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·综 述·

植物 CDPK 在响应逆境胁迫中的作用及机制

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摘 要：钙依赖性蛋白激酶(calcium-dependent protein kinase, CDPK/CPK)是一类 Ca^{2+}敏感的 Ser/Thr 蛋白激酶，在植物生长发育和逆境胁迫响应中发挥重要作用。CDPK 能够迅速感知细胞内瞬时 Ca^{2+}信号的变化，识别并磷酸化特异性底物，从而将 Ca^{2+}信号向下游传递并级联放大，广泛参与干旱、盐碱和伤害应激等逆境胁迫，调控植物生长发育以及相关基因表达、离子通道和气孔运动等。CDPK 的自磷酸化会影响其酶活性以及底物的选择性。CDPK 具有与多种底物结合并磷酸化的能力，除了参与呼吸暴发氧化酶同源物(respiratory burst oxidase homolog, RBOH)、丝裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)、植物激素等信号通路，CDPK 还可以与 14-3-3 蛋白结合，调控植物应对逆境胁迫和促进生长发育。本研究综述了植物 CDPK 的发现、结构、分类及其在逆境胁迫响应中的作用等方面的研究成果，并对其未来研究方向进行展望，为农作物抗逆性遗传改良提供了基因资源和理论依据。

关键词：钙依赖性蛋白激酶；抗逆性；生长发育；气孔运动；信号转导

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Functions and mechanisms of CDPKs in plant responses to abiotic stress

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Abstract: Calcium-dependent protein kinases (CDPKs/CPKs) are members of the Ca^{2+}-sensitive Ser/Thr protein kinase family and play a crucial role in plant growth and development and responses to abiotic stress. CDPKs are capable of rapidly sensing changes in intracellular Ca^{2+} signals and recognizing and phosphorylating specific substrates, thereby transmitting and amplifying Ca^{2+} signal cascades downstream. They are involved in plant responses to stress conditions such as drought, saline-alkali stress, and injuries and regulate plant growth and development, gene expression, ion channel activity, and stomatal movement. The autophosphorylation of CDPKs can affect their activities and substrate specificity. CDPKs have the ability to bind to and phosphorylate multiple substrates. In addition to participating in respiratory burst oxidase homolog (RBOH), mitogen-activated protein kinase (MAPK), and plant hormone signaling pathways, CDPKs can also bind to 14-3-3 proteins, which enables the regulation of plant responses to stress and promotes plant growth and development. This paper summarized the research findings on the discovery, structure, classification, and roles of CDPKs in plant responses to stress and proposed the future research directions, aiming to provide the genetic resources and a theoretical basis for improving the stress tolerance of crops.

Keywords: calcium-dependent protein kinases; stress tolerance; growth and development; stomatal movement; signal transduction

在植物生长发育过程中，经常遭受到各种逆境胁迫影响，这些胁迫会显著抑制植物生长发育，造成作物减产[1]。植物遭受胁迫通常可分为两大类：生物胁迫和非生物胁迫。生物胁迫是指由寄生于植物的病毒、真菌、细菌和其他致病性病原体产生的胁迫；而非生物逆境胁迫则是指与水分有效性、温度和土壤成分等环境参数波动直接相关的不利条件，包括盐分、干旱和低温等胁迫[2-4]。植物对逆境胁迫的反应多样且复杂，涉及形态、生理、细胞和分子防御等多个层面。为了在胁迫下生存并适应逆境，植物必须找到合适的策略来应对反复出现的胁迫[5]。因此，在长期适应胁迫过程中，植物逐渐进化出一系列耐受和抵抗胁迫的响应调控机制。

植物适应胁迫的能力取决于其可塑性，包括激活一些复杂的细胞和分子反应，如激素平衡和基因表达变化[2]。钙离子(Ca^{2+})作为多功能的第二信使，在几乎所有的非生物胁迫反应中都发挥着关键作用[6]。Ca^{2+}不仅与非生物胁迫的感知密切相关，还在信号转导中扮演重要角色[7]。Ca^{2+}信号主要通过钙调蛋白(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)感知并将特异的信号传递到下游，从而激活植物对各种胁迫的生理响应[8]。

CDPK 是一类 Ca^{2+}信号感知的 Ser/Thr 蛋白激酶家族，仅存在于植物、原生生物、卵菌纲和绿藻中，而在动物和真菌中不存在[9]。CDPK 分布于细胞的各个区域，包括质膜、细胞质、细胞核、内质网、线粒体、叶绿体、脂小体、过氧化物酶体和高尔基体等，广泛参与植物生长发育[10]。CDPK 在碳/氮代谢、细胞骨架调节、气孔运动调节、生长调节以及对生物和非生物逆境胁迫响应过程中发挥多重作用[11]，因此在学术界受到广泛关注[12-13]。鉴于此，结合本课题组前期对嗜盐作物甜菜(*Beta vulgaris*) BvCDPK 家族的研究成果，本文系统总结了植物 CDPK 的发现、结构与分类、表达调控机制和生物学功能，重点对 CDPK 响应各种非生物逆境胁迫中的研究成果加以综述，并对其未来研究方向进行展望，以期为农作物抗逆性遗传改良提供优异基因资源和理论支持。

1 植物 CDPK 的发现

高等植物的第一个编码 CDPK 蛋白激酶基因 *PsCDPK* 是在豌豆(*Pisum sativum*)中发现的，之后在大豆(*Glycine max*)中分离纯化到该蛋白激酶[14]。随后研究人员相继在拟南芥(*Arabidopsis thaliana*)[15]、小麦(*Triticum aestivum*)[16]、玉米(*Zea mays*)[17]、番茄(*Solanum lycopersicum*)[18]等植物中克隆和鉴定到 *CDPK* 基因(表 1)。本课题组采用生物信息学手段，从甜菜(*Beta vulgaris*)基因组中鉴定出 16 个 CDPK 成员，根据在染色体上的位置将其命名为 *BvCDPK1*−*BvCDPK16* (未发表数据)。序列分析显示，BvCDPK 基因家族成员的编码区序列(coding domain sequence, CDS)长度在 1 539 bp (*BvCDPK1*)到 1 881 bp (*BvCDPK9*)之间不等，蛋白质长度在 512−626 aa 之间，平均约为 554 aa；理论分子量(molecular weight, MW)在 57.11 kDa (*BvCDPK1*)到 70.97 kDa (*BvCDPK9*)之间不等；等电点(isoelectric point, pI)在 5.25 (*BvCDPK6*)到 9.24 (*BvCDPK12*)之间；蛋白质疏水性(grand average of hydropathicity, GRAVY)在−0.696 (*BvCDPK13*)到−0.35 (*BvCDPK1*)之间，所有 *BvCDPK* 的 GRAVY 均为负值，表明它们均是亲水性蛋白(未发表数据)。另外，不同物种 CDPK 基因家族成员数量有所不同。棉花(*Gossypium hirsutum*) CDPK 基因家族成员数最多，为 98 个[26]；而天蓝苜蓿(*Medicago truncatula*)最少，仅有 10 个[31]。在拟南芥、草莓(*Fragaria*×*ananassa*)和油菜(*Brassica napus*)中分别有 34、11 和 25 个成员[9,15,19]。由此表明，不同物种 *CDPK* 数量存在明显差异。此外，高等植物 *CDPK* 基因可能在进化过程中经历了基因扩增和非功能化的过程[22]。基因复制导致功能分化并增强同源物的相互作用[26]，则有助于提高植物的抗逆性。例如，小白菜(*Brassica rapa*)基因组中 CDPK 家族大小几乎是无油樟(*Amborella trichopoda*)基因组中 CDPK 家族的 2 倍[36]。

