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Chapter 20

Reactive Oxygen Species and Antioxidant Enzymes Involved in Plant Tolerance to Stress

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Additional information is available at the end of the chapter

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Abstract

Plants are continuously exposed to several stress factors in field, which affect their production. These environmental adversities generally induce the accumulation of reactive oxygen species (ROS), which can cause severe oxidative damage to plants. ROS are toxic molecules found in various subcellular compartments. The equilibrium between the production and detoxification of ROS is sustained by enzymatic and nonenzymatic antioxidants. Due to advances in molecular approaches during the last decades, nowadays it is possible to develop economically important transgenic crops that have increased tolerance to stresses. This chapter discusses the oxidative stress and damage to plants. In addition, it reports the involvement of antioxidant enzymes in the tolerance of plants to various stresses.

Keywords: ROS, abiotic and biotic stress, oxidative stress, antioxidative mechanisms, tolerant plants

1. Introduction

Crop yield depends on the plant's ability to adapt to different types of environmental adversities, which generally induce oxidative stress. Environmental stress induces the accumulation of reactive oxygen species (ROS) in the cells of plants, which can cause severe oxidative damage to the plants, thus inhibiting growth and grain yield. ROS are involved in processes such as growth, development, response to biotic and abiotic environmental stimuli, programmed cell death, and may act as signal transducers. Stressors, hormones, development, and other several metabolic routes can stimulate ROS production that in turn may induce other routes or act directly as defense compounds [1].

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Knowledge about the oxidative mechanisms in plants may contribute to the development of plants most well adapted to the environment and resistant to pathogens. Plants have defense mechanisms against oxidative damage that are activated during stress to regulate toxic levels of ROS. Antioxidant and nonantioxidant systems are involved in ROS detoxification.

During the last decades, antioxidant enzymes have been used to develop transgenic plants that have increased tolerance to several stresses. Therefore, this chapter will address the relation between abiotic and biotic stresses and ROS generation. The ROS production, major antioxidant enzymes involved in detoxification, and defense under stresses will be described. The involvement of the antioxidant enzymes in the tolerance of plants to various stresses will be also discussed.

2. Crop production and stress

Global agricultural production has tripled in the last 50 years because of increased demand due to population growth. Genetic breeding has improved crop yields per unit area. In 1960, the food requirement per capita was approximately 2,200 kcal/day. In 2009, the global food requirement per capita increased to more than 2,800 kcal/day. The global public spending on agricultural research and development rose markedly from 26.1 billion dollars in 2000 to 31.7 billion dollars in 2008; however, many challenges still remain in the agricultural sector [2].

Despite the efforts and progress achieved in recent decades in agriculture, growth and crop productivity are still negatively affected by several stress factors. Most crop plants grow in suboptimal environmental conditions, which prevent the plants from expressing their full genetic potential for development and reproduction, and consequently, these abnormal conditions lead to decreased plant productivity [3]. These stresses cause considerable production and economic losses worldwide.

Biological stress is an adverse force or condition that inhibits normal functioning of a plant [4]. These stresses may be biotic or abiotic. Biotic stresses include pathogens (viruses, bacteria, and fungi), insects, herbivores, and rodents. Abiotic stresses comprise cold (chilling and frost), heat (high temperature), salinity (salt), drought (water deficit condition), water excess (flooding), radiation (high-intensity ultra-violet and visible light), chemicals and pollutants (heavy metals, pesticides, and aerosols), oxidative stress (reactive oxygen species, ozone), wind (sand and dust particles in the wind) and soil nutrient deprivation [4, 5]. All of these factors may affect plant development and reproduction at different levels of severity.

Tolerance can be achieved by plant breeding or cultural practices that reduce losses, which is in turn accomplished by understanding the plant's response to its stressors and how they affect individual plants and plant processes [6]. Yield losses by oxidative damages occur because of an imbalance in plant synthesis and quenching. However, attributing this loss to the oxidative damage is difficult taking into account the several processes involved in ROS synthesis; however, stresses and oxidative damage are interlinked and are responsible for the yield losses [7] (Figure 1).

