

肌醇代谢在植物响应非生物胁迫中的作用

于 点, 郭卫冷, 丁 炀, 刘 磊, 郭 睿, 王 丹, 孙玉刚, 郭长虹
(哈尔滨师范大学生命科学与技术学院/黑龙江省分子细胞遗传与遗传育种重点实验室, 哈尔滨 150000)

摘要: 非生物胁迫制约了植物的生长和发育, 降低作物的产量, 严重时导致植物死亡。为了应对非生物胁迫, 植物在进化过程中形成了一系列胁迫响应机制, 包括肌醇(MI, myo-inositol)代谢途径。肌醇为一类化学性质稳定的极性小分子, 植物可通过积累其糖苷类衍生物参与渗透调节途径, 从而响应非生物胁迫。肌醇-1-磷酸合酶(MIPS, myo-inositol-1-phosphate synthase)、肌醇单磷酸酶(IMP, inositol monophosphatase)和肌醇加氧酶(MIOX, myo-inositol oxygenase)在肌醇的生物合成或分解过程中发挥作用, 它们通过调控植物中肌醇的含量, 以及后续一系列复杂的转化途径, 参与L-抗坏血酸(L-AsA, L-ascorbic acid)和部分细胞壁多糖的合成, 响应盐、干旱、碱和低温等非生物胁迫。本文综述了肌醇的结构、生物学作用、肌醇代谢途径相关酶和肌醇衍生物在植物响应非生物胁迫中的研究进展, 并对未来的研究方向进行了展望, 旨在为利用肌醇代谢增强植物对非生物胁迫的抗性, 培育抗逆植物品种提供理论基础。

关键词: 肌醇代谢; 非生物胁迫; 肌醇-1-磷酸合酶; 肌醇单磷酸酶; 肌醇加氧酶

The Role of Myo-inositol Metabolism in Plants Response to Abiotic Stress

YU Dian, GUO Weileng, DING Yang, LIU Lei, GUO Rui, WANG Dan, SUN Yugang, GUO Changhong
(College of Life Science and Technology, Harbin Normal University/ Key Laboratory of Molecular Cytogenetics and Genetic Breeding of Heilongjiang Province, Harbin 150000)

Abstract: Abiotic stress limits plant growth and development, causes yield losses in crops, and severe abiotic stress can even result in the death of plant. Plants have evolved a series of stress response mechanisms to adapt to abiotic stress, including the myo-inositol (MI) metabolic pathway. MI represents a class of small polar molecules with stable chemical properties. Plants can respond to a variety of abiotic stress by participating in osmoregulatory pathways through accumulating the glycoside derivatives of MI. Myo-inositol-1-phosphate synthase (MIPS), inositol monophosphate phosphatase (IMP), and myo-inositol oxygenase (MIOX) play a role in the process of the biosynthesis or decomposition of MI. They are involved in the synthesis of L-ascorbic acid (L-AsA) and cell wall polysaccharides by regulating the content of MI in plant and a series of subsequent complex transformation pathways, and ultimately response to abiotic stresses such as salt, drought, alkali, and low temperature. This paper reviewed the research progress of the structure, biological functions of MI, MI metabolic pathway-related enzymes and its derivatives in plants response to abiotic stresses, providing an outlook to the future research focuses. This study aims to provide a theoretical basis for enhancing plant resistance to abiotic stresses by utilizing MI metabolism and breeding stress-resistant plant varieties.

收稿日期: 2023-07-17 修回日期: 2023-08-02 网络出版日期: 2023-09-05

URL: <https://doi.org/10.13430/j.cnki.jpgr.20230717003>

第一作者研究方向为植物遗传学, E-mail: yudian227@163.com; 郭卫冷为共同第一作者

通信作者: 郭长虹, 研究方向为植物遗传学, E-mail: kaku3008@126.com

基金项目: 国家自然科学基金(U21A20182, 31972507); 国家科技攻关项目(2022YFE0203300); 黑龙江省博士后基金(LBH-Z21172); 哈尔滨师范大学研究生创新基金(HSDSSCX2022-36)

