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Role of oxidative stress enzymes in abiotic and biotic stress

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ABSTRACT

The study of the role of antioxidant enzymes in response to abiotic and biotic stress is of great importance in understanding plant responses to stress, biochemical changes, and their role in the formation of resistance to various factors. Studying these aspects will contribute to the implementation of targeted therapy in the event of exposure to a stress factor. The use of a plant model in this case is particularly acceptable, since oxidation processes under various types of stress, along with plants, are also found in the body of animals and humans. Oxidative stress caused in response to stress is caused by increased production of reactive oxygen species, which are represented as radicals. Under abiotic or biotic stress, the antioxidant system cannot cope with reactive oxygen species due to their insufficient synthesis, which leads to the death of individual parts of the plant or the entire organism. In any case, the protective response covers the entire plant, i.e. it is systemic and is aimed, on the one hand, at damage repair, on the other – at chemical self-defense. Secondary metabolism is activated in plants, phenols, terpenoids, and alkaloids accumulate, and intensive lignification and synthesis of structural cell wall proteins are observed. As a result of the analysis, the main aspects of the influence of stressors on the activation of the enzymatic antioxidant system, and, in particular, the enzymes superoxide dismutase, catalase and peroxidase and their role in the primary immune response of plants to stress are highlighted. It can be concluded that a more thorough study of the cascade of enzymatic reactions of plants to stress will make it possible to effectively select methods for the prevention and control of abiotic and biotic stresses.

Key words: Oxidative stress, Enzymes, Plants, Radicals, Active oxygen.
Article type: Review Article.

INTRODUCTION

The appearance of the first photosynthetic plants led to the accumulation of oxygen in the medium, which has two unpaired electrons with the same quantum number (spin). This feature makes oxygen capable of accepting electrons one at a time in a single reaction, which leads to a one-electron reduction of oxygen and causes the

