

植物SnRK家族的研究进展

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摘要: 植物在自然界中面临各种环境侵害时候, 如干旱、盐、低温和病菌袭击, 会启动自身的抵御机制来适应各种侵害。蔗糖非发酵相关的蛋白激酶(sucrose non-fermenting-1-related protein kinase, SnRK)是广泛存在于植物中的一类Ser/Thr蛋白激酶, 参与各种胁迫信号传导通路, 对植物抵御不良环境起到重要作用。植物中蔗糖非发酵相关的蛋白激酶共有38个成员, 可以分为3个亚家族: SnRK1、SnRK2和SnRK3。本文主要讨论SnRK家族的研究进展, 揭示SnRK家族在植物抗逆中的重要作用。

关键词: 信号通路; 蔗糖非发酵相关的蛋白激酶(SnRK); SnRK1; SnRK2; SnRK3

植物是固着生物, 不能随着周围环境的变化而迁移, 容易受到干旱、洪涝、冷、盐和病虫害等各种环境胁迫的侵害; 在长期的进化过程中, 植物形成了一套应对各种环境刺激的机制(Yu等2014)。其中, 蛋白质的磷酸化和去磷酸化修饰是植物应答环境胁迫信号的非常重要的机制。蔗糖非发酵相关的蛋白激酶(sucrose non-fermenting-1-related protein kinase, SnRK)是一类Ser/Thr蛋白激酶, 通过磷酸化修饰靶蛋白来调控多种信号途径的相互联系, 在植物胁迫应答过程中起着至关重要的作用(Yan等2014)。

SnRK在植物中广泛存在, 且具有保守性。SnRK依据蛋白质结构的差异性和相似性可以分为3个亚家族, 即SnRK1、SnRK2和SnRK3。其中SnRK1和酵母中SNF1与哺乳动物中AMPK存在着较高的序列相似性, 而SnRK2和SnRK3是植物所特有的一类蛋白激酶(Coello等2011)。研究表明, SnRK家族蛋白质具有激酶的活性, 主要通过磷酸化修饰来调节蛋白质的活性和基因的表达, 从而达到调节代谢的目的。目前, 对于SnRK1的研究还比较模糊, 这可能与其功能的多样性有关。SnRK1参与胁迫响应、代谢调节以及生长发育等过程(Halford和Hey 2009)。而对于SnRK2的研究较为深入, SnRK2在渗透胁迫和ABA信号传导中起到尤为重要的作用(Yoshida等2014)。SnRK3家族成员众多且有功能冗余, 主要通过和CBL互作调节各种生物和非生物胁迫反应(Yu等2014)。

1 SnRK1

SnRK1与酵母和哺乳动物中蔗糖非发酵相关的蛋白激酶在序列上高度保守(Crozet等2014), 且SnRK1能互补酵母中 $snf1$ 突变体的缺陷; 表明

SnRK1和SNF1存在一定的功能相似性。在结构上, SnRK1也由一个 α 催化亚基和 β 与 γ 两个调节亚基组成三元复合体(Carling等2012); 根据催化亚基的不同, 拟南芥中SnRK1分为SnRK1.1、SnRK1.2和SnRK1.3三个亚家族(Baena-Gonzalez等2007)。目前研究表明, SnRK1参与植物体内多种生理生化过程的调节, 是连接胁迫和新陈代谢的纽带(Halford和Hey 2009)。

植物中SnRK1在胁迫调节方面有着非常重要的作用。在豌豆中, SnRK1的活性减少50%~70%将导致蔗糖累积增加和种子成熟的缺陷, 包括蔗糖转换为种子内贮藏的养分和种子过早萌发(Radchuk 2005)。这些表型与ABA不敏感突变体 $abi3$ 的表型一致(Finkelstein 2013)。SnRK1的催化亚基KIN10超表达会引起拟南芥开花的延迟和长角果与子叶形成的缺陷(Tsai和Gazzarrini 2012a), 这种表型可以被 $fus3$ 突变体所缓解(Tsai和Gazzarrini 2012b)。在植物体内SnRK1和FUS3相互作用并调节FUS3蛋白质的稳定性, 且FUS3蛋白质也受到ABA的调节(Gazzarrini等2004)。研究表明SnRK1的活性受到PP2C的抑制(Rodrigues等2013), 而PP2Cs是ABA信号通路中抑制SnRK2活性的蛋白质家族(Umezawa等2009)。另外, SnRK1可以磷酸化ABA响应元件(ABREBs)和调节ABA信号途径中bZIP型转录因子ABI5和bZIP12的活性(Lastdrager等2014)。因此, SnRK1可能参与ABA信号的响应, 在ABA调节种子的成熟过程中发挥重要的作用(Baena-Gonzalez等2007)。

