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·专题论坛·

植物*GH3*基因家族生物学功能研究进展

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摘要 植物生长素早期响应基因*GH3*编码的酰胺合酶催化生长素、茉莉酸及苯甲酸衍生物与氨基酸结合, 形成相应的氨基酸复合物。当植物体内生长素浓度过高时, GH3蛋白催化生长素与氨基酸结合, 形成的复合物作为生长素贮存库。当生长素浓度过低时, 生长素-氨基酸复合物被蛋白水解酶水解为生长素, 重新参与生长素信号通路, 从而调控植物体内生长素动态平衡。当植物受到生物或非生物胁迫时, GH3蛋白催化茉莉酸和水杨酸与氨基酸结合, 参与植物胁迫响应。该文从GH3蛋白结构、*GH3*基因家族分类及其生物学功能方面总结了双子叶模式植物拟南芥(*Arabidopsis thaliana*)、单子叶模式植物水稻(*Oryza sativa*)及其它植物中*GH3*基因的研究进展, 为植物*GH3*基因家族的深入研究提供参考。

关键词 *GH3*基因, 生长素, 茉莉酸, 水杨酸, 胁迫响应

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植物激素在植物生长发育及环境响应过程中发挥至关重要的作用, 且在低浓度下就能产生明显的生理效应(黎家和李传友, 2019)。因此, 植物激素动态平衡在植物生命周期中受到严格调控。*GH3* (*Gretchen Hagen 3*)基因编码的酰胺合成酶催化生长素(IAA)、茉莉酸(JA)及水杨酸(SA)等植物激素与氨基酸结合, 调节植物激素的浓度, 反馈调节植物的生长发育及胁迫响应过程(Park et al., 2007a)。Hagen等(1984)最早在大豆(*Glycine max*)中发现*GH3*基因, 在施加2,4-二氯苯氧乙酸(2,4-D) 5分钟后, 大豆中*GH3*基因的表达水平迅速上调, 且转录水平不受蛋白质合成抑制剂处理的影响。因此, *GH3*与*AUX*/*IAA*和*SAUR*一起被称为生长素早期响应基因(Hagen and Guilfoyle, 1985, 2002)。之后相继在拟南芥(*Arabidopsis thaliana*)、水稻(*Oryza sativa*)和番茄(*Solanum lycopersicum*)等植物中分别鉴定出20、13和15个*GH3*基因(Conner et al., 1990; Staswick et al., 2005; Terol et al., 2006; Fu et al., 2011; Kumar et al., 2012)。此外, *GH3*基因也存在于非维管束植物中, 如小立碗藓(*Physcomitrella patens*) (Bierfreund et al., 2004)。Staswick等(2002)分析表明, *GH3*基因普遍存在于大多数植物中且家族成员较多, 可能存在基因功能冗余。本文主要综述*GH3*基因在模式植物拟南芥、水稻、番茄及马铃薯(*Solanum tuberosum*)中的研究进展, 以期为揭示*GH3*基因家族的生物学功能提供依据。

1 *GH3*基因及GH3蛋白的结构

植物生长素响应因子(auxin response factor, ARF)与生长素早期响应基因*GH3*启动子区域保守的生长素响应元件(auxin response element, AuxRE) TGTCTC序列特异性结合, 调控*GH3*基因表达(Ulmasov et al., 1995, 1997)。Liu等(1994)在大豆*GmGH3*启动子中发现至少含有3个独立的生长素响应元件, 可被生长素特异性诱导。其中生长素响应元件D1 (25 bp)和D4 (25 bp)包含在一段76 bp的序列中, 它们含有响应生长素所必需的TGTCTC序列(Ulmasov et al., 1995)。第3个响应元件E1含有植物核提取物中蛋白质的强结合位点Hex样元件(TGACGTGGC) (Liu et

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al., 1994)。除生长素响应元件之外，在*GH3*启动子中还发现了其它植物激素和胁迫的响应元件。例如，拟南芥*WES1*启动子区包含脱落酸(ABA)、水杨酸以及干旱和低温响应元件(Park et al., 2007a)。辣椒(*Capsicum annuum*) *CaGH3*启动子区不具有典型的TGTCTC序列，而是具有CATATG序列，并且在上游区域还发现乙烯响应元件(Liu et al., 2005)。谢小芳等(2010)对拟南芥和水稻等植物*GH3*家族基因进行分析，发现*GH3*基因一般包含3–4个外显子，0–6个内含子。其中拟南芥和水稻中存在不包含内含子的基因，说明植物*GH3*基因家族在进化过程中发生了内含子的插入和缺失。

张超(2021)在GH3家族中选取催化底物为JA和IAA的各5个GH3蛋白，研究发现这10个蛋白质二级结构中都包含α5、α6、β8-9和P-loop保守结构和Lys^{428}/Lys^{435}氨基酸残基(Wojtaczka et al., 2022)。而2个亚家族蛋白质功能的差异是由于亚家族I特异的Ser^{151}残基可以结合异亮氨酸，亚家族II特异的Lys^{146}残基与碱性氨基酸结合。Terol等(2006)对不同物种的49个GH3蛋白进行比对，发现所有GH3蛋白中都包含高度保守的^{192}SS (T) GTS (T) AG (Q, R) ERK^{202} (基序1)、^{392}YASSE^{396} (基序2)和^{484}YRVGD^{488} (基序3) 3个基序，高度保守的基序可能对应于GH3蛋白的功能结构域；他们还发现催化底物为IAA的蛋白中都具有^{C}motif, ^{D}motif存在于催化底物为JA的蛋白中, ^{E}motif存在于催化底物活性未知的拟南芥蛋白中。

