Chapter

Superoxide Dismutase: A Stable Biochemical Marker for Abiotic Stress Tolerance in Higher Plants

Mukesh K. Berwal and Chet Ram

Abstract

Superoxide dismutases (SODs) are ubiquitous metalloenzymes that constitute the first line of defense against reactive oxygen species (ROS). It constitutes one of the major enzymatic components of detoxification of superoxide radicals generated in biological system by catalyzing its dismutation to H_2O_2 and finally to H_2O and O_2 by catalase and peroxidase. Most plant species contain numerous SOD isoforms differing in their active site metal ions, namely Cu/Zn-SOD, Mn-SOD, and Fe-SOD. Many studies also reported that the tolerance level of plants is positively correlated with SOD activity as well as with the number of SOD isoforms, and established the fact that "More the SOD Activity, More the Stress Tolerance." Therefore, the SOD isozyme profile of any plant can be used as stable marker for stress tolerance in plant. In this chapter, we have discussed the role of SOD in abiotic stress tolerance, type of SODs, and correlation of its activity and its isoforms with stress tolerance level.

Keywords: superoxide dismutase, isoforms, ROS, stress tolerance

1. Introduction

Plants are sessile in nature and, as a result, they do not have the capability to escape from the site of unfavorable environment. As per circumstances, plants often face the challenges to grow under adverse environmental conditions such as water deficit or excess, high intense light, low or high temperature, salinity, heavy metals, UV rays, insect and pests attack, etc. These stresses wield adverse effects on plant growth and development by inducing many metabolic changes, such as the occurrence of an oxidative stress [1–3]. As a principal cause of global crop failure, abiotic stresses decrease average yields for major crops by more than 50% [4]. Abiotic stresses impact on growth, development and productivity, and significantly limit the global agricultural productivity mainly by impairing cellular physiology/biochemistry via elevating reactive oxygen species (ROS) generation. The production of ROS during abiotic stresses results from pathways such as photorespiration, the photosynthetic apparatus, and mitochondrial respiration. Additionally, pathogens and wounding or drought or osmotic stress have been also shown to activate the production of ROS by NADPH oxidases [5–8]. The enhanced production of reactive oxygen species (ROS) during stress can pose a threat to cells, but it is also thought that ROI act as signals for the activation of stress-response and defense pathways

[9, 10]. Thus, ROS can be viewed as cellular indicators of stress and as secondary messengers involved in the stress-response signal transduction pathway.

However, several anabolic and catabolic processes like photosynthesis and respiration occur as part of common aerobic metabolism. It has been proved that ROS are generated in different cellular compartments as mitochondria, chloroplasts, peroxisomes, cytoplasm or in the extracellular space, known as apoplast by action of different enzymes [11, 12]. In vegetative tissues, approximately 1–2% of total molecular oxygen consumption drives to the creation of ROS in normal conditions. This percentage increases when plants are subjected to stress conditions such as salinity, drought, cold stress, or high temperatures. ROS are the species generated through the reduction of molecular oxygen (O_2) that includes some free radicals such as superoxide ($O_2^{\bullet-}$), hydroxyl radical ($OH^{\bullet}$), alkoxyl ($RO^{\bullet}$), and peroxyl ($ROO^{\bullet}$), and nonradical products like hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$), etc. [11–13]. ROS generation is an unavoidable part and by-product in various metabolic processes, where 240 μM s^{-1} $O_2^{\bullet-}$ and 0.5 μM H_2O_2 can be observed in plants under optimal growth conditions. Further, abiotic stresses may significantly enhance the generation of varied ROS (and their reaction products) in plant cells, where stressed cells may exhibit accelerated ROS generation up to 720 μM s^{-1} $O2^{\bullet-}$ and 5–15 μM H_2O_2 [14, 15] (**Figure 1**).

