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镉超富集植物耐镉性的分子机制研究进展

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摘 要：土壤中的镉污染已经成为威胁生态系统和人类健康的严重环境问题。植物修复是一种绿色、经济、生态友好的土壤修复技术，超富集植物由于在植物修复中的巨大应用价值而备受关注。了解镉超富集植物的分子调控机制，对于Cd土壤修复具有重要理论指导意义。该文综述了国内外镉超富集植物耐镉性分子机制的研究现状，并对存在的问题和研究前景进行了展望。

关键词：超富集植物；镉胁迫；植物修复；分子机制

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土壤中的重金属污染已经成为全球性的严重环境问题[1-4]。在所有的重金属污染物中，镉(Cd)是最具有植物毒性的物质之一[4-6]。土壤中过量的Cd会被植物吸收，影响植物的生长、细胞结构、光合作用以及酶活性[7]，使农作物产量和质量下降，并通过食物链的富集作用进入人体，严重威胁人类健康[3,7-8]。近年来，我国由于土壤Cd污染而引发的“镉米”事件频发。如何解决土壤中的镉污染已经成为亟待解决的重要研究课题。

重金属在土壤中的自然净化过程一般需要上千年的时间，因此有必要采用人为的方法消除土壤中的重金属污染物。传统处理重金属的物理化学方法各有优点，但不同程度地存在着投资大、能耗高、操作困难、易产生二次污染等缺点[9]，特别是在处理低含量重金属污染时，操作费用和原材料成本过高。

1983年美国科学家CHANEY[10]首次提出了植物修复(Phytoremediation)的理论，即利用超富集植物清除土壤中的重金属污染。植物修复技术因其具有治理成本的低廉性、环境美学的兼容性和治理过程的原位性等优势，成为了具有广泛应用前景的技术。镉超富集植物也由于在植物修复中的巨大应用价值而备受关注[10-12]。镉超富集植物是指那些对Cd有很强的耐受能力，茎或叶中(或地上部)重金属达到临界含量标准100 mg/kg[13-14]且富集系数[15]和转移系数[16]均大于1的植物。目前，国内外已经筛选出的Cd超富集植物有：天蓝遏蓝菜(*Thlaspi caerulescens*)[17]、圆叶遏蓝菜(*Thlaspi rotundifolium*)[18]、巴丽芥菜(*Cardaminossis halleri*)[19]、宝山堇菜(*Viola baoshanensis*)[20]、东南景天(*Sedum alfredii* H.)[21-22]、龙葵(*Solanum nigrum* L.)[23]、*Thlaspi praecox*[24]、球果菜(*Rorippa globosa*)[25]、商陆(*Phytolacca acinosa* Roxb)[26]、三叶鬼针草(*Bidens pilosa* L.)[27]等。然而，这些Cd超富集植物都不同程度存在着生长缓慢、植株矮小、地上部生物量较小和地域性分布等缺点，严重制约了植物修复技术的有效性和广泛性应用[14]。

研究超富集植物耐重金属的分子机制有助于人们清楚了解植物的超富集调控机理，并有利于人们更加有效的利用相应途径来提高植物修复的成果[28]。该文总结了近年来国内外关于植物重金属应答的相关分子机制的研究进展，并对其存在问题、具体作用机制和调节网络进行了探讨和展望。

1 参与重金属胁迫应答相关的基因

植物在长期的进化过程中产生了一系列应对重金属胁迫的机制，如植物对重金属的螯合作用、根系富集作用、细胞壁束缚、跨膜转运以及抗氧化响应等[1,29]。近年来，对于植物超积累机制的研究越来越多的深入到分子水平，重金属应答过程中的很多基因已经得到了克隆与功能解析[30-33]。许多与胁迫相关蛋白和信号分子被证实参与到Cd胁迫应答过程中，包括*CAD1*(hydroxycinnamyl al-

