

# 植物自噬相关基因在响应逆境胁迫中的功能和作用机制

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**摘要:** 自噬是真核生物中进化保守的自我降解机制, 植物细胞自噬不仅在其生长发育过程中发挥重要作用, 而且参与应对各种生物和非生物逆境胁迫。植物可通过自噬降解多余或受损的细胞质物质和细胞器来抵御逆境胁迫。自噬的发生依赖于自噬相关基因(autophagy-related genes, ATGs), 转录因子能够直接结合 ATGs 启动子, 从而激活自噬并调节其转录水平和翻译后修饰。ATGs 还与激素直接或间接互动, 调控植物逆境胁迫应答反应。当受到盐分、干旱、极端温度、营养亏缺和病原菌等胁迫时, 植物 ATGs 被显著诱导, 自噬活性增强, 降解变性和未折叠蛋白质, 从而提高植物抗逆性。本文对植物 ATGs 发现、结构、分类及其在逆境胁迫响应中的作用等方面研究成果进行了综述, 并对其未来研究方向进行展望, 为农作物抗逆性遗传改良提供了基因资源和理论依据。

**关键词:** 自噬相关基因; 自噬活性; 调控机制; 逆境胁迫; 抗逆性

## Functions and mechanisms of autophagy-related genes in plant responses to adversity stresses

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**Abstract:** Autophagy is an evolutionarily conserved self-degradation process in eukaryotes. It not only plays a role in plant growth and development but also is involved in plant responses to biotic and abiotic stresses. Plants can initiate autophagy to degrade the surplus or damaged

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cytoplasmic materials and organelles, thus coping with abiotic and biotic stresses. The initiation of autophagy depends on autophagy-related genes (ATGs). The transcription factors can directly bind to the promoters of ATGs to activate autophagy and regulate their transcriptional levels and post-translational modifications. Furthermore, ATGs can directly or indirectly interact with plant hormones to regulate plant responses to stresses. When plants are exposed to salinity, drought, extreme temperatures, nutrient deficiencies, and pathogen stress, ATGs are significantly induced, which enhances the autophagy activity to facilitate the degradation of the denatured and misfolded proteins, thereby enhancing plant tolerance to adversity stresses. This article summarizes the discovery, structures, and classification of plant ATGs, reviews the research progress in the mechanisms of ATGs in plant responses to abiotic and biotic stresses, and prospects the future research directions. This review is expected to provide the genetic resources and a theoretical foundation for the genetic improvement of crops in responses to stress tolerance.

**Keywords:** autophagy-related genes; autophagy activity; regulation mechanisms; adversity stress; stress tolerance

由于固着生长的特性,植物经常暴露在不断变化的环境条件下,其中包括各种生物胁迫和非生物胁迫。为应对各种胁迫环境,植物通过降解受损或不需要的蛋白质和细胞器以维持细胞稳态<sup>[1]</sup>。自噬(autophagy)是生物中高度保守的自食过程,是指对受损蛋白质和特定化合物进行再循环,激活某些胁迫反应途径<sup>[2]</sup>。自噬被认为是植物适应逆境胁迫的重要机制之一<sup>[3]</sup>。

自噬可分为巨自噬(macroautophagy)、微自噬(microautophagy)和分子伴侣自噬(chaperone-mediated autophagy, CMA)等3种方式<sup>[4]</sup>。其中, CMA只在动物中发现,而在植物中以另一种形式存在,即超级自噬(mega-autophagy)<sup>[5]</sup>。自噬过程主要由自噬相关基因(autophagy-related genes, ATGs)参与完成<sup>[6]</sup>。迄今为止,在真核生物中已鉴定出的ATGs超过40个<sup>[7-8]</sup>,其中一半编码核心自噬蛋白。自噬主要受雷帕霉素靶蛋白(target of rapamycin, TOR)激酶信号通路调控,其过程包括自噬诱导、膜延伸及囊泡成核、自噬体延伸及扩展、物质降解等4个关键步骤<sup>[9]</sup>。TOR通过磷酸化ATG13,降低ATG13对ATG1

的亲合力,从而负调控自噬体形成。在胁迫条件下, TOR受到抑制, ATG13可与ATG1结合,进而促进磷酸化并触发自噬<sup>[10]</sup>。激活的ATG1激酶促进ATG9传递脂质到发育中的自噬体, ATG2/18在此过程中发挥协同作用,在液泡蛋白34(vacuolar protein sorting 34, VPS34)、VPS15以及ATG14和ATG6在内的蛋白复合物作用下与磷脂酰肌醇3-磷酸盐(phosphatidylinositol 3-phosphate, PI3P)共同促进膜的延伸及囊泡成核<sup>[11-12]</sup>。ATG7/10作为类泛素酶类参与ATG5/12/16共轭复合物形成,共轭复合物与ATG3/4/7促进ATG8与磷脂酰乙醇胺(phosphatidylethanolamine, PE)结合,并锚定到自噬体内膜及外膜上,促进自噬体的延伸及扩展。ATG8-PE偶联物和ATG12-ATG5复合物促进自噬体扩张并通过VTI12(vesical transport v-SNARE 12)介导向液泡运动,在液泡水解酶的作用下逐渐降解<sup>[7,13]</sup>。近年来,自噬过程因在植物生长发育和逆境胁迫响应过程中发挥着重要作用而备受学术界关注,也成为植物逆境生物学研究的热点之一。为促进ATGs在作物遗传改良中的功能探

索和应用, 结合本课题组对甜菜(*Beta vulgaris*) BvATGs 家族的研究成果, 本文就植物 ATGs 的结构和分类、调控机制及其在响应逆境胁迫中的作用等方面的研究成果加以综述, 并对其未来研究方向进行展望。

## 1 植物 ATGs 的发现

第一个自噬相关基因 *APG1* (AutoPhaGy1) 是在芽殖酵母(*Saccharomyces cerevisiae*)中被鉴定出来的, 从此开启了自噬研究新篇章<sup>[14]</sup>。随后, 研究人员相继在拟南芥(*Arabidopsis thaliana*)、茄子(*Solanum melongena*)、谷子(*Setaria italica*)和茶树(*Camellia sinensis*)等植物中鉴定到 ATGs 家族成员(表 1)。本课题组采用生物信息学手段, 从甜菜(*Beta vulgaris*)基因组中鉴定出 51 个 ATGs, 根据其拟南芥 ATGs 同源性和系统发育关系, 对其进行逐一命名(未发表数据)。序列分析显示, BvATGs 家族成员

的编码区序列(coding domain sequence, CDS)长度在 255 bp (*BvATG6b*)到 7 404 bp (*BvTOR*)不等。编码蛋白质的氨基酸长度在 84–2 467 aa 之间。分子量(molecular weight, MW)在 10.21 kDa (*BvATG6b*)到 277.30 kDa (*BvTOR*)之间。等电点(isoelectric point, pI)在 4.71 (*BvATG3*)到 9.59 (*BvVTI12a*)之间。蛋白质疏水性(grand average of hydropathicity, GRAVY)在 -0.659 (*BvATG6a-2*)到 0.237 (*BvATG18b*)之间。脂肪指数最高的是 *BvTOR*, 为 99.77; 最低的是 *BvATG6b*, 为 60.36。蛋白质不稳定指数最高的是 *BvATG13b*, 为 74.76; 最低的是 *BvATG6b*, 为 23.42 (未发表数据)。这些结果表明, 不同的 BvATGs 可能存在潜在的功能差异。另外, 不同物种 ATG 成员数量也有所不同。甘蔗割手密种(*Saccharum spontaneum*) ATGs 成员最多, 有 134 个<sup>[36]</sup>; 大麦(*Hordeum vulgare*) ATGs 成员最少, 只有 24 个<sup>[39]</sup>。