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formation of reactive oxygen species (ROS; Vuleta *et al.* 2016). ROS are constantly formed as a byproduct in mitochondria, chloroplasts, and peroxisomes, as a result of various metabolic processes. 95% of the oxygen consumed by the cell is restored in the mitochondria, the remaining 2-5% is involved in various enzymatic reactions (Lobna *et al.* 2016). This class of molecules is divided into: radical-superoxide (O_2), hydroxyl radical (OH'), non-radical molecules-singlet oxygen and H_2O_2 (Chai *et al.* 2012). Plants can be infected with pathogenic microorganisms – bacteria, fungi, viruses. Further events can unfold in two scenarios. The first is that the pathogen easily spreads through the plant, which "gets sick" and can die. The second is that the plant receives the signal of infection at the right time and resists infection, including a genetically determined protection program. This program is aimed at getting rid of the infection, preventing its spread, and increasing the immunity of the plant organism. The success of such a program depends on how quickly the plant "learns" about the attack (Debona *et al.* 2012). The pathogen attack is recognized by the corresponding receptors located in the plasmalemma. The receptor binds to one of the many metabolites released by a pathogenic microorganism, which is called an elicitor (Avinash & Umesha 2014). Binding to the elicitor activates the receptor and gives rise to the development of a protective program. Treatment with an exogenous elicitor is also perceived by the plant as a signal of an attack and initiates a defence program. This program begins with a phenomenon called the hypersensitivity reaction (Kebede *et al.* 2014). The hypersensitivity reaction is associated with the formation of necrosis and cell death in the zone of introduction of a pathogenic microorganism/virus. Thus, at the cost of the death of its own cells, the plant manages to get rid of the infection or, at least, prevent its further spread (Laz *et al.* 2018). Simultaneously with the hypersensitivity reaction, changes occur throughout the plant aimed at increasing immunity and resistance to the pathogen. The protective response is systemic in nature, i.e. it covers the entire plant, all its healthy tissues, and not just the attacked leaves. The implementation of the protection program involves the synthesis of many compounds. Secondary metabolism is necessarily activated, which is aimed at synthesizing compounds with fungicidal or bactericidal properties. These are primarily plant phenols, but also volatile monoterpenes and sesquiterpenes. Cell wall strengthening begins throughout the plant: the synthesis of lignin and extensins (structural glycoproteins of cell walls) becomes more intense (Zafar Ul hye *et al.* 2020). Of course, these changes are associated with the activation of the expression of many genes and the synthesis of many enzymes. As a rule, when plants are infected, both in affected and healthy tissues, the synthesis of secondary metabolism enzymes – phenylalanine-ammonium-lyase and halcon synthase, glutathione-S-transferases, and many others- increase. In response to a pathogen attack, previously "silent" genes are activated, the expression of which is exclusively associated with infection. These genes encode the de novo synthesis of so-called PR (Pathogenesis-related) proteins. PR-proteins include chitinases and glucanase that destroy the cell walls of fungi and bacteria, as well as enzymes necessary for the synthesis of plant antibiotics-phytoalexins, among which there are flavonoids, alkaloids and terpenoids. As a result of all these changes, the plant becomes more resistant to subsequent infection with this pathogen, i.e., it acquires Systemic Acquired Resistance (SAR) to it (Naveen *et al.* 2013). The first reaction of the plant to the attack of a pathogen is an oxidative explosion at the site of the introduction of the microorganism, which leads to a hypersensitivity reaction. Rapid absorption of oxygen by cells begins with the formation of a superoxide radical, and peroxide quickly formed with the participation of SOD begins to accumulate in cells located in this zone. The time of occurrence of such a reaction can vary from several minutes to hours, but, as a rule, an early and later oxidative explosion is observed. In some cases, O_2 generation in plant cells was detected as early as a few minutes after treatment with the fungal elicitor, while a later increase in ROS production occurred several hours later. At the very beginning, the oxidative explosion is caused by the formation of O_2 and H_2O_2 in the apoplast (Hashmi *et al.* 2019). There is no doubt that NADPH oxidases of cell walls are involved in this process. Activation of NADH-dependent peroxidase reactions is clearly manifested during pathogen introduction and is an integral part of the hypersensitivity reaction. As a result of these reactions, peroxide is formed directly or with the participation of SOD, which migrates from the apoplast to the cell. Somewhat later, ROS overproduction begins inside cells, especially in chloroplasts. Against this background, the activity of catalase and ascorbate peroxidase decreases in cells, which naturally contributes to an even greater accumulation of peroxide (Ramzan *et al.* 2020). Overproduction of O_2- and accumulation of H_2O_2 provoke cell death, resulting in necrosis on the leaves, areas of dead cells, which prevents the spread of infection. Interestingly, in areas of necrosis, cell death occurs not only due to oxidative damage, of course, but also peroxide damages cellular structures, however, at the same time it triggers an active program of cell death. Cell death in the hypersensitivity reaction has clear features of apoptosis. It is accompanied by chromatin fragmentation, and is generally considered