Foundation projects: National Natural Science Foundation of China (U21A20182, 31972507); National Key R & D Program of China (2022YFE0203300); Postdoctoral Foundation of Heilongjiang Province (LBH-Z21172); Graduate Student Innovation Fund of Harbin Normal University (HSDSSCX2022-36)

Key words: myo-inositol metabolism; abiotic stresses; myo-inositol-1-phosphate synthase; inositol monophosphatase; myo-inositol oxygenase

植物在生长发育过程中经常受到各种非生物胁迫的损伤,如盐、干旱、碱和低温等,长期非生物胁迫可以引起植物形态结构变化,影响植物体内渗透调节物质(如 Na^+ 、 K^+ 、脯氨酸和可溶性糖等)的含量,降低光合速率和抗氧化酶活性,触发细胞应激反应,使植物的生长发育和生理代谢等过程受损,严重制约植物的生长和作物产量^[1-2]。为了避免非生物胁迫带来的危害,植物通过渗透调节、离子和pH平衡、抗氧化系统等对非生物胁迫进行响应^[3]。肌醇(MI, myo-inositol)是一种小分子多元醇,是合成L-抗坏血酸(L-AsA, L-ascorbic acid)的重要前体,其代谢过程与细胞壁组分相关物质的生物合成、渗透调节能力提高和活性氧等清除生理过程密切相关^[4-5]。本文对参与肌醇代谢途径的物质和酶在植物响应非生物胁迫中的作用进行综述,旨在为通过调节肌醇代谢增强植物对非生物胁迫的抗性提供理论基础。

1 肌醇的结构特点及代谢途径

1.1 肌醇的结构特点

肌醇,即1, 2, 3, 4, 5, 6-六羟基环己烷,分子式 $\text{C}_6\text{H}_{12}\text{O}_6$,分子量180.16 g/mol,是葡萄糖的同分异构体。1850年,Scherer^[6]首次从牛肌肉中分离出肌醇。肌醇是一种环糖醇,根据其环上羟基相对位置的变化,可异构化产生其他8种可能的异构体形式,分别为鲨肌醇(Scyllo-inositol)、黏质肌醇(Muco-inositol)、D-手性肌醇(D-chiro-inositol)、L-手性肌醇(L-chiro-inositol)、新肌醇(Neo-inositol)、异肌醇(Allo-inositol)、外延肌醇(Epi-inositol)和顺肌醇(Cis-inositol)^[7]。相比于以上其他构型的同分异构体,肌醇在自然界中更常见。肌醇以游离或结合形式存在于真核生物中,调控细胞代谢活动,是脂质的重要组成部分^[8]。

在植物中,肌醇及其衍生物广泛分布,包括磷脂酰肌醇(PtdIns, phosphatidyl inositol)、肌醇半乳糖苷(Inositol galactoside)、肌醇磷酸盐(InsPs, inositol phosphates)等,植物利用胞质中肌醇及其衍生物的信号转导能力、调节渗透压和保护膜脂等特性作为响应环境胁迫生理机制的因子^[9]。磷脂酰肌醇是细胞膜磷脂的主要成分之一,占膜磷脂的10%~20%,通过肌醇基团位置磷酸化,产生7种不

同的磷脂酰肌醇磷酸盐(PIPs, phosphatidylinositol phosphates),在控制细胞骨架重组、增殖代谢、信号转导和基因表达中发挥作用^[10]。肌醇半乳糖苷由肌醇和UDP-半乳糖为底物形成,为棉子糖家族寡糖的生物合成提供半乳糖基供体,促进棉子糖的积累,提高渗透调节能力^[11]。肌醇磷酸盐由肌醇磷酸化产生不同的可溶性信号分子组成,如七磷酸肌醇、八磷酸肌醇等,可以作为第二信使将生物信号进一步传导^[12-13]。