拟南芥*AtGH3.11*/*JAR1* (茉莉酸抗性1)编码的酶与荧光素酶结构相似，荧光素酶属于腺苷形成酶家族(ANL adenylating enzymes)，该家族的特征是蛋白质中含有3个参与ATP/AMP结合的短且保守性较低的序列(Chang et al., 1997; Staswick et al., 2002; Gulick, 2009)。ATP存在时，腺苷形成酶催化2步反应：首先是腺苷酸酰基化，形成酰基-AMP中间产物；其次为氨基酸转移到腺苷酸化的酰基酸中间体(Gulick, 2009)。腺苷形成酶晶体结构是由1个大的N-末端结构域和1个较小的C-末端结构域组成的双结构域，在反应中C-末端结构域旋转180°，使活性位点在开放(ATP结合)和闭合(AMP结合)形式之间切换，分别在2步反应中允许底物结合(Gulick, 2009; Westfall et al., 2012; Round et al., 2013; Chen et al., 2017)。

2 *GH3*基因家族分类及其功能

拟南芥*GH3*基因家族有20个成员。根据蛋白同源性比对及其作用底物的特异性将GH3蛋白分为3个亚家族，它们分别催化JA、IAA和SA与氨基酸的结合(Staswick et al., 2002)。

GH3亚家族I催化JA与氨基酸结合，形成具有生物活性的茉莉酸异亮氨酸复合物(JA-Ile) (Staswick et al., 2002)。茉莉酸是植物体内重要的脂质激素，在植物胁迫响应中发挥重要作用。同时，茉莉酸作为重要的生长发育调节物质，参与调节植物生长发育的诸多过程(Wasternack and Hause, 2013; 李梦莎和阎秀峰, 2014; 黎家和李传友, 2019)。当植物受到机械损伤或昆虫啃食时，受伤部位迅速积累的JA被JAR1/AtGH3.11催化形成JA信号转导中的主要活性复合物JA-Ile。JA-Ile先被SCF^{COI1}受体识别，后招募茉莉酸响应抑制因子JAZ (jasmonate ZIM-domain)，形成SCF^{COI1}-JA-Ile-JAZ三元复合物(Yan et al., 2018)。形成的三元复合物使JAZ被26S蛋白降解，从而解除对转录因子(transcription factors, TF) MYC2的抑制作用，激活JA响应基因的表达(图1) (李梦莎和阎秀峰, 2014)。

GH3亚家族II催化IAA与氨基酸结合。生长素在植物整个生长发育过程中都发挥关键作用，它通过调控相关基因的表达参与植物根部形成、顶端优势、衰老及逆境胁迫响应等生理过程(Hagen and Guilfoyle, 2002)。植物体内普遍存在的天然生长素是吲哚-3-乙酸(IAA)。IAA活性由动态平衡、极性运输和生长素响应来调节(Qin et al., 2005)。GH3蛋白在维持植物体IAA动态平衡中发挥重要作用。当植物体内IAA浓度过高时，GH3蛋白催化IAA与氨基酸结合，形成IAA-氨基酸复合物使其失活，形成的复合物中IAA-Asp和IAA-Glu通过氧化代谢途径降解，也有一些复合物如IAA-Ala和IAA-Leu可作为植物体内的生长素贮存库。当植物体内IAA浓度过低时，作为贮存库的IAA-氨基酸复合物被蛋白水解酶水解，重新释放出IAA，返回到生长素信号转导途径，以此调节植物体内生长素的动态平衡(图2) (Westfall et al., 2010)。

此外，催化底物未知的GH3蛋白属于GH3亚家族III。目前仅发现*AtGH3-12*参与SA信号转导途径(Jagadeeswaran et al., 2007; Nobuta et al., 2007;

