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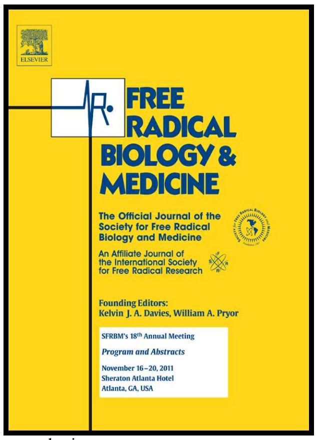

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Reactive oxygen species are crucial “pro-life “survival signals in plants

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Plants have a mainly sessile life-style, which means that they must accommodate a fluctuating and often hazardous environment that frequently poses biotic and abiotic challenges. Plant survival and seed production requires enormous molecular plasticity that allows continuous tuning of underpinning genetic and epigenetic programming of metabolism, physiology and morphology. Photosynthesis is the major driver of all plant processes, introducing the energy from sunlight into the biosphere and releasing oxygen from water. The driving force for photosynthesis sunlight is an almost limitless supply, and hence metabolic plasticity and flexibility has been achieved at the expense of photosynthetic efficiency. This evolutionary path has dictated that plants have become masters of redox control and signalling allowing exploitation of a wide range of ecological niches and highly variable as well as extreme environments. Photosynthesis and photorespiration are responsible for the high flux generation of a wide range of reactive oxygen species including singlet oxygen, superoxide, hydrogen peroxide. Even under optimal conditions, about 70% of the hydrogen peroxide production in the cells of C3 plants arises from photorespiration. This process generates vast amounts of hydrogen peroxide in the peroxisomes, at a rate that equals that of the oxygenation reaction of the primary enzyme of carbon assimilation, ribulose-1, 5-bisphosphate carboxylase/oxygenase in the chloroplasts. In addition, about 10% of the photosynthetic electron flux passes through pseudocyclic pathways generating large amounts of superoxide and hydrogen peroxide in the chloroplasts. These signals arising from photosynthetic reactions are integrated with the multitude of other reactive oxygen species producing systems in plant cells that are essential very similar in location and function to their animal counterparts. During evolution, various reactive oxygen species have been co-opted, directly and indirectly, into the regulation of the genetic and epigenetic programs that support plant growth and development as well as stress management. The intracellular functions of these important redox signals are controlled and often propagated by an extensive antioxidant system, comprising a network of enzymatic and non-enzymatic components that notably includes reactions linked to the intracellular ascorbate, glutathione and peroxiredoxin pools.

Plant reactive oxygen species and redox-associated pathways are tightly integrated with other signaling routes, including peptides and phytohormones. Redox-related communication pathways transmit information to the nucleus to steer the alterations in metabolism and physiology that are necessary for adaptation to a fluctuating and challenging environment. In this respect, there is significant overlap between plant and human paradigms, with regard to both the constraints of reactive oxygen species chemistry, organelle to nucleus signalling and the need for a high degree of signal specificity. As in animal biology and medicine, the field of plant redox biology has expanded enormously in recent decades, embracing a wide research community, whose ambition is to achieve food and nutrition security, ecosystem sustainability and economic growth in line with the United Nations Sustainable Development Goals (SDGs). Plant redox biologists not only seek to generate new knowledge that will transform agriculture and the food sector but their efforts will also contribute to the delivery of a more healthy lifestyle and wellbeing for all people on the planet.

Much of the current emphasis of plant research concerns the development of climate-resilient crops that are able to adapt rapidly to changing climatic conditions. Since reactive oxygen species signalling is a key aspect of how plants respond and cope with biotic and abiotic stress within the environment, any advance in our knowledge of the regulatory events governing stress-related reactive oxygen species signal transduction, is relevant to this goal. Suboptimal growth conditions can be caused by many environmental factors including drought, extremes of temperature, high salt or low soil nutrient availability that already cause significant losses in the yields of cultivated crops worldwide. The changing climate of the earth is predicted to increase the frequency of such environmental impacts and it is also likely to increase the threats from herbivore and fungal pathogens that will further threaten food security and hence have considerable societal impacts. For example, as the climate of the earth changes, there will be more frequent high temperature and drought stress events. Simultaneously, the global demand for plants as a source of food, feed and bioenergy is predicted to steadily increase as the population of the world exceeds 9 billion. Therefore, stress-tolerant crops are in high demand. The pending crisis in global food security has incentivized academic and industry-based research teams to make significant investments in research and development over the past decade directed at the generation of novel strategies and targets for the improvement of stress adaptation and protection in the major food and feed crops. This Special Issue of Free Radical Biology & Medicine, provides a set of expert reviews that together provide a comprehensive overview of how plants produce, perceive and transduce reactive oxygen species dependent signals, combined with unique personal insights into how this knowledge might impact research that tackles problems associated with human and (patho) physiologies.