1.2 肌醇的合成代谢途径

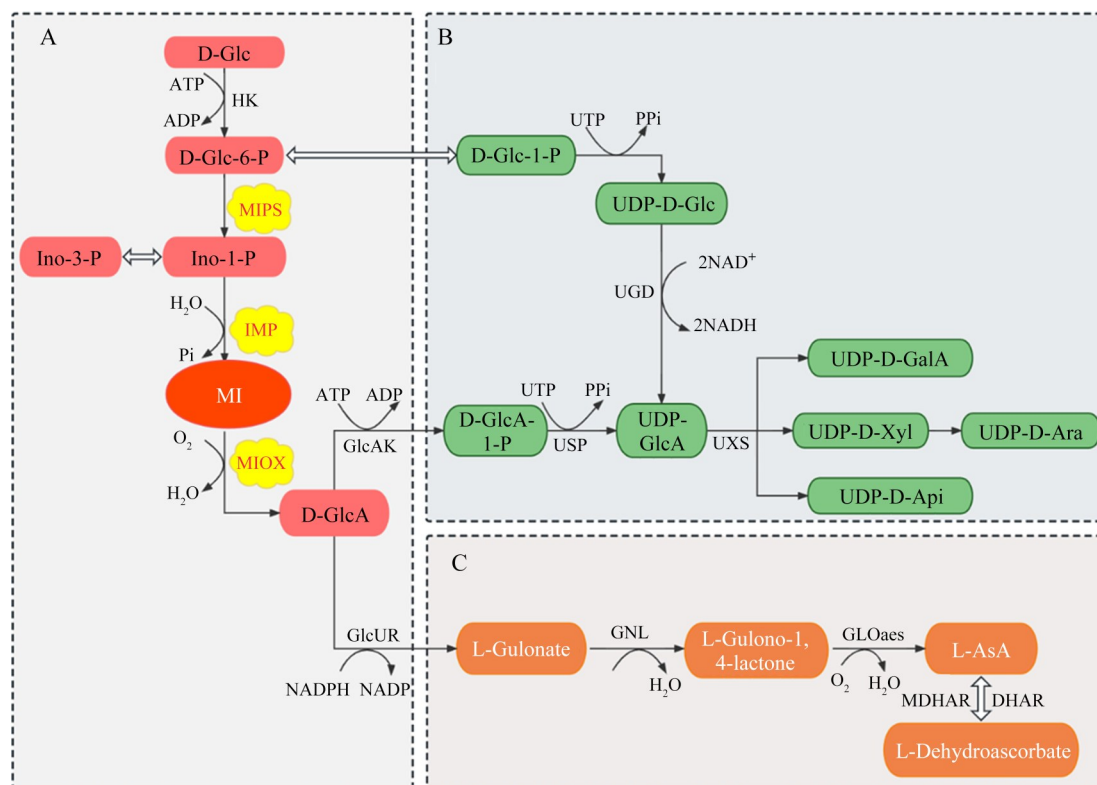
肌醇的生物合成由Loewus等^[8]利用放射性同位素标记实验证实,被称为Loewus途径,反应过程高度保守。首先,在肌醇-1-磷酸合酶(MIPS, myo-inositol-1-phosphate synthase)催化下,D-葡萄糖-6-磷酸(D-Glc-6-P, D-glucose-6-phosphate)转化为肌醇-1-磷酸(Ino-1-P, inositol-1-phosphate),随后肌醇单磷酸酶(IMP, inositol monophosphatase)催化肌醇-1-磷酸进行脱磷酸,生成游离的肌醇(图1),其中肌醇-1-磷酸合酶被认为是这一途径的限速酶^[14]。在真核生物中,肌醇-1-磷酸合酶具有高度保守的特性,目前已从多个物种中获得了肌醇-1-磷酸合酶基因^[15],如拟南芥^[16]、大豆^[17]、水稻^[18-19]、猕猴桃^[20]、杨树^[21]、棉花^[22]等。在大鼠^[23]、牛^[24]和人类大脑^[25]等动物中,肌醇单磷酸酶基因已被纯化并报道,在拟南芥^[26]、水稻^[27]等植物中肌醇单磷酸酶基因有部分报道,其他物种中肌醇单磷酸酶相关研究尚少。

