

Research Progress in Signal Transduction Mechanism of Cytokinin

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Abstract

Cytokinin (CK) is a kind of molecular purine derivative, which plays an important role in promoting cell division, delaying leaf senescence and inhibiting apical dominance. The signal transduction pathway of CK has always been a hot topic in the field of CK research, but there are few reports about its mechanism of action at the molecular biological level. In recent years, the application of molecular biology technology and the study of related mutants have promoted the study of CK signal transduction system at the molecular level, revealed the role of this signal transduction and other hormones, and initially established the model of CK signal transduction pathway. This paper reviews the signal transduction mechanism of CK from three aspects: signal transduction components, signal transduction mechanism and the interaction between signal transduction and other hormones.

Keywords

Cytokinin, Signal Transduction, Histidine Receptor Kinase, Response Regulator

细胞分裂素信号转导机制研究进展

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摘要

细胞分裂素(Cytokinin, CK)是一类分子嘌呤衍生物, 在促进细胞分裂、延缓叶的衰老以及抑制顶端优势等方面具有十分重要作用。CK信号转导途径一直是CK研究的热点领域, 但是从分子生物学水平阐明其作

用机理的报道还十分匮乏。近年来,对分子生物学技术的应用以及相关突变体的研究,促进了在分子水平上对CK信号转导系统的研究,揭示了该信号转导与其他激素之间的作用,同时初步建立了CK信号转导途径的模型。本文主要从信号转导组分、信号转导机制以及信号转导与其他激素的相互作用的等三个方面,对CK信号转导机制进行了综述。

关键词

细胞分裂素, 信号转导, 组氨酸受体激酶, 应答调节因子

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1. 引言

细胞分裂素(Cytokinin, CK)信号转导途径是一种与细菌双组分信号传导系统类似的磷酸化/去磷酸化级联放大系统。该系统最早在细菌中被发现,例如大肠杆菌基因组编码超过60种不同的双组分信号元件,它们能够对一系列不同的环境刺激作出反应[1][2],通常由感受环境刺激的膜定位的感应激酶和直接调控靶基因转录的反应调节因子组成[3]。土壤杆菌毒性基因、盐杆菌趋化性基因、假单胞菌和欧文氏菌的过敏性反应基因HRP均通过双组分信号转导系统进行调控[4]。细菌的双元组分系统的意义在于,阐明了细菌对环境变化作出反应的基本过程,为推进细菌行为、生态、生理生化研究奠定了基础。

拟南芥作为最常用的植物学研究模式生物,其CK信号转导系统包括感受CK信号的组氨酸受体激酶(arabidopsis histidine protein, AHK)、磷酸转运蛋白(arabidopsis histidine phosphotransfer protein, AHP)、应答调节蛋白(arabidopsis response regulator, ARR)组成[5]。通过组氨酸到天冬氨酸之间磷酸传递,植株能够感知各种环境刺激并调控自身基因的转录,对外界环境其作出相应的应答。

2. 细胞分裂素信号转导组分

2.1. 组氨酸受体激酶

CK组氨酸受体激酶主要由CRE1/AHK4、AHK2和AHK3组成[6]。它们具有相似的结构,均含有一个跨膜结构域,其中部分位于胞外用于信号输入和另一部分位于胞内用于信号输出。胞外部分有一个CHASE结构域,具有CK结合功能,而胞浆部分有组氨酸激酶和C末端,包含所有受体结构域酶功能所必需的高度保守残基的[7][8]。在早期研究当中,人们鉴定了CK突变体cre1对外源CK不敏感,呈现细胞数量减少和韧皮部缺乏表型,互补实验和CRE1等位基因测序显示该突变与AHK4基因相关,从而揭示了AHK4作为CK受体的功能[9][10]。受体激酶AHK2/AHK3可参与质体转录产物的积累,上述两种酶功能的缺失导致叶片细胞较少,叶绿素含量低[11][12]。AHK3在延缓叶片衰老过程中起着重要作用,AHK3基因突变将导致下游响应因子去磷酸化,进而调控下游基因表达[13]。

2.2. 磷酸转运蛋白

拟南芥磷酸转运蛋白AHP位于CK信号受体AHK下游,能够介导磷酸基团从激活的混合传感器组氨酸接受域到反应调节器的受体结构域的转移。拟南芥基因组编码5个含有激活所必需的高度保守残基AHP蛋白,以及一个缺乏组氨酸磷酸化位点的APHP1/AHP6,这些蛋白均以包含连续组氨酸残基的

