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·专题论坛·

植物环核苷酸门控离子通道研究进展

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摘要 环核苷酸门控通道(cyclic nucleotide-gated channels, CNGCs)是植物体内重要的阳离子通道, 在调控植物生长发育以及应对冷、热、盐和病原菌等胁迫中发挥重要作用。该文简要概述了植物CNGCs的分类、结构及表达定位, 并重点对其离子选择特征、调控机制以及生物学功能的最新研究进展进行综述, 以期增进对植物CNGCs蛋白的全面认识, 并为后续深入研究提供参考。

关键词 抗逆性, CNGCs, 离子选择性, 胁迫响应

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离子通道是植物体内介导离子沿电化学势梯度跨膜运输的孔道, 直接影响和调控细胞内离子的稳态平衡, 进而在渗透调节、信号转导及养分吸收和长距离运输中发挥关键作用(Pantoja, 2021)。近年来, 多种植物离子通道被鉴定和表征。环核苷酸门控通道(cyclic nucleotide-gated channels, CNGCs)是一种广泛存在于动植物中的阳离子通道, 介导K^+、Na^+和Ca^{2+}等一价和二价阳离子的转运(Duszyn et al., 2019; Jarratt-Barnham et al., 2021)。CNGCs在动物中的研究较为深入, 在植物中的研究则起步较晚。Schuurink等(1998)在筛选大麦(*Hordeum vulgare*)钙调素结合转运蛋白(CaM-binding transporter, HvCBT1)的过程中首次克隆到植物*CNGC*, 随后在拟南芥(*Arabidopsis thaliana*)、水稻(*Oryza sativa*)、小麦(*Triticum aestivum*)和棉花(*Gossypium hirsutum*)等植物中相继鉴定到其同源基因(Köhler and Neuhaus, 2000; Nawaz et al., 2014; Guo et al., 2018; Lu et al., 2022b)。其中, 模式植物拟南芥CNGCs的研究相对较为系统全面。AtCNGCs家族由20个同源蛋白组成(Mäser et al., 2001), 目前大部分蛋白的离子选择性已在细胞水平上被阐明。随着研究的不断深入, CNGCs在植物生长发育调控、生物及非生物胁迫响应中的重要作用已引起学术界的广泛关注。本文就植物CNGCs的分类、结构、表达定位、离子转运特征、调控机制以及生物学功能进行综述, 旨在为植物CNGCs的深入研究奠定基础。

1 植物CNGCs的分类与结构

根据氨基酸序列构建的系统进化树, 可将AtCNGCs分为4个亚家族(I、II、III和IV)。其中, 第I、II、III亚家族之间的亲缘关系较近; 第IV亚家族与其它亚家族的关系则相对较远, 并包括IVa和IVb两个亚组(Talke et al., 2003)。研究发现, 小麦、水稻、大豆(*Glycine max*)、白菜(*Brassica rapa*)、马铃薯(*Solanum tuberosum*)以及4个棉属植物CNGCs家族的系统发育关系均符合上述分类(Nawaz et al., 2014; Guo et al., 2018; Baloch et al., 2021; Lu et al., 2022b; Cui et al., 2023; 郝宇瑞等, 2023)。本课题组对荒漠植物霸王(*Zygophyllum xanthoxylum*)进行全基因组测序, 鉴定到24个ZxCNGCs成员, 同样分为I、II、III、IV四个亚家族, 并且第IV亚族包含IVa和IVb两个亚组(图1); 有趣的是, 其中*ZxCNGC1s*有9个同源基因, 与其近缘物种四合木(*Tetraena mongolica*)、盐生植物小花碱茅(*Puccinellia tenuiflorav*)和藜麦(*Chenopodium quinoa*)以及甜土植物桃金娘(*Rhodomyrtus*