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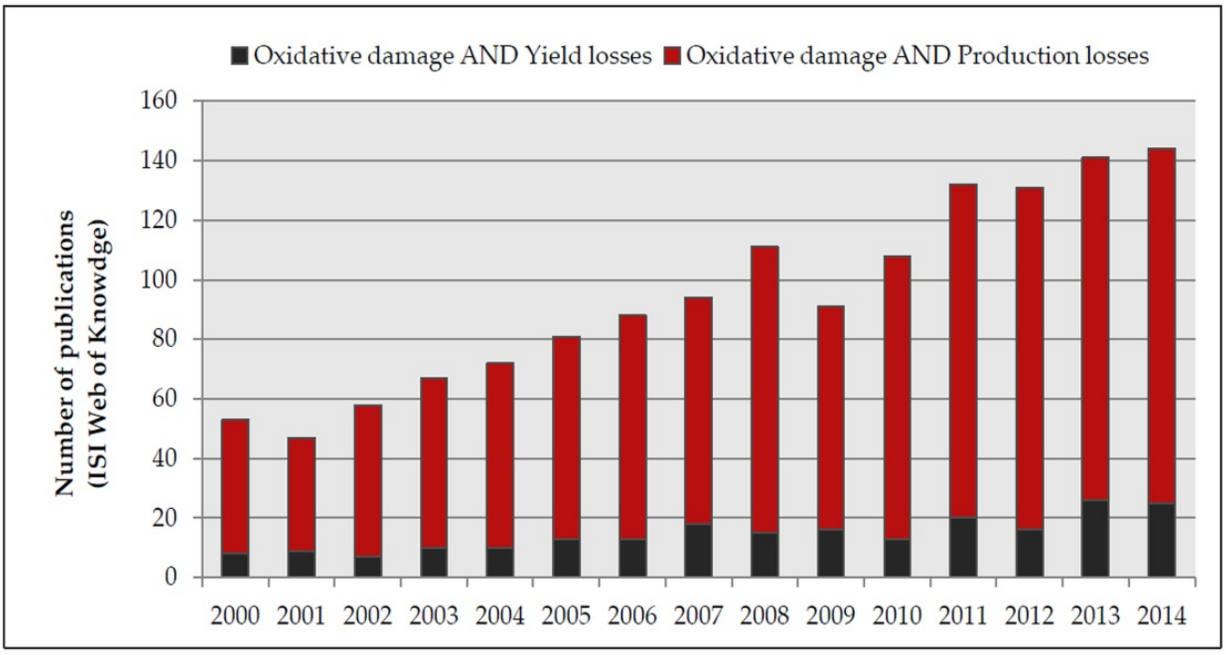


Figure 1. Evolution of the number of publications (2000-2014) addressing oxidative damage and yield/production losses. Total number of publications in 2000-2014 is 1,418. Source: ISI Web of Knowledge.

3. ROS generation

Environmental stress is directly correlated with increased accumulation of ROS. The equilibrium between production and scavenging of ROS may be disturbed by a number of biotic and abiotic factors, which may increase the intracellular levels of ROS [8]. When the level of ROS is increased and exceeds the defense mechanisms, the cell is in a state of oxidative stress [8, 9, 10, 11]. High concentrations of ROS are highly harmful to organisms, and when the symptoms persist, irreversible damage to the cells occurs, resulting in loss of physiological capacity and eventual cell death. Therefore, defense mechanisms against oxidative damage are activated during stress to regulate toxic levels of ROS [12] (Figure 2).

ROS are a group of free radicals, reactive molecules, and ions derived from oxygen. The most common ROS include singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\cdot -}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH\cdot$). These substances are highly reactive and toxic and can lead to oxidative destruction of the cell [8, 13]. ROS are found in various subcellular compartments such as chloroplasts, mitochondria, and peroxisomes due the high metabolic activity that normally occurs in these compartments [13]. ROS are generated in chloroplasts via the Mehler reaction, in mitochondria via electron transport, and in peroxisomes via photorespiration.

The glycolate oxidase reaction, fatty acid β-oxidation, enzymatic reactions of flavin oxidases and disproportionation of $O_2^{\cdot -}$ radicals are all metabolic processes responsible for the gener-

