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Review Article

Autophagy in Plants during Nutrient Starvation, Osmotic and Heat Stresses

Huda E. Mahood[1*]
[1]College of Agriculture/ Department of Horticulture University of Al-Qadisiyah, Iraq
*huda.enaya@qu.edu.iq

ABSTRACT

Autophagy is a prosurvivalpathway controlled by specific autophagy genes (Atgs)fort breaking down and self-digestion ofcases of severe components , particularly when exposed to stressors such as senescence, starvation, and hypoxia.Autophagy in plants contributes to growth, reproductive capacity, metabolic processes, senescence, endosperm and grain development, disease safety and microbial tolerance. Various transcriptomic, proteomic and metabolic networks are related to the autophagic response of plants to extracellular and intracellular stressors. Although research on mammalian autophagy is rapidly growing, greater research are required to understand the functions and importance of plant autophagy. All through study, I will explain the effects with plant autophagy research, the types, impacts and biological activities of autophagy in response to starvation, osmotic stress and extra temperatures.

Keywords
Autophagy, Nutrient Starvation, Osmotic, Heat, Stress

Introduction

If plants grow under stress or ageing, they decompose cytoplasmic molecules within the vacuole through a process calledautophagy [1].Autophagy occurs under basal conditions for clearance of unwanted substances and specifically upon exposure to various kinds of environmental stresses such as starvation[2,3].While auto-phagocytosis is activated, its double membrane bearing the nameautophagosome iscreated around the cargo and then attached to the vacuole where it is lysed and recycled [4]. Autophagy is already reported in plants to serve many functions such as resistance to the related biotic and abiotic stresses, degradation of damaged proteins in plants upon exposure oxidative stress and regulated cell death throughout pathogenic immune responses [5,6,7].Autophagy is generally accepted as prosurvival mechanism because it helps in rapid removal of damaged molecules and organelles inresponse to stress conditions [8, 9, 10] and modification of the immune system responseand the resistance of whole virulence or pathogens[11, 12, 13]. Consequently, autophagy can affect largest crop traits such as nutrient starvation tolerance, drought, heat, oxidative and salt stress, and immune response to diseases.Throughout this review, I will describe the characteristics, molecular mechanisms, and roles of autophagy in plant stress reactions.

Types of autophagy and Molecular pathways in plants

Autophagy in plant kingdoms can be divided into three different types: microautophagy, macroautophagy and mega-autophagy [1,14]. Most common molecular pathways may have been generalized as a cytosol-to-vacuole pathways. Microautophagy is marked by only a specific rupture of theirvacuolar membrane (tonoplast) and capture the cellular constituents for digestion [15,16].Microautophagy happens by seed germination in several plantsin order to digested starch granules and protein is stored in vacuoles[6, 17].Microautophagy molecular pathways do not appear to include any of the genes. In contrastmacrophautophagy, autophagy is controlledthrough ATG genes[16]. Macroautophagy has become one of the major type of autophagy through mammals and plants, but is also actually called autophagy. The autophagic pathway is regulated by autophagy-related proteins, which control the initiation, elongation, maturation, and fusion of the autophagosome mostly with the vacuole [18, 19, 20].Morphologically, the plant cargo is engulfed in the formation of new cytoplasmic vesicles resulting from enlargement phages or separate membranes that enclose the autophagosome-forming cytoplasm with a dual-membrane layer.The external autophagosome layer combines with the tonoplastic membrane leading. In the production ofinner vesicles called autophagic bodies. Autophagic membrane disruption produces the the intraluminal components using hydrolysis and recycle vacuoles[20]. In liquid culture and the whole plants, macroautophagy functions are described in reply to sucrose and nitrogen starvation and for several plant species throughout senescence [21, 22]. The third type of autophagy seems to be mega-autophagy typical of its final phase, during development of PCD or even in response to environmental factors[23, 24, 25]. Process begins when vacuolar membrane is permeable or ruptured.This triggers the release of vast quantities of hydrolases into the cytoplasm. Such enzymes absolutely dissolve the cytoplasm [27, 28,26].Typically some certain form of autophagy can happen within the cells on its own, with mega-autophagy following the other 2 kinds [27, 28,26].