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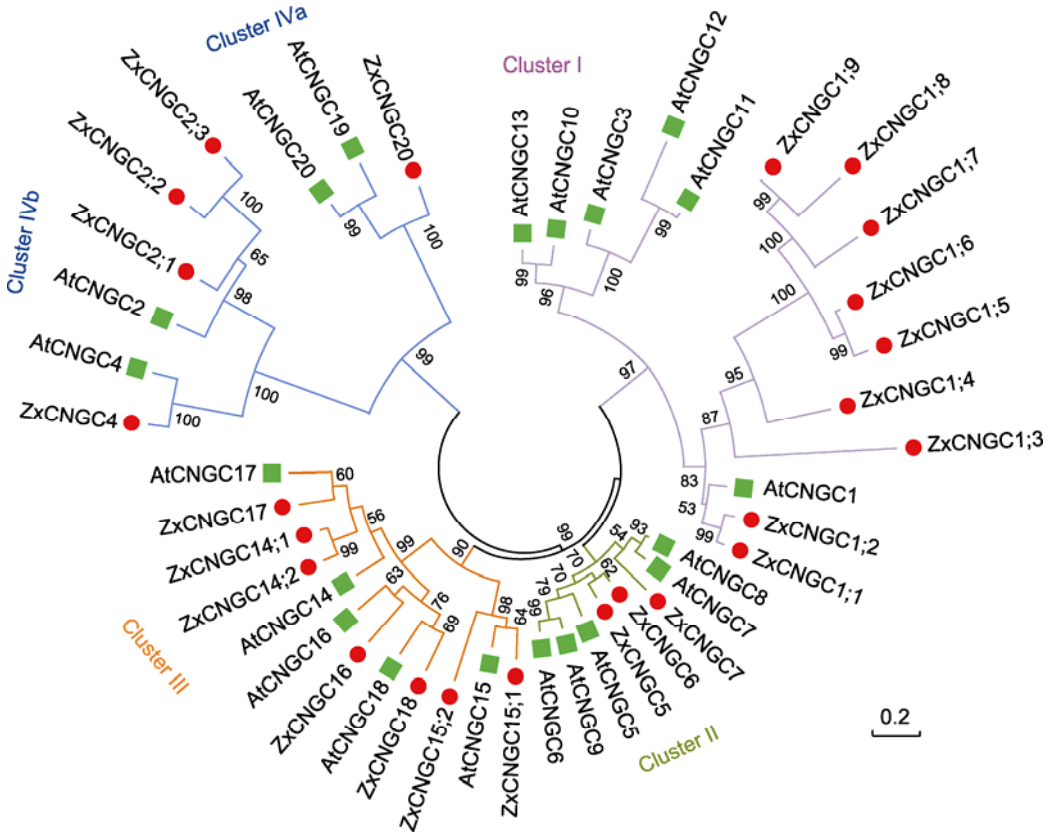


图1 ZxCNGCs和AtCNGCs蛋白的系统发育关系(改自Ma et al., 2024)

Figure 1 Phylogenetic relationship of ZxCNGCs and AtCNGCs proteins (modified from Ma et al., 2024)

表1 不同植物中*CNGC1*同源基因的数量(Ma et al., 2024)

Table 1 Number of *CNGC1* orthologs in different plants (Ma et al., 2024)

物种	霸王	四合木	小花碱茅	藜麦	桃金娘	毛果杨	葡萄	拟南芥
*CNGC1*基因数量	9	2	3	2	2	2	2	1

tomentosa)、毛果杨(*Populus trichocarpa*)、葡萄(*Vitis vinifera*)和拟南芥相比发生了明显扩张(Ma et al., 2024) (表1)。

植物与动物CNGCs以及植物Shaker型K^+电压门控通道的结构高度相似(Talke et al., 2003), 其核心结构为6个跨膜域(S1–S6) (图2)。其中, 作为电压传感器的S4带有正电荷, 能够感受和响应膜电位的变化, 具有电压门控的功能(Hua et al., 2003a; 刘海娇等, 2015); 位于S5与S6之间的孔状结构P环(pore loop)具有离子选择性(Chen et al., 2015)。植物CNGCs的N端和C端均位于胞质一侧。C端含有1个环核苷酸结合结构域(cyclic nucleotide-binding domain, CNBD)、1个钙调素(calmodulin, CaM)结合结构域(calmodulin-binding domain, CaMBD)以及1个可结合CaM的异亮氨酸-谷氨酰胺(IQ)基序, 其中CNBD和CaMBD部分重叠; C端还包含多个磷酸化位点及CNGC-CNGC相互作用结构域(图2) (Jarratt-Barnham et al., 2021)。N端较短, 包含CaMBD、磷酸化位点以及过渡金属结合位点(图2) (Chin et al., 2009; Demidchik et al., 2014)。植物CNGCs的CNBD结构域存在一段特异性保守基序“[LI]-X(2)-[GS]-X-[FYIVS]-X-G-X(0,1)-[DE]-LL-X(8,25)-[SA]-X(9)-[VLIT]-E-X-F-X-[IL]”。Zelman等(2012)发现, 基于此基序构建的系统进化树与利用CNGC蛋白全长构建的系统进化树相一致, 因此认为该基序可用于植物CNGCs的鉴定。

