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重金属镉 (Cd) 在植物体内的转运途径及其调控机制

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摘要: 重金属镉 (Cd) 的毒害效应与其由土壤向植物地上部分运输有关, 揭示 Cd²⁺ 转运途径及其调控机制可为提高植物抗镉性以及镉污染的植物修复提供依据。本文对 Cd²⁺ 在植物体内的转运途径, 特别是限制 Cd²⁺ 移动的细胞结构和分子调控机制研究进展进行了回顾。Cd²⁺ 通过共质体和质外体途径穿过根部皮层进入木质部的过程中, 大部分在皮层细胞间沉积, 少部分抵达中柱后转移到地上部分。为了免受 Cd²⁺ 的危害, 植物体产生了多种限制 Cd²⁺ 吸收和转移的生理生化机制: 1) 环绕在内皮层径向壁和横向壁上的凯氏带阻止 Cd²⁺ 以质外体途径进入木质部; 2) 螯合剂与进入根的 Cd²⁺ 螯合形成稳定化合物并区隔在液泡中; 3) 通过 H⁺/Cd²⁺ 离子通道等将 Cd²⁺ 逆向转运出根部。植物共质体和质外体途径转运重金属镉的能力以及两条途径的串扰尚待进一步明晰和阐明。

关键词: 重金属; 镉; 共质体途径; 质外体途径; 调控机制

Transport Pathways of Cadmium (Cd) and its Regulatory Mechanisms in plant

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Abstract: Heavy metal (HM) toxicity is a worldwide concern because it damages plants by altering their major physiological and metabolic processes. The heavy metal cadmium (Cd) is a nonessential element, and is a valid inhibitor of plant growth. The toxic effect of cadmium is closely related to its transfer from the soil to the plant above ground parts. Understanding the transport pathway and regulatory mechanism of cadmium in plants may improve plant resistance to this heavy metal, in addition to providing a theoretical basis for the phytoremediation soils contaminated by cadmium. In this paper, we reviewed the transport pathways of Cd²⁺ in plants and what limits its mobility based on the cytological structural and molecular regulation mechanism of plants. As the main organ for transporting water and nutrients to the plant body, the plant root is also the main organ that absorbs toxic metals, such as cadmium. During the process of Cd²⁺ transfer from the root cortex to the xylem, most Cd²⁺ is deposited between the cells of the root cortex, with some reaching stele, before being transferred to the plant organs, such as the leaves in the above ground part of the plant. The transport pathway of Cd²⁺ through the root cortex is mainly apoplastic, with the cytoplasmic accumulation of Cd²⁺ possibly causing apoplastic transport towards the vascular cylinder to decline. The transport pathway of Cd²⁺ in the vascular cylinder is also mostly apoplastic, with cytoplasmic accumulation reducing Cd²⁺ transfer to the xylem. Since the aboveground parts of plants are more

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susceptible to Cd^{2+} poisoning, two cellular strategies to restrict the absorption and transfer of cadmium have evolved. First, the Casparian strip surrounding radial wall and the endodermis wall prevents Cd^{2+} from entering the root xylem via the apoplastic pathway. In addition, the Casparian strip promotes Cd^{2+} transport via the endodermis, leading to vacuolar isolation and cytoplasmic precipitation. Second, heavy metal detoxification occurs by chelating Cd^{2+} to form stable compounds, which are then deposited inside the vacuole. Third, excess cadmium also activates oxidative stress defense mechanisms and the synthesis of heavy metal stress related proteins to minimize metal toxicity, which includes the use of metallothiones and ion channels, such as $\text{H}^+/\text{Cd}^{2+}$ binding or sequestering Cd^{2+} into vacuoles. For systematic improvements in the phytoremediation of heavy metal pollution, a more comprehensive understanding of cellular mechanisms involved in Cd avoidance, uptake, transport, and accumulation is required. Furthermore, the excluder strategy by extensive sequestration and retranslocation of cadmium through symplastic and apoplastic pathways should be confirmed and explored in future studies.