表 1 不同植物 ATGs

Table 1 The ATGs in different plant species

Species	Gene name	Gene number	Classification					References
			ATG1/ATG1 3 kinase complex	The ATG9/2/18 transmembrane complex	Phosphatidylinositol-kinase complex	ATG8/ATG12 ubiquitin-like conjugation systems	SNARE	
<i>Arabidopsis thaliana</i>	<i>AtATGs</i>	42	10	10	3	18	1	[15-16]
<i>Solanum melongena</i>	<i>SmATGs</i>	41	10	9	4	16	2	[17]
<i>Setaria italica</i>	<i>SiATGs</i>	37	6	11	4	14	2	[18]
<i>Camellia sinensis</i>	<i>CsATGs</i>	80	12	21	10	34	3	[19]
<i>Triticum aestivum</i>	<i>TaATGs</i>	108	17	11	27	53	/	[20]
<i>Pyrus bretschneideri</i>	<i>PbrATGs</i>	28	5	6	2	15	/	[21]
<i>Brassica napus</i>	<i>BnATGs</i>	127	31	27	13	48	8	[22]
<i>Oryza sativa</i>	<i>OsATGs</i>	33	5	8	3	17	/	[23]

(待续)

(续表 1)

Species	Gene name	Gene number	Classification					References
			ATG1/ATG13 kinase complex	The ATG9/2/18 transmembrane complex	Phosphatidylinositol-kinase complex	ATG8/ATG12 ubiquitin-like conjugation systems	SNARE	
<i>Ricinus communis</i>	<i>RcATGs</i>	34	8	9	3	14	/	[24]
<i>Vitis vinifera</i>	<i>VvARGs</i>	36	8	9	3	13	3	[25]
<i>Nicotiana tabacum</i>	<i>NtATGs</i>	30	8	8	3	9	2	[26]
<i>Medicago truncatula</i>	<i>MtATGs</i>	39	8	11	3	17	/	[27]
<i>Citrus sinensis</i>	<i>CsATGs</i>	35	6	9	3	14	4	[28]
<i>Zea mays</i>	<i>ZmATGs</i>	45	13	12	5	15	/	[29]
<i>Musa acuminata</i>	<i>MaATGs</i>	32	3	8	1	20	/	[30]
<i>Capsicum annuum</i>	<i>CaATGs</i>	29	5	9	3	12	/	[31]
<i>Rosa roxburghii</i>	<i>RrATGs</i>	40	11	9	3	17	/	[32]
<i>Brassica rapa</i>	<i>BrATGs</i>	64	19	12	5	25	3	[33]
<i>Gossypium hirsutum</i>	<i>GhirATGs</i>	40	9	13	2	16	/	[34]
<i>Gossypium arboreum</i>	<i>GarATGs</i>	33	7	13	2	11	/	[34]
<i>Gossypium herbaceum</i>	<i>GherATGs</i>	34	8	10	2	14	/	[34]
<i>Gossypium raimondii</i>	<i>GrATGs</i>	25	6	9	3	7	/	[34]
<i>Punica granatum</i>	<i>PgATGs</i>	58	12	15	6	21	4	[35]
<i>Saccharum spontaneum</i>	<i>SsATGs</i>	134	41	33	6	52	2	[36]
<i>Nelumbo nucifera</i>	<i>NnATGs</i>	28	7	7	3	10	1	[37]
<i>Populus trichocarpa</i>	<i>PtrATGs</i>	48	11	14	1	22	/	[38]
<i>Hordeum vulgare</i>	<i>HvATGs</i>	24	4	7	1	12	/	[39]
<i>Fagopyrum tataricum</i>	<i>FtATGs</i>	49	8	11	8	18	4	[40]
<i>Beta vulgaris</i>	<i>BvATGs</i>	51	21	9	6	13	2	Unpublished data

"/" indicates that no corresponding taxonomic ATG has been identified in the species.

## 2 植物 ATGs 的结构与分类

### 2.1 ATGs 结构

根据植物 ATGs 蛋白互作形式及其功能, 可将其分为 ATG1/ATG13 激酶复合物、ATG9/2/18 跨膜复合体、磷脂酰肌醇 3-激酶复合物 (phosphatidylinositol 3-kinase, PI-3K)、ATG8/ATG12 泛素偶联系统和可溶性 N-乙基马来酰亚胺敏感因子附着蛋白受体 (soluble N-ethylmaleimide-sensitive factor attachment protein receptor, SNARE) 这 5 类<sup>[41]</sup>。这些复合物驱动自噬体的形成并与液泡膜融合, 最终在液泡中降解。

ATG1/ATG13 激酶所有复合体均具有 30%–68% 的内在无序残基, ATG1 的 C 端结构域由 2 个微管相互作用和运输 (microtubule interacting and trafficking, MIT) 结构域组成, N 端为 Ser/Thr 蛋白激酶结构域; ATG13 含有 MIT 相互作用基序 (MIT interacting motifs, MIMs)、

Hop1p、Rev7p 和 MAD2 (HORMA) 结构域。ATG9/2/18 跨膜复合体中, ATG9 是唯一的跨膜蛋白, 由 4 个跨膜螺旋和 2 个侧向膜螺旋组成。PI-3K 含有 Beclin 1 的卷曲螺旋结构域 (coiled-coil domain, CCD)、ATG6/Beclin 1 的 C-末端  $\beta$ - $\alpha$  重复 (beta-alpha repeated, BARA)、自噬特异性结构域等, 该复合体的结构为 V 字形, V 字形结构的一条手臂由 ATG6-ATG14 异源二聚体和 Vps15 的 WD40 结构域组成, 而另一条手臂由 Vps34 和 Vps15 的螺旋结构域和激酶结构域组成。在 ATG8/ATG12 泛素偶联系统中, ATG8 和 ATG12 是泛素样蛋白, 具有共同的泛素样折叠, ATG8 保守的 C 端结构域由  $\beta$ 1- $\beta$ 4、 $\alpha$ 3 和  $\alpha$ 4 组成  $\beta$ -grasp 折叠结构, N 端结构域由  $\alpha$ 1 和  $\alpha$ 2 螺旋组成, 是 ATG8 相互作用蛋白结合位点; 而 ATG12 通过 E1 和 E2 酶与 ATG5 结合, 并促进 ATG8-PE 的脂化作用<sup>[42-43]</sup>。这些功能基团定位于空泡周围部位, 形成自噬前体结构, 自噬体的形成可能从这里开始 (图 1), 最

