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Autophagy - A Plant Survivor in Stress?

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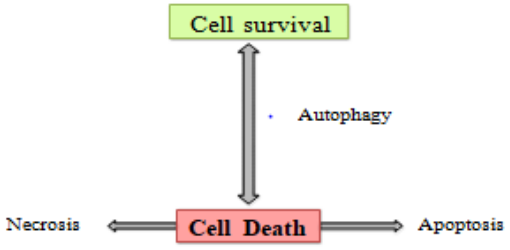
Abstract

Autophagy is a very crucial process in plants and is highly conserved in eukaryotes. Autophagy involves the recycling of cell component to maintain cell homeostasis but also help plants to cope up with adverse environmental stimuli. In this review we have discussed about how autophagy plays role of cell survival in different stress conditions leading to nutrient starvation in plants and also how autophagy can delay apoptosis or programmed cell death in plants.

Keywords: Autophagy; Abiotic stress; Apoptosis; Necrosis

Introduction

Cell Death in general refers to the process of aging. Cell Death is necessary to maintain the homeostasis of the body by removing unwanted or harmful cells that can lead to various diseases. Morphologically cell death is classified in three types: Apoptosis or Type I, Autophagic or Type II and Necrosis or Type III cell death (1). All these cell death process occurs through distinct mechanism but are also involved in regulation of one another. Increase in autophagy is generally related to cell survival but in certain extreme condition it also results in cell death. The three broad types of cell death is shown in (Figure 1).



Apoptosis and Autophagy are two distinct mechanism which are involved in the maintenance of organelles and proteins within a cell. Apoptosis and Autophagy can be induced within same cell in a sequential manner in response to various stress conditions. Number of cells in multicellular organaism are highly regulated by regulating cell division and cell death. Apoptosis is a process of programmed cell death in which unwanted cells are removed to ensure the quality of cells during embryonic as well as normal development. Apoptosis can be induced by various factors like bacterial infection, harmones, toxins, growth factors, Oxidative damage by reactive oxygen species etc. (2,3,4,5,6,7).

Autophagy is a cell survival process which protects cells from undergoing autophagy. Increased autophagy allows cell survival in nutrient deprived cells (8,9) as well as from various apoptotic stimuli and inhibit apoptosis (10). But in some cases Autophagy can also result in Type II programmed cell death (11,12,13). Apoptosis involves activation of cysteine-aspartic acid proteases called caspases that target proteins at specific aspartic acid sites (14,15,16) whereas autophagy is caspase independent (12).

Necrosis occurs when the cell are damaged by harmful factors such as injury or toxic materials. In necrosis plasma membrane is ruptures and lysis of cell occur (17,18) which also cause inflammation in the neighbor cells and tissues (19). Necrosis is also not associated with activation of caspases but it mediates cell death in response to damage (20,21). Release of HMGB1 is the pro inflammatory signal in necrotic cells (22).

Autophagy in Plants

Autophagy means self eating. It is a process which involves degradation and recycling of cellular components. Autophagy is a highly conserved process which is found in all the eukaryotes. Autophagy plays very important role in plant development and also helps plants to adapt and cope with different types of biotic and abiotic stress. Autophagy degrades the cellular components like cytoplamic organelles, proteins and other macromolecules and provide energy for cell survival and maintenance. In mammals three types of autophagy i.e. Microautophagy , Macroautophagy and chaperone mediated autophagy are found.

Microautophagy term was coined by Christian de duve. Microautophagy involves direct engulfment of harmful or toxic cargo in lysosomal membrane. Microautophagy can takes place by three means i.e. with lysosomal protusion, with lysosomal invagination or by endosomal invagination.

Macroautophagy is well studied in plants. In contrast to microautophagy, macroautophagy involves an intermediate component named autophagosome. Core Autophagy related genes (ATG) are involved in this process i.e. from its induction to the formation of autophagosomes. Autophagosomes are double membrane vesicles that fuse with lysosome to form

autolysosome and start autophagy. Molecular basis of Macrautophagy or simply autophagy was discoverewd by Professor Yoshimori Ohsumi who also identified several Autophagy related genes (ATG). More than 30 ATG genes have been reported in Plants. All these ATG genes work collaborately in Autophagy.

Chaperone mediated autophagy is highly selective in recognizing and degrading cytosolic proteins (23) and is unique in mammalian cells . CMA involves target recognition through heat shock chaperone protein Hsc70

(24) . HSC70 recognizes the substrate bearing pentapeptide KFERQ-like motif (25,26). CMA involves direct translocation of substrate protein to the lysosome through LAMP2A receptor, a splice variant LAMP2 gene (27).