Among the genes encoding different proteins associated with autophagy , one subgroup, like ATG1 to ATG10, ATG12 toATG14 and ATG16 to ATG18, as well as the respective specific genes were known it as central autophagosome formation mechanism[29, 30, 31].Identifying many autophagic-associated genes in plants hashelped to understand the process of autophagy. The development and presence of autophagic system in plantations were identified using Transmission Electron Microscopy (TEM) and detected by ATG8 immune response. This ATG8 is considered as main autophagy marker, which is responsible for autophagosome maturation, and fusion with vacuolesfor degradation. ATG8 may also lead to the diversification of common autophagy routes in plants [32, 33, 34, 26].

Autophagy Function During Starvation Stress

Starvation has been considered as the most common abiotic stress in plant to stimulate autophagy. Hypersensitivity with nitrogen and carbon starving was created in plants mostly as major morphology of atg mutants, originally described in Arabidopsis [35, 36, 37, 38],but also shown in maize [39]. All starvation of carbon and nitrogen is reported to trigger autophagy[40, 41].

Under conditions of carbon starvation plants degrade lipids and proteins in to other basic monomeric units and are using them as substitute sources of carbon [42, 43]. Data from Izumi et al . show that autophagy recycling can make a contribution to plant energy. They examined the relevance with autophagy through energy production and growth in Arabidopsis.Autophagy-deficient (atg) mutants demonstrates extra intense phenotypes when the sugar quality was reduced at night due to shorter photoperiods and/or starch-free mutations. Metabolic and transcription analysis results have demonstrated autophagy offers an alternative to sugar to energy production such as amino acids[74].Compared to control plants, starch-free mutations have less free amino acids that act as alternative energy sources as well as sending an electron to just the electron transport chain under carbon starving[42, 43]. More such results indicate also that concentrations of branched chain amino acids, aromatic amino acids and lysine in starchless ATG double mutations were much lower compared with single starchless mutations, results suggest which autophagy seems to be crucial to the source of amino acids throughout carbon starving. Two distinct observations have been noted in other original articles throughout the 6-day-long yellowing leaves of Arabidopsis plants cultivated without sugar, as well as in the four weeks old plant response to increasing darkness[45, 46]. Biochemical tests revealed also that atg mutation plants extracted produced few concentrations of free amino acids and possibly some partial carboxyl acids like malate, fumarate and dehydroascorbate compared to control plants, along with the higher concentration of many carbon compounds like fructose, glucose, and sucrose [45]. A research evaluating atg mutant plants exposed in 10 days with dark found subsequently that atg mutants produced lower levels with branched amino acid like valine , isoleucine and leucine , amino acid aroma (tyrosine) and lysine than wild plants [46]. Interestingly, it was observed which atg mutants produced larger amounts of dehydroascorbate, malate, fumarate and ,2-oxoglutarate however and produced reduced amounts of fructose and glucose.A differences of the carbon metabolites referred to in the two above research might well be related to the difference in age of the plants studied.

Autophagic response to nitrogen starvation was mostly analyzed and a metabolite strategy was used throughout petal leaves with atg-mutant arabidopsis thaliana sixty days old that grow at higher or lower concentrations of nitrogen [47]. Based on the study conducted by Masclaux-Daubresseand other authors, have shown that atg mutants produced the wide group of amino acids, like branched and phenylalanine aromatic amino acids, in addition to active compounds including, methionine, chikimate,glutamate and glutathione irrespective including its a nitrogen requirements used during development. The atg mutants, by contrast, yielded lower quercetins, anthocyanins and hexoses . Importantly, alcohol and aldonic acids of these sugars, including malonate, mannitol, gluconate and sorbitol, collected in atg mutants at larger levels , especially before forming through nitrogen-limiting conditions. Authors hypothesized that also loss of hexoses and the corresponding rise in sugars and acid suggested dysfunction in the atg mutants ofits redox control of sugar components [47]. This research and several others have also identified contortedlipid levels in relation to amino acids and carbohydrates.Metabolite detection of mutants in arabidopsis and rice atg indicatesthe significant role for autophagy throughout cell lipid homeostasis regulation [47, 50]. In mammalian studies of alcohol-induced fatty liver, it was found that enhanced autophagy of lipids (lipophagy) may be cytoprotective mechanism ameliorating the progress of alcohol liver disease [72]. However, more detailed approaches to lipidomy will probably berequired to better understand this type of plant autophagy.

