

· 专题论坛 ·

## 植物紫色酸性磷酸酶基因家族功能研究进展

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**摘要** 紫色酸性磷酸酶(PAPs)是一类广泛存在于植物体内的金属磷酸酯酶, 其羧基端含有1个保守结构域, 由5个保守基序和7个氨基酸残基构成。作为一种特殊的酸性磷酸酶, PAPs在酸性环境下能够有效催化磷酸酯或酸酐的水解, 释放出植物可以利用的磷酸基团。此外, PAPs在调节植物碳代谢、细胞壁合成和抵御病菌侵染等方面也发挥重要生理作用。该文简要介绍了PAPs的结构、家族成员及其调控因子, 并着重总结了近年来对PAPs生物学功能的研究进展, 为今后系统开展PAPs功能研究提供了理论参考。

**关键词** 紫色酸性磷酸酶, 生物学功能, 调控因子

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磷是植物生长发育过程中必需的六大营养元素之一, 对植物新陈代谢和正常生长发育有着极其重要的作用。磷元素不仅参与植物细胞内许多化合物的生物合成, 蛋白磷酸化和去磷酸化等生理生化过程, 而且对植物生长发育及作物产量形成等也有一定的影响 (James and David, 1992; Hammond et al., 2004)。尽管土壤中含有大量的磷, 但主要以磷酸酯和磷酸酐等有机形式存在, 不能被植物吸收和利用, 因此土壤中有效磷含量不足, 限制着植物的生长发育 (Vance et al., 2003; 刘涛等, 2016)。植物在缺磷状态下, 会表现出茎短而细、叶片基部变黄、植株矮小、生长延缓、分枝或分蘖减少、种子小且不饱满等缺素症状。农业生产上普遍采用外施磷肥来提高植物对磷素的吸收利用, 这不仅增加了农业生产成本, 而且施肥过量还会污染水环境, 导致水体富营养化, 同时加剧磷资源的消耗 (Vance, 2001; Cakmak, 2002; Smith and Schindler, 2009)。因此, 通过基因工程手段对植物进行改良, 研究植物磷营养代谢的生理学和分子生物学机制, 深入挖掘植物自身磷吸收利用潜力, 对节约磷矿资源、提高作物产量和品质以及保护生态环境具有重要意义 (周志高等, 2005)。

紫色酸性磷酸酶 (purple acid phosphatases, PAPs) 属于双核金属脱氢酶 (binuclear metallohydrolase) 家族, 是一种广泛存在于动物和植物体内的酸性磷酸酶类。在植物体的弱酸性 (pH4–7) 条件下, PAPs能够催化水解磷酸单酯和酸酐类有机物 (如ATP、ADP和糖脂) 并释放出无机磷, 供植物吸收利用, 从而提高植物对磷的利用率 (Olczak et al., 2003; 卢坤等, 2010)。Zimmermann等 (2004) 研究表明, 在低磷胁迫下, 植物体内和根际分泌的PAPs活性均显著提高, 因此该酶能够分泌到植物细胞外活化植物根际周围的有机磷, 从而促进植株体内磷素的再循环利用。植物PAPs的成功分离对研究植物磷营养代谢机制具有重要意义。近年来, 在植物中已鉴定出许多PAPs编码基因。本文将系统论述植物中紫色酸性磷酸酶的结构及其家族成员的分类, 并着重介绍紫色酸性磷酸酶生物学功能的研究进展。

### 1 植物PAPs的发现及其结构

1998年, Hiroshi等用同位素标记法, 发现低磷会诱导浮萍 (*Spirodela oligorrhiza*) 产生57 kDa的磷脂酰肌醇锚定磷酸酶, 该酶含有 $\text{Fe}^{3+}$ - $\text{Mn}^{2+}$ 双核金属中心,

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活性受到酒石酸抑制。这是首次在高等植物中发现紫色酸性磷酸酶(Nakazato et al., 1998), 由此揭开了植物PAPs研究的序幕。之后, 在单子叶和双子叶植物中均已鉴定出PAPs (Li et al., 2002; Zhang et al., 2011)。