1.3 肌醇的分解代谢途径

肌醇通过肌醇加氧酶(MIOX, myo-inositol oxygenase)氧合裂解转化为游离的D-葡萄糖醛酸(D-GlcA, D-glucuronic acid),随后生成不同的代谢物参与植物细胞壁合成和L-抗坏血酸合成。D-葡萄糖醛酸通过葡萄糖醛酸激酶(GlcAK, glucuronokinase)被激活为UDP-葡萄糖醛酸(UDP-GlcA, UDP-glucuronic acid)。UDP-葡萄糖醛酸在复杂的核苷酸糖相互转化途径中,能够生成UDP-D-半乳糖(UDP-D-GalA, UDP-D-galacturonate)或UDP-D-芹菜糖(UDP-D-Api, UDP-D-apiose),二者均为果胶的重要前体聚合物^[28],UDP-葡萄糖醛酸也可经过脱羧反应生成UDP-D-木糖(UDP-D-Xyl, UDP-D-xylose),再由UDP-阿拉伯糖(UDP-arabinose)向外

异构化(图1)^[29]。UDP-D-木糖能够在细胞质中合成,然后被运输到高尔基体,参与组成植物木聚糖合成^[30]。UDP-D-半乳糖、UDP-D-芹菜糖和UDP-D-木糖均为细胞壁合成物质的前体,形成的胶质和半纤维素等聚合物与其单糖约占细胞壁50%的生物量^[29]。在合成抗坏血酸途径中,D-葡萄糖醛酸转化为L-古洛糖-1,4-内酯(L-gulose-1, 4-lactone),随后

被氧化为L-抗坏血酸(图1)^[31-32]。肌醇加氧酶是肌醇分解代谢途径的关键酶,Charalampous等^[33]于1957年首次在鼠肾脏组织中提取出肌醇加氧酶,引起人们强烈关注。随着研究不断深入,目前在拟南芥^[34]、水稻^[35]、大豆^[36]、番茄^[37]、小麦^[38]、苹果^[39]、棉花^[40]和紫花苜蓿^[41]等种植物中分离到肌醇加氧酶基因。



A: 肌醇的合成分解途径; B: 肌醇参与细胞壁合成途径; C: 肌醇参与L-抗坏血酸合成途径。→代表物质单向合成, ⇌代表物质间可相互转化
A: Inositol synthesis and decomposition pathway; B: Inositol is involved in cell wall synthesis pathway; C: Inositol is involved in L-ascorbic acid synthesis pathway. → represents the unidirectional synthesis of substances, ⇌ indicates that substances can be converted into each other

图1 肌醇的代谢途径

Fig. 1 Metabolic pathway of inositol

2 肌醇的生物学作用

2.1 肌醇与L-抗坏血酸

L-抗坏血酸又叫维生素C(Vc, vitamin C),是自然界中一种常见的抗氧化剂。L-抗坏血酸通过调节植物中谷胱甘肽(GSH, glutathione)的氧化还原状态和环境诱导的氧化胁迫,减少植物的氧化应激^[42]。L-抗坏血酸参与的抗坏血酸-谷胱甘肽(AsA-GSH)循环是去除活性氧(ROS, reactive oxygen species)的一个有效的抗氧化系统,是清除过氧化氢(H_2O_2 , hydrogen peroxide)的主要代谢途径^[43]。提高L-抗坏血酸含量可能是增强作物生物量、非生物胁迫耐受性和植物修复能力的有效策

略^[44]。肌醇代谢途径相关酶可以通过调控肌醇的合成与分解从而影响植物合成L-抗坏血酸(图1)。Zhang等^[21]在杨树(*Populus euphratica* Oliv.)中过表达*PeMIPS1*, L-抗坏血酸总含量高于野生型, GSH/GSSH比值也优于野生型,证明过表达*PeMIPS1*会导致L-抗坏血酸的积累。Lorence等^[45]首次从拟南芥中克隆获得*AtMIOX4*,发现过表达*AtMIOX4*的拟南芥叶片中L-抗坏血酸含量增加了2~3倍。同样地, Lisko等^[44]研究发现,过表达*AtMIOX4*拟南芥叶片的L-抗坏血酸含量较野生型高约1.5倍,表明肌醇与L-抗坏血酸的合成可能存在直接关系。