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SnRK1也参与植物新陈代谢的调节。在能量饥饿条件下, SnRK1对于维持植物体内代谢平衡有着重要意义。遭受低能胁迫时, 植物体内有超过300个与合成代谢相关的基因受到SnRK1的抑制, 这些代谢过程包括蔗糖、淀粉、氨基酸、核苷酸和蛋白质合成等, 其中对蛋白质合成相关基因的抑制尤为明显(Baena-Gonzalez和Sheen 2008; Buchanan-Wollaston等2005)。另外, 大约有300个与植物分解代谢相关的基因受到SnRK1的调节, 这些基因参与植物体内氨基酸、细胞壁、蔗糖、淀粉和多糖的水解等过程。植物通过一系列的代谢调控来弥补能量的缺陷和碳源的损失, 其中蛋白质的降解是一个细胞成分回收再利用的关键过程(Baena-González等2007; Baena-Gonzalez和Sheen 2008)。此外, SnRK1可以诱导与代谢过程中相关蛋白酶体的表达, 如丙酮酸激酶PK、谷氨酸脱氢酶GDH和天冬氨酰合成酶ASN1等。这些蛋白酶参与体内多种代谢循环, 其中GDH普遍存在于高等植物的线粒体中, 在氮代谢中起到重要的作用; 同时在黑暗和碳胁迫时又能氧化脱铵为三羧酸循环提供碳源(Baena-Gonzalez和Sheen 2008)。因此, SnRK1在植物新陈代谢的调节中发挥重要作用。

2 SnRK2

越来越多的研究表明: 植物中所特有的蛋白激酶SnRK2在植物遭受逆境胁迫时起到至关重要的作用(Kulik等2011)。Anderberg和Walker-Simmons (1992)从小麦中克隆得到*PKABA1*基因是最早描述的SnRK2成员, 并且发现这个基因受到ABA和干旱的诱导。研究发现*PKABA1*在大麦的糊粉层中对GA所诱导的基因表达的抑制起到关键的作用。蚕豆中一个SnRK2家族成员AAPK, 在保卫细胞中受到ABA的诱导, 与气孔的运动有关(Li等2000)。拟南芥中SnRK2蛋白质家族共有10个成员, 即AtSnRK2.1~AtSnRK2.10。根据不同物种之间SnRK2s在进化上的同源性分析发现, 玉米SnRK2家族共有11个成员, 即ZmSnRK2.1~ZmSnRK2.11; 而水稻中也发现存在10个SnRK2成员, 即OsSAPK1~OsSAPK10 (Huai等2008; Saha等2014) (图1)。

研究发现, 大豆中的SPK1和SPK2基因被转到酵母中后可以被高浓度渗透胁迫所诱导(Monks等

2001)。SPK3和SPK4的超表达均可以增加植株对高渗透胁迫的响应; 然而, 它们又有所不同。SPK3受到外源ABA的诱导, 而SPK4不受外源ABA的影响(Baradaran等2013)。Kobayashi等(2004)分析了10个水稻SnRK2成员在成熟的水稻原生质体中的表达, 结果表明, 所有的SnRK2成员均受到高渗透胁迫的诱导, 而仅有SAPK8、SAPK9和SAPK10这3个成员受到ABA的诱导(Yoshida等2002)。拟南芥中, 除了SnRK2.9, 其他SnRK2家族成员在原生质体内均受到高渗透胁迫的诱导(Boudsocq等2004), 但只有SnRK2.2、SnRK2.3和SnRK2.6在ABA处理时强烈地被诱导, 而ABA对SnRK2.7和SnRK2.8只有微弱的诱导(Fujii和Zhu 2009)。这些表明, SnRK2在ABA依赖和ABA非依赖的信号通路中都起作用, 这可能与SnRK2蛋白质的结构有关(Yoshida等2014)。

2.1 SnRK2的结构

SnRK2通常是由140~160个氨基酸组成大约40 kDa的蛋白质。SnRK2与其他激酶的结构一样都是由催化区域和调节区域两部分组成(Kulik等2011)。SnRK2激酶的催化区域和SnRK1、SNF1和AMPK有42%~46%的氨基酸序列是相同的, 然而它们的羧基端是完全不同的(Halford等2003)。研究发现, AtSnRK2.6等在ABA依赖和ABA非依赖通路中都起作用, 而AtSnRK2.10仅仅在ABA非依赖的通路中行使功能(Vlad等2009)。因此, 推测SnRK2的结构中存在ABA依赖和非依赖的活化区域。