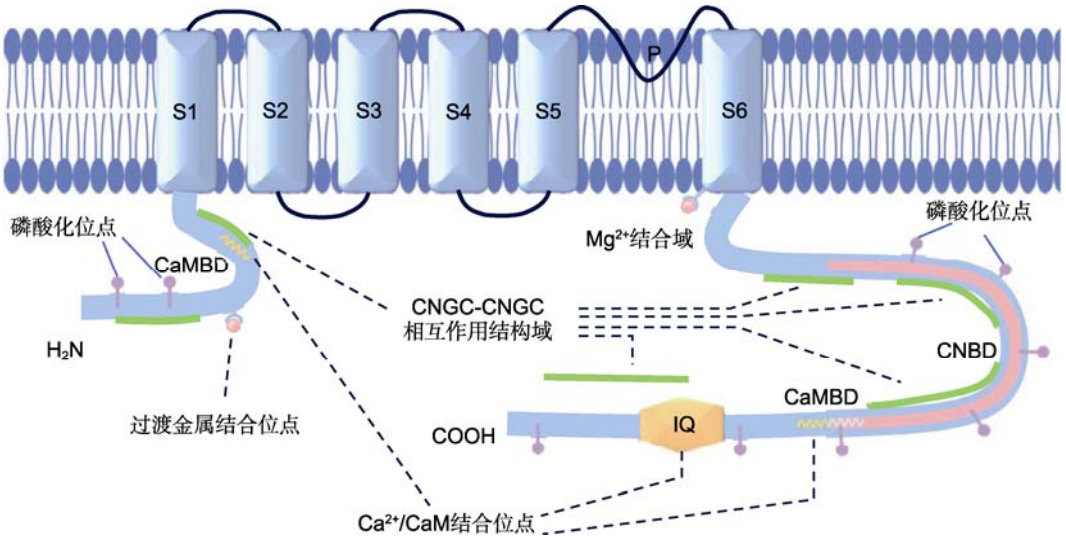


图2 环核苷酸门控通道(CNGC)的结构

S1–S6代表跨膜结构域。P: 磷脂; CaMBD: 钙调素结合结构域; CNBD: 环核苷酸结合结构域; IQ: 异亮氨酸-谷氨酰胺基序

Figure 2 Cyclic nucleotide-gated channel (CNGC) structure

S1–S6 represent the transmembrane domains; P: Phospholipids; CaMBD: Calmodulin-binding domain; CNBD: Cyclic nucleotide-binding domain; IQ: Isoleucine-glutamine motif

2 植物CNGCs的亚细胞定位

植物CNGCs成员多数定位于质膜。近年来，定位于线粒体内膜、叶绿体类囊体膜、核膜、内质网以及高尔基体囊泡的CNGCs相继被鉴定(Duszyn et al., 2019)。在拟南芥中, AtCNGC1、AtCNGC2和AtCNGC3等18个CNGCs定位于质膜(Ma et al., 2006; Chin et al., 2013; Pan et al., 2019)。值得注意的是，尽管之前的研究认为AtCNGC7、AtCNGC8、AtCNGC19和AtCNGC20定位于液泡膜(Chang et al., 2007; Yuen and Christopher, 2013)，但最新研究表明上述蛋白均定位于质膜而不是液泡膜(Meena et al., 2019; Pan et al., 2019; Yu et al., 2019, 2023; Peng et al., 2024) (表2)。除质膜外, AtCNGC10还定位于内质网及高尔基体囊泡；AtCNGC15及其在蒺藜苜蓿(*Medicago truncatula*)中的同源蛋白MtCNGC15a/b/c亦定位于核膜(Charpentier et al., 2016; Leitão et al., 2019)。在水稻中，根据PSORT亚细胞定位预测，发现13个OsCNGCs同源蛋白定位于质膜，其余3个成员(OsCNGC3、OsCNGC7和OsCNGC11)则定位于叶绿体类囊体膜和线粒体内膜(Nawaz et al., 2014)。目前, OsCNGC4、OsCNGC5、OsCNGC8、OsCNGC9、OsCNGC13、OsCNGC14和OsCNGC16，已通过在烟草(*Nicotiana tabacum*)中的瞬时表达证实定位于质膜(Xu et al., 2017; Wang et al., 2019; Cui et al., 2020; Lee et al., 2022)。

3 植物CNGCs的离子选择特征

作为一类重要的阳离子通道，多数CNGCs家族蛋白能够介导Ca^{2+}转运，部分成员对K^+、Na^+等一价和其它二价阳离子亦具有通透性。在拟南芥20个CNGCs中，除AtCNGC3、AtCNGC10和AtCNGC13外，其它17个CNGCs成员均介导Ca^{2+}转运(表2)。目前，已在非洲爪蟾卵母细胞(*Xenopus oocytes*)或人体胚胎肾细胞(human embryonic kidney cell, HEK293T)异源系统中通过膜片钳技术证实，AtCNGC1具有Ca^{2+}和Mg^{2+}通透性(Ma et al., 2024)。AtCNGC2和AtCNGC4能够介导环核苷酸(cNMP)依赖的Ca^{2+}和K^+吸收，同时AtCNGC2还可转运Li^+、Cs^+、Ba^{2+}和Sr^{2+}等一价和二价阳离子(Leng et al., 1999, 2002; Finka et al., 2012)；AtCNGC4还具有Na^+和Cs^+通透性(Balagué et al., 2003)。有趣的是，当AtCNGC2和AtCNGC4形成复合体时，对Ca^{2+}、Sr^{2+}、Ba^{2+}和K^+的通透性则不依赖于cNMP (Tian et al., 2019)。此外, AtCNGC5、AtCNGC6、AtCNGC7、AtCNGC8、AtCNGC9、AtCNGC14、AtCNGC18、AtCNGC19和AtCNGC20均在爪蟾卵母细胞或HEK293T细胞异源表达系统中

表2 拟南芥环核苷酸门控通道(CNGCs)的定位、离子选择性及其功能

Table 2 Localization, ion selectivity and function of cyclic nucleotide-gated channels (CNGCs) in *Arabidopsis*

