

Review Article

Role of selenium in regulation of plant antioxidants, chlorophyll retention and osmotic adjustment under drought conditions: a review

Abstract

Environmental change is ascending as one of the most unpredictable issue, the effects of which are observable as rise in the onset of regular abiotic stresses like no or irregular precipitation, ascend in worldwide normal temperature, floods and so on. Among all the abiotic stresses, drought stress has become a sector of interest for decades. Drought stress can be chronic in locations with low water accessibility or irregular precipitation during the time of plant development consequently decreasing its growth and yield through its impact on plant photosynthetic rate, increased load of reactive oxygen species, changes in plant water relations and so on. A great deal of examination has been done to study the varieties of changes in the plants at the morphological, physiological and cellular level to identify the methodologies for enhancing plant drought resistance. In this regard "selenium" (Se) is considered exceptionally significant for improving plant growth and development. Spraying drought stressed plants or pre-treating the seeds with low dosage of Se have been shown to be associated with upgraded plant drought resistance. The present study is aimed to frame a review on the regulation of plant defense system, chlorophyll retention and plant water relations so as to provide comprehensive

understanding into the changes caused by the application of Se which in turn are liable for improved plant drought tolerance.

Key words: —drought; plant; resilience; selenium

Introduction

The regularly changing ecological conditions have been faced by plants through evolutionary time, among which drought is most widely recognized and acts as one of the significant limitations to plant efficiency worldwide (Zaffar et al. 2018) more than any other abiotic stress (Lambers et al. 2008, Comas et al. 2013). Drought usually occurs normally, however the environmental change has quickened the hydrological procedures to make them set in faster with numerous results (Sourav et al. 2018). Intensity of drought stress depends on several factors, for instance rainfall amount and distribution, evaporative demands and moisture storing ability of soils (Saud et al. 2017). The arid and semi-arid areas of the globe, particularly in developing nations, are at incredible hazard since they are confronting intense deficiency of water (Marika et al. 2018) leading to plant death through extensive cell dehydration, stomatal closure and limited gaseous exchange (Jaleel et al. 2007), hormonal and nutritional imbalance and increased load of free radicals (Zaffar et al. 2018). In spite of its negative impact, serious natural conditions can incite intriguing adjustments in the plants that permit them to control water status, stay away from oxidative pressure and keep up fundamental capacities so as to endure the drought adversities (Elizamar et al. 2013). These adaptations lead to the emergence of new important tools for improving plant drought tolerance. As of late ameliorative role of plant hormones (Zhang et al. 2020), mineral supplements (Ejaz et al. 2011) and microbes like AM (Zaffar et al. 2018) have been assessed with little consideration on trace elements like selenium

Comment [B1]: Arbuscular mycorrhiza? Explain better.

(Se). Se is a component required by the plant at low concentrations and existing in the soil as selenite, selenite, natural Se and as inorganic selenide (McNeal and Balistreri 1989). In plants Se can be found both in inorganic and organic forms, including seleno amino acids and methylated compounds (Mirza et al. 2010). However, it has been reported that organic form of Se are dominant over the inorganic ones (Kiskinen et al. 2010). The membrane receptors responsible for accumulation of Se in the plant tissue have not been identified so far (Zhang et al. 2014), however it is expected that uptake of Se in selenate and selenite forms occurs respectively through high affinity sulfate transporters (Sors et al. 2005) and phosphate transporters (Li et al. 2008) depending on plant species (Kiskinen et al. 2010). In spite of the fact that Se isn't yet affirmed to be required by higher plants (Terry et al. 2000), a few investigations exhibit that at low doses it might apply valuable impacts, including plant development and help the plant out from the afflictions brought about by the drought stress. A portion of the important work accessible with respect to the job of Se in preventing the unfavorable impact of drought is talked about in this review as follows.

Regulation of active oxygen species (AOS) and antioxidants by Se

Almost all the abiotic stresses generate active oxygen species (AOS) in the plant system which is the result of partial reduction of atmospheric oxygen. Generally four forms of AOS are most common in plants subjected to various environmental stresses i.e. singlet oxygen (O^1_2), super oxide radical (O^-_2), hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH^\cdot) each with a specific oxidizing potential. Unlike normal oxygen the AOS are extremely reactive. The primary cellular AOS generation sites are chloroplasts, mitochondria, peroxisomes, apoplast, and plasma membranes (Singh et al. 2019). The enhanced production of AOS during environmental stresses

