

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 inturn 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 (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 Balistrieri 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 (Kiskenen 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. AOS are primarily generated in chloroplasts, mitochondria, peroxisomes, apoplast, and plasma membranes (Singh et al. 2019). 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 (Mitler 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 $\text{O}_2^{\cdot-}$ in the leaves. Generation of AOS has been reported to increase from less than $240 \mu\text{M S}^{-1} \text{O}_2$ to $240\text{-}270 \mu\text{M S}^{-1} \text{O}_2$ (Mitler 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).

Chu et al. (2010), Hasanuzzaman and Fujita (2011), Pukacka et al. (2011), Kumar et al. (2012), Pandey and Gupta (2015) 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 (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 $\text{O}_2^{\cdot-}$, 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, H_2O_2 accumulation and $\text{O}_2^{\cdot-}$ 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. The spontaneous

dismutation of $O_2^{\bullet-}$ to H_2O_2 in a non-catalysed by an SOD reaction and subsequent removal of $O_2^{\bullet-}$ 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 (Hawkes et al., 2010). (Hartikainen et al. 2000) Cartes et al. 2010 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 (Nesrine et al. 2018). It has been reported that exogenous application of Se in rice 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 (H_2O_2) content (Zahedi et al. 2020). 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 (Mostafa et al. 2020). 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 (Tailin et al. 2001).

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 (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). Reduced chlorophyll levels under drought stress have 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. It is considered as a typical symptom of pigment photo oxidation, 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 encoding a key enzyme in chlorophyll biosynthesis and affects the expression of genes related to chlorophyll biosynthesis decline markedly under drought conditions (Xing et al. 2018). Hortensteiner and Krautler (2011) 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 (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.

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 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 (Fahim et al. 2016), spinach (Saffaryazdi et al. 2012), lettuce (Duma et al. 2011), sorghum (Abbas 2012) etc. Djanaguiraman et al (2005) 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 (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 (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 (GB) (Ma and Turner 2006). The importance of solutes in maintaining plant cellular turgor pressure and adaptation to harsh environments has been, well defined by Drabble & Drabble in 1907. 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 (Papageorgiou and Murata 1995) and assist in scavenging of ROS (Wang et al. 2010). Role of osmolytes viz; Glycine Betaine and Proline in maintaining cellular integrity and osmotic adjustment under drought stress is also well known (Ashraf and Foolad 2007). 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 (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 (important enzyme in proline biosynthesis).
2. betaine aldehyde dehydrogenase, (glycine betaine accumulation).
3. myo-Inositol 6-O-methyltransferase, (accumulation pinitol) (Buchanan et al. 2000).

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 (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, wheat and maize (Germ et al. 2007; Nawaz et al. 2015a and Qiang-yun et al. 2008) mediated through its positive impact on osmotic and ionic balance to increase water uptake and reduce transpiration under drought stress conditions. Marika et al. (2018) 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 (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 enhances the accumulation of proline and soluble sugars hence protecting the plants from dehydration and oxidative stress under drought (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.

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