European Journal of Biology
Eur J Biol 2023; 82 (2): 154–160
DOI: 10.26650/EurJBiol.2023.1353293

RESEARCH ARTICLE

Selenium Toxicity Induced Physiological and Biochemical Alterations in Maize Seedlings

Mustafa Yildiz[1], Emre Pehlivan[1], Hakan Terzi[1]

[1]Afyon Kocatepe University, Department of Molecular Biology and Genetic, Faculty of Science and Literature, Afyonkarahisar, Turkiye

ABSTRACT

Objective: Selenium (Se) is not necessary for plants but alleviates the harmful effects of abiotic stresses. Indeed, high Se levels cause toxicity by inducing oxidative stress and disrupting several metabolic processes. However, the underlying mechanisms remain poorly understood.

Materials and Methods: The effects of Se toxicity on the morphological and physiological attributes of hydroponically grown maize (*Zea mays* L.) seedlings were illustrated. Five-day-old seedlings were subjected to 0 (control), 50, and 100 µM Se. After ten days, the treated seedlings were harvested to analyze growth, cell viability, photosynthetic pigments, lipid peroxidation, reactive oxygen species (ROS) accumulation, and enzymatic antioxidants.

Results: The results indicated that excess Se resulted in phytotoxicity, as demonstrated by reduced seedling growth, root activity, and chlorophyll accumulation but higher malondialdehyde content. Se also increased oxidative stress, as illustrated by the accumulation of ROS, lipid peroxidation, and loss of membrane integrity. The antioxidative system was induced to detoxify ROS through the superoxide dismutase, guaiacol peroxidase, and catalase enzymes. Excess Se increased catalase activity, while the opposite happened in superoxide dismutase and guaiacol peroxidase activities.

Conclusion: These results may improve the understanding of Se phytotoxicity in plants.

Keywords: Antioxidant enzymes, Growth, Oxidative Stress, Phytotoxicity, *Zea mays* L.

INTRODUCTION

Selenium (Se) is a non-metallic element in the soil, occurring in various inorganic forms. Se is essential for human and animal health due to its important role in stress defense systems.[1] Se, which can covalently bond with C, participates in the structural formation of various organic Se-containing compounds, including selenoamino acids and selenoproteins. Selenoproteins are required for maintaining the physiology in a wide variety of prokaryotes, archaea, and eukaryotes; but are absent in fungi or green plants.[2,3] However, Se stimulates the antioxidant mechanism at low concentrations and protects plants from oxidative stress but acts as a heavy metal and an oxidant at high concentrations.[4] Therefore, the beneficial role of Se at low concentrations has been extensively studied.[5]

While selenate, selenite, and organic Se compounds such as selenocysteine and selenomethionine can be quickly absorbed from the soil, the roots cannot take up colloidal elemental Se or selenides.[6] Se is chemically similar to S and shares a similar pathway of uptake and translocation in plants.[7,8] Selenate is taken up by sulfate transporters of the root cell plasma membrane.[9] However, excessive Se accumulation can affect amino acid concentrations and alter the levels of nitrogenous compounds and various secondary metabolites[10,11], which can cause phytotoxicity by directly affecting the metabolism.[12] Se-induced toxicity is mediated by increased ROS accumulation and oxidative stress[9] and negatively affects the accumulation of essential nutrients by disrupting the mineral balance in plants.[5] Se toxicity in rice seedlings causes chlorosis, reduced accumulation of photosynthetic pigments, growth inhibition, lipid peroxidation, and enhanced activity of antioxidant enzymes.[4,13] The phytotoxic mechanisms of Se in maize plants have been studied only to a limited extent. Therefore, this research was carried out to obtain information about plant responses to Se-induced toxic effects by investigating seedling growth, root activity, photosynthetic pigments, lipid peroxidation, ROS accumulation, and antioxidant systems in different tissues of maize plants.

Corresponding Author: Hakan Terzi **E-mail:** hakanterzi81@gmail.com
Submitted: 31.08.2023 • **Revision Requested:** 06.10.2023 • **Last Revision Received:** 10.10.2023 • **Accepted:** 20.10.2023 • **Published Online:** 08.12.2023

MATERIALS AND METHODS

Plant Material and Se Treatment

The seeds of the maize (*Zea mays* L.) cultivar "Capuzi" were surface sterilized using 1% NaOCl and washed five times with sterile distilled water. They were then placed in culture containers with two layers of wetted filter papers and germinated for 48 h in the dark and at 25°C. Homogeneous maize seedlings were transferred to 1 L hydroponic culture pots containing modified Hoagland nutrient solution. They were grown in a growth chamber under a 12 h:12 h photoperiod, 250 µmol m^{-2} s^{-1} light intensity, 25°C ± 1°C, and 60% relative humidity for three days. They were then transferred to a nutrient solution containing 0, 50, and 100 µM of sodium selenite (Na_2SeO_3) and cultivated for another ten days. The pH of the nutrient solution was adjusted to 6.0 and was renewed every two days.