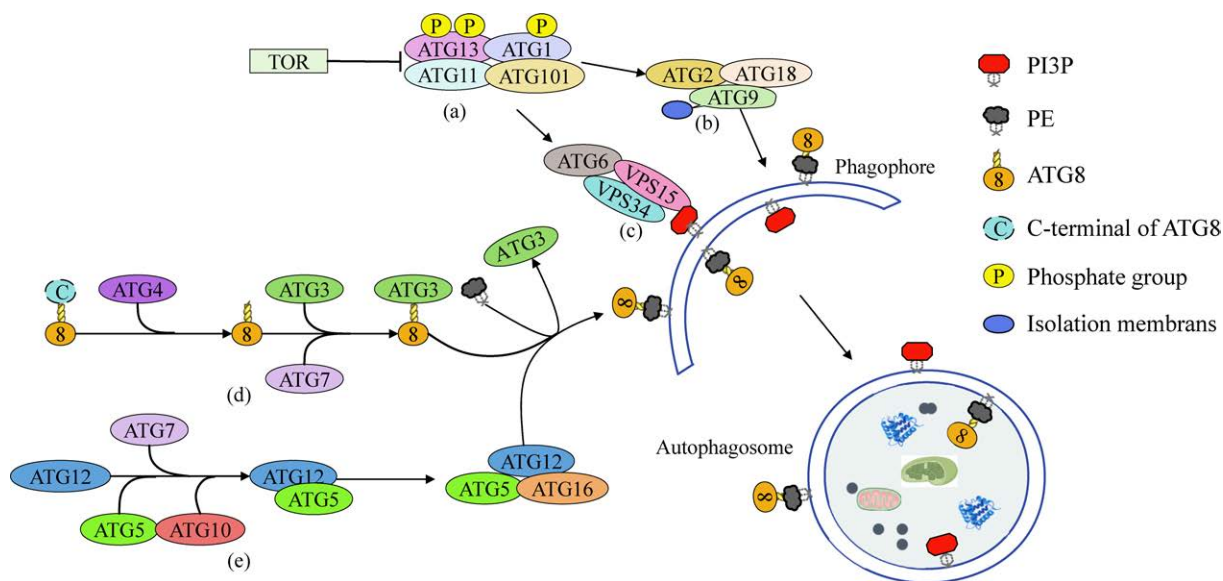


图 1 ATGs 互作蛋白和自噬体的形成过程<sup>[7]</sup> (a): ATG1/ATG13 激酶复合物; (b): ATG9/2/18 跨膜复合体; (c): 磷脂酰肌醇 3-激酶复合物 (PI-3K); (d): ATG8-PE 偶联系统; (e): ATG12/ATG5 偶联系统。

Figure 1 Interaction proteins of ATGs and formation processes of autophagosomes<sup>[7]</sup>. (a): ATG1/ATG13 kinase complex; (b): ATG9/2/18 transmembrane complex; (c): Phosphatidylinositol 3-kinase complex; (d): ATG8-PE conjugation system; (e): ATG12/ATG5 conjugation system.

后通过 SNARE 将自噬体正确靶向液泡。此外,还在 ATGs 家族中发现了 DIOX\_N、phox homology (PX)、PI-3K、chorein N、ThiF、RHOD、Hydrolase 4 和 DUF3385 等结构域。这些不同的保守结构域代表着 ATGs 家族成员在调控自噬过程中可能发挥不同的作用。

## 2.2 ATGs 分类

为进一步探究不同物种 ATGs 家族成员的进化关系,采用 Clustal W 软件对 42 个拟南芥 AtATGs、41 个茄子 SmATGs 和 51 个甜菜 BvATGs 氨基酸序列进行比对,利用 MEGA 11.0 软件构建系统发育树(图 2)。结果表明,ATGs 成员可被分为 5 个亚簇(A-E),但同一类 ATGs 分布在不同的亚簇,说明其蛋白结构可能存在较大差异。C 簇 ATGs 数最多,包含 I、III 和 IV 这 3 类 ATGs,有 36 个。其次是 E 簇和 A 簇, E 簇包含 I、III 和 IV 这 3 类 ATGs,有 34 个; A 簇包含所有类别的 ATGs,有 28 个。D 簇包含 I、II 和 IV 这 3 类 ATGs,有 21 个。B 簇包含 I、II 和 IV 这 3 类的 ATGs,有 15 个。在甜菜 BvATGs 基因家族中, A-E 亚簇分别含有 9、5、18、8、11 个成员。进一步分析发现, BvATGs 与茄科植物茄子 SmATGs 进化关系最近,而与十字花科植物拟南芥 AtATGs 进化关系较近(图 2)。

## 3 植物 ATGs 的调控机制

在植物中, ATGs 表达变化有助于其在特定发育阶段,对各种逆境胁迫信号作出反应,从而促进植物生长或存活。自噬的发生过程受到转录因子(transcription factors, TFs)、激素、互作蛋白、TOR 等多种因子的影响,调控植物生长发育及胁迫响应。

### 3.1 ATGs 转录和翻译后调控

转录调控是 ATGs 在环境胁迫下表达的关

键。在番茄(*Solanum lycopersicum*)中,热休克转录因子(heat-shock transcription factor A1a, HsfA1a)被诱导和激活后易位进入细胞核,并与 *SIATG10* 和 *SIATG18f* 启动子区域中的热激元件(heat-shock elements, HSE)结合,激活了 ATGs 的表达,促进不溶性泛素化蛋白聚集体的自噬降解,提高番茄存活率和抗旱性<sup>[44]</sup>。乙烯正向调控转录因子 5 (ethylene response factor 5, ERF5)直接结合 *SIATG8d* 和 *SIATG18h* 启动子中的干旱响应元件,激活其表达,从而刺激乙烯(ethylene, ET)诱导的番茄植株抗旱性的自噬<sup>[45]</sup>。拟南芥光信号途径中的核心转录因子 HY5 (elongated hypocotyl 5)在转录水平上负调控自噬,在正常氮(nitrogen, N)条件下, HY5 通过含有 ACGT 的顺式作用元件结合 *AtATG5* 和 *AtATG8e* 启动子区域并抑制其表达,进而抑制自噬,使细胞自噬活性保持在恒定水平;而在 N 饥饿条件下, HY5 蛋白积累受到抑制,解除对 *AtATG5* 和 *AtATG8e* 表达的抑制作用,从而激活自噬<sup>[46]</sup>。*AtWRKY53* 与组蛋白脱乙酰酶 9 (histone deacetylase 9, HDA9)和染色质重塑蛋白(powerdress, PWR)形成复合体,与 *AtATG9* 启动子中的 W-box 基序结合,并以 H3K27 去乙酰化依赖的方式抑制其表达,促进拟南芥叶片衰老<sup>[47]</sup>。此外, *WRKY24* 同源基因 *WRKY20* 被鉴定为参与木薯(*Manihot esculenta*)抗病的 *MeATG8a* 的上游调控基因, *MeWRKY20* 过表达上调 *MeATG8a* 的转录水平,增加 *MeWRKY20* 被自噬降解形成负反馈回路的可能性,从而增强免疫应答相互作用蛋白的信号传导,正向调控木薯对白叶枯病的抗性<sup>[48]</sup>。研究人员采用酵母单杂交和染色质免疫沉淀技术发现,番茄油菜素内酯(brassinosteroid, BR)途径的关键转录因子 BZR1 (brassinazole resistant 1)可直接结合 *SIATG2* 和 *SIATG6* 的启动子,通过转录上调 *SIATG2* 和