to be programmed cell death. Notably, in the zone of pathogen introduction, not only O_2- and H_2O_2 accumulation, but also NO synthesis occur. It is possible that O_2 and NO act as synergists and their interaction produces peroxynitrite, an even more powerful oxidizer than peroxide. In addition, there is evidence that H_2O_2 and NO act together in the induction of cell death (Ahmad *et al.* 2014). Considering the hypersensitivity reaction in plants, it is impossible not to mention the analogy that takes place in animal cells. Specialized cells, phagocytes and B-lymphocytes, when they come into contact with the surface of bacterial cells, begin to produce O_2 with the participation of NADPH oxidase, which is embedded in the phagocyte membrane. By provoking an oxidative explosion, phagocytes kill foreign cells (Ismail *et al.* 2011). If O_2^- and H_2O_2 over-formation in the necrosis zone causes local cell death, then in more distant tissues peroxide induces the development of systemic resistance (Tripathi & Mishra 2009). It is assumed that H_2O_2 migrates to the tissues surrounding the areas of necrosis, however, it is not yet very clear over what distances such diffusion is possible. In the tissues surrounding necrosis, peroxide, possibly together with NO, acts as a secondary messenger in triggering reactions leading to the synthesis of other signalling molecules, primarily salicylic acid. The content of salicylic acid dramatically increases in cells surrounding the necrosis zones, and it is believed that its synthesis is induced by hydrogen peroxide. It is possible that H_2O_2 induces the synthesis of benzoic acid hydrolase, an enzyme necessary for the formation of salicylic acid. Thus, due to its ability to cross membranes, H_2O_2 acts not only as an intracellular messenger, but also as an intercellular messenger (Diao *et al.* 2014). Thus, the formation of superoxide radical and hydrogen peroxide in the apoplast is one of the first reactions to stress associated with the attack of microorganisms and phytophages on the plant. This danger signal induces signal transduction pathways that lead to the synthesis of other signal molecules and take over the signal transmission pathway.

Superoxide Dismutase

Superoxide dismutase or metalloenzyme (SOD) is the most effective intracellular enzymatic antioxidant, which is ubiquitously present in all aerobic organisms and in all subcellular compartments prone to ROS-mediated oxidative stress. It is well known that various environmental stresses often lead to increased ROS generation, where SOD plays an important role in plant stress resistance and provides the first line of defence against the toxic effects of increased levels of oxidative stress. SOD removes O_2 by catalysing its dismutation, i.e., the rearrangement reaction of one molecule into two others: one O_2 molecule converted to H_2O_2 and the other is oxidized to O_2. The enzyme removes and therefore reduces the risk of OH formation through the metal-catalysed Haber-Weiss reaction, which is 10,000 times faster than spontaneous dismutation (Abbas *et al.* 2020). SOD are classified by their metallic cofactors into three known types: copper/zinc (Cu/Zn-SOD), manganese (Mn-SOD), and iron (Fe-SOD), which are localized indifferent cell compartments. Three Fe-SOD genes (FSD1, FSD2, and FSD3), three Cu/Zn-SOD genes (CSD1, CSD2, and CSD3), and one Mn-SOD gene (MSD1) were registered in the *A. thaliana* genome (García Limones *et al.* 2002). The activity of SOD isozymes can be detected by negative staining and identified by their sensitivity to KCN and H_2O_2. Mn-SOD is resistant to both inhibitors; Cu/Zn-SOD is sensitive to both inhibitors; Fe-SOD is resistant to KCN and sensitive to H_2O_2. The subcellular distribution of these isoenzymes is also different (Xie *et al.* 2017). Mn-SOD is found in mitochondria of eukaryotic cells and in peroxisomes; some Cu/Zn-SOD isoenzymes are found in cytosolic fractions, as well as in chloroplasts of higher plants (Rojas Beltran *et al.* 2000). Fe-SOD isozymes, which are often absent in plants, are usually associated with the region of chloroplasts in which they are present (Kużniak & Skłodowska 2005). Prokaryotic Mn-SOD and Fe-SOD, as well as eukaryotic enzymes. Cu/Zn-SOD are dimers, whereas Mn-SOD of mitochondria are tetramers. *Citrullus vulgaris* peroxisomes and glyoxysomes have been shown to contain Cu/Zn- and Mn-SOD activity, but there are no reports of extracellular SOD enzymes in plants. All forms of SOD are genetically encoded and target the corresponding subcellular compartments using amino-terminal targeting sequence. Several forms of SOD have been cloned from a variety of plants (Zelko *et al.* 2002). Upregulation of SOD is associated with the control of oxidative stress caused by biotic and abiotic factors and plays a critical role in plant survival under stress. A significant increase in SOD activity under salt stress was observed in various plants, including: Mulberry, *C. arietinum*, and *Lycopersicon esculentum*. Eidogan and Oz (2005) observed three bands of SOD activity (Mn-SOD, Fe-SOD, and Cu/Zn-SOD) in *C. arietinum* under salt stress. In addition, there was a significant increase in the activity of Cu/Zn-SOD and Mn-SOD isoenzymes under salt stress. Pan *et al.* (2006) studied the effect of salt and drought stress on *Glycyrrhiza uralensis* Fisch and found markedly increased SOD activity, but the additional