Determination of Growth Parameters

After exposure for ten days, ~8–10 seedlings were randomly selected from each group treated with a particular concentration of Se and harvested. The shoots and roots of the seedlings were separated, and their fresh weights were determined. The dry weights were determined after 48 h of drying at 80°C.

Determination of Root Activity by TTC Reduction

Root activity was analyzed by determining the activity of dehydrogenases in root tips using the TTC (2,3,5-triphenyl tetrazolium chloride) reduction test.[14] The root tips, ~1 cm long, were exposed to the TTC solution containing 0.8% TTC and 1% Tween-80 in 0.05 M potassium phosphate buffer (pH 7.4) for 2 h. The microscopic images were the taken with a digital camera.

Determination of Total Chlorophyll Content

Total chlorophyll content was determined using the Wellburn method.[15] The second leaves were collected, and ~100 mg were extracted with 10 mL methanol. The supernatants were obtained, OD_{653} and OD_{666} measured, and the chlorophyll content was estimated using the formulae:

$$\text{Chlorophyll a} = 15.65A_{666} - 7.34A_{653}$$
$$\text{Chlorophyll b} = 27.05A_{653} - 11.21A_{666}$$

Determination of Lipid Peroxidation Levels

The level of lipid peroxidation was determined by measuring the malondialdehyde (MDA) content.[16] Leaf tissues, 0.5 g, were homogenized with 0.1% trichloroacetic acid (TCA) and centrifuged at 11,500 × g for 15 min. The supernatant was mixed with 20% TCA containing 0.5% thiobarbituric acid and incubated at 95°C for 30 min. The OD_{532} and OD_{600} were observed, and the MDA content was calculated using the extinction coefficient (155 mM^{-1} cm^{-1}).

Histochemical Detection of Oxidative Damage

Hydrogen peroxide (H_2O_2) accumulation was determined histochemically using 3,3'-diaminobenzidine (DAB) solution.[17] Superoxide radicals ($O_2^{\bullet -}$) were determined after leaf and root tissues were incubated with 0.1% nitro blue tetrazolium (NBT) solution for 2 h in the dark.[18] Lipid peroxidation in the leaf and root tissues was determined using Schiff's reagent.[19] Membrane integrity at root tips was detected by treating the roots with 0.25% Evans blue solution for 1 h.[19] Leaf and root tissues were photographed using a digital camera.

Extraction and Assay of Antioxidant Enzymes

Fresh leaf and root tissues, 500 mg each, were homogenized separately with 50 mM phosphate buffer (pH 7.0). The homogenates were centrifuged at 14,000 rpm for 20 min. The supernatants were collected and stored for enzyme activity assays, and the total protein level was determined by the Bradford method.[20] Superoxide dismutase (SOD) activity was measured following the method of Beauchamp and Fridovich;[21] catalase (CAT) activity according to the method of Aebi;[22] and Guaiacol peroxidase (GPOX) activity by the method of Mika and Lüthje.[23]

Statistical Analysis

All experiments were carried out twice in triplicates. Statistical analyses were performed by analysis of variance using the SPSS 22.0 software (IBM, NY, USA). Duncan's multiple range test (DMRT) was used to compare the means.

RESULTS

Effect of Se on Seedling Growth

The fresh and dry weights of shoot and root tissues decreased significantly due to increased Se concentration ($P < 0.05$; Table 1). Under 50 and 100 µM Se, the shoot fresh and dry weights were reduced by 29.8% and 64.8%, and by 17.6% and 47.2%, respectively, compared to the control. The root fresh and dry weights decreased by 30.5% and 49.6%, and by 11.8% and 31.7%, respectively. In addition, visual symptoms of toxicity were observed in maize seedlings exposed to Se (Figure 1).

Effect of Se on Root Activity

The root activity in maize seedlings under Se determined by the TTC method revealed an intense red color in the root tips

Table 1. The effects of different Se concentrations on shoot and root fresh (FW) and dry weight (DW) of maize seedlings.