can pose a threat to cells by promoting oxidative stress which results in peroxidation of lipids, oxidation of proteins, damage to nucleic acids, enzyme inhibition, activation of programmed cell death (PCD) pathway leading to death of the cells (Mittler 2002, Kaushik and Aryadeep, 2014, Amna and Frank 2018). Oxidative stress has been reported in wheat (Usha and Pradhan 2012, Biehler and Fock 1996), sunflower (Sgherri et al. 1996), rapeseed (Hasanuzzaman and Fujita 2011) etc. due to increased generation of hydrogen peroxide (H_2O_2) and $O_2^{\cdot-}$ in the leaves. Generation of AOS has been reported to increase from less than $240 \mu M S^{-1} O_2$ to $240-270 \mu M S^{-1} O_2$ (Mittler 2002). Under drought stress, AOS production is increased through multiple pathways like reduction in the generation of $NADP^+$ through Calvin cycle, that ends up in the over reduction of electron transport chain. Discharge of electrons to Mehler reaction is taken into account as another contributing reason for inflated AOS load in plants under drought (Smirnoff 1993). Photorespiratory pathway is another justification for increased production ROS particularly once RuBP oxygenation is maximal due to CO_2 fixation (Noctor et al. 2002).

Comment [B2]: This character is present all text, please remove. Review the citations, there are text in the study that were not correctly cited.

Formatted: Subscript

Comment [B3]: Use ROS or AOS.

Comment [B4]: Ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase. Explain better.

Studies have shown that Se protect the plants from variety of abiotic stresses such as cold (Chu et al. 2010), drought (Hasanuzzaman and Fujita 2011), desiccation (Pukacka et al. 2011), and metal stress (Kumar et al. 2012, Pandey and Gupta 2015). Literature cited clearly indicates that Se at low doses overcomes the damage caused by oxidative stress during drought. Weronika and Barbara (2019) and Chang-Quan (2011) while respectively working on cucumber and *Trifolium repens* revealed that the capacity of two crops growing under drought and pre-treated with Se to generate $O_2^{\cdot-}$, H_2O_2 and OH^{\cdot} was significantly weaker when contrasted with the seedlings growing under drought alone which was visible by diminished MDA (an indicator of rate of lipid peroxidation brought by AOS) content and injury index. Pretreatment with Se resulted in elevated membrane stability index and root viability with a concomitant reduction in

the level of MDA content, H₂O₂ accumulation and O₂^{•-} generation in drought stressed wheat Heba (2014) and Yao et al (2012). Similar type of results pertaining to Se application have been reported by Hasanuzzaman and Fujita (2011) and Fabricio et al (2018) respectively in rape seed and rice growing under water deficit. Renwei et al (2013) has reported that Se works on AOS either by quenching the AOS or reducing their number. An appropriate concentration of Se may affect the level of AOS, through three processes: The spontaneous O₂^{•-}-dismutation to H₂O₂-(in a non-catalysed by an SOD reaction), the direct removal of O₂^{•-}-and H₂O₂-by Se compounds, and the regulation of antioxidant enzyme activity (Hartikainen et al. 2000, Cartes et al. 2010). Se as an essential microelement has recently gained importance in plant systems due to its effect on the antioxidative defense system (Nesrine et al. 2018). In rice it has been reported that exogenous application of Se mediated the drought tolerance by increasing the total antioxidant capacity particularly in shoots (Manal et al. 2014) which included catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX) and superoxide dismutase (SOD) followed by a reduction in lipid peroxidation and hydrogen peroxide (H₂O₂) content (Zahedi et al. 2020). Antioxidants act as free radical scavengers, by reacting with the AOS and demolishing them to become less active and less dangerous by accepting or donating electrons to remove the unpaired status of the radical (Mostafa et al. 2020). The results of other authors indicate that Se itself at lower concentrations acts as an antioxidant by significantly increasing the contents and activity of the components of the antioxidant defense system (Tailin et al. 2001).

Effect on chlorophyll content

Water deficit leads to the perturbation of most of the physiological and biochemical processes, among which reduction in leaf chlorophyll content is considered as the most critical

