Antioxidants and Antioxidant Enzymes in Higher Plants

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Preface

Generation and Scavenging of Reactive Oxygen Species (ROS) in Plant Cells: an Overview

Plant cells are provided with wide-ranging enzymatic and non-enzymatic antioxidant systems which are generally found adjacent to reactive oxygen species (ROS) production sites, with exceptional ability to elude the detrimental potential negative effects of ROS (i.e., oxidative stress), but also to restrain their signaling role under diverse circumstances (Corpas et al. 2015). Thus plants have developed several mechanisms whereby the endogenous content of antioxidant enzymes provides protection against the harmful effects of oxidative stress generated by abiotic/biotic sources (Gupta et al. 2016).

The main ROS are superoxide radicals (O_2^{-}) , hydrogen peroxide (H_2O_2) , hydroxyl radicals (OH), and singlet oxygen (¹O₂), and they are basically generated at every cell organelle, although the principal production compartments in plants are chloroplasts, mitochondria and peroxisomes (Fig. 1). In chloroplasts, O_2^{-} is produced at the level of the thylakoidal membrane, and especially at the photosystem I site, whereas the production site of ${}^{1}O_{2}$ is at the level of photosystem II (Asada 2006; Corpas et al. 2015). Superoxide radicals spontaneously dismutate into H_2O_2 , but they are also converted into H_2O_2 by the activity of superoxide dismutase (SOD) at the stroma. The main ROS generated in mitochondria are superoxide radicals, and this event is linked to complexes I and III located in the inner membrane (Corpas et al. 2015; Gupta and Igamberdiev 2015); whereas in peroxisomes, the O_2^{-} production is associated with both the matrix and membranes (Corpas et al. 2015, 2017). Peroxisomes are also the main production site of H_2O_2 (Foyer and Noctor 2003; Corpas 2015). In fact, several enzymatic systems are responsible for the direct production of H_2O_2 within these organelles (Corpas et al. 2015).

In higher plants, in addition to SOD, key ROS-scavenging/modulating proteins comprise a set of other enzymes including catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX), peroxiredoxins (Prx) and thioredoxins (Trx).



Fig. 1 Main reactive oxygen species (ROS) and antioxidants reported in organelles from plant cells. t,sCuZn-SOD: thylakoidal, stromal copper- and zinc-containing superoxide dismutase; t, sFe-SOD: thylakoidal, stromal iron-containing superoxide dismutase; Mn-SOD: manganese-containing superoxide dismutase; t,sAPX: thylakoidal, stromal ascorbate peroxidase; MDAR: monodehydroascorbate reductase; GR: glutathione reductase

In addition to the above scavenging antioxidant enzymes, a number of other enzymes found in several subcellular compartments are involved in preserving redox homeostasis either by directly scavenging specific ROS and ROS-byproducts or by replacing antioxidants; in some respects, these enzymes could be also described as antioxidants. Such enzymes include dehydroascorbate reductase (DAR), monodehydroascorbate reductase (MDAR), peroxidases (PODs) or glutathione S-transferases (GSTs), glutathione reductase (GR), and alternative oxidases (AOXs). Moreover, APX, MDAR, DAR, and GR are able to synergistically function through the so called ascorbate–glutathione cycle, which is broadly located within several cell organelles in plants (Fig. 1).

In plants, there are also non-enzymatic antioxidants, such as ascorbic acid (vitamin C, ASC), glutathione (GSH), tocopherols (vitamin E), and carotenes (provitamin A), which work in concert with antioxidant enzymes to tolerate the intracellular generation of ROS, and this may help in promoting plant growth and or development, cell cycle, hormone signaling, and sometimes also in strengthen the responses to abiotic/biotic environmental stressors. Furthermore, ascorbate and GSH participate as electron donors in the ascorbate–glutathione cycle, gaining their respective reduced status thanks to the electron provision given by NADPH.

In plants, over recent decades, ROS have gained importance in different features relating to heavy metal stress and its responses (Gupta et al. 2013), as well as under

other abiotic stress conditions, including, among others, salinity, high light, high temperatures, drought and wounding, which are usually associated with oxidative stress (Corpas et al. 2011). Many relevant enzymes intricated in the metabolism of ROS, which may subsequently take part in the protection mechanisms against the oxidative stress facilitated by heavy metal and other stressing agents, are metalloproteins (Palma et al. 2013). Under some physiological circumstances, ROS are always going to be balanced between productions and scavenging in all cell sections. Sometimes this balance can be disturbed by a number of contrary environmental factors, as indicated above. Therefore, ROS are assumed to be double-faced molecules also acting as signaling molecules regulating a large gene network and reacting against biotic and abiotic stress (Gupta and Sandalio 2011).

Nowadays, worldwide, many scientists are working on different molecular antioxidants and antioxidative enzymes and their role in higher plants. This special edited volume reviews a high number of antioxidants/antioxidative enzymes in one place and also updates current findings regarding their role at the cellular or molecular levels under different biotic and abiotic stresses. Namely, antioxidant enzymes such as SOD, CAT, APX, GR, Prx, Trx, class III peroxidases, MDAR, DAR, GR, and soluble antioxidants such as ASC, GSH, carotenoids, tocopherols, and flavonoids are covered in this edition. Figure 1 depicts the most relevant both enzymatic and non-enzymatic, located in the main antioxidants, oxygen-related organelles in plant cells-chloroplasts, mitochondria and peroxisomes. In chloroplasts, SODs are basically those containing copper/zinc and iron in their active sites and they can be either soluble in the stroma or anchored to thylakoidal membranes. APX also displays dual targeting, both in the stroma but also linked to thylakoids. However, in mitochondria, the only SOD reported is of the Mn-SOD class, and in peroxisomes all isozyme types (CuZn-SOD, Mn-SOD and Fe-SOD) have been reported (Palma et al. 2013). In chloroplasts, the whole ascorbate-glutathione cycle is functional, with the four enzymes (APX, MDAR, DAR and GR) working one after another; while in mitochondria and peroxisomes, the pairs APX–MDAR on the one hand, and DAR–GR on the other, seem to be the most likely to be operating. In a nutshell, the material in this book will bring great insight into the information collected and the recent successes within the field of antioxidants/antioxidants enzymes in higher plants.

