Effects of Selenium on Growth Parameters of Tomato and Basil under Fertigation Management

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Abstract. Tomato 'Abigail' (Solanum lycopersicum L.) and basil 'Perry' (Ocimum basilicum L.) were selected as model plants for selenium (Se) supplementation to evaluate a) effects of Se concentration in nutrient solution on Se content in different organs under fertigation, b) Se phytotoxicity threshold values, and c) mechanisms. Plants grown in a glasshouse were irrigated with 0, 1, 2, 5, and 10 mg Se/L in the first experiment, while with 0, 0.25, 0.5, 0.75, 1.0, and 1.5 mg Se/L in the second. Tomato plants accumulated Se linearly with rising Se concentrations, whereas accumulation in basil followed a saturation curve. Plants supplemented with 1.5 mg Se/L in the irrigation water accumulated 0.23 and 0.88 mg Se/g dry weight (DW) in tomato fruits and basil shoots, respectively. However, tomato roots, shoots and fruits DW were 56%, 36%, and 66% lower than in controls, respectively, and basil roots and shoots DW were 92% and 88% lower than in control, respectively. Calculated toxicity-threshold values were 1.27 mg Se/L for tomato and 0.44 mg Se/L for basil. Tomato crops were more tolerant than basil crops, although data suggested yield reduction at lower Se concentrations than those effecting biomass reductions. The results indicate that Se supplementation through drip irrigation may efficiently fortify tomato and basil. However, Se concentrations should be lower than 0.75 and 0.25 mg·L⁻¹ for tomato and basil, respectively, to avoid yield reduction and possible Se phytotoxicity.

Selenium is a nonmetal element belonging to the oxygen-sulfur-tellurium group, and is ranked 70th among the 98 elements

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that form the earth's crust. Se is found in sulfide ores such as pyrite, where it partially replaces the sulfur. Oxidation of pyritic parent material is an important natural source of Se in soil where human activities, such as mining, groundwater drawdown, and wetland drainage, have exposed pyritic materials to a more oxidizing environment (Strawn et al., 2002). Se content in most soils ranges from 0.01 to 2 mg·kg⁻¹, but can vary from ≈ 0 to > 10 mg·kg⁻¹ in certain regions (Fordyce, 2005). Se is distributed in the environment through natural processes of weathering; disposal of human, animal, and plant wastes; and emission of volcanic ash (Oldfield, 2002).

Se has been recognized as an essential trace element for animals and humans (Oldfield, 2002). Adult humans have a daily requirement of 55 to 70 µg Se. Se-deficiency diseases have been recognized in some regions: Keshan disease, an endemic cardiomyopathy, and Kashin-Beck disease, a deforming arthritis, were first identified in the Keshan region of China, where the soil is extremely low in Se (Chen et al., 1980; Tan and Huang, 1991). Diet is the main source of Se for humans and animals. Therefore, increasing Se concentrations in the tissues of edible crops by Se-fertilization strategies would improve the overall contribution of Se to human and animal diets (Carvalho et al., 2003). Plants play a unique role in recycling and delivering Se from the soil into the food chain, even though Se has not been yet confirmed as an essential plant micronutrient. In Finland, for example, selenate has been added to fertilizers since 1984 to increase the Se in soils (Alfthan et al., 2010; Wang et al., 1998), where the geochemical soil conditions are relatively uniform, two decades of supplementation of soils nationwide with fertilizers containing inorganic Se were safe and effective way of significantly increasing Se concentrations in most crop plants grown for human consumption (Alfthan et al., 2010). Great Britain has also undertaken efforts to develop soil amendment practices with inorganic Se to increase dietary Se intake through the Se biofortification of food crops (Rayman, 2012). Similarly, vegetables rich in Se contribute as much as 28% to 32% of humans' daily Se intake in northern Mexico (Kopsell et al., 2009). Malorgio et al. (2009) investigated the effects of Se fertilizer in a hydroponic system on growth of lettuce and chicory and Se content in the plant tissues. Addition of 0.5 and 1.0 mg·L⁻¹ Se in the nutrient solution had a positive effect on plant yield and increased Se content in the crops' leaves. Kopsell et al. (2009) reported a linear accumulation of Se up to 56 mg·kg⁻¹ in leaves of basil after foliar fertilization with three applications of 32 mg·L⁻¹ Se. In that study, daily Se application in the irrigation system seemed to be more efficient than foliar