如图2-A所示, SnRK2的N端为激酶区域, C端为调节区域。图中区域I为ABA非依赖的调节区域, 是所有的SnRK2成员都拥有的; 而区域II为ABA依赖的通路中PP2C和SnRK2绑定的区域(Kulik等2011; Yoshida等2006; Yunta等2011)。正是因为SnRK2的特殊结构, 所以SnRK2参与多种信号通路, 对植物的调节起到至关重要的作用。

2.2 SnRK2的调节及信号通路

渗透胁迫激活植物体内的信号通路, 迅速改变植物应答基因的表达和代谢, 从而帮助植物度过不良环境的胁迫(Kobayashi等2004)。SnRK2在渗透胁迫中被激活, 表明SnRK2参与渗透胁迫信号(Coello等2011)。在拟南芥中10个SnRK2家族成员同时突变时, *dec* (十突)突变体在没有聚乙二醇

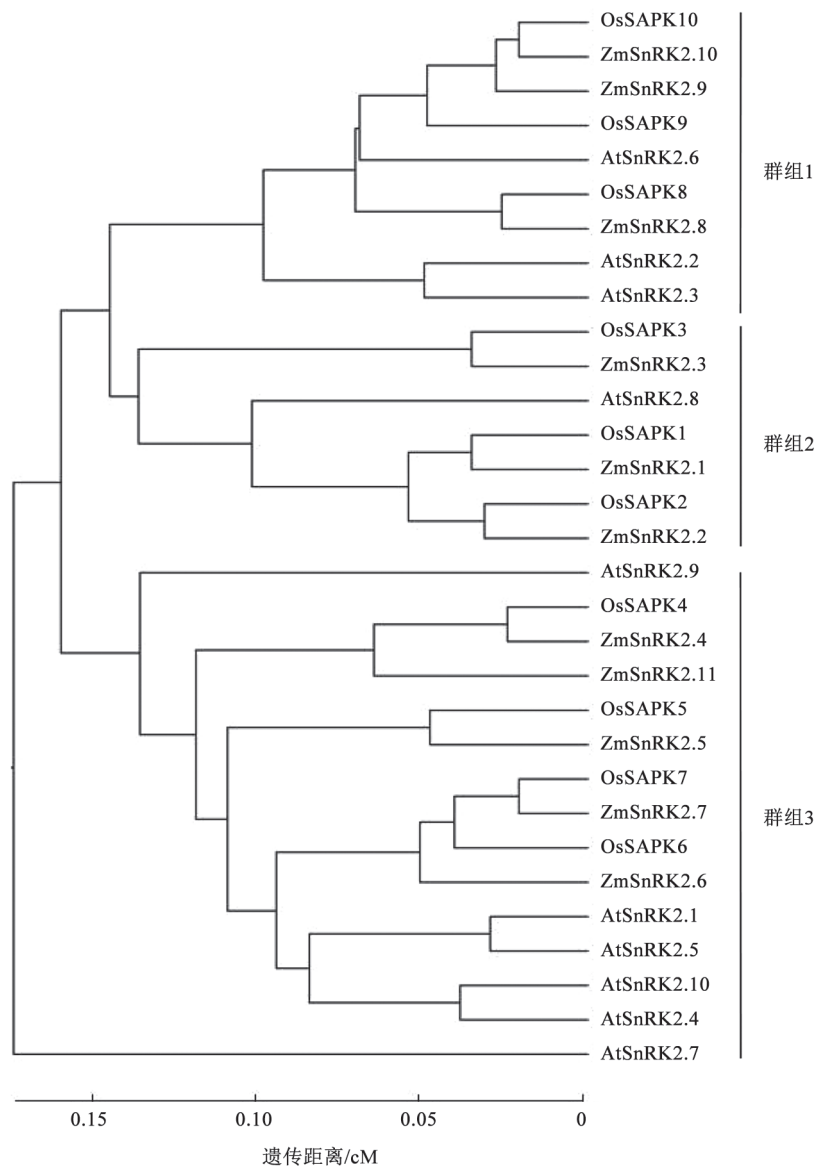


图1 拟南芥、玉米和水稻中SnRK2的系统发育树
Fig.1 Phylogenetic analysis of SnRK2s from *Arabidopsis*, maize and rice
应用MEGA 5.10软件作图。