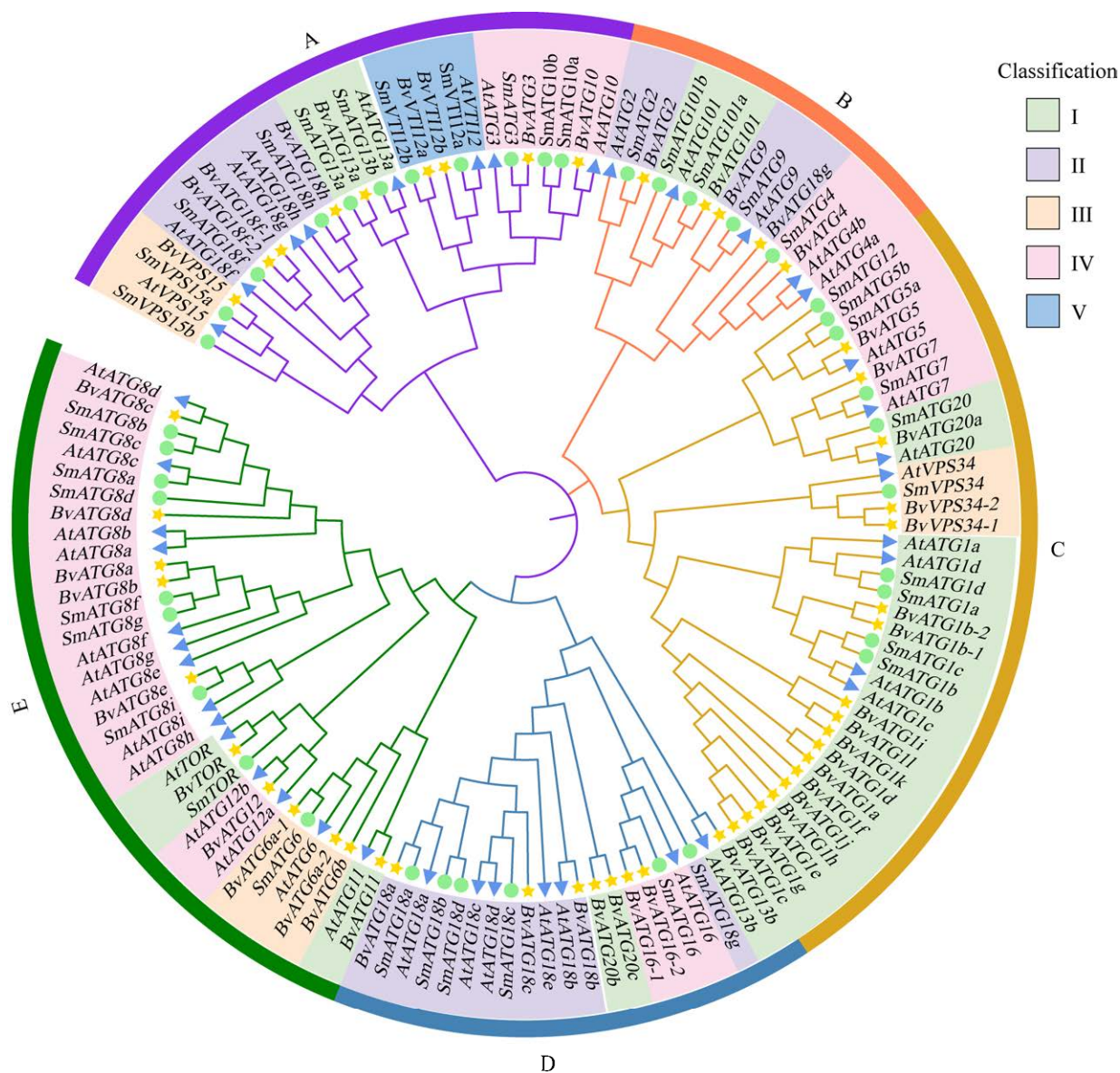


图2 高等植物 ATGs 基因家族的系统发育树 采用 MEGA 11.0 软件进行序列多重比较和系统进化树的构建。蓝色三角形表示拟南芥, 黄色五角星表示甜菜, 绿色圆形表示茄子。I: ATG1/ATG13 激酶复合物; II: ATG9/2/18 跨膜复合体; III: 磷脂酰肌醇 3-激酶复合体; IV: ATG8/ATG12 泛素样偶联系统; V: SNARE。ATGs 来源、名称和登录号已提交至国家微生物科学数据中心(编号: NMDCX0001706)。

Figure 2 Phylogenetic tree of the ATGs gene family in higher plants. The sequences multiple comparison and the phylogenetic tree construction were performed by MEGA 11.0 software. The blue triangles indicate *Arabidopsis thaliana*, the yellow pentagons represent *Beta vulgaris*, and the green circles indicate *Solanum melongena*. I: ATG1/ATG13 kinase complex; II: ATG9/2/18 transmembrane complex; III: Phosphatidylinositol 3-kinase complex; IV: ATG8/ATG12 ubiquitin-like conjugation systems; V: SNARE. The sources, names and accession numbers of ATGs are shown in National Data Center for Microbiological Science (No.: NMDCX0001706).

*SIATG6* 的表达, 从而提高番茄植株对冷胁迫和 N 饥饿的耐受性<sup>[49]</sup>。TGA 基序结合蛋白 9 (TGA motif-binding protein 9, TGA9) 被诱导表达并与 *AtATG8b* 和 *AtATG8e* 启动子上特定的 TGACG 基序结合, 上调 *AtATG8b*、*AtATG8e* 等基因的表达水平, 从而促进拟南芥细胞自噬, 提高幼苗对碳(carbon, C)饥饿的耐受性<sup>[50]</sup>。这些结果表明, 转录因子直接与 ATGs 启动子结合上调其表达, 从而有效激活自噬并调节其转录水平。

翻译后水平的自噬调节是植物适应各种环境胁迫的必要条件, 通过控制 ATGs 蛋白的丰度、稳定性和功能以响应上游信号。在营养充足条件下, 拟南芥 AtTOR 通过过度磷酸化 AtATG1 和 AtATG13 负向调节自噬, 从而降低 AtATG1 激酶的活性。相反, 营养或能量亏缺则会增加 AMP/ATP 比率, 并激活 AMPK/SnRK1、AMPK/SnRK1 正磷酸化 AtATG1, 从而激活自噬<sup>[51]</sup>。另外, 拟南芥 AtATG13a 可被高度磷酸化, 降低其对 ATG1a 激酶的亲和力; 在 C 饥饿条件下, 激活 type one 蛋白磷酸酶(type one protein phosphatase, TOPP)使 ATG13a 去磷酸化, 促进 ATG1a-ATG13a 复合物的形成和 ATG1a 磷酸化, 导致自噬活性升高, 而突变体 *atg13a* 对 C 饥饿耐受性增强<sup>[52]</sup>。在内质网(endoplasmic reticulum, ER)应激下, 拟南芥 AtATG18a 的磷脂结合活性可通过 Cys103 处的过硫化修饰以可逆方式激活, 负向调节自噬体的形成, 确保适当的生理反应<sup>[53]</sup>。此外, 拟南芥 RING 型 E3 泛素连接酶 1/2/6 (RING-type E3 ubiquitin transferase 1/2/6, SINAT1/2/6)可泛素化 ATG13 来调控自噬启动。在营养充足的条件下, 拟南芥肿瘤坏死因子受体相关因子家族蛋白 1a/1b (tumor necrosis factor receptor-associated 1a/1b, TRAF1a/1b)会激活 2 个环指 E3 连接酶 SINAT1/2, 泛素化并降解 ATG13a 和 ATG13b, 从而抑制自噬。相反, 在

营养亏缺条件下, SINAT6 通过与 ATG13 竞争性结合, 破坏 TRAF1a/1b 和 SINAT1/2 之间的相互作用, 稳定 ATG1/ATG13 复合物导致自噬激活<sup>[54]</sup>。由此可见, ATGs 基因通过翻译后修饰得到调控, 从而维持适当水平的胁迫反应。

