REDOX HOMEOSTASIS MANAGERS IN PLANTS UNDER ENVIRONMENTAL STRESSES

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REDOX HOMEOSTASIS MANAGERS IN PLANTS UNDER ENVIRONMENTAL STRESSES

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Spring forest with hornbeam trees and saw grasses in the locality of Baba, Czech Republic.
Personal photography of the Co-Editor Prof. Rene Kizek, University of Veterinary and Pharmaceutical Sciences, Brno, Czech Republic.

The production of cellular oxidants such as reactive oxygen species (ROS) is an inevitable consequence of redox cascades of aerobic metabolism in plants. This milieu is further aggravated by a myriad of adverse environmental conditions that plants, owing to their sessile life-style, have to cope with during their life cycle. Adverse conditions prevent plants reaching their full genetic potential in terms of growth and productivity mainly as a result of accelerated ROS generation-accrued redox imbalances and halted cellular metabolism. In order to sustain ROS-accrued consequences, plants tend to manage a fine homeostasis between the generation and antioxidants-mediated metabolisms of ROS and its reaction products.

Well-known for their involvement in the regulation of several non-stress-related processes, redox related components such as proteinaceous thiol members such as thioredoxin, glutaredoxin, and peroxiredoxin proteins, and key soluble redox-compounds namely ascorbate (AsA) and glutathione (GSH) are also listed as efficient managers of cellular redox homeostasis in plants. The management of the cellular redox homeostasis is also contributed by electron carriers and energy metabolism mediators such as non-phosphorylated (NAD+) and the phosphorylated (NADP+) coenzyme forms and their redox couples DHA/AsA, GSSG/GSH, NAD+/NADH and NADP+/NADPH. Moreover, intracellular concentrations of these cellular redox homeostasis managers in plant cells fluctuate with the external environments and mediate dynamic signaling in pant stress responses.

This research topic aims to exemplify new information on how redox homeostasis managers are modulated by environmental cues and what potential strategies are useful for improving cellular concentrations of major redox homeostasis managers. Additionally, it also aims to provide readers detailed updates on specific topics, and to highlight so far unexplored aspects in the current context.

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Table of Contents

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Editorial: Redox Homeostasis Managers in Plants under Environmental Stresses

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The Editorial on the Research Topic

Redox Homeostasis Managers in Plants under Environmental Stresses

Environmental stresses, grouped broadly into abiotic (physical environment e.g., drought, temperature regimes, UV-B radiation, salinity, and metals/metalloids) and biotic (e.g., pathogen, herbivore) significantly modulate the survival, reproduction, and productivity of plants/crops (Redondo-Gómez, 2013). In particular, environmental stresses caused by climate change, such as drought, high salinity, and low and high temperatures are predicted to become more severe and widespread (Osakabe et al., 2013). At cellular level, the sustenance of plant life under stressful environment is controlled by homeostasis in the usual redox reactions. Redox reactions can contribute various reactive oxygen species (ROS). One-, two-, and three-electron reduction of O_2 or excitation of triplet oxygen ($^3O_2$) can occur and cause the formation of superoxide radical ($O_2^{\bullet-}$) or hydroperoxyl radical ($HO_2^{\bullet}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($^{\bullet}OH$), and singlet oxygen ($^1O_2$), respectively. As integral signaling molecules, ROS regulate growth and development of plants, and also modulate their responses to biotic and/or abiotic stimuli (Baxter et al., 2014). However, beyond their steady-state cellular concentrations, ROS and their reaction products can modulate plant stress responses and/or severely impair the cellular redox homeostasis (Dietz, 2003; Oelze et al., 2008; Baxter et al., 2014; Juszczak et al.). Nevertheless, extreme environmental conditions are inevitable for plants and can excessively over-reduce or over-oxidize cellular environment. Previous conditions are likely to cause an imbalance in the generation and metabolism of ROS (and their reaction products), loss in the cellular redox homeostasis and finally the arrest in the cellular metabolism (Foyer and Noctor, 2009, 2012).