Plants have lot of antioxidant systems that protect them against these potential cytotoxic effects. Antioxidant enzymes are the most important components in the scavenging system of ROS. Major nonenzymatic antioxidants include ascorbic acid (AsA), glutathione (GSH), phenolic compounds, alkaloids, nonproteinaceous amino acids, and α-tocopherols. Alternatively, the battery of enzymatic antioxidants includes ascorbate peroxidase (APX), superoxide dismutase (SOD), glutathione reductase (GR), catalase (CAT), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), peroxidase (POX), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX), and glutathione-S-transferase (GST) [15]. Considering the major enzymatic antioxidants, SOD (EC 1.15.1.1) is ubiquitous metalloenzymes [16, 17] that constitute the first line of defense against reactive oxygen species (ROS). In living cells, SODs catalyze the dismutation of the superoxide radicals ($O_2^{\cdot-}$) into hydrogen peroxide (H_2O_2) and oxygen (O_2) and play an important role in protecting the cells against the toxic effect of superoxide radicals produced in different cell compartments [18]. In plants, the role of SOD during environmental adversity has received much attention since reactive oxygen species have been found to be produced during many stress conditions.

$$2O_2^- + 2H^- \rightarrow O_2 + H_2O_2$$

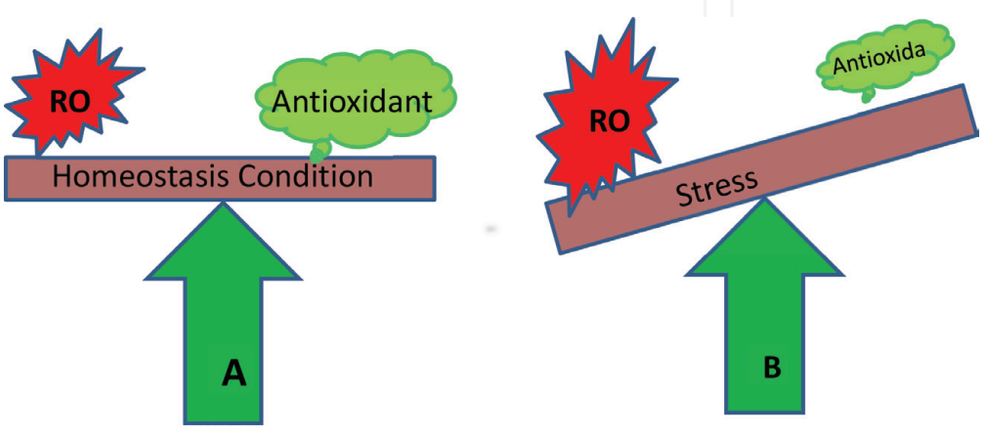

Figure 1.
The concept of homeostasis condition (A) and imbalance (B) between reactive oxygen species (ROS) and antioxidants.

2. Superoxide dismutase (SOD)

Superoxide dismutases (SODs: EC 1.15.1.1) are ubiquitous metalloenzymes [16, 17] that constitute the first line of defense against reactive oxygen species (ROS) and one of the most effective components of the antioxidant defense system in plant cells against ROS toxicity. Until reported in plants [19], SOD was recognized as a group of metalloproteins having no known function. Based on the metal cofactor at active site, SODs are categorized into three main groups and are believed to present in all oxygen-metabolizing cells and are also in all subcellular compartments like mitochondria, chloroplasts, nuclei, cytoplasm, peroxisomes, and apoplasts, etc. [20, 21]. It constitutes one of the major enzymatic components to detoxify superoxide radicals by catalyzing its dismutation to H_2O_2 [22]. By removing $O2^{\bullet-}$, SODs decrease the risk of $OH^{\bullet}$ formation via the metal catalyzed Haber-Weiss-type reaction because this reaction has a 10,000-fold faster rate than the spontaneous dismutation [11]. This enzyme is unique that its activity determines the concentrations of $O2^{\bullet-}$ and H_2O_2, the two Haber-Weiss reaction substrates, and it is therefore likely to be central in the antioxidant defense mechanism [23, 24]. The SOD system of higher plants exhibited into multiple isoforms, which are developmentally regulated and are highly reactive against exogenous stimuli. The significance in the efficiency of all SODs has been confirmed in the direct or indirect metabolism of diverse ROS and its reaction products in numerous studies [11, 19, 25]. According to the active site metal, the multiple SOD isoforms are classified into three major groups (types): Fe-SOD (iron cofactor), MnSOD (manganese cofactor), and Cu/ZnSOD (copper and zinc as cofactors; copper is the redox active catalytic metal). While in bacteria, another type of SOD called nickel SODs (Ni-SODs) has also been reported by many researchers with nickel as metal cofactor [19, 26–28]. These multiple SOD isoforms are designated to specific cell compartments namely Fe-SODs are located in plastids, Mn-SODs in mitochondrial matrix and peroxisomes, and they also have been found in cell wall, while Cu/Zn-SODs occur in cytosol, peroxisomes, plastids, and possibly extracellular space [19, 29–31]. All SODs are encoded by nuclear genes and targeted to their respective subcellular localization by an amino terminal guiding sequence (**Table 1**).

