尿囊素在植物抗逆应答中的作用

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摘要: 在高等植物中, 尿囊素是嘌呤降解途径上的一种中间产物, 不仅是氮素转运和存储过程中的重要物质, 而且在植物抗逆应答过程中也发挥着重要作用。本文总结了植物尿囊素的代谢途径、逆境胁迫响应以及尿囊素信号调控和转导的最新研究进展, 并对未来尿囊素在植物抗逆生理和育种方面的研究与应用做出展望。

关键词: 尿囊素; 代谢途径; 胁迫应答; 信号转导

尿囊素(allantoin, $C_4H_6O_3N_4$)是植物氮素循环系统的重要成员。自上世纪初Macalister (1912)首次在聚合草(*Symphytum officinale*)中提取出后, 尿囊素在植物体内一直被认为是嘌呤分解过程中的一种中间代谢物, 参与植物体内氮素转运、存储以及再利用等活动(Matsumoto等1978; Smith和Atkins 2002; Rentsch等2007)。此外, 国内早期的研究显示外源施加尿囊素可提高农作物的产量(谢德意等1993; 凌杏元和傅庭治1995; 许鸿源等1997)。近年来研究发现, 植物在病原菌侵染(Montalbini 1991)、低温(Kaplan等2004; Wang等2012)、营养缺乏(Nikiforova等2005)、暗处理(Brychkova等2008)、高盐(Kanani等2010; Wang等2016; Lescano等2016)以及干旱(Oliver等2011; Silvente等2012; Yobi等2013)等胁迫条件下, 均伴有尿囊素的积累。同时, 体内较高的尿囊素水平或者外施尿囊素又可诱导植物体的一系列胁迫应答反应(Takagi等2016; Watanabe等2014b)。由此可见, 尿囊素在植物的抗逆应答中也发挥着重要作用。本文旨在通过综述植物尿囊素的代谢途径及其参与植物胁迫响应的相关研究进展, 梳理尿囊素在植物抗逆应答过程中的作用方式, 拓展对尿囊素在植物抗逆生理中的认识, 为植物抗逆机理以及抗逆育种的研究提供新思路。

1 植物尿囊素的代谢途径

高等植物体内尿囊素合成的主要途径是通过嘌呤降解过程完成的(图1)。腺嘌呤核苷酸(adenosine monophosphate, AMP)与鸟嘌呤核苷酸(guanosine monophosphate, GMP)经过脱氨作用后, 均转化为黄嘌呤(xanthine), 又在黄嘌呤脱氢酶(xanthine dehydrogenase, XDH)的催化下生成尿酸(uric acid)。尿酸在尿酸氧化酶(urate oxidase, UOX)、尿囊素合酶(allantoin synthase, AS)作用下生成尿