Contrary various industrial activities, such as oil refineries, electrical utilities, and waste from glass, synthetic pigments, and semiconductor devices can contaminate soil and water bodies with Se (Mirbagheri et al., 2008; Terry et al., 2000). In addition, irrigation of semiarid farmlands in seleniferous regions is a common source of Se contamination, particularly in the presence of an impermeable subsurface layer, where leached Se can accumulate to toxic levels. This phenomenon has been well documented in the San Joaquin Valley of California, where high concentrations of Se $(\approx 300 \ \mu g \cdot L^{-1})$ in the subsurface agricultural drainage water caused a high incidence of deformity and mortality in waterfowl hatchlings at the Kesterson National Wildlife Refuge (Deverel and Millard, 1988; Fio et al., 1991; Fujii et al., 1988; Ohlendorf et al., 1986; Spallholz and Hoffman, 2002). Anthropogenic

application.

Se contamination of groundwater was documented in the Shimron wells located in the Yizre'el Valley in northern Israel (Michelson, 1990). A high concentration of Se (up to 37 $\mu g \cdot L^{-1}$) in the well water caused shutdown of two wells in the surrounding area (Michelson, 1990). This high Se concentration could enter the food chain and injure humans and animals. In humans, daily intake greater than 900 μg Se may result in toxicity, termed selenosis (Kopsell et al., 2009).

Plants accumulate selenate against its electrochemical potential gradient by active transport. Among the factors that affect Se status in the plant, species is the most important. Plants can be classified into three main groups according to their Se uptake: primary, secondary, and non-Se accumulators. The Se toxicity threshold for nonaccumulator plants varies from 2 to 330 mg·kg⁻¹ DW in rice and white clover, respectively (Terry et al., 2000). In contrast, Se-accumulator plants can hold Se concentrations of >4000 mg·kg⁻¹ with no toxic effects (Terry et al., 2000). Beath et al. (1937) found a Se level of 14,990 ppm in a sample of Astragalus racemosus, which is a primary accumulator. Also, most plants, even when grown in seleniferous soils, only contain ≈ 10 ppm Se, or less. Se can accumulate in plant tissues to levels that are toxic to the plant itself. In this case, high Se contents in the plant tissue can cause growth inhibition, yield reduction, chlorosis, and even plant mortality (Terry et al., 2000). Hurd-Karrer (1937) was the first to describe Se phytotoxicity (snow-white chlorosis) in wheat plants that were exposed to 20 mg Se/kg soil in a pot experiment. Se phytotoxicity in wheat was also investigated under field, glasshouse, and laboratory conditions by Lyons et al. (2005), In that study, no Se toxicity symptoms were observed in the field trials with rates of up to 120 g Se/ha as selenate, and in pilot trials with up to 500 g Se/ha applied to the soil or up to 330 g Se/ha applied to the foliage, with soils containing low sulfur (S) concentrations (2–5 mg·kg⁻¹). The critical tissue level for Se toxicity was 325 mg·kg⁻¹ on a DW basis, attained by adding 2.6 mg Se/kg to the growth medium as selenate. Solution concentrations above 10 mg Se/L inhibited early root growth of wheat in laboratory studies (Lyons et al., 2005).

The narrow margin between beneficial and harmful levels of Se has important implications for human health and crop production. Most studies have focused on either supplementation or toxicity aspects of Se, mainly through Se soil amendment or foliar fertilization. Se supplementation via fertigation could provide a practical and efficient method for crop fortification. Therefore, it is important to detail the relationships between Se concentrations in the nutrient solution, plant growth, and Se content. Using tomato and basil as model plants for crops with edible fruits and leaves, respectively, the specific objectives of the present study were to a) examine a wide range of Se concentrations in the irrigation water to determine the concentrations that can enrich basil and tomato

