综 述 Review

植物CBL-CIPK信号系统的功能及其作用机理

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摘要: 由类钙调磷酸酶B蛋白CBLs及其互作蛋白激酶CIPKs组成的信号系统是植物逆境胁迫信号传导的关键调控节点, 是近几年植物逆境胁迫生理与分子生物学研究领域中的重要热点之一。文章主要介绍了CBLs和CIPKs基本功能结构域、CBL-CIPK信号系统在各种生物和非生物逆境胁迫响应、营养物质吸收及植物激素应答中的生物学功能及其作用机理。

关键词: 钙信号; CBL-CIPK; 逆境胁迫; 营养; 植物激素

Functions and Action Mechanisms of CBL-CIPK Signaling System in Plants

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Abstract: The signaling system composed of calcineurin B-like proteins (CBLs) and CBL interacting protein kinases (CIPKs) is a key regulatory node in various stress signaling pathways in plants and has become a major area of research focus in the field of plant stress physiology and molecular biology. This review focused on basic functional domains of CBLs and CIPKs, and biological functions and action mechanisms of CBL-CIPK signaling system in responses to various biotic and abiotic stresses, nutrient uptake, and plant hormones.

Key words: calcium signaling; CBL-CIPK; stresses; nutrition; phytohormones

在植物细胞中, Ca^{2+}作为胞内第二信使, 参与调控植物多种逆境胁迫响应、植物各器官的形成与发育。根据外界刺激的不同, 胞内游离的Ca^{2+}浓度在时空上呈现不同特征的变化。钙感受器(calcium sensor)作为Ca^{2+}信号传导途径中的核心元件, 通过自身的EF手型(EF-hand)结构域与Ca^{2+}结合, 导致构象改变, 从而识别或解码Ca^{2+}信号并将信息传递至下游, 通过激酶的磷酸化作用或转录因子的调控, 最终使胞内Ca^{2+}信号转化为细胞生理反应(Batistič和Kudla 2012; Zhu等2013)。

在拟南芥中, 至今已鉴定出250多种具有EF手型结构域的蛋白, 其中包括4种最主要的钙感受器蛋白家族: 钙调蛋白(calmodulins, CaMs)家族、类钙调蛋白(calmodulin-like proteins, CMLs)家族、Ca^{2+}依赖型蛋白激酶(calcium-dependent protein kinases, CDPKs)家族和类钙调磷酸酶B蛋白(calcineurin B-like proteins, CBLs)家族(郑仲仲等2013)。有关这4类钙感受器的基本结构与功能近几年国内已有介绍(张俊文等2009; 唐仁杰等2013; 郑仲仲等2013)。其中, CBLs及其互作蛋白激酶CIPKs (CBL interacting protein kinases)组成的CBL-CIPK信号系统是植物逆境信号传导途径中的关键调控节点, 因而成为近几年植物逆境胁迫生理与分子生物学研究领域中的重要热点之一。本文在扼要介绍CBLs和CIPKs的功能结构域的基础上, 着重介绍最近几年有关CBL-CIPK信号系统的功能及其作用机理的研究进展。

1 CBL和CIPK的功能结构域

植物CBLs/SCaBPs (SOS3-like calcium-binding proteins)蛋白主要由N端和C端两个球状结构域组成, 每个结构域均含有一对EF手型(Sánchez-Barrena等2005)。在大多数物种中, CBL的EF手型的Ca^{2+}结合位点由12个相对保守的氨基酸组成, 每个CBL蛋白均拥有4个EF手型结构, 并以固定的顺

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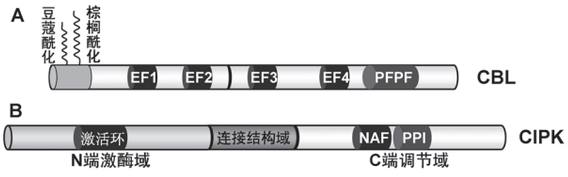