Autophagy is a catabolic process that is present in all eukaryotic cells and is important for cell homeostasis (28). This process is physiologically important in plants and is upregulated in any stress condition for plant survival (29). Mainly three types of Autophagy is reported in plants: micro-, macro- and mega autophagy. Out of three types , Macroautophagy is best studied and described in plants (30,31). Plant as a sessile organism has to face many environmental stress in form of nutrient deprivation, biotic and abiotic stresses. Autophagy helps plants to cope up with these stress condition within minutes by giving quick response to damage condition (32).

Molecular basis of plant autophagy was discovered by Professor Yoshinori ohsumi. He and his colleagues discovered several autophagy related genes (ATG) in yeast (33). Autophagy related genes are responsible for the regulation of autophagy process. More than 32 ATGs are involved in yeast autophagy (34) and homologues of these genes are also discovered in other plants species. Autophagy gene defective plants shows reduced growth, early senescence, reduced seed production and hypersensitivity to biotic and abiotic stresses. (35,36,37).

Unlike bulk degradation of cyplasmic compounds selective autophagy is defined as selective degradation of compound or protein through various receptor or adaptor proteins (38,39). ATG8 is reported to be involved in selective autophagy (40). ATG8 contains a ubiquitin interacting motif site (UIM) for autophagy receptors which helps ATG8 to control Autophagosomes size (41,42). These different sizes of autophagosomes can selectively degrade specific type of protein or call components like peroxisomes,chloroplast, ribosomes etc.

Autophagy: An important factor in plant survival

In this changing environment plants have to remobilize the nutrients efficiently to support its growth. Leaf senescence is one major process to remobilize and recycle plant nutrients from senescence leaf to the growing one and supports its growth (43). In plants nitrogen is the major nutrient and in nutrient limiting conditions remobilization of nitrogen becomes very important for plants. Efficient nitrogen remobilization can also decrease use of nitrogen fertilizers in agronomically important crops as it increase its yield (44,45,46,47). Autophagy genes are upregulated in plants during nutrient starvation and many reports in arabidopsis supports this (48,49,50,51,52,53). Studies in crop plants have also showed the importance of autophagy in crop plant yield during starvation or nutrient limiting conditions (54).

Autophagy plays an important role during seed and reproduction in normal conditions also apart from nutrient limiting and senescence condition. In Arabidopsis atg genes were upregulated during seed development (55) and endosperm development in maize (56). Autophagy gene atg6 is associated with pollen germination (57,58,59)). Under long day condition autophagy induced programmed cell death was observed in Wheat florets (60). In rice atg7 and atg8 were shown to play role in male sterility (61). Thus providing evidence for autophagy role in pollen and anther development (62). Autophagy also plays role in Xylem (63,64) and Phloem development (30,65). Atg5 mutant in Arabidopsis shows lower number of xylem cell (66).

Autophagy plays key role in immune response during biotic stress (67,68,69). Silencing of ATG8 in cassava (70) and wheat (71) shows increased disease susceptibility. WRKY transcription factors have been reported as autophagy regulators of biotic stress in plants (72). It has been reported that autophagy play important role in plant pathogen interactions(73) and provide immunity against necrotrophic pathogens(74,75). Autophagy also plays an important role in symbiotic interactions. An increase in transcript level of PI3K gene was reported after initiation of nodule formation (76).

Autophagy is induced during various abiotic stresses. The major abiotic stress are heat , cold, drought, high salinity, radiation etc. Autophagy gene atg5 and atg7 have been reported to play important role in heat tolerance in crop plants as silencing of these genes reduced autophagy induction under heat condition (77,78). It is also reported that Wrky play role in heat stress(79) and also in induction of autophagy during heat condition (77). Role of autophagy in drought condition is very well studied in plants.upregulation of autophagy related genes have been reported in many plants (80,81,82,83,84,85).

Conclusion

Increasing pollution and population, human beings have put the plants under severe threat for there own advantage and needs. Plants cant escape these environmental threat either by nature or through mankind. In these situation autophagy becomes an important mechanism for plants to overcome these environmental hazards. Autophagy is also a hope for man to understand its mechanism in plant survival so that they can use it for plant improvement especially for crop plant yield in stress conditions either biotic or abiotic.

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