Parameters	Se concentrations (µM)		
	0	50	100
Shoot FW mg plant $^{-1}$	2893 ± 75.0 ^{a}	2031 ± 97.4 ^{b}	1018 ± 92.2 ^{c}
Shoot DW mg plant $^{-1}$	158.0 ± 2.94 ^{a}	130.3 ± 11.3 ^{b}	83.5 ± 6.55 ^{c}
Root FW mg plant $^{-1}$	351.8 ± 18.2 ^{a}	244.5 ± 20.2 ^{b}	177.3 ± 21.6 ^{c}
Root DW mg plant $^{-1}$	17.4 ± 1.14 ^{a}	15.4 ± 0.92 ^{b}	11.9 ± 0.61 ^{c}

a – c; Different letters indicate significant differences among means according to DMRT analysis (P<0.05). Standard error (±SE).

Figure 1. Visual symptoms of Se toxicity in maize seedlings.

of the control seedlings, indicating a high cellular viability or oxidizing ability. Nonetheless, relatively low dehydrogenase activity was also evident in the root tips of Se-treated seedlings (Figure 2).

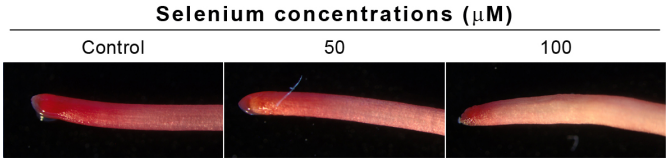

Figure 2. Root activity visualized by the TTC reduction assay in maize seedlings exposed to Se.

Effect of Se on Chlorophyll Content

The total chlorophyll content of leaf tissues reduced markedly by 30.4% and 60.8%, with an increase in Se concentration at 50 and 100 µM, respectively ($P < 0.05$; Figure 3).

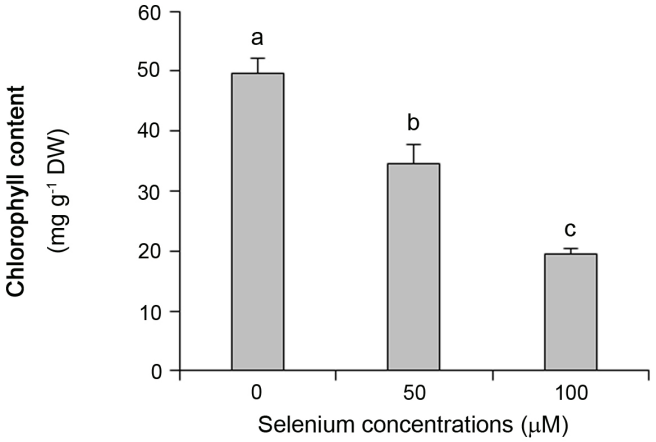

Figure 3. Effect of different Se concentrations on total chlorophyll content in leaf tissues of maize seedlings. Different letters (a – c) indicate significant differences among the means according to DMRT analysis (P<0.05).

Effect of Se on Lipid Peroxidation and ROS Accumulation

A significant increase in the MDA content indicated oxidative stress in plants exposed to Se (P<0.05; Figure 4). The MDA contents elevated by 1.37- and 1.47-fold under 50 and 100 µM Se, respectively. DAB staining detected a higher accumulation of H_2O_2 in the Se-treated seedlings compared to the control (Figures 5 and 6). Se-induced accumulation of $O_2^{\bullet -}$ was confirmed by histochemical staining with NBT. Lipid peroxidation was determined histochemically in leaves but not in roots. Additionally, the roots of maize seedlings treated with Se were stained extensively by Evans blue, indicating a loss of membrane integrity (Figure 6).

Effect of Se on Antioxidant Enzymes

The effects of excess Se on the activities of antioxidant enzymes and protein contents of the leaf and root tissues are depicted in Figure 7. Compared to the control, 50 and 100 µM Se suppressed SOD activity in the root tissues by 40.3% and 31.1%,

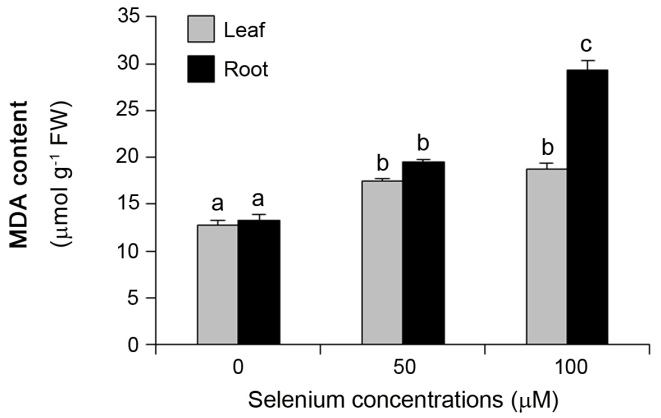

Figure 4. Effect of different Se concentrations on MDA content in leaf and root tissues of maize seedlings. Different letters (a – c) indicate significant differences among the means in each tissue according to the DMRT analysis ($P<0.05$).

