Programmed Cell Death in Fungus–Plant Interactions

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I. Introduction

Apoptosis was originally defined in mammals, where it plays a major role in controlling normal development. Apoptosis and several other forms of programmed cell death (PCD) have since been defined in metazoan as well as in plants, fungi and even in bacteria (Bredesen et al. 2006). For simplicity, when referring to cell death processes in plants and fungi we use the terms apoptosis or PCD throughout this chapter.

Hypersensitive cell death (HR) is a plant resistance response in which spreading of incompatible pathogens is restricted to a small number of plant cells. A hallmark of HR is appearance of small necroses that result from the local death of the host cells. Cell death observed during HR is preceded by enhanced production of reactive oxygen intermediates (ROI) and has typical markers of apoptosis. PCD is also observed during other types of plant–pathogen interactions including non-host as well as in compatible interactions. In some systems PCD is necessary for development of plant resistance, whereas in others it is harmful to the plant. Moreover, various pathogens developed ways to overcome, or even manipulate the plant PCD machinery for their advantage.

Apoptosis is also emerging as an important mechanism in fungi. Yeasts and filamentous fungi undergo cell death with classic markers of metazoan apoptosis during various stages of development. PCD is observed in fungi during vegetative incompatibility, in sexual and asexual reproduction, at stationary phase, and in aged cultures. Homologs of mammalian apoptotic genes have been identified in fungi, supporting a conservation of apoptotic machinery between mammals and fungi. Several recent studies also imply that fungal PCD might be involved in mediating fungus–plant interactions. In this chapter we review the literature on PCD in plants and fungi and the role it may play in mediating fungus–plant interactions.
II. Apoptosis

A. Apoptosis in Metazoan Organisms

Apoptosis is one of the main types of programmed cell death in multicellular organisms; it involves an orchestrated series of biochemical events leading to a characteristic cell morphology and death. Apoptosis is associated with maintenance of cell homeostasis, elimination of damaged cells, aging and differentiation, as well as the adaptive responses of cells to biotic and abiotic stresses (Danial and Korsmeyer 2004; Green 2005). Apoptosis is distinguished from necrosis by several morphological and cytological characteristics of the dying cells. Necrosis occurs by cell perturbation and usually provokes an inflammatory response and eventually cell lysis. Apoptosis is carried out in an orderly process; extracellular or endogenous signals trigger a chain of cellular responses that lead to non-inflammatory cell death. Apoptotic cells develop typical markers, including cell shrinkage, plasma membrane blabbing, chromatin condensation, specific DNA degradation (resulting in DNA laddering), swelling of the outer mitochondrial membrane, externalization of phosphatidylserine and formation of small vesicles from the cell surface also known as apoptotic bodies. At the end of the apoptotic response, apoptotic bodies are rapidly engulfed by phagocytes and adjacent cells and the cell content is recycled (Gozuacik and Kimchi 2007; Wilfried 2004).

1. Apoptotic Pathways

Apoptosis can follow two general routes, known as the extrinsic and intrinsic pathways. The extrinsic pathway is initiated by extracellular ligands, such as Fas and tumor necrosis factor (TNF), toxins, or other external signals that bind and activate death receptors on the cell membrane. The intrinsic pathway can be activated by cell damage or during specific developmental stages. Mitochondria play a central role in activation and regulation of the intrinsic pathway (Green 1998; Kroemer et al. 2007; Wang 2001). At the biochemical level apoptosis initiated by either pathway can be attributed to the activation of caspasases, a group of cysteine proteases that are the executors of apoptosis in mammals and other metazoan organisms (Reed et al. 2004). The intrinsic and extrinsic apoptotic networks include unique as well as common components. In the extrinsic pathway, activated death receptors belonging to the superfamily of cysteine-rich tumor necrosis factor receptor (TNFR) recruit adaptor proteins and pro-caspase 8 molecules, forming a death-inducing signaling complex (DISC) at the plasma membrane. DISC formation activates pro-caspase 8, which then acts to cleave and activate downstream caspases, including caspase 3 (Fig. 12.1). Activation of the intrinsic pathway causes release of certain mitochondrial proteins, which associate with and activate downstream components of the apoptotic machinery. Cytochrome c that is released to the cytosol binds apoptosis-inducing factor (Apaf1), which in

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Fig. 12.1. Extrinsic and intrinsic apoptotic pathways. The extrinsic path- way is mediated by membrane death receptors. The intrinsic pathway is mediated by mitochondria. Only major regulators are shown. Homologs of boxed proteins have been identified in fungi.