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cohol dehydrogenase 1)、*GSH1*(glutathione synthase1)、*AtPDR8*(pleiotropic drug resistance 8)、*AtATM3*(ATP-binding cassette transporter)、*PCS1*(phytochelatin synthase)、*PCR1*(Plant Cadmium Resistance 1)、*HMA3*(Heavy Metal ATPase 3)、*HsfA4a*(heat shock transcription A4a)、*HMA4*(Heavy Metal ATPase 4)、*ABCC1*、*ABCC2*(ATP-binding cassette transporters1,2)、*MT1a*(Metallothioneins 1a)、*Nramp5*(Natural Resistance and Macrophage Protein)和 *MAN3*(mannanase)[5-6,34-46]。尽管已经克隆了许多与镉超富集相关的直接效应基因,但是关于镉超富集植物的耐镉分子机制还存在许多问题,如:拟南芥中金属硫蛋白(Metallothioneins,MT)可以通过半胱氨酸上的巯基与重金属螯合,其表达水平与 Cd 的耐受性呈正相关[42],但超富集植物中 MT 的具体作用还不清楚;拟南芥中叶绿体上的转运因子 *HMA1* 是 Cd 耐受性相关基因,但只在 Cd 超富集植物 *Cardaminossis halleri* 中证实与锌超富集相关,而 *HMA1* 在其它 Cd 超富集植物中的功能研究尚鲜见报道[47];*HMA4* 是介导木质部装载过程的关键基因,在 Cd 超积累特性进化过程中具有重要作用,但已有的几个过量表达研究均没有找到与 Cd 相关的表型[48-51],暗示着 Cd 的超富集和耐受性可能是多个基因共同作用的结果。

从转录组水平整体观察 mRNA 的表达变化,有助于从宏观上把握植物超积累的主要分子机制,也有助于从中挑选关键基因,深入开展研究[52]。目前已经在几个物种开展了 Cd 胁迫条件下的转录组研究,如拟南芥[30,53]、豌豆[54]、龙葵[29]、大麦[55-56]、东南景天[57]、水稻[58]等。这些研究鉴定出大量与 Cd 胁迫应答相关的基因和转录因子,分别属于 *WRKY*[59]、*bZIP*[60]、*ERF*[61]和 *MYB*[62]等不同的基因家族,并且与其它胁迫相关的转录因子具有相同的信号转导通路,因此也可以被其它的逆境胁迫信号,譬如寒冷、干旱、水杨酸、茉莉酸和过氧化氢等激活[63]。尽管这些研究大大拓展了对 Cd 超富集植物耐镉性的认识,但是这些应答重金属胁迫的基因的表达调控机制,其中关键的调控因子等问题仍需要进一步研究。

2 参与重金属胁迫应答相关的调控因子

microRNA(miRNA)是小分子 RNA(Small RNA)中的一个重要类群,通过介导靶 mRNA 的降解或翻译,在转录后水平负调控靶基因的表达,是一种新型的表达调控因子[64-65]。已有的研究发现这些 Cd 相关的 miRNA 可以通过重金属转运、硫同化、抗氧化胁迫和生长素信号转导途径参与 Cd 胁迫应答,在植物对重金属胁迫的响应过程中发挥着重要作用[66-68]。如 miR159 和 miR167 分别通过调控重金属离子转运的重要蛋白 ABC 型转运蛋白(ATP-binding cassette)和 Nramp 蛋白家族(Natural Resistance-associated Macrophage Protein)发挥作用[69-70];miR395 通过参与调控硫饥饿诱导的低亲和力硫酸盐转运体(*SUL-TR2;1*)和 *APS1*、*APS3* 和 *APS4* 共 3 个 ATP 硫酸化酶基因(ATP sulphurylase,APS)参与重金属 Al、Cd 和 Hg 胁迫应答[68,71-72];miR398 通过靶向 2 种 SOD,即 Cu、Zn 超氧化物歧化酶(Cu Zn superoxide dismutase,CSD)中的 CSD1 和 CSD2,在 Al、Cd、Hg 和 Cu 等重金属的胁迫响应中发挥重要作用[68]。近年来,随着高通量测序技术的发展和应用,植物中越来越多重金属相关的 miRNA 得到克隆与鉴定,但是相比之下,它们的生物学功能的研究较少。miRNA 处于基因表达调控的中心位置,这些 miRNA 究竟如何发挥作用、其具体的功能与作用机制及参与的生物过程与信号通路等问题仍不清楚。