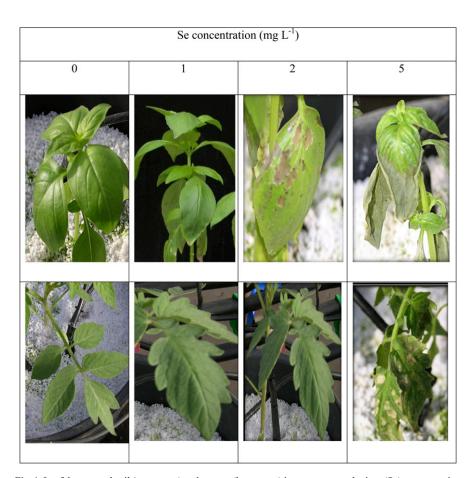


Fig. 1. Leaf damage to basil (upper row) and tomato (lower row) in response to selenium (Se) concentration (0, 1, 2, and 5 mg Se/L) in nutrition solution.

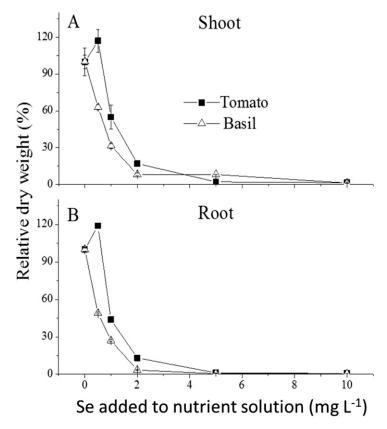


Fig. 2. Relative dry weight of (A) root and (B) shoot as affected by selenium concentration in nutrient solution

plants with Se without damaging yield and b) assess and study Se phytotoxicity threshold values and underlying mechanisms.

Materials and Methods

Experimental setup. The experiment was conducted at the Agricultural Research Organization's Newe Ya'ar agricultural research center in northern Israel, (lat. 32°70′ N, long. 35°18′ E). Basil (cv. Perry) and tomato (cv. Abigail) were selected as model plants for leaf and fruit crops, respectively, in controlled glasshouse experiments. Seedlings, 3 weeks after seeding when the second true leaf appeared, were planted in 10-L pots containing perlite no. 212 (Agrical, Habonim, Israel), and were drip irrigated three times a day to excess to obtain $\approx 30\%$ drainage, so that excess salts would leach from the pot. Plants were fertilized with Shefer fertilizer (Fertilizers and Chemicals, Haifa, Israel) containing (g· L^{-1}): nitrogen (N) (70), phosphorus (P) (14), potassium (K) (58), iron (0.71), manganese (0.35), zinc (0.17), copper (0.026), and molybdenum (0.019). The fertilizer solution was applied via the irrigation system at a dilution of 1:500 in the irrigation water. The experiments were conducted on split plots by plant type, with five replicates each (five pots) for each treatment (different Se concentrations). Se treatments were applied through the irrigation system as sodium selenate (Na₂SeO₄; Sigma-Aldrich, Saint Louis, MO) starting 1 week after planting. In the first experiment, plants were planted on 14 Oct. 2010, and Se concentrations of 0, 0.5, 1, 2, 5, and 10 mg·L⁻¹ were applied. Plants were grown for 1 month. In the second experiment, the Se concentrations were 0, 0.25, 0.5, 0.75, 1.0, and 1.5 mg·L⁻¹. In this experiment, plants were planted on 14 Dec. 2010 and grown for 3 months (until fruit ripening on the tomato plants). Electrical conductivity and pH of the irrigation water, shoot length, and toxicity symptoms were recorded once a week. After the end of the growing period, shoots (stem and leaves), fruits (second experiment), and roots were harvested separately and their fresh weights determined. They were then dried at 70 °C for 48 h and reweighed for DW determination. Basil shoots were harvested four times during the experiment, at 2-week intervals, starting from 23 Jan. 2011.

Chemical analysis. Three of the five replicates of each treatment were analyzed. Shoot, fruit, and root tissues were ground and digested with nitric and perchloric acid wet digestion (Miller, 1997) for calcium (Ca), magnesium (Mg), S, and Se analyses, and with concentrated sulfuric acid digestion for N, sodium (Na), P, and K, or extracted in distilled water for chloride (Cl) analysis. For the basil plants, only the last shoot harvest was analyzed. The K and Na concentrations were determined by flame spectrophotometry (Lachica et al., 1973), and ammonia-N and P concentrations by autoanalyzer. Ca, Mg, and Se concentrations were determined by atomic absorption spectroscopy (AAS 800; Perkin-Elmer, Shelton, CT) and S concentration was

determined by inductively coupled plasma emission spectroscopy (Varian, Australia). Cl⁻ concentration was measured by titration with silver nitrate according to Kolthoff and Kuroda (1951).