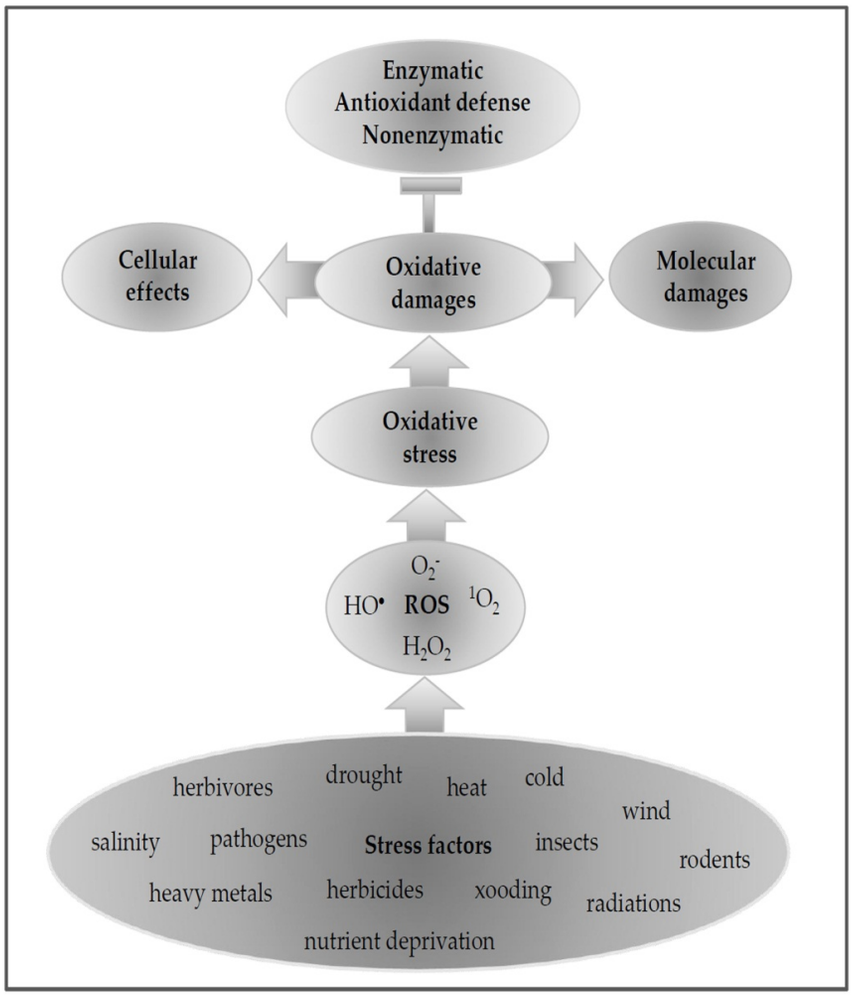


Figure 2. Stress factors, ROS generation, oxidative damage, and antioxidant defense. Several stress factors increased the ROS production, such as HO·, O^-_2, $^1O_2$, and H_2O_2. The increased ROS levels lead to oxidative stress. Consequently, oxidative damage at the molecular and cellular levels occurs. Defense mechanisms against oxidative stress are activated to neutralize toxic levels of ROS. Singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH·).

ation of H_2O_2 in different types of peroxisomes [14]. Cytoplasm, plasma membrane, apoplasts, endoplasmic reticulum, and extracellular matrix are also sources of H_2O_2. In the cytoplasm, the electron transport chain associated with the endoplasmic reticulum is the main source of H_2O_2/ROS [11]. H_2O_2 generation can also be via enzymatic sources such as plasma-membrane-localized NADPH oxidases, amine oxidases, and cell wall peroxidases [15, 16]. Different organelles and cellular compartments possess potential targets for oxidative damage, as well as mechanisms for eliminating excess ROS. However, the balance between production and elimination of ROS can be severely disturbed by several biotic and abiotic stresses [9, 15]. These disturbances in the ROS equilibrium can lead to a rapid increase in intracellular ROS levels, which can cause significant damage to cell structures [17]. The redox homeostasis is the equilibrium between the production and scavenging of ROS; however, when ROS production overcomes the cellular scavenging capacity, there occurs an unbalancing of the cellular redox

homeostasis resulting in a rapid and transient excess of ROS, known as oxidative stress [11, 12]. Thus, the antioxidant defense imbalance disrupts metabolic activities [18], causing severe oxidative damages to cellular constituents, which can lead to loss of function and even cell death [12].

ROS may affect many cellular functions, for example, they can damage nucleic acids (oxidation of deoxyribose, strand breaks, removal/deletion of nucleotides, modification of bases, and cross-linked protein-DNA), lipids (breaking of the chain and increasing the fluidity and permeability of the membrane), and proteins (site-specific amino acid modification, fragmentation of the peptide chain, aggregation of cross-linked reaction products, alteration of the electric charge, inactivation of enzymes, and increasing the susceptibility of proteins to proteolysis) and can activate programmed cell death [10, 11].

The balance between production and elimination of ROS at the intracellular level must be tightly regulated and/or efficiently metabolized. This is necessary to avoid potential damage caused by ROS to cellular components as well as to maintain growth, metabolism, development, and overall productivity of plants. This equilibrium between the production and detoxification of ROS is sustained by enzymatic and nonenzymatic antioxidants [13, 15].