Plants are equipped with several strategies to efficiently metabolize and tightly regulate the steady-state levels of cellular ROS (and its reaction products), and manage cellular redox homeostasis at its optimum. The list of major cellular redox homeostasis managers includes redox-related components such as proteinaceous thiol members such as thioredoxin, glutaredoxin, and peroxiredoxin proteins, and key soluble redox-compounds such as ascorbate (AsA) and glutathione (GSH). Electron carriers and energy metabolism mediators such as non-phosphorylated (NAD+) and the phosphorylated (NADP+) coenzyme forms and their redox couples DHA/AsA, GSSG/GSH, NAD+/NADH, and NADP+/NADPH also contribute to cellular redox homeostasis (Schafer and Buettner, 2001; Anjum et al., 2010, 2012a,b; Foyer and Noctor, 2011, 2012; Suzuki et al., 2012; Giordano, 2013). The cellular redox homeostasis has also been regarded as the major "integrator" of information from metabolism and the plant–environment relationship

(Foyer and Noctor, 2009). Hence, unveiling insights into the role and underlying mechanisms of redox homeostasis in plants under environmental stresses has been the major focus of current plant research (Schafer and Buettner, 2001; Foyer and Noctor, 2009, 2011, 2012; Anjum et al., 2010, 2012a,b; Suzuki et al., 2012; Giordano, 2013).

The present volume "Redox Homeostasis Managers in Plants under Environmental Stresses" updates the readers on the subject, and discusses research progress and current understanding on the subject. Among the significant 17 article types, original research reports exemplified new information on how redox homeostasis managers are modulated by environmental cues and what potential strategies are useful for improving cellular concentrations of major redox homeostasis managers. Additionally, detailed updates to specific topics and so far unexplored aspects were highlighted by focused review/mini-review articles.

Cellular redox homeostasis is impacted by abiotic factors that can cause elevations in ROS (and their reaction products) at varying levels in the major energy organelles, such as chloroplast and mitochondria (Das et al.). Soil salinity is a serious threat to crop productivity worldwide that causes oxidative stress through imposing ion toxicity, osmotic stress, and metabolic imbalance (Adem et al., 2014; Abd Elgawad et al.). Notably, salinity stress significantly impacts electron flow in the electron transport chain in these organelles, disturbs the status of adenine (ATP) and pyridine nucleotides (NADH, NADPH), and eventually leads to elevation in cellular ROS and lipid peroxidation (LPO; Srivastava et al.). However, the extent of salinity-impact on ATP, NADH, NADPH, cellular ROS, and LPO can be higher in glycophytes (such as *Brassica juncea*; salt-sensitive) when compared with halophytes (such as *Sesuvium portulacastrum*; salt-tolerant; Srivastava et al.). Redox active compounds, AsA and GSH can play a significant role in the protection of plants against a number of abiotic stresses including temperature (low/chilling and high) and drought (Anjum et al.; Awasthi et al.; Das and Roychoudhury; Lukatkin et al.). Notably, the cellular level of AsA and GSH can differ in *Vigna radiata* during its ontogeny under drought exposure (Anjum et al.). In addition, sulfur nutrition was revealed as a potential strategy for the management of improved cellular pools of these redox active compounds. The role of polyamines and brassinosteroids for the maintenance of the cellular redox homeostasis in plants exposed to major abiotic stresses was critically discussed by Saha et al. and Vardhini and Anjum, respectively. Montero-Palmero et al. showed that plant endogenous factors like ethylene can modulate the early oxidative stress induced by mercury (Hg). Monoterpenoid indole alkaloids and phenols can be used as a defense tool against stress factors and can also benefit plants depleted in GSH (Vera-Reyes et al.). Dehydrogenases involved in the regeneration of NADPH such as glucose-6-phosphate dehydrogenase (G6PDH), 6-phosphogluconate dehydrogenase (6PGDH), NADP-malic enzyme (NADP-ME), and NADP-isocitrate dehydrogenase (NADP-ICDH) can support the protection of plants against nitro-oxidative stress induced by adverse environmental conditions (Corpas and Barroso). Information is scanty in the literature on the mechanisms involved in the control of each mitochondrial enzyme at the post-translational level (Millar et al., 2011; Nunes-Nesi et al., 2013). To this end, Yoshida and Hisabori evidenced that oxidation can inactivate mitochondrial isocitrate dehydrogenase; whereas, the later can be reactivated by thioredoxin-dependent reduction in Arabidopsis.