2 植物 CDPK 的结构与分类

CDPK 是一类对 Ca^{2+}敏感的、最大的蛋白激酶家族，其通过直接利用 ATP 激活蛋白底物和 Ca^{2+}作为信号传递。典型的 CDPK 分子由具有 4 个功能区或结构域的多肽链组成(图 1A)，包括可变 N 端结构域(variable N-terminal domain, VNTD)、Ser/Thr 激酶催化结构域(Ser/Thr protein kinase domain, S/T KD)、自抑制结构域(auto-inhibitory junction domain, AJD)和含有 EF-hand 的类钙调素结构域(CaM-like regulatory domain, CaMLD)[11,22,30]。

表 1 不同植物 *CDPK* 基因

Table 1 The *CDPK* genes in different plant species

Species	Gene number	Gene name	Subgroup				Class	References
			I	II	III	IV		
Arabidopsis thaliana	34	*AtCPK1−AtCPK34*	10	13	8	3	Dicotyledon	[15]
Triticum aestivum	79	*TaCDPK1B−TaCDPK30D*	26	24	24	5	Monocotyledon	[16]
Zea mays	40	*ZmCDPK1−ZmCDPK40*	17	9	10	4	Monocotyledon	[17]
Solanum lycopersicum	29	*SlCDPK1−SlCDPK29*	13	8	6	2	Dicotyledon	[18]
Fragaria×ananassa	11	*FaCDPK1−FaCDPK11*	4	2	2	3	Dicotyledon	[19]
Ipomoea trifida	35	*ItfCDPK1−ItfCDPK35*	14	9	9	3	Dicotyledon	[20]
Ipomoea triloba	35	*ItbCDPK1−ItbCDPK35*	14	9	9	3	Dicotyledon	[20]
Brachypodium distachyon	30	*BdCDPK01−BdCDPK30*	11	8	8	3	Monocotyledon	[21]
Hevea Brasiliensis	30	*HbCPK1−HbCPK30*	11	8	9	2	Dicotyledon	[22]
Musa acuminate	44	*MaCDPK1−MaCDPK44*	14	11	13	6	Dicotyledon	[23]
Cicer arietinum	22	*CaCDPK1−CaCDPK22*	8	8	5	1	Dicotyledon	[24]
Setaria italic	29	*SiCDPK1−SiCDPK29*	13	6	8	2	Monocotyledon	[25]
Gossypium hirsutum	98	*GhCDPK1−GhCDPK98*	28	29	20	21	Dicotyledon	[26]
Trifolium repens	50	*TrCDPK01−TrCDPK50*	17	15	13	5	Dicotyledon	[11]
Medicago truncatula	24	*MtCDPK1−MtCDPK24*	9	9	5	1	Dicotyledon	[27]
Raphanus sativus	37	*RsCDPK1−RsCDPK37*	13	6	13	5	Dicotyledon	[28]
Solanum habrochaites	33	*ShCDPK1−ShCDPK33*	13	8	7	5	Dicotyledon	[29]
Gossypium barbadense	84	*GbCDPK1−GbCDPK84*	27	30	19	8	Dicotyledon	[30]
Medicago lupulina	10	*MlCDPK1−MlCDPK10*	4	2	3	1	Dicotyledon	[31]
Taraxacum koksaghyz	34	*TkCPK1−TkCPK34*	11	8	12	3	Dicotyledon	[32]
Lactuca sativa	34	*LsCPK1−LsCPK34*	12	7	11	4	Dicotyledon	[32]
Helianthus annuus	40	*HaCPK1−HaCPK40*	13	10	13	4	Dicotyledon	[32]
Chrysanthemum nankingense	34	*CnCPK1−CnCPK34*	14	6	9	5	Dicotyledon	[32]
Cynara cardunculus	30	*CcCPK1−CcCPK30*	10	7	8	5	Dicotyledon	[32]
Prunus persica	17	*PpCDPK1−PpCDPK17*	6	5	5	1	Dicotyledon	[33]
Ananas comosus	17	*AocCPK1−AocCPK17*	5	4	6	2	Monocotyledon	[34]
Chorchorus capsularis	18	*CcCDPK1−CcCDPK18*	8	5	4	1	Dicotyledon	[35]
Chorchorus olitorius	16	*CoCDPK1−CoCDPK16*	6	4	5	1	Dicotyledon	[35]
Beta vulgaris	16	*BvCDPK1−BvCDPK16*	5	5	5	1	Dicotyledon	Unpublished data

CDPK 可变 N 端结构域通常包含 20−200 个氨基酸残基，其中包括棕榈酰化位点和豆蔻酰化位点[20]。N 端结构域参与 CDPK 与细胞膜结合和底物特异性调控[37]。催化结构域是真核生物 Ser/Thr 蛋白激酶中高度保守的 11 个亚域之一，其中第 2 个亚域包含 1 个保守的 Lys 残基，可能是 ATP 的结合位点。自抑制结构域由最保守的 31 个富含碱性氨基酸组成，可以与催化区结合以抑制激酶活性[20]。在低浓度 Ca^{2+}下，自抑制域作为假底物，使得 CDPK 保持在失活状态(图 1B)。当 Ca^{2+}与类钙调素结构域的 EF-hand 结合时，自抑制假底物段从激酶催化位点释放，导致 CDPK 激活[37]。尽管大多数 CDPK 具有 4 个 EF-hand 结构，但也存在例外情况，不同 CDPK

