



植物亲环素基因功能研究进展

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摘要: 亲环素属于亲免疫素家族, 具有肽基脯氨酰顺反异构酶(PPIase)活性, 在生物界广泛分布, 存在于细胞质和各个细胞器中, 且在结构上高度保守。植物亲环素是一个多基因家族, 除具有一般亲环素的功能外, 还在一系列生物学过程中发挥重要作用, 如参与胁迫应答、代谢调控及植物的生长发育等。该文主要对近年来国内外有关植物亲环素基因的功能和研究进展进行综述, 为今后亲环素研究提供参考。

关键词: 亲环素; 基因; 生物学功能。

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Research Progress of Plant Cyclophilin Gene Functions

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Abstract: Cyclophilins (CyPs), members of the ‘immunophilin’ protein family, have peptidyl-prolyl-cis-trans isomerase activity and widely distribute in different organisms. They are highly conserved in protein structure and expressed in cytosol and various organelles. Plant CyPs are supper-family members and play significant roles in stress response, metabolic regulation and plant development besides their common functions. This review summarizes the functions and recent research progress of plant CyPs and aims to help their further characterization in the future.

Key words: cyclophilin; gene; biological function

亲环素(cyclophilin, CyP)能够与免疫抑制剂环孢霉素 A(cyclosporine A, CsA)特异结合, 具有肽基脯氨酰顺反异构酶(peptidyl-prolyl *cis-trans*-isomerase, PPIase)活性, 能够催化脯氨酸残基的顺-反异构化, 在富含脯氨酸蛋白质的折叠、输送和相互作用中都起到至关重要的作用。亲环素广泛存在于不同生物体中, 包括病毒、细菌、真菌、植物和动物, 通常出现在细胞质、内质网、高尔基体、细胞核、线粒体等细胞器中^[1]。亲环素分为单结构域和多结

构域两种类型, 单结构域亲环素具有一个高度保守的 PPIase 结构域, 多结构域亲环素除了 PPIase 域, 还有 WD、CCD、RP、RRM、Zn Finger 和 TPR 等结构域, 这些结构域参与蛋白质-蛋白质或蛋白质-核酸相互作用^[2]。植物亲环素是一个很大的家族, 拥有众多不同的结构、功能和组织定位。1990 年 Gas-ser 等^[3]首次从番茄(*Lycopersicon esculentum*)、玉米(*Zea mays*)、油菜(*Brassica napus*)中鉴定和分离了亲环素蛋白, 并在大肠杆菌中进行表达。随后,

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在拟南芥(*Arabidopsis thaliana*)、小麦(*Triticum aestivum*)、水稻(*Oryza sativa*)、大豆(*Glycine max*)、大白菜(*Brassica campestris*)等植物中相继鉴定和克隆到亲环素基因^[2]。前人的研究结果表明植物亲环素普遍存在并高水平表达于生长旺盛的分生组织中,在植物生长发育调节、胁迫应答以及代谢调控等方面均发挥重要作用。

1 拟南芥亲环素基因

在拟南芥基因组发现了 31 个亲环素基因,属于目前已鉴定的第二大亲环素基因家族。Marquez 等^[4]发现拟南芥亲环素基因存在可变剪接,编码了 41 个预测蛋白。迄今为止,只有 17 个亲环素基因功能得到解析(表 1)。

拟南芥亲环素基因与光合作用及光信号传导相关。AtCYP38 和 AtCYP20-3 在维持光合系统 II (PS II) 的完整性与氧化还原和光合蛋白复合物装配中起重要作用。AtCYP38 是位于叶绿体类囊体腔的多结构域亲环素,与叶绿素蛋白结合后帮助 PS II 复合物正确折叠和插入,并参与氧化还原复合物的正确装配,而 *Atcyp38* 突变体生长迟缓且对光敏感^[5]。位于叶绿体基质的 AtCYP20-3 是单结构域亲环素,仅在光合组织中表达且受光照强烈诱导,其 PPIase 活性受氧化还原作用的调节。它是将光合电子传递和氧化还原调节与半胱氨酸生物合成和外界胁迫应答联系起来的一个关键枢纽^[6]。2-半胱氨酸过氧化物氧化蛋白(2-CysPrxs)定位于叶绿体,具有硫醇过氧化物酶和分子伴侣等功能,AtCYP20-3 通过与 2-CysPrx 相互作用在叶绿体中形成一个对氧化还原敏感的调控单元^[7]。AtCYP18-3、AtCYP19-1 和 AtCYP19-3 参与光信号传导调控。*Atcyp18-3* 突变体对隐花色素和光敏色素介导的去黄化作用有缺陷表型,在蓝色和远红光下具有较长的下胚轴和茎^[8-9]。*AtCYP18-3*、*AtCYP19-1* 和 *AtCYP19-3* 在黑暗中表达降低,而在连续光照下 *AtCYP18-3* 的表达量增加^[9]。