Statistical analysis. Data were subjected to Tukey's honestly significant difference test, with a significance level P=0.05. Percentage results were transformed using arcsin transformation before the analysis.

Results and Discussion

The leaf injuries caused by excess Se are shown in Fig. 1. The toxicity symptoms were more pronounced in basil than in tomato. In the former, the leaf damage started at 2 mg Se/L, whereas for the latter, it started after application of 5 mg Se/L.

The effect of Se on shoot and root growth is presented in Fig. 2. Increasing Se concentration in the irrigation water dramatically decreased biomass in both tomato and basil plants'. Here too, tomato was less sensitive to Se than basil. Since these concentrations caused severe damage, in the second experiment, we

decreased them to a maximum of 1.5 mg Se/L. The toxicity symptoms could be a result of Se accumulation in the leaves, which in turn would cause physiological damage to the plant. Both basil and tomato plants accumulated Se in their tissues when introduced through the irrigation system. However, differences in the patterns of Se accumulation were noted between species. Tomato plants accumulated Se linearly with rising concentrations in the irrigation water in all analyzed tissues (Fig. 3), but the slope differed among roots, shoots, and fruits. The highest Se concentration was found in the shoot tissue, up to 0.36 mg·g⁻¹ DW at 1.5 mg Se/L in the irrigation water, whereas it was lowest in the fruits, reaching 0.23 mg·g⁻¹ DW at 1.5 mg Se/L and 0.1 mg·g⁻¹ DW at 0.25 mg Se/L treatment.

In basil root tissues, Se also accumulated linearly with rising Se concentration in the irrigation water, whereas in the shoots, accumulation followed a saturation curve best represented by a polynomial equation (Fig. 4). Se concentration in the basil shoots was four times higher than that in the root

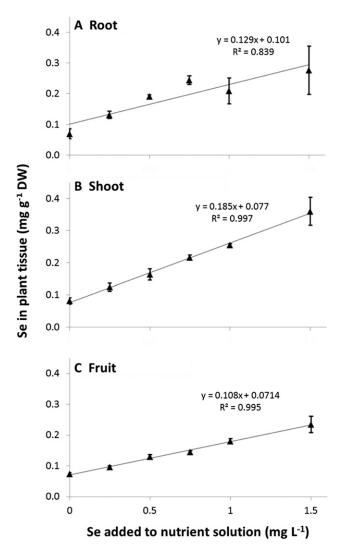


Fig. 3. Selenium (Se) concentration in (A) root, (B) shoot, and (C) fruit of tomato plants as a function of Se concentration added to the nutrient solution. Bars indicate standard errors (n = 3).