In plants, the major ROS-scavenging pathway is the ascorbate–glutathione cycle (AsA-GSH) in chloroplasts, cytosol, mitochondria, apoplast, and peroxisomes. This cycle plays a crucial role in controlling the level of ROS in these compartments [15]. The AsA-GSH cycle involves successive oxidation and reduction of ascorbate, glutathione, and NADPH catalyzed by ascorbate peroxidase (APX), monodehydroascorbate reductase (MDAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) [15, 18]. Thereby, the AsA-GSH cycle plays an important role in combating oxidative stress induced by environmental stress. Many components of the antioxidant system of plants are already well characterized into plant models, and disturbances or alterations in this system are an excellent strategy to investigate the different signaling pathways involving ROS.

3.1. Nonenzymatic antioxidants

Nonenzymatic antioxidants are found in all cellular compartments. These compounds may act directly in the detoxification of ROS and radicals, or they can reduce substrates for antioxidant enzymes [15]. Nonenzymatic components of the antioxidative defense system include the major cellular redox buffers ascorbate (AsA) and glutathione (GSH) as well as tocopherol, carotenoids, and phenolic compounds [10, 13, 18].

Ascorbate is found in organelles of most plant cell types and in the apoplast. AsA is a crucial component of the detoxification of ROS in the aqueous phase due to the ability to donate electrons in enzymatic and nonenzymatic reactions. AsA can directly eliminate $O_2^{\cdot -}$, $OH\cdot$, and $^1O_2$, and thus reduce H_2O_2 to water via the ascorbate peroxidase reaction [19]. AsA is generally maintained in its reduced state by a set of NAD(P)H-dependent enzymes, including monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase [13, 20, 21]. Moreover, AsA is involved in the regulation of cell division, the progression of G1 to S

phase of the cell cycle and cell elongation, and it participates in multiple functions in photosynthesis [22].

Glutathione is oxidized by ROS to form oxidized glutathione (GSSG), which is present in all cellular compartments. Along with its oxidized form, GSSG, GSH maintains the redox balance in cellular compartments. Several studies indicate that GSH is involved in regulating gene expression and the cell cycle due to the properties of the GSH:GSSH pair [15]. The glutathione and AsA antioxidants are abundant and stable and have appropriate redox potential to interact with numerous components and pathways.

Tocopherols (α, β, γ, and δ) is a group of lipophilic antioxidants [11]. The α-tocopherol is the largest scavenger of peroxyl radicals in lipid bilayers. The α-tocopherol present in the membrane of chloroplasts protects them against photooxidative damage [19].

Phenolic compounds are abundantly found in plant tissues, such as flavonoids, tannins, hydroxycinnamate esters, and lignin, and possess antioxidant properties [23].

3.2. Enzymatic antioxidants

Enzymatic components of the antioxidative defense system comprise several antioxidant enzymes such as superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), glutathione peroxidase (GPX, EC 1.11.1.9), guaiacol peroxidase (POX, EC 1.11.1.7), and peroxiredoxins (Prxs, EC 1.11.1.15), which catalyze ROS degradation, and enzymes of the ascorbate-glutathione (AsA-GSH) cycle, such as ascorbate peroxidase (APX, EC 1.1.11.1), monodehydroascorbate reductase (MDAR, EC 1.6.5.4), dehydroascorbate reductase (DHAR, EC 1.8.5.1), and glutathione reductase (GR, EC 1.8.1.7), that regenerate soluble antioxidants [13, 15, 18, 24]. This antioxidant system plays an important role in the maintenance of cell homeostasis and in the antioxidant response in plants.

Superoxide dismutases are enzymes that catalyze the dismutation of $O_2^{\cdot}$ to H_2O_2; therefore, they constitute a frontline in the defense against ROS. These enzymes may be attached to a metal ion (Cu/Zn, Mn, Fe, and Ni); thus, they are classified according to their subcellular location and metal cofactor. SODs are present in many organisms, such as bacteria, yeast, animals, and plants. Plants have multiple genes encoding SODs that can be regulated by development, tissue-specific and environmental signals [10, 25].

Catalases are responsible for the removal of H_2O_2 by reducing H_2O_2 to $2H_2O$. CATs are largely, but not exclusively, localized to peroxisomes. Plants possess multiple CATs encoded by specific genes, which respond differentially to various stresses that are known to generate ROS [9, 10].

