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植物CDPK在逆境胁迫与育种中的研究进展

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摘要:钙依赖性蛋白激酶(Calcium-dependent protein kinase, CDPK/CPK)是一类丝氨酸/苏氨酸(Ser/Thr)蛋白激酶,在植物生长发育和逆境胁迫响应过程中起重要作用。CDPKs通过自磷酸化以及对代谢酶、离子通道、转录因子和膜转运蛋白的磷酸化修饰,形成复杂的网络信号传导,以响应盐碱、干旱、低温等非生物胁迫。同时,CDPKs亦参与脱落酸(Abscissic acid, ABA)、水杨酸(Salicylic acid, SA)等激素的信号通路,调控植物的生长发育。本研究对植物CDPKs蛋白结构、分类、调控机制、以及逆境胁迫响应中的作用和育种应用等方面研究成果进行了总结综述,并提出未来CDPKs在育种领域的应用前景,以期为农作物抗逆性遗传改良和生物育种提供参考。

关键词:钙依赖蛋白激酶;信号转导;磷酸化;非生物胁迫;育种应用

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Research Progress of Plant CDPK in Abiotic Stress and Breeding

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Abstract: Calcium-dependent protein kinases (CDPK/CPK) are a class of Ca^{2+} -sensitive Ser/Thr protein kinases, which play important roles in plant growth and development, as well as in response to abiotic stresses. CDPKs could autophosphorylate or phosphorylate metabolic enzymes, ion channels, transcription factors, and membrane transporters, forming complex signaling networks to respond to abiotic stresses, such as salinity, drought, and low temperature. Meanwhile, CDPKs also participate in plant hormone signaling pathways such as abscissic acid and salicylic acid to modulate plant growth and development. This study reviews the research achievements concerning the structure, classification, regulatory mechanisms, roles in abiotic stress responses, and breeding applications of plant CDPKs. This paper also proposes future application prospects for CDPKs in the field of breeding, aiming to provide genetic resources and a theoretical basis for the genetic improvement of crop stress resistance and biological breeding.

Key words: Calcium-dependent protein kinase; Signal transduction; Phosphorylation; Abiotic stress; Breeding application

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植物在自然生长过程中不可避免地遭受多种生物与非生物逆境胁迫,如高盐、干旱、极端温度、病原菌侵染等,严重制约了植物的生长发育^[1]。而植物在长期进化中形成了复杂的信号传递网络系统,比如钙离子(Ca^{2+})信号传递通路和丝裂原活化蛋白激酶(Mitogen activated protein kinase, MAPK)等,以抵御逆境胁迫^[2]。 Ca^{2+} 作为第二信使,在植物感知胁迫信号并在启动响应中扮演着极其重要的角色。 Ca^{2+} 通过时空特异性波动激活下游级联反应,成为逆境感知的核心枢纽^[3]。钙信号传感器主要包括:钙调素蛋白(Calmodulin, CAM)、钙调素样蛋白(Calmodulin-like protein, CML)、钙依赖性蛋白激酶(Calcium-dependent protein kinase, CDPK/CPK)、钙调磷酸酶B蛋白(Calcineurin B-like protein, CBL)和CBL互作蛋白激酶(CBL-interacting protein kinase, CIPK)^[4]。这些 Ca^{2+} 传感器负责感知胞内 Ca^{2+} 浓度的波动变化,进而调控植物的生长发育、逆境响应以及触发免疫反应。不同的是,CDPKs是植物特有的钙传感器,兼具 Ca^{2+} 结合域(EF-hand)和激酶催化域,可直接将钙信号转化为磷酸化信号,无需其它中介蛋白^[5]。可见,CDPKs可以直接整合感应与响应功能来触发植物逆境信号转导,并使其成为了核心钙传感器。同时,CDPKs亦是植物中特有的一类Ser/Thr蛋白激酶。亚细胞定位发现,其定位于细胞质、细胞核、质膜、叶绿体或者线粒体等细胞器,其N-末端是CDPKs亚细胞定位和执行功能的关键调控区域^[6]。研究表明,CDPKs亦参与调控盐碱、干旱、低温、重金属等多种逆境胁迫响应,因其在植物生长发育及逆境胁迫响应中的重要功能,备受研究人员的关注,成为植物逆境生理和遗传育种研究的热点之一^[5]。本文系统综述了植物CDPKs结构和分类、调控机制,着重对CDPKs在响应逆境胁迫中的作用机制加以系统总结,并提出未来CDPKs在育种领域中的应用前景,以期为作物抗逆遗传优良及新品种培育提供理论依据。

1 植物 CDPK 的结构和分类

CDPKs的结构域组成主要由可变结构域、蛋白激酶结构域、自抑制结构域和钙调蛋白样结构域这四个部分组成^[7-8](图1)。可变结构域位于CDPKs

的N端,长度40~180个氨基酸,序列高度可变且无同源性,被认为可能参与蛋白质相互作用和亚细胞定位^[8-9]。蛋白激酶结构域是CDPKs的核心催化结构域,负责磷酸化底物,该结构域包含典型的真核Ser/Thr蛋白激酶的12个高度保守的亚基^[10]。自抑制结构域在非活性状态下,自抑制结构域与激酶结构域结合,抑制其活性^[11]。钙调蛋白样结构域是CDPKs的关键钙结合区域,含4个EF-hand基序(少数成员含1~3个),每个EF-hand由12个氨基酸构成的螺旋-环-螺旋结构并结合一个 Ca^{2+} 组成^[12]。当 Ca^{2+} 结合到钙调蛋白样结构域时,会引发构象变化,释放自抑制结构域,从而激活激酶^[8]。EF-hand序列的变异也会影响 Ca^{2+} 结合亲和力与激活阈值^[5]。除了经典的CDPKs,其家族还包括其他几类结构功能相关的蛋白激酶,共同构成植物钙信号转导网络的核心^[9]。通过构建CDPKs蛋白系统发育树,可以揭示物种特异性的扩展或独特的CDPKs亚类^[13]。例如,在拟南芥中,34个CDPK基因被分为四个主要类别^[7]。同样,在草莓(*Fragaria × ananassa*)中,将FveCPKs也分为四个亚组,每一亚组的蛋白都具有同源性^[14]。可见,通过对CDPKs进行全面的分类,可以更好地理解它们在植物生长发育和逆境响应中的作用。