Masclaux-Daubresse suggested a model for the alteration with nitrogen, carbon and redox homeostasis throughoutatg mutants influences the content of anthocyanin and salicylic acid, affecting the response of plants to stress Figure:(1).A model indicates which carbon structure, which derive via phenylalanine to be used for thedevelopment between both SA and anthocyanin is better driven by SA biosynthesis rather than anthocyanin. As cells die, anthocyanin-depleting antioxidants will then enhance oxidative stress and maintain SA output. It is still important to explore the carbon shift between anthocyanin and SA. Therefore, tracing 13C phenylalanine molecules to analyze carbon fluxes in mutants with autophagy would be beneficial [48].

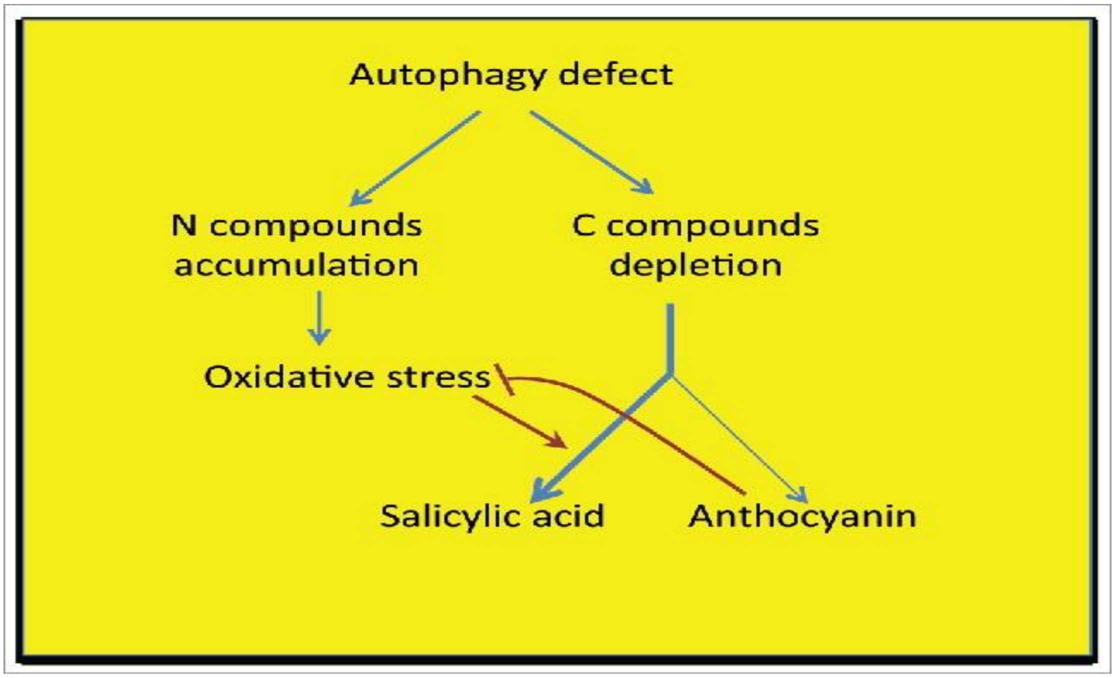

Figure 1. Alteration of the carbon , nitrogen and redox homeostasis in ATG mutants impacts the content of anthocyanin and salicylic acid, affecting the response of plants to stress [48].