### 3.2 ATGs 与信号通路

激素可以通过诱导自噬活性, 参与植物对各种逆境胁迫的反应。Rodriguez 等<sup>[55]</sup>采用外源激素乙烯前体(1-aminocyclopropane-1-carboxylic acid, ACC)、脱落酸(abscisic acid, ABA)、芸苔素内酯(brassinolide, BL)、生长素(1-naphthalene acetic acid, NAA)和细胞分裂素(6-benzylaminopurine, 6-BA)处理拟南芥, 诱导 GFP-ATG8a 和自噬受体 NBR1 快速积累, 表明自噬基因与激素信号之间存在联系。研究发现, 乙烯处理矮牵牛(*Petunia hybrida*)可促进衰老花瓣中 *PhATG8* 表达, 而使用乙烯抑制剂(1-methylcyclopropene, 1-MCP)处理后, *PhATG8* 表达被抑制<sup>[56]</sup>, 表明 ET 是调控 ATGs 基因表达的重要因子之一。另外, 自噬也调节 ET 的生物合成, *SIPI3K* 的过表达会增强转基因烟草(*Nicotiana tabacum*) ET 的生物合成, 加速花的衰老, 而 *PhATG6* 和 *PhPI3K* 的沉默则会抑制矮牵牛(*Petunia hybrida*) ET 生物合成基因 *PtACS* 的表达<sup>[57]</sup>。在苹果(*Malus pumila*)中, 过表达 *MdATG18a* 促进水杨酸(salicylic acid, SA)的积累, 致使 SA 途径中 ATGs 的表达也上调, 从而增强苹果对褐斑病的抗性<sup>[58]</sup>。研究表明, 高水平的 SA 会引起自噬介导的细胞程序性死亡(programmed cell death, PCD), *atg* 突变体在衰老和免疫过程中加速 PCD 的表型是通过 SA 依赖而不是完整的茉莉酸(jasmonic acid, JA)或 ET 信号通路<sup>[59]</sup>。在拟南芥中, tryptophan-rich sensory protein (*AtTSPO*)可被 ABA 瞬时诱导, 该基因的 ATG8 互作基序(ATG8 interaction motif, AIM)直接与 *AtATG8* 结合, 在自噬体中与



*AtATG8* 共定位, 通过自噬直接支持 TSPO 降解。在自噬缺陷 *atg5* 突变体中, 其降解被抑制<sup>[60]</sup>。同样地, 细胞内 ABA 升高可减轻硫化氢对 *AtATG4* 的过硫化, 从而增加 *AtATG4* 蛋白酶活性和促进自噬体的形成<sup>[61]</sup>。此外, 多个 AP2/EREBP (apetala2/ethylene responsive element binding protein) 可结合 *AtATG8s* 启动子区域并促进其表达; ARF8 (auxin response factor 8) 等 NAA 响应因子也可以结合 *AtATG8s* 基因的启动子区域, 提示了 NAA 处理可能影响 ATGs 基因的表达<sup>[50]</sup>。这些结果表明, ATGs 参与植物激素的生物合成和信号传导, 以调控植物生长发育和胁迫应答反应。

## 4 植物 ATGs 在响应逆境胁迫中的作用

盐分、干旱、营养亏缺、冷胁迫和热胁迫以及病虫害等逆境会对农业生产造成不利影响, 从而降低作物产量。自噬是植物重要的胁迫反应机制, 不仅影响 ATGs 的表达, 还诱导细胞自噬体的形成。大量研究表明, ATGs 在调控植物逆境胁迫响应中发挥重要作用(表 2)。

### 4.1 ATGs 调控盐胁迫响应

土壤盐碱化是一个全球性环境问题, 由于持续的盐胁迫, 导致至少 30% 的作物遭受不同程度的产量损失, 对粮食安全造成严重影响<sup>[89-90]</sup>。研究表明, ATGs 在植物应答盐胁迫中起重要作用(图 3)。盐胁迫可通过诱导植物自噬, 促进蛋白质的降解和再循环, 提供植物生存所需的大分子和能量。Zhang 等<sup>[91]</sup>发现盐胁迫下外源亚精胺(spermidine, Spd)通过激活黄瓜(*Cucumis sativus*) *CsATGs* 基因的表达和自噬体的形成, 抑制不溶性蛋白积累和泛素化, 从而正向调控黄瓜耐盐性; 而 *CsATG4* 和 *CsATG7* 沉默会降低 Spd 诱导的黄瓜耐盐性和自噬体的形成。同样地, 盐胁迫诱导小麦(*Triticum aestivum*)自噬

和 PCD 发生, 沉默 *TaATG2* 或 *TaATG7* 会显著抑制小麦自噬, 破坏 Na、Cl、K 和 Ca 等元素的吸收, 诱导过量活性氧(reactive oxygen species, ROS)的产生, 降低抗氧化活性, 使小麦耐盐性减弱, PCD 水平增加, 从而负向调控盐胁迫和程序化死亡<sup>[92]</sup>。此外, 盐胁迫可诱导苹果根系 *MdATG10* 表达, 过表达 *MdATG10* 会缓解盐处理对根系生长和活力的损害, 降低盐胁迫下苹果 Na<sup>+</sup> 积累, 诱导转基因植株离子稳态相关基因表达, 从而增强其耐盐性<sup>[93]</sup>。采用 RNA 测序(RNA sequencing, RNA-seq)和实时荧光定量 PCR (quantitative real-time PCR, qRT-PCR)技术研究发现, 棉花(*Gossypium hirsutum*)大多数 *GhATG8* 基因受盐胁迫诱导。进一步研究表明, *GhATG8f* 可通过增加超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)和过氧化氢酶(catalase, CAT)活性以及 Pro 积累来提高棉花耐盐性<sup>[94]</sup>。在盐水芹(*Eutrema salsugineum*)中, 盐胁迫下 ATGs 和过氧化物酶体通路中基因表达显著增加, 抗氧化活性增强, 表明盐水芹可能通过清除 ROS 和氧化蛋白来应对盐胁迫, 从而增强植物防御反应<sup>[95]</sup>。Khan 等<sup>[96]</sup>采用 JA 处理水稻幼苗后发现, 盐胁迫可能促进自噬, 导致自噬细胞死亡, ATGs 通过 JA 信号通路正向调控植物耐盐性。这些结果表明, ATGs 通过提高自噬水平来增强抗氧化活性, 从而提高植物耐盐性。

### 4.2 ATGs 调控干旱胁迫响应

干旱是影响全球农业地区的一个经常性和严重的气象挑战, 导致植物物种分布发生重大变化, 作物产量大幅下降<sup>[97]</sup>。研究表明, ATGs 在植物应答干旱胁迫中发挥重要作用(图 3)。干旱胁迫可显著促进 ATGs 的表达, 提高自噬活性, 从而清除氧化损伤蛋白和调节 ROS 水平, 提高植物抗旱性。苹果 *MdATG10* 的过表达可通

过调节气孔运动和增强自噬活性, 提高水分利用效率(water use efficiency, WUE), 从而增强苹果植株光合效率, 减少 ROS 积累, 正向调节植物抗旱性<sup>[98]</sup>。同样地, 过表达苹果 *MdATG8i* 和 *MdATG5a* 后转基因植株自噬活性增强, 渗透调节能力、光合能力和 WUE 均显著提高, 苹

果植株耐旱性明显提高<sup>[99-100]</sup>。在香蕉(*Musa acuminata*)中, 10 个 MaATG8s 家族成员响应干旱胁迫, 在拟南芥中过表达 *MaATG8f* 后, 可激活抗氧化相关酶活性, 抑制 ROS 积累, 同时调控 ABA 合成代谢和自噬活性, 正向调节植物抗旱性<sup>[101]</sup>。在小麦幼苗干旱胁迫后, 根组织的自