Mn-SOD isoenzyme was detected only under salt stress. It was concluded that heteromeric FSD2 and FSD3 act as ROS scavengers in maintaining early chloroplast development by protecting chloroplast nucleoids from ROS.

Peroxidase

Ascorbate Peroxidase (APX)

APX is believed to play the most important role in ROS neutralization and protection of cells of higher plants, algae, protozoa and other organisms. The APX family consists of at least five different isoforms, including the thylakoid (tAPX) and glyoxysomal membrane forms (gmAPX), as well as the stromal-soluble chloroplast form (sAPX) and the cytosolic form (cAPX; Noctor & Foyer 1998). APX has a higher affinity for H_2O_2 (mM range) than CAT and POD (mM range), and plays a more important role in controlling ROS-induced responses during stress. Enhanced APX expression in plants has been demonstrated under various stressful conditions. Increased leaf APX activity under Cd stress has been reported in *Ceratophyllum demersum*, *B. juncea*, *T. aestivum*, and *V. mungo* (Singh *et al.* 2008). Hsu & Kao (2007) reported that pretreatment of *O. sativa* seedlings with H_2O_2 under non-thermal shock conditions resulted in an increase in the activity of APX and protected rice seedlings from subsequent Cd stress. Increased APX activity was also found in *A. doliolum* exposed to salt stress (Srivastava *et al.* 2008). A significant increase in APX activity was observed under water stress in three varieties of *P. vulgaris* and *P. asperata*. Sharma and Dubey (2005) found that plants resistant to mild drought conditions have increased APX chloroplastic activity than controlled plants, but activity decreases with higher levels of drought stress.

It has been suggested that overproduction of APX increases POD activity, which enhances the body's ROS-scavenging system and leads to resistance to oomycete pathogens (Sarowar *et al.* 2005).

Guaiacol peroxidase (GPOX). APX can be distinguished from those isolated from plants by guaiacol peroxidase (GPOX) in terms of differences in sequences and physiological functions. GPOX degrades indole-3-acetic acid (IAA) and plays an important role in lignin biosynthesis and protection against biotic stresses by consuming O_2 and H_2O_2. GPOX prefers aromatic electron donors such as guaiacol and piragallol, which usually oxidize ascorbate, at a rate of about 1% of that of guaiacol (Asada 1999). GPOX activity varies significantly depending on the plant species and stress state. An increase in the content of ARCH is observed in Cd-exposed plants of *T. aestivum*, *A. thaliana*, and *C. demersum* (Cho & Seo 2005). Radotic *et al.* (2000) note an initial increase in GPOX activity in spruce needles exposed to Cd-stress, and showed that subsequent Cd-treatments caused a decrease in activity. Concomitant increases in GPOX activity have also been reported in both the leaves and root tissues of *Vigna radiate* and *O. sativa* under salt stress. Glutathione reductase (GR) is a flavo-protein oxidoreductase, found in both prokaryotes, and eukaryotes. It is a potential enzyme of the ASH-GSH cycle and plays an important role in the defence system against ROS, maintaining a reduced GSH status. It is mainly localized in chloroplasts, but a small amount of this enzyme is also found in mitochondria and the cytosol (Koji *et al.* 2009). Regions of GR1 and GR2 expression in rice, wheat, barley, and corn were studied by northern blotting, and increased regulation of HvGR1, HvGR2, and TaGR2 was found in response to Fe-deficient conditions rather than Fe-sufficient ones. Expression of eukaryotic GR from *B. campestris* (BcGR) and *E. coli* GR (EcGR) was studied in *E. coli* in pET-28a. Over-expressed BcGR in *E. coli* exhibited better growth and survival compared to the control, but much better growth was observed in the *E. coli* strain transformed with inducible EcGR in the presence of paraquat, SA, and Cd (Yoon *et al.* 2005).