tissues (0.88 and 0.18 mg·g⁻¹ DW, respectively) under the highest Se treatment. Shoot Se accumulation at the lowest Se concentration reached 0.12 mg·g⁻¹ DW. These results indicate the feasibility of Se supplementation through the irrigation system for both basil and tomato plants. However, relatively high Se concentrations were found in the edible parts of the tested crops, even at the lowest Se dosage in the irrigation water. Furthermore, basil accumulated Se more readily in its edible parts than tomato crops. Malorgio et al. (2009) investigated the effects of Se on chicory and lettuce production and storage. Growth, ethylene production and chlorophyll content were examined in plants grown in Se-enriched nutrient solutions on a floating hydroponic system. The addition of 0.5 and 1.0 mg Se/L to the nutrient solution resulted in increased Se concentration in the leaves, which had a positive effect on plant yield. In addition, Se was generally effective at decreasing ethylene production. The addition of 0.5 mg Se/L to the nutrient solution effectively prevented chlorophyll loss in lettuce plants. These results imply potential shelf life-prolongation characteristics of Se supplementation (Malorgio et al., 2009). Foliar supplementation was tested on basil and tomato plants in both growth chamber and field environments (Hawrylak-Nowak, 2008; Kopsell et al., 2009). A wide concentration of selenates (1-50 mg Se/L) did not cause plant injuries and only affected the physiological parameters to a small extent. There were visual symptoms of slight Se phytotoxicity when the tissue Se concentrations exceeded 25 and 20 µg·g⁻¹ DW for the basil cultivated in a chamber and in the field, respectively (Kopsell et al., 2009). In a greenhouse experiment, foliar application of Se $(10^{-1}, 10^{-4}, 10^{-5}, 10^{-6}, \text{ and } 10^{-7}\%)$, or application through drip irrigation (7.5 g·ha⁻¹) considerably increased total Se content in leaves, pulp, and skin (Golubkina et al., 2003). Analysis of Se distribution in the different plant organs showed Se concentrations of 198 $\mu g \cdot k g^{-1}$ in the leaves and 47.7 $\mu g \cdot k g^{-1}$ in the pulp (mesocarp and endocarp), while the concentration in the fruit skin (exocarp) was 208.8 μg·kg⁻¹. Carvalho et al. (2003) measured a significant difference in Se distribution between edible and nonedible tissues in tomato, strawberry, radish, and lettuce plants. For three of these crops, grown in the phytotron in pots with soil containing 1.5 mg Se/kg sand, more than 99% of the Se accumulated in nonedible parts (leaves, stems, and roots) and less than 1% in the edible tissues. However for lettuce, most of the Se was accumulated in the edible leaves. These results, similar to those obtained by Pezzarossa et al. (1999) in tomato plants, indicate that plants can be used as Se scavengers in Se-contaminated soils.

Despite the possibility of Se supplementation in crops, it caused significant phytotoxicity symptoms in both species tested. Several Se phytotoxicity mechanisms are possible: a) S nutrient deficiency and b) physiological plant stress as a result of Se interaction with biochemical processes. Relative roots (Fig. 5A) and shoots (Fig. 5B)

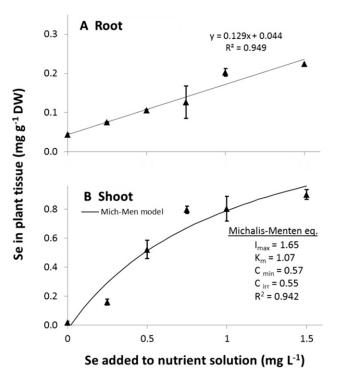


Fig. 4. Selenium (Se) concentration in (A) root and (B) shoot tissues of basil plants as a function of Se concentration added to the nutrient solution. Bars indicate standard errors (n = 3). Michalis–Menten model was fitted based on 0.55 mg·L⁻¹ Se in the irrigation water (C_{irr}); K_m and C_{min} are also given in mg·L⁻¹ units and the I_{max} is given in terms of mg Se/g DW for the whole experiment period.

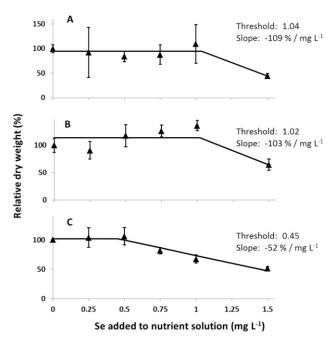


Fig. 5. Relative dry weight of (A) root, (B) shoot, and (C) fruit tissues of tomato plants compared with the corresponding control tissues as function of Se concentration in the irrigation water. Presented data are means \pm sp of three replicates. Different letters indicate statistically significant differences (P = 0.05%) between Se treatments. Curves, threshold, and slope values calculated from the von Liebig model.