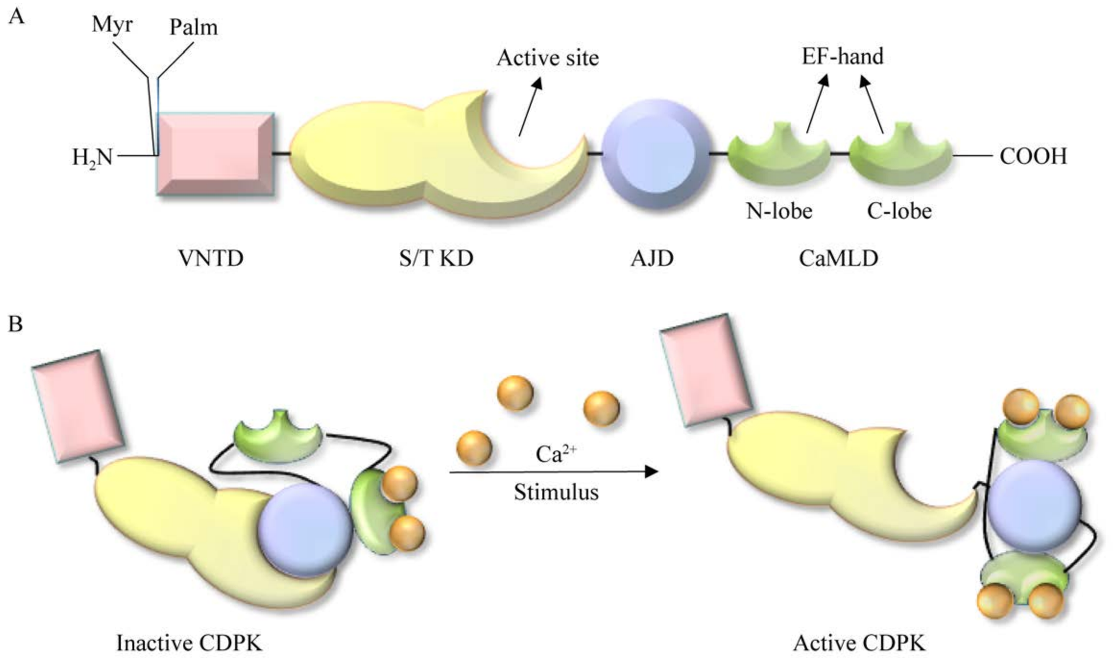

图 1 植物 CDPK 结构域(A)和激活机制(B)示意图[15] VNTD：可变 N 端结构域；S/T KD：Ser/Thr 激酶催化结构域；AJD：自抑制结构域；CaMLD：类钙调素结构域；Myr：豆蔻酰化位点；Palm 表示棕榈酰化位点

Figure 1 Diagram of CDPK structure domains (A) and activation mechanisms (B)[15]. VNTD: Variable N-terminal domain; S/T KD: Ser/Thr protein kinase domain; AJD: Auto-inhibitory junction domain; CaMLD: CaM-like regulatory domain; Myr: Myristoylation site; Palm: Palmitoylation site.

亚型中 EF-hand 的序列也不完全一致[22]，可能改变 Ca^{2+}结合，从而导致 CDPK 的 Ca^{2+}依赖性和酶活性不同[37]。西葫芦(*Cucurbita pepo*) CpCDPK25 只包含 2 个 EF-hand，而 CpCDPK19 和 CpCDPK27 则分别含有 9 个和 8 个 EF-hand，这可能是由于保守结构域的自我复制导致了基因结构变异，从而导致亚功能化或新功能化[38]。

Harmon 等[39]对拟南芥 34 个 *CDPKs* 进行序列相似性分析，并将其分为 I–IV这 4 个簇。尽管 *CDPK* 可以根据其在进化树上的位置进行分类，但没有显著的特征或序列差异可以区分这些簇[39]。为深入探究 CDPK 家族成员系统进化关系，本文采用 MEGA 11.0 软件对拟南芥、小麦、橡胶草(*Taraxacum koksaghyz*)和甜菜等 4 个物种的 162 个 *CDPK* 基因的氨基酸序列进行多重比对，并通过邻接算法(neighbor-joining，NJ)构建系统发育树(图 2)。结果表明，I 簇 *CDPK* 基因数最多，有 52 个，其次是II簇和III簇，分别有 51 个和 47 个，而IV簇 *CDPK* 基因数最少，只有 12 个(图 2)。在甜菜中，*BvCDPK1*、*BvCDPK6*、*BvCDPK9*、*BvCDPK10* 和 *BvCDPK14* 属于 I 簇，*BvCDPK4*、*BvCDPK5*、*BvCDPK7*、*BvCDPK13* 和 *BvCDPK16* 属于II簇，*BvCDPK2*、*BvCDPK3*、*BvCDPK8*、*BvCDPK11* 和 *BvCDPK15* 属于III簇，而 *BvCDPK12* 属于IV簇(图 2)。进一步研究发现，*BvCDPKs* 与菊科植物橡胶草 *TkCPKs* 进化关系最近，其次与十字花科植物拟南芥进化关系较近，而与禾本科作物小麦(单子叶植物)进化关系较远(图 2)。

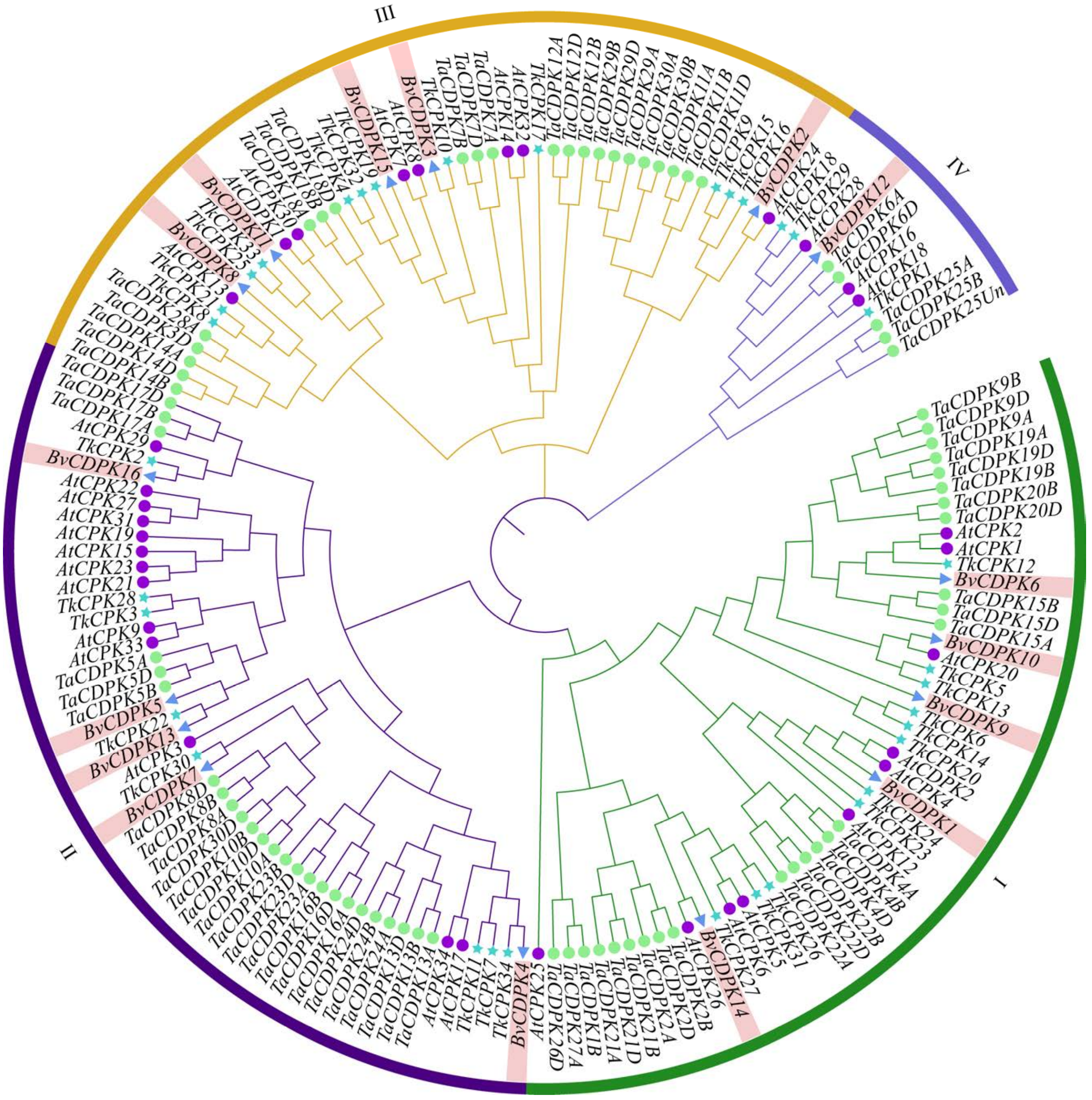

图 2　高等植物 CDPK 基因家族系统进化分析　采用 MEGA 11.0 软件进行序列多重比较和系统进化树的构建. 紫色圆形表示拟南芥，绿色圆形表示小麦，蓝色三角形表示甜菜，青色五角星表示橡胶草. CDPK 基因来源、名称和登录号已提交至国家微生物科学数据中心(登录号：NMDCX0001709)

Figure 2　Evolutionary analysis of CDPK gene family in higher plants. MEGA 11.0 software was used for sequence multiple comparisons and phylogenetic tree construction. Purple circles represent *A. thaliana*, green circles represent *T. aestivum*, blue triangles represent *B. vulgaris* and cyan stars represent *T. koksaghyz*. The source, name and accession number of *CDPKs* are shown in National Data Center for Microbiological Science (accession number: NMDCX0001709).