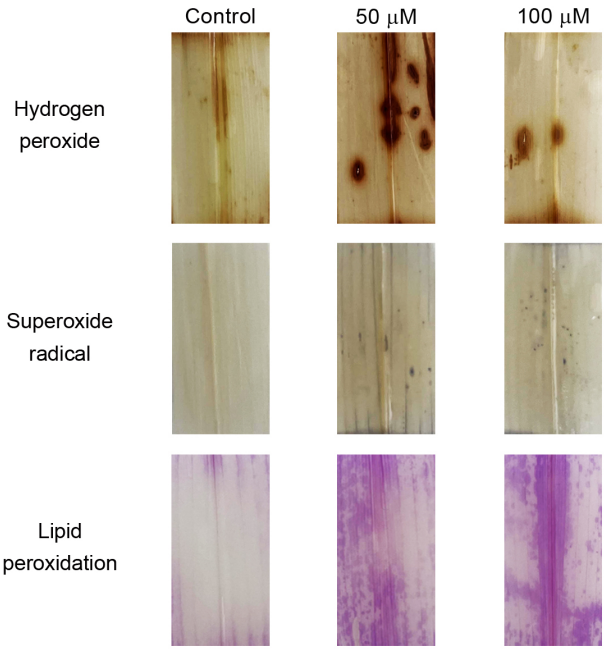

Figure 5. Histochemical analysis of hydrogen peroxide, superoxide radical, and lipid peroxidation accumulation in maize leaves.

respectively; and GPOX activity by 52.9% and 28.2%, respectively. On the other hand, SOD and GPOX activities in the leaf tissues were not significantly affected by Se. Se at 50 and 100 μM enhanced CAT activity in the leaves by 54.9% and 47.4%, respectively, compared to the control plants. However, the root CAT activity was remarkably elevated only at 50 μM Se. Se at 50 and 100 μM reduced the protein content of leaf tissues by 13.7% and 20.6%, but an increase of 21.7% and 34.5% in root tissues, respectively.

DISCUSSION

Although Se is known to have positive effects at low concentrations, it shows toxicity symptoms in plants at high concentrations. One of these symptoms is the reduction in biomass. In this work, an increasing concentration of Se significantly reduced the growth attributes of maize seedlings. Se-induced inhibition of growth was also detected in rice seedlings.[4] Excessive growth inhibition was associated with reduced stomatal density, disrupted stomatal arrangement, and diminished cell viability in *Arabidopsis thaliana*.[24] In a short-term experiment, selenate treatment promoted the Se contents in the rice seedlings grown with 0.1 mM sulfate. This suggested that under the S-limited conditions, plants can absorb selenate more efficiently, inducing toxicity and growth impairment. Excess Se reduced S concentrations in the roots of rice seedlings, indicating a competition between Se and sulfate uptake.[25] Reduced growth in maize seedlings may be related to impaired sulfate availability and damage induced by excessive Se to vital processes such as protein and chlorophyll biosynthesis.[12]

The reduction of colorless TTC to a water-insoluble red formazan depends on the efficient activity of respiratory dehydrogenases and indicates mitochondrial activity and viability in metabolically active cells.[26] The intensity of the red color is proportional to the metabolic activity of the cells, making it a reliable indicator of cell viability. In the present study, suppression in TTC reduction was determined in root cells to indicate cell viability in plants exposed to Se. A reduction in root activity was also reported under metal-induced stress.[27,28] However, low Se concentration (2.5 μM) elevated the TTC reduction capacity in *Phaseolus aureus* roots.[27]

Excess Se negatively affects many physiological and biochemical processes in plants. Among these, chlorosis is one of the most harmful effects due to decreased chlorophyll biosynthesis. A dramatic reduction in chlorophyll contents was observed in Se-treated maize seedlings. In the case of cowpea plants, foliar application of high Se concentrations inhibited photosynthesis and decreased the chlorophyll content, generating leaf chlorosis-related symptoms.[29] Elevated Se accumulation in leaf tissues can destroy chlorophyll molecules and increase oxidative stress.[30,31] Se reduces chlorophyll content in spinach plants by suppressing the activity of δ-aminolevulinate (ALA) dehydratase, which is required for chlorophyll biosynthesis.[32] Similarly, Se reduced ALA content in etiolated maize.[33] However, the Se-induced reduction in chlorophyll concentration may have resulted in lower photosynthetic yields and thus inhibited seedling growth.[13]