2.1 Superoxide dismutase in plants as stable marker for abiotic stress tolerance

Different types of environmental stresses such as heat, cold, drought, salinity, and chemical contaminants commonly result in enhanced production of reactive

SOD isozymes	Structure	Subcellular localization	Sensitivity
Cu/Zn-SOD	Homodimeric and homotetrameric	Cytosol, chloroplast, peroxisome, mitochondria	H_2O_2 and KCN
Mn-SOD	Homodimeric and homotetrameric	Mitochondria, peroxisome	$CHCl_3$:CH_3CH_2OH but not to H_2O_2 and KCN
Fe-SOD	Homodimeric and tetrameric	Cytosol, chloroplast, peroxisome, Mitochondria	H_2O_2 but not to KCN
Ni-SOD	Only reported in prokaryotes		

Table 1.
Types of plant SOD, subcellular location, and sensitivity.

oxygen species (ROS), and demand an effective scavenging system to prevent oxidative damage to living cells under such conditions. Thus, the understanding of the plant responses to these abiotic stresses has become a prerequisite in order to develop crop plants tolerating abiotic stresses. Nevertheless, as an important component of plant defense machinery within a cell, SODs are major enzymatic components of the cellular defense system against abiotic stress-accrued enhanced ROS. SODs are ubiquitous to aerobic organism and catalyze the dismutation of superoxide to molecular oxygen and hydrogen peroxide (H_2O_2). Under normal conditions, the resulting H_2O_2 is effectively scavenged by catalase and peroxidase enzymes. Hereunder, recent reports available on the modulation of SODs in abiotic-stressed plant species are discussed.

It has been observed under numerous studies that the higher the SOD activity or higher number of isoforms, greater the potential to remove ROS. The upregulation of SODs is implicated in combating over-produced ROS due to biotic or abiotic stresses and has a crucial role in the survival of the plant under stressful environment. Significant increase in total leaf SOD activities as well as some extra SOD isoforms (in some studies) has been reported in many plant species under various types of abiotic stresses, namely drought, salt, and heavy metals (Cu, Cd, etc.), in a number of crops like *Arabidopsis*, mulberry [32], tomato [33], *Brassica juncea* [34, 35], *Treaticum aestivum* [36], *Hordeum vulgare, Vigna mungo* [37], citrus [38], etc. The abundance of SOD transcripts is observed in response to various abiotic and biotic stresses to distinct the oxidative stress that exerts a significant role in stress tolerance. Over-expressing transgenic plants of various SOD isoforms increases enhanced tolerance to oxidative stress and to other environmental stresses. These results have been reported in many crops and model species including *Arabidopsis,* alfalfa, rice, potato, poplar, and tobacco [39]. There have been many reports in the development of stress tolerant plants with increased expression of different SODs namely over-expressed Mn-SOD in GM *Arabidopsis* [40] and tomato [41] exhibited higher tolerance to salt, Cu/Zn-SOD overexpression in tobacco plant exhibited tolerance toward multiple stresses [42]. Furthermore, Lee et al. [43] reported that combined overexpression of Cu/Zn-SOD and ascorbate peroxidase in GM *Festuca arundinacea* plant exhibited multiple tolerance against drought (Methyl vilogen), H_2O_2, Cu, and Cd.