蛋白	亚细胞定位	组织特异性	可渗透离子	功能	参考文献
AtCNGC1	质膜	根	Ca^{2+}、Mg^{2+}和Pb^{2+}	根的向地性生长; 重金属离子吸收	Sunkar et al., 2000; Ma et al., 2006, 2024; Moon et al., 2019
AtCNGC2	质膜	叶脉末端周围的细胞	Ca^{2+}、Mg^{2+}、K^+、Li^+、Cs^+、Rb^+、Sr^{2+}和Ba^{2+}	植物免疫; 叶片衰老; 耐热、耐寒性; 成花转变; 生长素稳态	Leng et al., 1999, 2002; Ma et al., 2010; Finka et al., 2012; Chin et al., 2013; Tian et al., 2019; Cui et al., 2020; Chakraborty et al., 2021
AtCNGC3	质膜	根表皮及皮层、叶脉	Na^+和K^+	离子稳态; 种子萌发; 植物免疫	Gobert et al., 2006
AtCNGC4	质膜	叶表皮、胚轴、根毛区、根的伸长区和分生区	Ca^{2+}、Mg^{2+}、Ba^{2+}、Sr^{2+}、K^+、Na^+和Cs^+	植物免疫; 程序性细胞死亡; 耐热、耐寒性; 成花转变	Balagué et al., 2003; Finka et al., 2012; Chin et al., 2013; Tian et al., 2019; Cui et al., 2020
AtCNGC5	质膜	保卫细胞和根毛	Ca^{2+}、Mg^{2+}和Ba^{2+}	耐盐性; 根毛生长; 生长素信号	Wang et al., 2013; Tan et al., 2020, 2023
AtCNGC6	质膜	保卫细胞和根毛	Ca^{2+}、Mg^{2+}和Ba^{2+}	耐盐性; 根毛生长; 生长素信号; 耐热性	Gao et al., 2012; Wang et al., 2013; Brost et al., 2019; Tan et al., 2020, 2023
AtCNGC7 AtCNGC8	质膜	花粉管尖端	Ca^{2+}	花粉管生长	Tunc-Ozdemir et al., 2013a; Pan et al., 2019
AtCNGC9	质膜	保卫细胞和根毛	Ca^{2+}	根毛生长; 生长素信号	Brost et al., 2019; Tan et al., 2020; 2023
AtCNGC10	质膜、内质网及高尔基体囊泡	叶肉细胞、叶片栅栏薄壁组织、叶表皮、根表皮及内皮层和花	Na^+、K^+和Pb^{2+}	离子稳态; 耐盐性; 根向地性生长; 花粉发育	Li et al., 2005; Christopher et al., 2007; Guo et al., 2008; Jin et al., 2015; Moon et al., 2019
AtCNGC11	质膜	–	Ca^{2+}、Pb^{2+}和Cd^{2+}	植物免疫; 细胞死亡	Urquhart et al., 2007; Moeder et al., 2011; Moon et al., 2019
AtCNGC12	质膜	保卫细胞	Ca^{2+}和Mg^{2+}	植物免疫; 细胞死亡; 生长素信号	Urquhart et al., 2007; Moeder et al., 2011; DeFalco et al., 2016; Tan et al., 2023
AtCNGC13	–	–	Pb^{2+}和Cd^{2+}	重金属离子吸收	Moon et al., 2019
AtCNGC14	质膜	根毛	Ca^{2+}	根毛生长; 根的向地性生长	Shih et al., 2015; Zhang et al., 2017; Brost et al., 2019; Serre et al., 2023
AtCNGC15	质膜及核膜	主根和侧根的根尖、侧根原基和保卫细胞	Ca^{2+}、Pb^{2+}和Cd^{2+}	根的发育	Moon et al., 2019; Leitão et al., 2019; Wang et al., 2021b
AtCNGC16	–	花粉管	Ca^{2+}和Cd^{2+}	逆境胁迫下的花粉育性	Tunc-Ozdemir et al., 2013b; Moon et al., 2019
AtCNGC17	质膜	–	Ca^{2+}和K^+	细胞扩张; 耐盐性	Ladwig et al., 2015
AtCNGC18	质膜	花粉管尖端	Ca^{2+}	花粉管的生长和导向	Gao et al., 2016; Pan et al., 2019
AtCNGC19	质膜	叶脉周围的叶肉细胞和根韧皮部	Ca^{2+}、Na^+、Pb^{2+}和Cd^{2+}	植物免疫; 耐盐性; 植食反应; 细胞死亡	Kugler et al., 2009; Moon et al., 2019; Meena et al., 2019; Yu et al., 2019, 2023; Jogawat et al., 2020
AtCNGC20	质膜	叶脉周围的叶肉细胞	Ca^{2+}、Na^+和Cd^{2+}	植物免疫; 耐盐性; 细胞死亡; 耐寒性	Kugler et al., 2009; Yu et al., 2019, 2023; Oranab et al., 2021; Peng et al., 2024

– 未知 – Unknown

具有Ca^{2+}通透性(Pan et al., 2019; Yu et al., 2019; Tan et al., 2020)。在酵母异源表达系统中的分析显示, AtCNGC3具有K^+和Na^+转运活性, 但不介导Ca^{2+}的转运(Gobert et al., 2006)。将AtCNGC11和12单独

