植物蛋白酪氨酸磷酸酶的生理功能研究进展

何含杰[1,2], 唐丽[2], 邓华凤[2,3,*], 邹志刚[1]

[1]中南林业科技大学林业生物技术湖南省重点实验室/湖南省生物发育工程及新产品研发协同创新中心, 长沙410018; [2]湖南杂交水稻研究中心, 杂交水稻国家重点实验室, 长沙410125; [3]南方粮油作物协同创新中心, 长沙410125

摘要: 植物蛋白酪氨酸磷酸酶与蛋白激酶共同控制可逆磷酸酶作用, 在植物的生长、器官发育、激素应答、信号传递和胁迫应答过程中发挥着重要的生理功能。文章主要介绍植物蛋白酪氨酸磷酸酶的分类、蛋白酪氨酸磷酸酶在其生长发育、非生物和生物胁迫应答中的生物学功能及其参与的信号途径, 以期为后续研究提供理论参考。
关键词: 蛋白酪氨酸磷酸酶; 胁迫应答; 生理功能; 信号途径

植物的发育进程受到多种机制的调控, 如可逆蛋白磷酸化作用等。可逆蛋白磷酸化作用被称为生命的"开关", 由蛋白磷酸酶(protein phosphatases)和蛋白激酶(protein kinases)共同调控, 蛋白磷酸酶可以对具有活性的靶蛋白进行去磷酸酶作用, 使其恢复原来的构象并丧失活性(Hunter 1995)。已有的研究结果表明, 蛋白磷酸酶在植物的生长和发育过程中发挥着重要的生理功能, 如激素信号的传递和调控、细胞的生长与繁殖、器官的形成与发育、器官衰老、非生物和生物胁迫应答等(Barford 1995; Hunter 1995; Asai等2002; Bartels等2009, 2010; Lumbreras等2010; 丁海东等2011; Macho等2014; Segonzac等2014; 肖冬等2014)。蛋白酪氨酸磷酸酶(protein tyrosine phosphatase, PTP)是蛋白磷酸酶家族中一类重要的磷酸酶, 在植物的生长发育过程中发挥着重要的生理功能(Tonks 2006)。蛋白酪氨酸磷酸酶的氨基酸序列中包含多个保守结构域, 其中磷酸酶催化区保守结构域为: (I/V)HCXAGXXR(S/T)G (Gupta和Luan 2003)。对蛋白酪氨酸磷酸酶的研究主要集中在人类(human)和拟南芥(*Arabidopsis thaliana*)中, 水稻(*Oryza sativa*)等物种中蛋白酪氨酸磷酸酶的研究则较少(Alonso等2004; Shankar等2015)。本文对植物蛋白酪氨酸磷酸酶的分类、生理功能及信号途径进行归纳与总结, 为蛋白酪氨酸磷酸酶的后续研究提供理论依据。

1 植物蛋白酪氨酸磷酸酶的分类

在植物中, 根据催化底物氨基酸的特异性, 可以将蛋白磷酸酶分为两大系统: 丝/苏氨酸磷酸酶系统(serine/threonine phosphatase system)和酪氨酸磷酸酶系统(tyrosine phosphatase system)。根据作用底物的特异性, 可以将蛋白酪氨酸磷酸酶分为两类, 即酪氨酸特异性磷酸酶(tyrosine-specific phosphatase)和双特异性磷酸酶(dual-specificity phosphatase, DSP), 其中前者只能水解Tyr残基上的磷酸基团, 而后者可以水解Ser/Thr/Tyr残基上的磷酸基团(Alonso等2004; Roma-Mateo等2007; Jammes等2011)。根据蛋白酪氨酸磷酸酶在细胞中的定位及结构特点, 可以分为两大类, 即受体型PTP (receptor PTP)和非受体型PTP (non-receptor PTP), 前者主要分布在质膜上, 而后者主要分布于细胞质中, 二者均存在于真核生物中(Van Vactor等1998; Gupta和Luan 2003)。已有的研究证实, 在拟南芥中含有24个PTP成员, 水稻中含有25个PTP成员, 玉米(*Zea mays*)中含有29个PTP成员, 且上述PTP成员中都含有典型的PTP成员、双特异性PTP (DSP)成员和低分子量PTP (low molecular weight PTP, LMWPTP)成员(Kerk等2002, 2008; Singh等2010; Shankar等2015)。