表 2 ATGs 在调控植物逆境胁迫响应中的作用

Table 2 Function of ATGs in regulating plant stress response

Stress responses	Gene name	Species	Function	References
Salinity stress	<i>PagATG18a</i>	<i>Populus alba</i> × <i>Populus tremula</i> var. <i>Glandulosa</i>	Mitigating membrane oxidation damage and Na <sup>+</sup> retention; ROS and oxidized products clearance	[62]
	<i>BnaATG8</i>	<i>Brassica napus</i>		[63]
	<i>AtATG8</i>	<i>Arabidopsis thaliana</i>		[64]
	<i>ZmATG3, ZmATG6, ZmATG8a, ZmATG10</i>	<i>Zea mays</i>		[65-66]
Drought stress	<i>AtATG8</i>	<i>Arabidopsis thaliana</i>	Repressing BR and activating ABA signaling; Heme clearance; degradation of aquaporin PIP2-7; Removal of ROS and oxidized products	[67]
	<i>MtATG1a, MtATG2, MtATG4, MtATG5, MtATG8a, MtATG18b</i>	<i>Medicago truncatula</i>		[27]
	<i>SiATG8a</i>	<i>Setaria italica</i>		[18]
	<i>PvATG8c</i>	<i>Phaseolus vulgaris</i>		[68]
Nutritional deficit stress	<i>AtATG5, AtATG18a</i>	<i>Arabidopsis thaliana</i>	Proteins and 26S proteasome degradation	[69-71]
	<i>OsATG1a, OsATG4a-b, OSATG5, OsATG6c, OsATG8a, OsATG8d-h, OsATG12, OsATG13b, OsATG16, OsATG18c-f</i>	<i>Oryza sativa</i>		[23]
	<i>ZmATG12, ZmATG5</i>	<i>Zea mays</i>		[72-73]
	<i>CsATG3a</i>	<i>Camellia sinensis</i>		[74]
	<i>PIATG3</i>	<i>Peronophythora litchii</i>		[75]
	Heat stress	<i>TaATG8</i>	<i>Triticum aestivum</i>	Degradation of ubiquitinated proteins and HSPs; Tapetum degeneration; Golgi apparatus reassembly
<i>AtATG8</i>		<i>Arabidopsis thaliana</i>		[77]
<i>SIAT11</i>		<i>Solanum lycopersicum</i>		[78]
Cold stress	<i>MsATG13</i>	<i>Medicago sativa</i>	Degradation of ubiquitinated proteins; NBR1-mediated selective autophagy	[79]
	<i>SIATG2, SIATG6, SIATG7, SIATG8, SINBRI</i>	<i>Solanum lycopersicum</i>		[80-82]
	Biotic stress	<i>NbATG8f</i>	<i>Nicotiana benthamiana</i>	The interaction between ATG proteins and virulence factors; Enhancing bacterial pathogenicity; Suppress host immune response
<i>NbATG3, NbATG5, NbBeclin1, NbATG7, NbATG8a</i>		<i>Nicotiana benthamiana</i>		[84]
<i>NbATG1, NbATG8, NbATG11, NbATG13</i>		<i>Nicotiana benthamiana</i>		[85]
<i>NbATG5, NbATG3</i>		<i>Nicotiana benthamiana</i>		[86-87]
<i>TaATG6, TaATG8</i>		<i>Triticum aestivum</i>		[88]

噬活性被激活, *TaATG8* 表达显著上调, 对于干旱的敏感性显著提高; 相反, 沉默 *TaATG6* 则会抑制植株自噬导致细胞死亡<sup>[102-103]</sup>。这些结果表明, ATGs 通过增强自噬活性从而提高植物对于干旱胁迫的耐受性。

此外, ATGs 可通过与多种信号分子相互作用应答干旱胁迫。研究发现, 蒺藜(*Medicago truncatula*)脱水蛋白 MtCAS311 (cold acclimation-specific 31)与 ATG8a 和干旱胁迫负调节因子 MtPIP2-7 (plasma membrane intrinsic protein 2-7) 互作, 在自噬中起正向调控作用; 通过促进 MtPIP2-7 的自噬降解, 从而降低其根系导水

率, 减少水分流失, 提高植株抗旱性<sup>[104]</sup>。Bao 等<sup>[105]</sup>发现拟南芥 *AtCOST1* (constitutively stressed 1)通过 ATG8 相互作用, 稳定性调控自噬。在正常条件下, *AtCOST1* 通过介导 *AtATG8* 的降解来抑制自噬; 而在干旱胁迫下, *AtCOST1* 被降解, 释放 *AtATG8*, 激活自噬, 增强植物耐旱性<sup>[105]</sup>。同样地, 施用 24-表芸苔素内酯 (24-epibrassinolide, EBR)会减轻干旱胁迫对桃 (*Prunus persica*)叶片造成的伤害, 降低 *PpATG* 表达水平并减少自噬体数量, 增强植物耐旱性<sup>[106]</sup>。干旱胁迫可显著诱导 *ERF5* 表达, *ERF5* 通过 DRE (drought response elements)基序直接结合

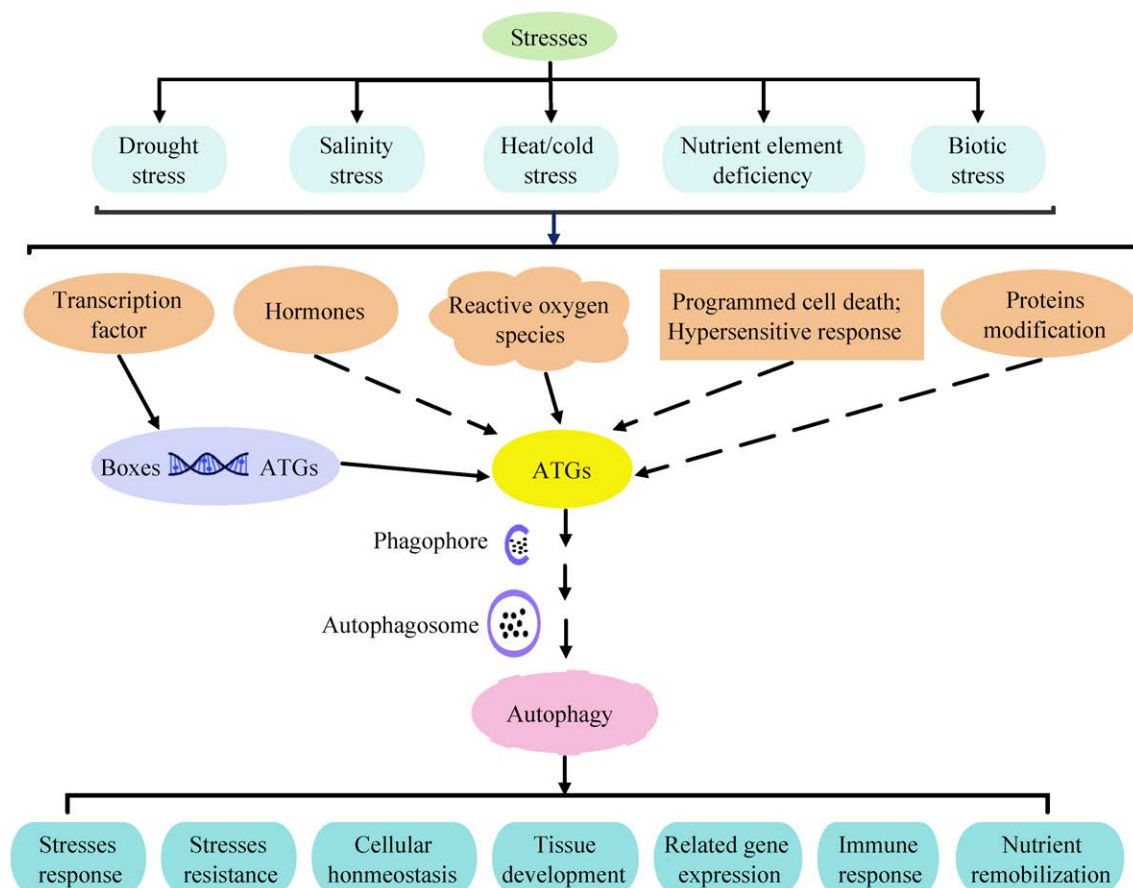


图 3 ATGs 调控植物逆境胁迫响应机制 黑色实线箭头均表示直接的诱导作用或激活作用; 黑色虚线箭头均表示间接的诱导作用或激活作用。

Figure 3 Regulatory mechanisms of ATGs in the response of plants to stress. Solid black indicate direct induction or activation; Dashed black arrows indicate indirect induction or activation.