或共同转入Ca^{2+}吸收缺陷型酵母菌株中均可促进Ca^{2+}的吸收(Urquhart et al., 2007)。AtCNGC10在大肠杆菌(*Escherichia coli*)和酵母异源表达系统中表达均可介导K^+以及Na^+的转运(Li et al., 2005)。本课题组利用酵母及HEK293T异源表达系统分析表明，霸王的2个ZxCNGC1同源蛋白ZxCNGC1;1以及ZxCNGC1;2均可介导Na^+、Ca^{2+}和Mg^{2+}的转运，但不介导K^+的转运(Ma et al., 2024)。另外，仅在植株水平上分析了部分AtCNGCs成员的离子选择性。例如，Moon等(2019)研究发现*AtCNGC1*、*AtCNGC10*或*AtCNGC13*的单突株系对Pb^{2+}胁迫具有更强的耐受性，推测上述蛋白介导Pb^{2+}的转运。

有研究表明，部分CNGC能够形成异源四聚体通道，通过相互作用介导Ca^{2+}转运，进而调控植株生长发育及胁迫响应。AtCNGC2和AtCNGC4能够形成Ca^{2+}通道复合体(Tian et al., 2019)；AtCNGC7或AtCNGC8能够与AtCNGC18形成异源四聚体，介导Ca^{2+}向胞质中转运(Pan et al., 2019)；AtCNGC19与AtCNGC20也能够形成Ca^{2+}通道复合体(Yu et al., 2019)。此外，在HEK293T细胞中，ZxCNGC2;1或ZxCNGC4均能介导Ca^{2+}和Mg^{2+}的转运，但未检测到Na^+或K^+的转运活性；而ZxCNGC2;1-ZxCNGC4复合体不仅能介导Ca^{2+}和Mg^{2+}转运，还能介导Na^+转运，但未检测到K^+转运活性(陈芹芹, 2022)。

4 植物CNGCs的调控机制

早期研究认为植物CNGC由cNMP和Ca^{2+}/CaM竞争性调节，CNGC通过与cNMP结合而被激活，引起Ca^{2+}内流，使得胞内Ca^{2+}增加，从而激活Ca^{2+}依赖蛋白激酶(CDPKs)，进而磷酸化下游靶蛋白(Talke et al., 2003)。近年来的研究表明，CNGC的通道活性并非绝对依赖于cNMP的激活。例如，AtCNGC11、AtCNGC12和AtCNGC14的离子通道活性均与cNMP无关(Zhang et al., 2019; Zeb et al., 2020)；在非洲爪蟾卵母细胞异源表达系统中，多数CNGCs异源四聚体表现出超极化激活的Ca^{2+}通道活性，不需要cNMP的激活(Tian et al., 2019)。因此，cNMP可能仅是CNGC发挥功能的辅助因子，而不是必需的门控配体。此外，胞内增加的Ca^{2+}亦能够激活CaM，后者通过与CNGC的CaMBDs结合，抑制cNMP与CNGC的结合，使得其通道活性减弱，从而限制Ca^{2+}向胞内转运，以确保植株对胞内Ca^{2+}信号的精密调节(Hua et al., 2003b; Lemtiri-Chlieh and Berkowitz, 2004)。进一步研究显示，除CaMBDs外，CaM还能够通过与IQ基序结合进而调控CNGCs (Zhang et al., 2019; Dietrich et al., 2020; Zhao et al., 2021)，表明CaM对植物CNGC的调节较为复杂，并非完全通过影响cNMP与CNGCs的结合。此外，有研究表明CNGCs的活性受磷酸化调控。例如，Ca^{2+}依赖的蛋白激酶AtCPK32能够显著增强AtCNGC18的通道活性(Zhou et al., 2014)；胞质激酶BIK1/PBL1能够磷酸化AtCNGC4，随后激活AtCNGC2-AtCNGC4复合体通道(Tian et al., 2019)；在水稻中，胞质受体激酶OsRLCK185通过磷酸化激活OsCNGC9，进而触发防御反应(Wang et al., 2019)。CNGC还受Ca^{2+}非依赖性蛋白激酶的激活。例如，AtCNGC5、AtCNGC6、AtCNGC9和AtCNGC12四个通道能够被Ca^{2+}非依赖性蛋白激酶AtOST1激活并起始胞内Ca^{2+}信号(Yang et al., 2024)；此外，植物CNGC还能够通过与其它转运蛋白相互作用进而发挥作用，如AtCNGC15与硝酸盐转运蛋白AtNRT1.1共同组装成“转运体-钙通道复合体(transceptor-channel complex)”，该复合体能够感应外界硝酸盐浓度变化，激活或关闭钙离子通道(Wang et al., 2021b)。

5 植物CNGCs的生物学功能

植物CNGCs家族成员众多，分别在不同生长发育阶段的不同器官中表达，具有多种生物学功能，尤其是通过介导Ca^{2+}转运调控胞内Ca^{2+}信号，进而在植物生长发育以及胁迫响应中发挥重要作用(表2)。

