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Regulation of Ca^{2+} in Plant Response Mechanisms under Cold Stress

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Abstract

Cold stress presents one of the major limitations for plant growth, development and yield worldwide, as well as distribution, especially in areas of north and high-latitude regions. Worldwide, the annual crop economic losses due to the low temperature above 0˚C is amount to hundreds billions of yuan. So an investigation of responses mechanism of cold stress in plant and improvement of its resistance has significant important value. Ca^{2+} acts as the second messenger coupling of extracellular signals and intracellular physiological response. It plays an important role in mediating plant growth and development, as well as involved in the regulation of various abiotic stresses. The review discusses the molecular mechanism of Ca^{2+} regulating cold stress in plant.

Keywords

Ca^{2+} Signaling, Cold Stress, Plant, Regulatory Mechanism

钙信号调控植物低温胁迫的分子机制研究进展

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摘 要

低温冷害是最为严重的自然灾害之一。低温冷害抑制植物的生长发育，全世界范围内每年因0℃以上的

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低温冷害造成的作物经济损失达数千亿元。因此研究植物的低温胁迫适应机理，提高其低温抗性不仅具有十分重要的科学意义，而且有着更为重要的现实价值。Ca^{2+}作为重要的第二信使不仅参与调控植物的生长发育过程，还参与调控各种生物与非生物胁迫应答。本文重点论述了Ca^{2+}调控植物低温胁迫应答的分子机制。

关键词

钙信号，低温胁迫，植物，应答机制

1. 引言

低温作为重要的非生物逆境被认为是世界最为严重的自然灾害之一。全世界范围内每年因零度以上的低温造成的作物经济损失达数千亿元[1]，在我国每年因低温冷害造成的作物生产损失可达3~5亿吨[2]。因此，研究植物的低温胁迫应答机制，提高其低温抗性具有重要的意义[1]。Ca^{2+}除了是植物必需的元素以外，还起到植物细胞膜保护剂的作用，能够稳定植物细胞膜和膜蛋白等；另外，Ca^{2+}也作为植物细胞内重要的第二信使，在植物的各种生物与非生物胁迫应答中起到信号转导的作用[2]。已经有许多研究报道 Ca^{2+}信号在植物低温应答过程中发挥重要的作用。本文综述了 Ca^{2+}信号在植物低温胁迫下的响应及Ca^{2+}参与植物低温应答的转导途径(图 1)，并对 Ca^{2+}信号与 CBF 依赖的低温应答通路的调控关系进行展望。

2. 低温胁迫下植物钙信号的响应

植物在正常生长条件下，其细胞内的 Ca^{2+}含量维持在较低的水平，一旦植物遭遇到不良环境胁迫后，细胞内的 Ca^{2+}水平在短时间内骤增，从而产生和放大钙信号[3]，在 Ca^{2+}信号转导过程中，Ca^{2+}能够与其下游的钙调素等钙结合蛋白结合，激活一系列的钙依赖的蛋白激酶，这些激活的蛋白激酶能够进一步通过调控下游的胁迫应答相关的基因表达，从而调控植物体内各种生理代谢响应[4]。对拟南芥和紫花苜蓿的研究发现，低温诱导的基因转录水平同低温诱导的钙离子流存在正相关关系[5]。低温胁迫一方面诱导Ca^{2+}从质膜流入细胞内，另一方面从中央液泡释放到细胞内最终导致细胞内 Ca^{2+}浓度上升[6]。采用微电极法分析胞外 Ca^{2+}水平变化，发现低温胁迫导致植物根组织中 Ca^{2+}流从胞外进入胞内，从而导致细胞内Ca^{2+}升高[7]。低温胁迫会抑制质膜上 Ca^{2+}通道的活性。在 Ca^{2+}信号转导过程中，Ca^{2+}跨膜运输离不开钙离子通道的调控作用。钙离子通道定位于质膜与细胞内膜，当植物遭遇外界不良环境刺激时，通道打开，胞外或胞内的 Ca^{2+}进入到细胞质中，导致胞内 Ca^{2+}水平瞬间升高，从而激活一系列防御响应[2]。细胞内Ca^{2+}浓度升高可以诱导磷酸酯酶 C 和 D 活性增强，导致三磷酸肌醇(IP3)和磷脂酸积累。IP3 能够通过其调控的钙离子通道进一步放大 Ca^{2+}信号。拟南芥 fry1 突变体同野生型相比积累更多的 IP3，提高了 *CBFs* 和 *COR* (cold responsive genes)基因的表达，具有更高的抗寒性[8]。定位在液泡膜上的 Ca^{2+}/H^{+}反向转运体 CAX1 具有将细胞质中的 Ca^{2+}转运到液泡中的作用。*cax1* 功能缺失突变体在非冷驯化条件下没有明显的表型，但是经过冷驯化以后，表现出明显的抗冻表型。这一研究表明，CAX1 通过向外转移细胞质中 Ca^{2+}