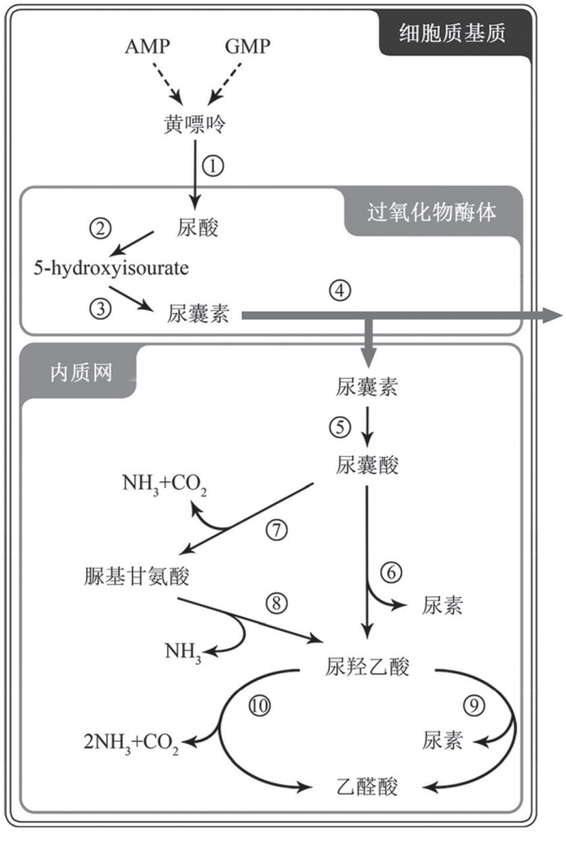

图1 植物尿囊素的代谢过程

Fig.1 Metabolic pathway of allantoin in plants

参照Zrenner等(2006)和Lescano等(2016)文献修改。①黄嘌呤脱氢酶; ②尿酸氧化酶; ③尿囊素合酶; ④酰脲渗透酶与尿囊素转运蛋白; ⑤尿囊素酶; ⑥尿囊酸酶; ⑦尿囊素脱氨酶(allantoin deaminase); ⑧脲基甘氨酸氨基水解酶(ureidoglycine amidohydrolase); ⑨尿羟乙酸裂解酶; ⑩尿羟乙酸水解酶。

收稿 2016-12-16 **修定** 2017-05-31
资助 河北省自然科学基金(C2015408022)和河北省大学生创新创业训练计划项目(201510100033)。
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囊素。其中, AMP和GMP向黄嘌呤的转化以及形成尿酸的过程均在细胞质基质中完成(Stasolla等2003), 尿酸到尿囊素的代谢在过氧化物酶体中进行(Hanks等1981)。随后, 尿囊素可以在酰脲渗透酶(ureide permease, UPS)及其他尿囊素转运蛋白(allantoine transporter)的作用下, 进入细胞质参与多种代谢活动(Schmidt等2004), 也可向外分泌到细胞间质, 参与氮素转运(Smith和Atkins 2002; Baral等2016); 或者排出植物体, 在化感作用中发挥作用(Wang等2007)。

尿囊素分解代谢主要在内质网进行(Werner等2013) (图1), 首先是在尿囊素酶(allantoinase)的作用下生成尿囊酸(allantoate)。随后通过两条途径形成尿羟乙酸(ureidoglycolate), 一条在尿囊酸酶(allantoicase)的作用下直接生成, 同时释放一分子尿素; 另一条途径是先转化为脲基甘氨酸(ureidoglycine), 同时释放一分子的NH_3和CO_2, 再生成尿羟乙酸和一分子NH_3。接下来尿羟乙酸被尿羟乙酸裂解酶(ureidoglycolate lyase)或尿羟乙酸水解酶(ureidoglycolate hydrolase)转化为乙醛酸(glyoxylate), 并分别生成尿素或NH_3和CO_2 (Zrenner等2006)。

2 植物体内尿囊素对逆境胁迫的应答

早期的研究认为, 高等植物氮素代谢与渗透胁迫响应存在某种联系(Morgan 1984)。环境中的水分胁迫是最典型、最直接的渗透胁迫, 因此, 尿囊素参与植物胁迫响应, 较多体现于植物干旱胁迫的相关研究中。

Oliver等(2011)研究发现, 在60%水分条件下, 抗旱型复原草(*Sporobolus stapfianus*)与干旱敏感型的*S. pyramidalis*相比, 体内尿囊素含量高出8倍。在大豆(*Glycine max*)中也存在类似现象。对干旱胁迫下(土壤持水量23%)大豆耐旱品种‘NA5009RG’和敏感性品种‘DM50048’的代谢组数据进行主成分分析(principal component analysis, PCA), 表明尿囊素的含量变化是区分抗旱品种和干旱敏感品种的一个主要标志(Silvente等2012)。此外, 对比耐旱性不同的菜豆品系发现, 干旱胁迫下, 各品系植株均发生酰脲类化合物(ureides)积累, 虽然干旱敏感品系中存在更高的酰脲水平, 但所积累的酰脲多为尿囊酸。而抗旱品系所积累的酰脲中, 尿囊素比例较高(Coleto等2014)。卷柏科植物*Selaginella lepidophylla*是一种可从轻度风干状态下恢复的耐旱植物, 其在水分胁迫下体内也有大量尿囊素积累(Yobi等2013)。对拟南芥(*Arabidopsis thaliana*)尿囊素酶基因功能缺失突变体*aln*进行基因芯片分析显示, *aln*植株中自发启动了脱落酸(abscisic acid, ABA)和茉莉酸(jasmonate, JA)两条应答途径, 且大量干旱和高盐胁迫响应相关基因显著上调表达(Watanabe等2014b)。