2 植物蛋白酪氨酸磷酸酶的生理功能

2.1 调控生长发育

在拟南芥中, 磷酸酶基因*AtPAS2* (*pasticcino2*)沉默表达会抑制突变体胚轴和幼苗的生长与发育(Bellec等2002; Da Costa等2006)。在水稻中发现, *OsMKP1* (*MAPK phosphatase1*)缺失后, 水稻的生长受到抑制, 同时提高植株体内蛋白激酶的活性(Katou等2007)。Gupta等(2002)发现, AtPTEN1

(phosphatase and tensin homolog1)是酪氨酸特异性磷酸酶, *AtPTEN1*被敲除后, 会导致拟南芥花粉发育缺陷; 而*AtPHS1* (*propyzamide hypersensitive1*)突变后, 会导致拟南芥中微管结构与根发育异常。后续研究证实, 在长日照条件下, 突变体*atphs1-5*表现为晚开花, 提高体内*FLC*的表达水平, 同时降低*CO*、*FT*的表达水平(Gupta等2002; Naoi和Hashimoto 2004; Tang等2016)。拟南芥*atmkp1*或*atptp1*突变体表现为植物矮化, 而*atibr5* (*indole-3-butyric acid response5*)突变体则表现为生长受到抑制, 同时抑制植株花瓣的生长, 推测其可能通过生长素或TCP信号途径发挥功能(Monroe等2003; Bartels等2009; Johnson等2015)。

2.2 调控非生物胁迫应答

AtDsPTP1 (dual-specificity PTP1)是双特异性蛋白酪氨酸磷酸酶, 其缺失突变体经渗透胁迫处理后, 增加植株体内游离脯氨酸的积累和提高抗氧化酶的活性水平, 降低MDA和ABA的含量, 推出其可能作为负调控因子参与渗透胁迫应答(Liu等2014)。*AtPTEN2* (*phosphatase and tensin homolog2*)编码的蛋白具有酪氨酸磷酸酶活性, 其转录活性受到盐和渗透胁迫的调控, 推测其可能参与植物的非生物胁迫应答(Pribat等2012)。*OsIBR5*可以被PEG-6000、H_2O_2、ABA诱导上调表达, 且其过表达烟草(*Nicotiana benthamiana*)植株对干旱和H_2O_2较对照敏感, 推测*OsIBR5*在干旱胁迫应答过程中发挥负调控作用(Li等2012)。*OsPFA-DSP1*可以被PEG6000、H_2O_2、ABA诱导上调表达; 在水稻和烟草中过表达*OsPFA-DSP1* (*plant and fungi atypical dual-specificity phosphatase1*), 转基因植株均表现为对干旱胁迫敏感, 表明OsPFA-DSP1作为负调控因子参与和调控干旱胁迫应答反应, 但是具体的调控机制尚不清楚(Liu等2012)。*AtMKP2*沉默表达后, 植株对氧化胁迫(臭氧)非常敏感, 而*AtMKP1*、*AtIBR5*基因被敲除后, 植株对盐等胁迫不敏感, 同时AtIBR5可以与AtCHS3形成二聚体并调控冷胁迫的应答(Lee和Ellis 2007; Strader等2008; Liu等2015)。后续的研究结果证实, UV-B处理可以促进AtMKP1的积累, 而机械损伤可以诱导TMKP1的表达并活化其蛋白酪氨酸磷酸酶活性, 推测其可能在非生物胁迫应答中作为正调控因子而发挥作

用(Gonzalez Besteiro和Ulm 2013; Ghorbel等2015)。体外实验证实, NtMKP1可以对蛋白激酶NtSIPK (salicylic acid induced protein kinase)去磷酸化并失活其激酶活性; 而在过表达*NtMKP1*烟草植株中则抑制NtWIPK (wound induced protein kinase)和NtSIPK的激酶活性, 但*NtMKP1*缺失后, 可以上调NtWIPK和NtSIPK激酶的活性水平, 推测其可能在烟草机械损伤中发挥负调控作用(Oka等2013)。

