JETIR.ORG ISSN: 2349-5162 | ESTD Year : 2014 | Monthly Issue
JOURNAL OF EMERGING TECHNOLOGIES AND INNOVATIVE RESEARCH (JETIR)
An International Scholarly Open Access, Peer-reviewed, Refereed Journal

BIOLOGY AND PHYSIOLOGY OF PLANT OXIDATIVE STRESS

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Abstract:

A key sign of stresses at the molecular level is the accelerated production of reactive oxygen species (ROS), which cause oxidative stress. A key sign of such stresses at the molecular level is the accelerated production of reactive oxygen species (ROS), which cause oxidative stress. ROS-induced oxidative damage can be alleviated by exogenous application of different chemical substances, such as amino acids and their derivatives, sugars, polyamines and vitamins, plant growth regulators to seeds (as seed priming), roots (as irrigation or soil incorporation), or leaves (as foliar application), at low concentrations. The systemic action of these chemicals improved various abiotic stress tolerances, including salinity, by increasing the antioxidant defense system and decreasing oxidative injuries at the cellular level. Some of the non-enzymatic antioxidants, such as ascorbic acid, glutathione and tocoferol were reported to be very effective in scavenging and detoxifying ROS.

Keywords: Antioxidants; Nano particles; Oxidative stress; Plants; ROS.

Plants are frequently exposed to abiotic and biotic stresses, and these stresses pose serious threats to plant growth and productivity. A key sign of such stresses at the molecular level is the accelerated production of reactive oxygen species (ROS), which cause oxidative stress. A key sign of such stresses at the molecular level is the accelerated production of reactive oxygen species (ROS), which cause oxidative stress. —which are oxygen radicals and their derivatives—such as hydrogen peroxide (H_2O_2) singlet oxygen ($^1O_2$), superoxide radicals ($O_2^{\bullet-}$), and hydroxyl radical ($OH^{\bullet}$). These are highly reactive and usually toxic. A key sign of such stresses at the molecular level is the accelerated production of reactive oxygen species (ROS), which cause oxidative stress (Hasanuzzaman et al 2019, Hasanuzzaman et al 2020, Hasanuzzaman et al 2021). Under normal circumstances, there is a balance between the generation and the elimination of ROS. However, this balance can be hampered by different biotic and abiotic stresses, resulting in the generation of a large number of ROS that should be counteracted by the antioxidant machinery in cells.

Enhancement in the antioxidant defense systems in plants is a very important task for plant biologists. Recent progress in plant molecular biology and biotechnology has been targeting the development of approaches that can be used to enhance the antioxidant defense systems in plants. New knowledge acquired through research on oxidative stress, abiotic stress, and biotic stress tolerance in plants will help us to apply stress-responsive determinants and to engineer plants with enhanced tolerance to stress.

Enhanced activities of antioxidant enzymes play a crucial role in upregulating the adaptation mechanisms of plants under oxidative stress (Miller et al 2010). Non-enzymatic antioxidants—such as ascorbate (AsA), glutathione (GSH), tocopherols (Toc), flavonoids, and carotenoids—and enzymatic antioxidants—such as superoxide dis- mutase (SOD), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), glutathione *S*-transferase (GST), glutathione peroxidase (GPX), and peroxidase (POD)—take part in scavenging ROS and protect the plants from oxidative damage (Hasanuzzaman et al 2019, Hasanuzzaman et al 2020).

Developed genomic tools have shown that antioxidant defense is crucial for defending the plant against oxidative stress (Billah et al 1910). Many researchers have revealed that modern genomics studies have advanced our capabilities of improving crop genetics, especially those traits relevant to abiotic stress management. Advanced genomics tools and the gene regulatory network of reactive oxygen species homeostasis for the appropriate planning of future breeding programs, which will assist sustainable crop production under salinity and drought conditions (Billah et al 1910).

Seleiman et al reported that sequential application of proline, AsA, and/or GSH rectifies ion imbalance and strengthens antioxidant systems in salt-stressed cucumber by improving growth characteristics, photosynthetic efficiency, relative water content and membrane stability index. Additional improvements were seen in AsA, Pro, and GSH; enzymatic activity; leaf and root K^+ and Ca^{2+} contents; and their ratios to Na^+, while the same sequential applications significantly reduced leaf and root Cd^{2+} and Na^+ contents (Seleiman et al 2020).

Endemic plants were found to have ample capacity for antioxidant defense, and those plants provide enhanced tolerance to oxidative stress. Accumulation of secondary metabolites is a defense mechanism, as reported by Hashim et al. They found that endemic endangered species viz. *Nepeta septemcrenata*, *Origanum syriacum* subsp. *Sinaicum*, *Phlomis aurea*, *Rosa arabica*, and *Silene schimperiana*) showed elevated phe- nols, AsA, Pro, flavonoids, and tannins content in response to different altitudes. Secondary metabolites progressively increased in the studied species that were associated with a significant decrease in the levels of antioxidant enzyme activity (Hashim et al 2020).