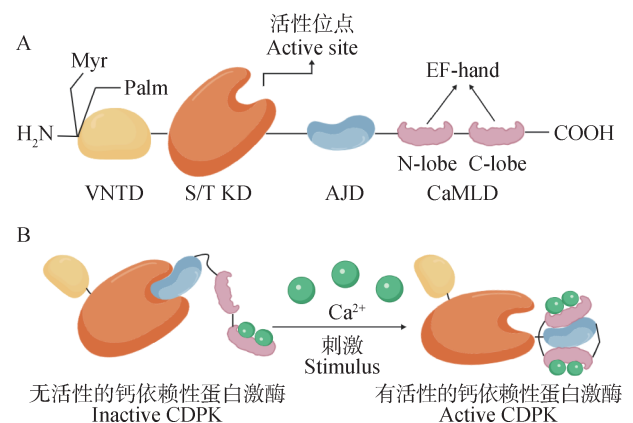


图1 植物 CDPK 结构模式图(A)和激活机制(B)示意图^[15]

Fig. 2 Diagram of CDPK structure domains (A) and activation mechanisms (B)

注: VNTD, 可变N结构域; S/TKD, Ser/Thr, 激酶催化结构域; AJD, 自抑制结构域; CaMLD, 类钙调素结构域; Myr, 豆蔻酰化位点; Palm, 棕榈酰化位点

Note: VNTD, Variable N-terminal domain, S/TKD, Ser/Thr, protein kinase domain; AJD, Auto-inhibitory junction domain; CaMLD, CaM-like regulatory domain; Myr, myristoylation site site, Palm, Palmitoylation site

2 植物CDPK的调控机制

2.1 CDPKs的活性调控

CDPKs的活性主要受到 Ca^{2+} 精确调控(图1)。低钙浓度下,自抑制结构域与Ser/Thr激酶结构域的活性位点结合,阻止底物结合,使CDPKs处于非活性状态;高钙浓度下, Ca^{2+} 结合到EF手性基序上,引起钙结合结构域的构象变化,进而解除自抑制结构域对激酶结构域的抑制,暴露活性位点,使CDPKs能够磷酸化底物,从而激活CDPKs活性^[16]。除了 Ca^{2+} 结合带来的构象变化,CDPKs自身的磷酸化也可精细调节其活性。CDPKs的自磷酸化现象普遍存在,且通常发生在Ser和Thr残基上,甚至在酪氨酸(Tyr)残基上也有发生,这种自磷酸化通常是 Ca^{2+} 依赖性的,并能促进激酶活性^[5]。研究表明,大豆CDPK β 和几个拟南芥同工酶(AtCPK4和AtCPK34)中观察到Tyr残基的自磷酸化并确定了Ser-8、Thr-17、Tyr-24、Ser-304和Ser-358为His(6)-GmCDPK β 的自磷酸化位点^[10]。另外,激素也会影响CDPKs的自磷酸化,在体外磷酸化实验中,ABA能够有效提高葡萄ACPK1、拟南芥AtCPK4和AtCPK11的自磷酸化水平,导致这三种CDPKs活性的增强^[17]。进一步研究表明,ABA主要以剂量依赖性方式激活AtCPK1,并且在果实发育过程中,AtCPK1的表达和酶活性与内源ABA浓度一致变化^[18]。虽然磷酸化通常会提高激酶活性,但在某些Tyr残基上的自磷酸化则可能起到抑制作用。研究表明,在大豆CDPK β 中,Tyr-24的自磷酸化似乎减弱了激酶活性,而Ser-8、Thr-17、Ser-304和Ser-358的自磷酸化则增强了激酶活性^[11]。因此,CDPKs的自磷酸化是一个复杂的调控过程,不同磷酸化位点可能对激酶活性产生不同的影响。

2.2 CDPKs对下游蛋白的调控

CDPKs通过磷酸化调控下游靶蛋白基因表达水平来发挥其功能,而这些靶蛋白涵盖了植物生长发育、逆境响应和免疫防御等多个方面。一般而言,CDPKs最直接的调控方式是通过磷酸化底物蛋白上的Ser或Thr残基来改变其活性或功能^[19]。体外实验证实,菠菜(*Spinacia oleracea*)CDPKs能够通过磷酸化其叶片中的蔗糖磷酸合酶(Sucrose phosphate synthase, SPS)的Ser-158位点来使其失活^[20]。另外,CDPKs还可磷酸化其它功能蛋白。例