拟南芥亲环素在植物生长发育中发挥重要作用。*Atcyp71* 突变体茎顶端分生组织发育不良、花形态改变、根生长受到抑制。Li 等^[10]研究发现 AtCYP71 不仅能与组蛋白 H₃ 结合调控基因沉默和器官发生,而且参与拟南芥染色质装配并调控基因表达。*Atcyp40* 突变体从幼苗到成熟期以及开花期都表现出发育不良、叶数减少和叶形态改变^[11]。Smith 等^[12]研究发现 AtCYP40 与 HSP-90 相互作

用调控植物的生长发育。位于叶绿体的 AtCYP20-2 参与 NADPH 脱水结构域的装配,是叶绿体脱氢酶复合物形成的重要分子伴侣^[13]。它会导致 BZR1 (brazzinazole-resistant1, BZR1) 转录因子的构象变化,有助于 BZR1 与开花基因 *FLD* (*Flowering Locus D*, *FLD*) 启动子中的顺式元件结合并调节 *FLD* 表达调控开花模式,而 *Atcyp20-2* 突变体表现提前开花表型^[14]。此外,位于线粒体的 AtCYP21-3 和 AtCYP21-4 具有高度保守的 PPIase 活性,在调控线粒体的通透性和细胞凋亡中起关键作用^[15]。

研究发现拟南芥亲环素还参与对高盐、低温和病菌感染等的胁迫应答。AtCYP19-2 在高盐和低温胁迫下表达增强^[16]; AtCYP19-4 响应高盐和低温胁迫^[17]; AtCYP19-1 和 AtCYP57 参与植物对抗细菌病原体丁香假单胞菌的防御反应^[18]; AtCYP40 则与翻译后基因沉默、microRNA 活性有关,与病毒复制蛋白结合后抑制了番茄丛矮病毒酶的装配^[19-20]。AtCYP18-3 不仅能与转运蛋白 VirD2 相互作用抑制根癌土壤杆菌入侵植物细胞^[21-22],而且与丁香假单胞菌 AvRpt2 蛋白酶的激活有关,有助于植物的先天免疫^[23]。Li 等^[24]研究还发现 AtCYP18-3 能催化病原菌效应蛋白 RPM1 的宿主靶蛋白 RIN4 磷酸化,激发植物细胞内由 RPM1 介导的防御反应。

拟南芥亲环素与植物激素信号转导也有关。AtCYP18-3 参与油菜素内酯与赤霉素信号转导,调控植物的生长和发育^[21]; 位于叶绿体的 AtCYP20-3 参与调控茉莉酸信号通路与细胞氧化还原信号传递^[25-26]; 位于内质网的 AtCYP20-1 则通过与蛋白磷酸酶相互作用参与生长素信号转导和磷酸酶活性的调控^[27]。

此外,位于类囊体的 AtCYP59 和 AtCYP65 是多结构域亲环素,AtCYP59 与 RNA 聚合酶 II 相互作用在转录和 per-mRNA 加工过程起到重要作用,而 AtCYP65 能够与泛素连接酶相互作用^[28-29]。AtCYP19-4、AtCYP20-1、AtCYP21-1、AtCYP21-2 和 AtCYP21-3 参与调控分泌途径,其中 AtCYP19-4 定位在内质网和高尔基体,通过调节鸟嘌呤核苷酸交换因子参与囊泡运输^[30]。