As in animal systems, the production and scavenging of reactive oxygen species is highly compartmentalized. Depending on the type of stimulus, reactive oxygen species can be generated– and scavenged- in any organelle or cellular compartment. This integrated system, not only provides optimized defense capacities that prevent the unregulated triggering of reactive oxygen species-induced cell suicide pathways, but also provides plant cells with highly sensitive and specific mechanisms to employ reactive oxygen species as signaling molecules in intra- and extracellular signaling (Czarnocka and Karpinski, 2018). Within the various communication systems between organelles, reactive oxygen species-induced reactive oxygen species release (RIRR) are beginning to emerge as important pathways involved in many different human pathologies and plant responses to environmental stresses. Zandalinas and Mittler (2018) describe the main features of RIRR pathways in plants and animals, highlighting the features of each system and how important parallels may be drawn.

Plant mitochondria are not only key production sites for superoxide and hydrogen peroxide in plants as they are in animals, but they also house the targets and sensors of signaling cascades for a variety of metabolic cues and environmental stresses. The mitochondria to nucleus anterograde and retrograde controls are described, together with the safeguards that allow an efficient and effective contribution of this crucial energy-generating organelle cellular and organellar redox homeostasis (Wang et al., 2018). The role of redox regulation of the alternative oxidase (AOX) and other mitochondrial proteins in NO production is considered in the paper by Vishwakarma et al. (2018) who compared the effects of hypoxia in transgenic Arabidopsis plants that either over express AOX or that have lower AOX levels. These authors present data suggesting that AOX functions feed into the haemoglobin-NO cycle to drive energy efficiency under hypoxia.

Communication between the mitochondria and the other major powerhouse of plant cells, the chloroplast and the nucleus, can be initiated by imbalances between the absorption of light energy and the capacity of photosynthetic carbon assimilation to use this energy productively in carbon gain. Mullineaux et al. (2018) provide an expert review that covers our current knowledge of photosynthetic regulation and provides a working hypothesis concerning how plants convey and translate superoxide and hydrogen peroxide signals to the nucleus to elicit appropriate changes of gene expression. In addition, these authors present an interesting comparison between the responses of chloroplasts to high light and the responses of animal cells to oxidative stress. The paper by Roach et al. (2018) provides further evidence of the important role of redox processes in the acclimation responses of plants to high light through stimulation of thiol/disulphide-based redox defence.

The transfer of redox equivalents between different cell compartments can also be mediated by organic acid metabolism in plants, in which malate dehydrogenases are particularly important. Igamberdiev and Bykova (2018) provide a timely and interesting discussion of the roles of organic acids, particularly through interconversions of malate and oxaloacetate or through the formation of pyruvate. These authors highlight the central position of organic acid metabolism in the equilibration of redox states between different cellular compartments, as well as in the support of ion gradients across the different cellular membranes, as well as in the regulation of the production of reactive oxygen and nitrogen species. Organic acid metabolism is intrinsically linked to the reduction/oxidation of the major redox couples in plants, including NAD/NADH and NADP/NADPH. Gakiere et al. (2018) provide an interesting overview of the current state of knowledge concerning how NAD metabolism in plants is regulated, together with its influences on other metabolic pools and on gene expression. These authors highlight the overall complexity of NAD dependent metabolic regulation, particularly in the mitochondria.

Not surprisingly, reactive oxygen species-derived organic molecules and reactive oxygen species-antagonistic compounds can have profound effects on reactive oxygen species homeostasis through interactions with specific metabolic and molecular targets. Reactive nitrogen and carbonyl species are considered to have profound effects on redox signaling systems. In particular, one important type of reactive nitrogen species, methylglyoxal (MG), which is a byproduct of the metabolic pathways that degrade carbohydrates, proteins and lipids, is emerging as a new and potentially important signaling agent in plants. Mostofa et al. provide a comprehensive update on our current knowledge concerning MG production and detoxification in plants. These authors also highlight the putative functions of glyoxalase systems in mediating plant defenses against abiotic stresses. The intimate interplay between nitric oxide and ROS signaling in plants is described in detail by C. Lindermayr (2018), who emphasizes the importance of ROS dependent post-translational modifications that direct affect nitrosoglutathione (GSNO)-reductase activities in plants. GSNOR holds a key regulatory position at the crossroads between ROS and NO signaling in plants and animals.