Ascorbate peroxidases are enzymes that play a key role in catalyzing the conversion of H_2O_2 into H_2O and use ascorbate as a specific electron donor. Plants have different APX isoforms that are distributed in distinct subcellular compartments, such as chloroplasts, mitochondria, peroxisomes, and the cytosol. The *APX* genes are differentially modulated by several abiotic stresses in plants [26, 27, 28]. The balance between SODs, CATs, and APXs is crucial for

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determining the effective intracellular level of $O_2^{\cdot}$ and H_2O_2, and changes in the balance of these appear to induce compensatory mechanisms [8, 9, 10].

Glutathione peroxidases are nonheme thiol peroxidases that catalyze the reduction of H_2O_2 or organic hydroperoxides to water. The GPX proteins have been identified in many life species [29]. In plants, the GPX proteins are localized to mitochondria, chloroplasts, and cytosol.

Peroxiredoxins are a family of thiol-specific antioxidant enzymes that are involved in cell defense and protection from oxidative damage. These enzymes are widely distributed in plant cells and are important proteins in chloroplast ROS detoxification [30]. The peroxiredoxins are a group of peroxidases that have reducing activity in their active sites via cysteine residues. These enzymes do not possess a prosthetic group and catalyze the reduction of H_2O_2, peroxynitrite, and a wide variety of organic hydroperoxides to their corresponding alcohols [31].

Guaiacol peroxidases are involved in H_2O_2 detoxification. The POX proteins are heme-containing enzymes that belong to class III or the "secreted plant peroxidases." Theses enzymes are able to undertake a second cyclic reaction, called the hydroxylic reaction, which is distinct from the peroxidative reaction. Due to the use of both cycles, class III peroxidases are known to participate in many different plant processes, from germination to senescence, auxin metabolism, cell wall elongation, and protection against pathogens [32].

Monodehydroascorbate reductase is a flavin adenine dinucleotide enzyme that catalyzes the regeneration of AsA from the monodehydroascorbate radical using NAD(P)H as an electron donor. Thereby, MDAR plays an important role in the plant antioxidant system by maintaining the AsA pool [24]. Isoforms of MDAR have been reported to be present in chloroplasts, the cytosol, peroxisomes, and mitochondria [33, 34].

Dehydroascorbate reductase is a thiol enzyme that maintains AsA in its reduced form. DHAR catalyzes the reduction of dehydroascorbate to AsA using GSH as a reducing substrate [18, 24]. It is present in various plant tissues, and its modulation activity has been reported in various plant species [35].

Glutathione reductase is an NAD(P)H-dependent enzyme. GR catalyzes the reduction of oxidized glutathione (GSSG) to reduced glutathione (GSH); it is a key enzyme of the AsA-GSH cycle; it protects cells against oxidative damage; and it maintains adequate levels of reduced GSH. A high GSH/GSSG ratio is essential for protection against oxidative stress [20].

The great increasing number of publications addressing APX, SOD, CAT, POX, GPX, Prxs, MDAR, DHAR, and GR enzymes are examples of positive responses to biotic and abiotic stresses by these enzymes. Over the past fourteen years, significant efforts have been made to understand plant antioxidant system mechanisms related to stresses, so the number of publications reporting antioxidant enzymes and biotic and abiotic stresses has increased substantially (Figure 3A and 3B, ISI Web of Knowledge database). These data show the relevance of studying these enzymes assisting in the understanding of its involvement with scavenging of cell toxic products in diverse species and the relation between oxidative stress and biological processes.

