

植物根系细胞抑制镉转运过程的研究进展

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摘要: 镉是我国重金属污染土壤中最常见的元素, 在酸性土壤中, 镉能在水稻和蔬菜等作物根系中大量富集, 并转运到地上部, 其中可食部分的镉含量直接影响食品的质量安全。植物根系的细胞壁、细胞膜和细胞器对镉具有识别能力, 能通过沉淀作用、络合作用和区域化作用等, 把大量的镉固定在根系内, 抑制其向地上部转运, 从而保证地上部各种生理活动的正常进行。本文综述了植物根系细胞各组分的控镉原理, 为发掘优异的种质资源和基因资源提供参考。

关键词: 镉; 根系; 细胞壁; 细胞膜; 转运

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Inhibiting Cadmium Transport Process in Root Cells of Plants: A Review

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Abstract: Cadmium (Cd) is the most common element found in the heavy-metal contaminated soils in China. Roots of rice and vegetables can concentrate Cd from acid soils, and then transport Cd to above-ground parts. Cd in edible part of plants directly influences the food safety. Cellwall, plasma membrane and organells of root cells in plant can discriminate Cd from other elements. A lot of Cd can be fixed in root cells by precipitation, complexation, compartmentation, and so on, to inhibit its transport from roots to shoot and guarantee the physiological activities in above-ground parts carrying out normally. This paper summarized recent advance on inhibiting Cd transport process in subcellular fractions of root cells of plants, which is in advantage of exploring excellent germplasms and gene resources in the future.

Keywords: cadmium; root; cellwall; plasma membrane; transport

镉(Cd)是我国重金属污染土壤中最常见的元素, 它虽然不是植物生长发育所依赖的必需元素, 却能在许多植物根系中大量富集。水稻根系中的 Cd 浓度可以比环境中的 Cd 浓度提高几百倍, 一般为 $150 \sim 1\,600 \text{ mg} \cdot \text{kg}^{-1} \text{ DW}$, 因品种类型、土壤理化特性和污染状况等因素的变化而变化^[1-4]。土壤溶液中的镉离子接

触到根系表皮组织时, 首先进入由细胞间隙、细胞壁微孔以及细胞壁到质膜之间的空隙等构成的“自由空间”, 然后通过主动吸收或被动吸收跨膜进入细胞质, 再经胞间连丝进行共质体运输, 或通过自由空间构成的质外体运输到达内皮层凯氏带处, 再跨膜转运到细胞质中进行共质体运输。因此, 进入根系的 Cd 被分解成就地贮存和继续转运两大部分。一部分 Cd 沉积在细胞壁上; 另一部分 Cd 穿过细胞膜进入到细胞质中, 其中的少部分继续进行跨膜运输, 进入液泡和其他细胞器中储存起来, 其余的 Cd 继续向地上部转运。不同水稻品种根系累积 Cd 的能力和向地上部转运 Cd 的效率差异非常显著。一般把能超量吸收 Cd

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并将其运移到稻米中的水稻品种称之为高镉积累品种;把吸收转运到稻米中的Cd含量较低的品种称之为低镉积累品种。本文围绕植物根系细胞壁、细胞膜和细胞器对根际环境中Cd的拦截作用及其植物种类间的多样性进行了综述,以期筛选和培育具有多种拦截功能的植物品种提供参考依据。

1 细胞壁对Cd的区域化作用

植物细胞壁由初生壁、次生壁和胞间层3部分组成。细胞分裂后,最初由原生质体分泌形成的细胞壁称之为初生壁,主要成分为纤维素、半纤维素,同时含有少量的结构蛋白。部分植物细胞(如根系表皮细胞)停止生长后,其初生壁内侧继续积累纤维素、木质素等物质而形成的细胞壁层称之为次生壁。次生壁厚而坚硬,使细胞壁具有很大的机械强度。两相邻细胞所共有的一层膜称之为胞间层或中胶层,主要成分为果胶质。有助于将相邻细胞粘连在一起,并可缓冲细胞间的挤压。细胞壁能将重金属离子隔离在胞外,主动参与植物对重金属胁迫的响应过程,进而降低进入原生质体的重金属离子数量^[5-6]。在镉超富集植物东南景天、天蓝遏蓝菜(*Thlaspi caerulescens* L.)和结缕草中,细胞壁中的Cd占绝大部分,细胞器和胞液所含的Cd较少,根、茎、叶均可通过细胞壁的区域化作用降低Cd的毒性^[7-9]。根系细胞壁上沉积的Cd约占水稻根系中Cd总量的45%~90%^[10]、小麦根系Cd的26%~32%^[11]、大麦根系Cd的36.3%~43.1%^[12]、高粱根系Cd的49.7%~54.2%^[13]、结缕草根Cd的58%~80%^[8]、互花米草根Cd的47.0%~54.6%^[14]。由此可见,细胞壁沉积是许多植物解除Cd毒性的主要方式。