Despite its widely known importance as crucial vitamin and plant derived anti-oxidant within human diets, the multifaceted roles of ascorbic acid (vitamin C) in plants are poorly-understood. With the exception of primates and some other animal groups, ascorbic acid is synthesized by all eukaryotes. Ascorbate is involved in iron uptake and transport in both plants and animals. However, ascorbate peroxidases (APX) are limited to plants, which mainly use ascorbate rather than glutathione in hydrogen peroxide detoxification. Together with catalases and peroxiredoxins, APX activity provides plants with high capacities for removal of the H_2O_2 produced by photosynthesis and photorespiration. In an expert and comprehensive review, N. Smirnoff provides a timely comparison of ascorbic acid metabolism and functions in plants and mammals. Evidence in support of the role of reactive oxygen species in the control of plant growth through their multifaceted interactions with phytohormones is provided in the paper by Caviglia et al. (2018). These authors show that deficits in antioxidant capacity lead to a greater production of the stress hormone ethylene, and altered transcript profiles of genes that contribute to the control of growth. Such responses may be particularly important in the control of the growth arrest that occurs when plants perceive environmental stresses. Plants will often stop growing upon perception of even mild stress, even though the environmental conditions may not be sufficiently severe to warrant this response. A crucial part of this response is the stress-triggered arrest of the cell cycle. The review by Foyer et al. (2018) discusses the concept of redox regulation of cell proliferation in animals and plants. Although the concept that reactive oxygen species fulfil both positive and negative roles in the regulation of the cell cycle is widely accepted, little is known about the precise mechanisms and redox-sensitive proteins that influence cell cycle progression in plants. These authors discuss the potential for redox control of known cell cycle regulators and consider how proteomics may be used to map critical redox modifications at the molecular level in plants. These authors provide a comprehensive overview on the portfolio of redox proteomics based strategies to experimentally validate the presence and importance of oxidized cysteine residues.

Another naturally-occurring dietary compound, isothiocyanate sulforaphane (SNF), is currently the subject of several clinical trials for a variety of disease states, including the evaluation of its therapeutic potential to ameliorate diabetic and cardiometabolic complications. Patel et al. (2018) provide a critical review of the mechanisms by which SNF activates the molecular regulators of the transcriptional pathways that are important in plant defenses. Plant-based products, such as red wine and tea are enriched in polyphenols. Epidemiological studies have indicated that regular intake of such plant secondary metabolites in polyphenol-rich diets are associated with a reduced risk of cardiovascular diseases. The proposed mode of action of these plant secondary metabolites is through the direct targeting of endothelial cells, which increases vasoprotective factors including NO to delay endothelial ageing. Oak et al. (2018) provide a detailed discussion of both the experimental and clinical evidence that supports the positive role of polyphenols in promoting endothelial and vascular health. It is interesting to note that SNF is able to prime both plant and mammalian responses through the activation of redox-sensitive genes. The use of priming through the application of naturally-occurring plant compounds is also an interesting concept for sustainable agriculture. In his paper, Gonzalez-Bosch (2018) describes plant-priming agents, highlighting the fact that many plant compounds including vitamins such as thiamine, riboflavin and quercetin, function through effects on redox signaling. This review also illustrates how priming agents promote a stronger and faster transcriptional response to stress by modulating the intracellular redox environment, and interacting with phytohormone signaling pathways particularly the stress-related hormones such as salicylic acid, jasmonic acid and ethylene.

A detailed map of the oxidative stress responses of mammalian and plant systems is already available at the level of transcriptional regulation. However, new insights continue to emerge concerning the impacts of reactive oxygen species and their subsequent effects at the post-transcriptional, post-translational and proteome levels. Van Ruyskensvelde et al. (2018) review the current knowledge on the post-transcriptional gene regulation during the oxidative stress response in plants. Although still an emerging field, the role of RNA-binding proteins on RNA homeostasis and diversity will reveal a new layer of regulation which affect cellular responses under oxidizing conditions. Two reviews focus on the relevance of oxidative post-translational modifications. In addition to Foyer et al. (2018) who used a bioinformatics approach to map out cysteine residues on known cell cycle regulators Huang et al. (2018) focus in their review on the functional consequences of sulfenylation of both mammalian and plant proteins. By comparing compendia of sulfenylated proteins in human and plants, these authors identify the significant evolutionary conservation of sulfenylated targets that participate in specific biological pathways and metabolic processes. Together with advanced methods for precise imaging and quantification that can be used to monitor local, subcellular and global reactive oxygen species dynamics with high selectivity, sensitivity and spatiotemporal resolution, these authors provide comprehensive sub-cellular maps of protein cysteine (and methionine) oxidation that will allow a better understanding of hydrogen peroxide signalling pathways that underpin stress responses. In addition, Ortega-Villasante summarizes current knowledge and innovations in plant reactive oxygen species imaging and in vivo detection, using chemical probes and fluorescent protein-based biosensors.

Taken together, the reviews and research studies presented in this special issue are important in providing a timely description of our current knowledge of reactive oxygen species-mediated processes in plants, particularly through redox signalling mechanisms that control plant growth and development in a fluctuating environment, as well as providing acclimation and tolerance to environmental stresses. In addition, the authors provide expert views and opinions concerning how this knowledge may be translated and applied to drive new strategies for plant improvement and the development of climate-resilient crops. These papers provide essential new insights into how redox processes may be deployed to enhance plant productivity and so ensure sustainable food production in the future.

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