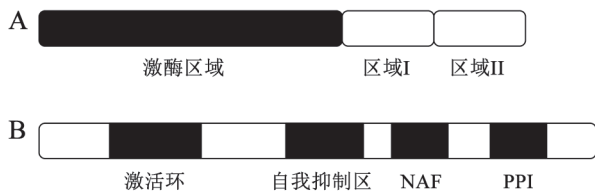


图2 SnRK2和CIPK的结构模型
Fig.2 The model of structure of SnRK2 and CIPK
参考Kulik等(2011)、Batistic和Kudla (2009)文献修改。A:
SnRK2的结构模型; B: CIPK的结构模型。

(PEG)处理时, 生长状况和野生型没有什么大的区别; 但是在含有PEG的培养基上生长时叶片明显发黄, 表明*dec*突变体对渗透胁迫高度敏感(Fujii等2011)。 *snrk2.2/2.3/2.6*三突在 $0.5\ \mu\text{mol}\cdot\text{L}^{-1}$ ABA处理时, 表现出对ABA不敏感的表现, 且在 $300\ \mu\text{mol}\cdot\text{L}^{-1}$ ABA处理时突变体仍能很好生长(Nakashima和Yamaguchi-Shinozaki 2013); 然而其他SnRK2家族成员的突变体并没有表现出明显对ABA响应的表现(Joshi-Saha等2011)。综上所述, 表明SnRK2参与

透胁迫信号通路可以分为: ABA依赖和ABA非依赖的两种调节途径(Yoshida等2014)。目前, 关于SnRK2调节的ABA非依赖通路的研究还不太清楚, 而对ABA依赖信号通路的研究已经相当深入。研究发现, 干旱和高盐胁迫引起植物激素ABA含量的累积, 而ABA的增加可以调节植物对高渗透胁迫的响应(Yoshida等2014)。植物细胞感受ABA浓度的波动是通过细胞膜上的受体来完成的。研究发现PYR/PYL/RCAR在结构上包含与ABA结合的

START结构域, 表明PYR/PYL/RCAR家族可能是ABA的受体蛋白家族(Park等2009)。当ABA不存在时, ABA响应通路中重要的蛋白激酶SnRK2将受到PP2C的抑制; 然而, 当ABA存在时, ABA和其受体结合形成复合体抑制PP2C的活性, 从而使SnRK2得以从PP2C的抑制状态中释放出来(Park等2009; Santiago等2012)。进而, SnRK2通过调节下游相关蛋白质的活性来调节胁迫响应基因的表达(图3)。

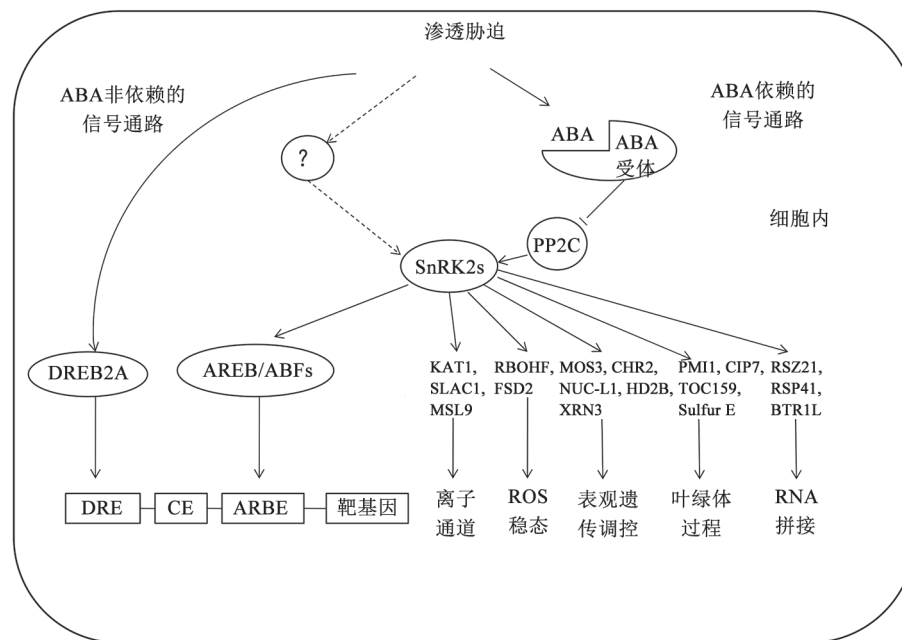


图3 响应渗透胁迫的ABA依赖和非依赖的信号通路

Fig.3 ABA-dependent signaling pathway and crosstalk with ABA-independent signaling in response to osmotic stress