紫色酸性磷酸酶因其在溶液中表现出特殊的紫色或粉色而命名, 而呈现粉紫色是由发色基团铁离子和酪氨酸之间的电子转移所致。PAPs的催化位点和结构域高度保守, 其结构的基本特征在于含有5个保守基序( $\beta/\alpha/\beta/\alpha/\beta$ )、7个结合金属离子的氨基酸残基(DXG/GDXXY/GNH(D/E)/VXXH/GHXH)和1个金属离子的双核中心(Schenk et al., 2000b)。菜豆(*Phaseolus vulgaris*)紫色酸性磷酸酶(KBPAP)的三级结构见图1。其三维大小为 $40 \times 60 \times 75 \text{ \AA}$ , 二聚体呈现出心形结构, 每个亚基具有1个N端结构域(120个氨基酸残基), 1个C端结构域(210个氨基酸残基)和Fe-Zn金属离子中心(Strater et al., 1995)。植物、哺乳动物和细菌PAPs的催化结构域都含有“三明治”形状的 $\beta/\alpha/\beta/\alpha/\beta$ 基序。植物PAPs的双核金属中心一般由 $\text{Fe}^{3+}$ - $\text{Zn}^{2+}$ 或 $\text{Fe}^{3+}$ - $\text{Mn}^{2+}$ 构成, 而动物PAPs的双核金属中心一般由 $\text{Fe}^{3+}$ - $\text{Fe}^{2+}$ 构成(Schenk et al., 2008; Jarenmark et al., 2011)。

## 2 PAPs的分类及植物PAPs家族分析

根据紫色酸性磷酸酶基因编码蛋白的结构和分子量大小, 可将PAPs蛋白成员分为2类: 一类为大分子量PAPs, 其单体亚基分子量约为55 kDa; 另一类为小分子量PAPs, 其单体亚基约为35 kDa。植物大分子量PAPs与真菌的同源蛋白进化关系较近; 而植物小分子量PAPs与动物的同源蛋白进化关系较近, 从而反映PAPs家族成员在结构和功能上进化出的多样性。

### 2.1 植物大分子量PAPs

大分子量的紫色酸性磷酸酶(high molecular weight PAPs, HMW PAPs)通常以同源二聚体的形式存在, 其单体分子量约为55 kDa, 此类PAPs在植物中所占比例较大, 并且与真菌和分枝杆菌的此类蛋白之间同源性较高(Schenk et al., 2000b)。

菜豆中克隆出的KBPAP (检索号P80366)分子量

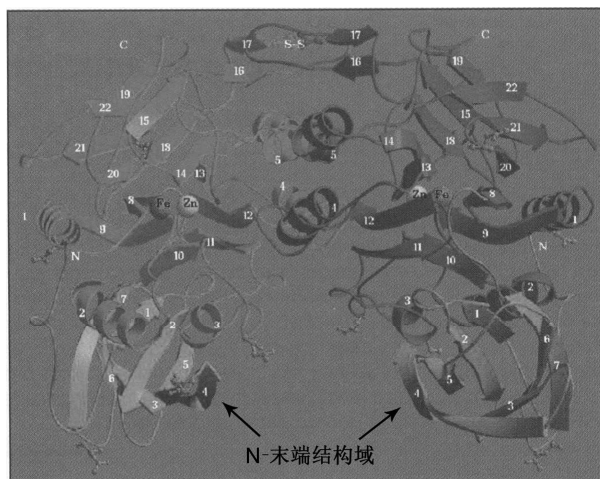


图1 菜豆紫色酸性磷酸酶(KBPAP)的三维结构(改自Strater et al., 1995)

Figure 1 3D-structure of KBPAP of *Phaseolus vulgaris* (modified from Strater et al., 1995)