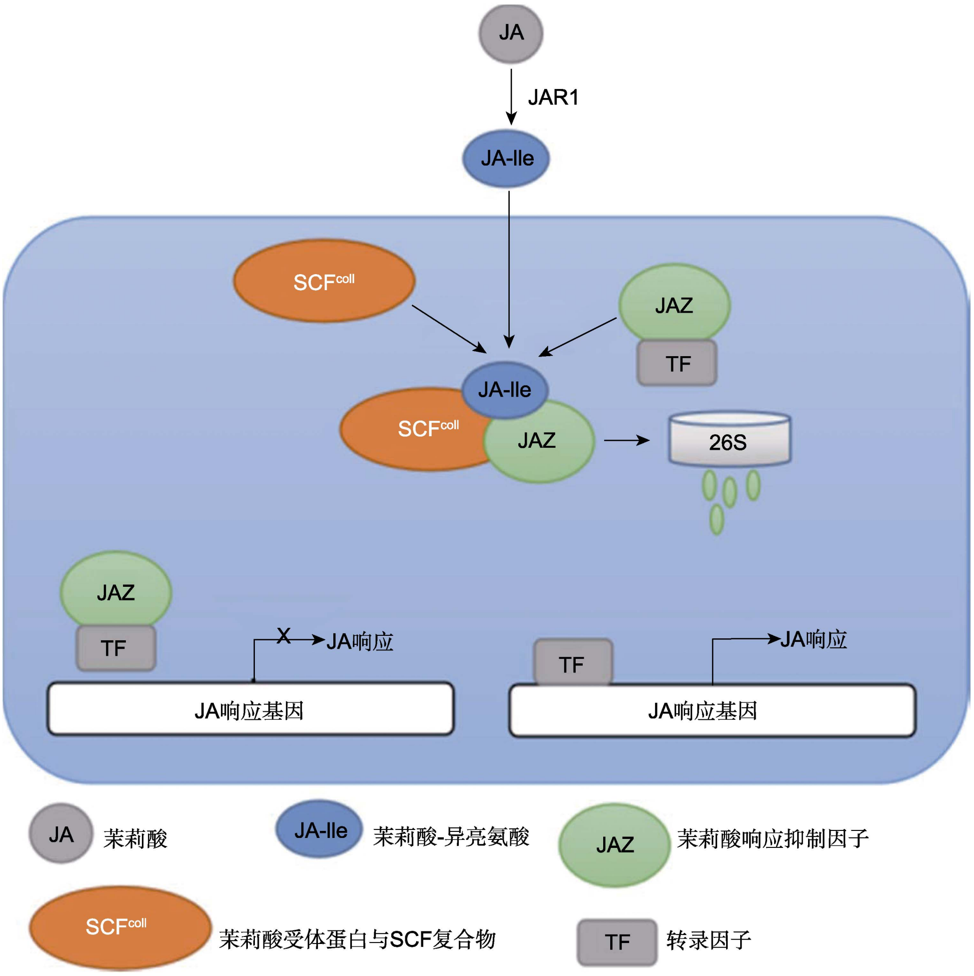

图1 茉莉酸信号转导通路(参考李梦莎和阎秀峰, 2014; Lee et al., 2022)

Figure 1 Jasmonic acid signal transduction pathway (refer to Li and Yan, 2014, in Chinese; Lee et al., 2022)

Okrent et al., 2009)。

3 拟南芥*GH3*基因家族的生物学功能

拟南芥20个*GH3*基因可分为3个亚家族。亚家族I包含*AtGH3.10*和*AtGH3.11*; 亚家族II包含*AtGH3.1*、*AtGH3.2*、*AtGH3.3*、*AtGH3.4*、*AtGH3.5*、*AtGH3.6*、*AtGH3.9*和*AtGH3.17*; 其余拟南芥*GH3*基因归为亚家族III (Staswick et al., 2002)。研究表明*GH3*基因在拟南芥生长发育及环境响应中发挥重要作用(表1; 图3)。

3.1 *GH3*基因家族参与生长发育调控

研究表明*GH3*家族基因调控拟南芥生长发育及形态建成。由*AtGH3s*基因表达引起的游离生长素含量变化影响拟南芥植株构型及根系发育。过表达*AtGH3.6*获得拟南芥*dfl1-D*矮化株系, 较野生型茎更短、叶更小和侧根数更少(Nakazawa et al., 2001)。*YDK1*/*AtGH3.2*过表达株系*ydk1-D*矮化突变体表现主根短、侧根数减少和顶端优势减弱, 并且*YDK1*表达受生长素响应因子ARF7调节(Takase et al., 2004)。*AtGH3.5*过表达株系同样表现出生长素缺陷表型, 具有更小的卷曲莲座叶, 更耐外源生长素类物质且主根缩短、侧根数减少(Zhang et al., 2007)。*AtGH3.9*过表达株系除了植株矮化外, 还表现出雄蕊变短和果荚短小(周苹等, 2015)。*AtGH3.17*过表达株系表现出短根、叶片卷曲、叶柄缩短和矮化等表型, 并且IAA-Glu含量显著增加, 油菜素内酯(BL)合成途径相关基因*DWF4*和*CPD*的表达量明显增高, 表明*AtGH3.17*除调节IAA

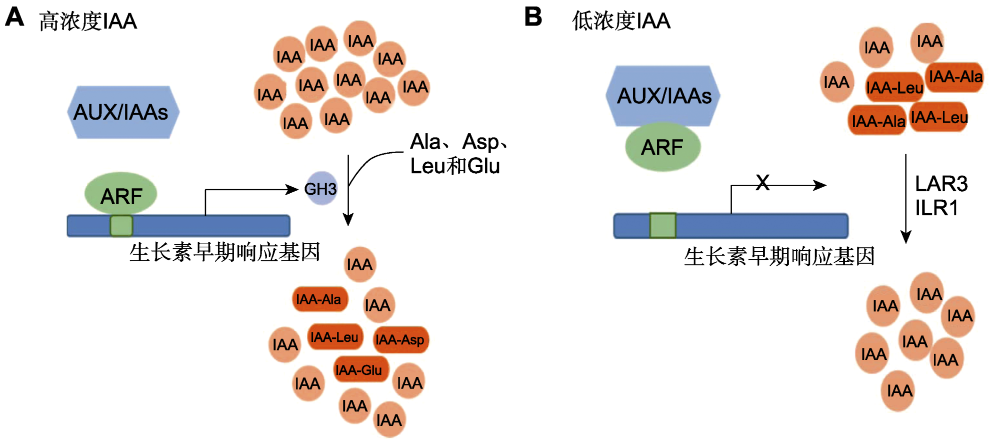

图2 植物体内生长素(IAA)动态平衡(参考Hagen and Guilfoyle, 2002; Woodward and Bartel, 2005)
(A) IAA浓度较高时, ARF与Aux/IAAs二聚体分离, ARF结合到相应的AuxREs并激活*GH3*表达, 催化IAA与氨基酸结合; **(B)** IAA浓度较低时, ARF与Aux/IAAs形成二聚体并关闭AuxREs, *GH3*基因转录受到抑制, 作为生长素贮存库的IAA-Ala和IAA-Leu由酰胺水解酶水解, 重新释放出IAA。

Figure 2 Auxin (IAA) dynamic equilibrium in plants (refer to Hagen and Guilfoyle, 2002; Woodward and Bartel, 2005)
(A) Under higher IAA concentration, ARF splits with Aux/IAAs dimer, and ARF binds to AuxREs and activates the expression of *GH3*, which catalyzes the binding of IAA to amino acids; **(B)** Under lower IAA concentration, ARF forms a dimer with Aux/IAAs and turns off AuxREs, *GH3* gene transcription is inhibited, and IAA-Ala and IAA-Leu, which are auxin reservoirs, are hydrolyzed by amidohydrolase to release IAA again.

