

# We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

4,800

Open access books available

122,000

International authors and editors

135M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index  
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?  
Contact [book.department@intechopen.com](mailto:book.department@intechopen.com)

Numbers displayed above are based on latest data collected.

For more information visit [www.intechopen.com](http://www.intechopen.com)



# 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  $\text{H}_2\text{O}_2$  and finally to  $\text{H}_2\text{O}$  and  $\text{O}_2$  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

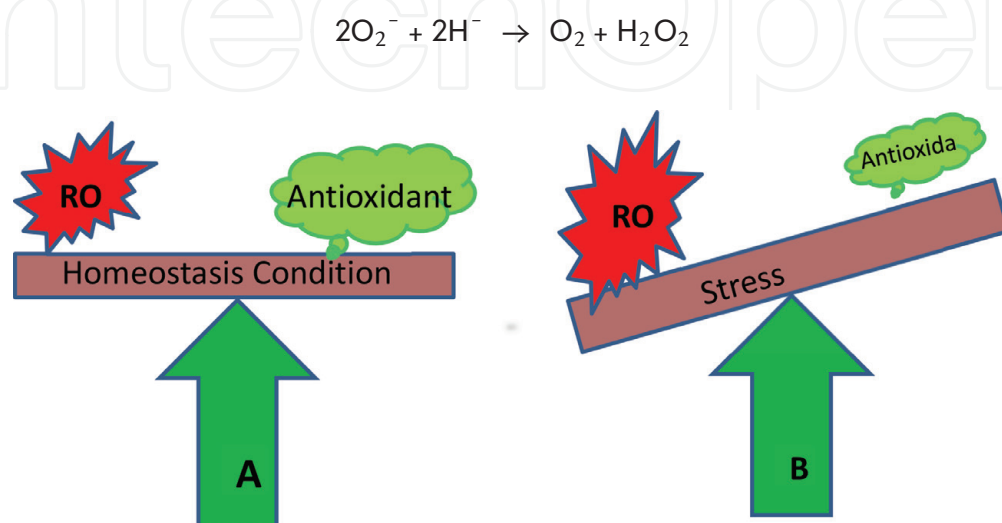
## 1. Introduction

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 yield 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 ( $O_2^{\cdot-}$ ), hydroxyl radical ( $OH^{\cdot}$ ), alkoxyl ( $RO^{\cdot}$ ), and peroxy ( $ROO^{\cdot}$ ), 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  $240 \mu M s^{-1} O_2^{\cdot-}$  and  $0.5 \mu M H_2O_2$  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  $720 \mu M s^{-1} O_2^{\cdot-}$  and  $5\text{--}15 \mu M H_2O_2$  [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  $\alpha$ -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.



**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  $O_2^{\bullet-}$ , 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  $O_2^{\bullet-}$  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.*

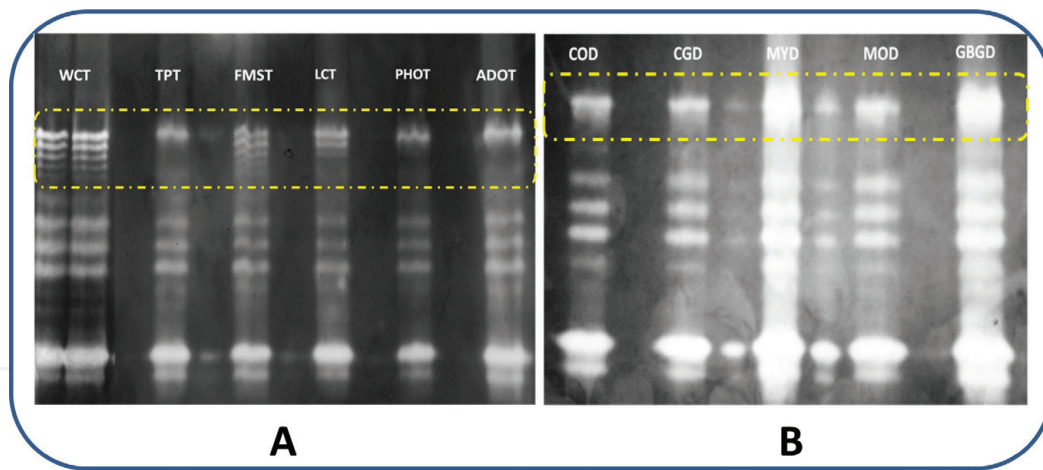


oxygen species (ROS), and demand an effective scavenging system to prevent oxidative damage to living cells under such conditions. Thus, the understanding of the plant responses to these abiotic stresses has become a prerequisite in order to develop crop plants tolerating abiotic stresses. Nevertheless, 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], *Triticum 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.