DW of tomato plants were not significantly affected by Se concentration in nutrient solutions with <1 mg Se/L relative to the control group with no Se supplementation in the nutrient solution. Tomato fruits were more sensitive to Se concentration, where significant biomass reduction was observed with

0.75 mg Se/L in the irrigation water, resulting in an 18% reduction in DW relative to control tomato plants (Fig. 5C). Treatment with 1.5 mg Se/L caused DW reductions in all three tomato tissues analyzed, with roots, shoots, and fruits being 56%, 36%, and 66% smaller than the respective control plant

tissues. The average toxicity-threshold values, calculated using the von Liebig model, for roots, shoots, and fruits were 1.04, 1.02, and 0.45 mg·L $^{-1}$, respectively, indicating that the fruits were more sensitive to Se in the nutrient solution, compared with the roots and shoots. As for fruit yield parameters, Se concentrations between 0 and 0.5 mg·L $^{-1}$ had no significant effect on the relative yield or relative fruit number (data not shown). Se at 1.5 mg·L $^{-1}$ reduced both parameters, to 51% and 42% of control plants. Tomato fruit total soluble solids did not differ significantly with rising Se concentrations in the nutrient solution (data not shown).

Biomass reduction in basil plants fits an exponential model in both root and shoot tissues (Fig. 6). Roots of basil plants exposed to 0.5 mg Se/L were 58% smaller than control plant roots, whereas at the same concentration no significant weight reduction was noted in the shoots. Basil shoots were harvested four times during the experiment, at 2-week intervals. An exponential decrease was observed in relative basil yield between harvests (Fig. 6B). The first three harvests were gradually affected by the Se treatments, as noted from the exponents -0.51, -1.78, and -1.99, in the first, second, and third harvest, respectively. The last harvest exponent value of -1.37 was slightly higher than the previous harvest, going against the general trend. This might be due to the change in temperature between the third and fourth harvests, increasing by an average of 2 °C. The higher temperature may have increased plant tolerance to the Se. A similar phenomenon was described by Lyons et al. (2005) in a hydroponic experiment in which a 4 °C increase was shown to increase wheat plant tolerance to Se concentrations in the nutrient solution. Thus, the effect of temperature on Se phytotoxicity warrants further investigation.

A dramatic reduction of 92% and 88% in roots and shoots DW, respectively, was found in plants irrigated with 1.5 mg Se/L. Figure 6 shows the effect of Se applied to the roots and shoots of basil plants. The basil roots were found to be more susceptible to Se concentration than the shoots. This was also noted by the differences in exponent values: –1.662 for the roots compared with an average of –1.39 for the shoots. Se phytotoxicity symptoms and biomass reduction are dependent on Se exposure period and dosage, as implied from the basil harvest results.

The solution Se concentration that resulted in a 50% DW reduction in the most sensitive tissue (fruits for tomato and roots for basil) compared with the control was termed Se₅₀. A Se₅₀ value of 1.27 mg Se/L was calculated for tomato fruit from the linear trend line between 0.5 and 1.5 mg Se/L (x-axis values) where significant statistical differences were found (Fig. 5C). The calculated Se₅₀ value for basil roots was 0.44 mg Se/L (Fig. 6A). According to Lyons et al. (2005) results, a Se₅₀ value of \approx 35 mg Se/L in the growth solution can be calculated for wheat crops. This result indicates that both basil and tomato crops are more susceptible

to Se concentration in the nutrient solution than wheat cultivars. It may also be concluded that tomato plants are more tolerant to higher Se concentrations in the irrigation water than basil plants.

Concentrations of macronutrients in tomato and basil plants are shown in Table 1. N, P, and K concentrations did not differ significantly in either of the crops with Se treatments and are not shown. A significant decrease in Ca concentration was observed in tomato roots and shoots with increasing Se concentration in the nutrient solution, whereas in basil, Ca concentration only

decreased in the shoots. These findings contradict those obtained in several studies conducted on tall fescue (Festuca arundinacea Schreb.), white clover (Trifolium repens L.), wheat (Triticum aestivum L.), and corn (Zea mays L.) crops, which showed an increase in plant Ca accumulation with increasing Se concentrations. According to Kinraide (2003), addition of solutes as CaCl₂, MgCl₂, or SrCl₂, or reduction in pH enhanced the uptake of Se by plant roots. This was explained by elevated plasma membrane surface activity of SeO₄⁻², caused by solute-induced reduction of plasma membrane surface negativity. Feng et al.