如,乙烯生物合成途径中的关键酶1-氨基环丙烷-1-羧酸合酶(1-Aminocyclopropane-1-carboxylate synthase, ACS)的某些基因类型如Type 1和Type 3 ACS也受到CDPKs的磷酸化调控,从而影响乙烯的产生^[21]。在拟南芥中,AtCPK12在缺氧条件下通过钙依赖性磷酸化其Ser-186残基迅速激活,使AtCPK12从细胞质穿梭到细胞核,与植物缺氧感应的核心调节因子VII组乙烯响应转录因子(Ethylene response factors, -VII, ERF-VII)相互作用并使其磷酸化,以增强ERF-VII稳定性^[22]。同时,CDPKs也参与各种信号级联反应,比如ZmCDPKs通过磷酸化离子通道和转运蛋白,启动离子平衡调节的信号级联,应对干旱、盐胁迫,ZmCPK35定位于保卫细胞,可直接磷酸化S型阴离子通道蛋白ZmSLAC1,促进阴离子外流,降低保卫细胞膨压,最终介导气孔关闭,减少水分流失^[23]。值得注意的是,CDPKs还可以与其他激酶如MAPK等相互作用,形成复杂的信号网络^[24]。例如,烟草(*Nicotiana tabacum*)中的NtCDPK2的升高会抑制MAPK激活乙烯的合成和感知,这表明CDPK和MAPK途径并非独立发挥作用,两条途径的协同控制着对胁迫的反应特异性^[25]。14-3-3蛋白家族是一类在真核细胞中广泛表达且高度保守的调节蛋白,其名称源于最初的电泳迁移特性^[26]。研究表明,谷氨酸受体样蛋白的Ser-860位点被CDPK磷酸化后,可以与14-3-3 ω 相互作用,参与拟南芥的盐胁迫响应^[27]。由此可见,CDPKs通过磷酸化其下游靶点,为14-3-3蛋白提供结合位点,从而调控靶蛋白的活性。以上研究表明,CDPKs的磷酸化作用在信号通路转导过程中发挥着重要的作用。

3 植物CDPK在响应逆境胁迫中的作用

3.1 CDPK在响应非生物胁迫中的作用

3.1.1 CDPKs参与盐胁迫响应 盐胁迫严重制约着植物的生长发育。CDPKs作为关键的 Ca^{2+} 传感器,负责将胞内钙信号转换为特异性磷酸化事件,进而调控下游靶基因应答,以提高耐盐性^[28](图2)。拟南芥中AtCPK12、AtCPK27、AtCPK1都被证实参与盐胁迫信号传导。盐胁迫下,与野生型拟南芥相比,AtCPK12表达被抑制的RNAi突变体幼苗显示出显著的生长抑制,包括地上部分生物量减少

以及整体发育迟缓,这表明CPK12-RNAi干扰植株在幼苗生长方面对盐胁迫更加敏感^[29]。AtCPK27是膜定位的蛋白激酶,AtCPK27的T-DNA插入突变体cpk27-1,在种子发芽和发芽后幼苗生长方面对盐胁迫的敏感性远高于野生型拟南芥。在离子通量测定中,cpk27-1突变体在长期盐处理后,排出钠离子(Na^+)和进入氢离子(H^+)的能力低于野生型拟南芥。此外,cpk27-1突变体在短期和长期盐处理后,盐诱发的过氧化氢(H_2O_2)产量均高于野生

型。表明AtCPK27通过促进 Na^+ 外排和 H^+ 内流来调控离子稳态,并且抑制 H_2O_2 的积累,在种子萌发和幼苗生长阶段增强拟南芥对盐胁迫的耐受性^[30]。除此之外,通过测量脯氨酸(Pro)、丙二醛(MDA)和 H_2O_2 的变化证实了cpk1突变体和AtCPK1过表达株系的耐受性降低和升高。表明AtCPK1缺失功能突变体对盐胁迫表现出超敏感性,而过表达AtCPK1的拟南芥植株则显著增强了对盐胁迫的抗性^[31]。

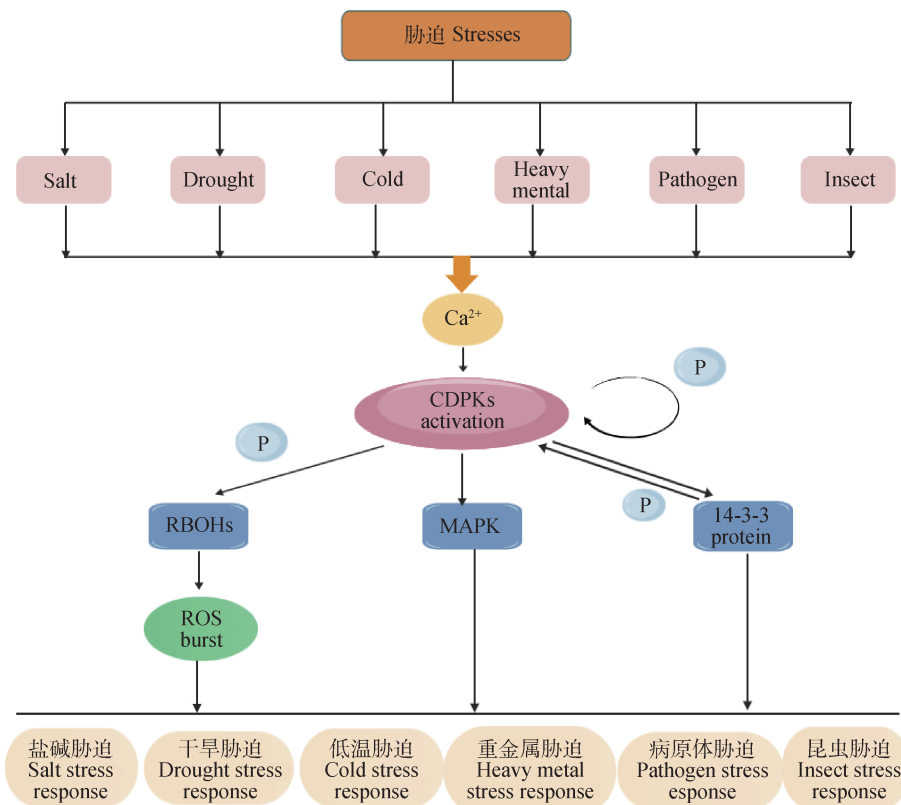


图2 CDPKs调控植物逆境胁迫响应示意图

Fig. 2 Schematic diagram of CDPKs regulating plant responses to abiotic stress

注:CDPKs调控植物胁迫响应的方式是通过 Ca^{2+} 激活,随后磷酸化下游蛋白(如RBOHs和14-3-3蛋白),从而应对逆境胁迫反应。CDPKs还可通过MAPK信号通路来响应外界的刺激