植物和微生物细胞壁对Cd的吸附固定主要靠细胞壁中纤维素、半纤维素、木质素、果胶等大分子物质提供的各种带负电的配位基团来完成,如羟基、羧基、醛基、氨基、磷酸基、胺基、酰胺基等^[5,15-16]。拟南芥细胞壁中果胶和半纤维素含量的下降会显著影响细胞壁对Cd的吸持能力^[17];但如果用一氧化氮(NO)增加根部细胞壁果胶、半纤维素含量,就能显著增加水稻根细胞壁中的Cd积累量和水稻的耐Cd能力^[18]。木质素是植物细胞次生壁的主要成分之一,其代谢活性和含量的变化与植物的耐Cd能力密切相关。在Cd处理下,大豆根生长受抑制,根木质素含量增加,并伴随着过氧化物酶(POD)和漆酶(LAC)活性的增加,同时,与木质素合成相关的POD基因表达也有所上调^[19];洋甘菊(*Matricaria chamomilla*)、柳树等植物根系中的

木质素也会显著增加^[20-21]。细胞壁中的一些酶蛋白则通过一系列生理生化反应参与到植物对Cd的固定化中。例如,亚麻(*Linum usitatissimum*)受到Cd胁迫时,与细胞壁形成密切相关的果胶甲酯酶(pectin methylesterase, PME)的活性显著增加^[22]。PME负责细胞壁中果胶的脱甲基化,对植物细胞生长发育有重要影响^[23-24]。一些无机离子如钙、锌、硅等通过增加Cd在细胞壁中的沉积和自由空间中交换态Cd的比重等途径缓解Cd对水稻的毒害,抑制水稻对Cd的吸收及其向地上运输^[25-30]。

2 细胞膜对Cd的阻控作用

细胞膜又称原生质膜,是分隔细胞内、外不同介质和组成成分的界面,主要由磷脂双分子层、膜蛋白以及糖和糖脂构成。原生质膜通过其上孔隙的开启程度和跨膜蛋白的特异性识别,能选择性地物质转运,实现屏蔽有害物质进入细胞质的目的。细胞膜进行物质转运的方式主要有被动运输和主动运输两大类。这两种运输方式对Cd在根系内的转运和积累都有显著的影响。

离子或小分子物质在膜上质子泵的作用下,逆浓度差或逆电位差进行跨膜转运的过程,称为主动运输。主动运输需要消耗大量热量并且需要载体。例如,位于根系细胞膜上的锌转运蛋白家族(ZRT)和铁转运蛋白家族(IRT)主要负责把环境中的Zn、Fe、Mn、Cd等重金属转运到细胞质中^[31]。至今发现了大约100种锌铁转运蛋白,分属于细菌、真菌动物和植物^[32]。OsIRT1和OsIRT2是水稻根系中的2种关键Fe转运载体,参与根系对Fe²⁺的直接吸收和Fe³⁺-PS螯合物的转运,它们对Cd²⁺的亲合性较高,过量表达时能够提高水稻对Cd²⁺的转运效率^[33-36]。水稻根系细胞膜上的自然抗性巨嗜细胞蛋白(natural resistance-associated macrophage protein)也与Cd的吸收转运密切相关。水稻中已发现至少有7个不同的基因(*OsNramp1*~*OsNramp7*)调控着金属离子的转运种类和转运能力,*Nramp1*主要负责Fe²⁺和Cd²⁺的转运,*Nramp5*主要负责Mn²⁺和Cd²⁺的转运^[3,37]。

水、尿素、二氧化碳等脂溶性物质由膜的高浓度侧向低浓度侧的扩散过程,称为自由扩散;非脂溶性物质在膜蛋白的帮助下,顺浓度差或电位差跨膜扩散的过程,称为协助扩散。这2种扩散本身不消耗能量,均属于被动运输。对于大多数金属离子而言,主要通过协助扩散过程进入根系细胞中。因为协助扩散需要