此外, 植物体内尿囊素含量也受其他胁迫的影响, 特别是近几年, 转录组学、代谢组学技术的发展不仅验证了早期的发现, 也显示了植物体内尿囊素含量与多数非生物胁迫响应呈正相关, 与生物胁迫响应呈负相关(表1)。

3 尿囊素参与植物抗逆应答的分子证据

对高等植物嘌呤降解途径的研究发现, 黄嘌呤脱氢酶抑制物别嘌呤醇(allopurinol)可抑制植物免疫应答过程中的过敏性坏死反应(Montalbini 1992), 而拟南芥黄嘌呤脱氢酶的缺失突变体表现出明显的抗逆性降低和早衰现象, 外源施加尿酸、尿囊素可消除突变体的上述不良表型(Nakagawa等2007; Watanabe等2010, 2014a)。因此认为, 嘌呤降解途径的某些中间产物可能参与了植物的抗逆应答过程。对黄嘌呤脱氢酶下游尿酸氧化酶突变体的研究发现, 尿酸氧化酶的功能缺失所导致的尿酸积累会对植物体产生严重甚至是致命的毒害(Hauck等2014), 这表明参与植物抗逆应答的嘌呤降解中间产物应处于尿酸下游。

Watanabe等(2014b)对拟南芥黄嘌呤脱氢酶、尿囊素酶、尿囊酸酶3个功能缺失突变体(*xdh*、*aln*、*aah*)的研究发现, *aln*植株中尿囊素的大量累积自发地启动ABA合成, 诱导体内免疫应答相关基因的表达, 提高了拟南芥突变体幼苗对非生物胁迫的耐受性, 但突变体*xdh*和*aah*未出现类似现象。此外, 野生型拟南芥外施尿囊素后, 表现出与*aln*植株相似的抗逆性提高表型。由此, 尿囊素在植物体抗逆应答中的作用得到了明确的分子证据。

4 尿囊素参与植物抗逆应答的作用机制

4.1 尿囊素信号的调控

尽管针对植物尿囊素的研究已有相当长的时间, 但在胁迫下植物体产生尿囊素的机理尚不明确。谢德意等(2001)曾以上世纪初的观测结果为

表1 不同胁迫条件下植物体内尿囊素含量及相关指标的变化

Table 1 Changes in allantoin levels and related indexes in plants under various stress conditions

