Aquaporins Link ROS Signaling to Plant Immunity

One of the most rapid defense reactions of plants to pathogen attack is the so-called oxidative burst, which constitutes the production of reactive oxygen species (ROS) at the site of an attempted invasion. In general, the oxidative burst is induced by the perception of typical microbial nonplant molecules, so-called microbe-associated molecular patterns (MAMPs; Bigeard et al., 2015). Well-known examples of MAMPs are bacterial flagellin or fungal chitin, which are sensed by plasma membrane localized pattern recognition receptors (Macho and Zipfel, 2014). In Arabidopsis (*Arabidopsis thaliana*), a plasma membrane-localized NADPH oxidase (RbohD) is mainly responsible for this MAMP-induced ROS burst and produces membrane-impermeable superoxide ($O\cdot-_2$), which is converted into hydrogen peroxide (H_2O_2) by superoxide dismutases (Liu and He, 2016), in the apoplast. Apoplastic H_2O_2 was then thought to diffuse through the plasma membranes and induce cytosolic signaling pathways to contribute to the plethora of defense reactions termed MAMP-triggered immunity (Bigeard et al., 2015).

ROS are also continuously produced as a result of aerobic metabolism or in response to abiotic stress conditions, and are not only toxic chemicals but also signaling molecules involved in several developmental processes (Apel and Hirt, 2004). Although H_2O_2 can cross plasma membranes to enter the cytosol and different organelles, this process is rather slow and inefficient but can be strongly facilitated by certain membrane proteins of the aquaporin family (Li et al., 2014). Although originally thought of as being simple water transporters, different aquaporins have different specificities and can also transport neutral substances, such as glycerol, ammonia, urea, boric and lactic acid, carbon dioxide, and last but not least H_2O_2 (Wu and Beitz, 2007). Because of the obvious relationship of the water status of a plant with abiotic stress, it is not surprising that ample evidence exists that aquaporins play key roles in the abiotic stress tolerance of plants (Li et al., 2014). The expression of certain aquaporins is regulated by abiotic stresses, and altered expression of specific aquaporins can influence abiotic stress tolerance in a range of plants (Li et al., 2014).

In this issue, the work by Tian et al. (2016) shows that aquaporins are also key in the immune response of plants against pathogens. The authors screened for altered expression of Arabidopsis AtPIP aquaporins by the bacterial pathogen *Pseudomonas syringae* pv *tomato* (*Pst* DC3000). Among these aquaporins, *AtPIP1;4* was found to be responsible to transport pathogen-induced apoplastic H_2O_2 to the cytoplasm of plant cells. Importantly, blocking the entry of H_2O_2 into cells in *Atpip1;4* knockout mutants did not affect pathogen-induced RbohD generation of H_2O_2, which accumulated to high apoplastic concentrations, but completely compromised plant defense responses and resulted in hypersensitivity to Pst DC3000. The authors also showed that the entire process can be mimicked by applying external H_2O_2 or using MAMPs such as a flagellin peptide or chitin fragments, thereby proving that *AtPIP1;4* is a key component of MAMP-triggered immunity in plants. These findings fill an important gap in our understanding of the molecular mechanism of ROS signaling in innate immunity, and also pave the way for appreciating the roles ROS play in biotic and abiotic stresses.

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