高度保守磷酸传递结构域作为磷酸化位点[14] [15] [16] [17]。在酵母双杂交实验中, AHP 能够与 AHK、ARR 因子结合, 并参与多步磷酸反应过程中[18] [19]。对基因功能分析表明, AHP1、AHP2、AHP3 和 AHP5 能够作为 CK 信号转导的正向调节因子, 而 AHP4 对 CK 信号响应很低, 某些情况下甚至起负调节作用, 相应的突变体则表现出抑制初生根伸长、侧根形成、下胚轴伸长以及诱导 CK 响应基因表达[20]。此外, 由于该蛋白的磷酸转运功能, AHP 主要定位于细胞质和核中, 并且在两者之间不断循环[6]。

2.3. 应答调节因子

拟南芥 CK 应答调节因子主要有两大类型: A 型 ARR 家族和 B 型 ARR 家族。

根据系统进化树分析, B 型 ARR 分为 3 个亚家族 11 个成员: 第一个亚家族包含 ARR1、ARR2、ARR10、ARR11、ARR12、ARR14、ARR18 共 7 个成员, 第二个亚家族包含 ARR13、ARR21 两个成员, 第三个亚家族也由两个成员 ARR19 和 ARR20 组成[21] [22]。B 型 ARR 的特点包含一个接受结构域和一个大的 C 端扩展结构域, C 端扩展结构域的关键保守特性是含有一个类似 Myb 的 DNA 结合域, 称为 GARP 结构域[23] [24]。B 型 ARR 可以作为转录因子具有转录激活功能, 在酵母杂交实验中, 通过其 GARP 结构域与下游基因 DNA 序列结合, 转录激活下游基因表达[24]。与其功能一致的是, 细胞亚定位结果显示 B 型 ARR 主要定位在细胞核中[25]。遗传分析结果表明, 至少 5 个 B 型 ARR 成员参与了对 CK 信号转导途径的调控, 其中 ARR1、ARR10 和 ARR12 在大多数经典的 CK 响应通路中起主要作用[26]。B 型 ARR 多突变体表现出抑制根的伸长、侧根形成和下胚轴伸长以及愈伤组织的体外诱导和芽形成等现象[4]。ARR1、ARR10、ARR12 功能缺失导致地上部分发育迟缓, 呈现初生根生长中止, 种子变大, 雌配子体发育缺陷等表型[26]。

A 型 ARR 应答调节因子包含有 10 个成员: ARR3、ARR4、ARR5、ARR6、ARR7、ARR8、ARR9、ARR15、ARR16 以及 ARR17, 并由 5 对高度相似氨基酸序列编码[27]。与 B 型 ARR 不同, A 型 ARR 包含一个接受结构域但不含有典型的输出结构域。A 型 ARR 绝大部分氨基酸序列是保守的, 但在 N 端和 C 端序列上存在差异, 这可能有助于下游信号的输出[14]。大部分的 A 型 ARR 在 CK 诱导下, 能够快速上调表达, 定量反映植株体内 CK 的水平, 因此常被作为 CK 含量的标记基因[28]。CK 对 A 型 ARR 的诱导表达不是在从头合成蛋白质的情况下, 并且 A 型 ARR 启动子通常包含多个 B 型 ARR 结合位点, 表明 CK 对其诱导是强烈且可重复的上调过程[29]。其他信号途径可以通过 A 型 ARR 影响 CK 信号途径, 例如, 生长素在顶端分生组织中对 ARR7 和 ARR15 的调节, WUSCHEL 在茎尖分生组织中对多个 A 型 ARR 的调节[30] [31]。ARR3、4、5、6、7、8、9、15 可作为 CK 信号的负调控因子, 在 CK 信号的负反馈通路中起重要作用, 降低对 CK 的敏感性[21] [31] [32]。此外, 拟南芥中还存在一类 CK 应答因子 CRF (cytokinin response factor), 共有 8 个成员, 依次为 CRF1、CRF2、CRF3、CRF4、CRF5、CRF6、CRF7 以及 CRF8, 其中 CRF6 被报道参与 CK 信号的下游传递[33] [34] [35]。