图1 植物CBL与CIPK功能结构域

Fig.1 Functional domains of plant CBLs and CIPKs

序和间距排列(图1-A)。因此, 所有CBL蛋白大小基本相似(23~26 kDa), 但同时存在一定程度上的变异(Weinl和Kudla 2009)。实际上, 典型的EF手型是CBL高度保守的结构元件之一, 负责对Ca^{2+}的高度亲和(Haeseleer等2002)。而这些不同程度上的变异很可能影响CBL蛋白对Ca^{2+}的亲和能力。目前, 对所有已知CBL中EF手型是否均具有Ca^{2+}结合能力尚无正式定论。有研究发现, CBL的N端含有豆蔻酰化(myristoylation)和棕榈酰化(palmitoylation)两个脂质修饰位点(Batistič等2008; 图1-A), 参与调控CBL-CIPK复合体的亚细胞定位。相反, C端有一保守的PFPF基序(PFPF motif) (图1-A), 其中P、M、L、F、P和F氨基酸残基完全保守。除AtCBL5/SCaBP4和AtCBL6/SCaBP2之外, 其他AtCBLs的PFPF结构域内均含有一Ser残基, 是AtCIPKs磷酸化作用靶点, 这一磷酸化机制能够促进CBLs与CIPKs之间的互作, 并参与对下游靶蛋白活性的调控(Du等2011), 是CBL-CIPK信号途径的重要调控机制之一。

CIPKs/PKSs (SOS2-like protein kinases)是一类植物特有的丝氨酸-苏氨酸蛋白激酶, 能与CBLs特异性互作。CIPKs通常由含有一个典型激活环的N端激酶域和C端调节域组成(图1-B)。在C端调节域中, 含有一个进化上高度保守的天冬酰胺-丙氨酸-苯丙酰胺(NAF)结构域, 这一结构域是介导CIPKs与CBLs互作所必需的(Albrecht等2001)。同时, 有文献报道邻近NAF结构域的PPI (protein phosphatase interaction)结构域能介导CIPKs与2C型蛋白磷酸酶PP2Cs (protein phosphatases 2C)的特异性结合(Weinl和Kudla 2009), 暗示激酶与磷酸酶通过拮抗作用来调控靶蛋白的活性。

CBL和CIPK蛋白最初在模式植物拟南芥(*Arabidopsis thaliana*)中被鉴定(Kudla等1999; Shi等1999)。在拟南芥基因组中, 共有10个*CBLs*和26个*CIPKs*同源基因。目前, 在水稻(*Oryza sativa*)、杨树(*Populus*)、玉米(*Zea mays*)、大麦(*Hordeum vulgare*)、小麦(*Triticum aestivum*)、大豆(*Glycine max*)等物种中也陆续被鉴定出多个*CBLs*和*CIPKs*同源基因(Kolukisaoglu等2004; Yu等2007; Chen等2011)。在植物进化过程中, *CBLs*和*CIPKs*基因数量的增加很可能与CBL-CIPK信号系统的功能进化相关(Weinl和Kudla 2009), 这有利于时空特异性Ca^{2+}信号的识别与解码, 暗示CBL和CIPK进化的复杂性与植物的环境适应性相一致。

2 CBL-CIPK的亚细胞定位机制

有研究表明, Ca^{2+}通道周围的Ca^{2+}浓度高于胞内的浓度(Dargan等2006), 表明特定部位的Ca^{2+}积累很可能是形成特异性Ca^{2+}信号的重要前提。一旦植物受到某一性质的外界刺激, 其胞内外钙库局部释放Ca^{2+}, 形成特异性Ca^{2+}信号, 由特定的CBL识别并由CBL-CIPK信号系统快速传递。不同CBL-CIPK复合体在胞内的区隔化(compartmentation) (Batistič等2010)决定了Ca^{2+}信号传导的空间特异性。

CBLs既能激活CIPKs激酶活性, 又能决定CBL-CIPK复合体的亚细胞定位, 有利于对下游靶蛋白的空间特异性识别。研究显示AtCBL1、AtCBL4、AtCBL5和AtCBL9的N端均含有一小段N-豆蔻酰化结构域, 从而介导这些CBLs的质膜定位(Batistič等2008)。相反, AtCBL2、AtCBL3、AtCBL6和AtCBL10在N端缺少这一豆蔻酰化位点, 但有一段延长的N端结构域, 使这些CBLs定位于液泡膜上(Batistič等2008, 2010), 其中AtCBL10的N端还存在一转膜结构域, 使其能定位在内体小泡(endosomal vesicles)中, 这对于AtCBL10与质膜的结合非常重要(Kim等2007; Batistič等2010)。此外, AtCBL7和AtCBL8因N端序列在进化中发生变异而定位于细胞质和细胞核中(Batistič等2010; Batistič和Kudla 2012)。CBLs亚细胞定位的多样性为CBLs在胞内执行多种生物学功能奠定了空间基础。