流，从而负向调控植物的抗冻性[9]。另外，在高等植物之中还存在另一类环核苷酸钙离子通道 CNGC (cyclic nucleotide gated calcium channel)，它能够通过调控 Ca^{2+}内流而提高植物的各种生物与非生物抗性[10]。Nawaz [11]在水稻发现 16 个 CNGC 基因，其中 10 个是由低温诱导上调表达。近年来，在水稻根细胞研究中发现低温受体蛋白 COLD1 (Chilling-tolerance Divergence 1)可与 G 蛋白互作，激活钙离子通道，导致根细胞中的钙离子内流加快，并改变膜电信号，从而激活钙离子信号通路，最终增强植物的耐寒性[12]。以上研究都表明，Ca^{2+}浓度迅速升高和钙离子通道开关在植物响应低温胁迫的过程中起到非常重要的作用。

3. 低温胁迫下钙信号的应答机制

3.1. Ca^{2+}转运系统

植物的细胞内 Ca^{2+}信号产生后，需要经过一个解码的过程，Ca^{2+}信号首先由 Ca^{2+}感受元件(Calcium sensor)感知，之后将 Ca^{2+}信号逐级放大，最终引发一系列的生理代谢响应[13]。钙－钙感受器－靶蛋白－关键基因是调控植物响应逆境胁迫的关键途径。目前研究比较深入地植物对环境信号的感知和传递的钙信使系统，主要包括钙离子－钙调蛋白(Ca^{2+}-CaM)、钙离子－钙调磷酸酶 B 类似蛋白(Ca^{2+}-Calcineurin B-Like protein (CBL))和钙离子－钙依赖性蛋白激酶(Ca^{2+}-CDPK) [14]。近年来，CBL-CBL-interacting protein kinases (CIPKs)信号在调控植物胁迫应答方面受到国内外学者的普遍关注[15] [16]。CIPK 信号是在高等植物中特有的一类丝氨酸/苏氨酸蛋白激酶，它能与 CBLs 特异性互作。CBL-CIPK 信号通路在植物 Ca^{2+}信号传递过程中起着重要作用。

3.2. Ca^{2+}参与植物低温应答的转导途径

CBLs 在检测到植物细胞产生的 Ca^{2+}信号后，通过激活下游 CIPKs 的激酶活性来实现 Ca^{2+}信号的转导[16] [17]。许多研究表明，植物 CIPKs 基因受多种逆境胁迫诱导表达，CBL-CIPK 信号网络在植物逆境应答过程中起关键作用[18] [19] [20] [21]。然而，关于 CBL-CIPK 信号调控植物低温胁迫应答的报道较少。在水稻中的研究表明，低温胁迫诱导 *OsCIPK*3 (*OsCK*1)表达，并且 *OsCIPK*3 (*OsCK*1)可能通过 Ca^{2+}信号依赖的方式调控植物的低温胁迫应答[22]。Xiang 等[23]研究发现，过表达 *OsCIPK03* 可以提高水稻的抗寒/冻性。在拟南芥中的研究发现，CBL1 与 CIPK7 互作共同调控植物的低温应答[24]。Deng 等[25]研究发现，异源表达小麦 *TaCIPK*14 基因能够提高番茄的抗寒性。

植物遭受低温等外界刺激后，其细胞膜流动性和结构发生改变，导致细胞膜上离子通道打开，从而引起细胞质中 Ca^{2+}水平瞬间激增，细胞内瞬间增加的 Ca^{2+}流被下游的钙信号感受器(CRLK1，CPKs 和 CIPKs)所感知，进一步将 Ca^{2+}信号向下游传递，从而调控低温应答基因响应[17]。Yang 等[26]报道，低温逆境下，CRLK1 与 MEKK1 互作，从而激活 MAPK 级联响应。Teige 等[27]在拟南芥中的研究发现，低温激活 MAP2K/MKK2 信号从而调控下游的 COR 基因表达。MKK2 作为 MAPK3/MEKK1 的下游信号，而作为 MPK4 和 MPK6 的上游信号参与调控植物的低温应答响应[28]。在拟南芥中，低温胁迫诱导升高的[Ca^{2+}]cyt 与 CaMs 结合，进一步在蛋白修饰水平调控下游的类受体激酶(RLKs)的活性以及激活 MEKK1-MKK2-MPK4 级联信号，从而诱发植物的低温胁迫应答[29]。低温胁迫诱导的[Ca^{2+}]cyt 浓度的升高还能通过调节 *CBF*2 和 *CAMTA*3 的表达，进而激活低温胁迫响应通路中的转录因子[30]。综上，低温首先降低细胞膜的流动性，细胞膜的这种改变被定位于质膜的钙离子通道或蛋白所感知，导致钙离子流的激活以及 CPKs、CIPKS、CRLK1 等钙响应蛋白激酶和 MAPK 级联响应，最终调控低温响应基因 COR 表达。低温胁迫下植物 Ca^{2+}信号转导途径见图 1。