Possible mechanisms involved in Se-mediated oxidative stress have been described to explain its harmful effects.[5] Se-induced inhibition in the antioxidant defense system causes the overproduction of ROS.[34] A significant increase in MDA content indicates oxidative stress in plants exposed to Se toxicity due to the overproduction of ROS.[4] Increased oxidative stress

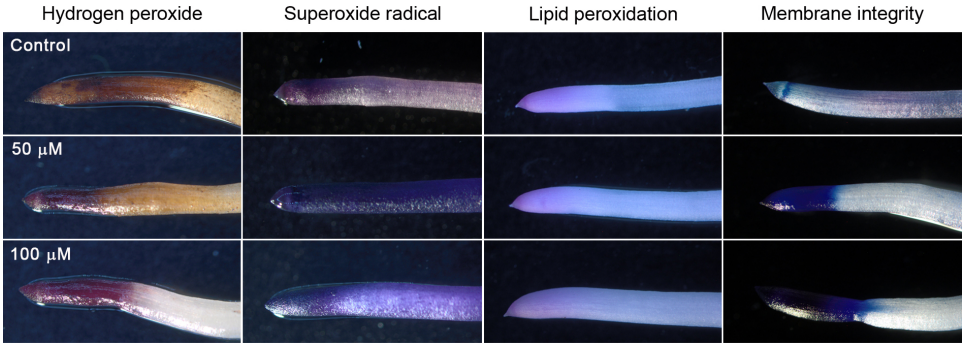

Figure 6. Histochemical analysis of hydrogen peroxide, superoxide radical, lipid peroxidation, and membrane integrity in maize roots.

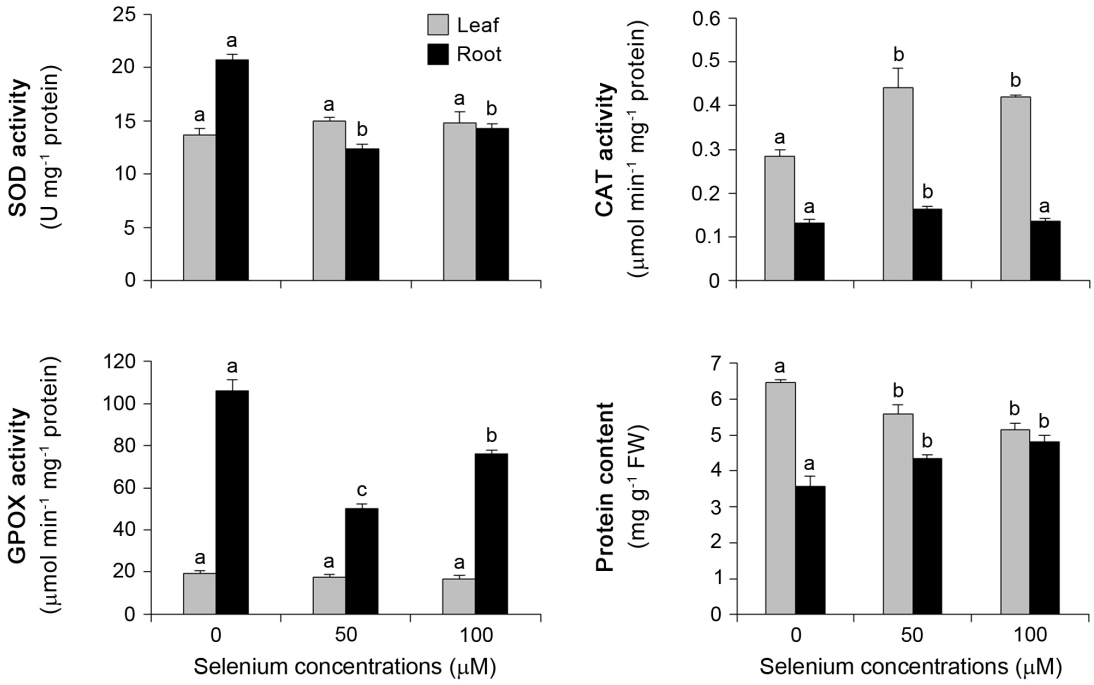

Figure 7. Effects of different Se concentrations on the activities of antioxidant enzymes and protein contents in leaf and root tissues of maize seedlings. Different letters (a – c) indicate significant differences among the means in each tissue according to the DMRT analysis (P<0.05).