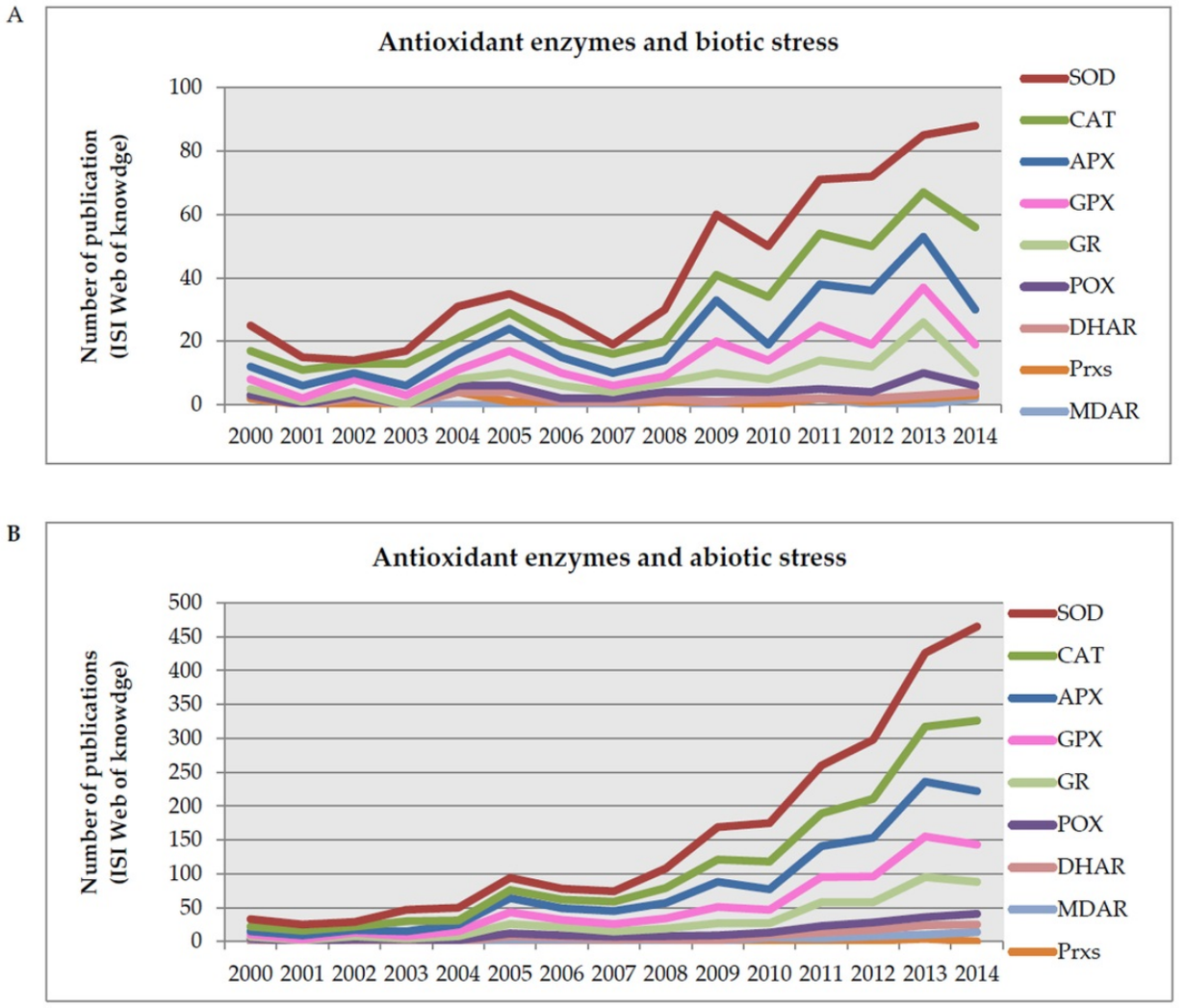


Figure 3. Evolution of the number of publications addressing antioxidant plant enzymes and biotic and abiotic stresses in the last fourteen years. (A) Data of the antioxidant enzymes and biotic stresses; (B) Data of the antioxidant enzymes and abiotic stresses. SOD (superoxide dismutase), APX (ascorbate peroxidase), CAT (catalase), GPX (gluthatione peroxidase), POX (guaiacol peroxidase), Prxs (peroxiredoxins), MDAR (monodehydroascorbate reductase), DHAR (dehydroascorbate reductase), and GR (glutathione reductase) enzymes. Source: ISI Web of Knowledge.

4. Stress conditions and plants tolerant to stress

Stressful conditions are the main factor limiting agricultural productivity because plants do not reach their full genetic potential [4, 17]. Environmental conditions affect growth and development and trigger a series of morphological, physiological, biochemical, and molecular changes in plants. The metabolic pathways of plant organelles are sensitive to changes in environmental conditions [36]. Consequently, all environmental adversities have led to the world's agriculture facing serious challenges to meet demand. The increased consumption, allocation of land for other uses, and use of chemical products with implications for health safety are some examples these challenges [37].

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The estimated world population for the year 2050 is nine billion people [2], and, consequently, the food demand will rise again. Therefore, it is necessary to increase the production and quality of food. Currently, the goal of many studies is the understanding of defense/tolerance mechanisms to different stresses in plants and to develop technologies and products that enable the generation of resistant/tolerant and more productive plants. Due to advances in molecular approaches, several crops of economic importance are being produced containing genes that encode stress tolerance using transformational technologies. Thus, several stress signaling and regulatory pathways have been elucidated and better understood.