表1 拟南芥*GH3*基因的生物学功能
Table 1 Functions of *GH3* genes in *Arabidopsis thaliana*

基因编号	基因名称	功能	参考文献
At2g14960.1	*AtGH3.1*	调节吲哚-3-乙酸(IAA)动态平衡	Staswick et al., 2005
At4g37390.1	*AtGH3.2/YDK1*	调控株高、主根伸长、侧根数与顶端优势	Takase et al., 2004; Staswick et al., 2005
At4g27260.1	*AtGH3.5/AtGH3a/WES1*	调控主根伸长及侧根数, 参与水杨酸(SA)与光信号途径	Staswick et al., 2005; Park et al., 2007b; Zhang et al., 2007, 2008
At5g54510.1	*AtGH3.6/DFL1*	调控生长素含量, 影响株高、叶形态、侧根数及非生物胁迫响应, 参与光信号途径, 影响下胚轴伸长	Nakazawa et al., 2001; 刘晓东等, 2016
At2g47750.1	*AtGH3.9*	调控株高、花器官以及果实发育	周苹等, 2015
At4g03400.1	*AtGH3.10/DFL2*	参与光信号途径, 影响下胚轴伸长	Takase et al., 2003
At2g46370.1	*AtGH3.11/JAR1/FIN219*	调控茉莉酸(JA)水平, 影响抗病性, 参与光信号转导途径	Staswick et al., 1998; van Loon et al., 1998; Overmyer et al., 2000; Rao et al., 2000; Hsieh et al., 2000
At5g13320.1	*AtGH3.12/PBS3/GDG1*	调控SA水平, 影响植物抗病性	Jagadeeswaran et al., 2007; Nobuta et al., 2007
At5g13370.1	*AtGH3.15*	调节吲哚丁酸(IBA)水平, 影响主根伸长与侧根数	Sherp et al., 2018
At1g28130.1	*AtGH3.17*	调控株高、根系发育及叶片形态, 参与油菜素内酯(BL)信号途径	周淑瑶等, 2023

含量外还参与BR信号途径(周淑瑶等, 2023)。值得注意的是, *AtGH3.15*过表达株系在主根伸长和侧根密度上对吲哚丁酸(IBA)处理有抗性, 但对IAA或JA处理无抗性, 说明*AtGH3.15*可能通过调节过氧化物酶体转化为IAA的IBA水平, 在生长素平衡中发挥作用(Sherp et al., 2018)。*atgh3.1-1*、*atgh3.2-1*、*atgh3.5-1*、*atgh3.9*和*atgh3.17-1*等单基因突变体可能由于存在基因功能冗余而未表现出明显的表型, 但因为突变体中生长素动态平衡调节机制受损导致主根生长对外源生长素类物质敏感(Staswick et al., 2005; Khan and Stone, 2007)。

3.2 *GH3*基因家族参与环境响应

植物在生长发育过程中常受到生物与非生物胁迫, JA和SA作为信号分子在植物胁迫响应中发挥重要作用。目前, *GH3*基因参与拟南芥胁迫响应的研究主要集中在少数几个*AtGH3s*基因中。Staswick等(1998)研究发现, *JAR1/AtGH3.11*突变体*jar1-1*、*jar1-2*和*jar1-4*经土壤腐霉菌侵染后, 病症比野生型更明显, 并表现对外源JA的敏感性降低及内源JA-Ile水平降低, 说明*JAR1*参与JA信号转导途径, 增强植物抗病性。对*JAR1*的进一步研究表明, *JAR1*参与非致病性根瘤菌引发的系统获得抗性(systemic acquired resistance, SAR), 还能减少臭氧对拟南芥的损伤(van Loon et al., 1998; Overmyer et al., 2000; Rao et al., 2000)。Zhang等(2007)发现*AtGH3.5*除调节IAA含量外, 还参与SA信号转导途径, *AtGH3.5*过表达导致SA积累增加, 及响应无毒病原体的病程相关蛋白PR-1表达量增加。研究表明, *atgh3.5*通过依赖NPR1和独立途径增强SA介导的防御反应(Zhang et al., 2008)。此外, 在*AtGH3.12*/*PBS3*等位基因*GDG1*突变体*gdg1*中, SA依赖性基因表达和防御受损, 响应病原体的SA积累受抑制。*gdg1*所有防御相关表型都可通过外源施加SA来挽救, 表明*GDG1*位于SA上游, 调节SA水平, 进而增强对病原体的抗性(Jagadeeswaran et al., 2007; Okrent et al., 2009)。*AtGH3.6*过表达株系游离IAA的含量减少, 导致抗旱性和耐盐性均低于野生型; 在干旱、ABA和高盐胁迫下, *AtGH3.6*基因的高表达抑制逆境响应基因*RD22*、*KIN1*、*RD29A*和*DREB1A*的表达, 表明*AtGH3.6*负调控拟