Interaction Between the Metabolism of ROS and Reactive Nitrogen Species (RNS)

As mentioned, antioxidant systems, both enzymatic and non-enzymatic, are crucial in plant cells to keep the production of ROS under physiological and adverse environmental conditions under control. However, it is important to bear in mind that these systems do not work alone and there are other molecules that have an interactive mechanism of regulation alongside ROS and antioxidants. In this sense, the free radical molecule, nitric oxide (NO) and derived molecules called reactive nitrogen species (RNS) can interact at different levels, as part of a complex network of signaling processes as well as a mechanism of response against different biotic/abiotic stresses. Figure 2 shows a simple model of the interaction of ROS and RNS metabolisms in plant cells and some of the antioxidant enzymes involved. Thus, O_2^{-} are dismutated by the enzyme SOD to generate H_2O_2 whose content is controlled by either catalase or APX, among others. O_2^{-} can also react with NO to generate peroxynitrate (ONOO⁻), which is a strong oxidant and nitrating molecule and can mediate a process of tyrosine nitration of some proteins such as catalase, MDAR or APX (Chaki et al. 2015: Mata-Pérez et al. 2016). On the other hand, NO can also react with the reduced GSH component of the ascorbate-glutathione cycle, to form S-nitrosoglutathione (GSNO). This metabolite is able to interact with SH-containing proteins by a process of S-nitrosylation affecting their function. Some target enzymes of this event are catalase, MDAR, DHAR and Prx (Begara-Morales et al. 2016). Moreover, these ROS/RNS molecules $(O_2^{-}, H_2O_2, H_2O_2)$ NO, ONOO⁻ or GSNO) can mediate either the process of cell signaling or initiate mechanisms of defense against pathogen or abiotic stresses.



Fig. 2 Simple model of the interaction of ROS and RNS metabolisms and involved antioxidative enzymes in plant cells. SOD: superoxide dismutase; APX: ascobate peroxidase; MDAR: monodehydroascorbate reductase; DAR: dehydroascorbate reductase; Prx: peroxiredoxin; GSH: reduced glutathione; GSNO: *S*-nitrosoglutathione; ONOO⁻: peroxynitrite; Protein-Tyr-NO₂: nitrated proteins; Protein-Cys-S-NO: nitrosylated proteins

Preface

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Contents

Plant Superoxide Dismutases: Function Under Abiotic Stress Conditions	1
Luis A. del Río, Francisco J. Corpas, Eduardo López-Huertas and José M. Palma	-
Studies of Catalase in Plants Under Abiotic Stress David W. M. Leung	27
Ascorbate Peroxidase Functions in Higher Plants: The Control of the Balance Between Oxidative Damage and Signaling Takanori Maruta and Takahiro Ishikawa	41
Glutathione Reductase: Safeguarding Plant Cells Against Oxidative Damage Rafael Zuccarelli and Luciano Freschi	61
Function of the Various MDAR Isoforms in Higher Plants	83
Peroxiredoxins: Types, Characteristics and Functions in Higher Plants José Rafael Pedrajas and José Antonio Bárcena	95
Redox Protein Thioredoxins: Function Under Salinity,Drought and Extreme Temperature ConditionsAingeru Calderón, Francisca Sevilla and Ana Jiménez	123
Biosynthesis and Regulation of Ascorbic Acid in Plants Takahiro Ishikawa, Takanori Maruta, Kazuya Yoshimura and Nicholas Smirnoff	163
Glutathione Metabolism and Its Function in Higher Plants Adapting to Stress Biao Gong, Shasha Sun, Yanyan Yan, Xin Jing and Qinghua Shi	181

Revisiting Carotenoids and Their Role in Plant Stress Responses: From Biosynthesis to Plant Signaling Mechanisms During Stress	207
Virgílio Gavicho Uarrota, Deivid Luis Vieira Stefen, Lucieli Santini Leolato, Diego Medeiros Gindri and Daniele Nerling	
Abiotic Stress Response in Plants: The Relevance of Tocopherols Ivna Štolfa Čamagajevac, Tanja Žuna Pfeiffer and Dubravka Špoljarić Maronić	233
Flavonoids (Antioxidants Systems) in Higher Plants and Their Response to Stresses Venkidasamy Baskar, Rajendran Venkatesh and Sathishkumar Ramalingam	253
Class III Peroxidases: Functions, Localization and Redox Regulation of Isoenzymes Sonja Veljović Jovanović, Biljana Kukavica, Marija Vidović, Filis Morina and Ljiljana Menckhoff	269

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Dharmendra K. Gupta is senior scientist of environmental biotechnology/ radioecology and has already published more than 80 refereed research papers/review articles in peer reviewed journals and edited 11 books. His field of research includes abiotic stress by radionuclides/heavy metals and xenobiotics in plants, the antioxidative system in plants, and environmental pollution (radionuclides/heavy metals) remediation through plants (phytoremediation).

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