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Unravelling the role of Chloroplasts in plant growth and innate immunity

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Introduction

The chloroplast is a vital component of photosynthetic cells in cyanobacteria, algae, and higher plants, since it is the organelle in which photosynthesis takes place. Chloroplasts are large plant cell organelles bounded by a double-celled composite membrane with an intermembrane space, called the chloroplast envelope. In addition to the inner and outer membranes, chloroplasts have a third internal membrane system, known as the thylakoid membrane, which is extensively folded. This thylakoid membrane divides the stroma, which lies inside the envelope but outside the thylakoid membrane, and the thylakoid lumen.

Chloroplast role in plant innate immunity

Plants undergo an increased demand for photosynthesis during the interaction with pathogens, as the biosynthesis of pro-defense molecules and, more generally, the induction of defense responses requires energy that is provided through photosynthesis. Moreover, virulent pathogens feed on plant carbon compounds, and some of them are able to use plant transporters of the SWEET family to promote sugar efflux, further increasing photosynthesis demand in host cells. However, instead of increased photosynthesis, several reports have revealed suppression of photosynthetic functions in infected plants, perhaps reflecting an active plant response to shut down carbon availability and limit pathogen growth or to favor the establishment of defense over other physiological processes, including photosynthesis, during pathogen attack. Along these lines, the chloroplast is emerging as a very dynamic signaling compartment that is able to sense perturbations (biotic and abiotic stresses) at the subcellular level and to integrate a multitude of intracellular signals in order to communicate those perturbations to other organelles.

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The chloroplast, together with the nucleus, cell membrane, and endoplasmic reticulum (ER), plays a critical role during the establishment of plant immunity against microbial attack and, in this context, the importance of efficient interorganellar signaling to achieve a synchronized whole-cell response during plant defense responses is becoming increasingly evident. The orchestration of this intracellular signaling is achieved by the action of the chloroplast as a receiver, an integrator, and a transmitter of specific signals that co-ordinate expression of nuclear and plastid genomes in order to sustain homeostasis. Plants are sessile organisms lacking an adaptive immune system. Nonetheless, they have developed a multilayered defense system that effectively protects them from a wide range of pathogens, including bacteria, viruses, and fungi. The immune system of plants can be divided into two layers of defense responses. The first line of defense is activated by the detection of conserved pattern-associated molecular patterns (PAMPs), by pattern-recognition receptors (PRRs), leading to PAMP-triggered immunity (PTI), a basal immune status effective against a broad spectrum of pathogens.

The chloroplast: a major production site of pro-defense molecules

Chloroplasts play a central role in plant immunity by hosting biosynthesis of several key defense-related molecules, including hormones and secondary messengers such as calcium and ROS SA biosynthesis and accumulation are tightly regulated since constitutive SA accumulation has negative impacts on plant fitness. SA biosynthesis is triggered during PTI and ETI, upon recognition of PAMPs and effectors, respectively. Plants synthesize SA through two distinct enzymatic pathways: the isochorismate (IC) and the phenylalanine ammonialyase (PAL) pathways. Both pathways commonly utilize chorismate, the end-product of the shikimate pathway, to produce SA, but the IC pathway, which is operative in plastids, is the predominant source of both basal and pathogen-induced SA production in Arabidopsis.

SA is a key signalling molecule in resistance against biotrophic and hemibiotrophic pathogens, although it has also been shown to be involved in the response to necrotrophic pathogens. SA plays a primary role not only in local PTI and ETI responses but also in systemic defense signalling during systemic acquired resistance (SAR), a long-lasting and broadspectrum induced resistance to secondary infection that follows the onset of local defenses.

In addition, SA is a central regulator of defense responses by crosstalk with other hormone signaling pathways in order to fine-tune plant responses with the minimal fitness cost (Microbial effectors are able to interfere with the production/function of prodefense molecules in the chloroplast Consistent with the importance of a balanced production of pro-defense molecules during plant–pathogen interactions, pathogens have developed sophisticated molecular mechanisms to subvert their biosynthesis and subsequent signaling for their own benefit. The central role of hormones during plant–pathogen interactions is highlighted by the significant number of pathogenic microbes that are able to produce hormones or hormone-mimicking molecules to disturb hormone homeostasis and cause disease.

Conclusions

The chloroplast plays a central role in energy production, redox homeostasis, and retrograde signalling to the nucleus that, we now know, collectively contribute to the outcome of the plant immune response. Plant cells rely on the integrated production and delivery of defence-related signals and molecules through different organelles to mount an efficient response to pathogen attack. In addition, organellar production of pro-defence molecules determines gene expression changes in the nucleus, and vice versa. Gaining knowledge on the organization and regulation of this interorganellar crosstalk during plant immune responses is an important task for future research.