参考Yoshida等(2014)、Wang等(2013)文献修改。图中实线箭头表示已知的激活作用, 虚线箭头代表未知的激活作用, ⊥代表抑制作用, 方形框代表基因, 其他图形框代表蛋白质。

2.3 SnRK2的下游

在ABA调节通路中, ABA响应基因的启动子区含有多个保守的ABA响应元件ABRE (Yoshida等2015)。相应的转录因子和ABRE结合启动ABA响应基因的表达, 而这些转录因子的活性受到磷酸化作用的调节。如AREBs/ABFs受到SnRK2激酶的调节(Yoshida等2015)。Furihata等(2006)发现ABFs在拟南芥体内的活性受到SnRK2.2/2.3/2.6的调节。随后, 研究发现群组1中的激酶磷酸化ABFs和ABI5在种子成熟和萌发过程中起到重要作用(Piskurewicz等2008)。水稻中的SAPK8、SAPK9

和SAPK10可以磷酸化TRAB1 (Kobayashi等2005); 小麦中PKABA1可以磷酸化TaABF (Johnson等2002)。因此SnRK2可以通过磷酸化ABFs来调节ABA响应基因的转录。

蚕豆中的AAPK在保卫细胞中受到ABA的诱导, 并且参与阴离子通道和气孔关闭的调节(Li和Assmann 1996)。拟南芥中 $srk2e/ost1/snrk2.6$ 突变体叶片气孔的正常关闭功能缺失, 导致在环境湿度快速减少时突变体叶片有较高的失水率而萎焉(Nakashima等2009)。SnRK2.6功能的缺失导致ABA介导的气孔运动丧失和对ABA不敏感的表现

(Liang等2015)。*snrk2.6*突变体在保卫细胞中损坏ABA激发ROS产物的形成,表明SnRK2.6在NADPH氧化酶的上游。NADPH由两部分组成,即AtrbohD和AtrbohF (Sirichandra等2009)。在体外AtrbohF和OST1可以互作,而在细菌中OST1可以磷酸化AtrbohF的N端部分,表明NADPH氧化酶可能是SnRK2.6的底物。

SLAC1是一个在保卫细胞中表达的S型的阴离子通道蛋白,并且在气孔响应高浓度CO₂和ABA时起作用(Tian等2015)。SLAC1的活性受到可逆的磷酸化的调节,其磷酸化状态是有活性的;且当SLAC1的活性上调时有助于气孔的关闭(Vahisalu等2008)。研究表明,OST1可以磷酸化SLAC1 (Geiger等2009)。当OST1和SLAC1共表达时,SLAC1被激活;然而加入PP2C时,SLAC1的活性消失(Brandt等2012)。研究表明SLAC1是SnRK2.6的底物。另外,钾离子通道蛋白KAT1活性下调对气孔关闭是必不可少的,这恰恰与SLAC1的作用相反;而SnRK2.6也可以磷酸化KAT1的C端区域来调节其活性。因此SnRK2.6磷酸化SLAC1和KAT1对于气孔的运动是至关重要的。综上表明,SnRK2s是离子通道非常重要的调节子。

ABA是植物体内非常重要的胁迫相关的植物激素,参与植物许多生理生化的过程;而SnRK2s是ABA通路中至关重要的蛋白激酶(Santiago等2012)。然而,对于ABA-SnRK2s的底物的研究还不够透彻。通过对SnRK2s底物组学的研究,发现有58个蛋白质可能是SnRK2s的底物。这些蛋白质涉及到多种生物过程,包括基因的转录、RNA的加工、后生调节、叶绿体过程和花期的调节等(图3, Wang等2013)。这些结果表明SnRK2s对于植物的渗透调节有着非常重要的作用,然而对于其下游基因了解还有待进一步的研究。

3 SnRK3

Ca²⁺作为第二信使,在植物中参与许多生物学过程(Weinl和Kudla 2009)。植物中Ca²⁺的浓度受到多种生物和非生物胁迫的影响,如光、干旱、低温、氧化胁迫、盐胁迫、激素、机械损伤和病原体侵袭等(Luan 2009)。当Ca²⁺浓度发生变化时,植物会感应到此信号,进而通过调节植物应激基因的表达来缓解外界刺激。然而,植物是如何来感知