Osmotic stress

Osmotic stress, like drought and high salinity, the most popular environmental stress that negatively affects the growth of plants [49, 19]. It is known that 6% of the earth 's land surface and 30% of the earth's irrigated lands were also suffering from high salt concentrations [50]. With climate change, the salinity and drought-prone regions will increase over time.There are some similar features of salt stress and drought stress they have specific regulating mechanisms in plants. Salt stress serves as ionic as well as osmotic stress to plants [51], While these two types of osmotic stress (salt and drought) can enhance ROS accumulation, causing disruption of the membrane, enzyme instability and oxidative protein damage [51]. As seen above, autophagy plays a prominent part in oxidized protein scavenging, indicating that autophagy could be active in the relation to osmotic stress.Autophagy was found to enhance the tolerance of salt and drought stress. For example, in Arabidopsis, mutants atg5, atg7, and RNAi-ATG18a, which apparently were unable to trigger autophagy via the drought stress [51, 52], indicating that autophagy is a mechanism for prosurvival in plants under environmental stressors such as drought conditions. Similar phenotypes in autophagous tomato and wheat plants [53, 54, 55] were also observed. At the other hand, ATG18a's overexpression in apples conferred increased autophagy and drought tolerance, thus promoting a central part for autophagy in the response to drought [56].

Abiotic and biotic stresses will stimulate plant developmentof ROS as signaling components for defense responses[57, 58].One key source of ROS is NADPH oxidase associated with the plasma membrane [59]. NADPH oxidase suppression inhibits autophagy during salt stress and nutrient starvation, not just under osmotic stress in Arabidopsis, indicating that NADPH oxidase-mediated ROS signaling seems to be essential in autophagy caused by salt and starvation, but not for autophagy caused by drought [51].

ROS build-up is also toxic to cells, leading to membrane damage, protein aggregation, and sometimes cell death, although ROS is essential for autophagy stimulation [57, 58].Throughout stressful drought, the side suggested role of autophagy is to improve the number of proteins. By activating ATG genes and inducing autophagy, the transcription factor HsfA1a was found to induce resistance to drought.In tomatoes, the silencing of HsfA1a resulted in increased aggregation with insoluble proteins, whereas the over-expression with HspA1a decreased the insoluble protein levels under drought stress[53]. This role is further confirmed by observing reduced insolubleprotein and less soluble protein oxidation in ATG18a-over-expressing apple lines [56].Ironically, overexpressing ATG18a in apple has also enhanced the antioxidant function during stress from drought. Improved by increasing H2O2-scavenging enzyme activity and increased gene expression in the ascorbate – glutathione (AsA – GSH) cycle, an H2O2 scavenging structure, have been noted throughout ATG18aoverexpressing apple compared to wild type under drought stress[56].

In addition, drought and salt and stress stimulate the expression of ATG genes as well as encourage to development of autophagosomesthat eliminate denatured proteins and damaged organelles, resulting in an improved stress tolerance.

Heat stress

Heat is a vital state of abiotic stress that can induce protein misinformation and denaturation. In normal protein conformations, autophagy plays an important role in clearing misfolded and potentially highly toxic proteins or protein aggregates [60, 61, 62, 63].

In response to elevated temperatures, the research article by zhou et al. provides important data promoting a role throughout heat for autophagy genes stress response in the excremental expression patterns of seven ARB genes (ATG5, ATG6, ATG7, ATG8a, ATG9, ATG10, ATG18a) and NBR1. After 8-ten hours during thermal pressure (45 ° C), when plants being toexhibit symptoms of dehydration, they found ATG and NBR1 genes the greatest increase in transcription grade. They also compared the agitation of the nine gens of the ATG8 gene family as well as observed which even ATG8a, ATG8e, and ATG8h had four to five inductions and urged others supporters of the genes two to three times after 10 hours of thermal stress at 45°C[52].