3 植物 CDPK 的调控机制

3.1 CDPK 自磷酸化

CDPK 具有下游信号传导能力并具有 Ca^{2+}传感器的特征[14]。CDPK 能够直接与 Ca^{2+}结合，通过底物特异性磷酸化来激活某些靶蛋白。磷酸化状态可调控多功能激酶对特定 Ca^{2+}信号的响应。CDPK 自磷酸化已被证明可以激活或抑制其激酶活性。大豆 GmCDPKb 的 Tyr_{24}位点体外自磷酸化会减弱酶的活性，而其他位点的 Ser 和 Thr 残基的磷酸化则会增强酶的活性[40]。自磷酸化还可能与 CDPKs 的 Ca^{2+}敏感性有关。如拟南芥 AtCPK28 在体外过度磷酸化时，其激活酶活性对较低的 Ca^{2+}敏感[41]。另外，烟草(*Nicotiana tabacum*) NtCDPK1 在 Ser_6 和 Thr_{21} 位点的 Ca^{2+}依赖性自磷酸化会降低其与地上部生长抑制因子(repression of shoot growth, RSG)的结合亲和力以及 RSG 的磷酸化效率，但在体外会增强一般底物髓磷脂碱性蛋白的磷酸化水平，表明位点特异性磷酸化也可决定底物的选择性[42]。此外，蓖麻(*Ricinus communis*) RcCDPK1 的 Tyr_{30}位点自磷酸化促进 VNTD 和 Ca^{2+}激活结构域之间的 Ca^{2+}依赖性互作，从而使得 RcCDPK1 在 Ser_{451}位点磷酸化细菌型磷酸烯醇丙酮酸羧化酶(bacterial-type phosphoenolpyruvate carboxylase , BTPC)[43]。这些结果表明，CDPK 自磷酸化不仅与细胞内的 Ca^{2+}敏感性有关，而且还与底物特异性有关。

3.2 CDPK 参与各种信号级联反应

CDPK 具有与多种底物结合并磷酸化的能力，这很可能涉及复杂的调控机制，从而决定 CDPK 激活和底物选择。CDPK 不仅与呼吸暴发氧化酶同源物(respiratory burst oxidase homolog, RBOH)、丝裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)和植物激素等信号通路相关，而且与 14-3-3 蛋白相结合。在油菜中，CDPK 与 RBOH 互作，过表达 *BnaCPK2* 后其与呼吸暴发氧化酶同源物 D (respiratory burst oxidase homolog D, RBOHD)相互作用，引发了活性氧(reactive oxygen species, ROS)积累和细胞死亡；BnaCPK6L 也与 RBOHD 互作和磷酸化，在 ROS 的过度积累和类超敏反应(hypersensitivity-like, HR)的细胞死亡中发挥重要作用[44-45]。此外，WRKY 转录因子 WSR1 与 CPK5/6/11 互作并被磷酸化，WSR1 促进水杨酸(salicylic acid, SA)和 ROS 的产生，导致叶片衰老[46]。CDPK 和 MAPK 两种信号通路间也可能存在交互作用，当植物受到刺激后，通常会同时激活 CDPK 和 MAPK。1-氨基环丙烷-1-羧酸合酶(1-aminocyclopropane-1-carboxylate synthase, ACS)可能会同时受到 CDPKs 和 MAPKs 的动态调控[47]。基因瞬时表达分析显示，在玉米原生质体中 CPK11 调控 *MPK5* 表达，从而激活防御功能和抗氧化酶活性[48-49]。这些结果表明，CDPK 通过参与多种信号通路发挥重要作用。大多数 *CDPK* 受到各种植物激素的诱导，山葡萄(*Vitis amurensis*) *VaCPK16* 和 *VaCPK32* 调控二苯乙烯(一种酚类次生代谢物)的生物合成[50]。此外，CDPK 也参与脱落酸(abscisic acid, ABA)信号转导(图 3)，ABA 可以促进 CDPK 的转录和翻译，而 CDPK 可磷酸化 ABF 调节 ABA 信号转导[51-53]。拟南芥 CPK6 通过磷酸化 ABA 应答元件结合因子(ABA responsive element binding factors, ABF)和 ABA 不敏感 5 (ABA insensitive 5, ABI5)来正向调控种子萌发、幼苗生长和抗旱性[54]。梅花(*Prunus mume*) PmCDPK8/11 和游龙梅(*P. mume* var.) PmvCDPK9/13 也与 ABI5 相互作用[55]。此外，油菜 BnaCPK6 与 BnaABF3/4、BnaABI5 以及 BnaAREB3 之间存在相互作用[56]。这些结果表明，CDPK 在核心 ABA 信号通路中调节应激反应基因的表达。

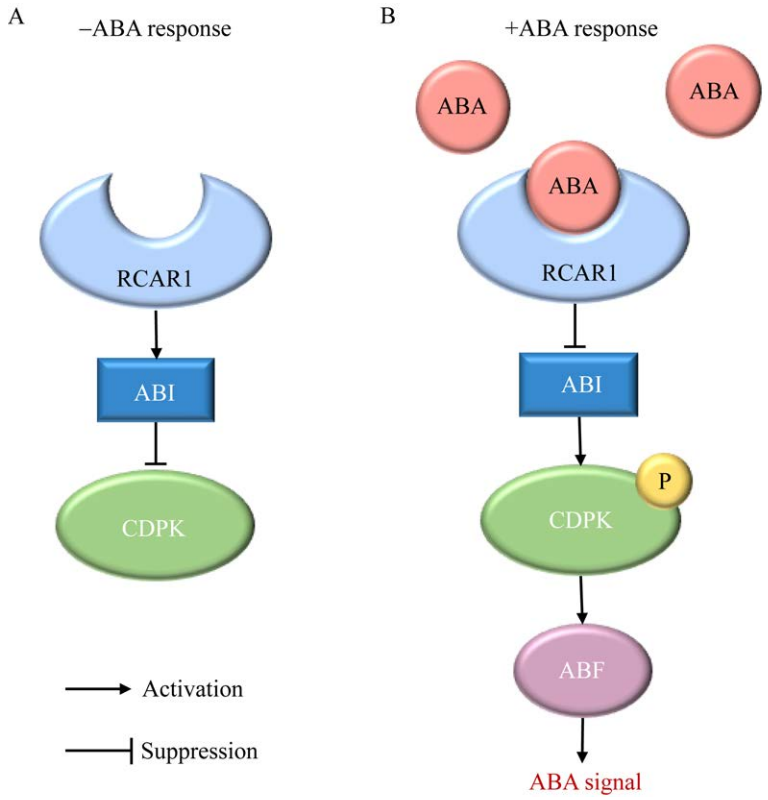

图 3　CDPK 在核心 ABA 信号通路中调节机制　A：在缺乏 ABA 的情况下，蛋白磷酸酶 ABI 抑制 CDPK 的自磷酸化，使其失去活性. B：当 ABA 受体 RCAR/PYR/PYL(标记为 RCAR1)感知 ABA 时，ABI 被细胞质 ABA 受体结合并失活，从而减轻对 CDPK 的抑制