Ca²⁺浓度的改变呢?研究表明:植物通过钙离子效应器蛋白来感应此信号。这些蛋白质在结构上都含有Ca²⁺结合区域——EF臂(Gifford等2007)。在拟南芥中目前发现有超过250种含有EF臂的蛋白质,可以分为四类,即CaM家族、CML家族、CDPK家族和CBL家族(Luan等2002)。然而,CBL蛋白家族并没有激酶活性,需要通过招募其相关的蛋白激酶形成复合体来传递信号;这类蛋白质叫做CBL相关的蛋白激酶即CIPK (Batistic和Kudla 2009)。CIPK蛋白家族是一个植物特殊的丝氨酸-色氨酸激酶家族(Batistic和Kudla 2009)。因为CIPK与酵母和哺乳动物中的蔗糖非发酵相关的蛋白激酶在结构上存在一定的相似性,所以也被称作植物蔗糖非发酵相关的蛋白激酶亚家族SnRK3 (Tominaga等2010)。

在结构上,CIPK蛋白质家族由一个N端激活区域和一个C端调节区域两部分组成(图2-B)。在正常条件下,CIPK的活性受到CIPK本身的自我抑制区域的抑制。当外界刺激引起Ca²⁺浓度的变化时,钙离子感受器CBL的EF臂区和钙离子结合,招募相应的CIPK蛋白质,并和CIPK调节区域的NAF结合形成复合体。从而CIPK的构象发生改变,CIPK激酶的活性被释放。另外CBL的N端区域准确的指导CBL-CIPK复合体到相应的细胞靶区,进而通过CIPK激酶磷酸化相应的靶蛋白来调节相应的响应(Kolukisaoglu等2004; Waadt等2008)

研究发现CBL-CIPK系统在低等植物和高等植物中都是普遍存在的。生物信息学分析发现在拟南芥中存在10个CBL蛋白质和26个CIPK蛋白质;水稻中有10个CBL蛋白质和33个CIPK蛋白质,而玉米中有8个CBL蛋白质和43个CIPK蛋白质(Chen等2011; Wang等2011; Xiang等2007)。因此在植物中可以形成多种CBL-CIPK复合体来行使不同的功能。目前,研究发现CBL-CIPK系统参与植物的多种生物和非生物胁迫。SOS通路是最早被发现的CBL-CIPK系统,主要参与植物细胞内的钠离子稳态的调节(Shi等2002)。在高浓度的盐胁迫的条件下,SOS通路可以通过调节植物细胞内Na⁺的平衡来增强植物对盐的耐受性。盐胁迫引起植物细胞内Ca²⁺浓度的变化,Ca²⁺和SOS3 (CBL4)结合,并招募SOS2 (CIPK24)形成复合体,在细胞膜上直接调节SOS1即Na⁺/H⁺反向转运体的活性(图4),从而来