5.1 CNGCs在植物生长发育中的作用

Ca^{2+}在细胞内的浓度变化形成周期性振荡，进而产生特异性的Ca^{2+}信号，该过程由多个负责编码Ca^{2+}信号的Ca^{2+}通道或转运蛋白完成(Luan and Wang, 2021; Wang et al., 2024)。部分CNGCs成员已被证实参与编码Ca^{2+}信号，进而调控生长发育，尤其在花粉管和根毛的极性生长中发挥重要作用(Luan and Wang, 2021)。AtCNGC7或AtCNGC8能够与AtCNGC18形成异源四聚体，在低钙条件下，CaM2与AtCN-

GC18-AtCNGC8复合体相互作用, 使得花粉萌发和花粉管正常生长; 当细胞中Ca^{2+}浓度达到峰值时, Ca^{2+}结合的CaM2从AtCNGC18-AtCNGC8复合体上解离, 进而抑制花粉萌发和花粉管生长(Gao et al., 2016; Pan et al., 2019)。AtCNGC5、AtCNGC6、AtCNGC9和AtCNGC14被证实是根毛尖端细胞中Ca^{2+}振荡的重要调节因子, 它们之间存在部分功能冗余, 其中AtCNGC14不仅对于根毛生长的调控尤为重要, 还在根的向地性生长中发挥关键作用(Brost et al., 2019; Tan et al., 2020; Zeb et al., 2020; Serre et al., 2023)。此外, 钙调磷酸酶B样蛋白AtCBL2/3既能够与其互作蛋白激酶AtCIPK12/19相互作用, 进而作为Ca^{2+}解码模块调控花粉管尖端的极化生长, 也能够募集AtCIPK13/18调控根毛生长, 而CNGCs可能通过介导Ca^{2+}转运在上述CBL-CIPK模块的上游发挥作用(Fang et al., 2024)。

CNGCs还参与植物中的其它生理过程。例如, AtCNGC5、AtCNGC6、AtCNGC9和AtCNGC12作为脱落酸(ABA)激活的Ca^{2+}通道在调控气孔关闭中发挥重要作用(Tan et al., 2023; Yang et al., 2024)。受体激酶BAK1以及SERK4通过磷酸化破坏CNGC19-CNGC20复合体的稳定性, 抑制Ca^{2+}信号的传递, 阻止细胞凋亡(Yu et al., 2019)。类受体激酶BTL2 (BAK-TO-LIFE2)可检测BAK1/SERK4的完整性, 当BAK1/SERK4缺失或受损时, BTL2的活性增强, 以激活钙离子通道AtCNGC20, 从而触发自身免疫反应; 且BAK1通过特定的磷酸化机制来限制BTL2的激活, 以避免过度免疫反应(Yu et al., 2023)。蒺藜苜蓿中核定位的MtCNGC15a/b/c介导Ca^{2+}振荡, 从而影响Ca^{2+}信号, 在豆科植物响应根瘤菌入侵及根瘤形成中发挥作用(Charpentier et al., 2016)。

5.2 CNGCs在抵御生物胁迫中的作用

植物中多个CNGCs成员参与响应Ca^{2+}依赖的免疫反应, 其中对AtCNGC2和AtCNGC4的研究最为深入。Tian等(2019)与Wang等(2024)阐明了AtCNGC2-AtCNGC4复合体在病原体相关分子模式(pathogen-associated molecular patterns, PAMPs)触发的免疫反应(PAMP-triggered immunity, PTI)中介导的Ca^{2+}信号转导途径: 在静息状态下, 植物模式识别受体(pattern-recognition receptors, PRRs)处于无活性状态, AtCNGC2-AtCNGC4复合体被CaMs抑制而关闭; 当病原体入侵时, PAMPs与PRRs结合, 并激活PRR的效应激酶BIK1 (BOTRYTIS-INDUCED KINASE1), 随后, AtCNGC2-AtCNGC4通道被BIK1磷酸化并激活, 从而引发胞质中游离的Ca^{2+} ($[Ca^{2+}]_{cyt}$)增加, 此过程起始Ca^{2+}信号并产生免疫反应; 当$[Ca^{2+}]_{cyt}$升高后, BIK1/PBL1磷酸化并激活液泡膜上的Ca^{2+}/H^{+}逆向转运蛋白(Ca^{2+}/H^{+} antiporters, CAXs), 将Ca^{2+}区域化至液泡中, 降低胞质中的Ca^{2+}浓度以解除Ca^{2+}信号, 从而调节生长和免疫响应之间的平衡。此外, AtCNGC3、AtCNGC11、AtCNGC12、AtCNGC19和AtCNGC20也被证实是病原体防御反应的正调节因子(Moeder et al., 2011; Yu et al., 2019; Jogawat et al., 2020; 刘梦娇, 2021)。水稻中也有多个OsCNGCs家族蛋白参与病原菌胁迫响应, 其中OsCNGC5和OsCNGC9正调控水稻的抗病性(Wang et al., 2019; Zheng et al., 2024)。在接种不同病原菌后, 苹果(*Malus pumila*)、烟草及大豆等植物中大量*CNGCs*的表达水平发生显著变化, 表明*CNGCs*可能在响应病原菌胁迫中发挥重要作用(Zhang et al., 2018; Nawaz et al., 2019; Cui et al., 2023)。