*SIATG8d* 和 *SIATG18h* 的启动子区域并激活其表达, 从而提高细胞自噬活性, 增强植物抗旱能力<sup>[45]</sup>。此外, 3-甲基腺嘌呤(3-methyladenine, 3-MA)处理和 *ATG6* 敲低均会抑制自噬, 加速干旱胁迫下小麦幼苗 PCD<sup>[103]</sup>。Williams 等<sup>[107]</sup>对来自澳大利亚的耐干旱草线形草沙蚕(*Tripogon loliiformis*)的研究发现, 脱水处理导致海藻糖大量积累, 从而触发 ATGs 上调表达, 进而赋予植物更强的抗旱性。这些结果表明, ATGs 可通过调节渗透稳态和提高水分利用效率来增强植物抗旱性。

### 4.3 ATGs 调控极端温度胁迫响应

热胁迫通过引起蛋白质异常折叠和变性来损害植物生长<sup>[108]</sup>。植物在受到热胁迫后, ATGs 转录水平迅速升高, 自噬活性增强, 一方面降解蛋白质聚集体, 维持蛋白质稳态和完整性; 另一方面促进叶片气孔关闭, 减少植株水分散失, 从而提高植物对高温的耐受性<sup>[109]</sup>。辣椒 (*Capsicum annuum*) *CaATG8e* 通过增加过氧化氢(H<sub>2</sub>O<sub>2</sub>)积累和抑制热休克反应(heat shock response, HSR)相关基因的表达来负调控辣椒耐热性<sup>[110]</sup>。过表达 *MdATG18a* 使得转基因苹果植株自噬活性升高, 抗氧化能力增强, ROS 积累减少, 叶绿体受损程度减弱, 热胁迫耐受性增强<sup>[111]</sup>。此外, 高温胁迫还可促进花药细胞壁和小孢子的自噬<sup>[112]</sup>, 敲除 *AtATG2*、*AtATG5*、*AtATG7* 和 *AtATG10* 后, 番茄花粉发育和花药开裂严重受损, 说明热胁迫下自噬在绒毡层退化和花粉发育中起作用。在热胁迫下, 花药中 HsfA1a 可直接调控 *SIATG10* 转录, 从而增强花粉自噬体的形成和热胁迫下番茄花药的自噬水平, 正向调控花粉和花药的耐热性<sup>[113]</sup>。对拟南芥野生型和 *atg5* 突变体在热胁迫前后的转录组分析表明, 自噬对热诱导的热休克蛋白(heat shock proteins, HSPs)基因表达影响不大, 但在

植物热胁迫反应早期, 自噬对许多其他胁迫和防御相关基因的表达起着积极的作用<sup>[114]</sup>。这些结果表明, ATGs 参与调控植物的热胁迫反应和耐热性(图 3)。

低温也会影响植物细胞酶活性和膜功能, 使细胞代谢不稳定或自噬<sup>[115]</sup>。研究表明, 在低温胁迫下, *MsATG13* 转基因烟草增加 Pro 含量和抗氧化酶活性, 增强冷胁迫条件下的抗氧化防御能力; 另外, *MsATG13* 过表达降低超氧阴离子自由基(O<sub>2</sub><sup>-</sup>)和 H<sub>2</sub>O<sub>2</sub> 的水平, 可见 *MsATG13* 通过调节自噬和抗氧化水平增强植物的抗寒性<sup>[79]</sup>。在番茄中, BZR1 可直接与 *ATG2*、*ATG6*、*NBR1a* 和 *NBR1b* 的启动子结合, 并在冷胁迫下上调这些基因的表达, 从而导致自噬增加和 NBR1 蛋白水平升高, 并促进功能性蛋白(PsbS, VDE 和 D1)的积累, 增强番茄抗寒性<sup>[80]</sup>。这些结果表明, ATGs 在植物响应低温胁迫过程中也扮演着重要作用。

### 4.4 ATGs 调控营养亏缺胁迫响应

在营养亏缺胁迫下, ATGs 可重新动员营养物质, 为植物生存提供必要的氨基酸、脂肪酸和糖等能量<sup>[116]</sup>。无机磷酸盐(inorganic phosphate, Pi)和氮是植物生长的必需营养物质<sup>[117]</sup>。低 Pi 优先增加拟南芥根分生区的自噬通量, 其中大多数 *AtATGs* 由 N 饥饿高度诱导, 但在 Pi 饥饿下受诱导的程度相对较低。在 *AtATG8* 家族中, *AtATG8a*、*AtATG8f*、*AtATG8g* 和 *AtATG8h* 在地上部分因 Pi 饥饿而上调, *AtATG8f* 和 *AtATG8h* 在根中因 Pi 饥饿显著上调, 维持细胞 Pi 的稳态<sup>[118-119]</sup>。过表达 *SiATG8a* 的小麦植株通过调节磷相关转运基因(*TaPHR1*, *TaPHR3*, *TaIPS1* 和 *TaPT9*)的表达, 提高了转基因小麦根、茎、叶的磷含量, 从而提高小麦籽粒产量<sup>[120]</sup>。在苹果中过表达 *MdATG10* 可显著缓解低氮胁迫下植株的生长抑制和光合系统的损伤, 上调氮吸

收与同化相关基因 *MdNRT1.1*、*MdNRT2.4*、*MdNRT2.5* 和 *MdNRT2.7* 的表达水平,促进对氮的吸收,从而增强细胞自噬活性以及对低氮胁迫的耐受性<sup>[121]</sup>。同样地,过表达 *MdATG9* 使得转基因苹果愈伤组织中 *MdATG3a*、*MdATG5*、*MdATG8c*、*MdATG8i* 和 *MdATG10* 的转录水平增加,糖和游离氨基酸含量提高,硝酸盐同化基因 *MdNRT1.1*、*MdNRT2.5*、*MdNIA1* 和 *MdNIA2* 表达上调,从而增强转基因植株对氮缺乏的耐受性<sup>[122]</sup>。*OsATG8b* 过表达可显著增强转基因拟南芥的自噬通量,有效缓解氮胁迫下的生长抑制,促进植株生长发育,赋予转基因植株对氮饥饿更强的耐受性,并提高产量和氮利用效率(nitrogen use efficiency, NUE)<sup>[123]</sup>。类似地,番茄 *SIATG6* 依赖性自噬也可通过上调 *NRT1.1* 和 *NRT1.2* 转录水平,调节氮的摄取和利用以及碳同化,减轻氧化损伤,从而调节番茄植株的营养循环和再动员来促进低氮耐受性<sup>[124]</sup>。