and high MDA content in maize leaves due to Se application indicated membrane disruption. Similarly, foliar Se application at high concentrations of 150 g ha^{-1} induced a drastic increase in H_2O_2 concentration and lipid peroxidation in cowpea leaves.[29] On the contrary, foliar application of Se ranging from 20 to 80 ppm in coffee plants decreased lipid peroxidation and H_2O_2 levels, highlighting the antioxidant capacity of Se in combating ROS.[35] Conversely, Se-induced oxidative damage was also demonstrated by the histochemical localization of $O_2^{\bullet-}$, H_2O_2, and lipid peroxidation. In addition, lipid peroxidation severely affected membrane integrity in root cells, as observed through the high uptake of Evans blue reagent by roots. *In vitro* studies have revealed that Se reacts with glutathione, causing excessive $O_2^{\bullet-}$ and, subsequently, H_2O_2 accumulation.[36] Se elevated oxidative stress in rice seedlings, and H_2O_2 accumulation was the leading cause of Se-related toxicity.[4] Se-induced toxicity disrupted chloroplast and mitochondrial structure and function, leading to the overproduction of ROS.[5]

Plant cells possess a dedicated defense strategy, such as enzymatic antioxidants to detoxify ROS.[37] In the present study, antioxidant enzymes were differentially regulated to scavenge ROS produced under excess Se. For instance, Se decreased SOD and GPOX activities in root tissues, while it did not cause any significant effects in leaf tissues. Se-induced reduction of SOD activity was also observed in wheat and lettuce plants.[38,39] Numerous studies have revealed that excess Se diminished GPOX activity.[40–42] On the other hand, the activity of CAT, another H_2O_2 detoxifying enzyme, increased with Se supplementation, as observed in rice seedlings.[4] However, a reduction was ob-

served in certain plant species.[39,42] Foliar Se application at >100 ppm exceeded the toleration limits of the leaves of coffee plants exercising a pro-oxidant function, as observed by the increased ROS production and decreased activities of SOD, CAT, and APX.[35] However, rice seedlings exposed to Se presented higher CAT and APX activities and higher GSH contents, which probably counteracted the deleterious effects of ROS.[25] Differential regulation of antioxidant enzymes depending on the level of Se exposure suggests that varied mechanisms may play a role in overcoming Se toxicity.

CONCLUSION

Se exposure inhibited the growth of maize seedlings due to reduced photosynthetic pigment content and increased oxidative stress markers. Plants exposed to Se displayed high levels of $O_2^{\bullet -}$, H_2O_2, lipid peroxidation, and loss of membrane integrity. Maize seedlings regulated the antioxidant system to detoxify the Se-induced ROS accumulation, modulated by SOD, GPOX, and CAT. Further research on the impacts of Se on the transcriptome and proteome in plants can provide a better understanding of the effects of Se in maize.

Acknowledgments: The authors also wish to thank Afyon Kocatepe University's Foreign Language Support Unit for language editing.

Peer Review: Externally peer-reviewed.

Author Contributions: Conception/Design of Study- M.Y., H.T.; Data Acquisition- H.T., E.P.; Data Analysis/Interpretation- M.Y., H.T., E.P.; Drafting Manuscript- M.Y., H.T.; Critical Revision of Manuscript- M.Y., H.T.; Final Approval and Accountability- M.Y., H.T., E.P.

Conflict of Interest: Authors declared no conflict of interest.

Financial Disclosure: Authors declared no financial support.

ORCID IDs of the authors

Mustafa Yildiz 0000-0002-6819-9891
Emre Pehlivan 0000-0001-9405-0524
Hakan Terzi 0000-0003-4817-1100