Catalase

Catalases are tetrameric gem-containing enzymes that have the ability to break down hydrogen peroxide to water and molecular oxygen, making them essential for ROS detoxification. Catalases have one of the highest activity coefficients accepted for the characterization of all enzymes: 1 CAT molecule can cleave 2.6 million H_2O_2 molecules in 1 minute. It is important that catalases participate in the removal of hydrogen peroxide concentrated in peroxisomes by oxidases involved in beta-oxidation of fatty acids, photorespiration, and purine catabolism. Catalase isoenzymes have been extensively studied in higher plants, for example, *H. vulgare*, 4 in cotyledons of *Helianthus annuus* (Azpilicueta *et al.* 2007), and as many as 12 isozymes in *Brassica*. Maize contains 3 isoforms of catalases (CAT1, CAT2, and CAT3), whose genes are expressed and regulated independently on different chromosomes. CAT1 and CAT2 are localized in peroxisomes and cytosol, respectively, and CAT3 in mitochondria. *E. coli* catalase is encoded by the katE gene, which is over-expressed in *O. sativa*, making the plant resistant to salt stress. In addition, catalases react with certain hydroxides, such as methylhydroperoxide (MeOOH). A variable catalase response was observed under heavy metal stress. This activity decreased in *Glycine*

max, *Phragmites australis*, *Capsicum annuum*, and *A. thaliana*, but it also increased under cadmium stress in *O. sativa*, *B. juncea*, *T. aestivum*, *C. arietinum*, and *V. Mungo* roots (Khan & Singh 2008). Pretreatment of rice seedlings with hydrogen peroxide under non-stressful temperature conditions led to an increase in catalase activity, which subsequently protected the seedlings from exposure to cadmium. Eidogan and Oz (2005) showed in their work that a significant increase in CAT activity was observed in *C. arietinum* leaves when treated with salt. Similarly, increased CAT activity in *C. arietinum* roots appeared after NaCl and Cu^{2+} stress. Simova Stoilova *et al.* (2010) reported increased CAT activity in wheat under drought conditions, which was particularly high in sensitive varieties. During the study of CAT (Cu/Zn SOD) genes in maize, attention waso focused on chloroplasts of *Brassica campestris* L. ssp. *pekinensis* cv. Tropical Pride and it was noted that irradiation of plants with SOD + CAT *B. campestris* up to 400×10^{-9} SO_2, also increases the drought resistance of plants. It was further reported that increasing the activity of SOD or CAT alone has a negligible effect on the tolerance of 400 ng mL^{-1} of SO_2 in *B. campestris* transformed by the SOD and CAT genes of *E. coli*. It was noted that co-transformed strains that over-expressed both SOD and CAT showed high resistance to SO_2 (Tseng *et al.* 2007).

Fight against ROS

Many different studies were conducted on different plant cultures to study the relationship between the level of AOF and ROS and stress resistance. For example, Deya Eldeen and co-workers (Radwan *et al.* 2008) studied the antioxidant status and protein composition of horse beans infected with legume yellow mosaic virus (BYMV) and studied the effect of salicylic acid (SC) on their level. As a result of their research, it was found that when the antioxidant status changes, alterations in the activity of AOF and the content of various metabolites are observed. During salicylic acid therapy, CAT, POD, and ROS were inhibited, but SOD activity was increased. The enzymatic activity depended on the SC content in the medium. A higher concentration of H_2O_2 and MDA (malondialdehydes) was observed in leaves infected with the virus, and subsequent treatment with SC resulted in a lower concentration of MDA and reduced damage due to lipid peroxidation. Moreover, an increase in the amount of phenolic compounds and flavonoids was observed in the treatment of SC. SC-therapy also affected the quality and quantity of proteins, since when plants were infected, they had more protein. In particular, accumulations of insoluble pathogenic related proteins, and during SC-therapy, new protein profiles appeared on electrophoresis, both soluble and insoluble, which also depended on the amount of SC in the medium. The case of SC treatment is considered to be a method by which the plant's protective response to infection can be initiated and activated.