2 水稻亲环素基因

水稻基因组中含有 29 个亲环素基因,与拟南芥一样存在可变剪接,编码了 46 个预测蛋白^[31],但相关的功能研究较少,目前只报道了 7 个基因的功能,

表 1 已报道的拟南芥亲环素及其功能

Table 1 The reported cyclophilins and their functions in *Arabidopsis thaliana*

基因名称 Gene	基因座 Gene locus	亚细胞定位 Subcellular localization	基因功能 Function	参考文献 Reference
<i>AtCYP18-3(ROC1)</i>	At4g38740	叶绿体 Chloroplast	与根瘤土壤杆菌 VirD2、丁香假单胞菌 AvRpt2 蛋白酶以及植物 RIN4 蛋白作用;参与油菜素类固醇、隐花素以及光敏色素的信号转导 Interacting with <i>A. tumefaciens</i> VirD2 protein, <i>P. syringae</i> AvRpt2 protease and the plant RIN4 protein; involved in hormone (brassinosteroid) regulation	[21-24]
<i>AtCYP18-4(ROC5)</i>	At4g34870	细胞质 Cytoplasm	响应光照胁迫应答 Responding to light stress	[9]
<i>AtCYP19-1(ROC3)</i>	At2g16600	细胞质 Cytoplasm	参与植物对抗细菌病原体的防御反应;响应光照胁迫 Involved in plant defense response against <i>P. syringae</i> ; responded to light stress	[9,23]
<i>AtCYP19-2</i>	At2g21130	细胞质 Cytoplasm	在高盐和低温胁迫下增强表达 Induced under high salt stress and low temperature stress	[16]
<i>AtCYP19-3(ROC2)</i>	At2g56070	细胞质 Cytoplasm	与细胞内钙蛋白 CaM 相互作用;响应光照胁迫应答 Interacting with intracellular calcium protein CaM; responding to light stress	[49,9]
<i>AtCYP19-4</i>	At2g29960	内质网 ER;高尔基体 Golgi apparatus	通过调节鸟嘌呤核苷酸交换因子 GNOM 参与囊泡运输 Involved in vesicle trafficking by modulating the function of guanine nucleotide exchange factor GNOM	[30]
<i>AtCYP20-1(ROC7)</i>	At5g58710	内质网 ER	参与磷酸酶活性的调节 Involved in protein phosphatase 2A (PP2A) regulation	[27]
<i>AtCYP20-2</i>	At5g13120	叶绿体 Chloroplast	参与 NAD(P)H 脱氢酶复合物形成;引起 BZR1 蛋白的构象变化从而改变开花模式 Involved in NAD(P)H dehydrogenase complex formation; causing conformational change in brassinazole-resistant (BZR1) protein (thereby altering flowering pattern)	[13-14]
<i>AtCYP20-3(ROC4)</i>	At3g62030	叶绿体 Chloroplast	将光合氧化还原信号连接到半胱氨酸生物合成和应激反应,与 SAT1(半胱氨酸生物合成酶)有关;参与茉莉酸信号调控 Linking light and redox signals to cysteine biosynthesis and stress response, interacting with SAT1 (essential enzyme in cysteine biosynthesis); involved in jasmonate signaling	[6,25-26]
<i>AtCYP21-3</i>	At2g47320	液泡 Vacuole 线粒体 Mitochondria	参与调控线粒体的通透性并在坏死和凋亡性细胞死亡中起关键作用 Involved in the permeability transition pore of mitochondria and playing a crucial role in necrotic and apoptotic cell death	[15]
<i>AtCYP21-4</i>	At3g66654	叶绿体 Chloroplast 线粒体 Mitochondria	参与调控线粒体的通透性并在坏死和凋亡性细胞死亡中起关键作用 Involved in the permeability transition pore of mitochondria and playing a crucial role in necrotic and apoptotic cell death	[15]
<i>AtCYP38</i>	At3g01480	叶绿体 Chloroplast	参与光合系统 II 超级复合物和放氧复合物的装配和加工;PPIase 自抑制 Involved in assembly and maintenance of PS II and oxygen evolving complexes; PPIase auto-inhibition	[5-7]
<i>AtCYP40</i>	At2g15790	细胞质 Cytoplasm	参与植物茎端营养生长;翻译后基因沉默,HSP90 介导的 RISC 组装,抑制 Tombus 病毒复制酶组装 Involved in vegetative shoot maturation; post-translational gene silencing; HSP90-mediated RISC assembly; inhibition of Tombus virus replicase assembly	[11-12,19-20]
<i>AtCYP57</i>	At4g33060	细胞核 Nucleus	参与植物对丁香假单胞菌的防御反应 Involved in plant defense response against <i>P. syringae</i>	[18]
<i>AtCYP59</i>	At1g53720	细胞核 Nucleus	通过与富含精氨酸(SR)蛋白和 RNA 聚合酶 II 的相互作用参与转录和 pre-mRNA 加工 Involved in transcription and pre-mRNA processing via interaction with serine/arginine-rich(SR) proteins and RNA polymerase II	[28]
<i>AtCYP65</i>	At5g67530	细胞核 Nucleus	与泛素连接酶相互作用 Interacting with ubiquitin ligase	[29]
<i>AtCYP71</i>	At3g44600	细胞质 Cytoplasm	参与器官发生,表观遗传基因沉默,染色质组装和组蛋白 H ₃ 修饰 Involved in organogenesis, epigenetic gene silencing, chromatin assembly and histone H ₃ modification	[10]