Figure 3　Regulatory mechanisms of CDPK in the core ABA signaling pathway. A: In the absence of ABA, the protein phosphatase ABI inhibits the autophosphorylation of CDPK, rendering it inactive. B: When the RCAR/PYR/PYL ABA receptor (denoted as RCAR1) senses ABA, ABI is bound by the cytoplasmic ABA receptors and inactivated, thereby reducing inhibition on CDPK.

CDPK 还与开花因子、金属离子和硝酸盐等信号通路相互作用。例如，CDPK 可以磷酸化开花位点(flower locus T, FT)与碱基区/亮氨酸拉链(basic leucine-zipper, bZIP)转录因子 FD 相互作用，从而诱导植物延迟开花[57]。在拟南芥根系中，过量锰(Mn)可诱导 Ca^{2+} 信号被 CPK4/5/6/11 解码，这些激酶可磷酸化并激活 Mn 转运蛋白 MTP8，从而促进 Mn 的解毒[58]。然而，Mn 亏缺触发根系伸长区 Ca^{2+}信号，激活 CPK21/23 激酶，促进 Mn 转运蛋白 NRAMP1 在 Thr_{498} 位点磷酸化，$NRAMP1^{Thr}$ 磷酸化进一步增加其转运活性，从而增强植物对 Mn 吸收能力和对 Mn 亏缺的耐受性[59]。硝酸盐-CDPK 信号可磷酸化保守的 NIN 样蛋白(nin-like protein, NLP)，从而影响下游转运蛋白、氮同化和碳氮代谢等过程。CPK10/30/32 通过调节初级硝酸盐信号网络，促进植物地上部生长和根系的建成[60]。梨(*Pyrus bretschneideri*) PbrSLAH3 被 CDPK 磷酸化来控制其活性，PbrSLAH3 与 PbrCPK32 的交联可能参与根系 NO_3^-的转运[61]。在灰绿藜(*Chenopodium glaucum*)中，干旱或盐胁迫下，过表达 *CgCDPK* 可诱导转基因烟草植

株与 *CgbHLH001* 同源的 *NtbHLH* 的表达，表明 *CgCDPK* 与 *CgbHLH001* 之间存在相关性[62]。在拟南芥中，AtCPK28 可与 E3 泛素连接酶 AtPUB25 和 AtPUB26 结合并磷酸化保守氨基酸残基 Thr_{95} 和 Thr_{94}，从而增强对 AtBIK1 的多泛素化[63]。这些结果表明，CDPK 在不同信号通路中起重要作用，并调节植物的生长发育。

14-3-3 蛋白存在于所有真核生物中，与磷蛋白相互作用可以调节蛋白质功能并影响多种细胞过程[64]。CDPK 与 14-3-3 蛋白相互作用，调节植物生长发育。拟南芥 AtCDPK 可以磷酸化谷氨酸受体样蛋白 3.7 (glutamate receptor-like 3.7, GLR3.7)的 Ser_{860} 位点，该蛋白与 14-3-3ω 相互作用，并通过调节 Ca^{2+}信号在盐和 ABA 反应中发挥重要作用；GLR3.6 的 $Ser_{861/862}$ 与 14-3-3ω 相互作用，且 CDPK16 特异性磷酸化 GLR3.6 的 Ser_{856}位点[13]。这些结果表明，CDPK广泛参与植物的各种信号通路，对植物应对不利环境和促进生长发育至关重要。

4 植物 CDPK 的生物学功能

CDPK 在植物中广泛分布，在根、茎、叶、花等不同组织中均有表达。CDPK 蛋白参与植物体内多种信号转导及生理代谢调控。

4.1 CDPK 调节植物气孔运动

气孔是植物与大气之间气体交换的门户，存在于叶片和其他器官的表面，由两个保卫细胞组成[65]。气孔可以调节气体交换，平衡 CO_2 吸收和水分损失，并维持植物的水分状态和叶片蒸腾作用[66]。植物面对干旱胁迫时，关闭气孔以防止水分流失。在拟南芥中，S 型阴离子通道 AtSLAC1 对此起着关键作用[67]。如图 4 所示，SLAC1 和 SLAC3 调节保卫细胞中阴离子平衡；液泡膜双孔钾离子通道(two-pore K^+ channel, TPK)对维持体内 K^+稳态至关重要[68]；Ca^{2+}/H^+逆向转运蛋白可以防止 Ca^{2+}在胞质中过度积累[69]。此外，SA 和 ABA 都可诱导气孔关闭。研究表明，CDPK 依赖的 Ca^{2+}信号识别可能是保卫细胞中 SA 信号和 ABA 信号整合的关键机制[67,70]。在干旱胁迫下，玉米 ZmSLAC1 对于气孔关闭起着至关重要的作用，其活性受到 ZmCPK35 和 ZmCPK37 的调控，从而通过促进 ABA 和 Ca^{2+}的诱导来实现气孔关闭[67]。ABA 不仅通过调节离子通量对气孔关闭产生快速影响，还通过调控基因表达对植物发育产生长期影响，增强植物对干旱的适应能力[71-72]。另外，干旱胁迫激活 CaCDPKs 可能通过磷酸化和调控保卫细胞离子通道，以 ABA 依赖方式调节气孔运动，从而降低鹰嘴豆(*Cicer arietinum*)的蒸腾速率和水分损失[24]。在拟南芥中，34 个 *AtCDPK* 基因中大约有 20 个在保卫细胞中有不同水平的表达，这意味着它们可能在气孔运动过程中具有协调一致的功能[15]。例如，AtCPK3 对于 CO_2控制的气孔开启和关闭是必不可少的[73]。AtCPK9 在气孔 ABA 信号传导中具有负向调控作用[74]。此外，AtCPK33 还调节保卫细胞外向型整流钾通道 GORK 的活性[75]。同时，AtCPK33 激酶活性对于独角金内脂(strigolactones, SLs)诱导的气孔关闭也至关重要，然而 SLs 是否能刺激 AtCPK33 激活 GORK 活性还有待研究[76]。这些结果表明，CDPK 以 ABA 依赖的方式来调控气孔运动，提高作物水分利用效率，限制水分蒸发损失，以适应各种逆境胁迫。

4.2 CDPK 调节植物生长发育

CDPK 在植物中广泛存在，并且它们的功能与其组织特异性表达相关。小麦 *TaCDPK* 上游启动子序列中，发现大量与光、植物激素和非生物胁迫响应相关的顺式作用元件，表明 *TaCDPK* 表达在不同组织和生长阶段有所差异[77]。类似地，在苜蓿(*Medicago lupulina*)[31]、二穗短柄