Key Words: heavy metal; cadmium; symplastic pathway; apoplastic pathway; regulatory mechanism

镉(Cd)是一种毒性很强的重金属,对植物生长和发育而言属于非必需元素,轻度胁迫导致植物叶片干枯萎黄,根茎缩短,侧根数量减少,降低营养元素吸收,而重度胁迫则会减少叶绿素含量,扰乱水分平衡,抑制抗氧化酶活性,引起活性氧(reactive oxygen species, ROS)合成积累,降低细胞膜通透性,导致细胞损伤,进而显著抑制植物生长^[1-2]。当前,自然环境中植物地上部分的镉含量呈现增加趋势,既是环境中镉污染程度增加所致,也是植物自身在镉胁迫下进化的结果^[3]。随着对镉污染环境本土植物的不断筛选,一些镉的超累积植物不断被发现^[4]。

重金属镉发挥毒性的关键步骤是其被吸收进入根内并向植物地上部分运输,该过程受到植物外部和内部条件的影响。其中,影响根吸收镉的外部条件如土壤镉浓度、有机物含量、pH 值、氧化还原电位、温度和其它元素浓度等研究进展已有评述^[5]。由于植物地上部分对镉毒害作用更加敏感,为了减少 Cd^{2+} 向地上部分的转移,植物体内部阻碍 Cd^{2+} 进入木质部和韧皮部并限制其向上转运的机制已经引起了人们的关注。研究发现,细胞内部的螯合剂可以将镉螯合后隔离在液泡中,阻止 Cd^{2+} 以共质体途径(symplastic pathway)横向运输,减少抵达木质部和韧皮部 Cd^{2+} 的数量,进而减弱重金属镉向地上部分运输。在细胞外部,镉沿着细胞壁中的空隙从表皮、皮层到内皮层,经质外体途径(apoplastic pathway)进入木质部向上转运至植物的枝叶中^[6]。由于植物内皮层细胞壁中不透水的凯氏带会阻止 Cd^{2+} 的运输,因此 Cd^{2+} 进入内皮层后又转为共质体途径^[7]。本文着重回顾了镉转运途径及其调控机制研究进展,为植物抗镉性机制和镉污染防治提供理论依据。

1 植物体内 Cd 的吸收和转运途径

土壤中的镉在转移进入植物体内各组织器官后才会产生毒害效果,共质体途径是指 Cd^{2+} 从植物根毛细胞膜上的通道进入,再利用细胞与细胞间的胞间连丝,经由皮层、内皮层及周鞘进入根内导管细胞,而质外体途径则是土壤中的 Cd^{2+} 经由根吸收之后不进入细胞内,而是沿着细胞壁中的空隙从表皮、皮层到内皮层,进入木质部和韧皮部^[6]。镉通过以上两种运输途径抵达维管束并向枝叶转运,随着植物的生长和新陈代谢,逐渐被稀释或排出体外,进而减少对植物的危害。虽然植物地上部分的镉含量会随着土壤中镉浓度的增加而增加,但达到一定程度后就不再升高,如龙葵(*Solanum nigrum*)和中国石竹(*Dianthus chinensis*)地上部分的镉含量最高分别为 1110 和 414 mg/kg ^[8]。由于镉毒害严重威胁植物生长,导致其光合作用和蒸腾作用几乎停止,进而影响离子转运,因此,植物产生了多种限制 Cd^{2+} 吸收和转移的生理生化机制以利于植物生长发育。研究发现,植物根系中的 Cd^{2+} 含量通常高于地上部分,且地上部分对镉更加敏感,表明植物可能通过限制镉进入根中具有传导水分和养分功能的木质部和韧皮部,以减少 Cd^{2+} 向地上部分的转运^[9]。

1.1 影响镉在植物体内转运的外部因素

重金属镉并非地壳中含量丰富的元素,通常在岩石中伴随大量的锌而形成,土壤中镉含量的范围在 0.1—2 $\mu\text{g/g}$ ^[10]。Cd 在土壤溶液中溶解后,以水合离子、复杂的有机或无机化合物的形态存在,镉向植物体内迁移受到诸多因素的影响,如土壤 pH 值、有机质含量、土壤中存在的其它元素和氧化还原电位等,其中土壤 pH 值和有机质含量是影响 Cd^{2+} 在土壤中被植物吸收的主要因素。一方面,酸碱环境能够决定土壤颗粒表面电荷的正负性质和 Cd^{2+} 的存在形态,对于 pH 值较高的碱性土壤, Cd^{2+} 的迁移能力较低^[11]。另一方面, Cd^{2+} 容易和土壤有机质的功能团如羧基、烯醇羟基、醇羟基等形成有机镉络合物而降低活性^[12]。研究发现,植物根系分泌的可溶性有机物质导致根际土壤中 Cd^{2+} 进入根部表皮受阻^[13]。与此同时,铁、锰等金属元素的氧化物对土壤中 Cd^{2+} 也具有吸附作用,可使其失去迁移能力^[14]。