主要与逆境胁迫应答相关(表 2)。

位于高尔基体的 OsCYP21-4 参与高盐和活性氧胁迫应答以及脱落酸(ABA)信号响应。由于缺乏编码 PPIase 以及结合 CsA 所必需的氨基酸残基,OsCYP21-4 不具有 PPIase 活性。OsCYP21-4 超表达可以提高植物对盐和 H₂O₂ 的耐受性,但此

过程的确切分子机制目前尚不明确,可能是通过调节过氧化物酶活性发挥作用^[32]。

OsCYP2 作为控制活性氧(ROS)水平的关键调节因子,在防止细胞的氧化损伤、保护光合作用中起着至关重要的作用。Ruan 等^[33]研究表明 OsCYP2 可以调控抗氧化酶的活性,控制 ROS 的水平。OsCYP2 表达受盐胁迫诱导,且被生物钟调节。另外,OsCYP2 也可能在其他胁迫中作为关键成分参与信号通路,如 PEG、热害、冷害和 ABA 等。OsCYP2 超表达转基因植株中氧化酶活性提高而脂质过氧化物降低,并且多重胁迫耐受性增加,在高盐胁迫下植株主根和地上部变长、叶绿素含量增加^[34]。Kumari 等^[35]研究发现在大肠杆菌和酵母中超表达 OsCYP2 能增加其对盐度、高温以及氧化胁迫的耐受性。

Lee 等^[36]的研究表明 OsCYP18-2 在水稻中过表达能够增强耐旱性并改变干旱条件下抗胁迫相关基因的表达和 pre-mRNA 剪接模式。干旱和盐胁迫作用能诱导 OsCYP18-2 和转录调控因子基因 OsSKIP 的表达,OsSKIP 与 OsCYP18-2 结合导致 OsCYP18-2 从细胞质转移到细胞核参与调控抗胁迫相关基因的转录,并能增加植物对干旱胁迫的耐受性。

OsCYP19-4 受多种胁迫诱导,低温处理会激活 OsCYP19-4 启动子使表达量提高 10 倍以上。OsCYP19-4 具有肽酰-脯氨酰-顺反式异构酶活性,过表

达 OsCYP19-4 水稻植株的耐冷性增强,同时分蘖数和穗数显著增加,表明可通过 OsCYP19-4 增强耐冷性以及提高生物量的潜力^[37]。虽然 OsCYP19-4 没有 PPIase 活性,但 Lee 等^[38]用酵母双杂交和 BiFC 等方法证实,在低温条件下其选择性剪接产生的 OsCYP19-4 AS 异构体能够和 AtRCN1(编码 1 个蛋白磷酸酶的亚基)相互结合增加水稻耐寒性。