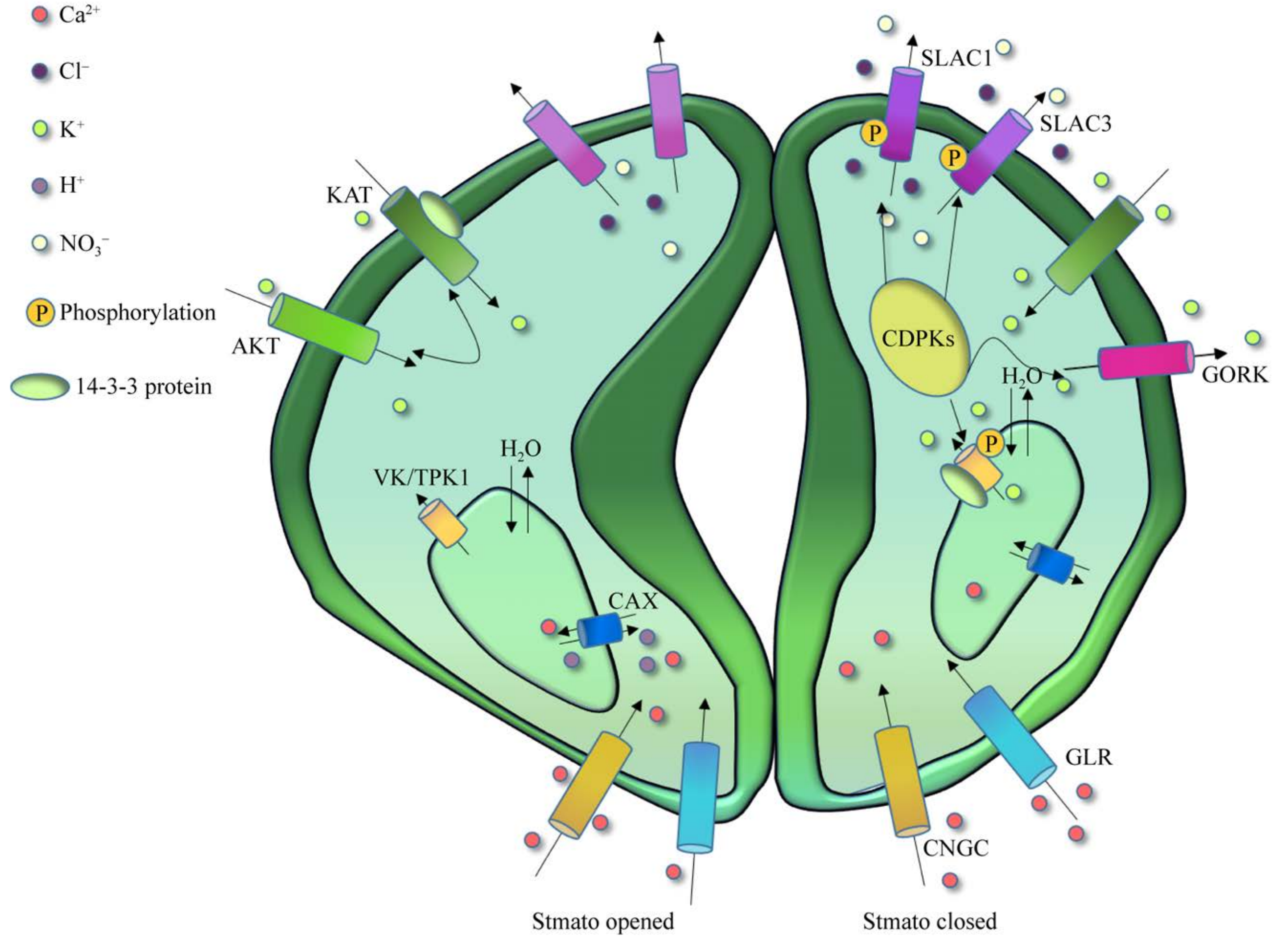

图 4　CDPK 在气孔运动中的调控作用　图中内向整流 K$^+$通道有 KAT 和 AKT；外向整流 K$^+$通道有 GORK；环核苷酸门控通道(cyclic nucleotide gated channel, CNGC)和谷氨酸受体样家族(glutamate receptor-like, GLR)可以参与 Ca^{2+}的转运

Figure 4　Regulatory role of CDPK in stomatal movement. The K$^+$ uptake channels include KAT and AKT. GORK is a K$^+$ efflux channel. The cyclic nucleotide gated channel (CNGC) and the glutamate receptor-like (GLR) family participate in Ca^{2+} transport.

草(*Brachypodium distachyon*)[21]和西瓜(*Citrullus lanatus*)[38]中，CDPK 家族成员也参与调节不同组织或器官(如花、叶片、根和茎等)的生长发育。另外，*CDPK* 也在花粉及花药中表达。拟南芥 *AtCPK17* 和 *AtCPK34* 在花粉管极性生长中起重要作用，它们通过调节水通道蛋白来维持花粉管伸长所需的膨压[78]，且在花粉管生长速度和花粉传递效率中起调控作用。AtCPK16 在体外可磷酸化自抑制 Ca^{2+}-ATPase ACA8 的多个位点，其敲除突变体的花粉萌发率低[79-80]。*cpk2/6/20* 三突变体表现出花粉管生长减缓的表型[81]。此外，*CPK11* 和 *CPK24* 也在花粉管中表达，并共同调节 Ca^{2+}依赖性抑制花粉管向内整流 K$^+$通道 SPIK/AKT6 的活性[82]。另外，水稻(*Oryza sativa*) *OsCPK29* 与花粉发育也有关[83]，而小麦 *TaCDPK13* 在花药中的表达量在花期达到最大[84]。

这些结果表明，*CDPK* 在植物生长发育过程中发挥着重要作用。

研究表明，CDPK 也参与植物的形态建成。马铃薯(*Solanum tuberosum*) StCDPK1 参与块茎的转变和发芽，影响茎和根的维管系统[85]。长蒴黄麻(*Chorchorus olitorius*) *CoCDPK6*/*7*/*11*/*12* 及其同源基因黄麻(*C. capsularis*) *CcCDPK18*/*17*/*10*/*8* 在纤维细胞中高表达，可能参与纤维细胞的发育[35]。水稻 *OsCPK12* 主要在幼嫩器官中表达，其突变体会导致叶片过早衰老，并参与氮代谢，过表达该基因可能会对水稻的产量产生积极影响[86-87]。此外，过表达 *CPK30* 可损害根系生长素外排蛋白 PIN 的极性，导致根系向地性丧失和根尖异位生长素积累[88]。CDPK 还参与调节植物营养摄取和平衡过程。CPK10/30/32 通过磷酸化调控转录因子 NLP7 的活性[60]，而 NLP7 则控制 NO_3^-/NH_4^+平衡[89]。CDPK 还参与重金属的摄取。CPK31 调节有毒亚砷酸盐(As^{3+})的吸收[76]。在水稻中，CDPK 家族的几个成员在镉(Cd^{2+})胁迫下表现出磷酸化增加[90]。由此可见，CDPK 在调控植物形态建成、营养和生殖生长等过程具有重要作用。

