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Programmed Cell Death in Plants

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Abstract

Programmed cell death (PCD) is an essential process required to perform vital functions in plants. PCD processes are expressed as inherent part of development in various cell types or tissues and are also triggered in response to various biotic and abiotic stresses. The two major types of PCD are Developmentally controlled PCD (dPCD) and Pathogen- triggered PCD (pPCD) which occurs through different mechanisms with similar components are discussed in this article.

Keywords: programmed cell death (PCD), developmentally controlled PCD, pathogen- triggered PCD, apoptosis, necrosis

Introduction

Programmed cell death

- Sequence of events leading to controlled and organized destruction of the cell
- Physiological and genetically controlled cell death process involved in selective elimination of unwanted cells
- Plays important role in defence and development in plants

Two distinct forms of cell death as described by Kerr et al., 1972:

Apoptosis:

- Characterized by cell shrinkage, nuclear condensation and fragmentation
- Eventually the breakup of the cell into 'apoptotic bodies'

Necrosis:

- Uncontrolled form of cell death
- Often follows overwhelming cellular stress
- Cell is unable to activate its apoptotic pathways
- Swelling of cells is the defining feature of the morphological change.

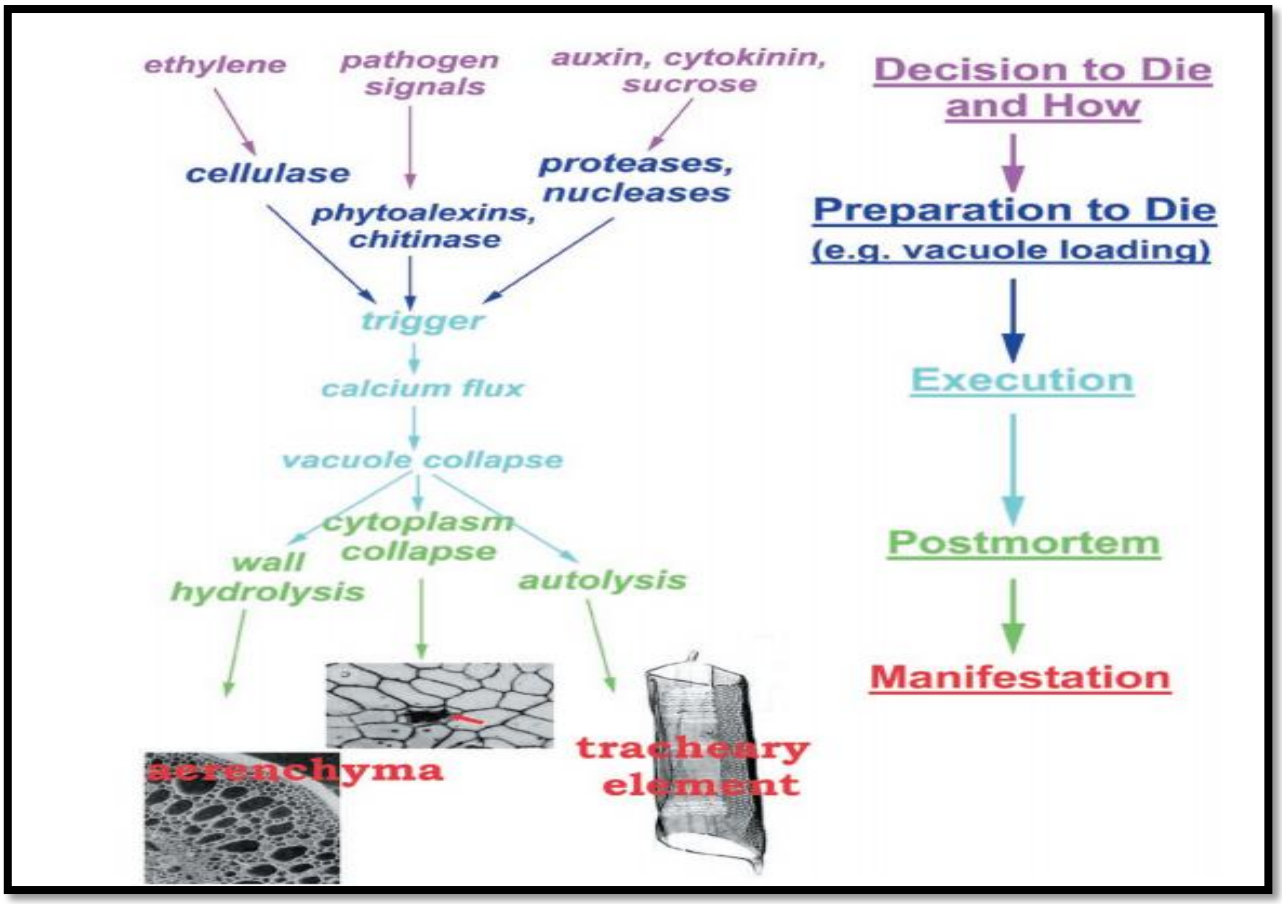

Fig.1 mechanism of PCD in plants

Important functions played by Cell death in plant development:

- Removes cells and recycles many important nutrients of the cell like carbon, nitrogen and phosphorous.
- Sculpting tissues like lysigenous aerenchyma, aleurone layers during germination, flower primordia during floral abortion
- Initiation of hypersensitive response and self-eliminated of cells invaded by pathogens
- Terminal differentiation of tissues like the formation of vessel members and tracheids
- Cell death as a coping mechanism to abiotic stresses

PCD plays important role in plants mostly in 2 ways; as

1. Inherent part of development (dPCD)

2. Response to biotic and abiotic stresses (pPCD)

Developmentally controlled PCD (dPCD):

- Occurs during vegetative and reproductive development
- Final differentiation step/ ends vital function of senescing, not required cells/ storage function.
- Morphologically characterized by vacuolar type of cell death.

Pathogen- triggered PCD (pPCD):

- Elicited on host plant by invading agents.
- Morphologically characterized by necrosis and vacuolar pcd.

The molecular regulation of PCD:

Hormonal signaling in PCD

dPCD	pPCD
• Different phytohormones like jasmonic acid, ethylene, auxin and strigolactones are involved in dPCD signaling, exact networks still unknown. • Ethylene is best-characterized. • Eg. Ethylene contributes to the elimination of the persistent synergid via cell fusion and nuclear degradation, terminating pollen tube attraction in *Arabidopsis.*	• Salicylic acid is strictly required for the establishment of pPCD. • Tight regulation of positive feedback loops between SA and ROS is essential to ensure rapid amplification of defense responses. • Eg. *Phytophthora parasitica* produces a toxin that promotes auxin accumulation at infection sites, resulting in inhibition of SA-mediated cell death and increased pathogen growth.

Factors triggering PCD:

dPCD

- Several cellular signals, including calcium fluxes, accumulation of reactive oxygen species (ROS), and cytoplasmic acidification are important in PCD triggering
- High levels of ROS can kill a cell directly by causing membrane leakage, whereas lower levels of ROS can have diverse signaling functions

pPCD

- Cytoplasmic immune receptor-mediated recognition at the site of attack is the main pPCD trigger during plant-biotrophic/hemibiotrophic pathogen interactions.
- Membrane-associated immune receptor- like kinases (RLKs) also regulates cell death.
- Apoplast is the source of many potential pPCD triggers like RLK ligands, ROS, nitric oxide (NO) and proteases.

Regulation and execution of PCD:

dPCD

- Upon triggering signals, PCD execution and post mortem corpse clearance is initiated through activation of a multitude of lytic enzymes activated or released from safe storage compartments to degrade cellular components.

- Genes like BFN1 are involved in execution of dPCD. For eg. in the Lateral Root Cap of Arabidopsis, BFN1 is responsible for DNA degradation, as

pPCD

- Transcriptomic meta-analysis in pPCD identified a set of genes most of which are involved in defense, rather than specifically in pPCD. best understood TF promoting pPCD and defense responses - Arabidopsis MYB30, which is involved in the SA amplification loop that controls pPCD.

- Calcium is an important regulator that contributes to triggering pPCD ensuring its timely and controlled execution.

the bfn1 mutant exhibits non-degraded nuclear remnants at the root surface. BFN1 protein is released from the endoplasmic reticulum (ER) upon PCD initiation.

- Nucleases and proteases are also involved in PCD execution and corpse clearance. For several proteases, caspase-like activities were found, for instance vacuolar processing enzymes (VPEs) or certain subunits of the proteasome.

- Metacaspases (MCs), have also been implicated in dPCD. Eg. In spruce suspensor, mcII-Pa activates autophagy, which is necessary for PCD execution and prevents the switch to a necrotic form of cell death.

- Autophagy can be a positive or negative regulator of pPCD depending on the pathosystem.
- Several caspases and metacaspases also play important role in pPCD. The Arabidopsis metacaspase AtMC1 acts synergistically with autophagy to promote pPCD whereas Wheat metacaspase4(TaMCA4) overexpression enhances pPCD caused by effector-mediated recognition of the hemibiotrophic fungus *Puccinia striiformis* and contributes to disease resistance, whereas its silencing causes the opposite effect.
- Equally important as positive regulation for pPCD establishment are negative regulators to confine the damage to cells destined to die. Autophagy and catalases have been shown to prevent runaway pPCD.

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