



Role of Selenium in Regulation of Plant Antioxidants, Chlorophyll Retention and Osmotic Adjustment under Drought Conditions: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. Author ZMD designed the review and wrote the first draft of the manuscript. Authors MAM, MAA, AM and ARD helped in adding details to the topic and managed the literature searches. Authors SUH and ZAD added mechanisms of different pathways, conclusion and incorporated recommendations of the reviewers. All authors read and approved the final manuscript.

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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

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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 inturn are liable for improved plant drought tolerance.

Keywords: Drought; plant; resilience; selenium.

1. 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 [1] more than any other abiotic stress [2,3] Drought usually occurs normally, however the environmental change has quickened the hydrological procedures to make them set in faster with numerous results [4]. Intensity of drought stress depends on several factors, for instance rainfall amount and distribution, evaporative demands and moisture storing ability of soils [5]. 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 [6] leading to plant death through extensive cell dehydration, stomatal closure and limited gaseous exchange [7] hormonal and nutritional imbalance and increased load of free radicals[1]. 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 [8] These adaptations lead to the emergence of new important tools for improving plant drought tolerance. As of late ameliorative role of plant hormones [9], mineral supplements [10] and microbes like AM [1] have been assessed with little consideration on trace elements like selenium (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 [11]. In plants Se can be found both in inorganic and organic forms, including seleno amino acids and methylated compounds [12]. However, it has been reported that organic form of Se are dominant over the inorganic ones [13]. The

membrane receptors responsible for accumulation of Se in the plant tissue have not been identified so far [14], however it is expected that uptake of Se in selenate and selenite forms occurs respectively through high affinity sulfate transporters [15] and phosphate transporters [16] depending on plant species [13] In spite of the fact that Se isn't yet affirmed to be required by higher plants [17] 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.

2. 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. AOS are primarily generated in chloroplasts, mitochondria, peroxisomes, apoplast, and plasma membranes [18]. The enhanced production of AOS during biotic and abiotic stresses damage cells by promoting oxidative stress which results in, oxidation of proteins, peroxidation of lipids, nucleic acid degradation, enzyme inhibition, activation of programmed cell death [19-21]. Oxidative stress has been reported in wheat [22,23], sunflower ([24] rapeseed [25] etc. due to increased generation of hydrogen peroxide (H_2O_2) and O_2^- in the leaves. Generation of AOS

has been reported to increase from less than 240 $\mu\text{M S}^{-1} \text{O}_2$ to 240-270 $\mu\text{M S}^{-1} \text{O}_2$ [19]. 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 [26]. Photorespiratory pathway is another justification for increased production ROS particularly once RuBP oxygenation is maximal due to CO_2 fixation [27].

Chu et al. [28], Hasanuzzaman and Fujita [25], Pukacka et al. [29], Kumar et al. [30], Pandey and Gupta [31] reported that selenium protects plants against several abiotic stresses viz; cold stress, drought stress, desiccation and heavy metal toxicity. Literature cited clearly indicates that Se at low doses overcomes the damage caused by oxidative stress during drought. Weronika and Barbara [32] and Chang-Quan [33] 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^- , H_2O_2 and OH^- 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, H_2O_2 accumulation and O_2^- generation in drought stressed wheat Heba [34] and Yao et al. [35]. Similar type of results pertaining to Se application have been reported by Hasanuzzaman and Fujita [25] and Fabricio et al. [36] respectively in rape seed and rice growing under water deficit. Renwei et al. [37] has reported that Se works on AOS either by quenching the AOS or reducing their number. The spontaneous dismutation of O_2^- to H_2O_2 in a non-catalysed by an SOD reaction and subsequent removal of O_2^- and H_2O_2 by Se compounds, is achieved under an optimum concentration of selenium in plants. Due to similarity of selenium to sulphur, it utilizes sulphur pathways and is absorbed by cells at higher concentrations. It is then used in cysteine biosynthesis and instead of normal amino acid selenocysteine is formed which is 21st genetically encoded amino acid. This amino acid is used to produce glutathione peroxidase protein that reduce ROS at the expense of glutathione [38,39]. Cartes et al. [40] also reported selenium

dependent regulation of antioxidant enzymes. Se as an essential microelement has recently gained importance in plant systems due to its effect on the antioxidative defense system [41]. It has been reported that exogenous application of Se in rice mediated the drought tolerance by increasing the total antioxidant capacity particularly in shoots [42] which included catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX) and superoxide dismutase (SOD) followed by a reduction in lipid peroxidation and hydrogen peroxide (H_2O_2) content [43]. Antioxidants react with the AOS thus leaving them less active and less toxic by accepting or donating electrons to remove the high affinity electron pair of the ROS radical [44]. Several authors also reported that Se itself acts as an antioxidant at lower concentrations by significantly increasing the contents and activity of the components of the antioxidant defense system [45].

