



Oxidative Stress and Antioxidant Machinery in Stressed Plants

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Because of the steady increase in the negative effects of climate change, higher plants are found to be the most affected as a result of their falling under the effects of many environmental; biotic and abiotic stresses. These stresses cause great threats to growth and productivity of plants. The master signal of these stresses at the level of molecular biology is the overproduction of reactive oxygen species (ROS), which cause oxidative stress. As a result, the agricultural sector suffers huge losses, which has the greatest negative impact on global food security [1].

Environmental stresses include biotic and abiotic stresses, the latter group in particular cause a decrease in the activity of the photosynthetic machinery in plants and facilitate the acceleration of ROS accumulation. The ROS, which are greatly reactive and usually toxic, are oxygen radicals and their derivatives, including superoxide radicals ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), hydroxyl radical (OH^{\cdot}), and singlet oxygen (1O_2). Due to stress, the overproduction of these ROS generates adverse conditions, hampering the normal growth of plants due to disturbances in metabolic processes and redox homeostasis. As a result, damage to macromolecules (e.g., protein oxidation, membrane lipid peroxidation, and nucleic acids damage) can be stimulated, and eventually death of plant cells [2-6]. As well established in recent years, ROS have been reported as central control molecules in plants, and their roles in early signaling events established by normal cell metabolic functions and environmental stresses [1,7]. Even in natural environments, plants are constantly subjected to stresses, including abiotic in particular such as high temperatures, salinity stress, drought, heavy metals, etc., which have a significant impact on the agricultural sector worldwide and thus the economy

is greatly lost. However, when plants are grown under normal conditions, a balance between the production and removal of ROS is explored, but this balance has been reported to be impeded by different environmental stresses, and thus the overproduction of different types of ROS in plant cells is explored. In this case, an efficient antioxidant machinery must be stimulated in plant cells to mitigate the harmful effects of these types of ROS.

Improving the efficiency of the antioxidant system in stressed plants is of interest to biologists so that plants can overcome the harmful effects of stress and give satisfactory growth and yield. Therefore, plant biotechnology and molecular biology have recently advanced to develop efficient approaches, which can improve the antioxidant machinery in plants [1]. However, more precise studies on oxidative stress and antioxidant defense systems in stressed plants are required, especially for stress-sensitive plants, to come up with a more efficient approach to increasing plant stress tolerance.

Attenuation of the harmful impacts of ROS in plant cells is a critical requirement in favor of stressed plants to produce satisfactory yields. For this purpose, efficient activities of non-enzymatic and enzymatic antioxidants (i.e., antioxidant defense system) must be accessed, as they play pivotal roles in the upregulation of adaptation mechanisms of plants under oxidative stress [1-12]. Ascorbate (AsA), glutathione (GSH), tocopherols (TOCs), carotenoids, flavonoids, etc., are low molecular mass non-enzymatic antioxidants. To integrate into the activity of antioxidant mechanisms, superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase

(APX), glutathione reductase (GR), glutathione peroxidase (GPX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione S-transferase (GST) are antioxidant enzymes. All of these different antioxidants are involved in the detoxification of different types of ROS to protect plants, in whole or at least in part, from oxidative damage [1-18], which has been reported through all possible combinations of advanced modern genomics and molecular approaches [9].

If the production of different types of ROS is higher than the ability of the plant's endogenous antioxidant systems to eliminate them, this leads to oxidative stress and, ultimately, plant cell death. Therefore, to overcome this problem, investigators are trying to adopt/develop effective and environmentally friendly strategies based on innovative technologies to increase the plant's endogenous antioxidant systems to enable stressed plants to perform higher through sustainable treatments [10]. The promotion of the antioxidant defense system is known to correlate with stress tolerance in plants and is greatly associated with the applications of exogenous antioxidant and/or biostimulators to stress-tolerant or stress-sensitive plants [2-19]. For example, sequential application of proline, AsA, and/or GSH corrects ion imbalance (i.e., improvements in leaf and root K^+ and Ca^{2+} contents, as well as minimized leaf and root Cd^{2+} and Na^+ contents) and promotes the antioxidant defense systems (i.e., extra improvements in AsA, proline, and GSH contents, as well as enzymatic activities) in salt-stressed cucumber plants. This positive finding led to enhanced growth traits and photosynthetic machinery and restoration of leaf tissue disintegration [15]. Additionally, the recent information is available about the AsA-GSH pathway in relation to tolerance to oxidative stress, as well as plant antioxidant defense mechanisms and ROS response and function under stress conditions [20,21].

By condensing the antioxidants and the contents of secondary metabolites, it has been explored that some plants have a great capacity of antioxidants; tolerance mechanisms to defend against oxidative damage. These tolerance mechanisms include accumulation of secondary metabolites like levels of phenols, AsA, proline, flavonoids, and tannins, which gradually increase along with levels of antioxidant enzyme activities in response to different altitudes [22]. Exogenous applications of various plant growth stimulators, including amino acids, especially proline, as well as polyamines, vitamins, plant growth regulators and/or nutrients to seeds and/or plant foliage can attenuate oxidative

damage stimulated by ROS. The systemic actions of these plant growth (bio)stimulators promoted tolerance to different abiotic stresses by elevating the activities of antioxidant defense systems and suppressing oxidative damage at the cellular level [2,23-34]. Assertiveness of the impacts of selenium (Se) application on normal or stressed plants has been reported, with access to Se application raising the nutritional and quality values of foods in Se-deficient environments and promoting the tolerance of olive trees and common bean plants to oxidative stress. These findings signaled that trace elements, including Se, have pivotal functions in the ability of plants to adapt to stress [4,35]. Se has diverse positive impacts on plants, as its application alone or in integration with other elements can raise the plant's tolerance to oxidative stress [36]. Application of Se and/or B markedly increased plant growth via promoting enzyme (e.g., CAT, POD, APX, GR, GPX, Gly I and II, MDHAR, DHAR, and GST) activities and suppressing the levels of malondialdehyde (MDA) and H_2O_2 under salinity stress [37]. In addition, several reports display that applications of exogenous plant hormones can attenuate oxidative damage in plants. Treatment with gibberellic acid, jasmonic acid, salicylic acid and/or zeatin-type cytokinins led a decrease in toxic ion contents (Na^+ and Cl^-) and an increase in photosynthetic machinery, antioxidant enzyme activities, and nutrient contents (N, K^+ , and Mg^{2+} , as well as K^+/Na^+ ratio), as well as levels of RNA, DNA, chlorophylls and carotenoids, thus improving the growth and productivity of stressed plants [6,17,38-42]. Like plant hormones, the low molecular mass antioxidants, including AsA, GSH, and TOCs are absolutely essential in improving plant growth and productivity by enhancing the various components of the antioxidant defense systems and suppressing oxidative stress damage [16,20,43]. At present, treatment with nanoparticles (NPs) such as nano-Se and nano-P improved the growth and productivity of stressed plants by promoting different antioxidant defense system components and suppressing damages stimulated by oxidative stress [4,10,44].

Conclusion

So far, promising findings have been obtained by the exogenous use of antioxidants, plant hormones, and different explored plant growth promoting (bio)stimulators, including natural plant extracts in controlling the adverse impacts of different environmental stresses at the field and greenhouse levels. However, more research is still needed in this regard.

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