物种	胁迫条件	观测结果	参考文献
水稻	Yoshida培养基+140 mmol·L^{-1} NaCl	尿囊素含量上升111倍	Wang等2016
(*Oryza sativa*)	低温或缺水大田(广州、沈阳)	幼苗存活率与体内尿囊素含量成正比	Wang等2012
	Yoshida培养基+7.5 mmol·L^{-1} $NaHCO_3$	尿囊素含量上升, 缺锌耐性品系和敏感品系分别上升(1.6±0.02)和(2.0±0.03)倍	Rose等2012
	无锌离子Yoshida培养基+7.5 mmol·L^{-1} $NaHCO_3$	尿囊素含量上升, 缺锌耐性品系和敏感品系分别上升(1.7±0.12)和(3.3±0.30)倍	Rose等2012
拟南芥	水培+50 mmol·L^{-1} NaCl	尿囊素含量上调3倍	Kanani等2010
(*Arabidopsis thaliana*)	1/2MS+250 mmol·L^{-1} NaCl	尿囊素含量显著上升	Lescano等2016
	1/2MS+150 mmol·L^{-1} NaCl	*UOX*与*AS*表达量显著上升, *ALN*表达量显著下降	Lescano等2016
	4°C下冷处理	尿囊素含量显著上升	Kaplan等2004
	1/2MS且硫元素含量减少89%	尿囊素含量上升4.77~15.09倍	Nikiforova等2005
	暗处理6 d	野生型尿囊素含量显著上升; 黄嘌呤脱氢酶突变株体内尿囊素含量无显著变化	Brychkova等2008
	暗处理6 d+恢复9 d	野生型存活率大于75%, 黄嘌呤脱氢酶突变体植株存活率低于50%	Brychkova等2008
	1/2MS+25~200 μmol·L^{-1} $CdCl_2$	尿囊素含量显著上升	Nourimand和Todd 2016
	土培, 喷施500~1 500 μmol·L^{-1} $CdCl_2$	野生型植株尿囊素含量显著上升, 尿囊素酶活性显著下降; 尿囊素酶突变株体内3种抗氧化酶(SOD、APX、CAT)活性显著高于野生型	Nourimand和Todd 2016
	Pseudomonas syringae pv. *tomato* (*Pst*)菌株DC 3000灌根	接种24 h, 尿囊素酶突变株体内病程相关蛋白的基因*PR-1*表达量显著低于野生型	Takagi等2016
	Pectobacterium carotovorum subsp. *carotovorum* (*Pcc*)菌株EC1的生理盐水菌悬液注射于离体叶片	接种3 h, 尿囊素酶突变株体内抗真菌防御蛋白的基因*PDF1.2*表达量显著低于野生型	Takagi等2016
小麦	*Fusarium graminearum*菌株PH-1孢子	酰脲转运相关基因表达量显著上调	Lysøe等2011
(*Triticum aestivum*)	悬液注射于花期小花		

UOX: 尿酸氧化酶基因(*URATE OXIDASE*); *AS*: 尿囊素合酶基因(*ALLANTOIN SYNTHASE*); *ALN*: 尿囊素酶基因(*ALLANTOINASE*); SOD: 超氧化物歧化酶(superoxide dismutase); APX: 抗坏血酸过氧化物酶(ascorbate peroxidase); CAT: 过氧化氢酶(catalase); *PR-1*: *PATHOGENESIS-RELATED PROTEIN 1*; *PDF1.2*: *PLANT DEFENSIN 1.2*。

基础推测, 胁迫条件下光合产物供应不足是植物产生尿囊素积累的主要原因。Lescano等(2016)的研究表明, 渗透胁迫可上调尿囊素合成途径中*UOX*和*AS*的表达, 而抑制分解途径中*ALN*的表达, 最终致使尿囊素水平提高。此外, 在干旱、高盐、低温、自然衰老以及外施ABA条件下, 黄嘌呤脱氢酶基因(*XANTHINE DEHYDROGENASE*, *XDH*)的转录水平都出现不同程度的响应(Hesberg等2004), 说明*XDH*的表达水平也可能影响植物体内尿囊素的产生。

除胁迫对基因表达的影响, 胁迫条件下酶的活性变化也可能对植物体尿囊素水平产生影响。研究发现, 刺槐(*Robinia pseudoacacia*)和拟南芥中尿囊素酶的蛋白序列都存在一个高度保守的金属结合位点, 尿囊素酶在不同金属离子或不同离子浓度下, 其活性表现出极大的差异, 极易受到重金属离子的抑制(Yang和Han 2004; Ho等2011)。随后, Nourimand和Todd (2016)用重金属盐$CdCl_2$处理拟南芥, 发现植株体内尿囊素酶活性明显降低, 而*ALN*的表达量虽然降低但不显著, 说明尿囊素酶活性受到抑制, 也可使植株体内尿囊素水平提高, 继而产生抗逆应答信号。