3. 细胞分裂素信号转导机制

当植物细胞表面接受 CK 信号时, 质膜上的 AHK 能够结合 CK 并发生自磷酸化, 并将磷酸基团由激酶区保守的组氨酸残基转移至信号接收区保守的天冬氨酸残基上[36]。随后, 天冬氨酸的磷酸基团被传递到胞质中的 AHP 上, AHP 进入细胞核并将磷酸基团传递给一系列 ARR [37]。在这些反应调节因子中, A 型 ARR 负调控 CK 信号, B 型 ARR 则激活靶基因转录进而调节 CK 下游反应, 并且 B 型 ARR 能够和 A 型 ARR 启动子区域结合, 进而调控 A 型 ARR 表达。此外, A 型 ARR 作为 CK 的负调控因子可以抑制 B 型 ARR 的活性, 从而形成一个负反馈调节来调控 CK 信号, 进而引发下游的一系列生化活性反应, 调节植株正常生长发育[38] (图 1)。

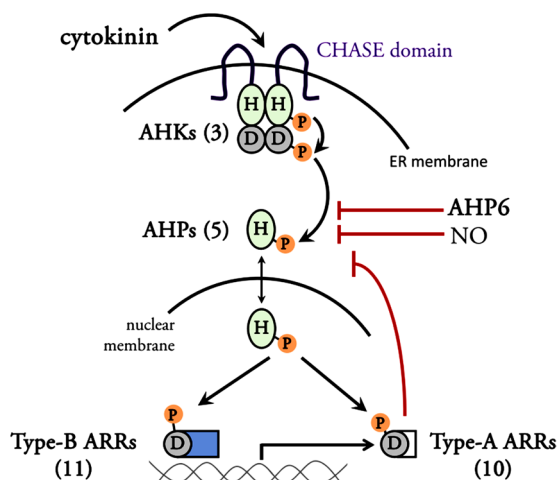


Figure 1. Signal transduction mechanism of cytokinin [39]

图 1. 细胞分裂素信号转导机制示意图[39]

4. 细胞分裂素与其他激素信号途径

CK 与 IAA (indole-3-acetic acid)在植株正常生长过程中,起相互促进又互相抑制作用。在愈伤组织中,CK 与 IAA 共同促进细胞的分化,而对于侧根的形成则互相拮抗。在胚根早期发育过程中,IAA 可以诱导 ARR7 和 ARR15 的表达,进而抑制 CK 对细胞的积累作用[40]。

独角金内酯(strigolactone, SL)在植物根中合成,向上运输至叶腋处,抑制腋芽的生长。SL 的合成与植物自身的生长状况相关,植物营养状况良好时,SL 含量会增加,反之则下降[41] [42]。最近,SL 被报道能够通过 D53 激活水稻细胞分裂素氧化酶 OsCKX9 表达,进而调控水稻 CK 水平。呈现水稻分蘖数增加,穗子变小的表型[43]。

CK 能够促进细胞分裂和组织分化,乙烯(ethylene)则促进植株衰老和果实的成熟,两者均在植物生长发育中起到至关重要的作用。ACS 是乙烯合成途径的关键酶,CK 可以通过 ACS 诱导乙烯合成[44]。一方面可能是 CK 将 ARR 信号直接传递给乙烯,另外一方面可能是 CK 信号途径中的 AHP 与乙烯受体 ETR1 产生互作[45]。

CK 与赤霉素(gibberellic acid, GA)均能促进细胞分裂和伸长、种子萌发、下胚轴和茎秆伸长、根的生长[46]。spy 是 GA 信号转导相关突变体,突变体中 A 型 ARR 被抑制表达,普遍认为 SPY 通过影响 CK 双组分信号转导系统,进而使 A 型 ARR 活性受到抑制[47]。但是,CK 是否能够影响 GA 的合成途径还不是很清楚。

5. 展望

近年来,人们在 CK 信号转导途径研究中取得了许多重要进展。然而,对 CK 受体成员及其功能研究还没有一个清晰的轮廓,不能完全确定信号转导途径中起主要作用或直接作用的基因。因此,对相关专一性受体及其生物学功能的研究,不仅有助于理解 CK 与受体结合的下游调控机制,而且有利于 CK 信号引起的不同生理反应机制的探索。随着分子生物学技术的发展和对相关突变体的深入研究,人们对 CK 信号转导机制的认识将会逐步深入。

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