factor which consequently reduces the plant growth and yield (Rahdari et al. 2012). However, the decreased chlorophyll content during drought stress depends on the duration and severity of drought level (Zhang and Kirkham, 1996). The reduction in chlorophyll content under drought stress has been reported in maize (Majid 2012), rice (Shamima et al. 2020), tomato (Sivakumar et al. 2017), soybean (Wensen et al. 2018) and so many other agricultural and horticultural crops of economic importance. The decrease in chlorophyll content under drought stress has been considered a typical symptom of pigment photo oxidation, chlorophyll disintegration (Shakeel et al. 2011) and over production of AOS (Majid et al. 2011). Meeta et al. (2013) reported that a substantial decrease in chlorophyll synthesis occurs due to significant reduction in δ aminolevulinic acid (ALA) content and δ aminolevulinic acid dehydratase (ALAD) activity both of which have a crucial role to play in chlorophyll biosynthesis. Recently it has been reported that AhPORA protein, which encodes a key enzyme in chlorophyll biosynthesis and genes related to chlorophyll biosynthesis decline markedly under drought conditions (Xing et al. 2018). Hortensteiner and Krautler (2011) have regarded HemaA (GlutamyltRNA reductase 1) and ChlH (magnesium-chelatase subunit) as the key enzymes of Chl biosynthesis. However, their down-regulation during drought stress contributes to inhibition of chlorophyll biosynthesis. Further Muhammad et al (2018) has reported that Chl biosynthesis process is severely repressed and degradation process is induced by the drought stress by upregulation of pheophorbide a oxygenase (PAO) which catalyses the degradation of chlorophyllide a into non-fluorescent Chl catabolites.

Comment [B5]: Has the literature ever reported the effect of Se on these specific enzymes?

Optimal exogenous supplementation of Se reduces the effect of drought induced stress and modulates the photosynthetic functions by increasing chlorophyll content (Feng et al. 2013). Seppanen et al (2003) and Balal et al (2016) reported that exogenous Se supply minimizes the

Formatted: Indent: First line: 0.5", Space Before: 12 pt, Tab stops: Not at 1.43"

damage to the chloroplasts and helps to maintain photosynthetic pigments under environmental stress conditions. Enhancement in chlorophyll content under drought has been reported in many crops like maize (Fahim et al. 2016), spinach (Saffaryazdi et al. 2012), lettuce (Duma et al. 2011), sorghum (Abbas 2012) etc. Djanaguiraman et al (2005)-found that low Se concentrations alter chlorophyll biosynthetic pathway to increase pigments in plants. It has been reported that increase in chlorophyll content by Se supplementation under drought stress is due to enhanced activity of antioxidative enzymes (Germ et al. 2007) which inhibit the lipid peroxidation and maintain the integrity of the cellular and subcellular membranes of some cell organelles like chloroplast which are considered vital for synthesis and localization of leaf pigments (Hartikainen, 2000, Malik et al. 2012). Increase in chlorophyll content may be attributed to effect of Se on protection of chloroplast enzymes (Salwa et al. 2012) and increased cell metabolic rate which enhances the chlorophyll synthesis and retard chlorophyll degradation (Shikha and Meetu 2016). Further, delay in leaf tissue senescence and increase in polyamine level especially putrescine which is having an important role in chlorophyll biosynthesis by selenium application is considered as an important factor for chlorophyll content increase under drought stress (Kakkar 2002). Selenium application has been found to promote the uptake of nitrogen and magnesium both of which are the structural components of chlorophyll which become limiting under drought conditions hence affect its biosynthesis.

Role in cell osmotic adjustment

Plants adapt to drought either by decreasing water loss or by maintaining the water uptake. Maintaining of water uptake is facilitated within the plant cell by osmotic adjustment which is widely recognized to have a role in plant adaptation to dehydration mainly through

Comment [B6]: Was this verified in plants without water stress?

Comment [B7]: Então a aplicação de se tem dois efeitos sob a clorofila? Evita a oxidação e ajuda indiretamente na absorção de N e Mg?

Formatted: Indent: First line: 0.5", Space Before: 12 pt, Tab stops: Not at 1.43"

turgor maintenance and the protection of specific cellular functions by defined solutes (Abraham 2016). Osmotic adjustment in response to drought was first recognized more than four decades ago (Neil 2018) by Greacen and Oh (1972) in pea roots, by Morgan (1977) in wheat leaves, by Turner et al. (1978a) and Jones and Turner (1978) in sorghum leaves. Plants protect themselves against drought by over-expression of some osmoprotectants which include sugars like sucrose, glucose and fructose (Sanchez et al. 1998), inorganic cations like potassium, magnesium, chloride and nitrate and amino acids like proline and glycine betaine (Ma and Turner 2006). Drabble & Drabble (1907) already recognized the importance of solutes in maintaining plant cellular turgor and adaptation to harsh environments. Accumulation of these solutes lower down the cell water potential, hence favour the water uptake to maintain the cell turgor pressure even under harsh environment besides stabilizing the tertiary structure of proteins and photosynthetic apparatus (Papageorgiou and Murata 1995) and detoxify AOS (Wang et al. 2010). Glycine betaine (GB) and proline are two major organic osmolytes that accumulate in plant species in response to environmental stresses like drought, salinity, extreme temperatures, UV radiation and heavy metals. Although their actual roles in plant osmotolerance remain controversial, both compounds are thought to possess positive effects on enzyme and membrane integrity besides their adaptive roles in mediating osmotic adjustment in plants grown under stress conditions (Ashraf and Foolad 2007). In addition to its function as an osmolyte, Pro is a scavenger of reactive oxygen species (ROS) thereby modulating the redox homeostasis of the cell and operating as a supply of energy and as a signal molecule interacting with other metabolic pathways during periods of stress (Sharma et al. 2011, Szabados and Savouré 2010). It has been proposed that accumulation of compatible solutes in response to drought stress requires the metabolic pathways that biosynthesize these solutes. Drought turns

on several genes which govern the biosynthesis of these solutes. The genes in turn encode the enzymes such as