与CBLs相比, CIPKs自身并不具备可识别的亚细胞定位信号。多数CIPK-GFP融合蛋白信号显示CIPK定位于细胞质和核内, 双分子荧光互补分析揭示CIPKs亚细胞定位取决于与其互作的CBLs (Batistič等2010; Batistič和Kudla 2012)。例如, AtCBL10-AtCIPK24主要定位于液泡膜; 当AtCIPK24

与AtCBL4互作时则定位于质膜。同样, AtCIPK1通过与AtCBL1/9或AtCBL2互作而分别被定位到质膜或液泡膜上(Kim等2007; Weinl和Kudla 2009)。不同CBLs能够将同一CIPK定位于细胞不同部位, 执行不同的功能, 使得CBL-CIPK信号系统的功能多样化。

3 CBL-CIPK信号系统的作用机理

反向遗传学和生物化学等现代分析手段加速了人们对CBLs和CIPKs生理学功能的认识。目前, 对CBL-CIPK信号系统调控各种非生物胁迫、脱落酸(ABA)和营养物质的吸收已有深入研究, 但对其调控生物逆境胁迫响应和对生长素应答等方面的研究近几年才刚刚起步, 但进展迅速。

3.1 病原体与植物防御反应

植物在进化中形成了复杂的免疫防御体系来应对病原体的侵染, 其主要通过PTI (pattern-triggered immunity)和ETI (effector-triggered immunity)两种防御机制对病原体侵染作出免疫反应, 其中ETI主要通过局部程序性细胞死亡(PCD)即超敏反应(HR)来阻止病原体的扩散。陈析丰等(2010)分析了白叶枯病菌(*Xanthomonas oryzae*)侵染对15个水稻*OsCIPKs*转录的影响, 发现有5个*OsCIPKs* (*OsCIPK1*、*2*、*10*、*11*和*12*)的表达上调, 暗示水稻OsCIPKs参与白叶枯病菌侵染的响应。另有研究表明, 水稻OsCIPK14/15参与调控多种霉菌TvX/EIX诱发的防御反应包括PCD、线粒体功能障碍、植保素的合成和发病相关基因的表达等(Kurusu等2010a)。酵母双杂交分析表明, OsCIPK14/15与OsCBL4互作, 且*OsCBL4*的表达受MAMPs/PAMPs (microbe/pathogen-asssociated molecular patterns)的诱导(Kurusu等2010a), 而OsCIPK14/15参与调控由MAMPs/PAMPs诱导的ROS (reactive oxygen species)形成(Kurusu等2010b)。这些研究结果暗示, OsCBL4-OsCIPK14/15可能通过调控由NADPH氧化酶RBOHs (respiratory burst oxidase homolog B)介导的ROS形成来直接或间接地激活多种防御反应(图2)。

最近, 利用VIGS (virus-induced gene silencing)分析技术发现, 烟草*NbCBL10*和*NbCIPK6*的沉默抑制了由细菌、卵菌、线虫和病毒等病原体效应蛋白(Pto/AvrPto)所诱导的PCD, 同时也减少了由丁香假单胞菌(*P. syringae*)侵染所诱导的病斑数目并减缓其生长速度。这一研究结果表明NbCBL10-NbCIPK6参与调控病原体诱导的细胞死亡和植株免疫反应, 很可能作为不同病原体免疫防御途径中的调控节点。进一步的研究表明, 在烟草(*Nicotiana tabacum*)中, 烟草或番茄CBL10-CIPK6信号系统能与NADPH氧化酶RBOHB互作, 并且调控ROS的产生(de la Torre等2013)。因此, 当病原体侵染植物时, 胞内产生大量的Ca^{2+}信号, 被CBL10所感知, 然后依次激活其互作蛋白激酶CIPK6和RBOHB的活性, 导致ROS信号的形成, 从而激活由ROS介导的PCD和病原体免疫反应(图2)。

