Plant Science 197 (2012) 114–121

Contents lists available at SciVerse ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review

A comparison between nuclear dismantling during plant and animal programmed cell death

Fernando Domínguez, Francisco Javier Cejudo*

Instituto de Bioquímica Vegetal y Fotosíntesis, Universidad de Sevilla and CSIC, Avda Américo Vespucio 49, 41092 Sevilla, Spain

ARTICLE INFO

Article history:
Received 9 May 2012
Received in revised form
14 September 2012
Accepted 25 September 2012
Available online 2 October 2012

Keywords:
Apoptosis
Plant
Programmed cell death
Nuclease
Nuclear dismantling

ABSTRACT

Programmed cell death (PCD) is a process of organized destruction of cells, essential for the development and maintenance of cellular homeostasis of multicellular organisms. Cells undergoing PCD begin a degenerative process in response to internal or external signals, whereby the nucleus becomes one of the targets. The process of nuclear dismantling includes events affecting the nuclear envelope, such as formation of lobes at the nuclear surface, selective proteolysis of nucleoporins and nuclear pore complex clustering. In addition, chromatin condensation increases in coordination with DNA fragmentation. These processes have been largely studied in animals, but remain poorly understood in plants. The overall process of cell death has different morphological and biochemical features in plants and animals. However, recent advances suggest that nuclear dismantling in plant cells progresses with morphological and biochemical characteristics similar to those in apoptotic animal cells. In this review, we summarize nuclear dismantling in plant PCD, focusing on the similarities and differences with their animal counterparts.

Contents

1. Introduction

Programmed cell death (PCD) is a process of organized destruction of cells that maintains cellular homeostasis and is essential for the successful development of multicellular organisms [1]. PCD is an important process in plants, as in other multicellular organisms, not only for development [2], but also as a mechanism of immunity against pathogen attack [3]. Plant developmental cell death affects to determined cell types at precise stages of development and is characterized by the rupture of the vacuolar tonoplast and subsequent release of hydrolases, which degrade the cellular content and, in some cases, the cell wall. Cell death in biotic stress depends of the type of pathogens, but free radicals seem to exert an important function [4].

The plant cell has peculiar characteristics, most notably the presence of the cell wall and vacuoles, which suggest that the process of PCD takes place with different morphological features from apoptosis of animal cells. Indeed, most of the morphological features of mammalian apoptosis are not found in plant cells undergoing PCD and, thus, it has been proposed that cell death in plants does not take place by the process of apoptosis; however, the degree of conservation of plant and animal cell death programmes is at the moment a matter of debate [4]. The notion that plants seem to have evolved different mechanisms for PCD is reinforced by the biochemical analyses of the components involved in the execution of cell death in different plant systems. Despite

* Corresponding author. Tel.: +34 954489511; fax: +34 954460065.
E-mail address: fjcejudo@us.es (F.J. Cejudo).

0168-9452/$ – see front matter © 2012 Elsevier Ireland Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.plantsci.2012.09.009

intense search, caspases have not been found in plants whereas they are the most characteristic proteases executing apoptosis in animal cells. Still, there are caspase-like proteases involved in plant PCD [5]. Analyses carried out in different plant systems have identified several types of proteases involved in cell death, which include metacaspases [6], subtilisin-like proteases [7], and vacuolar processing enzymes [8]. Therefore, both morphological and biochemical characteristics suggest that plants and animals have developed different strategies that perform cell death.

The study of PCD has been a major field of research in different animal model systems not only because it is an essential process to understand development, but also because deregulation of PCD causes alterations of the cellular homeostasis, which have important implications associated with diseases, including cancer or neurodegenerative processes [9]. At the morphological level, animal PCD takes place by two well-established mechanisms, apoptosis and necrosis [10]. Apoptosis is characterized by active plasma membrane blebbing and cell fragmentation, forming the so-called apoptotic bodies, which are eventually engulfed by phagocytes. In parallel, the nucleus undergoes dramatic modifications, which include disorganization of the nuclear envelope, chromatin condensation and internucleosomal degradation of DNA in fragments of 180–200 bp and multimers of it, forming a characteristic ladder, which constitutes a hallmark of apoptosis [11]. In contrast, necrosis is characterized by the rupture of the plasma membrane and the consequent degradation of intracellular contents. Necrosis lacks the morphological features of apoptosis, notably the formation of apoptotic bodies. Increasing attention has been devoted to autophagy, a process of cell self-digestion in which cellular components are engulfed in vesicles, called autophagosomes, prior to their degradation by lysosomes. It is well-established that autophagy has pro-death functions, but this process may also have pro-survival functions, and the relationship of autophagy with apoptosis is still the subject of intense debate [12].