1. 1-Pyrroline-5-carboxylate synthase, a key enzyme in the proline biosynthetic pathway.
2. betaine aldehyde dehydrogenase, an enzyme involved in glycine betaine accumulation.
3. myo-Inositol 6-O-methyltransferase, a rate-limiting enzyme in the accumulation of the cyclic sugar alcohol called pinitol (Buchanan et al. 2000).

In addition to the above mentioned enzymes expression of glyceraldehyde-3-phosphate dehydrogenase increases during osmotic stress, perhaps to allow an increase of carbon flow into organic solutes for osmotic adjustment (Buchanan et al. 2000).

Maintenance of favorable water relations is a prime defense strategy followed by plants to overcome drought adversities. It has been stated that Se foliar application resulted in less negative water potential in potato (Germ et al. 2007), wheat (Nawaz et al. 2015a) and maize (Qiang-yun et al. 2008) mediated through its positive impact on osmotic balance and ion homeostasis to increase water uptake and reduce transpiration under drought stress conditions. The increase in proline, potassium concentrations and nitrogen metabolism in aerial parts of plants grown in Se-rich substrates, seems to prove that Se-biofortification increased plant resistance to water shortage conditions (Marika et al. 2018). In rice the improved growth of Se pre-treated plants was associated with increase in the level of proline and glycine betaine (Khattab et al. 2014). Among 140 putative NAC or NAC like genes, twenty of the genes act as stress responsive genes including OsNAC5 (Fang et al. 2008) having a role in the production of osmolytes. Overexpression of OsNAC5 genes because of Se pretreatment in rice plants leads to

Comment [B8]: NACs are plant-specific proteins with several roles in plant development and stress response. Write in context.

accumulation of proline and soluble sugars hence protecting the plants from dehydration and oxidative damage under stressed conditions (Khattab et al. 2014). It has been reported that Se stimulates the amylase activity, which bring about its decomposition into simple sugars under water deficit conditions, which actively take in the osmotic adjustment (Fahim et al. 2016).

Conclusion

Selenium is an essential element which is required by plants in traces and it triggers various intrinsic regulatory mechanisms pertaining to stresses including drought. As it is absorbed using sulphur transporters and also accesses sulphate assimilation pathway and influences production of S-organic compounds which are vital in response to abiotic stresses. It also interacts with molybdenum pathways. Therefore managing such interactions are useful in biofortification and in other stress responsive compounds like glucosinolates and antioxidants. Furthermore at low concentrations selenium can improve crop productivity by increasing the capacity of plants to tolerate stress.

References

Abbas S. M. (2012). Effects of low temperature and selenium application on growth and the physiological changes in sorghum seedlings. *Journal of Stress Physiology and Biochemistry*. 8(1): 268-286.

Abraham B. (2016). Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. *Plant Cell and Environment*, 40(1): 4-10.

Amna M., Frank V. B. (2018): Reactive oxygen species in plant development. The Company of Biologists Ltd Development, 145, dev164376. doi:10.1242/dev.164376

Comment [B9]: The conclusion is different from the topics discussed in the review. I suggest rewriting. The conclusion should contain the three topics discussed in the review with If: Regulation of active oxygen species (AOS) and antioxidants by Se/ Effect on chlorophyll content/Role in cell osmotic adjustment.

Comment [B10]: It was not discussed in the review

Comment [B11]: It was not discussed in the review.

Ashraf M., Foolad M.R. (2007): Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany*, 59: 206-216.

Balal R. M., Shahid, M. A., Javaid, M. M., Iqbal, Z., Anjum, M. A., Garcia-Sanchez, F. (2016): The role of selenium in amelioration of heat-induced oxidative damage in cucumber under high temperature stress. *Acta Physiologia Plantarum*, 38: 1–14.

Biehler K., Fock H. (1996): Evidence for the Contribution of the Mehler-Peroxidase Reaction in Dissipating Excess Electrons in Drought-Stressed Wheat. *Plant Physiology*, 112(1):265-272.