位于类囊体的 OsCYP20-2 是具有 PPIase 活性的亲环素基因,能提高烟草和拟南芥抗胁迫能力。超表达该基因能增强大肠杆菌和酵母细胞抗高温高盐胁迫的能力和水稻抗高盐胁迫的能力^[39]。Trivedi 等研究发现 OsCYP25 响应多种胁迫应答,并在高盐、高低温和干旱环境下表达显著增加^[40]。OsCYP1 响应高盐胁迫作用,能够抑制稻瘟病菌附着孢形成和菌丝生长,从而参与调控水稻生长发育^[41]。

除了逆境应答,水稻亲环素还参与生长素信号通路调控。Kang 等^[42]研究发现 OsCYP2 作为分子伴侣参与生长素响应蛋白的降解,在水稻侧根的起始过程中发挥重要作用。Oscyp2 突变体表现出生长素响应缺陷,在根部有多种生长素相关生长发育表型。酵母双杂和体外 pull-down 实验证明 OsCYP2 可以与共分子伴侣 SKP1 的 G2 等位抑制子 OsSGT1 蛋白结合,表明 OsCYP2 通过与 OsSGT1 的互作参与生长素信号转导过程。此外,研究发现 OsCYP19-4 与生长素转运有关,调控低温胁迫响应基因表达^[37]。

表 2 已报道的水稻亲环素及其功能
Table 2 The reported cyclophilins and their functions in rice

基因名称 Gene	基因座 Gene locus	亚细胞定位 Subcellular localization	基因功能 Function	参考文献 Reference
OsCYP-1	LOC_Os01g02080	叶绿体 Chloroplast	响应高盐胁迫应答,抑制稻瘟病菌的生长 Responding to high salt stress, inhibiting the formation of rice blast fungus growth	[41]
OsCYP-2	LOC_Os02g02890	细胞质 Cytoplasm	参与生长素调控信号机制,调控侧根生长;通过 ROS 清除增加水稻苗耐盐性;在烟草、大肠杆菌和酵母中超表达后增加其多重胁迫耐受性 Involved in auxin regulatory signal mechanism, regulate of lateral root growth; Increasing salt tolerance of rice seedlings by ROS removal; increasing the multiple stress tolerance of tobacco, <i>E. coli</i> and <i>S. cerevisiae</i> after overexpressed	[33-35,42]
OsCYP18-2	LOC_Os08g44520	细胞质 Cytoplasm	调控相关抗胁迫基因的转录,增加植物干旱胁迫的耐受性 Regulating the transcription of stress-resistance genes, and increasing the tolerance of plants to drought stress	[36]
OsCYP19-4	LOC_Os06g49470	分泌(腔)Lumen	与生长素转运有关,对冷胁迫显著响应 Involved in auxin transportation, and significantly responding to cold stress	[37-38]
OsCYP20-2	LOC_Os05g01270	叶绿体 Chloroplast	参与调控烟草和拟南芥胁迫耐受性 Involved in regulation of tobacco and <i>Arabidopsis</i> stress tolerance	[39]
OsCYP21-4	LOC_Os07g29390	线粒体 Mitochondria	参与调控线粒体通透性、细胞凋亡,响应多种胁迫 Involved in regulation of mitochondrial permeability, apoptosis, responding to a variety of stress	[32]
OsCYP-25	LOC_Os09g39780	分泌(腔)Lumen	响应高温、高盐胁迫 Responding to high temperature and high salt stress	[40]

3 其他植物亲环素基因

菠菜 TLP40 是位于类囊体膜中的多功能酶,参与叶绿体生物发生和细胞内信号转导。作为 AtCYP38 同源物,它不仅调控光系统 II 特异性蛋白磷酸酶的活性,还参与调控光合体系 II 中多个关键蛋白去磷酸化以及蛋白质加工运输和转运。TLP40 与 AtCYP38 具有 82% 序列相似性,AtCYP38 不具有 PPIase 活性而 TLP40 是功能性 PPIase,这可能是因为 TLP40 含有保守的 PPIase 结构域和结合磷酸酶结构域等^[43-44]。

番茄中与 OsCYP2 最相近的 LeCYP1 属于细胞溶胶亲环素家族,参与调控生长素信号转导,影响植物生长发育^[45-46]。*Lecyp1* 突变体表现出多种生长素不敏感表型,包括向地性应答迟缓、缺失侧根、顶端优势降低、维管发育变异以及结实减少等^[47]。