Note: CDPKs regulate plant stress responses by being activated by calcium ions, followed by the phosphorylation of downstream proteins (such as RBOHs and 14-3-3 proteins), thereby effectively responding to stress. CDPKs can also mediate responses to external stimuli through the MAPK signaling pathway

在多种植物中也发现有许多CDPKs与盐胁迫相关。比如在水稻中,OsCPK12对盐胁迫耐受性有正向调控作用,过表达OsCPK12的植株表现出增强的耐盐性,叶片中 H_2O_2 的积累量低于野生型,这表明OsCPK12通过调节活性氧(Reactive oxygen species, ROS)水平来提高耐盐性^[32]。有实验证明,沉默TaCDPK27后,小麦幼苗在盐胁迫下根和叶长度缩短、ROS积累增加、超氧化物歧化酶(Superoxide

dismutase, SOD)等抗氧化酶活性降低^[33]。证实了TaCDPK27通过调控ROS稳态和抑制盐诱导的程序性细胞死亡,正向调控小麦幼苗的耐盐性^[33]。并且小麦中TabZIP60通过与TaCDPK30相互作用,一方面直接结合并上调TaNCED2等ABA合成相关基因的表达,促进ABA积累;另一方面上调TaLEA1等胁迫响应基因的表达,同时通过提高可溶性糖含量、降低MDA含量增强植株抗逆性,最终

介导小麦的盐耐受性^[34]。例如在银杏(*Ginkgo biloba*)中CDPKs与ROS清除、MAPK信号及类黄酮合成过程密切相关,类黄酮是银杏叶中的主要活性成分,*GbMYB41*是一个关键的调控因子,与银杏中的类黄酮生物合成正相关,CDPKs可能调控*GbMYB41*或其它类黄酮合成途径中关键酶的基因表达,影响类黄酮的合成量^[35-37]。紫花苜蓿(*Medicago sativa*)中克隆得到*MsCDPK3*基因,通过过表达和RNAi实验证实其能显著增强紫花苜蓿盐碱胁迫耐受性,*MsCDPK3*可以通过正调控ABA信号通路,降低活性氧积累和膜损伤、优化离子平衡,最终提升紫花苜蓿耐盐碱能力^[38]。综上,CDPKs通过感知钙信号、调控离子平衡、减轻氧化损伤以及整合激素应答等多层次机制,在植物盐胁迫响应中发挥核心作用^[39]。

3.1.2 CDPKs参与干旱胁迫响应 植物为了应对干旱胁迫,逐步进化出一系列复杂的形态、生理、生化和分子层面的适应机制,以提高水分利用效率,维持生命活动^[40-41]。CDPKs参与调控植物体内与抗旱相关的基因表达^[42](图2),例如,在小麦中,*TaCDPK1-5A*对干旱和ABA信号敏感,它与*TaMAPK4-7D*和*TaABF1-3A*形成一条信号通路,被激活的*TaABF1-3A*转录因子调控多个与干旱胁迫相关的基因,包括*TaP5CS1-1-B*、*TaPIN3-5A*和*TaSLAC1-3-2A*,它们分别通过参与Pro的生物合成、参与促进根系生长和参与气孔关闭的调控等生理过程正向调节干旱适应性^[43]。另外,拟南芥中的CPK家族,比如*AtCPK6*可以通过磷酸化ABF和ABI5转录因子,正向调节ABA信号传导和干旱耐受性^[44]。此外,二穗短柄草(*Brachypodium distachyon*)植株经干旱胁迫处理后,通过RT-PCR检测发现*BdCDPK14*在胁迫后表达量明显升高,表明其参与二穗短柄草抗旱胁迫反应^[45]。这些研究进一步支持了CDPKs在干旱胁迫响应中的重要性。ABA是植物响应干旱胁迫的关键植物激素,许多CDPKs基因参与ABA信号通路^[46]。玉米的*ZmCPK4*在拟南芥中过表达后,转基因株系在种子萌发、幼苗生长和气孔运动中对ABA敏感性显著增强,同时干旱胁迫耐受性提升,证实了*ZmCPK4*是CDPK/ Ca^{2+} 介导的ABA信号通路正调控因子,通过调控气孔运动参与玉米对干旱胁迫的响应^[47]。另外,CDPKs可以通过磷酸化ABA信号通路中的关键组分,如ABA响应元件结合转录因子(ABRE/

ABFs),从而介导ABA信号转导^[48]。例如,玉米亚硫酸氧化酶基因(*Zea mays sulfite oxidase gene*, *ZmSO*)是玉米中参与硫代谢、胁迫响应的关键基因。*ZmSO*基因的表达受到ABA的调控,含有两个ABRE元件的*ZmSO*基因能够增强植物的抗旱性^[49]。可见CDPKs可以通过感知钙信号进而磷酸化转录因子来对响应ABA等信号通路共同构建了复杂的耐旱机制。