Buchanan, B. B., Gruissem, W., Jones, R. (2000): *Biochemistry & Molecular Biology of Plants*. American Society of Plant Physiologists, Rockville, MD

Cartes P., Jara A. A., Pinilla L., Rosas A., Mora M. L. (2010): Selenium improves antioxidant ability against aluminium induced oxidative stress in ryegrass roots. *Annals of Applied Biology*, 156: 297-307.

Chang-Quan W. (2011): Water stress mitigation by selenium in *Trifolium repens* L. *Journal of Plant Nutrition and Soil Sciences*, 174(2): 276-282.

Comas L. H., Becker S. R., Cruz V. M., Byrne P. F., Dierig (2013): Root traits contributing to plant productivity under drought. *Frontiers in Plant sciences*, 5(4): 442.

Chu, J., X. Yao Zhang Z. (2010). Responses of wheat seedlings to exogenous selenium supply under cold stress. *Biological Trace Element Research*, 136: 355-363.

Djanaguiraman M., Devi D.D., Shanker A.K., Sheeba A., Bangarusamy U. (2005): Selenium-an antioxidative protectant in soybean during senescence. *Plant and Soil*, 272: 77-86.

Drabble E., Drabble H. (1907): The relation between the osmotic strength of cell sap in plants and their physical environment. *Biochemical Journal*, 2: 117–132.

Ejaz A. W., Rashid A., Saifullah M. Y., Ashraf E. (2011): Role of mineral nutrition in alleviation of drought stress in plants. *Australian Journal of Crop Science*, 5(6):764-777.

Elizamar C. S., Manoel B. A., André D. A. N. and Carlos D. S. J. (2013): Drought and its consequences to plants-from individual to ecosystem. In book: *Responses of Organisms to Water Stress*.

Fabricio R. A., Geanderson N., S., Karina C. G., Herlon B.F., Kamila R.D. S., Luiz, R.G.G., Valdemar F., andre R. D. (2018): Selenium protects rice plants from water deficit stress. *Ecotoxicology and Environmental Safety*, 164(30): 562-570.

Fahim N., Muhammad N., Muhammad Y. A., Muhammad N. T., Bilal Z., Muhammad S., Rana N. S., Muhammad A. (2016): Selenium supplementation affects physiological and biochemical processes to improve fodder yield and quality of maize (*zea mays* l.) under water deficit conditions. *Frontiers in Plant Sciences*, 7: 1438.

Fang Y., You J., Xie K., Xie W., Xiong L. (2008): Systematic sequence analysis and identification of tissue-specific or stress-responsive genes of NAC transcription factor family in rice. *Molecular Genetics and Genomics*, 280: 547–563.

Feng R., Wei C., Tu S. (2013): The roles of selenium in protecting plants against abiotic stresses. *Environmental and Experimental Botany*, 87:58–68.

Formatted: Portuguese (Brazil)

Germ M., Kreft I., Stibilj V., Urbanc-Bercic O. (2007): Combined effects of selenium and drought on photosynthesis and mitochondrial respiration in potato. *Plant Physiology and Biochemistry*, 45: 162–167.

Greacen E. J. S., Oh (1972): Physics of root growth. *Nature New Biology*, 235: 24-25.

Hartikainen H., Xue T., Piironen V. (2000): selenium as an antioxidant and pro-oxidant in rye grass. *Plant and Soil*, 225: 193-200.

Hasanuzzaman M., Fujita M. (2011): Selenium pretreatment upregulates the antioxidant defense and methylglyoxal detoxification system and confers enhanced tolerance to drought stress in rapeseed seedlings. *Biological Trace Element Research*, 143:1758–1776.

Heba M. I. (2014): Selenium pretreatment regulates the antioxidant defense system and reduces oxidative stress on drought-stressed wheat (*Triticum aestivum* L.) plants. *Asian Journal of Plant Sciences*, 13(3):120-128.

Hortensteiner S., Krautler B. (2011): Chlorophyll breakdown in higher plants. *Biochimica et Biophysica Acta (BBA)-Bioenergetics*, 1807:977-988.

Jaleel C.A., Manivannan P., Sankar B., Kishorekumar, A., Sankari, S., Panneerselvam, R. (2007): Paclobutrazol enhances photosynthesis and ajmalicine production in catharanthus roseus. *Process Biochemistry*. 42:1566-1570.

Jones M. M., Turner N. C. (1978): Osmotic adjustment in leaves of sorghum in response to water deficit. *Plant Physiology*, 61:122–126.

Kakkar, R. K. (2002). Polyamine research in plants-a changing perspective. *Plant Physiology*, 116(3): 281-292.