Knowledge about the oxidative mechanisms in plants may contribute to the development of plants most well adapted to the environment. The maintenance of high antioxidant capacity to remove toxic levels of ROS has been related to increased stress tolerance of crop plants. Several studies show that maintaining a high level of antioxidant enzymes will help a plant to protect itself against oxidative damage by rapidly scavenging the toxic levels of ROS in its cells and restoring redox homeostasis.

Considerable progresses have been achieved in the development of plants tolerant to oxidative stress due to transgenic plants with altered levels of antioxidant genes to improve tolerance and productivity. This fact can be observed in Figure 4, which shows the increasing number of publications addressing antioxidant genes and its relation to tolerant plants in the last fourteen years (Figure 4). It highlights that SOD, CAT, and APX genes are the main antioxidant genes involved in the tolerance of plants to stresses, followed by GPX, GR, POX, DHAR, MDAR, and Prxs, respectively. These studies reflect the importance and advances in comprehension of the antioxidant mechanisms and tolerance to stresses.

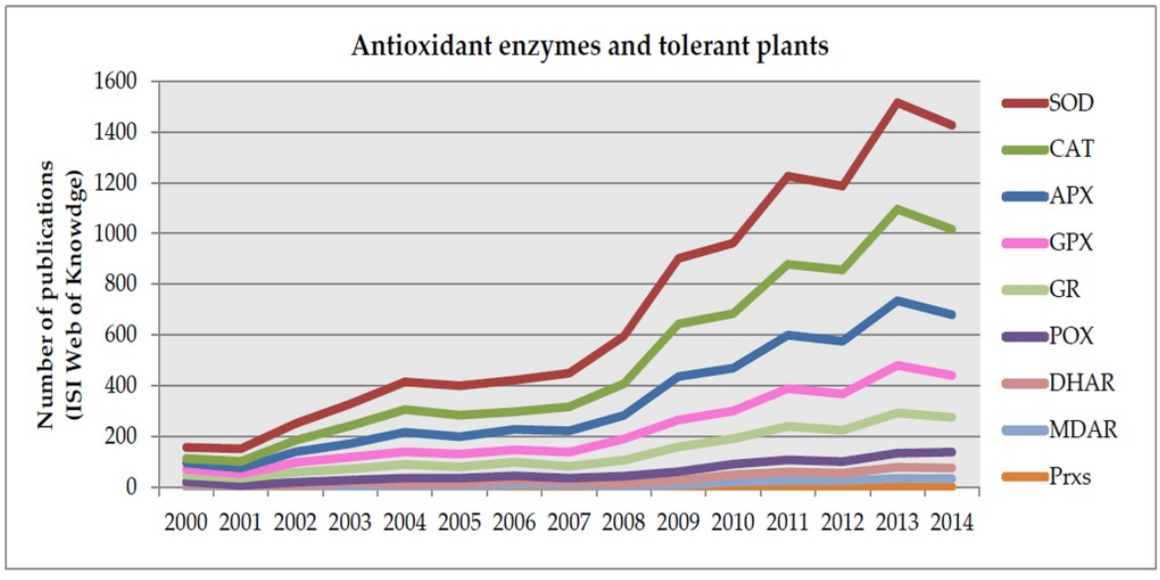


Figure 4. Evolution of the number of publications addressing antioxidant enzymes and plants tolerant to stresses in the last fourteen years. SOD (superoxide dismutase), APX (ascorbate peroxidase), CAT (catalase), GPX (gluthatione peroxidase), POX (guaiacol peroxidase), Prxs (peroxiredoxins), MDAR (monodehydroascorbate reductase), DHAR (dehydroascorbate reductase), and GR (glutathione reductase) enzymes. Source: ISI Web of Knowledge.

Furthermore, the increased antioxidant activity has been reported to lead to better performance or tolerance response to several stresses. Using transgenic approaches, several species were studied aiming at the improvement of tolerance to stress enhancing antioxidant capacity of antioxidant genes. Table 1 shows some examples of the successful and positive responses obtained with regard to increased tolerance to cold, drought, heat, salt, hydrogen peroxide, methyl viologen, and metals stresses (Table 1). Improved tolerance using antioxidant genes are attributed by high antioxidant activity and more efficient ROS elimination. Plants expressing or overexpressing one or more antioxidant genes have more antioxidant capacity; consequently, plants can more efficiently eliminate excess ROS and protect their cellular components against toxic effects of ROS produced during the exposure to stress. As a consequence, plants suffer less oxidative injury and can tolerate a stress condition more effectively.

