

**Role of Chloroplasts in Plant's Defense Activation**

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**SUMMARY**

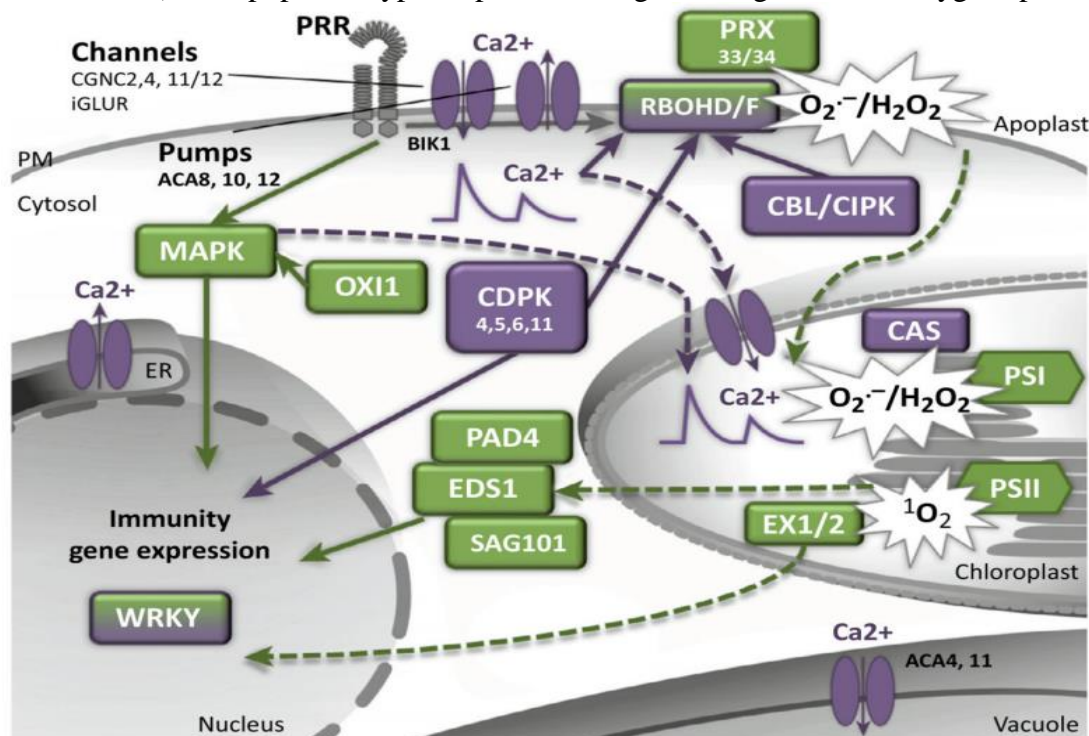
Chloroplasts are photosynthetic organelles enabling photoautotrophy and emerging as hubs in integrating environmental stimuli and determinants of downstream responses. They are the site of synthesis of phytohormone precursors, such as jasmonic acid and salicylic acid, secondary metabolites and defense compounds, underpinning resistance to pathogens and are also key contributors to redox homeostasis, including the generation of ROS and reactive nitrogen species (RNS), which in turn influence nuclear gene expression via retrograde signaling (RS).

**INTRODUCTION**

A plant's initial response to a broad spectrum of different stresses, including pathogens, is through integrated signalling modules that recognize a common set of second messengers like calcium, reactive oxygen species (ROS), nitric oxide (NO) and lipid molecules etc. Until recently, these studies have predominantly focused on the nucleus, cell wall and their associated immune components, including activated kinase signaling and transcriptional reprogramming (Lu and Yao, 2018). Apart from the cell wall, cell membrane and nucleus, there are other organelles in the cells which are also found actively contributing for effective immunity. One among them is, chloroplast, beyond its central position in oxygenic photosynthesis and primary metabolism it integrates, decodes and responds to environmental signals. It is involved in the synthesise of phytohormones and a diverse range of secondary metabolites, combined with retrograde and reactive oxygen signalling, thereby grabbing capacity to perceive and respond to biotic stresses.

**Chloroplast signals modulating defense responses**

During plant defence, recognition of PAMPs by PRRs activates plasma membrane-localized NADPH oxidase (Zhou *et al.*, 2019) and apoplasmic type III peroxidases generating, Reactive oxygen species (ROS).



**Fig 1: Reactive oxygen species (ROS) and calcium signaling pathways during plant immunity**

Relating to this, ROS generation is also observed in chloroplast by oxygen reduction during electron transport and by oxidase enzymes in peroxisomes (Smirnoff and Arnaud, 2019). The prominent routes for cROS generation are oxygen photoreduction at PSI (Mehler reaction) and possibly via the PSII electron acceptor plastoquinone (Vetoshkina *et al.*, 2017). Singlet oxygen ( $^1\text{O}_2$ ), a highly reactive species, is formed in PSII by transfer of excitation energy from triplet-state Chl and is the major ROS involved in ETI-induced lipid peroxidation (Zoeller *et al.*, 2012).

Emerging evidence suggests a biphasic interaction comprising the generation of extremely rapid early PTI-mediated  $\text{Ca}^{2+}$ /ROS signals. This may prime the chloroplast for subsequent transcriptional and physiological reprogramming. Within 20 min of pathogen perception, a  $\text{Ca}^{2+}$  flux is generated in the chloroplast, which is regulated by the thylakoid associated calcium-sensing protein (CAS). Pathogen perception might be signaled to the chloroplast by a MAPK cascade, direct transfer of calcium from the cytosol to the chloroplast and thus activating downstream retrograde signaling to the nucleus (Stael *et al.*, 2015). PTI triggers certain plasma membrane (PM) components, encoding both an N-myristoylation site and a chloroplast transit peptide signal, to relocalize to chloroplasts enhancing PTI and mechanistically linking PM and chloroplast signaling components (Puche *et al.*, 2020).

### Chloroplast proteins with central roles in immunity

Calcium-sensing protein (CAS) is phosphorylated in a calcium-dependent manner, implicating involvement of chloroplastic kinases in CAS signaling.  $\text{Ca}^{2+}$  flux is generated in the chloroplast after perception of pathogen, followed by activation of CAS and these changes in  $\text{Ca}^{2+}$  are necessary for callose deposition and stomatal closure possibly via chloroplast-derived ROS, which upregulate nuclear encoded defense-related genes and largely suppress chloroplast-related genes, such as those associated with photosynthesis and plastid sigma factors and thus CAS appears to mediate the generation of Retrograde Signalling (Stael *et al.*, 2012).

### Chloroplast-derived fatty acids and lipids in plant defense

JA and AzA are derived from FAs present on chloroplastic membrane lipids, highlighting the importance of chloroplastic lipids in signaling. It also act as major site for the synthesis of plant hormones like salicylic acid, abscisic acid indirectly involving in the generation of plant defence against biotic and abiotic stress.

### Chloroplast-to-Nucleus Retrograde Signaling

Chloroplasts are a central hub in plant metabolism, enabling them to act as environmental sensors and communicate via a diversity of retrograde signals to the nucleus that act to redirect nuclear gene expression via retrograde signaling such that it enhances transcription of those genes which are involved in generation of signals that activate defense thereby restricting the spread of the pathogen at the site of infection.

### CONCLUSION

The chloroplast is a complex and a critical hub connecting plant defense responses to primary anabolic functions. Finally, identifying the chloroplast targets of effectors and characterizing their interaction will be challenging but will provide important insights into how pathogens have evolved to target chloroplast components. Collectively, a better understanding of Chloroplast immunity might help in developing more resilient crops.

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