Kamrun N., Mirza H., Md. Mahabub A., and Masayuki F. (2015): Glutathione-induced drought stress tolerance in mung bean: coordinated roles of the antioxidant defense and methylglyoxal detoxification systems. *AoB Plants*, 7. <https://doi.org/10.1093/aobpla/plv069>

Kaushik D., Aryadeep R. (2014): Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Frontiers in Environmental Science*, 2: 53.

Keskinen R., Turakainen M., Hartikainen H. (2010): Plant availability of soil selenate additions and selenium distribution within wheat and ryegrass. *Plant and Soil*, 333: 301–313.

Khattab H.I., Emam M.A., Emam M.M., Helal N.M., Mohamed M. R. (2014): Effect of selenium and silicon on transcription factors *nac5* and *dreb2a* involved in drought-responsive gene expression in rice. *Biologia Plantarum*, 58 (2): 265-273.

Kumar M., Bijo A.J., Baghel R.S., Reddy C.R.K. Jha B. (2012): Selenium and Spermine alleviates cadmium induced toxicity in the red seaweed *Gracilaria dura* by regulating antioxidant system and DNA methylation. *Plant Physiology and Biochemistry*, 51: 129–138.

Lambers H., Chapin F., Pons T. (2008): *Plant physiological ecology*. Springer, New York, p 540.

Ma Q., Turner D.W. (2006): Osmotic adjustment segregates with and is positively related to seed yield in F₃ lines and crosses between *Brassica napus* and *B. juncea* subjected to water deficit. *Australian Journal of Experimental Agriculture*, 46:1621-1627.

Majid K. (2012). The effect of drought stress on leaf chlorophyll content and stress resistance in maize cultivars (*Zea mays*). *African Journal of Microbiology Research*, 6(12): 2844–2848.

Majid K., Roza G., Shahzad J., Roghayyeh Z. E. (2011): The leaf chlorophyll content and stress resistance relationship considering in Corn cultivars (*Zea mays*). *Advances in Environmental Biology*, 5(1):118-122.

Malik J. A., Goel S., Kaur N., Sharma S., Singh I., Nayyar H. (2012): Selenium antagonises the toxic effects of arsenic on mungbean (*Phaseolus aureus* Roxb.) plants by restricting its uptake and enhancing the antioxidative and detoxification mechanisms. *Environmental and Experimental Botany*, 77: 242–248.

Manal E., Hemmat I. K., Helal N. M., Deraz A. E. (2014): Effect of selenium and silicon on yield quality of rice plant grown under drought stress. *Australian Journal of Crop Science*, 8(4):596-605.

Marika B., Roberto D. Amato., Simona C., Maria C., Fontanella, C. A., Palmerini G. M., Beone A., O., Valeria N., Gianpiero M., Emidio A., Daniela B. (2018): Soil selenium (Se) biofortification changes the physiological, biochemical and epigenetic responses to water stress in *Zea mays* L. by inducing a higher drought tolerance. *Frontiers in Plant Sciences*, 9: <https://doi.org/10.3389/fpls.2018.00389>

McNeal J. M., Balistreri L. S. (1989): Geochemistry and occurrence of selenium: an overview. In: LW Jacobs, ed. *Selenium in agriculture and the environment*. Madison, WI, USA: Soil Science Society of America Special Publication 23: 1– 14.

Meeta J., Mini M., Rekha G. (2013): Effect of peg-6000 imposed water deficit on chlorophyll metabolism in maize leaves. *Journal of Stress Physiology and Biochemistry*, 9(3): 262-271.

Mirza H. M., Anwar H., Masayuki F. (2010): Selenium in higher plants: Physiological role, antioxidant metabolism and abiotic stress tolerance. *Journal of Plant Sciences*, 5: 354-375.

Mitler R. (2002). Oxidative stress, antioxidants and stress tolerance. *Trends in Plant Sciences*, 7: 405–410.

Morgan J.M. (1977): Differences in osmoregulation between wheat genotypes. *Nature*, 270: 234–235.

Mostafa R., Hussein E. E. B., Farouk G., Wael M. S. (2020): Selenium application in two methods promotes drought tolerance in *Solanum lycopersicum* plant by inducing the antioxidant defense system. *Scientia Horticulturae*, 266(6):118.

Muhammad S. H., Mahantesh M. K., Muhammad K. R., Tariq P., Jiu S., Muhammad F., Sudisha J., Chen W., Jinggui F. (2018): Drought stress revealed physiological, biochemical and gene-expressional variations in ‘Yoshihime’ peach (*Prunus Persica* L) cultivar. *Journal of Plant Interactions*, 13(1): 83-90.