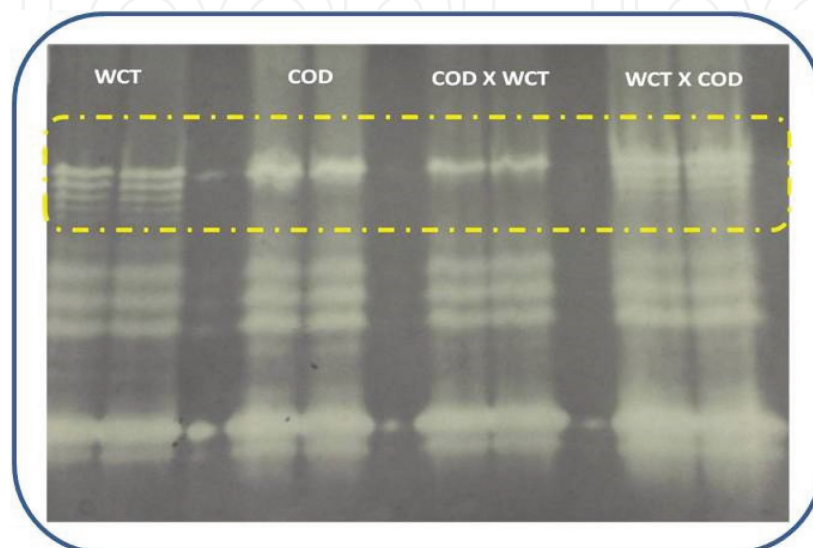
Rajgopal et al. [45] also studied the tolerance level of different coconut cultivars including the abovementioned cultivars on the basis of some physiological parameters like stomatal conductance, leaf water potential, and epicuticular wax content and scored them with 1–20 rank and WCT X WCT and FMST 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<sub>2</sub>O<sub>2</sub> 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.

IntechOpen

#### Author details

Mukesh K. Berwal\* and Chet Ram  
ICAR-Central Institute for Arid Horticulture, Bikaner, Rajasthan, India

\*Address all correspondence to: [mkbiochem@gmail.com](mailto:mkbiochem@gmail.com)

#### IntechOpen

© 2018 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 



## References

- [1] Diaz-Vivancos P, Clemente-Moreno MJ, Rubio M, Olmos E, Garcia JA, Martínez-Gómez P, et al. Alteration in the chloroplastic metabolism leads to ROS accumulation in pea plants in response to plum pox virus. *Journal of Experimental Botany*. 2008;**59**:2147-2160
- [2] Hernandez JA, Rubico M, Olmos E, Ros-Barcelo A, Martinez-Gimez P, et al. Oxidative stress induced by long-term plum pox virus infection in peach (*Prunus persica* L. cv. GF305). *Physiologia Plantarum*. 2004;**122**:486-495
- [3] Hernandez JA, Escobar C, Creissen G, Mullineaux P. Role of hydrogen peroxide and the redox state of ascorbate in the induction of antioxidant enzymes in pea leaves under excess light stress. *Functional Plant Biology*. 2004;**31**:359-368
- [4] Tuteja N, Tiburcio AF, Fortes AM, Bartels D. Plant abiotic stress: Introduction to PSB special issue. *Plant Signaling & Behavior*. 2011;**6**:173-174
- [5] Hammond-Kosack KE, Jones JDG. Resistance gene-dependent plant defense responses. *The Plant Cell*. 1996;**8**:1773-1791
- [6] Orozco-Cardenas M, Ryan CA. Hydrogen peroxide is generated systemically in plant leaves by wounding and systemin via the octadecanoid pathway. *Proceedings of the National Academy of Sciences United States of America*. 1999;**96**:6553-6557
- [7] Cazale AC, Droillard MJ, Wilson C, Heberle-Bors E, Barbier-Brygoo H, Lauriere C. MAP kinase activation by hypo-osmotic stress of tobacco cell suspensions: Towards the oxidative burst response? *The Plant Journal*. 1999;**19**:297-307
- [8] Pei ZM, Murata Y, Benning G, Thomine S, Klüsener B, Allen GJ, et al. Calcium channels activated by hydrogen peroxide mediate abscisic acid signaling in guard cells. *Nature*. 2000;**406**:731-734
- [9] Desikan R, A-H-Mackerness S, Hancock JT, Neill SJ. Regulation of the Arabidopsis transcriptome by oxidative stress. *Plant Physiology*. 2001;**127**:159-172
- [10] Knight H, Knight MR. Abiotic stress signaling pathways: Specificity and cross-talk. *Trends in Plant Science*. 2001;**6**:262-267
- [11] Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry*. 2010;**48**:909-930
- [12] Sandalio LM, Rodriguez-Serrano M, Romero-Puertas MC, del-Río LA. Role of peroxisomes as a source of reactive oxygen species (ROS) signaling molecules. *Subcellular Biochemistry*. 2013;**69**:231-255
- [13] Halliwell B, Gutteridge JMC. *Free Radicals in Biology and Medicine*. Oxford: Oxford University Press; 2007
- [14] Mittler R. *Oxidative Stress in Plants*. 2011. <http://biology.unt.edu/ros/pages/rosmetabolismdoc>
- [15] Hasanuzzaman M, Hossain MA, daSilva JAT, Fujita M. Plant responses and tolerance to abiotic oxidative stress: Antioxidant defense is a key factor. In: Bandi V, Shanker AK, Shanker C, Mandapaka M, editors. *Crop Stress and its Management: Perspectives and Strategies*. Berlin: Springer; 2012. pp. 261-316
- [16] Fridovich I. Superoxide dismutase. *Annual Review of Biochemistry*. 1975;**44**:147-159