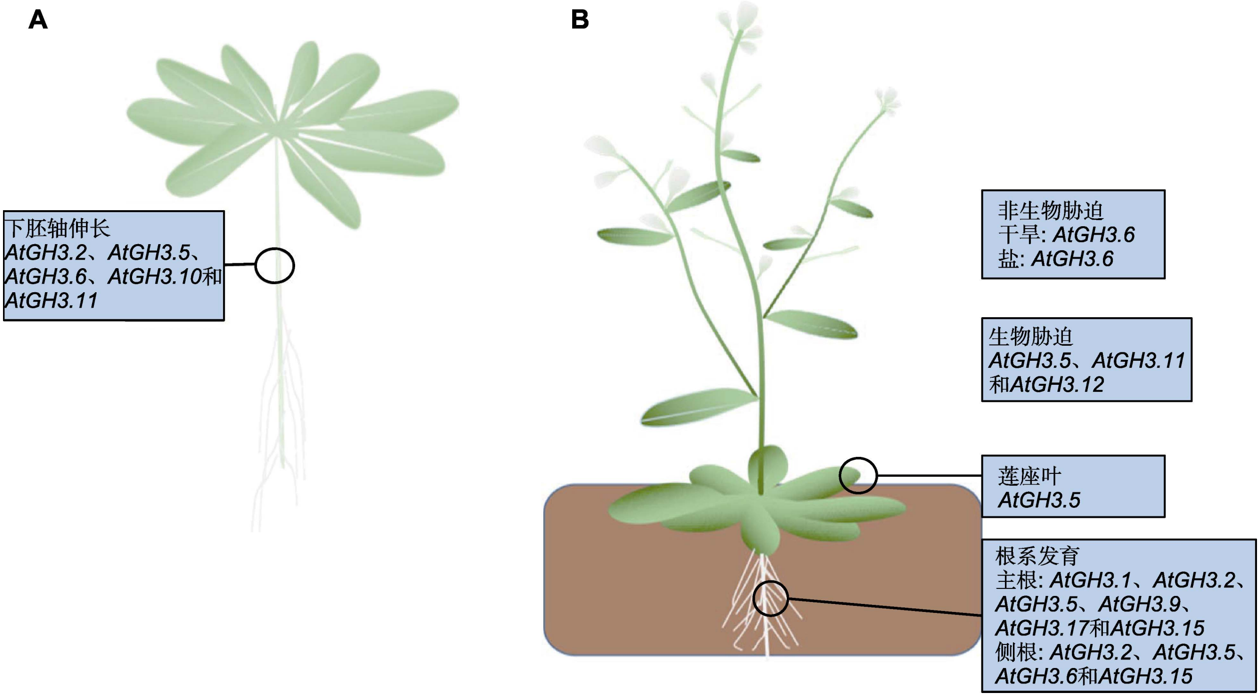

图3 拟南芥生长发育中*GH3*基因的功能(参考Staswick et al., 1998, 2005; van Loon et al., 1998; Hsieh et al., 2000; Overmyer et al., 2000; Rao et al., 2000; Nakazawa et al., 2001; Takase et al., 2003, 2004; Park et al., 2007b; Jagadeeswaran et al., 2007; Nobuta et al., 2007; Zhang et al., 2007; 2008; 周苹等, 2015; 刘晓东等, 2016; Sherp et al., 2018; 周淑瑶等, 2023)
(A) 拟南芥幼苗; **(B)** 拟南芥成熟植株

Figure 3 The function of *GH3* genes in *Arabidopsis* growth and development (refer to Staswick et al., 1998, 2005; van Loon et al., 1998; Hsieh et al., 2000; Overmyer et al., 2000; Rao et al., 2000; Nakazawa et al., 2001; Takase et al., 2003, 2004; Park et al., 2007b; Jagadeeswaran et al., 2007; Nobuta et al., 2007; Zhang et al., 2007; 2008; Zhou et al., 2015, in Chinese; Liu et al., 2016, in Chinese; Sherp et al., 2018; Zhou et al., 2023, in Chinese)
(A) *Arabidopsis* seedling; **(B)** *Arabidopsis* mature plant

南芥逆境响应(刘晓东等, 2016)。光是影响植物生长发育的重要环境因素之一。植物响应外界光信号, 通过合成生长素等植物激素进一步灵活地调控基因表达。外源光信号和生长素信号通路之间的整合使植物得以协调外界环境刺激与内在生长发育, 达到适应环境、优化生长的目的。Xu等(2018)发现了生长素信号与光信号互作的新机制——蓝光受体CRY1和光敏色素B (phyB)分别与AUX/IAA互作, 抑制生长素引起的AUX/IAA蛋白降解, 减弱生长素信号, 进而抑制下胚轴伸长。拟南芥*GH3*基因突变后, 在受到光信号调控时表现出一定的表型。*dfl1-D*在蓝光、红光和远红光下具有较短的下胚轴, 且侧根生长受抑制(Nakazawa et al., 2001)。红光和蓝光下*DFL2*过表达株系同样表现出短的下胚轴, 而在红光下反义表达时导致长下胚轴表型(Takase et al., 2003)。远红光下*AtGH3.5*过表达株系*wes1-D*下胚轴明显比对照短, 但突变体*wes1*下胚轴比对照长(Park et al., 2007b)。综上, *AtGH3s*基因参与生长素与光信号途径, 共同调节拟南芥下胚轴伸长。此外, *AtGH3.11*等位基因*FIN219*突变体*fin219*在连续远红光下表现长下胚轴表型, 并作用于光形态建成抑制因子COP1的上游, 推测远红光通过调控*FIN219*基因, 进而负调控*COP1* (McNellis et al., 1994; Osterlund et al., 1999; Hsieh et al., 2000)。

4 水稻*GH3*基因家族的生物学功能

水稻*GH3*家族13个基因分2个亚家族, *OsGH3.3*、*OsGH3.5*、*OsGH3.6*和*OsGH3.12*属于亚家族I, 其余*GH3*基因属于亚家族II。目前水稻*GH3*家族基因的生物学功能相继被揭示, 研究表明*GH3*基因在水稻生长发育、胁迫响应以及基础免疫等方面起作用(表2; 图4)。