Temperature stress induced the induction of ATG genes in crop species, particularly in tomatoes and peppers, and enhanced autophagosome formation [64, 65, 66]. The relations between 2-Cys peroxiredoxins and ascorbate in autophagosome formation throughout heat response to stress in tomato plants were examined by Cheng et al.In plants with impaired 2-CP1/2 activities, as well as increased autophagosomal development also with aggregation of oxidized and insoluble proteins, higher transcript levels of autophagy-related genes ATG5 and ATG7 were observed.On the other hand, silencing ATG5 or ATG7 raised the levelof 2-CP transcripts and protein but reduced resistance to heat stress.The 2-CPs thus achieve a crucial functionthroughout tolerance to heat stress in tomatoes[65, 66].The interesting study by Zhai et al. investigated autophagy and cytoplasmic puncta formation (markers of autophagosomes) in two lines of pepper with different thermal tolerance. The frequency of upregulatedCaATG genes was found as well as the increase in puncture area was obviously greater throughout the thermo-tolerant line R9 than in the thermosensitive line B6 genes.These two results (from tomato and pepper) show that autophagy can give plants a heat tolerance [67].

Heat or heat triggered ROS could even produce toxic effects including the aggregation of proteins [57].Abiotic stresses like high heat trigger damage to variouscellular structures and macromolecules like denaturation and aggregation of proteins [68]. It appears that denatured and or impaired cellular proteins are omnipresented by quality control machines for plant cellular proteins and are activated by NBR1 for autophagic degradation.Elevated concentrations of insoluble detergent resistant protein aggregates are developed in autophagy-deficient mutants that are toxic and can cause cell death [52]. Have also shown that most insoluble proteins collect through heat stress in defective autophagy plants in Arabidopsis and tomato [65, 52], suggesting that autophagy can act to remove protein aggregates.

For heat tolerance, the transcription factor WRKY33 is needed at Arabidopsis [69]. Two of WRKY33's Arabidopsis homologues were found in WRKY33a and WRKY33b tomatoes. Silencing has impaired heat tolerance, indicating their heat stress function, either WRKY33a or WRKY33b. In WRKY33a-or WRKY33b-silent plants, heat activation of the autophagy-related genes ATG5, ATG7, NBR1a and NBR1b was affected, noting that WRKY33s could have been beneficial autophagy regulators in tomatoes [65].

Melatonin was found to up regulate severalATG genes and increaseautophagosome formation and subsequent degradation of aggregated proteins under the heatstress [70,73].Melatonin enhances thermo tolerance by encouraging defense of cellular proteins in tomato plants. This endogenous amounts of melatonin increased gradually with some increase temperature. Increased melatonin rates through exogenous application or endogenous manipulation of the two heat-induced photoinhibition in tomatoes through genetic means. In the meantime, melatonin mitigated the rates of heat-induced insoluble protein aggregation and ubiquitisation through triggering heat shock protein expression and autophagy activation, thus conferencing cytoprotective functions [70].

Conclusions

In this review, we gave a brief review on plant autophagy in crop species, specifically under common stressors such as starvation, drought, salt and heat stresses. Global analyzes, including such transcriptome research, were conducted to elucidate ATG gene expression profiles and to Discover unique transcriptional autophagy regulatory systems.In addition, protein profiling and metabolism are being used progressively to study the impact of autophagy on plant growth.However, most problems stay available as well as further studies are required to build a detailed view of plant autophagy and to understand better its regulatory mechanism at the levels of transcription, translation and post-translation. There are, however, few integrative studies currently underway on plant autophagy.The use of etiolated Arabidopsis seedlings mostly as cell line clearly demonstrated the significance of autophagy in early seedling facilities by integrating metabolomic data with proteomic data[71]. In addition, transcriptomic data were embedded with Arabidopsis rosette leaves metabolic data to reveal connection amongboth autophagy, transcription and metabolism in plants and to detect the various impacts resulting from deficient autophagy [47].

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