为111 kDa, 属于大分子量PAP。KBPAP是1个二聚体酶, 包含2个糖基化的亚基, 2个亚基通过二硫键共价相连。每个亚基包含432个氨基酸残基和5个N-糖基化的天冬酰胺残基, 并且同时具有N-端和C-端2个结构域。C-端结构域分子量较大, 具有催化功能; N-端结构域较小, 由2个 $\beta$ -折叠组成。每个 $\beta$ -折叠由3个反向平行的 $\beta$ -链构成, 且不具有金属磷酸酶催化活性(Klabunde et al., 1994, 1995)。

### 2.2 植物小分子量PAPs

小分子量的紫色酸性磷酸酶(low molecular weight PAPs, LMW PAPs)以单聚体形式存在, 与哺乳动物和蓝藻体内的小分子量PAPs极为相似, 单体分子量一般约为35 kDa, 在结构上仅保留了典型的C-端结构域(Schenk et al., 2000a, 2000b)。菜豆根中提取的PvPAP3, 分子量为34 kDa, 属小分子量PAPs, 具有较高的热稳定性, 作用底物为ATP。PvPAP3定位于细胞质膜。低磷条件下, PvPAP3可在大豆(*Glycine max*)叶片和根中诱导表达, 并在磷高效基因型中表达量迅速增加(Liang et al., 2010)。马铃薯(*Solanum tuberosu*) StPAP1基因编码LMW PAPs, 类似于哺乳动物的PAPs, 在茎和根部高表达并对低磷环境敏感; 而StPAP2和StPAP3编码2种典型的植物HMW PAPs, 分别在茎和根部受低磷诱导表达(Zimmer-

mann et al., 2004)。

### 2.3 PAPs家族及其进化关系

目前, PAPs已在多种植物中被鉴定和分离, 通过对拟南芥(*Arabidopsis thaliana*)和大豆等植物中的PAPs进行系统研究, 发现拟南芥中存在29个PAPs基因(Li et al., 2002), 大豆中存在35个PAPs基因(Li et al., 2012), 水稻(*Oryza sativa*)中存在26个PAPs基因(Zhang et al., 2011)。将这些植物PAPs与已报道的烟草(*Nicotiana tabacum*)、玉米(*Zea mays*)、小麦(*Triticum aestivum*)和菜豆等物种PAPs的氨基酸序列比对, 构建进化树进行聚类分析(Tian and Liao, 2015), 可将其分成4个家族(图2)。

PAPs家族I所包含的种类最多, 该家族可进一步分为I-1和I-2两个亚家族。I-1亚家族成员已被证实参与植物磷和碳代谢途径(Hur et al., 2010; Sun et al., 2012a)。目前, 已报道的I-2亚家族蛋白均具有植酸酶活性(Zhang et al., 2008; Kuang et al., 2009)。PAPs家族II是一个多功能家族, 参与植物抗病、磷饥饿诱导和细胞壁合成等多种生物学过程(Kaida et al., 2010; Robinson et al., 2012a; Ravichandran et al., 2013)。PAPs家族III和IV成员相关研究报道较少, 已鉴定的GmPAP3和PvPAP3与植物响应非生物逆境胁迫和磷利用效率有关(Li et al., 2008; Liang et al., 2010)。

## 3 植物PAPs的生物学功能

紫色酸性磷酸酶在植物各个组织均有分布, 参与各种生命活动(Zhu et al., 2005)。多数PAPs蛋白能够非特异性水解很多含磷脂键的化合物(包括ATP、PEP和植酸等), 释放磷酸基团(Olczak et al., 2003)。PAPs在植物不同生长发育过程中, 具有多种生物学功能, 具体功能由其在植物体内作用的对象决定。近几年, 越来越多的植物紫色酸性磷酸酶被鉴定和克隆出来。我们对植物PAPs的生物学功能进行了总结, 详见表1。