3.2 植物耐盐性与Na^+运输

低浓度Na^+对植物生长有一定的刺激作用, 但高浓度将造成细胞离子失衡, 引起高渗透胁迫。已知拟南芥SOS (salt overly sensitive)信号途径是调节植物耐盐性的重要机制。拟南芥钙结合蛋白SOS3/AtCBL4和SCaBP8/AtCBL10通过与蛋白激酶SOS2/AtCIPK24互作, 分别在质膜和液泡膜上执行各自的生物学功能, 保护植株免受盐胁迫的伤害(Qiu等2004; Kim等2007)。虽然AtCBL4和AtCBL10都能与AtCIPK24互作, 激活SOS1, 但AtCBL4在根部特异性表达, 而AtCBL10主要作用在地上部分, 且它们异位表达后并不能相互恢复各自的突变表型(Quan等2007)。根细胞主要通过AtCBL4-AtCIPK24信号系统调控质膜Na^+/H^+逆转运蛋白SOS1, 而地上部分则通过AtCBL10-AtCIPK24复合体不仅调控SOS1活性, 还可能激活AtNHX (vacuolar Na^+/H^+ exchanger)或未知转运体将Na^+区隔于液泡中(Qiu等2004; Kim等2007; Quan等2007; 图2、3)。以上研究表明CBLs特异性亚细胞定位决定了CBL-CIPK的特定生物学功能。进一步分析表明, SOS2/AtCIPK24未能磷酸化SOS3/AtCBL4, 但能磷酸化SCaBP8/AtCBL10, 并受盐的诱导。这一磷酸化作用既稳定了AtCBL10-AtCIPK24之间的互作, 也促进了质膜Na^+/H^+逆转运蛋白SOS1的活性, 表明磷酸化机制是AtCBL10-AtCIPK24调控植株耐盐性的重要机制(Lin等2009; 图3)。

在其他物种中, 如水稻(Martínez-Atienza等2007)、白杨(*Populus trichocarpa*) (Tang等2013)、苹果(Hu等2012)和番茄(*Solanum lycopersicum*) (Huertas等2012)等中也同样存在相似的SOS信号途径。此外, 分别过表达拟南芥*AtCIPK16* (Roy等