Nawaz F., Ashraf M. Y., Ahmad R., Waraich E. A., Shabbir R. N., Bukhari M. A. (2015a): Supplemental selenium improves wheat grain yield and quality through alterations in biochemical processes under normal and water deficit conditions. *Food Chemistry*, 175: 350–357.

Neil C. T. (2018): Turgor maintenance by osmotic adjustment: 40 years of progress. *Journal of Experimental Botany*, 69(13): 3223–3233.

Nesrine A., Mario M., Leila R. (2018): An approach to alleviate the impact of drought stress with selenium amendment. *Iranian Journal of Science and Technology, Science, A. Transaction A.* 42(1): 283-288.

Noctor G., Veljovic-Jovanovic S., Driscoll S., Novitskaya L., Foyer C. H. (2002): Drought and oxidative load in the leaves of C₃ plants: a predominant role for photorespiration? *Annals of Botany*, 89(7): 841-850.

Pandey C., Gupta M. (2015): Selenium and auxin mitigates arsenic stress in rice (*Oryza sativa* L.) by combining the role of stress indicators, modulators and genotoxicity assays. *Journal of Hazardous Materials*, 287: 384–391.

Papageorgiou, G.C., Murata, N. (1995): The unusually strong stabilizing effect of glycine betaine on the structure and function of the oxygen-evolving photosystem II complex. *Photosynthesis Research*. 44: 243-252.

Pukacka S., Ratajczak E., Kalemba E. (2011): The protective role of selenium in recalcitrant *Acer saccharium* L. seeds subjected to desiccation. *Journal of Plant Physiology*, 168: 220-225.

Qiang-yun S., Turakainen M., Seppanen M., Makela P. (2008): Effects of selenium on maize ovary development at pollination stage under drought stress. *Agriculture Sciences in China*, 7: 1298–1307.

Rahdari P., Tavakoli S., Hosseini S.M. (2012): Studying of salinity stress effect on germination, proline, sugar, protein, lipid and chlorophyll content in Purslane (*Portulaca oleraceae* L) leaves. *Journal of Stress Physiology and Biochemistry*, 8(1):182–193.

Renwei F., Chaoyang W., Shuxin Tu. (2013): The role of selenium in protecting plants against abiotic stresses. *Environmental and Experimental Botany*, 87: 58-68.

Saffaryazdi A., Lahouti M., Ganjeali A., Bayat H. (2012): impact of selenium supplementation on growth and selenium accumulation on spinach plants. *Notulae Scientia Biologicae*, 4: 95-100.

Salwa M. A. (2012): Effects of low temperature and selenium application on growth and the physiological changes in sorghum seedlings. *Journal of Stress Physiology and Biochemistry*, 8(1):268-286.

Sanchez-Blanco M.J., Morales M.A., Torrecillas A., Alarcón J.J. (1998): Diurnal and seasonal osmotic potential changes in *Lotus creticus* plants grown under saline stress. *Plant Sciences*, 136: 1-10.

Saud S., Fahad S., Yajun C., Ihsan M.Z., Hammam H.M., Nasim W., Amaullah J. R., Raif M., Alharby H. (2017): Effects of nitrogen supply on water stress and recovery mechanisms in kentucky bluegrass plants. *Frontiers in Plant Sciences*, 8: 983.

Seppanen M., Turakainen M., Hartikainen H. (2003): Selenium effects on oxidative stress in potato. *Plant Sciences*, 165: 311-319.

Sgherri C. L. M., Pinzino C., Navari-Izzo F. (1996): Sunflower seedlings subjected to increasing stress by water deficit: Changes in O_2^- production related to the composition of thylakoid membranes. *Physiologia Plantarum*, 96:446-452.

Shakeel A. A., Xiao-yu X., Long-chang W., Muhammad F. S., Chen M., Wang L. (2011): Morphological, physiological and biochemical responses of plants to drought stress. *African Journal of Agricultural Research*, 6(9): 2026-2032.

Shamima N., Shukanta S., Hasna H. B. Rifat S.(2020): Impacts of drought stress on growth, protein, proline, pigment content and antioxidant enzyme activities in rice (*Oryza Sativa* var. brridhan-24). Dhaka University Journal of Biological Sciences, 29(1): 117-123.

Sharma S., Villamor J.G., Verslues P.E. (2011): Essential role of tissue-specific proline synthesis and catabolism in growth and redox balance at low water potential. *Plant Physiology*, 157: 292-304.

Shikha G., Meetu G. (2016): Alleviation of selenium toxicity in *Brassica juncea* L. salicylic acid-mediated modulation in toxicity indicators, stress modulators, and sulfur-related gene transcripts. *Protoplasma*, 253(6):1515-1528.