4.2 尿囊素信号的转导

通过生理学、反义遗传学和代谢组学分析显示, 尿囊素能够激活ABA信号途径(Watanabe等2014b)。ABA途径是植物体内重要的胁迫响应机

制之一。一般认为, 植物体内ABA是通过源自类胡萝卜素前体库的合成途径以及糖苷化ABA去糖苷化两条途径获得(Seo和Koshiba 2002; Priest等2006; Rai等2011)。最近, 对拟南芥的研究发现, ABA合成突变体*aba2-1*与糖苷ABA去糖苷化突变体*bglu18*均表现尿囊素钝化表型。野生型植株中被尿囊素激活的胁迫应答基因(既有ABA相关基因, 也存在JA相关基因), 无论是在*aba2-1*还是在*bglu18*突变体中都没有表现出显著上调, 说明尿囊素可以通过激活ABA的两条来源途径来激活ABA信号通路, 继而诱导植物体抗逆应答过程(Takagi等2016)。

植物中myelocytomatosis protein 2 (MYC2)是一种特异性结合G-box序列及其相关序列位点的转录因子, 为JA途径核心元件(Dombrecht等2007), 其基因*MYC2*受ABA诱导表达(Abe等1997)。正常情况下, MYC2会同转录抑制因子jasmonate ZIM-domain (JAZ)蛋白结合, 不具有活性。仅当JA信号物质茉莉酸-L-异亮氨酸(jasmonoyl-L-isoleucine, JA-Ile)作用下, JAZ才能释放有转录因子活性的MYC2 (Chini等2007)。被释放的MYC2正调控植物体对机械和采食损伤的应答, 负调控乙烯介导的抗病应答(Lorenzo等2004)以及水杨酸(salicylic acid, SA)途径(Laurie-Berry等2006), 并能够进一步促进JA的合成(Takagi等2016)。可见, MYC2对生物性和非生物性胁迫的调控特点, 与上述尿囊素对胁迫的响应现象相似。最近, Takagi等(2016)在对突变体*jar1-1* (JA-Ile合成突变体)和*myc2-3* (MYC2转录因子突变体)的研究中发现, 相对于野生型, 两个突变体植株均表现尿囊素钝化表型, 证实了JA信号以及MYC2在尿囊素发挥作用的过程中均是必不可少的。

ABA途径与JA途径的关系密切。多种抗逆应答过程往往需要两种信号途径共同发挥作用(Munemasa等2011; García-Andrade等2011; De Ollas等2015; Liu等2016)。ABA与JA途径虽然都可以被高水平的尿囊素诱导(Watanabe等2014b), 但对于该过程中信号的传导途径尚有不同认识。目前较多的观点认为ABA作为上游信号诱导了JA途径(刘新等2002; Lorenzo等2004; Takagi等2016), 原因是*MYC2*可以受到ABA的诱导而上调表达, 而MYC2在脱离了JAZ蛋白后, 又可以促进JA的合成。根据以上理论, Lorenzo等(2004)推测, 该过程中JA途径处于ABA的下游位置, 但目前尚缺乏研究证据。而与之相反, Anderson等(2004)认为在干旱胁迫下, 植物体内ABA途径是由JA信号所诱导的。综上, 尿囊素如何引起JA的响应以及尿囊素是否存在其他未知途径来诱导JA信号等问题, 都需要后续研究来进一步阐述。最近, Aleman等(2016)证明, 在ABA的作用下, MYC2会改变对不同序列的结合活性, 这种机制也可能在抗逆应答的调控过程中起着重要作用。