2.3 调控生物胁迫应答

在拟南芥中, *AtMKP1*缺失后可以提高对病原菌的抗性, 同时降低与其互作蛋白激酶的活性; 烟草*NtMKP1*缺失后, 不仅可以提高WIPK和SIPK的激酶活性, 还可以增强对病原菌*Botrytis cinerea*、*Mamestra brassicae*和*Spodoptera litura*的抗性, 二者在植物病原菌防御中发挥负调控作用(Ulm等2002; Anderson等2011; Oka等2013)。*AtMKP2*缺失后, 增强植株对病原菌的抗性, 同时提高蛋白激酶的活性, 此结果与*AtMKP1*的生理功能相似, 但具体的调控机制则不相同(Lumbreras等2010; Vilela等2010)。Bartels等(2009)发现, *AtMKP1*和*AtPTP1*同时缺失后, 拟南芥突变体植株的生长受到抑制, 同时抑制细胞内病原菌的增殖和扩散, 提高植株对*Pst* DC3000 (*Pseudomonas syringae* DC3000)的抗性。与野生型水稻植株相比, 在水稻中过表达*OsPFA-DSP2*, 可以提高植株对稻瘟病原菌(Z1菌株)的敏感性, 增大叶片受损面积, 同时提高叶片内过氧化氢的合成与积累, 推测其可能通过过氧化氢介导的信号途径发挥负调控功能(He等2012)。突变体*ospfa-dsp2*的表型与野生型'日本晴'水稻植株的表型一致, 无显著性差别, 推测可能原因是存在同源基因并发挥类似功能。后续研究发现, 植物蛋白酪氨酸磷酸酶OsPFA-DSP2在白叶枯病菌的应答过程也是发挥负调控作用, 且与OsMPK9存在显著的物理互作(结果未发表)。以上研究结果说明, 植物蛋白酪氨酸磷酸酶在生物胁迫应答过程发挥重要的作用。

3 植物蛋白酪氨酸磷酸酶参与的信号途径

植物蛋白酪氨酸磷酸酶在植物的生长、发育、胁迫应答、信号传导等过程中发挥着重要的生理功能(Pitzschke和Hirt 2010; Andreasson和Ellis 2010) (如图1)。蛋白酪氨酸磷酸酶AtIBR5是生长
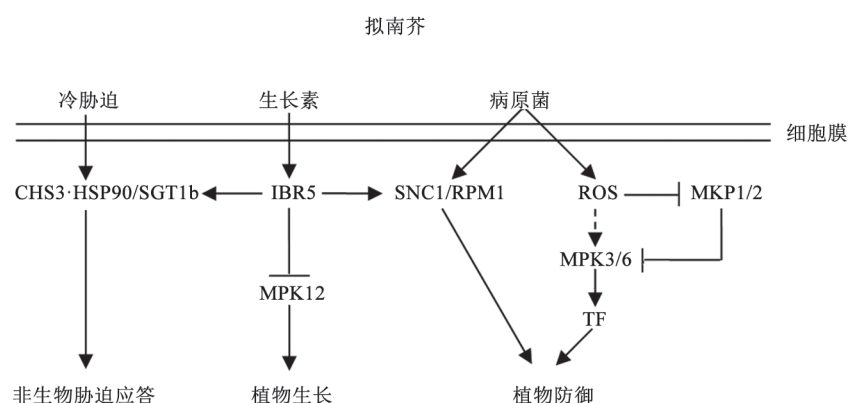
图1 蛋白酪氨酸磷酸酶在拟南芥中的信号途径
Fig.1 Signaling pathways of protein tyrosine phosphatases in *Arabidopsis*