Berwal et al. [44] studied the SOD isozymes pattern of 13 coconut genotypes comprising six tall, five dwarfs along with two reciprocal hybrids of WCT (tall) with COD (dwarf). Among the genotypes studied, a significant variation was observed in SOD enzyme activity as well as in SOD isoforms pattern. A total of 8–14 SOD isoforms were detected in different coconut cultivars (**Figures 2** and **3**). The variation was observed only in Mn-SOD isoforms, while Fe-SOD (two) and Cu/Zn-SOD (five) isoforms were similar in all the analyzed cultivars; these isoforms have already been identified in coconut by Kumar et al. [25]. Mn-SOD isoforms varied from one to five in numbers. Among the tall cultivars, WCT, FMST, and WCT X COD showed highest number (five) of Mn-SOD isoforms as well as highest enzymatic activity followed by LCT while TPT, PHOT, and ADOT showed only single isoform for Mn-SOD. All dwarfs studies showed that they had similar SOD isozyme profile for all SODs, that is, one Mn-SOD, five Cu/Zn-SOD, and two Fe-SOD isoforms. They also observed that Mn-SOD does not follow the Mendelian pattern of inheritance, that is, reciprocal crosses showed Mn-SOD isoform pattern similar to their mother palm.

Rajgopal et al. [45] also studied the tolerance level of different coconut cultivars including the abovementioned cultivars on the basis of some physiological parameters like stomatal conductance, leaf water potential, and epicuticular wax content and scored them with 1–20 rank and WCT X WCT and FMST secured first and second ranks, respectively. Since, Berwal et al. [44] reported maximum SOD isoforms in WCT and FMST cultivars and the same are already reported as

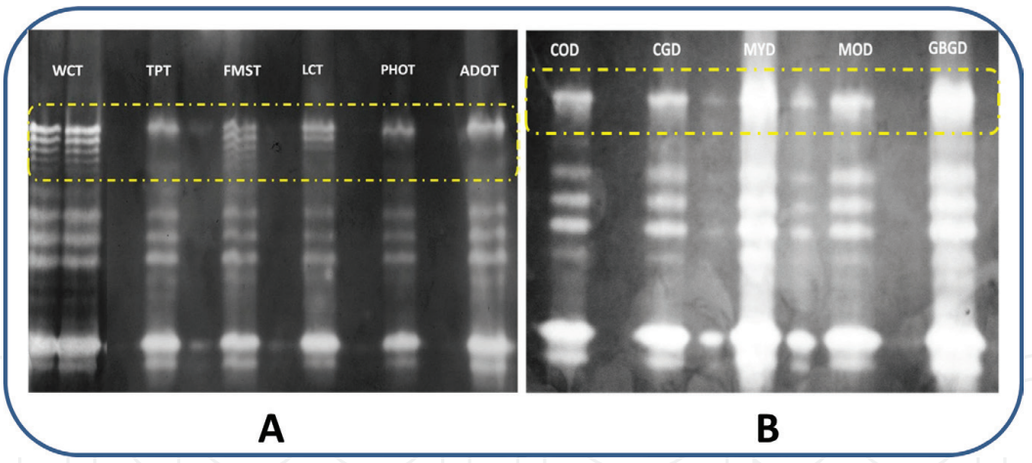

Figure 2.
Manganese superoxide dismutase (Mn-SOD) isoform variability in coconut genotypes (circled): (A) tall accessions and (B) dwarf accessions [44].

highest stress tolerant cultivars. Similarly, Kumar et al. [38] evaluated basal enzymatic antioxidative metabolism in the developing leaves of commercially grown citrus such as grapefruit, Hamlin (sweet orange), and kumquat. Young leaves of kumquat exhibited lower rates of lipid peroxidation and H_2O_2 generation as compared to grapefruit and sweet Hamlin. The total superoxide dismutase (SOD) activity, which catalyzes the transmutation of superoxide ion to H_2O_2, was two-fold higher in kumquat than grapefruit and sweet orange. Kumquat also showed more superoxide dismutase isoforms activities (**Figure 1**. Isoforms of superoxide dismutase (SOD; Panel A) and band intensities (Panel B) in developing leaves of different genotypes of citrus and kumquat at pp. 93, Kumar et al. [38]).