The nucleus is the major target of the cell degradation machinery at the onset of PCD. In apoptotic animal cells, the nucleus undergoes a massive reorganization, which includes the condensation of chromatin and internucleosomal fragmentation of DNA [11]. Condensation of chromatin has also been described in different plant systems. This is the case of nuclei from nucellar cells undergoing PCD during wheat grain development, the chromatin of which condenses in a morphologically similar manner as occurs in apoptotic animal cells [13]. Similarly, DNA laddering is also a hallmark of PCD in different plant systems such as pea carpel senescence [14]. However, it should be noted that both chromatin condensation and DNA laddering are not as consistent PCD markers in plants as they are in animal cells. Therefore, despite the clear morphological and biochemical differences of PCD in plants and animals, the phase of nuclear dismantling seems to have similarities in both types of cells. Indeed, factors involved in nuclear dismantling from plant cells are able to induce apoptotic morphology and DNA fragmentation in human cells [15], which suggests the possibility of common mechanisms in PCD of cells from both kingdoms, at least at the stage of nuclear dismantling.

In this review, we will summarize the current knowledge of the process of nuclear dismantling during PCD in plant systems, discussing the similarities and differences with the process in animal systems.

2. An overview of nuclear dismantling in animal cells

The content of the nucleus, the nucleoplasm, is separated from the cytoplasm by a complex membranous nuclear envelope formed by outer and inner nuclear membranes, which define the perinuclear space. The nuclear envelope is penetrated by nuclear pore complexes that mediate the nucleo-cytoplasmic interchange in both directions [16]. The nuclear matrix at the internal side of the nuclear envelope acts as a skeleton defining nuclear size and shape. Several nuclear membrane proteins localized to the inner side of the nuclear envelope provide binding sites for chromatin and nuclear matrix in animals and plants. In animal cells the nuclear matrix is composed of lamins and lamin-associated proteins [17], nuclei of plant cells lack this structure, with scaffold and structural support exerted by coiled-coil proteins [18].

Morphological and biochemical analyses have led to considerable advances of our knowledge of nuclear dismantling during animal apoptosis [11]. The protein profile of the nucleus in cells undergoing apoptosis is modified by the appearance of transcription factors, protein kinases, proteases and DNases, among other proteins. These proteins are probably translocated from the cytoplasm, as schematically shown in Fig. 1. One of the earliest events taking place during nuclear dismantling is the proteolysis of matrix attachment region-binding proteins, which anchor chromatin to the scaffold [19]. This limited cleavage may open nuclease sites on the chromatin structure allowing fragmentation of DNA, which facilitates the subsequent proteolysis of the bulk of nuclear matrix proteins (Fig. 1). Several membrane proteins localized to the inner side of the nuclear envelope, such as lamin B receptor, lamin-associated polypeptide 2α and nucleoporin Nup 153, are connected to chromatin. The cleavage of these proteins promotes the detachment of chromatin from the nuclear envelope, which results in nuclear pore clustering. Finally, it has been speculated that cleavage of components of the nuclear pore complex and the nuclear transport machinery may stimulate an increase in nuclear pore permeability, facilitating protein translocation from the cytoplasm into the nucleus [19].

Post-translational modifications of nuclear proteins seem to have an important function in nuclear dismantling during apoptosis. Histones H2, H3 and H4, lamins and HMGA1a protein are hyperphosphorylated, whereas histone H1 is dephosphorylated just before DNA fragmentation [19]. It is worth comparing nuclear envelope disassembly during mitosis and apoptosis because disorganization of this structure may share common mechanisms in both processes. Nup98, a peripheral nucleoporin localized on both sides of the nuclear envelope, contains 13 phosphorylation sites that are successively phosphorylated by mitotic kinases, driving nuclear pore complex disassembly and nuclear envelope permeabilization during mitosis [20]. Hyper-phosphorylation of Nup98 and other nucleoporins also seems to have a key regulatory role in apoptosis. The post-translational modifications of nuclear proteins are presumably important for three events: chromatin condensation, accessibility of nucleases to DNA and the breakdown of the lamina.

3. Similarities in nuclear dismantling in animal and plant cells undergoing PCD

As mentioned above, animal cell nuclei undergo very characteristic morphological changes during apoptosis. The nucleus becomes fragmented and the fragments move to apoptotic bodies, which are subsequently phagocytosed by macrophages, parenchymal or neoplastic cells and degraded by phagolysosomes [21]. Therefore, the nucleus of apoptotic animal cells becomes degraded inside another cell. In contrast, in plant cells undergoing PCD, the nucleus is not degraded in another cell, which is a clear difference of nuclear dismantling between plant and animal cell death.

Despite these differences, nuclear extracts of etopoxide-induced apoptotic human cells triggered apoptotic morphology of plant cell nuclei [15]. In the same way nuclear extracts from wheat nucellar cells undergoing PCD induce apoptotic morphology