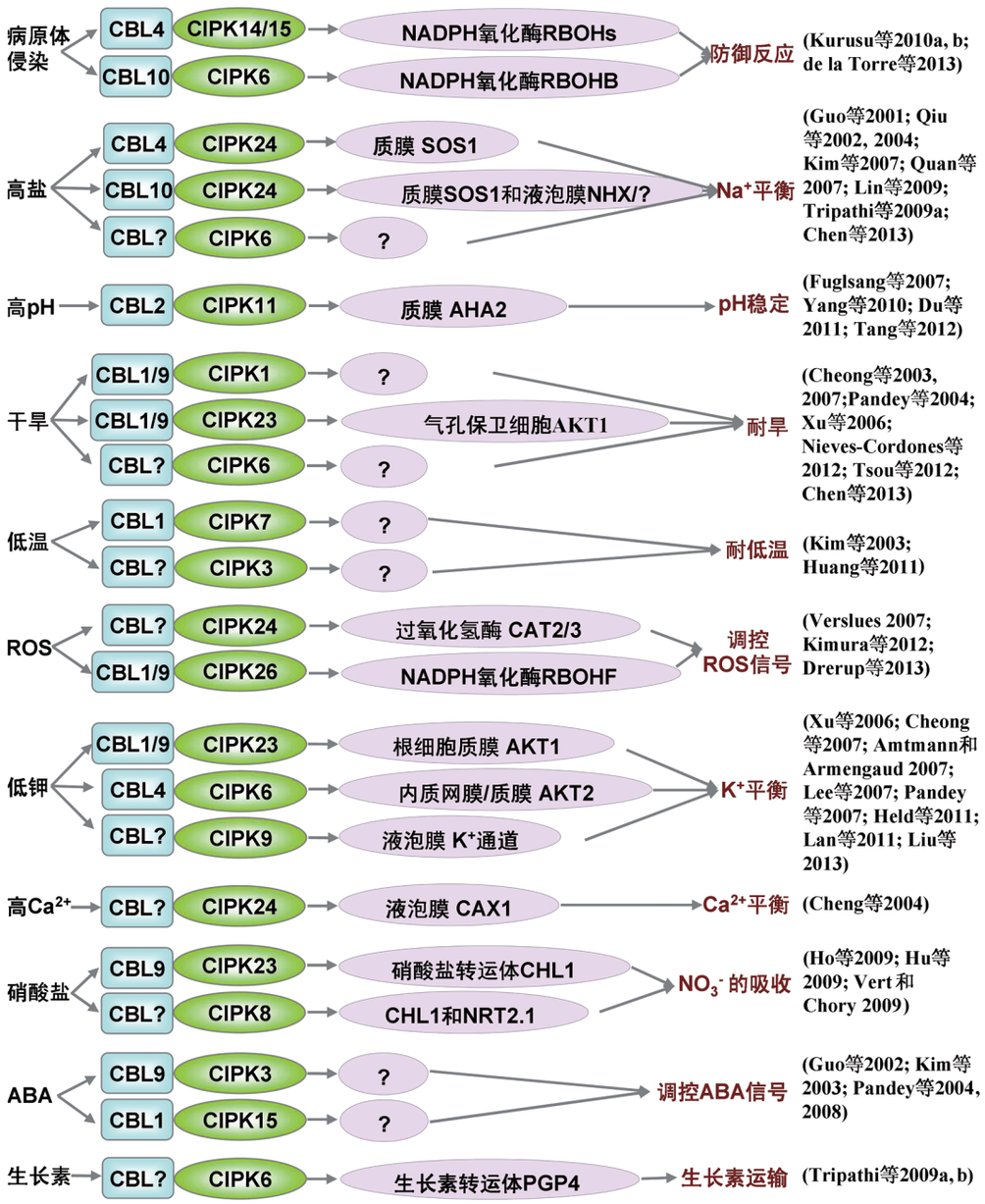

图2 CBL-CIPK信号系统调控植物逆境胁迫响应的作用机理

Fig.2 Action mechanisms underlying CBL-CIPK regulation of plant stress responses

2013)、盐生大麦*HbCIPK2* (Li等2012)、小麦*TaCIPK29* (Deng等2013)和油菜(*Brassica napus*)、苹果(*Malus*)、棉花(*Gossypium* spp.)、鹰嘴豆(*Cicer arietinum*)等物种的*CIPK6* (Tripathi等2009a; Wang等2012; He等2013)均能明显提高转基因植株的耐盐性, 表明由SOS信号途径介导的耐盐机制在草本植物和木本植物中非常保守。

3.3 pH的调节与H^+的平衡

植物细胞处于pH不断变化的环境之中, 伴随着植物细胞对各种胁迫的响应。早期研究发现, AtCBL2/SCaBP1-AtCIPK11/PKS5复合体通过阻止氢泵-ATP酶AHA2 (H^+-ATPase)与14-3-3蛋白的互作来抑制AHA2的活性(Fuglsang等2007), 从而阻止胞内H^+的外排(图2、3)。进一步的研究发现,