Singh R.K., Soares B., Goufo P., Castro I., Cosme F., Pinto-Sintra A.L., Inês A., Oliveira A. A., Falco V. (2019): Chitosan upregulates the genes of the ROS pathway and enhances the antioxidant potential of grape (*Vitis vinifera* L. 'Touriga Franca' and 'Tinto Cão') tissues. *Antioxidants*, 8: 525.

Sivakumar R., Nandhitha G. K., Nithila S. (2017): Impact of drought on chlorophyll, soluble protein, abscisic acid, yield and quality characters of contrasting genotypes of tomato (*Solanum lycopersicum*). *British Journal of Applied Science & Technology*, 21(5): 1-10.

Smirnoff N. (1993): The role of active oxygen in the response of plants to water deficit and desiccation. *New Phytologist*. 125:27–58.

Sors T. G., Ellis D. R., Na, G. N. Lahner B., Lee S., Leustek T. (2005): Analysis of sulfur and selenium assimilation in astragalus plants with varying capacities to accumulate selenium. *Plant Journal*, 42: 785–797.

Sourav M., Ashok M., Kevin E., Trenberth (2018): climate change and drought: a perspective on drought indices. *Current Climate Change Reports*, 4(2): 145-163.

Szabados L., Savaouré A. (2010): Proline: a multifunctional amino acid. *Trends in Plant Sciences*, 15: 89-97.

Tailin X., Helina H., Vieno P. (2001): Antioxidative and growth-promoting effect of selenium on senescing lettuce. *Plant and Soil*, 237(1):55-61.

Terry N., Zayed A. M., De Souza M. P., Tarun A. S. (2000): Selenium in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, 51:401-423.

Usha C., Pradhan B. (2012): Drought stress-induced oxidative stress and antioxidative responses in four wheat (*Triticum aestivum* L.) varieties. *Archives of Agronomy and Soil Science*, 58(6):1-14.

Wang C., Zhang I., Yuan M., Ge Y., Liu Y., Fan J., Cui Z., Tong S., Zhang S. (2010): The microfilament cytoskeleton plays a vital role in salt and osmotic stress tolerance in *Arabidopsis*. *Plant Biology*, 12: 70-78.

Wensen W., Cheng W., Dayu P., Yakun Z., Bin L., Jianwei J. (2018): Effects of drought stress on photosynthesis and chlorophyll fluorescence images of soyabean (*Glycine Max*) seedlings. *International Journal of Agricultural and Biological Engineering*. 11(2): 196-201.

Weronika J., Barbara P. (2019): Effect of selenium on alleviating oxidative stress caused by a water deficit in cucumber roots. *Plants*, 8(7): 217-235.

Xing L., Limei L., Meijuan L., Liangchen S., Siman L., Baihong Z., Xiaoyun L., Kui G., Ling L. (2018). AhGLK1 affects chlorophyll biosynthesis and photosynthesis in peanut leaves during recovery from drought. *Sci Rep* **8**, 2250. <https://doi.org/10.1038/s41598-018-20542-7>

Yao X., Chu J., Liang L., Hou G. (2012): Selenium improves recovery of wheat seedlings at rewatering after drought stress. *Russian Journal of Plant Physiology*, *59*(6): 701-707.

Zaffar M. D., Amjad M., Malik A., Mushtaq A. M. (2018): Review on arbuscular mycorrhizal fungi: an approach to overcome drought adversities in plants. *International Journal of Current Microbiology and Applied Sciences*, *7*(3):1040-1049.

Zahedi H, Noormohammadi G, Shirani Rad AH, Habibi D, Akbar Boojar M. M. (2009): Effect of zeolite and foliar application of selenium on growth, yield and yield component of three canola cultivar under conditions of late season drought stress. *Notulae Scientia Biologicae*, *1*(1):73–80

Zhang J., Kirkham M. B. (1996): Antioxidant response to drought in sunflower and sorghum seedlings. *New Phytologist*, *132*: 361-373.

UNDL

Zhang M. U., Tang S., Huang X. U., Zhang F., Pang Y., Huang Q., Yi Q. (2014): Selenium uptake, dynamic changes in selenium content and its influence on photosynthesis and chlorophyll fluorescence in rice (*Oryza sativa* L.). *Environmental and Experimental Botany*, 107: 39-45.

Zhang Y., Li Y., Hassan M.J. (2020): Indole-3-acetic acid improves drought tolerance of white clover via activating auxin, abscisic acid and jasmonic acid related genes and inhibiting senescence genes. *BMC Plant Biology*, 20(1): 150.

UNDER PEER REVIEW