- [17] Jackson CA, Moore AL, Halliwell B, Foyer CH, Hall DO. Subcellular localization and identification of superoxide dismutase in the leaves of higher plants. *European Journal of Biochemistry*. 1978;**91**:339-344
- [18] Del Rio LA, Sandalio LM, Altomare DA, Zilinskas BA. Mitochondrial and peroxisomal manganese superoxide dismutase: Differential expression during leaf senescence. *Journal of Experimental Botany*. 2003;**54**:923-933
- [19] McCords JM, Fridovich I. Superoxide dismutase. *The Journal of Biological Chemistry*. 1969;**44**(22):6049-6055
- [20] Alscher RG, Erturk N, Heath LS. Role of superoxide dismutases (SODs) in controlling oxidative stress in plants. *Journal of Experimental Botany*. 2002;**53**(372):1331-1341
- [21] Fink RC, Scandalios JG. Molecular evolution and structure—function relationships of the superoxide dismutase gene families in angiosperms and their relationship to other eukaryotic and prokaryotic superoxide dismutases. *Archives of Biochemistry and Biophysics*. 2002;**399**(1):19-36
- [22] Hossain Z, Lopez-Climent MF, Arbona V, Perez-Clemente RM, Gomez Cadenas A. Modulation of the antioxidant system in citrus under waterlogging and subsequent drainage. *Journal of Plant Physiology*. 2009;**166**:1391-1404
- [23] Bowler C, Van Montagu M, Inze D. Superoxide dismutase and stress tolerance. *Annual Review of Plant Physiology and Plant Molecular Biology*. 1992;**43**:83-116
- [24] Kandhari P. Generic differences in antioxidant concentration in the fruit tissues of four major cultivars of apples [Master thesis]. College Park: University of Maryland; 2004
- [25] Kumar M, Sugatha P, Hebbar KB. Superoxide dismutase isozymes and their heat stability in coconut (*Cocos nucifera* L.) leaves. *Annals of Biology*. 2014;**30**(4):593-597
- [26] Reddy CD, Venkaiah B. Isoenzymes of superoxide dismutase from mung bean (*Phaseolus aureus*) seedlings. *Current Science*. 1982;**20**:987-988
- [27] Werner K, Heinz R, Andrea P. Purification of two SOD isozymes and their sub-cellular localization in needles and roots of Norway spruce (*Picea abies* L.). *Plant Physiology*. 1992;**100**:334-340
- [28] Pradedova EV, Isheeva OD, Salyaev RK. Superoxide dismutase of plant cell vacuoles. *Membrane and Cell Biology*. 2009;**26**(1):21-30
- [29] Kukavica B, Mojovi M, Vucinic Z, Maksimovic V, Takahama U, Veljovic-Jovanovic S. Generation of hydroxyl radical in isolated pea root cell wall, and the role of cell wall-bound peroxidase, Mn-SOD and phenolics in their production. *Plant and Cell Physiology*. 2009;**50**:304-317
- [30] Pilon M, Ravet K, Tapken W. The biogenesis and physiological function of chloroplast superoxide dismutases. *Biochimica et Biophysica Acta*. 2011;**1807**:989-998
- [31] Miller AF. Superoxide dismutases: Ancient enzymes and new insights. *FEBS Letters*. 2012;**586**:585-595
- [32] Harinasut P, Poonsopa D, Roengmongkol K, Charoensataporn R. Salinity effects on antioxidant enzymes in mulberry cultivar. *Science Asia*. 2003;**29**:109-113
- [33] Gapinska M, Sklodowska M, Gabara B. Effect of short- and long-term salinity on the activities of antioxidative enzymes and lipid peroxidation in tomato roots. *Acta Physiologiae Plantarum*. 2008;**30**(1):11-18