2.2 肌醇与细胞壁

植物细胞壁是由纤维素、半纤维素、果胶和少

量结构蛋白等构成的网状结构,与植物生长发育密切相关,维持细胞的基本形态,为植株提供机械支撑,是植物细胞区别于动物细胞的基本特征之一^[46]。此外,细胞壁还在营养物质转运、抵御外界环境胁迫等方面发挥广泛的作用^[47-48]。肌醇通过分解可转化为UDP-葡萄糖醛酸,UDP-葡萄糖醛酸作为合成核苷酸糖的主要前体,形成植物细胞壁的半纤维素和果胶聚合物(图1)。Loewus等^[49]在离体的成熟草莓(*Fragaria*)和欧芹(*Petroselinum*)叶中注入带2-³H或2-¹⁴C标记的肌醇,发现有56%的放射性标记进入到细胞壁多糖中,首次证明了肌醇与细胞壁多糖有着紧密的代谢关联。Kanter等^[29]用³H标记肌醇后,发现³H-肌醇出现在细胞壁聚合物中,

细胞壁水解后的产物分离显示糖醛酸、阿拉伯糖和木糖具有放射性,并且两种肌醇加氧酶基因敲除拟南芥均显示³H-肌醇掺入细胞壁的量显著减少,表明*MIOX1*和*MIOX2*在该通路中发挥功能,证明了肌醇加氧酶基因为细胞壁聚合物提供糖类的作用。这些研究为植物中参与细胞壁多糖生物合成的功能性肌醇氧化途径提供了强有力的证据。

3 植物肌醇代谢对非生物胁迫的响应

目前,植物肌醇代谢相关基因在多种非生物胁迫中的作用已经取得了一定的研究进展,如盐、碱、干旱和极端温度等(表1)。

表 1 植物肌醇代谢相关基因对非生物胁迫的响应
Table 1 Responses of inositol metabolism-related genes to abiotic stress in plant

基因名称 Gene name	胁迫类型 Stress type	表达模式 Expression pattern	转入植物 Transferred plant	参考文献 Reference
<i>PeMIPS</i>	盐	上调	杨树	[21]
<i>SjMIPS</i>	盐	上调	—	[50]
<i>MdMIPS1</i>	盐、干旱	上调	拟南芥、苹果	[51-52]
<i>AdMIPS</i>	盐、干旱	上调	—	[20]
<i>MjMIPS1</i>	盐、干旱、低温	上调	烟草	[53]
<i>CaMIPS2</i>	盐、高温	上调	鹰嘴豆	[54]
<i>TaMIPS-D</i>	低温、高温	上调	水稻	[55]
<i>GhMIOX09</i>	盐	上调	—	[40]
<i>MhMIOX2</i>	盐	上调	杨树、拟南芥	[39]
<i>AtMIOX4</i>	盐、干旱、低温、高温	上调	拟南芥	[44-45, 56]
<i>MsMIOX</i>	盐、盐碱、干旱、寒冷	上调	紫花苜蓿	[41]
<i>GsMIOX1a</i>	碱	上调	棉花	[36]
<i>GhMIOX04</i>	干旱	上调	—	[40]
<i>OsMIOX</i>	干旱	上调	水稻	[35, 57]
<i>TaMIOX</i>	干旱、低温、高温	上调	拟南芥	[38]
<i>GhMIOX03</i>	低温	上调	—	[40]
<i>SlMIOX</i>	氧化胁迫、失水	上调	番茄	[37]
<i>OsIMP</i>	低温	上调	烟草	[27]

—表示该基因未进行转基因实验
— indicates that the gene has not been genetically modified

3.1 盐胁迫

盐胁迫会阻碍种子萌发、生长发育、开花和结果,对植物产生不利影响^[21, 58]。盐渍土壤中高浓度的Na⁺限制了植物对水分和养分的吸收,引起渗透胁迫和离子胁迫,进而导致氧化应激,引起一系列的次级应激^[59]。而且盐胁迫影响光捕获复合物的

形成,抑制细胞分裂,导致植物生理及分子变化^[60]。Cui等^[20]克隆并鉴定了猕猴桃(*Actinidia Deliciosa* cv. Qin Mei)肌醇-1-磷酸合酶基因,通过盐胁迫下不同组织中的基因表达分析,发现盐胁迫能够不同程度地诱导猕猴桃叶片、韧皮部和根*AdMIPS*的转录和肌醇-1-磷酸合酶活性,在盐胁迫处理5 d和10 d