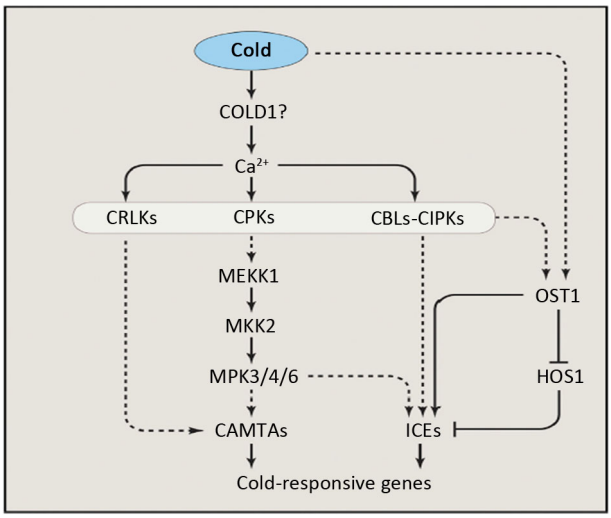

Figure 1. Ca^{2+} signaling transduction pathway under cold stress
图 1. 低温胁迫下 Ca^{2+}信号转导途径[18]

4. 钙信号与 CBF 信号的潜在调控关系

低温诱导植物体内的冷响应基因(*CORs*)表达，*CORs* 基因编码一些保护性的蛋白质，如脱水素，这类蛋白质能够保护植物免受低温伤害。CBFs/DREBs (C-repeat (CRT)-binding factors/dehydration-responsive element (DRE) binding factors)是作用于 *CORs* 基因上游的一类重要的转录因子[31]。截止目前，CBF 信号通路是公认的低温信号转导途径。低温胁迫下植物的 CBF 转导途径见图 2。CBF 通过结合 COR、LT1 (Low temperature Induced)、KIN (Cold-induced)及 RD (Responsive to Dehydration)等类型低温调节基因启动子区域的 CRT (C-repeat)/DRE (Dehydration Response Element)顺式作用元件上，诱导其表达，从而提高植物的抗寒性[32] [33] [34]。研究发现，苹果 bHLH 转录因子 MdCIbHLH1 (Cold-Induced bHLHl)可以通过正调控 *MdCBF*2 表达，提高了苹果植株的抗寒性。同时，该基因也可以结合到拟南芥 *AtCBF*3 启动子上的顺式调控元件[35]。Zhao 等[36]研究发现香蕉 *MaMYC*2 转录因子可以与 MalCEl 互作，进一步调节 *MaCBF1*、*MaCBF*2、*MaCORl*、*MaKIN*2、*MaRD*2 及 *MaRD5* 等基因的表达，提高香蕉果实的抗寒性。Shi 等[37]通过对拟南芥乙稀突变体的分析，证实 EIN3 也可以负调控 *CBFs* 基因的表达。近期的研究发现，低温诱导 SnRK2.6/OST1 上调表达，这一诱导的 SnRK2.6 蛋白进一步磷酸化 ICE1，从而激活 CBF-COR 依赖的低温信号应答途径[38] [39]。Liu 等[40]研究表明，定位于质膜的冷响应蛋白激酶 1 (cold-responsive protein kinase 1, CRPK1)磷酸化 14-3-3 蛋白，磷酸化的 14-3-3 蛋白进入细胞核与 CBF 蛋白互作调控其稳定性，从而实现 CRPK1-14-3-3 模块精细地调控植物的低温应答响应。Ca^{2+}信号感受器可能通过某种未知机制调控 ICE1，CBF 的转录水平及蛋白稳定性，从而进一步调控植物的低温抗性。另外，Li 等[41]研究发现，低温激活的蛋白激酶 MPK3 和 MPK6 能够磷酸化 ICE1，降低其转录活性及蛋白稳定性，抑制 *CBF* 基因表达，从而负调控植物的低温抗性。