5 植物 CDPK 在响应逆境胁迫中的作用

5.1 CDPK 与植物耐盐性

盐胁迫对植物的生长和发育产生严重影响，包括抑制光合作用、扰乱离子稳态和膜脂过氧化，威胁着农业生产和粮食安全[91]。CDPK 在植物应答盐胁迫中起重要作用(图 5)。在拟南芥中，AtCPK3 和 AtCPK6 正向调控盐胁迫响应，增强植物耐盐性；而 AtCPK21 和 AtCPK23 则负向调控盐胁迫[15]。在银杏(*Ginkgo biloba*)中，盐胁迫下 GbCDPK/CIPK 基因家族的 5 个成员参与离子渗透潜在信号的转导[92]。鹰嘴豆 CaCDPK 可能调控盐胁迫下植物根系 Na^+的转运、区隔化以及维持细胞内 Na^+/K^+稳态[24]。本课题组对嗜盐作物甜菜 *BvCDPK* 在响应盐胁迫中的作用进行了深入研究，采用 qRT-PCR 技术对不同浓度盐处理后的甜菜 *BvCDPK* 表达模式分析发现，甜菜叶和根中的 *BvCDPK* 表达均受盐胁迫的调控，表明 BvCDPK 在盐胁迫应答中具有潜在作用(未发表数据)。此外，CDPK 还参与芒果(*Mangifera indica*)盐胁迫反应，但其耐盐机理研究较少[93]。在玉米中，ZmCPK11 通过调控叶中 Na^+/K^+稳态，防止盐诱导的叶绿素降解和光系统 II 损伤，从而提高植物的耐盐性；此外，ZmCPK11 还在 ABA 诱导的 ROS 产生及其清除系统中发挥作用[48]。油菜 CDPK 通过调节 NO、酶和非酶抗氧化剂含量，以及调控次生代谢产物，有效提高植物耐盐性[94]。在盐胁迫下，甘草(*Glycyrrhiza uralensis*) GuCPKs 在根系特异性表达，可能与草酸和黄酮类化合物合成相关[95]。这些结果表明，CDPK 在植物响应盐胁迫中发挥重要作用。

5.2 CDPK 与植物抗旱性

干旱胁迫限制植物生长发育，为了应对这种胁迫，植物在形态、代谢和分子等方面进化出多样化适应机制[96]。CDPK 在植物响应干旱胁迫中扮演重要角色(图 5)。在干旱条件下，胞质 Ca^{2+}浓度变化会激活 CDPK，并促进 ABA 释放[97]。ABA 在调节干旱应答中起重要作用[98]。CDPKs 磷酸化 ABA 相关的转录因子 ABFs/AREB，增强其转录活性，提高植物抗旱性[99]。油菜 BnaCPK5 通过磷酸化 BnaABF3 和 BnaABF4 来调节脱水诱导(responsive to dehydration, RD)基因 *RD29B* 表达，从而正向调节植物抗旱性[100]。在小麦中，干旱胁迫会显著提高 TaCPK34 蛋白丰度，*TaCPK34* 可直接或间接调节 ABA 依赖型基因表

图 5 CDPK 调控植物逆境胁迫响应机制 黑色实线箭头表示 CDPK 调控植物胁迫响应途径；P 表示磷酸化；CDPK 可自磷酸化，还可磷酸化 WRKY 转录因子、RBOH 和 14-3-3 蛋白；另外，CDPK 与 14-3-3 蛋白可互相调节

Figure 5 Regulatory mechanisms of CDPK in plant response to adversity stress. The solid black arrows indicate that CDPK regulating plant stress response pathway. P represents phosphorylation. CDPK can undergo autophosphorylation and also phosphorylate WRKY transcription factors, RBOH, and 14-3-3 proteins. Additionally, CDPK and 14-3-3 proteins can regulate each other.

达，从而响应干旱胁迫[101]。此外，TaCDPK13 与 TaNOX7 互作并激活其产生 ROS，调节植物对干旱胁迫的耐受性[84]。毛竹(*Phyllostachys edulis*) *PheCPK1* 是一个负调控因子，参与干旱胁迫的应答，该基因不仅激活胁迫相关基因表达，还显著降低 ROS 清除能力[102]。过表达 *GmCDPK3* 显著增强转基因大豆对干旱胁迫的耐受性[103]。水稻 OsCPK4/10/13 也参与干旱胁迫应答，OsCDPK1 赋予水稻幼苗耐旱性[104]。这些结果表明，CDPK 通过调节抗氧化能力和渗透稳态来增强植物的抗旱性。

5.3 CDPK 与极端温度耐受性

极端温度(高温和低温)会导致植物代谢失调并抑制其生长[105]。研究发现，CDPK 参与调控植物对极端温度的耐受性(表 2)。在香蕉(*Musa acuminate*)中，低温处理后 *MaCDPKs* 被诱导[23]。

表 2　CDPK 在植物响应逆境胁迫中的作用
Table 2　The role of CDPK in plant response to adversity stress

Specie name	*CDPK*	Function	Reference
Arabidopsis thaliana	*AtCPK3*	Positive regulation of salt stress; CPK3-TPK1 pathway	[15]
	AtCPK6	Positive regulation of salt stress; phosphorylation of ABF and ABI5 can positively regulate seed germination, seedling growth and drought resistance	[15,54]
	AtCPK8	Interact and phosphorylate CAT3, mediate ABA-dependent stomatal movement, regulate H_2O_2 homeostasis and improve drought resistance	[96-97]
	AtCPK10	Interact with HSP1 to regulate heat stress	[15]
	AtCPK21/23	Negative regulation of salt stress	[15]
	AtCPK27	Positive regulation of salt stress; regulating H_2O_2 and ion homeostasis	[91]
Oryza sativa	*OsCDPK1*	Negative regulation of GA biosynthesis, expression and activation of 14-3-3 protein; participated in rice drought resistance	[104]
	OsCPK12/13/21	Salt resistance	[104]
	OsCPK21	Salt resistance; exogenous ABA was added	[106]
Phyllostachys edulis	*PheCPK1*	The scavenging ability of ROS was reduced; negative regulation of drought stress	[106]
Solanum tuberosum	*StCDPK5*	Participated in the outbreak of ROS mediated by StRBOHB	[107]
Brassica napus	*BnaCPK2*	Interaction with RbohD triggered ROS accumulation and cell death	[44]
	BnaCPK6L	Interaction with RbohD plays an important role in the cell death of ROS and hypersensitivity-like (HR)	[45]
	BnaCPK5/6/11	Interact with BnaWSR1 and phosphorylate, promote the production of SA and ROS, and eventually lead to leaf senescence	[46]
Zea mays	*ZmCPK4*	Regulating drought resistance of maize through stomata regulated by ABA	[108]
	ZmCPK11	Activate defense function and antioxidant enzyme activity by regulating the expression of *MPK5* gene; regulating the steady state of sodium and potassium in leaves to improve the salt tolerance of maize	[48-49]
	ZmCPK35/37	Regulating ZmSLAC1 protein to improve drought resistance	[67]
Nicotiana tabacum	*NtCDPK1*	Negative regulation of transcription factor RSG, involved in the feedback regulation of gibberellin; interacting with 14-3-3 protein	[109]
Vitis amurensis	*VaCPK16/32*	Synthesis of positively regulated stilbene	[109]
	VaCPK20	Increase the expression of stress response genes such as COR47, NHX1, KIN1 or ABF3, to improve their cold resistance; increase the content of resveratrol in grapes to improve the resistance of grapes to biological stress	[110-112]
	VaCPK30	Participate in cold and drought tolerance	[50]
Solanum lycopersicum	*LeCPK2*	The production of ethylene is regulated by phosphorylating LeACS2, thus the immune signal is regulated	[113]
	SlCDPK23	Participated in ABA-responsive drought resistance	[18]
Triticum aestivum	*TaCDPK2/4/13*	Directly or indirectly regulate ABA-dependent gene expression and improve drought resistance	[101]
	TaCPK34	Interact with TaNOX7 to produce ROS, which improves drought resistance	[84]