*AdMIPS*表达量分别是对照组的1.5倍和3.5倍,表明*AdMIPS*受到盐胁迫的调节。肌醇代谢相关酶可在植物中增加超氧化物歧化酶、过氧化氢酶和过氧化物酶等抗氧化酶活性,降低有害物质含量,通过积累可溶性糖缓解渗透胁迫来抵抗盐胁迫带来的损害。如在杨树(*Populus euphratica* Oliv.)中过表达*PeMIPS1*^[21],在杨树(*Malus hupehensis* Rehd.)和拟南芥中过表达*MhMIOX2*^[39],与野生型相比,转*PeMIPS1*杨树、转*MhMIOX2*杨树和拟南芥在盐胁迫下活性氧清除酶活性增加,过氧化氢和丙二醛含量降低。Tan等^[53]从黄花苜蓿(*Medicago falcata* L.)中克隆出*MfMIPS1*并在烟草中过表达,发现盐胁迫下肌醇-1-磷酸合酶的活性升高,并且肌醇产量增加,从而使作为活性氧清除剂的半乳糖醇和棉子糖的水平有所增高以抵抗盐胁迫。苹果(*Malus domestica* Borkh.)中*MdMIPS1*可以增加盐胁迫下转*MdMIPS1*拟南芥的根长及鲜重,转*MdMIPS1*苹果通过积累可溶性糖来缓解渗透胁迫,降低过氧化氢和丙二醛含量,增强超氧化物歧化酶、过氧化物酶和抗超氧阴离子活性,并且在胁迫下内质网应激相关基因(*Bip1*、*Bip2*和*Bip3*等)和植物盐过度敏感途径(SOS)相关基因(*SOS1*、*SOS2*、*SOS3*和*NHX1*)上调,说明*MdMIPS1*可通过改善盐胁迫下氧化系统来降低氧化胁迫和内质网应激,以及维持胁迫下离子稳态^[51]。本课题组通过基因家族分析和实时荧光定量PCR分析表明,在盐胁迫下,紫花苜蓿(*Medicago sativa* L.)肌醇加氧酶基因家族亚族I的*MsMIOX01*-*MsMIOX06*表达上调,肌醇加氧酶的酶活性在盐胁迫下提高,为*MIOX*基因在响应盐胁迫中的作用提供了理论依据^[41]。肌醇衍生物也会参与对盐胁迫的响应,在盐胁迫下的磷脂酰肌醇-5-磷酸酶基因突变体拟南芥相比于野生型叶片明显发白,具有更高的盐敏感性,进一步研究发现磷脂酰肌醇-5-磷酸酶基因突变体拟南芥内吞作用减弱,根中活性氧含量和 Ca^{2+} 内流减少,盐诱导标记基因*RD29A*具有较高的表达,表明膜结合的磷脂酰肌醇通过协调内吞作用、活性氧产生、 Ca^{2+} 内流和应激反应基因的诱导,调节拟南芥耐盐性^[61]。

3.2 干旱胁迫

植物在生长发育的过程中,干旱胁迫会造成渗透胁迫,影响植物吸收水分和矿质营养,导致细胞脱水,改变植物的生理生化平衡^[62]。干旱胁迫的加剧也会使植物活性氧过量积累,导致蛋白质、膜脂和其他大分子氧化损伤,植物生长受到抑制^[43]。Hu