Kaur 等^[48]研究证明小麦亲环素 TaCYPA-1 具有 PPIase 活性,TaCYPA-1 表达能够增强大肠杆菌耐热性,但其作用机理仍不清楚。TaCYPA-1 与 AtCYP19-3 的序列相似性达 72.67%,可以与钙调节蛋白 CaM 发生钙离子依赖性相互作用^[49-50]。此外,小麦亲环素 TaCYPB 参与蛋白质的折叠与装配,调控小麦的正常生长与成熟^[51]。Yu 等^[52]发现亲环素 TaCPY 与小麦-簇毛麦 6VS/6AL 易位系抗病性相关。

蓖麻亲环素 RcCYP1 定位于细胞质中具有高度 PPIase 活性,在蛋白质的折叠过程中作为分子伴侣发挥重要作用^[53]。来自柑橘的 CsCYP-1 通过与含 TPR 结构域的氧化还原硫蛋白转录激活因子与 RNA 聚合酶 II 结合调控转录过程^[54-55]。来自小麦的 TaCYPA-1^[56]、来自长春花的 Cat r 1 CYP^[57]与 CsCYP-1 具有高度的结构和序列相似性,表现出与 CsCYP-1 相似的功能。此外,研究发现长春花花粉的 Cat r 1 CYP^[57]和来自桦树(*Betula verrucosa*)花粉的 Betv7^[58]属于亲环素过敏原家族。

来自不同物种的植物亲环素参与多种胁迫应答,例如高低温、高盐、干旱、物理挫伤和病原菌等。土豆 StCyP 的积累受多种胁迫条件影响,在高低温、干旱和物理挫伤作用下显著增加,且物理挫伤和真菌感染时其 mRNA 含量显著增加从而有效抵抗病原体的侵袭^[59]。黄花羽扇豆亲环素 LpCYP 在物理挫伤、高低温和高盐胁迫下积累增多,且在胚轴中的含量比叶片中更高^[60]。水芹亲环素 ThCYP1 广泛分布在细胞中且在细胞核中含量最多,它的表达

量受盐、双氧水和高温等诱导,在烟草细胞中异位表达该基因能够增加耐盐性^[61]。蚕豆亲环素 pCyPB 定位于叶绿体,参与光响应和高温胁迫应答,其可以与去环孢素 A 形成复合物抑制钙调磷酸酶的活性^[62]。大白菜中的 C-CyP 有抗真菌活性,能抑制真菌病原体生长^[63]。在烟草中表达花生亲环素 AdCYP 能增强对病原体寄生疫霉的抗性^[64]。Kinoshita 等^[65]研究发现 VcCYP 参与蚕豆细胞的防御反应。辣椒 *CaCyP1* 在成熟的根、茎、叶和花中表达,而且受病原菌诱导^[66]。Kanakala 等^[67]发现烟草亲环素 NtCYPB 具有抑制黄叶卷曲病毒 TYLCV 传播的作用。TYLCV 是单链病毒,对番茄和其他几种作物造成严重损害,NtCYPB 在植物体内表达能改变 TYLCV 的转录模式从而导致 TYLCV 传播减少,为深入研究农作物抗虫提供基础。

此外,土豆、红藻以及水芹亲环素参与激素信号调控过程。土豆 StCyP 对甲基茉莉酸酯(MeJA)和 ABA 有响应,且在 ABA 作用下含量显著增加^[59]。在烟草中表达红藻 *GjCyP-1* 发现其受赤霉素(GA3)、吲哚乙酸(IAA)和玉米素(ZT)信号调控^[68]。水芹亲环素基因 *ThCYP1* 对 ABA 有显著响应^[61]。