CNGCs除参与植物免疫反应外, 还参与植物对植食性昆虫取食的响应。植物防御食草动物取食由茉莉酸(jasmonic acid, JA)依赖的信号级联介导, *AtCNGC19*的表达能够被食草昆虫的取食行为诱导, 引起Ca^{2+}向胞质中转运, CaM1、CaM4和CaM7感知Ca^{2+}浓度升高并通过激活下游蛋白促进JA的生物合成, 进而触发植物对虫害的防御反应(Yan et al., 2018; Meena et al., 2019)。

5.3 CNGCs在抵御非生物胁迫中的作用

5.3.1 在抵御外界温度变化中的作用

植物CNGCs在温度胁迫诱导的Ca^{2+}信号转导中发挥关键作用。部分CNGCs参与响应热胁迫。例如, AtCNGC6介导热胁迫诱导的Ca^{2+}内流, 并影响热激蛋白的表达以增强植株的耐热性(Peng et al., 2019); 白菜*CNGC1* (*BrCNGC1*)、*BrCNGC3*、*BrCNGC10*、*BrCNGC17*和*BrCNGC29*在高温胁迫下上调表达(Li et al., 2019)。此外, CNGCs亦在植物响应冷胁迫中发挥作用。最新研究表明, AtCNGC20通过介导Ca^{2+}的转运正调节拟南芥的耐寒性, 在低温胁迫早期, 酪氨

酸硫酸肽受体激酶PSY1R (Plant Peptide Containing Sulfated Tyrosine1 Receptor)被激活，进而磷酸化AtCNGC20并增强其活性；而在长期低温胁迫下，冷响应蛋白激酶CRPK1 (Cold-Responsive Protein Kinase1)磷酸化并降解AtCNGC20，从而降低植株的耐寒性(Peng et al., 2024)。OsCNGC9也可通过OsSAPK8蛋白激酶的磷酸化正调控水稻的耐寒性(Wang et al., 2021a)。在低温胁迫下，甘蓝(*B. oleracea*) *BoCNGC17*和*BoCNGC23*、烟草*NtCNGC6*和*NtCNGC7*、芒果(*Mangifera indica*) *MiCNGC9*和*MiCNGC13*以及茄子(*Solanum melongena*) *SmCNGC1a*的表达水平均显著上调(Kakar et al., 2017; Nawaz et al., 2019; Zhang et al., 2023; Jiang et al., 2023)。此外, CNGC2和CNGC4在拟南芥耐热性和耐寒性中均发挥重要作用。AtCNGC2和AtCNGC4对植株耐热性的影响依赖于发育阶段，*AtCNGC2*的缺失导致植物幼苗期耐热性增强，但生殖期耐热性降低(Finka et al., 2012; Katano et al., 2018; Lu et al., 2022a)；同时，二者正调控植物幼苗期的耐寒性，其单突变体株系在低温条件下均表现出下胚轴缩短、鲜重及存活率降低(Cui et al., 2020)。水稻OsCNGC14和OsCNGC16也在植株耐热和耐寒中发挥作用(Cui et al., 2020)。

5.3.2 在抵御干旱胁迫中的作用

干旱胁迫可显著诱导烟草*CNGC1* (*NtCNGC1*)、*NtCNGC6*和*NtCNGC7*等在叶中的表达，表明NtCNGCs参与烟草对干旱的响应(Nawaz et al., 2019)。干旱胁迫下，甜橙(*Citrus sinensis*) *CsCNGC1.4*、*CsCNGC2.1*和*CsCNGC4.2*在叶中的表达显著上调，而*CsCNGC4.6*的表达显著下降(Zia et al., 2022)。此外, Gao等(2020)发现外源多巴胺可通过促进*CNGC*和*CAM*/*CML*家族基因的表达激活Ca^{2+}信号通路，从而提高苹果的抗旱性。本课题组对霸王进行转录组分析，结果表明9个*ZxCNGC1s*中有7个主要在根中表达，并且在干旱或盐处理下均上调表达(Ma et al., 2024)。