### 3.1 调节植物的磷代谢

植物PAPs与土壤有机磷的分解吸收及植株体内磷素的再利用有密切关系, 很多植物来源的PAPs都具有酸性磷酸酶活性, 能够将植物体内外的有机磷水解成

无机磷, 供植物吸收利用。根据PAPs是否具有分泌到细胞外的性质, 可将其分为细胞内酸性磷酸酶(intracellular acid phosphatase, IAP)和分泌型酸性磷酸酶(secreted acid phosphatase, SAP)。细胞内酸性磷酸酶主要水解植物体内磷库的磷, 进行细胞内磷素的再利用; 分泌型酸性磷酸酶则被分泌出细胞外, 活化土壤中的有机磷组分, 释放出供植物利用的无机磷(Wasaki et al., 2003)。细胞内的无机磷含量与IAP和SAP活性密切相关。在磷饥饿诱导下, IAP会迅速催化植物体内储存的有机磷, 释放无机磷, 保证磷源的供应(Veneklaas et al., 2012)。随后, 植物会诱导合成SAP并且分泌到细胞外, 水解植物体外的磷源, 将释放的无机磷吸收到植物体内(Wasaki et al., 2003)(图3)。拟南芥AtPAP12和AtPAP26分别是2个主要的细胞内和分泌型酸性磷酸酶。缺磷条件下, 它们被检测到过量表达(Wang et al., 2014)。在磷胁迫下, 可检测到番茄(*Solanum lycopersicum*)悬浮细胞中IAP和SAP先后被诱导表达(Kusudo et al., 2003)。

### 3.2 参与植物应对逆境

大豆酸性磷酸酶3基因(*GmPAP3*)定位在线粒体(活性氧产生的主要部位), 其表达受盐和氧胁迫诱导, 可能在非生物逆境响应过程中发挥作用。将*GmPAP3*过表达植株分别进行盐、PEG以及农药胁迫处理, 对比野生型发现过表达植株的根长增加。此外, *GmPAP3*能够通过抑制活性氧(ROS)的积累, 减轻盐和过氧化胁迫造成的损伤(Liao et al., 2003; Li et al., 2008)。酸性磷酸酶15基因(*AtPAP15*)在拟南芥中组成型表达, 具有植酸酶活性。在*atpap15*突变体材料中, 抗坏血酸盐(ascorbic acid sodium salt, AsA)的含量下降, 植酸的含量升高, 植物对氧胁迫逆境的抗性降低。反之, 在*AtPAP15*过量表达的转基因拟南芥中, AsA含量升高, 抗性增强。*AtPAP15*通过水解植酸盐释放出肌醇和无机磷, 肌醇参与抗坏血酸合成途径, 进而调节植物的逆境适应性(Zhang et al., 2008)。

### 3.3 调节植物的碳代谢

Sun等(2012b)研究表明, *AtPAP2*是一种尾部锚定蛋白, 含有N-端信号肽和C-端膜锚定信号肽。*AtPAP2*在拟南芥角果、茎、花、根和开始衰老的叶中高度表



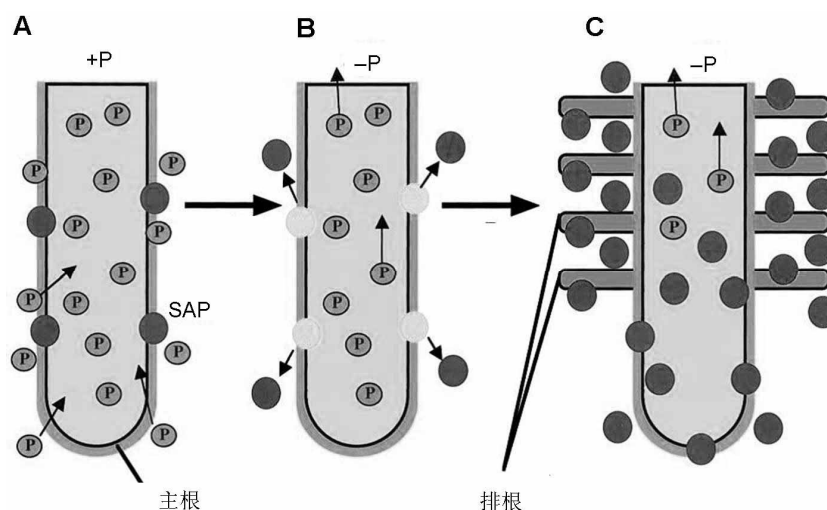


图3 缺磷情况下分泌型酸性磷酸酶的诱导表达及其根际分泌与排根形成示意图(改自Wasaki et al., 2003)