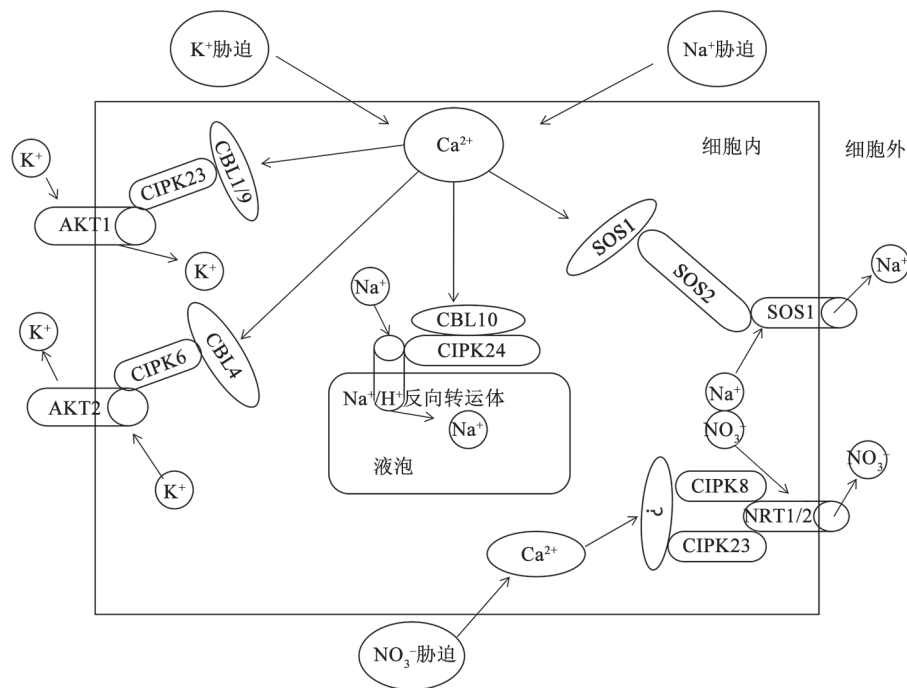


图4 CBL-CIPK调节细胞内钾离子、钠离子和硝酸根离子稳态的机制

Fig.4 Regulation of ion (Na^+ , K^+ and NO_3^-) homeostasis by CBL-CIPK

参考Manik等(2015)、Yu等(2014)文献修改。图中圆形框代表离子,其他图形框代表蛋白质,实线箭头代表激活或者离子运动方向。

调节细胞内 Na^+ 的输出(Halter等2000; Ishitani等2000)。另外, CBL10同样也和CIPK24相互作用调节钠离子的平衡。然而, 与CBL4所不同的是, CBL10是主要在茎和叶片中起作用而CBL4主要在根部起作用, 且CBL10定位在液泡膜上而CBL4定位在细胞膜上(Kim等2007)。在液泡膜上, CBL10-CIPK24复合体通过调节 Na^+/H^+ 反向转运体NHX来调节 Na^+ 由细胞质进入到液泡中(Kim等2007)。

钾离子是植物生长发育所必需的基本离子, 钾离子的运输同样受到CBL-CIPK系统的调节(Luan等2009)。当土壤中钾离子浓度过低时, 植物一般表现出叶片萎黄等症状, 影响植物生长(Luan等2009)。研究表明, 植物对于土壤中钾离子的吸收是依赖于定位在植物根部细胞膜上的钾离子通道蛋白家族(Anderson等1992)。AKT1是一个钾离子吸收的通道蛋白, 拟南芥中CBL1/9-CIPK23复合体通过调节AKT1的活性, 来调节细胞内钾离子的浓度(Li等2006; Xu等2006)。在植物根细胞中CIPK23也可以调节HAK5, 一个高效的钾离子运输蛋白(Ragel等2015)。另外, 在植物保卫细胞内CIPK23也可以通过调节AKT1的活性来参与植物

对水胁迫的响应(Lee等2009)。AKT2亦是与 K^+ 吸收相关的通道蛋白, CBL4-CIPK6通过调节其从内质网运输到质膜来调节AKT2的活性(Held等2011)(图4)。

另外, CBL-CIPK复合物还参与植物中多种生物过程。在拟南芥中, CBL1-CIPK1可能参与ABA依赖的胁迫响应; 而CIPK1和CBL1同源关系较近的CBL9形成复合体时, 却是参与ABA非依赖的胁迫响应(D'Angelo等2006)。CBL9-CIPK3在植物种子萌发时对植物激素ABA起负调节作用(Pandey等2008); CIPK7和CBL1相互作用参与冷胁迫响应(Huang等2011); CIPK8和CIPK23通过调节硝酸盐转运蛋白来调节植物对硝酸盐的响应(Hu等2009); CIPK11在干旱、ABA、盐和蔗糖胁迫时被诱导表达, CIPK11和CBL2相互作用调节质膜中 H^+ -ATPase AHA2的活性(Fuglsang等2007); CIPK26和ABA信号通路中的PP2C家族的ABI1、ABI2和ABI5相互作用, 在种子萌发中起正调节作用(Lyzenga等2013); 另外, CBL1/9-CIPK26复合体也参与NADPH氧化酶的调节(Drerup等2013)。CIPK15在ABA响应中起到负调节子的作用(Zhu等2007)。然

而, 由于基因功能冗余等原因, 对于CIPK2/4/5/10/12/13/17/18/19/20/21/22/25功能的研究还不是很清楚, 需要进一步研究。

在玉米和水稻中, CIPK蛋白家族也参与各种生物和非生物响应。玉米中CIPK16和CBL3/4/5相互作用, 并且在幼苗阶段受到盐、ABA、高温、干旱和脱水胁迫的诱导(Chen等2011); 而CIPK1/3/8/17/18在水胁迫条件下受到ABA、CaCl₂和H₂O₂的不同程度的诱导; 表明玉米中多种CIPK蛋白质的功能与多种非生物胁迫相关(Tai等2013)。在水稻中, CIPK03/12/15/19/31参与不同的非生物胁迫信号通路, 包括盐、ABA、冷、干旱、光和营养物等(Xiang等2007)。