REFERENCES

1. Reis AR, El-Ramady H, Santos EF, Gratao PL, Schomburg L. Overview of selenium deficiency and toxicity worldwide: Affected areas, selenium-related health issues, and case studies. In: Pilon-Smits E, Winkel L, Lin ZQ, eds. *Selenium in Plants: Molecular, Physiological, Ecological and Evolutionary Aspects*. Springer, Cham; 2017:209–230.
2. Castellano S, Novoselov SV, Kryukov GV, et al. Reconsidering the evolution of eukaryotic selenoproteins: A novel nonmammalian family with scattered phylogenetic distribution. *EMBO Reports* 2004;5:71–77.
3. Santesmasses D, Mariotti M, Guigó R. Computational identification of the genomes' selenocysteine tRNA (tRNASec). *PLOS Comput Biol*. 2017;13:e1005383. doi: 10.1371/journal.pcbi.1005383
4. Gouveia GCG, Galindo FS, Lanza MGDB, et al. Selenium toxicity stress-induced phenotypical, biochemical and physiological responses in rice plants: Characterization of symptoms and plant metabolic adjustment. *Ecotox Environ Safe*. 2020;202:110916. doi: 10.1016/j.ecoenv.2020.110916
5. Hasanuzzaman M, Bhuyan MHMB, Raza A, et al. Selenium in plants: Boon or bane? *Environ Exp Bot.* 2020;178:104170. doi: 10.1016/j.envexpbot.2020.104170
6. White PJ. Selenium metabolism in plants. *Biochim Biophys Acta* 2018;1862(11):2333–2342.
7. Golob A, Gadžo D, Stibilj V, Djikić M, Gavrić T, Kreft I. Sulphur interferes with selenium accumulation in Tartary buckwheat plants. *Plant Physiol Bioch*. 2016;108:32–36.
8. González-Morales S, Pérez-Labrada F, García-Enciso EL, Leija-Martínez P, Medrano- Macías J, Dävila-Rangel E. Selenium and sulfur to produce *Allium* functional crops. *Molecules* 2017;22:558. doi: 10.3390/molecules22040558
9. Gupta M, Gupta S. An overview of selenium uptake, metabolism, and toxicity in plants. *Front Plant Sci*. 2017;7:2074. doi: 10.3389/fpls.2016.02074
10. Bielecka M, Watanabe M, Morcuende R, et al. Transcriptome and metabolome analysis of plant sulfate starvation and resupply provide novel information on transcriptional regulation of metabolism associated with sulfur, nitrogen, and phosphorus nutritional responses in Arabidopsis. *Front Plant Sci*. 2015;5:805. doi: 10.3389/fpls.2014.00805
11. Schiavon M, Lima LW, Jiang Y, Hawkesford MJ. Effects of selenium on plant metabolism and implications for crops and consumers. In: Pilon-Smits EAH, Winkel LHE, Lin ZQ, eds. *Selenium in Plants: Molecular, Physiological, Ecological and Evolutionary Aspects.* Springer, Cham; 2017:275–357.
12. Reis AR, Boleta EHM, Alvez CZ, et al. Selenium toxicity in upland field-grown rice: seed physiology responses and nutrient distribution using the μ-XFR technique. *Ecotox Environ Safe*. 2020;190:110147. doi: 10.1016/j.ecoenv.2019.110147
13. Mostofa MG, Hossain MA, Siddiqui MN, Fujita M, Tran LSP. Phenotypical, physiological, and biochemical analyses provide insight into selenium-induced phytotoxicity in rice plants. *Chemosphere*. 2017;178:212–223.
14. Clemensson-Lindell A. Triphenyltetrazolium chloride as an indicator of fine-root vitality and environmental stress in coniferous forest stands: applications and limitations. *Plant Soil* 1994;159:297–300.
15. Wellburn AR. The spectral determination of chlorophylls a and b as well as total carotenoids, using various solvents with spectrophotometers of different resolution. *J Plant Physiol*. 1994;144:307–313.
16. Heath RL, Packer L. Photoperoxidation in isolated chloroplasts I. Kinetics and stoichiometry of fatty acid peroxidation. *Arch Biochem Biophys.* 1968;125:189–198.
17. Deuschle K, Funck D, Forlani G, et al. The role of Δ1-pyrroline-5-carboxylate dehydrogenase in proline degradation. *Plant Cell* 2004;16:3413–3425.
18. Lehotai N, Peto A, Bajkan S, Erdei L, Tari I, Kolbert Z. *In vivo* and *in situ* visualization of early physiological events induced by heavy metals in pea root meristem. *Acta Physiol Plant*. 2017;33:2199–2207.
19. Singh HP, Batish DR, Kaur G, Arora K, Kohli K. Nitric oxide (as sodium nitroprusside) supplementation ameliorates Cd toxicity in hydroponically grown wheat roots. *Environ Exp Bot.*

2008;63:158–167.