载体或离子通道,所以具有特异性、饱和性和竞争型抑制3个显著的特点。例如,位于植物细胞质膜上的Shaker家族离子通道,主要调节K的选择性吸收,其中AKT1对钾离子的转运率既受外界K⁺浓度的影响,又受Na⁺、Ca²⁺和质子的调控^[38-39]。植物根系对Cd²⁺的吸收与K⁺有相似之处,既受根系周围环境中Cd浓度的影响^[40-42],又受Ca²⁺、Zn²⁺、K⁺等阳离子的影响^[43-45],存在明显的竞争性抑制现象。遗憾的是,根系细胞膜上的离子通道如何调控Cd吸收转运的分子机理尚不清楚。

3 细胞器对镉的区隔化作用

细胞器是细胞中通过生物膜与细胞中其他部分分隔开来的、功能上独立的亚细胞结构,与细胞质基质一起统称为细胞质。细胞器拥有的细胞内膜与细胞膜具有相似的结构和功能,也能通过选择性吸收把Cd转运到细胞器内,通过区隔化作用减弱或消除Cd对细胞质中各种正常生理活动的干扰。参与多种重金属转运的重金属ATPase(HMA)不仅存在于细胞膜上,而且广泛分布与叶绿体、高尔基体、液泡、内囊体等细胞器的质膜上^[31]。

液泡的区隔化作用是植物防御重金属毒害的重要机制。液泡作为植物细胞一类特殊的细胞器,对于维持整个细胞和组织的渗透压起着非常重要的作用。液泡中的物质类型非常丰富,主要有无机盐、有机酸、糖类、脂类、蛋白质、树胶、鞣酸类、生物碱和花色素苷等物质,这些代谢物能与金属离子形成络合物或螯合物而降低其毒性。如位于水稻根系厚壁组织、薄壁组织和周皮细胞的液泡膜上的OsHMA3、位于拟南芥根系细胞液泡膜上的HMT1等重金属转运蛋白,能把大量的Cd从细胞质中转运到液泡中。胁迫时间越长,根系向地上部分转运的Cd越多,茎叶中的积累量与根系中积累量的差距越小^[46-48]。Cd与植物螯合肽(PCs)结合后能转运至液泡中区隔起来,限制其向地上部转运^[49]。但也有研究发现敏感型大麦根系和叶片中的PC2和PC3含量都显著高于耐镉大麦,说明根系合成较多的PC2和PC3有助于Cd从根部向地上部的转运^[12]。

4 结论与展望

对于农田生态系统中,植物根系中的Cd积累量直接反映了土壤中的Cd活性。Cd在根系细胞各组分中的不同分布则反映基因的调控作用。对于大多数植

物而言,细胞壁对Cd²⁺的区域化隔离是降低Cd的移动性、削弱其生理毒害的一种重要策略。细胞壁中的多糖、蛋白质和木质素等成分能与Cd形成相对稳定的络合物,当环境中出现较高浓度的Cd时,植物根系能通过增加细胞壁厚度来提高其结合Cd²⁺的能力。细胞膜是防止细胞外物质自由进入细胞的屏障,它的选择透性保证了细胞内生化的反应环境的相对稳定性。细胞膜上的载体蛋白和通道蛋白专门负责各种离子的转运,是重金属离子进出细胞的必经之路。Cd是植物生长发育的非必需元素,只能通过其他必需元素的专性通道或离子选择性较低的共用通道进入细胞内。因此,未来研究应在以下2个方面进一步加强。

(1)根系细胞壁Cd固定机理的研究。植物根际土壤中的营养元素和植物体内抗逆基因的表达水平都会影响根系细胞壁的发育对Cd的固定效应,研究Cd胁迫下细胞壁变化的基本规律和分子调控机制,研究能够稳定提高根系细胞壁捕获Cd的技术手段,就能使进入原生质体的Cd大幅度下降,保证细胞的正常代谢活动。

(2)载体蛋白和离子通道调控机理的研究。许多以主动运输为主的载体蛋白和以被动运输为主的离子通道是Cd跨膜运输的主要途径,必需元素的含量和基因的表达水平都会影响Cd的跨膜运输效率。但植物根系对Cd的敏感性远远超过其他元素,通过提高膜蛋白的识别能力,提升根系组织中各种载体蛋白和离子通道蛋白的拦截作用,就有可能大幅度降低污染环境中植物根系细胞内的Cd浓度及其向地上部的转运效率,生产出质量安全的农产品原料,进而加工出质量安全的食品,达到保障农业生产和改善农田生态环境的双重目的。

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