5. 展望

目前，虽然关于钙离子调控植物低温应答的机理研究已取得很大的进展，然而对于植物感受低温信号的受体激酶，以及该受体是如何将低温信号传递到次级信使 Ca^{2+}尚未有定论。因此，在以后的研究中，Ca^{2+}信号是如何与低温信号感受器作用，并将低温信号进一步放大将会是一个非常重要的研究领域。尤其是 Ca^{2+}信号通路与 CBF 低温应答通路的关键互作蛋白的研究尤为重要。综上所述，深入研究 Ca^{2+}

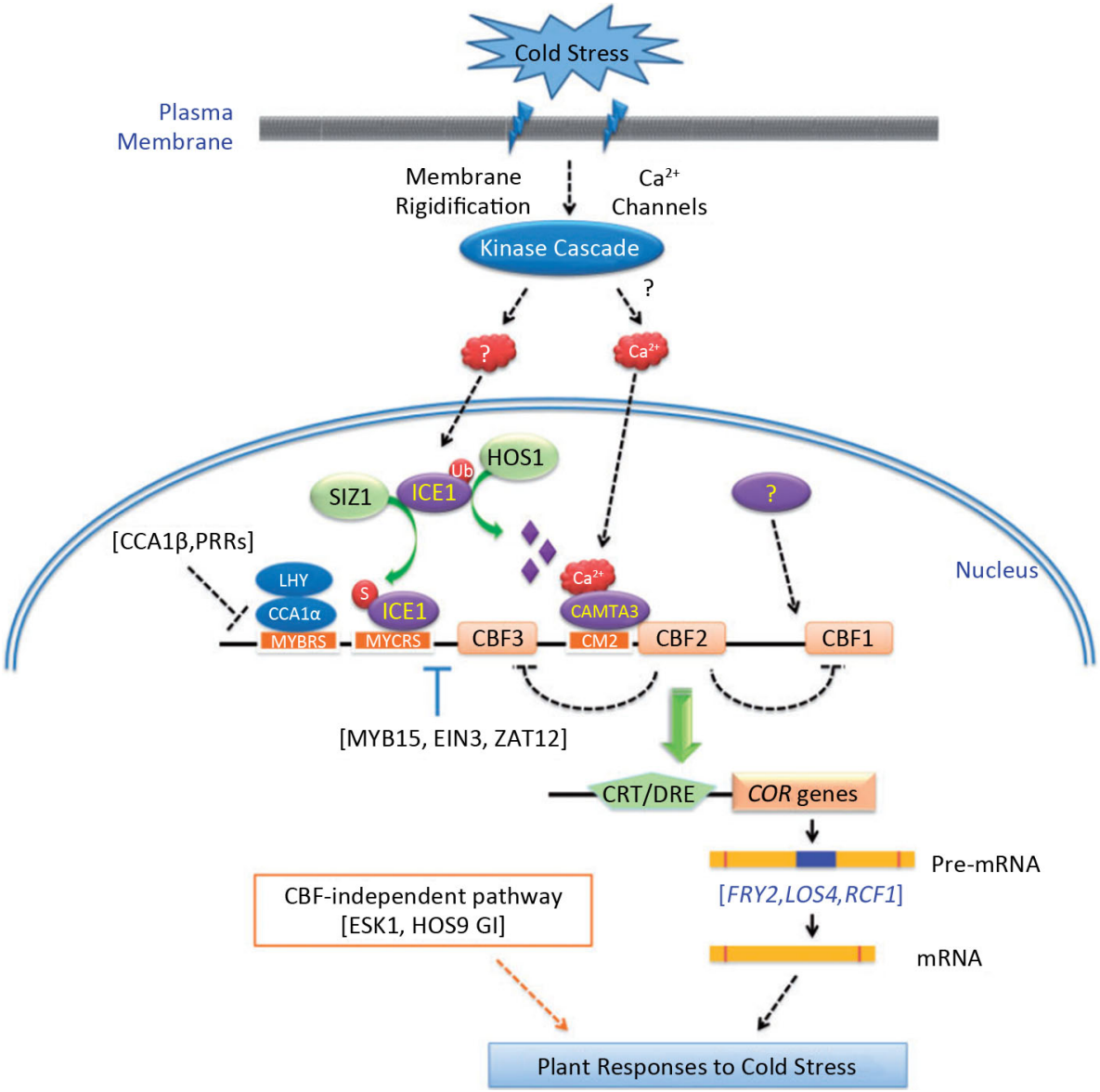

Figure 2. The signaling transduction pathway of CBF-regulated response to stress in plants
图 2. 植物 CBF 冷信号转导途径[35]

依赖的低温信号转导机制将有助于揭示植物低温胁迫应答的机理，同时也为选育耐寒作物及牧草新品种提供理论支撑。

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