Mainali 等^[69]对大豆亲环素基因家族进行了全基因组分析,共确定了 62 个大豆亲环素基因(*GmCYP1-GmCYP62*),在 18 条染色体中都有分布,是迄今为止已知最大的亲环素基因家族,这也是第一次在全基因组水平对豆科物种的亲环素基因家族开展研究。*GmCYPs* 组织定位分析显示其基因特异性表达模式受生物因素影响较小,在嫩芽和成熟植物中均有表达,而在发育过程中的嫩芽中表达更高^[70-71]。在胁迫应答过程中,玉米和大豆亲环素 mRNA 积累有显著差异且发生时间不同。高温胁迫下,玉米亲环素 mRNA 显著增加而大豆亲环素没有变化。盐胁迫下,玉米亲环素 mRNA 积累出现的时间比豆类早,但冷胁迫下则正好相反^[72]。表 3 概括了已报道的其他植物亲环素基因及其功能。

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植物亲环素具有多种亚细胞定位和功能,除了参与蛋白质的合成与折叠、作为分子伴侣发挥 PPIase 活性、参与调控 DNA 降解以及作为钙离子释放的通道,还参与植物中叶绿体的光保护和氧化还原调节、植物的生长发育,并在逆境胁迫应答以及激素

表 3 其他已报道的植物亲环素及其功能

Table 3 Other reported plant cyclophilins and their functions

亲环素 Cyclophilin	来源物种 Source species	基因功能 Function	参考文献 Reference
<i>Betv7</i>	桦树 <i>Betula verrucosa</i>	一种花粉过敏原 A pollen allergen	[58]
<i>Cat r 1 CYP</i>	长春花 <i>Catharanthus roseus</i>	一种花粉过敏原 A pollen allergen	[57]
<i>TLP40</i>	菠菜 <i>Spinacia oleracea</i> L.	参与调控光系统Ⅱ特异性蛋白磷酸酶的活性和多种关键蛋白质脱磷酸化,并与蛋白质加工运输及转运有关 Involved in the regulation of photo-system Ⅱ-specific protein phosphatase activity, involved in the regulation of photosynthetic system Ⅱ in a variety of key protein dephosphorylation, and playing a role in protein processing and transportation	[43-44]
<i>LeCYP1</i>	番茄 <i>Lycopersicon esculentum</i>	参与 PSⅡ的装配和维护以及与类囊体膜中磷酸酶相互作用 Involved in assembly and maintenance of PSⅡ and interaction with phosphatase in thylakoid membrane	[45-47]
<i>TaCYPA-1</i>	小麦 <i>Triticum aestivum</i>	增加大肠杆菌耐热性,与细胞内钙蛋白 CaM 相互作用,参与 PPIase 氧化还原机制的调控 Increasing the heat resistance of <i>E. coli</i> , interacting with intracellular calcium protein CaM, involved in regulation of the PPIase oxidation and reduction mechanism	[48-50]
<i>TaCYPB</i>	小麦 <i>Triticum aestivum</i>	参与蛋白亚基的有效折叠与装配,参与小麦成熟 Involved in the efficient folding and assembly of protein subunits, involved in wheat maturation	[51]
<i>TaCYP</i>	小麦 <i>Triticum aestivum</i>	与小麦-簇毛麦 6VS/6AL 易位系抗病性相关 Associated with disease resistance of the wheat- <i>Haynaldia villosa</i> 6VS/6AL translocation line	[52]
<i>RcCYP1</i>	蓖麻 <i>Ricinus communis</i> L.	在蛋白质的重折叠中作为分子伴侣发挥重要作用 Playing critical roles in the protein refolding as molecular chaperones	[53]
<i>CsCYP</i>	柑橘 <i>Citrus sinensis</i>	与柑橘黄单胞菌效应蛋白 PthA、植物 Tdx 以及 RNA 聚合酶Ⅱ相互作用 Interacting with the bacterial effector protein PthA, the plant Tdx, and RNA polymerase Ⅱ	[54-55]
<i>StCyP</i>	马铃薯 <i>Solanum tuberosum</i>	响应逆境、激素、机械损伤和病原菌 Responding to stress, hormone, mechanical damage and pathogen	[59]
<i>LpCYP</i>	羽扇豆 <i>Lupinus polyphyllus</i>	响应多种胁迫,在叶片中表达较高 Responding to multiple stress, highly expressed in leaves	[60]
<i>ThCYP1</i>	盐芥 <i>Thellungiella halophila</i>	增加烟草耐盐性 Increasing the salt tolerance of tobacco	[61]
<i>pCyPB</i>	蚕豆 <i>Vicia faba</i> L.	与 CsA 结合抑制钙调磷酸酶的活性,受光和热激诱导 Inhibiting the activity of calcineurin by interaction with CsA, induced by light and heat shock	[62]
<i>C-CyP</i>	大白菜 <i>Brassica pekinensis</i>	响应生物逆境,具有抗真菌活性,能抑制真菌病原体生长 Responding to biological stress, having antifungal activity to inhibit the growth of fungal pathogens	[63]
<i>AdCYP</i>	花生 <i>Arachis hypogaea</i>	异位表达增强烟草对病原体寄生疫霉的抗性 Increased the resistance of transgenic tobacco with its ecotopic expression to <i>Phytophthora parasitica</i>	[64]
<i>VcCYP</i>	蚕豆 <i>Vicia faba</i> L.	参与蚕豆细胞的防御反应,且在细胞原生质体中比根和叶中表达高得多 Involved in the defensive response of <i>Vicia faba</i> bean cells and much more expressed in cell protoplasts than in roots and leaves	[65]
<i>CaCyP1</i>	辣椒 <i>Capsicum annum</i> L.	响应逆境,受病原菌以及植物激素的诱导 Responding to stress, induced by pathogenic bacteria and plant hormones	[66]
<i>NtCYPB</i>	烟草 <i>Nicotiana tabacum</i> L.	改变了黄叶卷曲病毒 TYLCV 转录模式,减少 TYLCV 传播 Changing the transcriptional pattern of yellow leaf curl virus TYLCV, and reducing the transmission of TYLCV	[67]
<i>GjCyP-1</i>	红藻 <i>Griffithsia japonica</i>	参与种子萌发及植物生长,响应激素应答 Involved in seed germination and plant growth, responding to hormones	[68]
<i>ZmCYP</i>	玉米 <i>Zea mays</i> L.	响应低温、高盐胁迫应答,且 mRNA 发生积累 Responding to low temperature, high salt stress with mRNA accumulation	[72]
<i>GmCYP</i>	大豆 <i>Glycine max</i>	在嫩芽和成熟植物中表达,在嫩芽表达更高,响应低温、盐胁迫应答 Expressed in young shoots and mature plants with higher expression in young shoots, responding to low temperature, salt stress	[69-71]