3. EFFECT ON CHLOROPHYLL CONTENT

Water stress leads to disturbance in several physiological and chemical processes, among which reduction in leaf chlorophyll content is considered as the most critical factor which consequently reduces the plant growth and yield [46]. However, the decreased chlorophyll content during drought stress depends on the duration and severity of drought level [47]. Reduced chlorophyll levels under drought stress have been reported in maize [48], rice [49], tomato [50], soybean [51] and so many other agricultural and horticultural crops of economic importance. It is considered as a typical symptom of pigment photo oxidation, disintegration [52] and over production of AOS [53]. [54] 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 encoding a key enzyme in chlorophyll biosynthesis and affects the expression of genes related to chlorophyll biosynthesis decline markedly under drought conditions [55]. Hortensteiner and Krautler [56] have regarded HemA (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 [57] 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.

Optimal exogenous supplementation of Se reduces the effect of drought induced stress and modulates the photosynthetic functions by increasing chlorophyll content [58]. Seppanen et al. [59] and Balal et al. [60] reported that exogenous application of Selenium minimizes the damage to the chloroplasts which helps in maintaining the levels of photosynthetic pigments under abiotic stress conditions. Enhancement in chlorophyll content under drought has been reported in many crops like maize [61], spinach [62], lettuce [63], sorghum [64] etc. Djanaguiraman et al [65] reported that low Se concentrations in plant tissues alter chlorophyll biosynthetic pathways. It has been reported that increase in chlorophyll content by Se supplementation under drought stress is due to enhanced activity of antioxidative enzymes [66] 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 [39,67]. Increase in chlorophyll content may be attributed to effect of Se on protection of chloroplast enzymes [68] and increased cell metabolic rate which enhances the chlorophyll synthesis and retard chlorophyll degradation [69]. 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 [70]. 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.

4. 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 [71]. Osmotic adjustment in response to drought was first recognized more than four decades ago [72] by Greacen and Oh [73] in pea roots, by Morgan [74] in wheat leaves, by [75] and Jones and

Turner [75] in sorghum leaves. Plants protect themselves against drought by over-expression of some osmoprotectants which include sugars like sucrose, glucose and fructose [76] (chez et al. 1998), inorganic cations like potassium, magnesium, chloride and nitrate and amino acids like proline and glycine betaine (GB) [77]. The importance of solutes in maintaining plant cellular turgor pressure and adaptation to harsh environments has been, well defined by Drabble & Drabble in [78]. 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 cellular proteins and photosynthetic apparatus [79] and assist in scavenging of ROS [80]. Role of osmolytes viz; Glycine Betaine and Proline in maintaining cellular integrity and osmotic adjustment under drought stress is also well known [81]. Proline is not only an osmolyte but it is also an ROS scavenging and signal molecule under drought conditions and thus helps in maintaining the redox homeostasis of cell and uninterrupted energy supply to the cell [82,83]. 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 inturn encode the enzymes such as

1. 1-Pyrroline-5-carboxylate synthase (important enzyme in proline biosynthesis).
2. betaine aldehyde dehydrogenase, (glycine betaine accumulation).
3. myo-Inositol 6-O-methyltransferase, (accumulation pinitol) [84].

In addition to the above mentioned enzymes expression of glyceraldehyde-3-phosphate (3GP) dehydrogenase increases during osmotic stress, perhaps to allow an increase of carbon flow into organic solutes for osmotic adjustment [84].

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, wheat and maize [66,85,86] mediated through its positive impact on osmotic and ionic balance to increase water uptake and reduce transpiration under drought stress conditions. Marika et al. [6] have reported a marked increase in Proline and Potassium content as well as enhanced nitrogen

metabolism in selenium biofortified tissues. Selenium pretreated rice plants exhibited enhanced production of GB and Proline, consequently better growth [87]. Among 140 putative NAC or NAC like genes, twenty of the genes act as stress responsive genes including OsNAC5 [88] having a role in the production of osmolytes. Overexpression of OsNAC5 genes because of Se pretreatment in rice plants enhances the accumulation of proline and soluble sugars hence protecting the plants from dehydration and oxidative stress under drought [87]. 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 [88].

5. 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.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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