

On How to Build a Larger and Healthier Arabidopsis ROSette Using a Mitochondrial Protein (Spoiler: Reactive Oxygen Species)

Cellular respiration is at the core of central metabolism, generating energy out of simple hydrocarbon molecules. This energy runs fundamental functions of the cell. A collateral effect of aerobic metabolism is the production of reactive oxygen species (ROS) with potential to damage biological molecules and structures. The cell has myriad sets of mechanisms to control the damage derived from respiration (Noctor and Foyer, 2016). The chloroplast and mitochondria are the organelles par excellence of ROS production that have acquired different strategies to avoid or mitigate their impact (Huang et al., 2016). Interestingly, the ROS within organelles or at the inner side of the plasma membrane can additionally help the plant under certain situations, such as abiotic stress (Colombatti et al., 2019; Wang et al., 2020).

In eukaryotes, one of these strategies requires the activity of the OXIDATION RESISTANCE (OXR) protein family responsible for the prevention of oxidative DNA damage and induction of antioxidant enzymes using a still-unknown mechanism. The physiological relevance of OXRs is supported by strong phenotypes in loss-of-function mutants across species, such as neurological disorders in mammals (Finelli and Oliver, 2017). In Arabidopsis (*Arabidopsis thaliana*), the OXR family is composed of six genes and is part of a protective mechanism to restrain respiration-associated damage (Colombatti et al., 2019; Torti et al., 2020).

In this issue of *Plant Physiology*, Mencia et al. (2020) establish that the specific action of the OXR2 mitochondrial protein results in a significant improvement in Arabidopsis protection against bacterial pathogens. Using plants with altered expression levels of OXR2, they showed that ROS, produced through the isochorismate pathway, is associated with the enhanced defense response of OXR2-overexpressing (oeOXR2) plants and the increased susceptibility of the *oxr2* mutant.

Mencia et al. (2020) describe several OXR2-mediated events related to the salicylic acid (SA)-defense response of Arabidopsis. Analyzing the transcriptional profile of oeOXR2 plants, they found an important transcriptomic overlap between noninfected oeOXR2 plants and wild-type plants infected with a biotrophic pathogen and, to a lesser extent, an overlap with mutants related to hormonal pathways. Therefore, the

ectopic expression of OXR2 triggers a molecular response emulating the presence of a pathogen and activates hormonal pathways related to defense responses of the plant. Among the events leading to the improved resistance of oeOXR2 plants to *Pseudomonas syringae* pv *tomato* DC3000 they found increased levels of SA and ROS, enriched nuclear localization of NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1 associated with an increment of glutathione oxidation in the cell, and high expression of SA-marker genes, even before exposure to the pathogen. The *oxr2* mutant showed contrasting behavior, with a delayed defense response leading to increased susceptibility to the pathogen and triggering a lower production of SA with low induction of some early and late SA-marker genes. Altogether, OXR2 expression levels somehow control the activation of the SA response, alter the oxidation environment in the cell, and at least partially modulate ROS production in plant tissues. It remains unclear how OXR2 expression levels are associated with resistance levels depending on the pathogen. If Arabidopsis plants become more resistant to *P. syringae* pv *tomato* DC3000 through the induction of OXR2, it is unclear why other pathogens, such as the hemibiotroph oomycete *Phytophthora parasitica* and the necrotrophic fungus *Sclerotinia sclerotiorum*, repress OXR2 expression (Mencia et al., 2020). It will be interesting to test the ability of oeOXR2 plants to defend against *P. parasitica* and *S. sclerotiorum* and to identify Arabidopsis ecotypes in which OXR2 is not down-regulated by these pathogens during the infection process. The pathogen's ability to control OXR2 expression levels as part of the infection process could be another entry point for pathogens into the plant (Fig. 1).

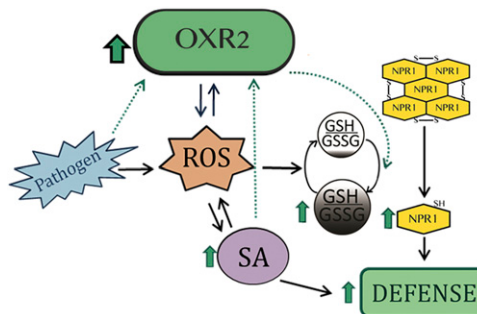


Figure 1. The OXR2 mitochondrial protein modulates multiple layers leading to pathogen resistance. Figure reprinted from Mencia et al. (2020).

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Previous reports showed that increased SA levels accompanied by high endogenous ROS have a penalty on rosette growth, as observed for the *cpr5* mutant (Meng et al., 2017). However, *oeOXR2* plants bearing high levels of both SA and ROS are still able to produce larger rosettes compared with wild-type plants, opening interesting questions with potential biotechnological impact (Colombatti et al., 2019; Mencia et al., 2020). Using *oeOXR2* plants, Mencia et al. (2020) also identified altered expression for several genes related to growth-promoting hormones like gibberellins and cytokinins. If these genes are at least partially responsible for the phenotype of larger rosettes and enhanced pathogen tolerance, could they be part of a novel layer of regulation of the growth-defense tradeoff? Could ROS levels and ROS compartmentation control the expansion of green tissues while modulating the pathogen infection? Now, there is strong evidence that the plant microbiome, including belowground and aboveground plant-associated bacteria, influences plant growth, health, and stress resilience (Rudrappa et al., 2008). If *OXR2* is able to directly or indirectly modulate the plant microbiota, it might indirectly influence plant growth and defense.

The study by Mencia et al. (2020) identifies a series of events required for this puzzling connection between ROS, mitochondria, and environmental stress. Yet, the contribution of *OXR2* in natural conditions remains unclear, including in the face of different types of pathogens, light and temperature fluctuations, and water deficit. Can *OXR2* be a novel marker for crop breeding programs to manipulate SA-inducible defenses with a low penalty in growth? Since crop-breeding programs are now integrating multiple avenues, it might be relevant to explore the contribution of ROS and *OXR*-related genes in complex traits.

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