4.1 *GH3*基因家族参与生长发育调控

水稻株型是决定其产量的核心因素之一。水稻株型的形成主要取决于植株高度、分蘖数及分蘖角度等。其中, 生长素的含量和分布对植株形态建成产生重要影响。水稻根系类型为须根系, 不定根和侧根是其生长后期营养和水分吸收的主要器官, 根系发育同样影响水稻生长发育及产量。*OsGH3.8*过表达植株表现出矮化和分蘖数增加, 且具有更短的根和更少的不定根, 可育性和种子发芽率大幅降低(Ding et al., 2008)。*TLD1*/*OsGH3.13*功能获得突变体*tld1-D*分蘖数增加, 叶夹角增大, 矮化, 还表现出细秆、种子细长、短穗和侧根减少。在正常生长条件下, 地上部组织中*TLD1*被抑制, 但在干旱胁迫下被显著诱导(Zhang et al., 2009)。*OsGH3.2*过表达株系表现出矮化、叶片变小、不定根和根毛减少等表型(Du et al., 2012)。Liu等(2022)发现, 与野生型相比, *osgh3.2*突变体表现出短根, 且具有更短的不定根及更多的侧根与不定根。此外, 水稻中过表达*OsGH3.1*获得*LC1*过表达株系, 因其游离IAA含量减少而表现出半矮化和叶夹角增大等表型, 且对BR信号敏感(Zhao et al., 2013)。

4.2 *GH3*基因家族表达受ARF等转录因子调节

生长素处理使水稻细胞内*microRNA167*水平升高, 降低靶基因*OsARF8*的表达, 受OsARF8正向调控的*OsGH3.2*表达水平降低(Yang et al., 2006)。OsARF19正调控*OsGH3.5*的表达, 调节生长素含量,

表2 水稻*GH3*基因的生物学功能

Table 2 Functions of *GH3* genes in rice

基因编号	基因名称	功能	参考文献
LOC_Os01g57610.1	*OsGH3.1*/*LC1*	调控株型, 参与油菜素内酯(BL)信号途径与抗病性	Domingo et al., 2009; Zhao et al., 2013
LOC_Os01g55940.1	*OsGH3.2*	调控株型和根系发育, 响应低温和干旱胁迫	Du et al., 2012; Liu et al., 2022
LOC_Os01g12160.1	*OsGH3.3*	参与茉莉酸(JA)信号转导途径	Hui et al., 2019
LOC_Os05g50890.1	*OsGH3.5*/*OsJAR1*	调控水稻株高和叶夹角, 参与光信号途径	Riemann et al., 2008; Zhang et al., 2015
LOC_Os05g05180.2	*OsGH3.6*	参与JA信号转导途径	Hui et al., 2019
LOC_Os07g40290.1	*OsGH3.8*	调控株型及根系发育, 影响种子发芽率和可育性, 参与抗病性	Ding et al., 2008
LOC_Os11g08340.1	*OsGH3.12*	参与JA信号转导途径	Hui et al., 2019
LOC_Os11g32520.1	*OsGH3.13*	调控株型及根系发育, 响应干旱胁迫	Zhang et al., 2009

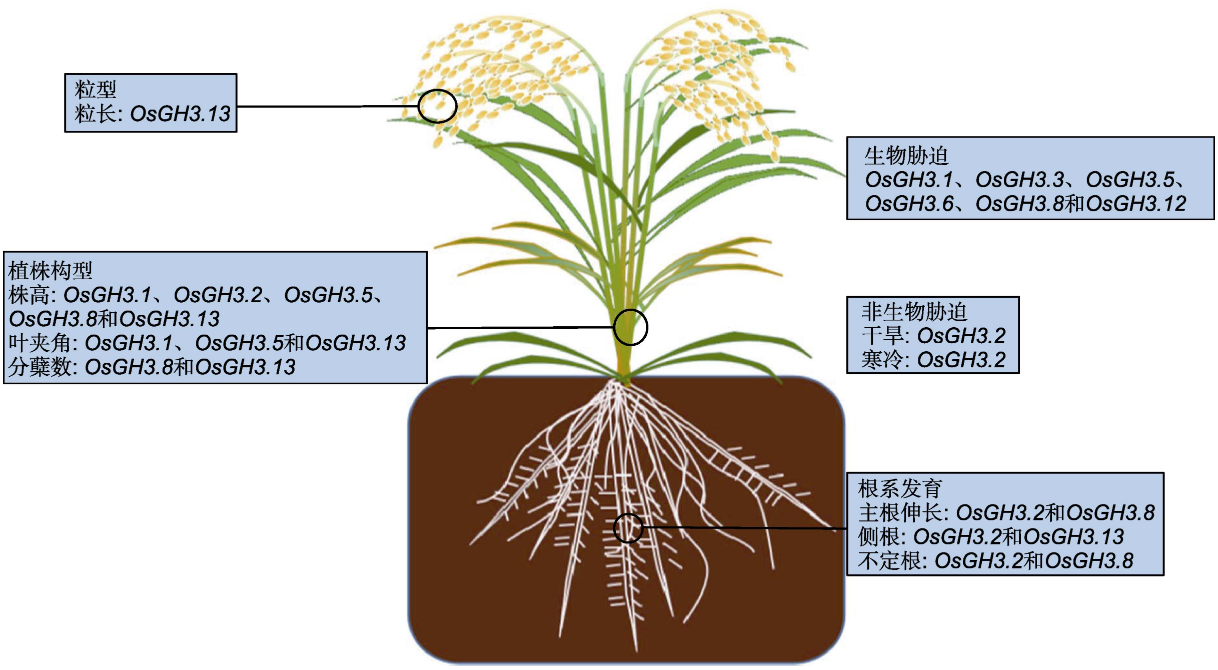

图4 水稻生长发育中*GH3*基因的功能(参考Yang et al., 2006; Qiu et al., 2007; Ding et al., 2008; Domingo et al., 2009; Tao et al., 2009; Zhang et al., 2009, 2015; Du et al., 2012; Zhao et al., 2013; Dai et al., 2018; Hui et al., 2019; Liu et al., 2022)

Figure 4 The function of *GH3* gene in rice during growth and development (refer to Yang et al., 2006; Qiu et al., 2007; Ding et al., 2008; Domingo et al., 2009; Tao et al., 2009; Zhang et al., 2009, 2015; Du et al., 2012; Zhao et al., 2013; Dai et al., 2018; Hui et al., 2019; Liu et al., 2022)