通路调控等方面发挥重要作用。其中植物亲环素作为胁迫应答蛋白参与不同的信号传导通路,例如叶绿体亲环素可以与多种叶绿体蛋白如铁硫蛋白复合

物、硫氧还蛋白和抗氧化蛋白相互作用,线粒体亲环素参与调控线粒体通透性导致的细胞凋亡,而分泌亲环素主要参与协调细胞顶端优势和根细胞增殖。

但植物亲环素调节氧化还原的机制和 PPIase 活性的作用机理仍需进一步阐明。

可变剪接异构体可以编码具有不同功能的蛋白质,从而增加功能多样性^[73]。Lu 等^[31]发现水稻亲环素基因的可变剪接能力受胁迫影响,表明可变剪接是水稻适应非生物胁迫的有效调控途径。在水稻中,OsCYP19-4 在冷胁迫下表达量显著上升,而且通过可变剪接产生 8 个转录变体和 4 种不同的蛋白质异构体,它的转基因超表达植物低温耐受性显著增强^[38]。OsCYP19-4.2 和 OsCYP19-4.3 通过与调控蛋白磷酸酶活性的 AtRCN1 相互作用,在生长素传导和抗冷胁迫中起作用,但 OsCYP19-4 可变剪接

异构体参与冷胁迫应答的具体分子机制还不清楚。

植物亲环素能响应各种生物和非生物逆境诱导表达并发生 mRNA 积累,表明在植物对环境的不断适应的演化过程中它们发挥了重要作用。通过研究亲环素的时空表达有助于深入阐明亲环素基因的表达和调控机理,为进一步研究亲环素功能奠定基础。目前亲环素研究已经取得了一定进展,但对部分植物亲环素蛋白家族还仅仅进行了生物信息学分析,植物亲环素参与胁迫应答、作为分子伴侣帮助蛋白质折叠、通过表观遗传调控基因表达等的作用机理仍不明确,有待于进一步深入研究。

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