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Editorial

Plant redox biology—on the move

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Redox reactions underpin cellular energy exchange and are therefore essential to life. Beyond this essential function, it has become clear that plants have evolved modules that can detect redox states, thereby providing information on cellular and subcellular conditions during developmental processes and interactions with the environment. Since the pioneering studies of light-dependent redox regulation of photosynthetic enzymes in the 1960s (Buchanan 1980), the field of redox biology has extended its reach to almost all aspects of plant physiology and in fact far beyond to encompass virtually any kind of organism, developmental or signaling process, as well as pathology or disease. It is now evident that plants organize a multiplicity of different reactions in which reactive molecular species, redox modifications, and redox proteins act to regulate cellular homeostasis (Zaffagnini et al. 2019). Recent studies have elucidated the organization and biological significance of this complex redox network in planta. This focus issue exemplifies the pervasive roles of thiol redox regulation, reactive oxygen and nitrogen species in integrating metabolism, environmental acclimation, stress responses, and plant development. It combines eight topical focus reviews and multiple research papers to capture current views and perspectives of these recent developments and to provide novel insights into plant redox biology.

Six papers provide insights into intraorganellar redox systems and redox signals involved in intracellular communication. The update of Cejudo et al. (2021) highlights new functions of peroxiredoxins and antioxidative systems in the redox regulation of chloroplast metabolism. Plant chloroplasts contain two different thiol-redox systems, the ferredoxin–thioredoxin (Trx) system which allows the regulation of chloroplast metabolism in response to light, and the NTRC, a NADPH-dependent Trx-system, which integrates the use of NADPH in this redox network. It is now becoming evident that both reductive systems work in concert with thiol-dependent antioxidative systems to modulate the redox-state of chloroplast enzymes in response to light, and to allow their rapid oxidative inactivation in the dark, by mediating the transfer of electrons from reduced enzymes via Trxs to hydrogen peroxide. This provides a new model of chloroplast redox regulation with NADPH and hydrogen peroxide acting as input and final sink of electrons, respectively, which is proposed to be linked to the signaling function of the chloroplast.

As confirmed by elegant studies using in-vivo redox biosensing, chloroplast-derived photo-oxidative stress causes changes in hydrogen peroxide and oxidation of glutathione in other cell compartments (Ugalde et al. 2021). Novel evidence for the importance of the chloroplast NADPH redox poise for photosynthetic performance has been provided by Höhner et al. (2021), showing that PHOSPHOGLYCERATE DEHYDROGENASE 3, an oxidoreductase in leaf chloroplasts with strong preference to reduce stromal NAD(H) instead of NADP(H), is required for full photosynthetic activity, specifically in fluctuating light

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environments. While these studies have mainly been focused on Arabidopsis, new work in algae by Milrad et al. (2021) establishes bidirectional energy transfer between H_2 and NADPH to be crucial to maintain the plastid redox balance under light fluctuations.

In addition to chloroplasts, peroxisomes and mitochondria are important redox signaling nodes in intracellular communication and stress responses. The review of Sandalio et al. (2021) updates our knowledge of peroxisomal redox homeostasis and the roles of ROS and NO in the functionality, biogenesis, and abundance of these organelles, as well as their roles as redox hubs in metabolic regulation, signaling, and interorganellar crosstalk. As outlined in the update, there is an emerging function of peroxisomes as highly dynamic organelles capable of changing their number, size, and morphology and adjusting the speed in response to environmental redox changes. Peroxisomal hydrogen peroxide regulates cellular processes also outside organellar boundaries, including pathogen-associated processes, DNA repair systems, cell cycle, and phytohormone-dependent signaling. Van Aken (2021) provides an update of the latest research concerning the organization and operation of plant mitochondrial redox systems, and their effects on cellular metabolism and signaling. Recent breakthroughs are discussed concerning mitochondrial retrograde signaling pathways, which communicate the functional status of mitochondria to change nuclear gene expression in response to interorganellar signals and physiologically relevant stress conditions.

ROS and RNS are known to play critical and integrative roles in multiple stress signaling (Baxter et al. 2014). Four papers in this Focus Issue provide novel insights into the role of these redox signals to control abiotic and biotic stress responses and to regulate plant growth and development. In their update, Bleau and Spoel (2021) review recent progress in understanding selective redox-signaling mechanisms that shape plant–pathogen interactions. Novel evidence is discussed that highlights the importance of chloroplast-generated ROS production in response to pathogen infection, as well as major advances in our understanding of how pathogens can manipulate plant redox systems. In the letter of Fichman and Mittler (2021) transgenic plants expressing roGFP1 in the cytosol were used to show that a wound-induced ROS wave is accompanied by a systemic whole plant change in redox levels. Also fluctuations in O_2 concentrations affect the plant cellular redox balance and the formation of ROS and RNS during the onset of hypoxia and upon re-oxygenation. The update of Sasidharan et al. (2021) provides an insightful view on our current understanding of how these redox signals integrate in low-oxygen signaling and adaptation of plants. Novel evidence is discussed that ethylene, a key regulator of submergence responses in plants, is tightly linked to ROS and RNS homeostasis and signaling. In addition to external changes in O_2 concentrations, there are also developmental transitions in the O_2 status of meristems and reproductive plant organs which may contribute to regulate plant growth and development. Considine and Foyer (2021) review recent progress in oxygen- and ROS-dependent regulation of plant growth, development and differentiation through multiple interlinked signaling pathways. Novel evidence is discussed highlighting convergence points for oxygen and ROS signaling to occur on proteins such as ROP2 GTPase, RBOHD, and Trx *h* to regulate meristematic activity via TOR kinase activity.

Finally, two papers focus on emerging tools enabling ever-increasing spatiotemporal resolution and imaging of redox status components, as well as cysteine redoxome profiling in plants. The update of Müller-Schüssele et al. (2021) summarizes recent progress in the development and use of genetically encoded biosensors for live monitoring of plant redox and energy physiology to understand plant redox dynamics and energy metabolism on a cellular and subcellular level. The update highlights methodological advances that have been instrumental to dissect the dynamics of several distinct redox couples and energy physiology in plants. In their update, Willems et al. (2021) provide an overview of contemporary proteomic strategies for cysteine redoxome profiling, enabling systematic characterization of diverse oxidative post-translational modifications.

The topics covered in the updates and research articles provide compelling evidence of the centrality of redox signaling and redox-dependent regulation to plant physiology. With this knowledge in mind, it is apparent that redox-dependent regulation is relevant to almost all aspects of plant function. Therefore, the researcher should ask by which mechanism redox regulation might affect the process under consideration. Redox biology will continue to develop further and certainly is on the move.

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