3.1.3 CDPKs参与低温胁迫响应 CDPKs在植物应答低温胁迫中起着不可或缺的作用(图2)。许多CDPKs基因在低温胁迫下表现出差异表达模式^[50]。玉米中的*ZmCPK1*被鉴定为CDPKs家族的一员,转基因拟南芥后冷处理并进行电解质渗漏实验,发现转基因株系的半致死温度低于野生型,抗冻性增强,证实*ZmCPK1*对低温胁迫的负调控作用^[51]。草莓的FaCDPK1在根、匍匐茎、分生组织、花、叶片中均有表达,果实中仅在白色阶段开始积累转录本,且成熟果实经4℃低温处理5~10 h后,其转录本水平显著升高,表明FaCDPK1可能参与草莓果实发育及低温响应过程^[52]。并且在白三叶草(*Trifolium repens*)中也发现了相关基因的表达, RNA-seq和qRT-PCR验证显示,多数*TrCDPK*基因在低温胁迫早期显著上调表达,其中*TrCDPK4*、*TrCDPK8*、*TrCDPK19*等基因表达量最高可达对照的32倍,证实*TrCDPK*基因在白三叶草低温胁迫早期响应中起关键调控作用^[53]。另外,研究发现,一些特定的CDPKs直接参与了植物的耐寒性调控。例如,从野生番茄(*Solanum pennellii*)中分离出的*SpCPK33*基因,主要定位于质膜,其过表达可显著提高转基因番茄的耐寒性^[54]。雪莲(*Sasussurea involucrata*)中的*SikCDPK1*基因过表达可增强烟草的耐寒性,其转录组分析表明*SikCDPK1*可以通过参与MAPK信号通路并调节转录因子(包括WRKY、AP2、MYB、bHLH和NAC)的表达水平来应对寒冷^[55]。在桃果实中,对CDPKs基因家族的全基因组分析发现,CDPK-RBOH途径可能参与提高果实的冷害耐受性^[56]。CDPKs在植物响应逆境胁迫中扮演着核心角色^[50](表1)。

3.1.4 CDPKs参与重金属胁迫响应 重金属的积累会对植物生长、代谢和生理过程产生广泛而深远的负面影响^[57]。当植物暴露于重金属胁迫时,会诱导细胞质 Ca^{2+} 水平的快速升高^[58]。这种 Ca^{2+} 的升高信号被CDPKs精确识别和解码,进而激活一系列

表 1 CDPK 在植物响应逆境胁迫中的作用

Table 1 The role of CDPK in plant response to stress conditions

物种名称 Specie name	CDPK	作用 Function	参考文献 Reference
拟南芥 <i>Arabidopsis thaliana</i>	<i>AtCPK1</i>	参与盐胁迫响应;磷酸化脱落酸信号通路中的关键蛋白。 Salt stress response;Key proteins in the phosphorylation abscisic acid signaling pathway.	[31]
	<i>AtCPK12</i>	响应盐胁迫;激活脱落酸信号负调控因子 ABI2,并磷酸化脱落酸信号正调控因子 ABF1 与 ABF4。 Response to salt stress;Stimulate the ABA signaling negative regulator ABI2, and phosphorylate the ABA signaling positive regulators ABF1 and ABF4.	[29]
	<i>AtCPK27</i>	调节活性氧与离子平衡,正向调控盐胁迫信号转导过程。 Regulate the balance of reactive oxygen species and ions, and positively modulate the salt stress signaling transduction process.	[30]
玉米 <i>Zea mays</i>	<i>ZmCPK4</i>	整合胁迫信号,调控 ABA 途径及与生长发育相关的基因。 Integrate stress signals, regulate the ABA pathway and genes related to growth and development.	[47]
	<i>ZmCPK1</i>	其存在会抑制植物对冷胁迫的主动响应。 The presence can inhibit the plant's active response to cold stress.	[51]
水稻 <i>Oryza sativa</i>	<i>OsCPK12</i>	磷酸化 OsCATA 与 OsCATC 可维持 H ₂ O ₂ 稳态,从而正向调控水稻氧化胁迫耐受性;同时降低对稻瘟病的抗性。 Phosphorylation of OsCATA and OsCATC maintains H ₂ O ₂ homeostasis, thereby positively regulating oxidative stress tolerance in rice;Reduce resistance to rice blast disease.	[32]
	<i>TaCDPK27</i>	受负调控的小麦白粉病抗性,其功能与小麦自噬相关;正向调控小麦耐盐性。 Resistance to wheat powdery mildew is subject to negative regulation, and its function is related to wheat autophagy.;Positive regulation of wheat salt tolerance.	[33]
	<i>TaCDPK30</i>	与 TabZIP60 互作调控 ABA 合成,从而介导小麦耐盐性。 Interact with TabZIP60 to regulate ABA synthesis, thereby mediating salt tolerance in wheat.	[34]
	<i>TaCDPK1</i>	增强植物对低磷胁迫的耐受性。 Enhancing the plant's tolerance to low-phosphorus stress.	[43]
紫花苜蓿 <i>Medicago sativa</i>	<i>MsCDPK3</i>	可通过正调控 ABA 信号通路,降低活性氧积累与细胞膜损伤、优化细胞离子平衡来提升耐盐性。 Enhances salt tolerance by positively regulating the ABA signaling pathway, reducing reactive oxygen species accumulation and membrane damage, and optimizing ion homeostasis.	[38]