从而控制水稻株型，*OsARF19*与*OsGH3.5*过表达株系都表现出叶夹角增大和矮化等表型(Zhang et al., 2015)。Dai等(2018)研究发现，*microRNA156*负调控靶基因*OsSPL7*的表达，减弱*OsSPL7*对*OsGH3.8*表达的抑制作用，引起IAA含量的变化，从而影响水稻株高与分蘖数。*OsbZIP49*过表达株系中IAA-Asp和IAA-Glu积累增加，局部游离生长素与色胺水平降低，表明OsbZIP49直接结合*OsGH3.2*和*OsGH3.13*启动子区并激活其表达，从而调控局部生长素含量，影响水稻分蘖角度(Ding et al., 2021)。

4.3 *GH3*基因家族参与环境响应

病原菌感染可诱导IAA积累，而IAA诱导膨胀蛋白的表达，使细胞壁松弛。松弛的细胞壁是植物生长的关键，但也使植物容易受到病原菌感染。*OsGH3.1*和*OsGH3.8*过表达引起游离IAA含量显著降低，抑制细胞生长和细胞壁松弛，从而增强水稻对病原菌的抗性(Ding et al., 2008; Domingo et al., 2009)。*OsGH3.2*过表达株系游离IAA含量降低，氧化损伤减轻，质膜透性降低，表现出较强的耐冷性，并对干旱胁迫敏感(Du et al., 2012)。*OsWRKY13*和*OsWRKY45*是JA信号响应正调控基因(Qiu et al., 2007; Tao et al., 2009)。Hui等(2019)发现这2个基因在*OsGH3.3*、*OsGH3.5*、*OsGH3.6*和*OsGH3.12*过表达株系中被显著激活表达，表明这4个基因通过调节JA响应基因的表达增强水稻对白叶枯病菌的抗性。*OsGH3.5*/*OsJAR1*为*AtJAR1*的同源基因，在水稻JA和光信号转导途径中发挥相同作用(Riemann et al., 2008)。在远红光和蓝光下，*osjar1*突变体胚芽鞘比野生型更长，表明*OsJAR1*参与光下胚芽鞘伸长的抑制。

5 其它植物中*GH3*基因家族

目前，我国主要经济作物番茄和柑橘类以及粮食作物马铃薯和小麦(*Triticum aestivum*)中*GH3*的生物学功能研究有了新进展(表3)。

5.1 番茄*GH3*基因家族

在茄科植物番茄中鉴定到15个*GH3*家族基因。王慧敏(2015)研究发现，与野生型相比，*SlGH3.2*过表达株

表3 其它植物*GH3*基因的生物学功能

Table 3 Functions of *GH3* genes in other plants

物种名称	基因编号	基因名称	功能	参考文献
番茄	*Solyc01g107390.4.1*	*SlGH3.2*	调控株高、结实率及种子大小	王慧敏, 2015; 艾国, 2017
	Solyc02g092820.4.1	*SlGH3.4*	调节吲哚-3-乙酸(IAA)含量, 影响抗病性	陈潇, 2017
	Solyc07g054580.3.1	*SlGH3.8*	调控IAA含量, 影响植物生长发育	Sun et al., 2020
	Solyc12g005310.2.1	*SlGH3.15*	调控株高、叶片形态及侧根数目	艾国, 2017
马铃薯	–	*StGH3.1*/*StGH3.5*	参与茉莉酸(JA)信号转导途径	张超, 2021
柑橘	*Cs1g22140*	*CrGH3.1*	调节IAA含量, 影响抗病性	Chen et al., 2016
	Cs8g04610	*CrGH3.6*	调控株高和叶片形态, 影响抗病性	邹修平等, 2019
	Ciclev10017968m.g/ *Ciclev10019393m.g*	*CrGH3.4*/*CrGH3.7*	参与胁迫响应	庞少萍等, 2015
小麦	*TraesCS1A02G425100.1*/ *TraesCS2B02G210600.1*/ *TraesCS3A02G301200.1*/ *TraesCS3B02G335300.1*/ *TraesCS3D02G300600.1*	*TaGH3.2a*/ *TaGH3.7*/ *TaGH3.11*/ *TaGH3.13*/ *TaGH3.15*	参与根系发育和非生物胁迫响应	Jiang et al., 2020

系明显矮化，结实率低，且种子显著变小。*SlGH3.4*过表达株系根中游离IAA浓度降低，显著抑制菌根共生和一些生长素响应基因表达，同时丛枝表现为生长素缺陷的发育畸形(陈潇，2017)。在番茄中过表达*SlGH3.15*基因，过表达株系表现出由节间距缩短所致的矮化、叶片卷曲及侧根变少，且过表达植株体内游离IAA含量减少(艾国，2017)。番茄YABBY2b转录因子直接结合*SlGH3.8*启动子并抑制其表达，正调控植物生长；*yabby2b*突变体表现出矮化和较小的花和果实，表明*SlGH3.8*负调控植物的生长发育(Sun et al., 2020)。

5.2 马铃薯*GH3*基因家族

马铃薯是我国五大主食之一，其营养价值高、适应能力强且产量大，是全球第三大粮食作物，仅次于小麦和玉米(李超等, 2021)。*StGH3.1*和*StGH3.5*具有与拟南芥*JAR1*相似的功能，*StGH3.1*和*StGH3.5*过表达株系中JA-Ile含量在不同胁迫处理时间下均明显高于其它株系，而RNAi株系的植物激素含量则较低。青枯菌侵染*RNAistgh3.1*和*RNAistgh3.5*时马铃薯叶片出现萎蔫；接菌诱导的RNAi干扰植株内菌落数和叶片过氧化物积累量均高于其它株系(张超, 2021)。