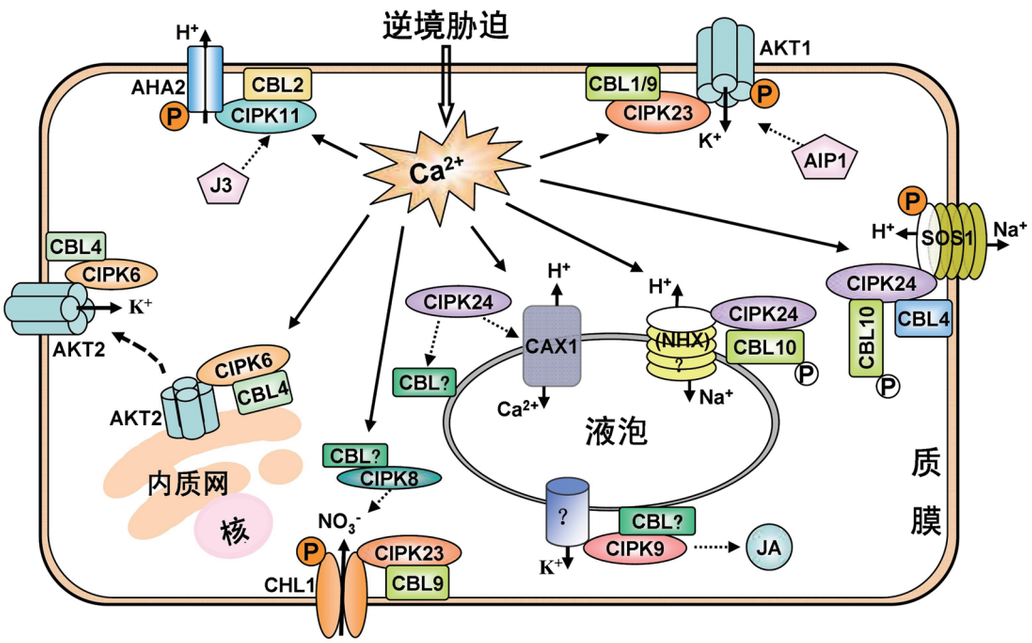

图3 植物CBL-CIPK信号系统与细胞离子转运调控机制

Fig.3 Plant CBL-CIPK signaling system and regulatory mechanisms of cellular ion transport

参考Luan (2009)、Tokas等(2013)、Weinl和Kudla (2009)文献并作修改。

AtCIPK11/PKS5能特异性地磷酸化AtCBL2/SCaBP1 C端的Ser216残基, 而这一位点突变恢复了AHA2的活性(Du等2011), 充分表明AtCBL2/SCaBP1的磷酸化是该信号系统调控AHA2活性的重要机制。相反, 分子伴侣J3 (DnaJ homolog 3; heat shock protein 40-like)通过抑制PKS5的磷酸化作用来激活AHA2的活性, 从而促进胞内H^+的外排, 使植物在碱性环境下存活(Yang等2010)。

3.4 干旱、低温胁迫

干旱既能诱导*AtCIPK6*的表达(Chen等2013), 又能促进AtCBL1/CBL9与AtCIPK1特异性互作, 通过ABA依赖或非依赖的方式作出应答, 以维持植物细胞渗透平衡(Cheong等2003; Pandey等2004; 图2)。另外, 过表达*AtCBL5*也能提高植物对干旱和高盐的耐受能力, 但不依赖于ABA (Cheong等2010)。已知AtCBL1/CBL9与AtCIPK23互作能够调控AKT1介导的根细胞K^+吸收与运输(Xu等2006; Cheong等2007)。遗传学分析发现, *Atcipk23*和*Atakt1*突变体植株均表现出耐旱性(Cheong等2007; Nieves-Cordones等2012), 表明植物通过抑制CBL1/CBL9-CIPK23-AKT1介导的保卫细胞K^+的内流使叶片气孔关闭, 减少植物水分损失, 从而对干旱胁迫作出间接响应(图2)。相反, 在水稻中, *OsCIPK23*的RNA干涉株系对干旱敏感, 而过表达*OsCIPK23*诱导多种耐旱相关基因的表达但并未减少叶片的水分损失(Yang等2008), 表明水稻*OsCIPK23*通过调控下游的干旱响应基因间接参与对干旱的响应。以上研究结果表明CBL-CIPK在不同物种中参与调控不同耐旱机制, 以适应不同生存环境。

同样, AtCIPK3通过依赖或不依赖于ABA的方式对低温、高盐及干旱等非生物胁迫作出响应, 成为多种逆境胁迫信号交互对话(cross-talk)的重要调控位点(Kim等2003; 图2)。另外, *AtCIPK7*的表达受冷诱导, 亲和色谱法分析证明AtCIPK7在活体内与AtCBL1互作。这一研究结果表明AtCBL1-AtCIPK7信号系统介导植物冷胁迫响应(Huang等2011; 图2)。

3.5 氧化胁迫及ROS信号

酵母双杂交显示, 过氧化氢酶CAT2、CAT3及二磷酸核苷激酶NDPK2均能与AtCIPK24互作(Verslues等2007; 图2), 而这些蛋白均参与H_2O_2的分解代谢, 暗示AtCIPK参与调控ROS介导的信号

途径。有证据表明, AtCBL1/CBL9和AtCIPK26通过两种方式来协同激活拟南芥NADPH氧化酶RBOHF (respiratory burst oxidase homolog F)的活性, 即Ca^{2+}直接结合RBOHF的EF手型和Ca^{2+}诱导的磷酸化(Drerup等2013; 图2)。以上研究结果表明CBL-CIPK信号系统正调控ROS的形成, 并与ROS信号途径交互对话。