素的受体, 外源或内源生长素将信号传递至AtI-BR5, AtIBR5与AtMPK12互作并使其去磷酸化, 进而调节拟南芥的生长, 该调控方式是独立于TIR1介导的信号通路外的一种新的调控机制(Monroe-Augustus等2003; Strader等2008; Lee等2009)。冷胁迫可诱导AtCHS3 (chilling-sensitive mutant3)蛋白的表达与积累, 而AtIBR5可以与AtCHS3/HSP90/STG1b互作并形成聚合体, 保护AtCHS3蛋白的完整性, 进而提高拟南芥植株的抗逆性(Liu等2015)。最近的报道还证实, 拟南芥受到病原菌*Pst* DC3000侵染时, *atibr5*植株对病原菌较对照敏感, 同时AtIBR5与AtSNC1 (suppressor of *npr1-1*, constitutive1)互作, 抑制下游*PR* (pathogenesis resistance)基因的表达, 进而负调控拟南芥的生物胁迫应答(Liu等2015; Shankar等2015)。因此, 植物蛋白酪氨酸磷酸酶AtIBR5作为一个关键的调控点, 在植物的生长、激素应答和胁迫应答过程中发挥着重要的作用。

拟南芥受到病原菌侵染时, 可以促进植株体内ROS的产生和积累(Torres 2010; Feng和Shan 2014; Mittler 2016)。如图1所示, 一方面, ROS可以通过MAPK级联反应激活MPK3/6的活性, 而活化的MPK3/6通过调控下游转录因子(transcription factor, TF)的转录与表达, 进而提高拟南芥植株的免疫应答能力; 另一方面, ROS可以抑制细胞内蛋白酪氨酸磷酸酶AtMKP1/2的活性, 而AtMKP1/2可以与蛋白激酶AtMPK3/6互作并通过去磷酸酶作用抑制其激酶活性, 进而抑制下游TF的转录与表达, 从而降

低拟南芥植株对病原菌的抗性(Lee和Ellis 2007; Bartels等2009; Lumbreras等2010; Jalmi和Sinha 2015)。因此, 蛋白酪氨酸磷酸酶AtMKP1/2作为负调控因子在拟南芥病原菌应答过程中发挥作用。

4 总结与展望

综上所述, 蛋白酪氨酸磷酸酶在植物的生长、器官发育、非生物胁迫和生物胁迫应答等过程中发挥着重要的生理功能。蛋白酪氨酸磷酸酶的研究存在以下几个问题: (1)生物信息学分析结果显示, 大部分蛋白酪氨酸磷酸酶的生物学功能尚不明确, 有待于进一步研究; (2)多数蛋白酪氨酸磷酸酶调控的上下游基因或蛋白因子尚未完全鉴定, 因而调控植物生长和胁迫应答的机制未阐明; (3)在植物中沉默或过量表达蛋白酪氨酸磷酸酶基因, 是否影响植物内源性激素的合成与积累以及是否通过植物激素信号途径来发挥其生理功能, 仍未得到解释。

已有的研究主要集中在模式植物拟南芥中, 且其参与的信号通路及调控机制研究的较为详细; 而针对水稻、烟草等物种中蛋白酪氨酸磷酸酶的研究与报道则较少。因此, 加大对植物中蛋白酪氨酸磷酸酶生物学功能及调控机制的研究, 既可以丰富植物酪氨酸磷酸酶的研究成果, 也可以通过基因敲除技术为作物的分子育种提供理论依据。

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Recent advance on physiological function of protein tyrosine phosphatases in plants

HE Han-Jie[1,2], TANG Li[2], DENG Hua-Feng[2,3,*], ZOU Zhi-Gang[1]

[1]*Key Laboratory of Forestry Biotechnology/Cooperative Innovation Center of Engineering and New Products for Developmental Biology of Hunan Province, Central South University of Forestry and Technology, Changsha 410018, China; [2]Key Laboratory of Hybrid Rice, Hunan Hybrid Rice Research Center, Changsha 410125, China; [3]Southern Regional Collaborative Innovation Center for Grain and Oil Crops in China, Changsha 410125, China*

Abstract: In plant, protein tyrosine phosphatases (PTPs) and protein kinases control reversible phosphorylation, and the former plays critical roles in growth, organism development, hormones response, signal transduction and stresses response. This paper focused on classification, biological function and signaling pathways of PTPs in growth, abiotic and biotic stresses responses, in order to provide theoretical basis for future scientific research.

Key words: protein tyrosine phosphatase; stresses response; physiological function; signaling pathway