综上所述, 我们参考Takagi等(2016)提出的尿囊素作用模型, 修改并推测构建尿囊素对植物体抗逆应答机制的模型(图2)。

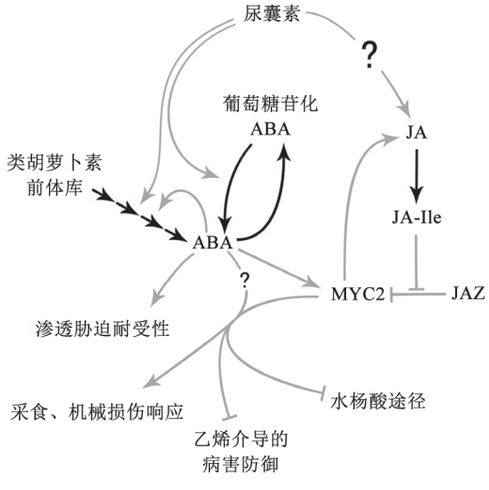

图2 尿囊素诱导植物抗逆应答的可能机制

Fig.2 The potential mechanism of allantoin-induced stress response in plants

黑箭头为代谢路径; 灰箭头为激活调控; 灰色横条为抑制调控; 问号表示该模型中信号传导途径尚不明确。

5 展望

在逆境条件下, 植物体中的多种代谢活动受到抑制, 因此, 代谢中间产物累积的现象时有发生。其中, 许多物质可以作为诱导植物体抗逆应答的信号因子或激发子(单守明等2014; 汪和贵等2016)。如细胞壁降解中间产物寡聚糖类化合物作为植物抗性激发因子, 早已有了较为清晰的认识(王克夷1989; 罗建平和贾敬芬1996; 何亚飞等

2016)。尿囊素作为一种嘌呤降解中间产物, 其在植物抗逆应答中的作用正被逐渐揭示。在特定胁迫条件下, 植物嘌呤降解代谢过程受到影响, 致使植物体内尿囊素产生积累。而这种尿囊素的积累可以作为抗逆应答信号, 调动植物体特定的应答过程。

基于GEO (https://www.ncbi.nlm.nih.gov/geo/)数据库所进行的转录组数据分析为未来的进一步研究提供了重要信息: (1)寡糖chitooctaose (一种壳聚寡糖)或乙烯处理可使拟南芥*ALN*表达量显著下降(Libault等2007; Alonso等2003); 拟南芥独脚金内酯(strigolactone)合成突变体中*ALN*表达量显著上升(Mashiguchi等2009)。以上结果暗示尿囊素信号可能与其他信号通路或者激素调节机制存在交叉, 进一步了解各个信号途径之间的互作可作为后续研究的重要方向。(2)拟南芥*GLABROUS 1* (*GL1*)基因编码一个R2R3型myeloblastosis protein (MYB)转录因子, 其突变体*gl1*植株中*UOX*与*ALN*的表达水平在高盐胁迫下无应答迹象(Chan等2011), 而在野生型植株中两者的表达均受到显著影响, 表明MYB可能参与尿囊素对胁迫信号的应答响应, 也预示通路上游可能存在更加复杂的响应机制。(3)植物中多个microRNA (miRNA)家族能够对不同胁迫做出响应(雷凯健和安国勇2014), 拟南芥miRNA突变体*jaw*中*ALN*表达量显著上升(Palatnik等2003); 过表达拟南芥miR159a、miR164b也使*ALN*表达量显著上升(Schwab等2005)。说明部分miRNA对尿囊素代谢相关基因的调控发挥了作用, 但其作用机理尚需进一步阐述和梳理。

随着植物尿囊素相关研究的深入, 关于抗逆育种的一些新思路也逐渐清晰起来。在分子育种方面, 以现有理论为基础, 可尝试对植物尿囊素代谢途径上一些关键酶进行遗传操作, 通过调控尿囊素的响应水平, 以期达到提高植株特定抗逆性的目的。此外, 尿囊素作为植物抗逆应答体系中的重要一员, 其浓度水平及其代谢途径上的相关指标, 可作为筛选优良种质资源的评价依据, 为常规育种的材料选择提供新的参考。

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Roles of allantoin in plant defense responses

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Abstract: Allantoin, involved in nitrogen storage and transport, is a metabolic intermediate of purine catabolism in high plants. In addition, allantoin also plays essential roles in mediating plant responses to stresses. This review summarizes the recent research on the metabolic pathway, stress response and signaling transduction mechanisms of allantoin. Furthermore, the potential research direction towards allantoin in plant stress resistance is also addressed.

Key words: allantoin; metabolic pathway; stress responses; signaling transduction

Received 2016-12-16 Accepted 2017-05-31
This work was supported by Natural Science Foundation of Hebei Province (C2015408022) and College Students' Innovative Entrepreneurial Talents Training Program of Hebei Province (201510100033).
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