20. Bradford MM. A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein dye binding. *Anal Biochem*. 1976;72:248–254.
21. Beauchamp C, Fridovich Y. Superoxide dismutase: Improved assays and an assay applicable to acrylamide gels. *Anal Biochem*. 1971;44:276–287.
22. Aebi H. Catalase *in vitro*. *Method Enzymol.* 1984;105:121–126.
23. Mika A, Lüthje S. Properties of guaiacol peroxidase activities isolated from corn root plasma membranes. *Plant Physiol*. 2003;132:1489–1498.
24. Molnár Á, Kolbert Z, Kéri K, et al. Selenite-induced nitro-oxidative stress processes in *Arabidopsis thaliana and Brassica juncea. Ecotox Environ Safe*. 2018;148:664–674.
25. Cardoso AFS, Gomes FTL, Antonio JRR, et al. Sulfate availability and soil selenate adsorption alleviate selenium toxicity in rice plants. *Environ Exp Bot.* 2022;201:104971.
26. Mingji X, Chongling Y, Jing Y, Lily W. Impact of phenanthrene on organic acids secretion and accumulation by perennial ryegrass, *Lolium perenne* L., root. *B Environ Contam* Tox. 2009;83:75–80.
27. Malik JA, Goel S, Kaur N, Sharma S, Singh I, Nayyar H. Selenium antagonises the toxic effects of arsenic on mung bean (*Phaseolus aureus* Roxb.) plants by restricting its uptake and enhancing the antioxidative and detoxification mechanisms. *Environ Exp Bot.* 2012;77:242–248.
28. Hawrylak-Nowak B, Dresler S, Matraszek R. Exogenous malic and acetic acids reduce cadmium phytotoxicity and enhance cadmium accumulation in roots of sunflower plants. *Plant Physiol Biochem*. 2015;94:225–234.
29. Lanza MGDB, Silva VM, Montanha GS, Lavres J, de Carvalho HWP, dos Reis AR. Assessment of selenium spatial distribution using μ-XFR in cowpea (*Vigna unguiculata* (L.) Walp.) plants: Integration of physiological and biochemical responses. *Ecotox Environ Safe*. 2021; 207:111216. doi: 10.1016/j.ecoenv.2020.111216
30. Akbulut M, Çakir S. The effects of Se phytotoxicity on the antioxidant systems of leaf tissues in barley (*Hordeum vulgare L.*) seedlings. *Plant Physiol Biochem*. 2010;48:160–166.
31. Silva VM, Boleta EHM, Lanza MGDB, et al. Physiological, biochemical, and ultrastructural characterization of selenium toxicity in cowpea plants. *Environ Exp Bot*. 2018;150:172–182.
32. Saffaryazdi A, Lahouti M, Ganjeali A, Bayat H. Impact of selenium supplementation on growth and selenium accumulation on spinach (*Spinacia oleracea* L.) plants. *Not Sci Biol*. 2012;4:95–100.
33. Jain M, Panwar M, Gadre R. Influence of selenium supplementation on δ-aminolevulinic acid formation in greening maize leaf segments. *Res J Phytochem*. 2017;11:111–117.
34. Józwiak W, Politycka B. Effect of selenium on alleviating oxidative stress caused by a water deficit in cucumber roots. *Plants* 2019;8:217. doi: 10.3390/plants8070217
35. Mateus MPB, Tavanti RFR, Tavanti TR, Santos EF, Jalal A, dos Reis AR. Selenium biofortification enhances ROS scavenge system increasing yield of coffee plants. *Ecotox Environ Safe.* 2021;209:111772. doi: 10.1016/j.ecoenv.2020.111772
36. Spallholz JE. On the nature of selenium toxicity and carcinostatic activity. *Free Radical Bio Med.* 1994;17:45–64.
37. Mittler R, Vanderauwera S, Gollery M, Van Breusegem F. Reactive oxygen gene network of plants. *Trends Plant Sci*. 2004;9:490–498.
38. Xue T, Hartikainen H, Piironen V. Antioxidative and growth-promoting effect of selenium on senescing lettuce. *Plant Soil* 2001;237:55–61.
39. Łabanowska M, Filek M, Kościelniak J, Kurdziel M, Kuliś E, Hartikainen H. The effects of short-term selenium stress on Polish and Finnish wheat seedlings—EPR, enzymatic and fluorescence studies. *J Plant Physiol*. 2012;169(3):275–284.
40. Nowak J, Kaklewski K, Ligocki M. Influence of selenium on oxidoreductive enzymes activity in soil and in plants. *Soil Biol Biochem*. 2004;36:1553–1558.
41. Kong L, Wang M, Bi D. Selenium modulates the activities of antioxidant enzymes, osmotic homeostasis and promotes the growth of sorrel seedlings under salt stress. *Plant Growth Regul*. 2005;45:155–163.
42. Mroczek-Zdyrska M, Wójcik M. The influence of selenium on root growth and oxidative stress induced by lead in *Vicia faba* L. *minor* plants. *Biol Trace Elem Res*. 2012;147:320–328.

How to cite this article

Yildiz M, Pehlivan E, Terzi H. Selenium Toxicity Induced Physiological and Biochemical Alterations in Maize Seedlings. Eur J Biol 2023; 82(2): 154–160. DOI:10.26650/EurJBiol.2023.1353293