(A) 磷充足条件下, SAP聚集在根表皮细胞周围, 只有少量SAP分泌; (B) 磷胁迫条件下, SAP在12小时内从根部迅速分泌, 但在长时间保持较低水平; (C) 组织中磷含量明显下降后, 根系成簇排列, 形成排根, SAP分泌量显著增加。

Figure 3 Schematic model of SAP expression and formation of cluster root under phosphorus deficiency (modified from Wasaki et al., 2003)

(A) Under sufficient P conditions, SAP localizes around the epidermal cells of roots, and only a small amount of SAP is secreted; (B) After P stress treatment, SAP is released from roots rapidly within 12 h, however, SAP secretion remains at a low level for a long time; (C) After the decrease of P content in tissues, cluster roots form and SAP secretion significantly increases.

达, 但在叶和成熟的种子中表达量相对较低(Sun et al., 2012a)。AtPAP2在C-末端具有保守的疏水结构域, 这决定了其亚细胞定位及对叶绿体和线粒体的双向靶定; 同时, C-端锚定信号肽的存在直接影响AtPAP2的基因功能, 将C-端信号肽去掉, AtPAP2将无法继续行使功能(Sun et al., 2012a)。AtPAP2过量表达的拟南芥、亚麻芥(*Camelina sativa*)和马铃薯转基因植株抽苔提前, 生长速度加快, 叶片光合速率提高10%–20%, 种子体积及生物量增加; 同时, 蔗糖磷酸合酶的活性显著升高, 嫩枝含有更高水平的糖类(蔗糖和己糖)、丙氨酸和脯氨酸等三羧酸循环(TCA)代谢产物(Sun et al., 2012a; Zhang et al., 2012, 2014)。此外, AtPAP2转基因植株的ATP含量升高, 细胞壁合成相关酶(果胶酯酶和纤维素合酶)基因表达量上调(Sun et al., 2013; Liang et al., 2014, 2015)。AtPAP2是第1个被证实参与碳代谢的紫色酸性磷酸酶。最新研究表明, AtPAP2能与线粒体和叶绿体中参与RNA编辑的MORFs因子互作, 控制相应蛋白进出线粒体和叶绿体的效率, 最终调节质体基因的表达(Law et al., 2015; Zhang et al., 2016; Sun et al.,

2017)。

### 3.4 参与植物细胞壁合成

烟草中, NtPAP12可催化重组的木糖苷酶磷酸化和去磷酸化以及葡萄糖苷酶去磷酸化, 抑制木葡聚糖降解, 增加木聚糖的合成; 还可通过葡萄糖苷酶去磷酸化, 抑制纤维寡糖的降解, 进而增加纤维素和胼胝质的合成。NtPAP12过表达株系糖苷酶活性下降, 质外体中木葡聚糖和纤维寡糖含量上升, 细胞壁主要成分(木聚糖、胼胝质和纤维素)的含量增加, 证实NtPAP12能够调节木糖苷酶以及葡萄糖苷酶的活性, 从而促进细胞壁的合成(Kaida et al., 2008, 2009, 2010)。拟南芥AtPAP10与烟草NtPAP12的功能相似性较高, 能够活化 $\beta$ -葡聚糖合成酶, 推测其可能参与初生壁的合成(Kaida et al., 2003)。

## 4 植物PAPs基因的表达调控

不同PAPs在植物体内的表达模式不尽相同, 它们分工合作, 在转录水平、翻译水平和翻译后水平受到调

控。绝大部分植物PAPs的表达水平不仅与植物体内的无机磷含量相关,而且与植物所处的逆境(氧和盐胁迫等)环境有关。对26个水稻PAPs编码基因进行启动子元件分析,发现其中12个基因的启动子含有顺式作用元件P1BS (PHR1-binding site), P1BS是水稻磷信号代谢途径转录因子 *OsPHR2* 的结合元件 (Rubio et al., 2001)。PHR1在水稻中的同源基因为 *OsPHR2* (Zhou et al., 2008)。通过对*OsPHR2*过表达材料进行定量检测表明,其中10个PAPs受到*OsPHR2*诱导表达(Zhang et al., 2011)。与水稻PAPs类似,拟南芥*AtPAP10*、*AtPAP12*和*AtPAP15*等在转录水平受到PHR1正调控(Wang et al., 2011; Robinson et al., 2012b)。