锌或铁亏缺同样会诱导细胞自噬,并且自噬可以补充  $Zn^{2+}$  和  $Fe^{2+}$ ,纠正细胞内 Zn-Fe 失衡<sup>[125]</sup>。当环境中的 Zn 含量较低时,ATGs 表达可提高植物的锌生物利用效率。在缺锌条件下,*atgs* 突变体萎蔫的程度更为严重<sup>[126]</sup>。Zn 亏缺会诱导自噬降解各种靶标,以增加游离  $Zn^{2+}$  的水平并维持植物中的活性氧稳态。有趣的是,当 Zn 过量时,自噬也会被诱导,通过向培养基中补充高水平的 Fe,可以抑制 *atg* 突变体中过量的 Zn 诱导症状,以维持植物 Zn-Fe 稳态<sup>[127]</sup>。在 Zn-Fe 稳态中,转录因子 bZIP19 和 bZIP23 可能是在 Zn 亏缺/过量条件下启动/抑制植物自噬的开关,而 E3 泛素连接酶 BRUTUS (BTS) 可能参与 Fe 亏缺条件下自噬的启动<sup>[125]</sup>。此外,ATGs 也参与植物硫饥饿的调节。与野生型相比,拟南芥突变体 *atag5* 的 S 元素从莲座叶到种子的再迁移受损,自噬以不依赖 SA 的

方式控制硫的再动员,从而影响莲座叶到种子的 S 通量,表明 ATGs 参与调控 S 的运输<sup>[128]</sup>。这些结果表明,营养亏缺可通过提高 ATGs 表达增强细胞自噬活性,促进营养物质循环和再分配。

#### 4.5 ATGs 调控病害胁迫响应

自噬在植物调控病原微生物胁迫响应中也发挥重要作用(图 3)。研究发现,细胞自噬可限制病毒在寄主体内的复制和积累<sup>[129]</sup>。当受到病原菌侵染时,植物会激活 ATGs 基因表达,从而抑制或清除外来病原菌,增强植物的抗病性。在拟南芥中,AtATG18a 磷酸化修饰在调节其自噬功能和防御灰霉菌(*Botrytis cinerea*)方面起负向作用,BRI1 (brassinosteroid insensitive 1) 相关受体激酶 1 (BRI1-associated receptor kinase 1, BAK1) 与 AtATG18a 发生互作并直接磷酸化 AtATG18a,BAK1 突变阻断 AtATG18a 的 4 个磷酸化位点(Ser361、Thr241、Ser328 和 Thr387),从而通过增加自噬活性来增强植物对坏死性病原体的抵抗力<sup>[130]</sup>。类似地,棉花卷叶木尔坦病毒(cotton leaf curl Multan betasatellite, CLCuMuB)的  $\beta$ C1 蛋白通过与负自噬调节因子细胞溶质甘油醛-3-磷酸脱氢酶(cytoplasmic glyceraldehyde-3-phosphat dehydrogenases, GAPCs)结合,诱导自噬发生,破坏 NbGAPC 与 NbATG3 互作,加速自噬通量和自噬活性,抵抗病毒侵染<sup>[131]</sup>。NbP3IP 通过与水稻条纹病毒(rice stripe virus, RSV)编码的 RNA 沉默抑制蛋白 p3 互作,介导 p3 的降解,从而影响 p3 的沉默抑制活性并诱导自噬,负向调控病毒感染<sup>[132]</sup>。此外,WRKY24 被证实可以与 *MaATG8f* 和 *MaATG8g* 启动子上的 W-box 结合,正向调控自噬基因的转录,提高自噬活性,增强自身的防御能力,从而降低真菌侵染对植物的威胁<sup>[133]</sup>。同样地,  $CaCl_2$  处理能够显著诱导梨(*Pyrus bretschneideri*) 叶片中 *PbrATG1*、*PbrATG5*、*PbrATG6*、*PbrATG7*、

*PbrATG8c* 和 *PbrATG10* 的转录水平, 提高梨的自噬活性, 促进 SA 的积累及抗氧化活性, 增强植株对葡萄座腔菌(*Botryosphaeria dothidea*) 的抗性<sup>[134]</sup>。

植物可通过调节自噬抵御病原菌侵染, 而病原菌也会进化出复杂的策略来调控自噬从而直接或间接促进病毒侵染。研究发现, 大麦(*Hordeum vulgare*) 条纹花叶病毒(barley stripe mosaic virus, BSMV)的  $\gamma$ -b 蛋白通过与 ATG7 直接结合破坏 ATG7-ATG8 的相互作用抑制宿主植物自噬, 破坏自噬介导的植物抗病毒防御反应, 从而促进感染<sup>[135]</sup>。番茄卷叶云南病毒(tomato leaf curl Yunnan virus, TLCYnV)编码的 C2 蛋白直接与 ATG7 的泛素激活结构域互作, 竞争性地破坏本氏烟草(*Nicotiana benthamiana*) 和茄子 ATG7-ATG8 的结合, 抑制自噬活性, 促进病毒感染<sup>[136]</sup>。同样地, 本氏烟草叶片在竹花叶病毒(bamboo mosaic virus, BaMV)感染期间, 上调 ATGs 表达, 并且感染后细胞中富含 ATG8f 的自噬体颗粒数量增加, 表明 ATGs 正向调控植物 BaMV 的积累<sup>[137]</sup>。与野生型植株相比, 小麦 *TaATG8j* 沉默植株叶片经条形柄锈菌(*Puccinia striiformis* f. sp. *tritici*, *Pst*)侵染后, 坏死细胞数量减少, 表明沉默植株超敏反应(hypersensitive response, HR)受到限制; 同时 *TaATG8j* 沉默植株可提高对 *Pst* 的敏感性, 促进菌丝生长和分枝, 植株抗性降低<sup>[138]</sup>。此外, 在木薯中, 甘油醛-3-磷酸脱氢酶(glyceraldehyde-3-phosphate dehydrogenase, GAPDH)可与 MeATG8b 和 MeATG8e 互作, 并抑制自噬活性; 在野生型和 *MeGAPDHs* 沉默植株中, 敲除 *MeATG8b* 和 *MeATG8e* 均可降低对萎蔫病黄单胞菌(*Xanthomonas axonopodis* pv. *manihotis*, Xam)抗性, 可见 GAPDH 通过负向调控自噬影响抗病能力<sup>[139]</sup>。这些研究结果表明, ATGs 在调控植物抗病性中起着重要

的作用。

## 5 展望

ATGs 介导的自噬是真核生物进化过程中高度保守的自我降解过程, 在调控植物生长发育和逆境胁迫响应中扮演着重要角色。目前有关植物 ATGs 的研究主要集中在逆境胁迫响应及自噬核心机制等方面。然而, 同一 ATGs 可调控多种胁迫响应, 而同一胁迫响应又可能受到多个 ATGs 响应, 并且不同物种中 ATGs 的功能和调控网络也存在特异性。此外, 植物激素、WRKY、MAPK 和  $Ca^{+}$  信号分子与 ATGs 串扰方面的机制仍不明确。因此, 该领域未来的研究可从以下几方面着手:(1) 利用病毒诱导基因沉默、CRISPR/Cas9 基因编辑等技术, 深入挖掘自噬信号途径中的关键 ATGs 及调控因子和靶标基因, 解析逆境胁迫响应调控网络。(2) 探索 ATGs 表达对自噬活性的调控, 并深入研究自噬与细胞凋亡之间的关系及其作用机理。(3) 探究 ATGs 与植物激素、WRKY、MAPK 和  $Ca^{+}$  信号分子之间的网络联系及其与各信号途径的交互作用机制。利用分子遗传学、细胞生物学和生物化学等方法揭示逆境胁迫下植物 ATGs 的功能及其调控机制, 有望为农作物抗逆性和作物遗传改良提供重要的靶点和优异基因资源, 为其在生物育种以及提高作物产量和品质等方面提供新思路。

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