类似地，梅花[114]、西瓜和甜瓜(*Cucumis melon*)[38]等植物的 *CDPK* 基因也受到低温诱导。在多毛番茄(*S. habrochaites*) CDPK 基因家族中，*ShCDPK6* 和 *ShCDPK26* 受冷胁迫影响最大，其次是 *ShCDPK19*，表明 *CDPK* 不同成员可能在冷胁迫下发挥不同作用[29]。苹果(*Malus domestica*) *MdCPK1a* 过表达可通过降低转基因烟草 *NtRbohD* 表达水平，增加超氧化物歧化酶(superoxide dismutase) *NtSOD*、谷胱甘肽过氧化物酶(glutathione peroxidase) *NtGPX* 和过氧化氢酶(catalase) *NtCAT* 等基因表达，从而增强转基因植株对冷胁迫的耐受性[115]。在二穗短柄草中，BdCDPKs 参与极端温度胁迫的响应[21]。茶树(*Camellia sinensis*) CsCDPK20 和 CsCDPK26 在热胁迫中发挥积极调节作用[116]。拟南芥 AtCDPK 参与调控热胁迫，而番茄 *SlCDPK21* 被热处理显著诱导[15,18]。此外，川党参(*Codonopsis tangshen*) *CtCDPKs* 在热应激后表达上调[117]。这些结果表明，CDPK 作为极端温度胁迫响应信号通路的调节因子，具有用于作物抗寒性和耐热性遗传改良潜力。

5.4 CDPK 与植物抗病性

植物通过精准的免疫系统感知和防御病原体并适应病原微生物环境。钙信号是免疫信号转导中的重要部分[8,118]。钙信号能够激活 CDPK，反过来，CDPK 又与其他信号互作，调节植物的防御体系，抵抗微生物免受伤害。OsCPK4 在水稻先天免疫中起负调控作用，其通过促进细胞质受体类激酶(receptor-like cytoplasmic kinases) OsRLCK176 降解，以及调节 OsRLCK176 磷酸化状态来调控植物免疫[119]。野草莓(*Fragaria vesca*) *FvCDPKs* 在致病性病原菌感染后表达上调[120]，而菠萝(*Ananas comosus*) AcoCPK1/3/6 负向调控菠萝对病原菌的抗性[34]。此外，AtCPK1 通过增加白藜芦醇生物合成而促进植物生长[121]。应激条件下 AtCPK1 可通过调节初级代谢感知系统获得抗性信号系统[122]。AtCPK3 在病毒侵染后表现出持续增加，而在其他处理(如干旱、盐分)下则表现出明显降低或无显著变化，因此该蛋白可作为检测植物病毒感染的有效手段[123]。这些结果表明，CDPK 在植物免疫中发挥重要作用，参与调节免疫信号传递和抵御病原体的侵袭。

CDPK 可以与 MAPK 级联协同或独立地调节病原体相关分子模式触发的免疫信号，或通过磷酸化 WRKY 转录因子来调节免疫基因的表达。CDPK 还可通过磷酸化 RBOHs 来调节 ROS 产生，并通过磷酸化不同的底物来调节效应物触发的免疫信号[21,114]。辣椒(*Capsicum annuum*) CaWRKY40 可促进对青枯菌感染(*Ralstonia solanacearum infection*, RSI)和高温高湿(high-temperature and high-humidity, HTHH)应激免疫反应，而 CaCDPK29 则通过磷酸化 CaWRKY27b 来调控 CaWRKY40，从而促进 CaWRKY40 正向调节辣椒 RSI 免疫反应和耐热性[124]。Flagellin 22 (flg22)是细菌鞭毛蛋白中的一个保守小肽，其诱导的免疫是研究植物与微生物相互作用的最经常使用的模式系统之一[125]。在 flg22 或木聚糖酶处理后，拟南芥 I 和 III 簇 CDPKs 被鉴定为免疫诱导的磷酸化蛋白[126]。研究表明，IV簇 CDPKs 磷酸化一系列底物，包括 RLCKs、PUB E3 连接酶和 MAPKs，维持免疫系统稳态[127]。最近研究还发现，CDPK 参与病原体诱导的 AtSR1 磷酸化反应。CDPK 和 MAPKs 级联通过改变 AtSR1 稳定性、磷酸化状态和植物防御过程中的亚细胞定位来调节 AtSR1 功能[128]。另外，ROS 的产生与植物细胞内 Ca^{2+}直接相关[129-130]。Ca^{2+}-ROS 信号的明显重叠和 Ca^{2+}-MAPK 级联之间的交互也与生物入侵有关[129]。利用宿主选择性毒素和非宿主选择

性毒素对茄链格孢(*Alternaria solani*)进行结合实验，发现 CDPK1 和 CDPK2 与它们结合并抑制 NADPH 氧化酶依赖性 ROS 的产生[131]。在拟南芥中，AtCPK28 通过促进免疫信号激酶 BIK1 降解来促进免疫系统稳定，并在从营养到生殖过程中发挥作用[132]。这些结果表明，植物通过钙信号和 CDPK 调节来感知和应对病原体的攻击，从而增强植物免疫能力和抗病性。

6 展望

CDPK 是参与多种应激反应的主要信号分子，识别 Ca^{2+}信号后通过对的磷酸化来调节信号途径，在调控植物生长发育和应对各种逆境胁迫中具有重要作用。目前研究主要集中于 CDPK 在植物抗逆性的作用以及对离子通道和其他蛋白激酶的调控等方面。然而，单个 CDPK 可能参与多种胁迫响应，而单一胁迫响应可能会受到多个CDPK调控。此外，有关CDPK与ABA、MAPK、WRKY、RBOH 和 SnRK 等信号级联及其互作组分的研究还相对较少。因此，该领域未来的研究重点在于阐明 CDPK 的生理功能和调控机制。研究可从以下几方面着手：(1) 采用过量表达、基因组编辑、RNA 干扰等技术手段，探究嗜盐作物或盐生植物 CDPK 调控非生物胁迫响应的作用机制。(2) 探索 CDPK 相互作用调节因子，深入研究 *CDPK* 对内源底物如 14-3-3 蛋白、NADPH 和 NOX 等的交叉磷酸化调节机制，以及对下游靶基因的影响。(3) 探究 *CDPK* 的下游事件及其与 ABA、MAPK、WRKY、RBOH 和 SnRK 等信号级联的关系，解析 *CDPK* 的信号网络。

随着生物技术的发展，CDPK 调控植物响应逆境胁迫的作用机制及其信号通路将被揭示，有望为农作物抗逆性和品质遗传改良提供优异基因资源，其在生物育种以及提高作物产量和品质等方面有着广阔的应用前景。

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