3.6 K^+的吸收与稳态

K^+参与调控植物信号传导、新陈代谢与生长发育, 因而维持细胞K^+稳态对植物正常生长发育极为重要。AtCBL1/AtCBL9-AtCIPK23和AKT1互作蛋白磷酸酶AIP1 (AKT1-interacting PP2C 1)通过磷酸化/去磷酸化机制调控质膜K^+通道AKT1 (*Arabidopsis* K^+ transporter 1)的活性和细胞K^+吸收, 从而维持胞内K^+平衡(Xu等2006; Cheong等2007; Lee等2007; 图2、3)。在其他物种中, 也存在相似的K^+通道调控机制(Cuéllar等2013), 表明这一调控机理在进化上相对保守。此外, AtCBL4通过与AtCIPK6互作来介导另一K^+通道AKT2从内质网膜到质膜的转定位, 并激活质膜定位的AKT2活性(Held等2011; 图3), 该过程依赖于Ca^{2+}和CBL4的豆蔻酰化和棕榈酰化双重脂质修饰, 但不依赖于AtCIPK6的磷酸化作用。这很可能是CBL-CIPK信号系统调控离子通道活性的新机制。

另有研究表明, *Atcipk9*突变体对低钾呈现超敏反应, 但不影响对K^+的吸收(Pandey等2007), 推测AtCIPK9与某一AtCBL互作后, 可能激活液泡膜K^+通道活性, 从而介导液泡内K^+释放到胞质中, 另一种可能是参与茉莉酸(JA)介导的低钾适应性响应(Amtmann和Armengaud 2007; 图3)。但过表达*AtCIPK9*或*AtCBL3*对低钾敏感, 胞内K^+含量有所下降(Liu等2013), 这可能是过表达*AtCIPK9*或*AtCBL3*抑制了根系对K^+的吸收。在低钾条件下, 突变体*Atcipk9*和*Atcbl3*的根与地上部分的K^+含量比值与野生型相比明显降低, 暗示AtCIPK9可能通过转运并合理分配K^+从而维持胞内K^+平衡。这些研究结果表明, 在低钾胁迫下, 不同CBLs可能通过与不同CIPKs互作来调节细胞不同部位的K^+通道的开与关, 以维持胞内K^+的稳态。

3.7 Ca^{2+}的平衡

Ca^{2+}作为胞内重要信使参与各种信号途径, 因此保持胞内Ca^{2+}的平衡对植物正常生长发育至关重要。酵母双杂交分析表明, AtCIPK24/SOS2与液泡膜Ca^{2+}/H^+逆转运蛋白CAX1 (cation exchanger 1)特异性互作不依赖于AtCBL4/SOS3, 很可能是由于AtCIPK24/SOS2通过与未知液泡膜定位的AtCBL互作所致, 从而调控CAX1的活性和胞内Ca^{2+}的平衡(图2)。同时, CAX1的活性不依赖于AtCIPK24/SOS2的激酶活性, 并且在高盐胁迫下, CAX1提高了植株对盐胁迫的敏感性。因此推测, 当植物受到高盐胁迫时, 某一未知AtCBL与AtCIPK24/SOS2结合从而抑制AtCIPK24/SOS2与CAX1之间的互作, 使CAX1自我抑制, 促进液泡Ca^{2+}释放到胞质中; 而正常条件下, AtCIPK24/SOS2通过非磷酸化方式激活CAX1, 将胞质中多余的Ca^{2+}转运到液泡中贮存(Cheng等2004; 图3)。这一发现为Ca^{2+}调控和Na^+转运过程提供了一种偶联机制。有关该信号系统的具体调控机理仍需进一步研究。

3.8 硝酸盐的吸收

硝酸盐(NO_3^-)是大多数陆生植物的主要氮源, 在植物营养、辅酶因子合成及信号传导中具有重要生物学功能。植物细胞对硝酸盐的吸收主要依赖于两种不同亲和力的转运系统。不同浓度的硝酸盐条件下, NO_3^-分别与硝酸盐双亲和转运蛋白CHL1/NRT1.1 (chlorate resistant 1/nitrate transporter 1.1)的高/低亲和位点结合, 诱导其构象改变, 使AtCBL9-AtCIPK23通过磷酸化/去磷酸化机制调节CHL1/NRT1.1对硝酸盐的亲和性, 从而使CHL1/NRT1.1能够感知较大范围的硝酸盐浓度的波动, 以双重亲和形式对不同浓度的硝酸盐作出高低两种亲和水平的应答(Ho等2009; 图2、3)。