下游的信号通路(图 2)^[42]。比如,重金属胁迫可导致 ROS 的过量产生,进而引发氧化胁迫,CDPKs 的激活可以参与调控抗氧化酶的活性,通过 ROS 的清除和从而减轻氧化损伤^[59]。在拟南芥中发现 AtCPK5 和 AtCPK11 正向调控植物对高锰胁迫的耐受性,二者可与液泡膜上的锰转运体 MTP8 直接互作,并磷酸化其 Ser31 和 Ser32 位点以增强转运活性,将胞质中过量锰转运至液泡隔离,从而缓解锰毒害^[60]。另有研究表明,多种 CDPKs 同源基因在响应重金属胁迫时表现出表达量的显著上调^[15]。例如,在杨树(*Populus tomentosa*)中,研究人员鉴定了 20 个 *PtCDPKs* 基因,其中 *PtCDPKSK5*、*PtCDPK24* 等在砷胁迫下表达量发生变化,表明它们参与对重金属的响应^[61]。同时,活化的 CDPKs 可以直接磷酸化细胞核内的转录因子,从而调节与重金属解毒、螯合、转运等相关的基因表达,例如 WRKY 转录因子已被证实是 CDPKs 的下游靶标,参与植物免疫和胁迫响应基因的调控^[62]。已有实验证实了 CaCDPK29 在 Ca²⁺ 激活下磷酸化 CaWRKY27b 的 Ser137 位点,促使其从细胞质转运

至细胞核,通过与 CaWRKY40 蛋白互作增强其对 *CaPR1*、*CaNPR1* 等靶基因的 W-box 结合能力,同时三者形成正反馈环路放大防御信号来应对胁迫^[63]。

值得注意的是,镉(Cd)是一种常见的有毒重金属,严重影响植物生长发育和品质^[64]。一般而言,Cd 胁迫可导致植物体内 ROS 积累、细胞膜损伤和光合作用效率下降^[65]。CDPKs 在感知 Cd 诱导的 Ca²⁺ 信号后,通过调控胞内镉离子转运蛋白(如 NRAMP、HMA、ZIP、ABC 等)的活性,或通过调节抗氧化酶如 SOD 的表达和功能,从而影响 Cd 在细胞内的积累、运输和解毒过程^[66]。美洲商陆(*Phytolacca americana*)属多年生草本植物,因对重金属的超强耐受与富集能力,成为重金属污染土壤修复的核心材料,有实验探究在其 20 mg·L⁻¹ Cd 胁迫下的表达模式,发现 *PaCDPK1*、*PaCDPK7* 和 *PaCDPK12* 在胁迫下均上调^[67]。这反映了钙信号及其感知者 CDPKs 在植物应对重金属胁迫中的重要性。

3.2 CDPKs在响应生物胁迫中的作用

3.2.1 CDPKs在病原体抵抗中的作用 植物通过两类先天免疫反应来抵御病原体感染:病原相关分子模式(Pathogen-associated molecular patterns, PAMP)触发的免疫和效应子触发的免疫(Effector-triggered immunity, ETI)^[68]。CDPKs在这两种免疫反应中均扮演着重要的角色(图2)。当植物识别到病原体相关的分子模式时,细胞内 Ca^{2+} 浓度会迅速升高,CDPKs能够直接感知这种 Ca^{2+} 信号的增加并被激活,活化的CDPKs会磷酸化下游靶蛋白,例如呼吸爆发氧化酶同源物D/F,从而导致ROS的产生^[69]。CDPKs同样参与ETI,其中植物识别特定的病原体效应子,并触发更强烈的防御反应,包括程序性细胞死亡以限制病原体扩散^[9]。实验证实,oscpk17突变体和OsCPK17沉默株对细菌性病害更敏感,PAMP诱导的ROS爆发和防御基因表达显著减弱。OsCPK17作为免疫正调控因子可与类受体酪氨酸激酶OsRLCK176互作并将其Ser83位点磷酸化,从而抑制植物U-box型E3泛素连接酶OsPUB12对OsRLCK176的泛素化降解,增强OsRLCK176的稳定性与免疫功能^[70]。研究表明,小麦条锈病由小麦条锈菌(*Puccinia striiformis* f. sp. *tritici*, Pst)引起,沉默TaCDPK7后,小麦对Pst的抗性显著降低,表现为过氧化氢积累减少40%、真菌生物量增加30%、防御相关基因表达下调及病原菌菌丝生长增强,最终证实TaCDPK7通过促进ROS积累和病程相关基因表达,正向调控小麦对Pst的抗性^[71]。另外,对洋葱的AcCDPK1-OE和AcCDPK5-OE过表达株系接种烟草疫霉后病斑面积显著减小,ROS早期积累增加、抗氧化酶活性提升,最终证实AcCDPK1和AcCDPK5通过调控ROS代谢和下游抗病基因表达正向增强植物对烟草疫霉的抗性,且AcCDPK1功能强于AcCDPK5^[72]。蒺藜苜蓿是豆科生物学和基因组学研究的模式物种^[73]。在蒺藜苜蓿(*Medicago truncatula*)中以酵母诱导子(YE)处理模拟病原体侵染,通过微阵列数据分析MtCDPKs和MtCRKs的表达变化MtCDPK4、MtCDPK8、MtCDPK16等多个基因在YE处理2小时后表达量显著升高,提示这些基因快速响应病原体信号,可能参与早期防御反应启动^[74]。因此,CDPKs在对植物病原体胁迫中扮演重要的角色。