5.3 柑橘*GH3*基因家族

目前已在柑橘中鉴定出11个*GH3*基因，萘乙酸(NAA)和柑橘溃疡病诱导*CrGH3.1*和*CrGH3.6*基因的表达(Chen et al., 2016)。*CrGH3.1*过表达显著降低游离生长素的含量，抑制细胞分裂和伸长，从而增强抗病能力并抑制病原体的传播。*CrGH3.6*过表达株系表现出植株分枝增多且下垂，叶片向上卷曲、变小及颜色浅，气孔密度增大，表皮细胞变短，溃疡病抗性显著增强；*CrGH3.6*过表达株系游离IAA和JA含量均显著降低，而SA含量显著增高，暗示*CrGH3.6*可能参与IAA、JA和SA信号转导途径(邹修平等，2019)。*CrGH3.4*和*CrGH3.7*受低温、高盐以及PEG (干旱)胁迫诱导，表明其参与柑橘的逆境响应。*CrGH3.4*和*CrGH3.7*在叶中受ABA、ACC (乙烯前体)、MeJA和SA诱导，在根中却受抑制，呈现相反的表达模式(庞少萍等, 2015)。

5.4 小麦*GH3*基因家族

Jiang等(2020)研究表明, 36个TaGH3蛋白可分3组。在盐和渗透胁迫下，大多数候选*TaGH3*基因在根中比叶中表达水平更高，暗示这些蛋白参与根的生长发育。一些*TaGH3s*响应非生物胁迫而被显著诱导，特别是在干旱条件下, *TaGH3.2a*、*TaGH3.7*、*TaGH3.11*、*TaGH3.13*和*TaGH3.15*被上调。qRT-PCR分析表明，盐胁迫和渗透胁迫下，很多*TaGH3*基因在小麦叶片和根中的表达存在差异，表明*TaGH3*家族基因在响应环境胁迫中发挥重要作用。

6 总结与展望

*GH3*是生长素早期响应基因家族之一，其编码的酰

胺合成酶是植物激素水平的调节因子。已有研究表明GH3催化植物激素与氨基酸结合，形成的植物激素-氨基酸复合物维持IAA、JA和SA的动态平衡或活性，在优化植物生长及增强抗逆性方面发挥重要作用。*GH3*与ARF和*AUX*/*IAA*作为生长素信号通路的重要组成部分协同发挥作用，调控植物的生长发育。ARF调控*GH3*的表达，引起游离IAA含量变化，影响农作物株高、叶夹角、分蘖角度及根系发育，进而影响植株整体发育。值得注意的是，拟南芥ARF17对不同*GH3*基因的调控作用差异很大，对某些*GH3*基因起正调控作用，对另一些*GH3*基因则具有负调控作用(Mallory et al., 2005)，表明植物生长素响应因子对植物*GH3*基因的作用情况复杂，有待进一步研究。此外，在生物或非生物胁迫下，*GH3*通过调控植物激素动态平衡来影响植物生长发育，还通过激活JA及SA等信号途径来提高植物的抗逆性。然而，目前对于*GH3*参与SA信号转导途径的具体作用机制尚不明确。在多种植物*GH3*基因启动子区还发现赤霉素、脱落酸和茉莉酸甲酯等响应以及胁迫响应相关调控元件，这对于*GH3*基因在植物生长发育和胁迫响应中潜在功能的挖掘具有一定意义。对多种植物的生物信息学分析也鉴定出更多的*GH3*基因，但*GH3*基因功能研究目前主要集中在拟南芥和水稻。由于植物GH3家族成员较多，存在基因功能冗余，因此大多数植物中GH3的生物学功能尚不清楚。CRISPR/Cas9作为常用的基因编辑系统，是实现基因精准编辑的有效工具，因其能靶向任意序列、同时靶向多个靶点且切割效率高而被广泛应用于基因功能研究(Xie et al., 2014)。基于CRISPR/Cas9系统改造升级建立的CRISPR/dCas9是用于调控基因组转录与表观遗传修饰的系统，该系统中dCas9蛋白失去剪切DNA的能力，但仍可与VP64和EDLL等转录激活因子融合，激活特定基因的表达(Lowder et al., 2017, 2018)。因此，CRISPR/Cas9和CRISPR/dCas9系统的灵活性和靶位点选择的广泛性为植物*GH3*家族功能冗余基因研究提供了有力支持。此外，逐渐成熟的单细胞测序技术通过分析细胞之间遗传和蛋白质信息的差异，在植物单细胞水平进行基因组或转录组测序分析，可帮助人们深入理解*GH3*在调控植物细胞发育中的分子机制及相关基因调控网络，推进*GH3*基因在植物生长发育过程中的生物学功能研究。

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Research Advances in Biological Functions of *GH3* Gene Family in Plants

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Abstract The amide-synthase encoded by the auxin early response gene *GH3* in plants could catalyze the combination of auxin, jasmonic acid and benzoic acid derivatives with amino acids respectively to form the corresponding amino acid complex. Under the high auxin concentration in plants, GH3 protein catalyzes the combination of auxin and amino acid, which acts as the auxin sink in plants. Under the low auxin concentration, the auxin-amino acid complex is hydrolyzed to auxin by proteolytic enzymes and re-participates in the auxin signaling pathway, thus regulating the dynamic balance of auxin levels in plants. When plants are subjected to biological or abiotic stress, GH3 protein catalyzes jasmonic acid and salicylic acid to bind to amino acids and participate in plant stress response. In this study, we summarized the research progress of *GH3* gene in dicotyledonous model plant *Arabidopsis thaliana*, monocotyledonous model plant rice, and the other plants from the aspects of GH3 protein structure, *GH3* gene family classification and its function, and provided some references for further study of *GH3* gene family in plants.

Key words *GH3* gene, auxin, jasmonic acid, salicylic acid, stress response

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