratio were found at Köksal cv. F1 under low Mn-rate. Higher toxicity of Mn in aerial parts than in roots is a

characteristic shared by many species Li et al. (2010; Rezai and Farboodnia, 2008). It can result from the fact that the inhibition of Mn uptake or its retention in roots is not a common strategy for maintaining normal growth under Mn excess. Under high Mn-rate significantly higher shoot dry matter was detected at Adana cv. Dolmalık. Under both optimal and high Mn-rates, there were no significant differences stated among genotypes regarding root dry matter. Excess Mn accumulation as compared to optimal Mn level caused to growth and biomass depression for eggplant genotypes. These results are similar to experiments with peas (Rezai and Farboodnia, 2008) and tomato (Akinci et al. 2010) that Mn toxicity limited plant growth and biomass.

High Mn-rate Köksal cv. F1 recorded the highest root:shoot ratio followed by low Mn-rate and medium rate accordingly (Table 2). There is more than one reason for decreased eggplant biomass yield under Mn-stress caused by the accumulation of manganese. Generally, excessive or toxic manganese concentrations influence negatively plant nutrition. The highest Mn-concentrations cause toxic symptoms on plants and probably symptoms with regarding to deficit of other nutrients, occurring for example on leaves (Kleiber, 2014).

Similar results were obtained by Mou et al (2011) in grape cultivars under 15–30 mM Mn-rates. These results suggest that genotypic differences in Mn concentration significantly influenced the fresh and dry biomasses, particularly in eggplant genotype of Köksal cv. F1 plants grown under low Mn-rate. Like our study, Mn concentrations on Mn toxicity were often below 5 mM in previous studies (Sarkar et al., 2004). In our study, plant growth in two eggplant genotypes was stimulated by as low as 0.000025 mM, 0.2 mM Mn, or 0.4 mM Mn. Savvas et al. (2009) and Kleiber (2014) reported that manganese nutrition had a significant influence on tomato yielding, while Chohura et al. (2009) and Kołota et al. (2013) claimed that in research on microelements the form of ions is also important. The optimal content of manganese in a nutrient solution is varied depending on a cultivar (Kleiber, 2014).

Table 2. Shoot and root dry weight and root:shoot ratio of eggplant genotypes (Adana cv. Dolmalık and Köksal cv. F1) grown under different concentrations.

Mn rates	Shoot dry weight (g plant^{-1})		Root dry weight (g plant^{-1})		Root:shoot ratio (g g^{-1})	
	Adana D	Köksal F1	Adana D	Köksal F1	Adana D	Köksal F1
Low	11.2 b	13.0 a	1.70 b	3.37 a	0.15 b	0.26 a
Optimal	15.2 A	14.0 A	2.80 B	3.37 A	0.18 B	0.24 A
High	14.5 a	10.6 b	3.27 a	3.47 a	0.23 b	0.33 a
***F*-test**						
Genotype	***		**		**	
Mn rate	**		***		***	
Genotype × Mn rate	***		**		ns	

[z] Values denoted by different letters (lower, upper and underlined case letters for low, optimal and high Mn supply, respectively) are significantly different between genotypes within columns at $p < 0.05$. Significance of main and interaction effects F values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

Changes in Total Leaf Number, Branch Number and Leaf Area

Total leaf number and total leaf area were significantly affected by genotypes, Mn-rate, and genotypes X Mn-rate interaction. There were significant differences among genotypes with respect to branch number but there were no significant differences found in Mn-rate and genotypes X Mn-rate interaction regarding branch number. Increasing Mn concentration in the nutrient solution increased the total leaf number by almost 25.0%, branch number 76.67% and total leaf area 4.58% at high Mn-rate than low Mn-rate under hydroponic conditions. Decreasing Mn concentration in the nutrient solution significantly increased the total leaf number at the eggplant genotype of Köksal cv. F1. However, no visible foliar Mn deficiency symptoms were observed. Though, there were no significant differences stated among genotypes regarding total leaf number under both optimal and high Mn-rates. In hydroponics, excessive accumulation of this element can be avoided by monitoring Mn levels in water used to prepare the growing medium and correctly adjusting its pH because the availability of Mn increases with a decreasing pH (Ducic and Polle, 2005). Nevertheless, the risk associated with Mn concentration in plant products is often underestimated.

Regarding branch number, there were no significant differences stated among eggplant genotypes under low, optimal and high Mn-rates. In contrast to our study, Maher and Thomson (1991) stated that reduced growth of tomato seedlings was associated with high levels of manganese in the plant. With respect to total leaf area, significantly higher values were noted at the eggplant genotype of Köksal cv. F1 under low, optimal and high Mn-rates (Table 3). Previous investigations have shown that the growth and yield of tomato may be restricted by both Mn deficiency and Mn toxicity (Shenker et al., 2004). In our study, the eggplant plants were more severely affected at the low than high Mn-rates in terms of total leaf number, branch number and total leaf area. In contrast to our study, Akinci et al. (2010) claim that under low Mn-rate (50 mg L^{-1} Mn) and control (0 mg L^{-1} Mn) total leaf area of tomato plants increased significantly as compared to moderate (100 mg L^{-1} Mn) and high Mn-rates (200 mg L^{-1} Mn).

The Effects in the Root Systems

Eggplant plants under low Mn supply produced higher total root length and total root volume than plants under high and optimal Mn supply (Table 4). In the present study, root parameters were variously affected by Mn rates in different cultivars.