3.2.2 CDPKs在抵抗昆虫中的作用 当植物遭受

昆虫啃食时,会触发一系列防御反应,包括产生次生代谢产物作为抵抗昆虫和病原体的武器,例如酚类化合物、生物碱、糖苷和萜类化合物等^[75]。CDPKs作为信号转导的关键组分,参与调控这些防御性次生代谢产物的合成(图2)。除此之外,CDPKs参与植物的系统性免疫反应,例如诱导系统性抗性(Induced systemic resistance, ISR)或类ISR反应^[76]。这使得植物在局部受到攻击后,能够增强其在全身范围内的防御能力,从而有效抵御后续的昆虫或病原体侵扰^[77]。CDPKs能够磷酸化NADPH氧化酶,从而激活ROS的生成,ROS不仅对入侵者具有直接毒性作用,还能作为信号分子,进一步激活下游防御反应,包括MAPK信号级联和防御基因的表达^[78]。例如,马铃薯中的StCDPK14和StRbohB的相互作用有助于BTH诱导的马铃薯块茎伤口愈合,并且StCDPK23的过表达也通过调节StRbohB促进了马铃薯块茎的伤口愈合这与ROS的生成密切相关^[78-79]。还有研究人员利用CRISPR-Cas9技术构建了GhCPK突变体文库,以筛选抗虫基因,这为鉴定棉花中与抗虫性相关的特定CDPKs提供了新途径^[80]。可见,CDPKs作为植物钙信号转导的核心组分,在植物抵抗昆虫侵害中发挥着不可或缺的作用。

4 植物CDPK在育种领域的应用

4.1 CDPKs在作物产量和品质形成中的作用

CDPKs不仅与胁迫响应相关,也参与植物正常的生长发育过程,包括花粉管伸长、种子发育和次生代谢产物合成^[81]。例如,精确的 Ca^{2+} 信号调控对于花粉管的延伸至关重要,而CDPKs能够解码这些 Ca^{2+} 信号,进而影响花粉管的生长,最终影响植物的繁殖^[82]。众所周知,作物产量受开花时间、株高、分蘖数、籽粒数和籽粒重量等多种性状的影响。研究表明,水稻基因组中鉴定出31个CDPKs基因,其中OsCPK25和OsCPK26表达的上调或下调都会影响水稻雄蕊数量增加,暗示着CDPKs在作物生殖器官发育中具有重要的作用^[83]。可见,同时作物品质同样受到遗传和环境因素的综合影响,涉及代谢物的合成和代谢^[84]。CDPKs作为重要的信号分子,可能通过调控代谢途径间接影响作物营养成分和感官品质^[85]。例如,水稻OsCPK17通过调控SPS调控蔗糖代谢合成,进而提高糖含量,影响其品质的形

成^[86-87]。通过基因编辑等手段调节 CDPKs 的活性或表达,可实现对作物产量组分和营养品质的优化。

4.2 CDPKs 在协同调控抗逆性和产量平衡中的作用

在作物育种中,如何兼顾抗逆性和产量平衡是育种家面临的重要难点挑战。CDPKs 作为连接 Ca^{2+} 信号与下游反应的关键枢纽,为解决这一难题提供了新的思路。利用 CDPKs 基因,可以培育出在逆境条件下依然能够维持较高产量的作物品种^[88]。通过基因工程手段,将抗逆性强的 CDPKs 基因导入到高产品种中,或者通过分子标记辅助选择,筛选出具有优良 CDPKs 基因的种质资源,可以提高作物的抗逆性和产量^[89]。植物在生长和防御之间需要维持微妙的平衡。CDPKs 在协调植物生长和防御反应中发挥作用,确保植物在受到胁迫时,能够合理分配资源,维持生长和产量^[90]。科研人员还可以通过细胞筛选技术,结合基因编辑、细胞培养和选择性筛选等方法,可以加速具有抗逆性状的细胞或组织的筛选和培育,从而培育出更能适应环境挑战的农作物品种来提高产量^[91]。而且未来可将多个与抗逆性和产量相关的 CDPKs 基因聚合在一起,培育出具有更强抗逆性和更高产量的作物品种。这些方法都表明了 CDPKs 在协同提高作物抗逆性和

产量的育种中具有重要的应用前景。

4.3 CDPKs 在育种领域的应用前景

CDPKs 的功能多样性使其成为现代植物育种的重要靶点。随着基因组学、分子生物学和基因编辑技术的发展,对 CDPKs 基因家族的深入研究为作物改良提供了新途径^[92]。(图 3)目前,已在多种植物中进行了 CDPKs 基因家族的全基因组鉴定和表达分析,包括拟南芥、番茄、水稻等^[93-95]。为理解 CDPKs 基因的结构、进化和表达模式奠定了基础,并为后续的功能验证和育种应用提供了宝贵信息。特别是,CRISPR/Cas 系统,为精确改良作物性状提供了强大的工具,可通过编辑 CDPKs 基因来增强作物的抗逆性^[96]。例如,通过敲除敏感基因或敲入抗性基因,可以提高植物对非生物胁迫和生物胁迫的耐受性^[97]。CRISPR/Cas9 系统还可以用于对 CDPKs 基因进行点突变、缺失或插入,以及调节其转录活性,从而开发出更具抗逆性的作物^[96]。结合基因组学和分子标记技术,可以更高效地筛选和培育具有增强抗逆性的新品种。此外,竞争性等位基因特异性 PCR (Kompetitive allele specific PCR, KASP) 等高通量基因分型系统也可以应用于主要作物对生物和非生物胁迫的耐受性研究^[98]。通过识别与 CDPKs 基因相关的分子标记,育种家可以进行标记辅助选择,加速具有优良抗逆性状的品种的开发。