Gene	Native specie	Target specie	Stress tolerance	Reference
Ascorbate peroxidase	*Brassica campestris*	*Arabidopsis thaliana*	heat	[38]
	Puccinellia tenuiflora	*Arabidopsis thaliana*	salinity, hydrogen peroxide	[39]
	Jatropha curcas	*Nicotiana tabacum*	salinity	[40]
	Hordeum vulgare	*Arabidopsis thaliana*	zinc, cadmium	[41]
Superoxide dismutase	*Arachis hypogaea*	*Nicotiana tabacum*	salinity, drought	[42]
	Tamarix androssowii	*Populus davidiana* x *P. bolleana*	salinity	[43]
	Pisum sativum	*Oryza sativa*	drought	[44]
	Oryza sativa	*Nicotiana tabacum*	salinity, water, PEG-treatment	[45]
Catalase	*Brassica oleracea*	*Arabidopsis thaliana*	heat	[46]
	Brassica juncea	*Nicotiana tabacum*	cadmium	[47]
	Triticum aestivum	*Oryza sativa*	cold	[48]
Glutathione peroxidase	*Triticum aestivum*	*Arabidopsis thaliana*	salinity, hydrogen peroxide	[49]
Peroxiredoxins	*Solanum tuberosum*	*Solanum tuberosum*	heat, methyl viologen	[50]
	Festuca arundinacea	*Festuca arundinacea*	heat, methyl viologen	[51]
	Suaeda salsa	*Arabidopsis thaliana*	salinity, cold	[52]
Monodehydroascorbate reductase	*Malpighia glabra*	*Nicotiana tabacum*	salinity	[53]
	Acanthus ebracteatus	*Oryza sativa*	salinity	[54]
	Avicennia marina	*Nicotiana tabacum*	salinity	[55]

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Gene	Native specie	Target specie	Stress tolerance	Reference
Dehydroascorbate reductase	*Oryza sativa*	*Oryza sativa*	salinity	[56]
Gluthatione reductase	*Brassica campestris*	*Nicotiana tabacum*	methyl viologen	[57]
Ascorbate peroxidase/ Superoxide dismutase	*Rheum austral/Potentilla astrisanguinea*	*Arabidopsis thaliana*	cold	[58]
	Manihot esculenta	*Manihot esculenta*	methyl viologen, hydrogen peroxide, cold	[59]
	Solanum tuberosum	*Solanum tuberosum*	heat, methyl viologen	[60]
Catalase/Superoxide dismutase	*Gossypium hirsutum*	*Gossypium hirsutum*	salinity, methyl viologen	[61]

Table 1. Some examples of the transgenic plants with potential stress tolerance expressing antioxidant genes

Some antioxidant enzymes such as SOD, CAT, APX, and GPX are better studied (Figure 3 and 4), but in general all enzymes have potential defense antioxidant activity helping in scavenging ROS in different ways, either by dismutation of $O_2^{\bullet}$ to H_2O_2, reduction of H_2O_2, maintenance of the AsA pool, or of the adequate levels of GSH and GSSG, that all together maintain the antioxidant balance. In addition, antioxidant enzymes act in different subcellular compartments, thereby assisting in the ROS detoxification in organelles such as chloroplasts, mitochondria, peroxisomes, and in the cytosol. Besides, ROS-scavenging enzymes in various subcellular compartments might have a synergistic effect to improve stress tolerance in plants [59].

Many attempts aiming to increase the tolerance of plants to environmental stresses using antioxidant genes have been made by researchers. However, due to the great complexity of the antioxidant system and plant stress tolerance, we cannot state that ROS scavenging is the only factor that determines the level of tolerance, because other factors and several genes pathways are involved in the stress tolerance in plants. Furthermore, it must be emphasized that stresses often occur in combination; thus, the relation between ROS signaling mechanisms in different stress responses is very complex [62]. When under the effect of a combination of stresses, the plants respond differently than when experiencing just a unique type of stress [63]. Moreover, this can range depending on the plant species and cultivation area. Complexity of the tolerance mechanisms in plants is also a key factor because sometimes the alteration of one gene in the pathway can influence the expression of others, various genes and pathways being involved [64].

5. Conclusions

Plants activate antioxidant defense mechanisms under stresses, which helps in the maintenance of the structural integrity of the cell components and presumably alleviates oxidative

damage. Several antioxidant enzymes contribute to plant defense. The manipulation of ROS-scavenging enzyme systems is a worthwhile approach to produce transgenic plants with enhanced tolerance to a wide range of stress conditions; however, this needs to be further explored as many enzymes and isoforms can be involved, and ROS is only one of the potential parameters of plant tolerance against environmental variations and biotic stresses.

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