等^[52]发现,在干旱胁迫条件下,过表达*MdMIPS1*苹果的电导率和丙二醛含量均显著低于野生型植株,而超氧化物歧化酶和过氧化物酶活性则显著提高。*MdMIPS1*增强了胁迫下转基因苹果的肌醇合成、可溶性糖和脯氨酸的合成并增加了气孔孔径。说明*MdMIPS1*通过增加苹果抗氧化防御系统的活性、改善渗透调节和光合作用,由此增强了植株的耐旱性。Alok等^[38]发现带*TaMIOX*启动子的转基因拟南芥经干旱处理12 h和24 h后,*TaMIOX::Uida*表达量比野生型拟南芥高出3倍和5倍,表明*TaMIOX*启动子能够受干旱胁迫诱导。Li等^[40]从8种棉花(*Gossypium*)基因组中鉴定出75个肌醇加氧酶成员,对12个海岛棉(*Gossypium barbadense* L.)和12个草棉(*Gossypium herbaceum* L.)肌醇加氧酶基因的表达进行分析,发现在干旱胁迫下海岛棉*GbMIOX02*和*GbMIOX08*基因表达量明显上调,草棉*GhMIOX04*基因表达量在胁迫后24 h达到峰值。还有研究表明,过表达*OsMIOX*的水稻(*Oryza sativa* L.)可以增加脯氨酸的合成,加强活性氧清除和减少氧化损伤,从而提高水稻干旱胁迫耐受性^[35]。本课题组在紫花苜蓿毛状根中过表达*MsMIOX2*,发现在干旱胁迫下过表达*MsMIOX2*紫花苜蓿的毛状根长度明显长于野生型对照,而毛状根中的超氧阴离子和过氧化氢含量则显著低于对照^[41]。Perera等^[63]制备缺失肌醇磷酸盐-5-磷酸酶的拟南芥,发现离体叶片失水率降低30%,干旱诱导的脱水反应元件结合蛋白转录因子*DREB2A*和*DREB2A*调控基因的表达水平增加了两倍以上,肌醇磷酸盐-5-磷酸酶能够特异性溶解肌醇-1,4,5-三磷酸并终止信号,因此表明肌醇-1,4,5-三磷酸在*DREB2A*干旱信号通路中起着负调控因子的作用。

3.3 碱胁迫

碱胁迫是制约植物生长发育、影响作物生产力的非生物胁迫之一^[64]。碱胁迫会形成高pH胁迫,主要形成离子危害、渗透胁迫和氧化胁迫,活性氧积累从而影响植物根系对矿质元素的吸收,阻碍植物的各种生理代谢活动,抑制植物正常生长^[65]。Chen等^[36]鉴定到大豆(*Glycine soja* Sieb. et Zucc.)*MIOX*家族存在5个成员,其中*GsMIOX1a*在碱胁迫下显著上调表达,并在6 h时达到最高水平。过表达*GsMIOX1a*拟南芥在碱胁迫下,其脯氨酸水平升高,过氧化物酶活性增加,*atmiox1*突变体拟南芥的游离脯氨酸水平降低,过氧化物酶活性低于野生型,并且过表达*GsMIOX1a*拟南芥中碱胁迫应答和

诱导标记基因如 H^+ 转运焦磷酸酶基因 *H⁺-Ppase*、NADP-苹果酸酶基因 *NADP-ME*、抗冻蛋白基因 *KIN1* 和脱水诱导基因 *RD29B* 的表达水平也上调,这表明 *GsMIOX1a* 在拟南芥中能够正向调控碱胁迫。本课题组发现,紫花苜蓿所有 *MsMIOX* 基因在盐碱胁迫 12 h 时均显著上调表达,肌醇加氧酶的酶活性显著提高, *MsMIOX2* 蛋白可以提高酵母和紫花苜蓿毛状根的耐盐碱能力^[41]。