另有研究指出, 高浓度硝酸盐快速诱导*AtCIPK8*基因的表达, 而AtCIPK8通过控制硝酸盐转运体CHL1和NRT2.1的表达水平正调控硝酸盐的低亲和应答(图2、3); *Atcipk8*突变后抑制硝酸盐响应基因及硼转运体BOR1的表达(Hu等2009)。这些结果暗示AtCIPK8参与调控硝酸盐的吸收及早期应答、维持NO_3^-和其他阴离子之间的平衡。

3.9 植物激素应答

3.9.1 ABA信号 ABA作为植物衰老、逆境应答的重要信号分子, 参与调控胚芽发育、种子成熟与休眠、根和茎的生长、叶的蒸腾和植株对多种逆境胁迫的响应。研究发现, AtCIPK15/PKS3作为负调节蛋白与AtCBL1/SCaBP5形成复合体, 特异性

地调控ABA信号转导途径(图2)。此外, AtCIPK15与PP2C型磷酸酶ABI2 (ABA-insensitive 2)互作, 共同调控下游靶蛋白的磷酸化状态, 从而调控ABA相关基因的表达(Guo等2002)。而AtCBL9与AtCIPK3特异性互作正调控种子萌发期对ABA的响应(Kim等2003; Pandey等2008; 图2)。最新研究显示, AtCIPK6 (Chen等2013)、AtCIPK26 (Lyzenga等2013)及AtCIPK14 (Qin等2008)作为ABA信号途径的成员共同参与调控植株对ABA信号的响应。水稻功能缺失突变体*Oscipk31*的种子萌发和幼苗生长均表现出对ABA、盐及甘露醇等胁迫的高度敏感(Piao等2010)。这些研究结果表明, CBL-CIPK信号系统参与调控ABA介导的信号途径。

3.9.2 生长素运输 植物通过改善根系构型以适应多变的土壤环境, 而生长素和ABA介导的信号途径通过交互对话方式协同调控植株侧根发育(Tripathi等2009b)。研究发现, AtCIPK6除了参与调控逆境胁迫响应外(Chen等2013), 还参与调控植物生长素运输(Tripathi等2009a)。*Atcipk6*突变体表现出生长素运输活性下降和发育缺陷症状如子叶融合、下胚轴膨大及侧根退化等, 这些表型症状与生长素转运蛋白PGP4 (P-gly-coprotein)突变体*pgp4*极为相似, 暗示*AtCIPK6*有可能通过调控PGP4介导的生长素运输来影响植株的发育(Tripathi等2009b; 图2)。然而, 目前仍没有证据表明CIPKs是否参与调控生长素的合成或信号传导。

4 总结与展望

综上所述, 植物CBL-CIPK信号系统对Ca^{2+}信号的识别与解码至关重要, 该信号系统能够将上游的Ca^{2+}信号的时空特异性变化转换成下游的细胞生理反应, 参与调控各种逆境胁迫响应、胞内外离子平衡、营养物质吸收和对各种植物激素的应答。CBLs与CIPKs之间的互作机制以及Ca^{2+}的调控作用赋予了CBL-CIPK信号网络特异性的调控能力。

在CBL-CIPK研究领域中, 急待解决以下几个问题: 首先, 病原体侵染是如何触发宿主细胞CBL-CIPK信号系统以及病原体自身是否具有相应的对策机制? 其次, 一旦遭遇某一或多种逆境, 宿主细胞通过什么机制来快速有效地组织相对应的CBL-CIPK信号系统, 从而作出正确的响应; 第三, 分析鉴定受CBL-CIPK信号系统调控的下游靶蛋白, 将丰富和完善植物逆境信号传导和耐逆境分子机制; 最后, 值得一提的是, 从野生种质资源中分离和克隆*CBLs*和*CIPKs*等位基因, 将为培育高耐逆境作物新品种提供新的野生基因资源。

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