3 镉超富集植物耐镉性的分子机制研究展望

目前,在 Cd 胁迫下进行的分子机制研究,大多采用的是单独的转录组学测序或单独的 Small RNA 测序进行分析,二者联合的组学分析并不多见。对研究对象同时开展 miRNA 和 mRNA 高通量测序,有助于从基因组水平上了解基因的整体表达变化以及 miRNA 的调控机制。而且,以往对 Cd 超富集植物的研究主要集中在蔷薇类植物十字花科上。所以,对其它 Cd 超富集植物的深入研究,尤其是菊类 Cd 超富集植物的研究,对于深入理解超富集植物耐 Cd 分子调控机制具有独特优势。这些问题的探索,将有助于进一步了解植物吸收转运和积累镉的整体过程与机制,进而有望人为地调控其中的某些过程,以提高植物对镉污染的耐受能力或减少对镉的吸收。也有助于加深对转录调控因子和信号通路的研究,为分子育种提供科学依据与具体的基因材料,最终使植物修复得到广泛的应用。

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Research Progress on the Molecular Mechanism Underlying Cadmium Hyperaccumulation Tolerance

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Abstract:Contamination of soil by cadmium was a severe environmental problem,which represented a direct contact risk to humans and ecological recipients. Phytoremediation had been regarded as a suitable technique for the pollution control

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硒延缓果蔬成熟衰老与抗逆机理研究进展

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摘　要:硒是人和动物必需的微量元素,对防治疾病、增进健康和延缓衰老具有重要意义。现主要从硒的植物学功能、硒对果蔬生长发育的影响、硒延缓果蔬成熟衰老及提高果蔬抗逆性等方面概述了富硒果蔬研究的意义,并着重阐述了硒在延缓果蔬成熟衰老和诱导抗性等方面的作用机理及研究中存在的问题和未来研究方向。旨在为探索硒在果蔬采后贮藏保鲜中的应用及开发富硒果蔬提供理论和科学依据。

关键词:硒;果蔬;成熟衰老;抗逆性;贮藏保鲜

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硒是生态环境中一种重要元素,同时也是一种人体必需的微量元素,对人和动物具有多种生物学功能。硒元素和硒的化合物可以保卫细胞,抵抗铊、镉、汞、砷、铅等有毒物质和清除自由基等作用,对防治疾病、保持健康和延缓衰老具有非常重大的意义。有研究学者曾指出,缺硒可导致人体发生多种疾病,如癌症、肝病、冠心病、白内障、克山病等[1-2]。全球缺硒国家和地区约40多个,我国将近72%的县(市)呈不同程度的硒缺乏,其中近1/3为严重缺硒地区[3]。

人体日常摄入硒量至今暂时未有统一剂量。1988年中国营养学会给出建议的标准是50 μg/d,国际硒学会于1979年给出的标准是60 μg/d[4]。TAYLOR等[5]对我国多个省市的调研发现,当前我国成人每日硒的摄入量仅为26 μg左右,相比较营养学会给出的标准低得多,说明我国广泛缺硒,有些区域重度缺硒。日常膳食中适量添加硒能增强人体对疾病的免疫力,减少由硒缺乏所导致的疾病。补硒制品分为有机硒制品和无机硒制品。很长一段时期,人体补充硒的途径主要是食用亚硒酸钠片和它的强化食盐等无机硒类富硒食品和含硒产品。然而,人体对这些无机硒制品吸收率很低,并且这些化合物在人体中可能会产生副作用[6]。相对而言,人体对有机硒产品的吸收率高,且不会发生毒性效应,可储存在人体器官组织内,人们补硒的首选便是有机硒制品[7]。目前已通过相关试验证实,最有效和安全的补硒途径就是食用富有机硒食品[8-9]。由此可见,研究生物富硒和制定富硒农产品标准及发展富硒功能农业很有前景和意义。

硒在植物的生长过程中扮演着重要角色,是硒富集植物发育所需的微量元素之一,同时也是当前研究的热点之一。植物可将无机硒转化变有机硒,是硒在自然界流通中极其重要的一环。不少学者的研究结果证明,硒在植物体内以有机硒化物状态为主,但不同植物间存在一定差异性。施用硒肥可有效改善作物品质,有助于生

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of heavy-metal contaminated soil for green, safe technology and the properties of efficiency, economy and ecological harmony. Hyperaccumulators had recently gained considerable interest because of their potential use in phytoremediation. Understanding the molecular mechanisms of hyperaccumulation may help in enhancing the performance of hyperaccumulators for phytoremediation. This paper reviewed recent insights and existing problems of hyperaccumulators, and the directions of research in this area were introduced.

Keywords: hyperaccumulators; cadmium stress; phytoremediation; molecular mechanism