Despite the higher superoxide dismutase activity in kumquat, it had substantially lower H_2O_2 than grapefruit and Hamlin; and this is well-known that kumquat has greater resistance towards oxidative stresses. Gueta-Dahan et al. [46] also reported in citrus, callus, and cold-acclimated mandarin fruits and suggested higher SOD activity conferred greater resistance to salt and chilling stress (Figure 8. SOD activities in salt-sensitive (L) and salt-tolerant (R) citrus cells at pp. 465). Vysniauskiene et al. [47] reported higher SOD activity in frost-resistant potato hybrids than that of in frost-sensitive *Solanum tuberosum* "Matilda."

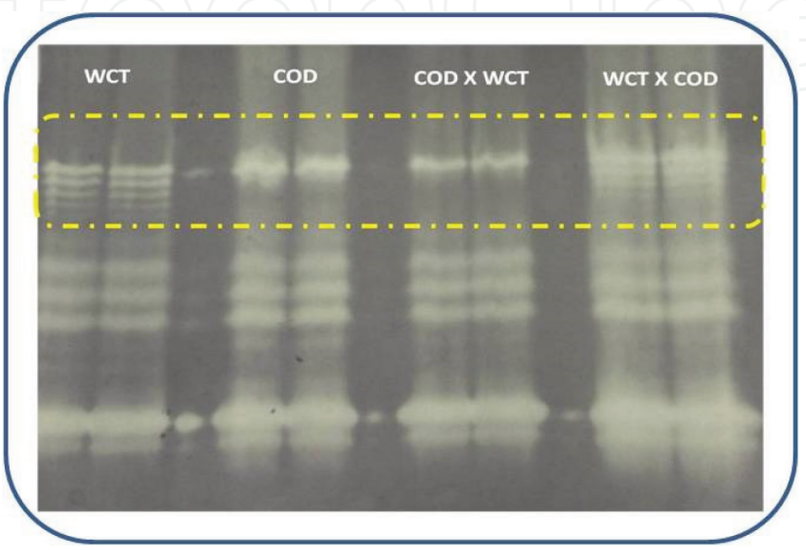

Figure 3.
Manganese superoxide dismutase (Mn-SOD) isoform pattern of WCT, COD, and their reciprocal crosses [44].

Activities of cytosolic and chloroplastic Cu/Zn-SOD isozymes and cytosolic APX (cAPX), as well as their corresponding mRNA transcripts, were increased by drought treatment of pea plants [48]. Similarly, osmotic stress increased the Mn-SOD transcript abundance in maize [49]. The higher level of gene expression corresponding to this isozyme as well as for Cu/Zn-SOD, were also increased by chilling stress in tobacco plants [50]. It has been reported in many studies that higher level of Mn-SOD is linked with abiotic stress tolerance and Melchiorre et al. [51] reported photo-oxidative stress tolerance, lower oxidative damage, and higher H_2O_2 in *Triticum aestivum* plant transformed with Mn-SOD gene from *Nicotiana plumbaginifolia*. Wang et al. [40] also reported overexpression of Mn-SOD gene in *Arabidopsis* leads to salt tolerance. Similarly, Rubico et al. [52] reported mild water stress tolerance and higher photosynthetic activity in *Medicago sativa* L. plants transformed with Mn-SOD and Fe-SOD from *Nicotiana plumbaginifolia* and *Arabidopsis thaliana*.

3. Conclusion

Superoxide dismutase is known as the first line of defense against oxidative stresses in plants and play most vital role is scavenging the reactive oxygen species produced during metabolic processes as well as under abiotic stress conditions. From the above discussion, it is clear that the plant has more native or induced SOD activity that showed more tolerance toward abiotic stresses. Many studies have proved that higher the native SOD activity along with more number of SOD isoforms makes the plants more capable to scavenge the ROS generated during stressed condition more effectively. As reported by Berwal et al. [44] in coconut and Kumar et al. [38] in citrus species that the cultivar having more number of native SOD isoforms showed more tolerance against drought stress. Therefore, the native SOD isozyme profile can be used as a stable biochemical marker for screening of crop germplasm for abiotic stress tolerance.

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