- [34] Mobin M, Khan NA. Photosynthetic activity, pigment composition and antioxidative response of two mustard (*Brassica juncea*) cultivars differing in photosynthetic capacity subjected to cadmium stress. *Journal of Plant Physiology*. 2007;**164**:601-610
- [35] Li Y, Song Y, Shi G, Wang J, Hou X. Response of antioxidant activity to excess copper in two cultivars of *Brassica campestris* ssp. *chinensis* Makino. *Acta Physiologiae Plantarum*. 2009;**31**:155-162
- [36] Khan NA, Samiullah S, Nazar R. Activities of antioxidative enzymes, Sulphur assimilation, photosynthetic activity and growth of wheat (*Triticum aestivum*) cultivars differing in yield potential under cadmium stress. *Journal of Agronomy and Crop Science*. 2007;**193**:435-444
- [37] Guo T, Zhang G, Zhou M, Wu F, Chen J. Effects of aluminium and cadmium toxicity on growth and antioxidant enzyme activities of two barley genotypes with different Al resistance. *Plant and Soil*. 2004;**258**:241-248
- [38] Kumar N, Ebel RC, Roberts PD. Antioxidant isozyme variability in different genotypes of citrus and kumquat. *Journal of Crop Improvement*. 2011;**25**(1):86-100. DOI: 10.1080/15427528.2011.545280
- [39] Van Camp W, Willekens H, Bowler C, Van Montagu M, Inze D, Reupold-Popp P, et al. Elevated levels of superoxide dismutase protect transgenic plants against ozone damage. *Nature Biotechnology*. 1994;**12**:165-168
- [40] Wang Y, Ying Y, Chen J, Wang XC. Transgenic Arabidopsis overexpressing Mn-SOD enhanced salt-tolerance. *Plant Science*. 2004;**167**:671-677
- [41] Wang Y, Wisniewski M, Meilan R, Uratsu SL, Cui MG, Dandekar A, et al. Ectopic expression of Mn-SOD in *Lycopersicon esculentum* leads to enhanced tolerance to salt and oxidative stress. *Journal of Applied Horticulture*. 2007;**9**:3-8
- [42] Badawi GH, Yamauchi Y, Shimada E, Sasaki R, Kawano N, Tanaka K, et al. Enhanced tolerance to salt stress and water deficit by over expressing superoxide dismutase in tobacco (*Nicotiana tabacum*) chloroplasts. *Plant Science*. 2004;**166**:919-928
- [43] Lee SH, Ahsan N, Lee KW, Kim DH, Lee DG, Kwak SS, et al. Simultaneous over expression of both Cu/Zn superoxide dismutase and ascorbate peroxidase in transgenic tall fescue plants confers increased tolerance to a wide range of abiotic stresses. *Journal of Plant Physiology*. 2007;**164**:1626-1638
- [44] Berwal MK, Sugatha P, Niral V, Hebbar KB. Variability in superoxide dismutase isoforms in tall and dwarf cultivars of coconut (*Cocos nucifera* L.) leaves. *Indian Journal of Agriculture Biochemistry*. 2016;**29**(2):184-188
- [45] Rajgopal V, Kastiribai KV, Voleti SR. Screening of coconut genotypes for drought tolerance. *Oleagineux*. 1990;**45**:2015-2220
- [46] Gueta-Dahan Y, Yaniv Z, Zilinskas BA, Ben-Hayyim G. Salt and oxidative stress: Similar and specific responses and their relation to salt tolerance in citrus. *Planta*. 1997;**203**(4):460-469
- [47] Vysniauskiene R, Ranceliene V, Radziunaite-Paukstiene A, Spalinskas R. The UV-B impact upon the enzyme of antioxidant system superoxide dismutase (SOD) of potato somatic hybrids. *Biologia*. 2007;**53**:67-70
- [48] Mittler R, Zilinskas BA. Regulation of cytosolic ascorbate peroxidase and other antioxidant enzymes during the progression of drought stress and

following recovery from drought. *Plant Journal*. 1994;5:397-405

[49] Zhu D, Scandalios JG. Differential accumulation of manganese-superoxide dismutase transcripts in maize in response to abscisic acid and high osmoticum. *Plant Physiology*. 1994;106:173-178

[50] Tsang EWT, Bowler C, Herouart D, Van Camp W, Villarroel R, Genetello C, et al. Differential regulation of superoxide dismutases in plants exposed to environmental stress. *The Plant Cell*. 1991;3:783-792

[51] Melchiorre M, Robert G, Thippi V, Racca R, Lascano HR. Superoxide dismutase and glutathione reductase overexpression in wheat protoplast: Photooxidation stress tolerance and change in cellular redox state. *Plant Growth Regulation*. 2009;57:57-68

[52] Rubio MC, Gonzalez EM, Minchin FR, Web KJ, Arrese-Igor C, Ramos J, et al. Effect on water stress on antioxidant enzymes of leaves and nodules of transgenic alfalfa overexpressing superoxide dismutase. *Physiologia Plantarum*. 2002;115:531-540