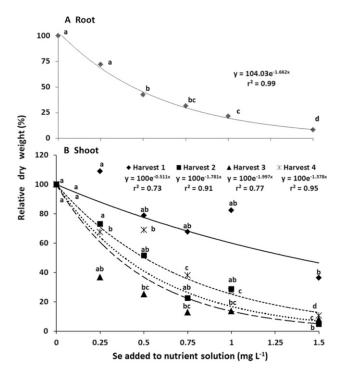


Fig. 6. Relative dry weight of (A) roots and (B) shoots yield of four harvests collected at 2-week intervals of basil plants compared with control plants as a function of Se. concentration in the nutrient solution. Different letters indicate statistically significant differences (P = 0.05%) between Se treatments.

Table 1. Average concentration of macroelements in different tissues of tomato and basil plants irrigated with different selenium (Se) concentrations.

	Se concn. in nutrient	Total content $(g \cdot kg^{-1})$							
		Ca		Mg		Na		Soluble Cl ⁻	
Tissue	solution $(mg \cdot L^{-1})$	Tomato	Basil	Tomato	Basil	Tomato	Basil	Tomato	Basil
Root	0	22.7 a	6.8 a	7.6 a	6.6 a	15.4 a	13.8 a	101.0 a	73.0 a
	0.25	16.3 ab	8.3 a	6.1 a	6.4 a	14.3 a	12.9 a	91.5 a	70.5 a
	0.5	14.4 ab	7.4 a	6.8 a	7.4 a	13.9 a	15.7 a	98.5 a	80.0 a
	0.75	14.6 ab	8.4 a	6.0 a	7.1 a	15.6 a	12.9 a	105.8 a	38.3 b
	1.0	16.8 ab	9.6 a	6.3 a	8.7 a	11.1 a	9.2 b	77.0 a	_
	1.5	11.3 b	8.6 a	4.7 a	5.3 a	12.5 a	6.4 b	72.7 a	_
Shoot	0	34.5 a	33.2 a	14.3 a	7.1 a	8.2 ab	1.0 a	244.4 a	66.4 ab
	0.25	30.4 ab	26.0 a	11.9 ab	7.6 a	10.2 a	0.8 a	219.9 ab	85.1 a
	0.5	30.7 ab	27.1 a	12.3 ab	6.7 a	9.2 a	0.8 a	177.5 bc	75.3 a
	0.75	28.1 ab	19.3 ab	10.1 bc	6.3 a	6.1 ab	0.7 a	173.2 cd	82.9 a
	1.0	26.2 ab	19.0 ab	9.1 bc	5.6 a	3.8 b	0.6 a	110.6 de	48.0 b
	1.5	19.5 b	15.0 b	7.8 c	4.9 a	3.4 b	1.0 a	71.6 e	49.1 b
Fruit	0	2.1 a	_	1.7 ab	_	2.1 a	_	60.3 ab	_
	0.25	1.3 a	_	1.8 a	_	2.2 a	_	85.1 a	_
	0.5	1.2 a	_	1.4 ab	_	2.0 a	_	75.3 a	_
	0.75	1.3 a	_	1.3 b	_	1.8 a	_	83.0 a	_
	1.0	1.4 a	_	1.3 b	_	1.7 a	_	49.0 b	_
	1.5	1.5 a	_	1.3 b	_	1.5 a	_	49.1 b	_

Different letters indicate statistically significant differences (P = 0.05) between Se treatments.

(2009) observed a decrease in Ca concentration in chinese brake fern plants (*Pteris vittata* L.) when Se concentration was <2 mg·L⁻¹ in nutrient solution. This decrease in Ca concentration might be explained by differences in plant physiology between the different species.

