

# Signaling and Communication in Plants

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Editors

# Reactive Oxygen Species in Plant Signaling

 Springer

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# Preface

Oxygen (O<sub>2</sub>) appeared in significant amounts in the Earth's atmosphere over 2.2 billion years ago, largely due to the evolution of photosynthesis by cyanobacteria (Halliwell 2006). The O<sub>2</sub> molecule is a free radical, as it has two impaired electrons that have the same spin quantum number. This spin restriction makes O<sub>2</sub> prefer to accept its electrons one at a time, leading to the generation of the so-called reactive oxygen species (ROS). The chemical nature of these species dictates that they can create damage in cells. This has contributed to the creation of the "oxidative stress" concept; in this view, ROS are unavoidable toxic products of O<sub>2</sub> metabolism and aerobic organisms have evolved antioxidant defences to protect against this toxicity (Halliwell 1981; Fridovich 1998). Indeed, even in present-day plants, which are full of antioxidants, much of the protein synthetic activity of chloroplasts is used to replace oxidatively damaged D1 and other proteins (Halliwell 2006). Yet, the use of the "oxidative stress" term implies that ROS exert their effects through indiscriminate widespread inactivation of cellular functions. In this context, ROS must not be able to react with lipids, proteins or nucleic acids in order to avoid any damage to vital cellular components.

However, genetic evidence has suggested that, in planta, purely physicochemical damage may be more limited than previously thought (Foyer and Noctor 2005). Thus, the concept of "oxidative stress", which implies a state to be avoided, was re-evaluated and the term "oxidative signaling" was created (Foyer and Noctor 2005). This means that ROS production, which was originally considered as an exclusively harmful process, is also an important component of the signaling network that plants use for their development and for responding to environmental challenges. The evolution of efficient antioxidant systems has most likely enabled plant cells to overcome ROS toxicity and to use these reactive species as signal transducers (Mittler 2006).

Results obtained during the last decade have highlighted the role of ROS as signals in plants, and it is now widely accepted that ROS are key regulators of plant metabolism, morphology, and development. The role of ROS as signals for gene expression has been evidenced (Desikan et al. 2001; Vanderauwera et al. 2005), and it is now known that ROS modulate the activity of key signaling compounds such as MAP kinases (Rentel et al. 2004). Furthermore, ROS can induce protein modifications, and thiol changes have been suggested as a widespread mechanism by which ROS might affect the activity and function of proteins (Cooper et al. 2002).

The identification of ROS-generating enzymes has demonstrated that plant cells can initiate ROS production for the purpose of signaling, and that the spatio-temporal characteristics of this production are likely to play an important role in the transduction of ROS signals (Mittler 2006). It is now obvious that sophisticated processes regulate these characteristics, which lead to the generation of inter-compartmental gradients, at least of hydrogen peroxide ( $H_2O_2$ ). Transport of  $H_2O_2$  through vesicle trafficking (Leshem et al. 2006) is most probably an important component of this process. Moreover, the facilitated diffusion of  $H_2O_2$  across membranes through specific aquaporins (Bienert et al. 2007) appears to play a crucial role in the establishment of such  $H_2O_2$  gradients. On the other hand, it appears that oxidation of target molecules by ROS is a part of how plants perceive and respond to environmental and developmental triggers (Foyer and Noctor 2005). Among the processes where ROS involvement has been evidenced, one can first cite the plant pathogen defense. During this process, ROS are produced by plant cells via plasma membrane-bound NADPH-oxidases, cell wall-bound peroxidases and amine oxidases in the apoplast (Bolwell 1999; Grant and Loake 2000). ROS production leads to programmed cell death (Bolwell 1999) and orchestrates the plant hypersensitive disease resistance response (Levine et al. 1994). Moreover, it has been shown that  $H_2O_2$  can mediate the systemic expression of defense-related genes (Orozco-Cardenas et al. 2001). ROS appear to also play an important role in plant development and functioning. They are essential signals in stomatal closure in response to abscisic acid and elicitors (Pei et al. 2000). They are involved in root hair growth (Foreman et al. 2003) and auxin signaling and gravitropism (Joo et al. 2001). ROS induce the expression of genes encoding proteins required for peroxisome biogenesis (López-Huertas et al. 2000). Moreover, it has recently been shown that DELLAs proteins regulate plant growth and defense processes by modulating the levels of ROS (Achard et al. 2008).

The volume of research into the roles of ROS in plants is currently growing. Thus, the purpose of this book is to present recent advances in this field. The constitutive chapters are mainly arranged around four topics: (1) the generation of ROS, their network signalling, including the retrograde signalling from the chloroplast to the nucleus and the cross-talk with hormone signaling, (2) the signaling role of ROS produced in some sub-cellular compartments, (3) the role of ROS in plant growth, development, functioning and stress acclimation, and (4) their role in biotic and abiotic interactions. In thanking the authors for their contributions, we are convinced that the forthcoming years will bring new exciting insights into this field. Unravelling the sensing and transduction of ROS, including the post-translational regulation, the modulation of their concentration at subcellular level, and the interaction networks with the reactive nitrogen species, as well as their possible role in epigenetic processes, will shed new light on ROS action in plants.

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