3.4 低温胁迫

低温胁迫会抑制植物的生长和发育,破坏细胞膜,甚至导致细胞死亡^[66]。在低温胁迫下,黄花苜蓿 *MfMIPS1* 的表达量在 4 h 开始升高,在 24 h 达到最高水平,紫花苜蓿 *MsMIPS* 在 8 h 被诱导并保持,同时,黄花苜蓿和紫花苜蓿的肌醇浓度均逐渐升高,说明肌醇的合成在黄花苜蓿和紫花苜蓿响应寒冷胁迫中发挥重要作用^[53]。Zhang 等^[27]在水稻中获得 *OsIMP*,多重比对结果表明, *OsIMP* 的氨基酸序列与短花药野生稻、拟南芥、蒺藜苜蓿、玉米和小麦的 *IMPs* 序列具有较高的相似性。在低温胁迫下,过表达水稻 *OsIMP* 的转基因烟草比野生型更耐寒,在 2 °C 处理 48 h 后几乎没有受到损伤。转基因烟草的超氧化物歧化酶、过氧化氢酶和过氧化物酶活性以及肌醇的含量较野生型显著增加,具有较低水平的过氧化氢、丙二醛含量。Alok 等^[38]发现,小麦 (*Triticum aestivum* L.) 中肌醇加氧酶基因启动子区域存在寒冷响应顺式元件, *TaMIOX::UidA* 拟南芥在低温胁迫处理下表现出显著的 GUS 活性,低温处理 12 h 和 24 h 后的 *TaMIOX::UidA* 表达量分别是野生型的 3 倍和 7 倍,认为 *TaMIOX* 可以作为探究小麦响应低温胁迫的潜在候选基因。本实验室发现,紫花苜蓿在冷胁迫下肌醇加氧酶活性显著增加,转染 pYES2-*MsMIOX2* 的酵母细胞在低温胁迫下活力更强,证明 *MsMIOX2* 能够响应低温胁迫^[41]。He 等^[67]在马铃薯 (*Solanum tuberosum* L.) 中过表达肌醇半乳糖苷合酶 *ScGolSI*,低温胁迫下转基因马铃薯的电导率和丙二醛含量均低于野生型, *ScGolSI* 诱导冷胁迫下棉子糖系列寡糖 RFO 代谢通路相关基因肌醇-1-磷酸合酶基因 *MIPS*、水苏糖合成酶基因 *STS*、棉子糖合成酶基因 *RS* 的表达上调,并影响糖代谢中可溶性碳水化合物成分的平衡,提高了转基因马铃薯植株的耐冻性。肌醇半乳糖苷合酶是分解肌醇半乳糖苷的第一步,继而合成棉子糖家族寡糖,从而也证明肌醇衍生物参与植物响应低温

胁迫。

4 展望

近年来,关于植物肌醇代谢相关基因响应盐、碱、干旱及低温等非生物胁迫的作用已取得一定的进展。关于肌醇-1-磷酸合酶和肌醇加氧酶这两个酶的相关研究报道较多,然而肌醇单磷酸酶作为肌醇合成途径的酶,肌醇单磷酸酶基因在响应非生物胁迫方面功能还没有被深入研究。另外,肌醇代谢相关基因的研究大多是在拟南芥、水稻、烟草等模式植物中开展的,尽管在苹果、杨树、小麦等植物中也取得了一定的进展,包括本课题组发现紫花苜蓿的 10 个 *MsMIOX* 基因在盐、干旱、盐碱和低温胁迫条件均有不同程度的响应, *MsMIOX2* 蛋白可提高酵母细胞和苜蓿毛状根的非生物胁迫耐受性,但是其他重要作物如大豆、玉米等的肌醇-1-磷酸合酶基因、肌醇加氧酶基因以及肌醇单磷酸酶基因等肌醇代谢相关基因在响应非生物胁迫中的功能还有待进一步研究。

肌醇途径是植物 L-抗坏血酸合成途径之一,肌醇途径能够有效提高植物体内 L-抗坏血酸的合成效率。但部分研究者持有不同态度,认为植物中积累的 D-葡萄糖醛酸作为肌醇代谢产物对 L-抗坏血酸的合成只起到微弱的作用,植物或许通过其他途径进行主要的 L-抗坏血酸合成^[68-69]。作为一种非酶抗氧化剂, L-抗坏血酸能与还原谷胱甘肽协同作用,防止脂质膜过氧化物和光合功能丧失,是对过氧化氢过度积累的一道强有力的防线。因此探究肌醇代谢相关酶参与植物合成 L-抗坏血酸的途径对于植物抵抗非生物胁迫具有重要意义,这仍是需要继续探讨的一个问题。

在各种非生物胁迫下,肌醇通过渗透调节途径调控植物的生理响应研究较多,但其中的具体调控机制仍不完善。肌醇代谢相关基因的应激响应依赖于上游信号的调控,今后可重点从肌醇-1-磷酸合酶基因、肌醇单磷酸酶基因和肌醇加氧酶基因由哪些上游基因调控,并且如何启动信号传导发挥作用,是否与其他蛋白互作以及如何通过植物各种多糖参与渗透调节等方面进一步深入探究和完善。全面解析肌醇分子调控机制,明确肌醇代谢相关基因响应非生物胁迫的机理,可为后续解析植物抗逆的生物学功能提供理论基础,为作物遗传改良提供新的思路。

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