ROS-induced oxidative damage can be alleviated by exogenous application of different chemical substances, such as amino acids and their derivatives, sugars, polyamines and vitamins, plant growth regulators to seeds (as seed priming), roots (as irrigation or soil incorporation), or leaves (as foliar application), at low concentrations. The systemic action of these chemicals improved various abiotic stress tolerances, including salinity, by increasing the antioxidant defense system and decreasing oxidative injuries at the cellular level (Costa et al 2018).

Se biofortification increased the nutritional and qualitative values of foods in Se-deficient regions and increased the tolerance of oxidative stress in olive trees. This result indicated that trace elements have important functions in the adaptability of plants (Del Pino et al 2021). A key sign of such stresses at the molecular level is the accelerated production of reactive oxygen species (ROS), which cause oxidative stress. This element alone or in combination with other elements could provide increased plant oxidative stress tolerance, (Hasanuzzaman et al 2020). The study conducted by Rahman et al revealed that supplementation of Se, boron (B), and Se + B enhanced the activities of APX, MDHAR, DHAR, GR, CAT, GPX, GST, POD, Gly I, and Gly II. This supplementation consequently diminished the H_2O_2 content and MDA content under salt stress and improved the growth parameters. The results reflected that exogenous Se, B, and Se + B enhanced the enzymatic activity of the antioxidant defense system and the glyoxalase systems under different levels of salt stress. This ultimately alleviated the salt-induced oxidative stress. Se+B supplementation was more effective than a single treatment (Rahman et al 2021).

A key indicator of such stresses at the molecular level is the accelerated production of reactive oxygen species (ROS), which cause oxidative stress. Al-Harthi et al performed seed priming with gibberellic acid (GA) and jasmonic acid (JA) and subsequently, the plants (summer squash) were grown in saline media. They observed that GA and JA resulted in a reduction of the concentration of Na^+, Cl^-, and the chlorophyll (Chl) *a*/*b* ratio. Increasing the activity of SOD, CAT, and APX the quantities of K^+ and Mg^{2+}; the K^+/Na^+ ratio; and the quantities of RNA, DNA, Chl *b*, and carotene, ameliorated the growth of salinized plants (Al-harthi et al 2021).

Salicylic acid was also found to be very protective against oxidative stress due to its metabolic functions. This hormone was found to enhance antioxidant defense and osmolyte metabolism, which was the main cause of oxidative stress tolerance in watermelons exposed to B toxicity (Moustafa-Farag et al 2021). Exogenously applied SA promoted photosynthesis and consequently, biomass production in watermelon seedlings treated with a high level of B by reducing B accumulation, lipid peroxidation and the generation of H_2O_2, while significantly increasing levels of the most reactive ROS, $OH^\bullet$ (Moustafa-Farag et al 2021).

In combination methyl jasmonate and SA were found to mitigate drought- induced oxidative damages in *Phaseolus vulgaris* as observed by Mohi-Ud-Din et al. Combined application of these phytohormones remarkably enhanced the drought tolerance of plants by improving the physiological activities and antioxidant defense system (SOD, CAT, POD, GPX, and GST as well as the enzymes of the AsA–GSH cycle). Phytohormones lowered the generation of $O_2^{\bullet-}$ and H_2O_2 and the malondialdehyde (MDA) content (Mohi-Ud-Din et al 2021).

Some of the non-enzymatic antioxidants, such as AsA, GSH, and Toc, were reported to be very effective in scavenging and detoxifying ROS. Foliar application of α-Toc significantly improved the yield in tested okra varieties by increasing the activity of antioxidants (CAT, GPX, SOD, and AsA), accumulation of glycine betaine, and total free Pro in fruit tissues under saline and non-saline conditions. However, these effects were dose-dependent (Naqve et al 2021). Manipulating production practices or growing techniques can also help in mitigating oxidative stress in plants. Bitter melon (*Momordica charantia* L.) - grafted cucumber seedlings showed significantly improved heat-induced growth inhibition and photoinhibition, maintained better photosynthesis activity, and accumulated greater biomass than self-grafted seedlings (Tao et al 2021).

Several aminoacids and peptones are involved in the stimulation of physiological and metabolic functions of plants (Soad et al 2010, Emanuil et al 2021). The application of peptone decreased Cd uptake and decreased levels of MDA, H_2O_2, and electrolyte leakage in spinach by increasing the activity of antioxidant enzymes. It indicated that peptone is a promising plant growth regulator that represents an efficient approach for the phytoremediation of Cd-polluted soils and enhancement of spinach growth, yield, and tolerance under a Cd-dominant environment (Emanuil et al 2021). Nanoparticles (NPs) have shown increasing attention in research focusing on enhancing the growth progress and development of plants (Do Espirito Santo Pereira et al 2021). NPs have recently become more commonly employed in commercial products and industrial applications (Yan and Chen 2018). There are many studies where NPs are commonly used as growth regulators and stress elicitors (Mittal et al 2021).

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