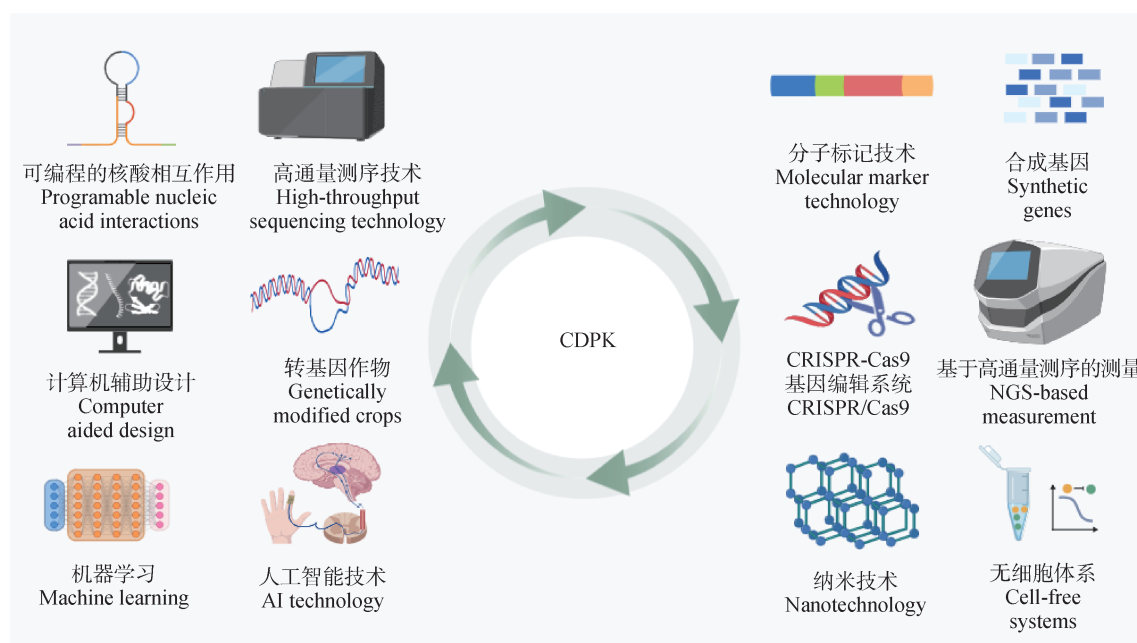


图3 CDPK 结合多种生物技术示意图

Fig. 3 Illustration of CDPK's integration with various biotechnological methods

虽然基因组编辑提供了更精确的工具,但传统的转基因方法仍可用于将来自其他物种或经过修饰的 *CDPKs* 基因导入作物中,以增强其抗逆性^[99]。这种方法有助于将特定 *CDPKs* 的抗逆功能引入目标作物,从而改善其在不利环境下的生长发育。研究表明,将 *CDPKs* 相关的抗逆基因与快速育种相结合,快速验证基因功能并培育出抗逆新品种^[100]。例如,非编码 RNA(ncRNA)在植物生长发育和胁迫响应中也发挥重要作用,研究 *CDPKs* 与 ncRNA 之间的相互作用有望为作物改良提供新途径^[101]。此外,代谢组学可以预测植物在胁迫环境下的代谢标记,与 *CDPKs* 研究结合有助于理解和筛选抗逆性状^[102]。特别是,在植物基因工程中,传统的基因传递方法,如电穿孔法和农杆菌介导的转化法,面临着物种依赖性、效率低、成本高以及 DNA 随机整合到宿主基因组等局限性。而纳米载体可以通过穿透生物屏障并保护所载物质不被降解,精确地靶向组织、细胞和细胞器,实现 DNA 或 RNA 的精确递送,为 *CDPKs* 基因的转化和功能验证提供了新的平台^[103]。因此,通过结合分子生物学、基因组学、生物信息学和先进育种技术,*CDPKs* 有望成为未来作物抗逆育种的重要靶点。

5 展望

CDPKs 在植物生长发育、逆境响应和信号转导中扮演着核心角色。鉴于 *CDPKs* 在植物抗逆性和生长发育中的关键作用,对其进行基因工程改造或利用其信号通路,可显著改善作物性状,提高农业产量和应对全球气候变化的能力。目前,对于不同物种中 *CDPKs* 家族的鉴定和分析仍在不断完善和丰富,不同物种 *CDPKs* 结构和功能存在相似性。然而,*CDPKs* 可调控多种胁迫响应,而同一种胁迫响应又可能会受到多个 *CDPKs* 调控,是否有更高效的信号通路来调节植物抗逆性仍有待深入研究。

尽管 *CDPKs* 在作物改良中前景广阔,但仍面临一些挑战:*CDPKs* 基因家族通常庞大,成员间可能存在功能冗余,使得单个基因的改造效果有限。尽管基因编辑技术发展迅速,但某些作物的转化效率仍是瓶颈,且脱靶效应仍需关注和最小化。鉴于此,关于 *CDPKs* 的未来研究方向可从以下几个方面进行:(1)解析 *CDPKs* 的特异性,探究不同 *CDPKs* 成员如何实现功能分化,例如通过亚细胞定位、时

空表达模式差异以及特异性底物的结合来明确信号特异性;(2)探究 *CDPKs* 与其他钙传感器如何通过信号整合,共同解码复杂的钙振荡模式,并触发精确的生理响应;(3)深入阐明 *CDPKs* 与 MAPK 级联两者如何协同或交叉调控下游靶点,形成更强的防御体系;(4)结合基因编辑技术,同时对多个 *CDPKs* 基因或其上下游调控基因进行精确改造,以实现更好的抗逆与产量的平衡;(5)整合不同组织层面的多组学数据,构建复杂的 *CDPKs* 介导的信号转导网络,预测关键调控节点,为作物抗逆遗传改良提供优异基因资源。

综上,*CDPKs* 作为植物信号转导网络中的关键调控枢纽,在提升作物抗逆性和改良产量性状方面具有巨大的应用潜力。未来随着基因编辑等技术不断成熟,以及对 *CDPKs* 复杂调控机制的深入理解,有望通过对 *CDPKs* 基因的精准操作,定向培育出兼具高产耐逆韧性的作物新品种,为全球粮食安全和农业新质生产力贡献力量。

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