Tomato and basil shoots and roots Cl concentrations decreased on exposure to increasing Se concentration levels (Table 1). Shennan et al. (1990) documented a 40% reduction in Se uptake by tomato cv. UC82B under high Cl salinity treatment. The effect of high Cl concentration corresponded closely with the \approx 40% reduction in selenate activity calculated for the high salt solutions in that study. As both are negatively charged, it could be assumed that Se has a counter effect on Cl activity. Se and S amounts (mg plant/ DW) in tomato and basil are summarized in Figs. 7 and 8, respectively. Tomato fruit S concentration did not differ significantly from Se concentrations (data not shown). In root tissues of both crops, S levels decreased with increasing Se concentrations in the irrigation water and with Se accumulation in the tissue (Figs. 7A and 8A). The competitive nature of selenate and sulfate with each other has been shown previously as inhibition of selenate uptake by sulfate (Hurd-Karrer, 1937; Kopsell and Randle, 1999; Leggett and Epstein, 1956; Pezzarossa et al., 1999; Shennan et al., 1990; White et al., 2004, 2007). In contrast, however, shoot S content increased with Se concentration, following a similar pattern in the shoot tissue of tomato and basil crops (Figs. 7B and 8B, respectively). These results are consistent with previous observations that increasing selenate concentration in the rhizosphere increases shoots S concentrations (Banuelos et al., 1990; Kopsell and Randle, 1999; Lyons et al., 2005; White et al., 2004). Sulfate is translocated in an acropetal direction, and reduction takes place in the chloroplasts. It is believed that selenate and sulfate follow similar translocation and incorporation patterns (Kopsell and Randle, 1999). These observations have been interpreted as resulting from either selenate or Se metabolites antagonizing the repression of sulfate transporters by sulfate and its metabolites (White et al., 2004). According to this hypothesis, S may accumulate to toxic levels in plant shoots as a result of decreased S transport selectivity. The S concentration results at the highest Se concentration in our experiment (1.5 mg·L⁻¹) indicated an increase of 42% and 140% relative to the control tomato and basil shoots, respectively. The excess of S may be metabolized to organic nonprotein forms or remain as sulfate. Due to the highly similar properties of Se and S, Se may be able to replace S in biochemical systems. However, the differences in size and ionization properties of S and Se may result in significant alterations in protein structure (Terry et al., 2000). The Se atom is larger than that of S with a radius of 0.5 Å compared with 0.37 Å, respectively. As a consequence, the bond between two Se atoms is about one-seventh longer and one-fifth weaker than the disulfide bond. Nonspecific integration

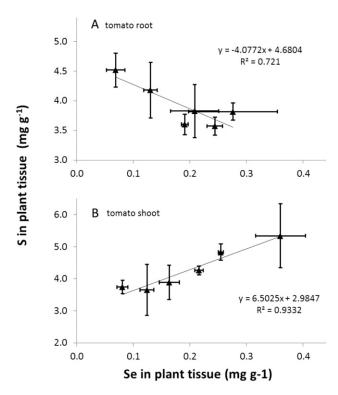


Fig. 7. Concentration of sulfur in (A) root and (B) shoot tissues of tomato plants as a function of selenium concentration in the shoots and roots. Bars indicate standard error (n = 3).

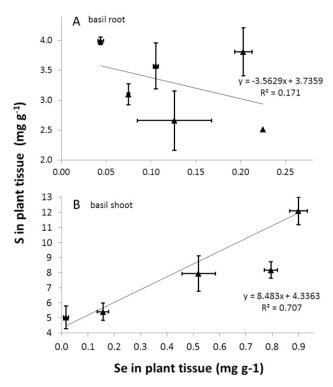


Fig. 8. Concentration of sulfur in (A) root and (B) shoot tissues of basil plants as a function of selenium concentration in the shoots and roots. Bars indicate standard errors (n = 3).

of the amino acids SeCys and SeMet into proteins is believed to be the major contributor of Se toxicity in plants (Sors et al., 2005). For example, in the case of SeMet as a substitute for Met, the bleaching induced by excess Se may be due to inhibition of porphobilinogen

synthetase, an enzyme required for chlorophyll biosynthesis (Smith and Watkinson, 1984). Furthermore, selenate may inhibit glutathione biosynthesis and interfere with the in vivo reduction of nitrate in leaves (Aslam et al., 1990; Dekok and Kuiper, 1986).

Conclusions

We conclude that Se supplementation through fertigation is an efficient way to fortify tomato and basil. However, Se concentrations should be lower than 0.75 and 0.25 mg·L⁻¹ for tomato and basil, respectively, to avoid yield reduction and possible Se phytotoxicity. Tomato and basil differ in their accumulation patterns and concentrations of, as well as tolerance to Se supplemented through the irrigation system. Tomato plants were found to be more tolerant than basil crops, although data indicate that yield may be reduced at lower Se concentrations, even before biomass reduction is noted. The long-term effects of supplementation with low concentrations of Se could have implications for the feasibility of Se nutrition by fertilization on certain crops.

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