大部分PAP都具有N-端信号肽,这个信号肽对PAP蛋白的锚定和生物学功能具有重要作用。信号肽定位预测表明,少数PAPs定位于线粒体(Zhang et al., 2011)。虽然很多细胞内和分泌型酸性磷酸酶编码基因已被克隆,但是其表达调控机制和分子生物学功能还不是很清楚。低磷胁迫下, *AtPAP10*和*AtPAP12*的表达受到诱导,由此可知这2个基因存在转录水平的调控; *AtPAP26*在转录水平没有变化,但是细胞内外*AtPAP26*蛋白含量显著增加,表明该基因受到转录后水平的调控(Tran et al., 2010b)。另外, *AtPAP1*也被证实可能受到转录后水平的调控(Wang et al., 2011)。由于*AtPAP10*、*AtPAP12*和*AtPAP26*蛋白的N-端都存在至少1个糖基化修饰位点,故这些蛋白的糖基化修饰可能直接影响它们的细胞定位(Tran et al., 2010b),但具体的糖基化调控方式尚有待研究。

## 5 展望

植物PAPs是植物体对低磷应答反应及其信号转导途径的重要调控因子。克隆与解析PAPs基因功能,对认识植物对磷高效利用的分子机制、解决当前土壤有效磷不足以及植物磷缺乏等问题具有重要意义。通过对植物各物种PAPs家族的不同成员进行分析,发现除与金属离子活性中心结合的5段氨基酸序列高度保守外, PAPs蛋白分子大小和氨基酸序列均存在较大差异,暗示PAPs成员间存在功能多样性。近年来,已从高等植物中分离鉴定出许多PAPs的编码基因,它们参与了次生壁合成、活性氧代谢和抵御病原菌侵染等

各种生命过程,但大多数植物PAPs基因的功能未知,值得进一步挖掘和探讨。

此外,虽然许多植物细胞内和分泌型酸性磷酸酶编码基因已被克隆,但其表达调控机制至今未有详尽的解释。磷胁迫条件下, *AtPAP26*在转录水平并未发生变化。免疫印迹检测显示, *AtPAP26*在蛋白水平受到缺磷诱导,但是其在蛋白水平具体的调控机制还不清楚(Tran et al., 2010a; Robinson et al., 2012b)。序列分析和生化实验证明,大多数植物紫色酸性磷酸酶都具有翻译后糖基化修饰的功能。糖基化修饰可调节酶的定位、溶解性、稳定性和动力学特征。现已发现不同物种PAPs家族的很多成员也存在潜在的N-端糖基化修饰位点,但糖基化如何改变PAPs定位及动力学活性还有待探讨。未来对PAPs的研究如果能够解释上述问题,将对阐明植物PAPs的功能以及调控大有帮助。

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## Research Progress into the Function of Purple Acid Phosphatase Gene Family in Plants

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**Abstract** Purple acid phosphatases (PAPs) are members of the metallo-phosphoesterase family identified from a wide range of plants. They are characterized by the presence of five conserved structure motifs and seven amino acid residues in the C-terminal. PAPs have mostly been studied for their potential involvement in phosphorus acquisition and redistribution because of their ability to catalyze the hydrolysis of activated phosphate esters and anhydrides under acidic conditions. Recent studies also showed that PAPs play important roles in modulating plant carbon metabolism, cell wall synthesis and pathogen resistance, etc. This review focuses on the structure, family members and regulatory factors of PAPs, with special emphasis on the recent progress of their biological functions, which will provide theoretical reference for further study of PAPs in plants.

**Key words** purple acid phosphatases (PAPs), biological function, regulatory factors

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