5.3.3 在抵御盐胁迫中的作用

在拟南芥中, *AtCNGC1*、*AtCNGC10*、*AtCNGC19*和*AtCNGC20*的表达丰度受盐胁迫诱导(Balagué et al., 2003; Jin et al., 2015)。在NaCl或KCl处理下, *atcngc3*突变体幼苗的长势略优于野生型，表明*AtCNGC3*负调控植物的耐盐性(Gobert et al., 2006)。盐胁迫下*AtCNGC19*和*AtCNGC20*在根中的表达量升高，且超表达*AtCNGC19*或*AtCNGC20*能够提高植株的耐盐性(Oranab et al., 2021)。*BrCNGC7*、*BrCNGC10*、*BrCNGC12*、*BrCNGC13*、*BrCNGC19*、*BrCNGC22*和*BrCNGC23*在白菜根中的表达受到盐胁迫诱导上调(Li et al., 2019)。在棉花中，*GhCNGC32*或者*GhCNGC35*的沉默均会降低植株的耐盐性(Lu et al., 2022b)。此外，本课题组在分析荒漠植物抗逆机制的过程中，发现多浆旱生植物霸王生境土壤中有效Na^+含量仅为盐生植物盐地碱蓬(*Suaeda salsa*)的1/66，但其叶中能够积累与盐地碱蓬相当的Na^+，并将其区域化至液泡中用于渗透调节，表明霸王根系具有极强的Na^+吸收能力(Wang et al., 2002, 2004; Wu et al., 2011; Janz and Polle, 2012; Ma et al., 2012; Yuan et al., 2015)。最近的研究表明，霸王ZxCNGC1;1和ZxCNGC1;2对Na^+具有极高的通透性，在正常的胞内电压(–80 – –120 mV)下即可开放；而甜土植物水稻OsCNGC1仅在消耗过多能量使胞内电压达到–180 mV时才能开放；模式植物拟南芥AtCNGC1则在任何检测电压下均无Na^+通透性(Ma et al., 2024)。可见, ZxCNGC1;1和ZxCNGC1;2能够介导“节能型”的Na^+吸收，进而在维持旱生植物霸王的积盐特性中发挥重要作用，这揭示了积盐型植物高效吸收Na^+的分子基础(Ma et al., 2024)。

5.3.4 在抵御重金属胁迫中的作用

部分CNGCs已被证实参与重金属离子的吸收和转运。*AtCNGC16*或者*AtCNGC20*的突变均减弱了植株对Cd^{2+}胁迫的耐受性；*AtCNGC11*、*AtCNGC13*、*AtCNGC15*或*AtCNGC19*的突变降低了拟南芥体内Pb^{2+}和Cd^{2+}积累(表2) (Moon et al., 2019)。在烟草中，多个*NtCNGCs*在Cd^{2+}胁迫下上调表达，可能参与植物对Cd^{2+}胁迫的响应(Nawaz et al., 2019)。此外，拟南芥AtCNGC5、AtCNGC6以及AtCNGC2-AtCNGC4复合体能够介导Ba^{2+}的转运，可能在植物应对Ba^{2+}胁迫中发挥作用(表2) (Wang et al., 2013; Tian et al., 2019)。

6 展望

植物CNGCs是重要的阳离子通道, 在调节植物生长发育和抵御生物与非生物胁迫中发挥重要作用。综合目前的研究进展, 我们认为未来关于植物CNGCs有以下4个研究方向。

(1) 20多年来, CNGCs在模式植物拟南芥中已进行了较为系统且深入的研究, 为其它植物CNGCs的研究奠定了良好的基础。近年来, 多种植物CNGCs的功能也相继被报道, 但仍主要集中在水稻等抗逆性较弱的栽培作物, 且相关研究尚处于起步阶段。分布于极端生境中的旱生或盐生植物具有极强的抗逆能力, 其CNGCs通道蛋白可能进化出有别于甜土植物的功能。本课题组发现霸王*ZxCNGC1s*发生显著扩张, 其中ZxCNGC1;1和ZxCNGC1;2介导Na^+吸收的能力远高于OsCNGC1, 而AtCNGC1不具备Na^+吸收能力。我们认为这是霸王在长期适应干旱、高温及土壤贫瘠等荒漠生境过程中形成的独特的抗逆机制。因此, 挖掘旱生或盐生植物的*CNGCs*, 分析其编码蛋白在逆境适应中的作用机制, 可为栽培作物抗逆性遗传改良奠定理论基础并提供优异的基因资源。

(2) 目前仍有部分AtCNGCs成员的离子选择性仅依据其编码基因在转录水平上对不同离子的响应进行推测, 并未在细胞水平上验证。明确CNGCs的亚细胞及组织定位, 并在细胞及植株水平上鉴定分析其离子选择性, 对于深入了解其功能与作用机制至关重要。

(3) CNGC能够以四聚体的形式发挥作用, 但是目前的研究大多关注单个CNGC的功能, 多数CNGCs家族蛋白之间的相互作用有待深入研究。

(4) CNGCs的通道活性受到非常复杂且严格的调控, 明确其调控因子并解析相关机制亦是值得关注的研究方向。

作者贡献声明

石雅琦: 作图, 撰写并修改论文; 刘海双、柯瑾和马清: 修改论文; 王锁民: 构思、指导撰写并修改论文。

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Research Advances in Cyclic Nucleotide-gated Ion Channels in Plants

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Abstract Cyclic nucleotide-gated channels (CNGCs) are important cation channels that play pivotal roles in the regulation of growth and development, as well as in response to stresses such as cold, heat, salt, and pathogen attacks in plants. In this review, we briefly outline the classification, structure and location of CNGCs in plants, and comprehensively summarize the recent research progress on their ionic selectivity, regulatory mechanisms, and biological functions, in order to enhance our understanding of plant CNGCs and provide a reference for future research.

Key words stress tolerance, CNGCs, ionic selectivity, response to stress

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