Table 3. Total leaf number, branch number and total leaf area of eggplant genotypes ("Adana cv. Dolmalık" and "Köksal cv. F1") grown under different concentrations.

Mn rates	Total leaf number (LN plant^{-1})		Branch number (BN plant^{-1})		Leaf area (cm^2 plant^{-1})	
	Adana D	Köksal F1	Adana D	Köksal F1	Adana D	Köksal F1
Low	25.0 b	40.3 a	5.3 a	4.7 b	2274.1 b	3316.7 a
Optimal	34.7 A	32.3 A	12.3 A	11.3 A	2855.0 B	3424.9 A
High	41.3 a	40.3 a	8.7 a	9.0 a	2593.0 b	3253.7 a
***F*-test**						
Genotype	**		***		***	
Mn rate	**		ns		***	
Genotype × Mn rate	***		ns		***	

[z] Values denoted by different letters (lower, upper and underlined case letters for low, optimal and high Mn supply, respectively) are significantly different between genotypes within columns at $p < 0.05$. Significance of main and interaction effects F values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

Total root length, root volume and average root diameter were significantly ($p < 0.001$) affected by genotype, Mn-rate and the interaction of genotype X Mn-rate. Plants under low Mn supply exhibited usually an improved performance in root growth and root morphological development than plants grown under high and optimal Mn supply. The eggplant genotype of Adana cv. Dolmalık produced significantly higher total root length and root volume than "Köksal cv. F1" under low, optimal and high Mn-rates. Köksal cv. F1 produced significantly higher average root diameter under low, optimal and high Mn-rates as compared to Adana cv. Dolmalık. This reason might be the eggplant genotype of Adana cv. Dolmalık under stressful conditions produces more root surface but lower root diameter. A large root system is considered to be an advantage for nutrient acquisition (Lynch, 2013), especially for elements with low mobility in soils, such as Mn. Deficiency of Mn is known to negatively affect the extension of the main root axis as well as the formation of lateral roots (Broadley et al., 2012). A recent study on Douglas fir showed that root growth relied on hydroponic Mn concentration (Ducic and Polle, 2007).

Bromfield (1978) and Sonneveld and Voogt (1980) also stated a tendency for Mn to be depleted in the root zone of soilless-grown crops and ascribed this phenomenon to immobilization of soluble Mn by oxidizing bacteria, which are common in nutrient solutions. It seems, therefore, that in our experiment, part of the Mn supplied to the plants through the nutrient solution was immobilized by microorganisms. The microbial oxidation of Mn in nutrient solution is beneficial when Mn is supplied at excessively high rates but potentially harmful if Mn is supplied at rates close to the standard requirements for plant uptake.

Similar to our study, Mou et al. (2011) stated that in a grape cultivar of Jinshou and Shuijin, except for the root volume increased by 15 mM Mn treatment, root length and root area were decreased with an increase in Mn concentration. Root diameter was increased with an increase in Mn levels in all grape cultivars except for Shuijin at an extremely high Mn level (60 mM). For root hairs, grape cultivars of Jinshou and Shuijin were much more affected by Mn than grape cultivar of Combier. At the concentration of 30 mM Mn treatment, pronouncedly decreased root hair elongation and hair density in grape cultivars of Jinshou and Shuijin was found although it had little effect in cultivar Combier; while under 60 mM Mn treatment, root hairs were torn down, and little hair remained in root surface in all cultivars. In contrast to our study, they stated that in grape cultivar of Combier root area and root volume increased with the increasing of Mn levels (ranged from 0 to 30 mM), but all these three root parameters were decreased under higher Mn^{2+} levels (45–60 mM).

Table 4. Total root length, root volume and average root diameter of eggplant genotypes (Adana cv. Dolmalık and Köksal cv. F1) grown under different concentrations.

Mn rates	Total root length (m plant^{-1})		Total root volume (cm^3 plant^{-1})		Av. root diameter (mm)	
	Adana D	Köksal F1	Adana D	Köksal F1	Adana D	Köksal F1
Low	43.95 a	24.42 b	2.78 a	1.91 b	0.29 b	0.38 a
Optimal	35.87 A	16.73 B	2.62 A	2.00 B	0.31 B	0.41 A
High	35.71 a	24.74 b	2.39 a	1.94 b	0.29 b	0.36 a
***F*-test**						
Genotype	***		***		***	
Mn rate	***		***		***	
Genotype × Mn rate	***		***		**	

[z] Values denoted by different letters (lower, upper, and underlined case letters for low, optimal and high Mn supply, respectively) are significantly different between genotypes within columns at $p < 0.05$. Significance of main and interaction effects F values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

Conclusions

In conclusion, our results showed that shoot, root growth, leaf physiological and root morphological parameters were significantly affected by different Mn rates. Both excessive and insufficient Mn concentrations resulted in reduction of shoot fresh and dry matter, branch number, total leaf area, and leaf total chlorophyll content in the two stated genotypes. Köksal cv. F1 has proven to be Mn-efficient under low Mn rates. While Adana cv. Dolmalık is responsive under high Mn rates. This further indicates that deficit and excess Mn nutrition could negatively affect the crop yield of eggplant.

Compliance with Ethical Standards

Conflict of interest

The authors declared that for this research article, they have no actual, potential or perceived conflict of interest.

Author contribution

The contribution of the authors to the present study is equal. All the authors read and approved the final manuscript. All the authors verify that the Text, Figures, and Tables are original and that they have not been published before.

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Data availability

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