Dikilitas *et al.* (2011) investigated the dependence of the degree of infection on the antioxidant status of tomatoes and the quality of their fruits. If the plants are infected when they are young, the symptoms may become more severe. However, symptoms may vary depending on the variety. Symptoms of viral infection in pepper plants usually develop within 1-3 weeks after infection. When plants are attacked by pathogens, they respond by activating various defence mechanisms, including rapid production and accumulation of ROS. On the other hand, the content of phenolic compounds increases in response to the defence mechanism. The overall antioxidant status, overall oxidative status, and oxidative stress levels, as well as the content of phenolic compounds in virus-infected peppers, reflect the state and resistance of pepper plants. As a result, it was found that the accumulation of bound and free phenol increased CB after a viral infection in pepper. The change may be the result of a protective mechanism against infection of the fetus. Although the content of phenolic compounds increased, no antioxidant activity was observed in infected pepper plants, which may be the result of insufficient accumulation of antioxidant metabolites due to severe infection (Ighodaro & Akinloye 2018).

CONCLUSION

There is documented evidence that various abiotic and biotic stresses, such as drought and infection with various viruses, respectively, lead to an overproduction of ROS in plants that are highly reactive and toxic, ultimately leading to oxidative stress. In general, the involvement of ROS in various metabolic processes in plant cells can have general consequences. Oxidative stress is a condition in which ROS or free radicals are generated extra - or intracellularly, which can have toxic effects on cells. These species can affect the properties of the cell membrane and cause oxidative damage to nucleic acids, lipids, and proteins, which can make them non-functional. However, cells are equipped with excellent antioxidant defense mechanisms to detoxify the harmful effects of ROS. Antioxidant protection can be either non-enzymatic (e.g., glutathione, praline, a-tocopherols, carotenoids, and flavonoids) or enzymatic (e.g., superoxide dismutase, catalase, glutathione peroxidase, and glutathione reductase).

ROS are also currently considered key regulatory molecules that are vital for cells, but they cause cellular damage when produced in excess, or when the antioxidant defense system is not functioning properly. Free radicals can also interact with each other and with antioxidant systems. It is the balance of all components that determines their good or bad effects of ROS on the cells of living systems (Ahmad *et al.* 2014). Redox reactions in the cell play a twofold role, and this was first described in pathogenesis, but now it is also shown in various conditions of biotic and abiotic stress. Therefore, it is necessary to control the concentration of ROS in the cell. This means that it is necessary to study the mechanism of ROS production and purification, its targets, and molecular functions. It is well known that plant cells and their organelles, such as the chloroplast, mitochondria, and peroxisomes, use antioxidant defence systems to protect against induced ROS and oxidative stress (Diao *et al.* 2014). Numerous studies have also established that induction of the cellular antioxidant system is important for protection against ROS. Higher expression of ROS-absorbing enzymes, such as SOD isoforms (Mn-SOD, Cu/Zn-SOD, Fe-SOD), CAT, APX, GR, DHAR, GST, and GPX, resulted in resistance to biotic and abiotic stress in various plant cultures due to their effective ROS-neutralizing ability. Pyramiding of genes responsible for the work of ROS-absorbing enzymes can also be used to produce plants with abiotic stress resistance. Thus, plants capable of producing and/or controlling the level of cellular ROS concentration can be useful for regions with harsh climates, as they will be able to withstand severe environmental conditions.

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