总之, 植物中CIPK蛋白家族参与多种生物和非生物胁迫, 在植物生长发育中起到至关重要的作用, 是植物为适应环境而进化出的植物特有的必不可少的蛋白质家族。

4 讨论与展望

在自然条件下, 植物经常要面临各种各样的生物和非生物胁迫, 如干旱、极端温度、盐和病虫害等。植物中蔗糖非发酵相关的蛋白激酶家族通过其上游的信号传递来调节相关基因的表达和蛋白质的活性, 来响应自然灾害使植物尽可能的幸存下来。目前, 关于SnRK家族的研究已经非常多, 但是对其功能的研究仍有许多不清楚的地方。植物受到胁迫时可能会导致体内能量状态的失衡, 引起低能综合症(LES)。植物中SnRK1和雷帕霉素的靶蛋白(TOR)在调节低能综合征有非常关键的作用(Tome等2014)。如当蔗糖浓度偏低时, SnRK1被激活抑制一些基因的表达和启动分解代谢从而来响应低能综合症; 然而当蔗糖浓度高时TOR起作用调节一些蛋白翻译和植物生长响应, 而SnRK1的活性受到海藻糖-6-磷酸(T6P)的抑制(Lastdrager等2014)。植物在不同能量状态时, SnRK1和TOR起到相反的作用, 它们之间存在着怎样的联系? 植物是通过什么机制来感应不同的能量状态? 又是通过什么信号通路来调节SnRK1的活性? 目前发现T6P在高浓度蔗糖调节下可以抑制SnRK1的活性, 但是具体的机制还不清楚; 这些问题有待进一步的研究。

SnRK2在ABA通路中起到的作用已经研究的

较为透彻, 但是对于SnRK2在渗透胁迫信号中的作用还有很多需要研究的地方。目前对于SnRK2的磷酸化普遍认为是SnRK2的自我磷酸化, 然而SnRK2的自我磷酸化对于SnRK2的作用是否是充足的还不太清楚。SnRK2.10是ABA非响应的蛋白激酶, 研究发现SnRK2.10并不和PP2C家族成员相互作用(Umezawa等2009), 然而在正常情况下SnRK2.10也没有被激活, 表明可能还存在其他的机制在ABA非响应的调节机制抑制SnRK2的活性。如上所述, SnRK2家族都受到渗透信号的激活, 而ABA响应的SnRK2在正常情况下是受到抑制的, 渗透信号是如何解除这种抑制状态的机制还不清楚。

Ca²⁺作为植物的第二信使, 其浓度的变化引起植物体内各种生理生化的反应。SnRK3作为Ca²⁺信号通路中非常关键的蛋白激酶可以调节植物体内胁迫响应和代谢响应。然而, 关于SnRK3功能的研究可能由于基因冗余等原因还不透彻, 有待进一步研究。另外从图2-B中可以看到CIPK蛋白家族还含有保守的PPI区域, PPI区域是蛋白磷酸酶PP2C家族的识别区域; 而PP2Cs也在ABA通路中起到非常重要的作用, 因此PP2Cs可能是连接ABA通路和其他通路的关键因子。

植物体内的调节是非常复杂且相互联系的, 各种信号通路之间也存在着必然的联系。SnRK家族参与胁迫和新陈代谢等多种生理生化过程, 和其他调节通路之间一定存在着某种联系, 对于这种联系的研究可能是以后SnRK研究的方向。总之, SnRK对于植物在恶劣的环境的生存有着至关重要的作用, 然而还有许多功能还没有研究透彻, 需要进一步的研究。

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Research progress of plant family of SnRK

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Abstract: In nature, plants are frequently exposed to harmful environmental conditions such as drought, salt, cold and pathogen attack. In order to survive, plants sense and respond to the change of their environment through various defense mechanisms. Sucrose non-fermenting-1-related protein kinase (SnRK) is a family of Ser/Thr protein kinase that generally exists in plants. When plants are subjected to environment stress, SnRK will be induced and participate in many signal transduction pathways to defense detrimental environment conditions. SnRK family comprises 38 members, which are subdivided into three sub-families: SnRK1, SnRK2, and SnRK3. In this summary, the research progress of the family of SnRK will be described to reveal the importance of SnRK family in plants.

Key words: signal pathway; sucrose non-fermenting-1-related protein kinase (SnRK); SnRK1; SnRK2; SnRK3

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