Insights into the role of redox active compounds AsA and GSH, proteinaceous thiol members such as thioredoxins, peroxiredoxins, and glutaredoxins, electron carriers and energy metabolism mediators phosphorylated (NADP) and non-phosphorylated (NAD+) coenzyme in the ROS-metabolism and the maintenance of redox homeostasis in abiotic stressed-plants were also critically discussed (Kapoor et al.). Notably, the enzymes of the AsA-GSH pathway, a key part of the network of reactions involving enzymes and metabolites with redox properties can have various subcellular isoforms, differ from each other (with respect to their spatial and temporal expression), and can also be differentially regulated by stress types (Anjum et al., 2010, 2012a,b; Gill and Tuteja, 2010). The knowledge gap available on the major mechanisms underlying the regulation of major isoforms of the AsA-GSH pathway enzymes was provided by Pandey et al. These authors provided major insights into the gene families of the AsA-GSH pathway, and also described their roles in the management of cellular redox homeostasis in plants exposed to abiotic and biotic stress conditions. Carvalho et al. elaborated the information available on the main mechanisms underlying plant tolerance to stresses (abiotic and biotic) via phenolic compounds (such as simple flavonoids like anthocyanins). Furthermore, it has recently been demonstrated that condensed proanthocyanidins (tannins) are solubilized into the vacuole or linked to cell wall polysaccharides and largely control the nutraceutical properties of the grape berry and its derivatives such as wine (Tenore et al., 2011; De Nisco et al., 2013).

An improved cellular redox homeostasis and plant-tolerance to environmental challenges are also achieved by employing several seed/plant-priming strategies (Tanou et al.; Bhanuprakash and Yogeesha, 2016). Notably, extreme abiotic and biotic stresses can severely impact or kill the organisms; whereas, low stress levels can exhibit priming effects and benefit stressed-plants (Hadacek and Bachmann). In an attempt to understand this idiosyncratic phenomenon, Hadacek and Bachmann explored the phenomenon of life from a more chemical perspective, elaborated insights into chemical structure diversity and recapitulated the basic reaction chemistry of low-molecular-weight metabolites (LMWMs). Additionally, contributions of LMWMs to a homeodynamic systems chemistry of living organisms were also dissected. Non-metabolized and/or elevated levels of ROS (and its reaction products) are the major violators of cellular redox homeostasis in stressed plants. However, the science of cellular redox homeostasis is lagging behind due to a major problem related with the quantification ROS and also with the identification of their short lifetime. Thus, the technique of electron paramagnetic resonance (EPR) spectroscopy could be a panacea to the said issue and can allow disentangling the origin of specific ROS and transient alterations in their cellular levels (Steffen-Heins and Steffens).

Herein, research reports discussing "cellular redox homeostasis in plants" in context with stresses caused by climatic changes (such as drought and salinity) and toxic chemicals (such as Hg) were least explored. Also, report is scanty on the "cellular redox homeostasis in plants" vs. biotic factors. However, contributions gathered herein concluded that the "cellular redox homeostasis in plants" is central to the plant stress defense, and the future investigations in this area can help in dissecting more insights into plant responses to environmental stresses. Recent advances in the subject were nicely presented and elaborated, and also identified and listed important open questions and challenges in the article types. Further, this research topic advocates to intensify and integrate biochemical, physiological and molecular-genetic studies on various aspects of the "cellular redox homeostasis in plants." Contributions included in this e-book can be useful for budding scientists working on the subject, and can also encourage further dialog, research and development on the "cellular redox homeostasis in plants."

AUTHOR CONTRIBUTIONS

NAA prepared the first draft of this "*Editorial*." All authors listed, have made substantial, direct and intellectual contribution to the work, and approved it for publication.

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