1.2 Cd^{2+} 进入根表皮层的途径

研究发现,土壤溶液中镉离子进入根部表皮层主要有 3 种方式:1) 根部表皮细胞的质膜处,存在由植物呼吸释放出的 CO_2 和 H_2O 生成的 H_2CO_3 解离而来的 H^+ 和 HCO_3^- , H^+ 迅速与 Cd^{2+} 交换吸附,使 Cd^{2+} 被吸附在植物根系表皮细胞表面,这种交换吸附不需要能量且速度很快,为 Cd^{2+} 以质外体途径进入表皮细胞做好准备^[15];2) Cd^{2+} 是非必需元素,却可以占用特异度低的必需元素如 Fe^{2+} 、 Zn^{2+} 和 Ca^{2+} 的离子通道进入植物细胞, Cd^{2+} 通过锌、钙转运通道时与锌转运蛋白和钙转运蛋白结合,以共质体途径进入根表皮细胞,该转运过程受到转运蛋白 ZIP (zrt-, irt-like protein) 家族中的 IRT1 转运蛋白的控制^[16];3) 为使根际土壤溶液中离子利用率升高,植物根部会积极分泌麦根酸等小分子化合物,而麦根酸可以有效螯合 Cd^{2+} 形成金属配位体复合物,使 Cd^{2+} 以螯合物的形式通过 YSL (yellow-stripe 1-like) 蛋白,最终进入根细胞^[17]。

植物根部吸收土壤溶液中 Cd^{2+} 和被土壤颗粒吸附的 Cd^{2+} 的部位主要在根尖,其中,根毛区吸收离子最为活跃,占镉吸收的绝大部分^[18]。意大利五针松 (*Pinus pinea*) 和海岸松 (*Pinus pinaster*) 根际表面会附着大量 Cd^{2+} ,但其根尖上发达的根冠具有筛选离子并阻止镉侵入的功能^[19]。对玉米 (*Zea mays*) 根中镉的沉积格局观察发现,在低镉浓度下 Cd^{2+} 主要累积在根的顶端或距根尖 3 cm 的区域^[20]。

1.3 Cd^{2+} 进入根木质部的途径

本课题组对镉胁迫条件下玉米幼苗的镉沉积显微观察发现, Cd^{2+} 通过共质体和质外体两种途径进入根木质部,图 1 示意了 Cd^{2+} 在玉米根中的运输途径。 Cd^{2+} 通过共质体途径进入玉米的中柱,最后 Cd^{2+} 又经过质外体扩散到导管或管胞。质外体途径中的 Cd^{2+} 在向中央皮层扩散时,受到外皮层凯氏带的阻碍 (图 1①)。当 Cd^{2+} 到达发育正常的内皮层时,内皮层细胞壁中的凯氏带一方面会阻止 Cd^{2+} 的继续扩散 (图 1②),另一方面,对于以共质体途径进入木质部的 Cd^{2+} ,凯氏带也会阻止其通过质外体途径返回中央皮层 (图 1③),使得木质部保持了较高的 Cd^{2+} 浓度。共质体途径中的 Cd^{2+} 能够顺利穿过发育不正常缺失凯氏带的外皮层细胞 (图 1④) 和具有正常凯氏带外皮层的短细胞 (图 1⑤) 而进入细胞质,但不能穿过正常外皮层的长细胞 (图 1⑥)。

镉进入根细胞后通过共质体途径到达中柱鞘,该转运方式主要通过胞间连丝完成。有关 Cd^{2+} 的共质体转运形式尚不清楚,可能的形式有 Cd^{2+} 和镉螯合物两种。重金属镉通过共质体途径进入木质部主要利用重金属酶 $\text{P}_{1\text{B}}\text{-ATP}$,如 *AtHMA2* 和 *AtHMA4* 编码转运蛋白,也有可能和 YSL 蛋白质结合进入木质部^[16]。此外,拟南芥 (*Arabidopsis thaliana*) *AtPDR8* 基因编码的三磷酸腺苷 (ATP, adenosine triphosphate) 转运体已经被证明能够将 Cd^{2+} 从根毛和表皮细胞的细胞膜上导出^[21]。业已证明,外皮层作为环境变化的屏障控制着水和离子的吸收^[22]。大多数被子植物的外皮层与内皮层同时发育,外皮层是阻碍 Cd 进入根内的初级屏障,外皮层的存在可有效降低 Cd^{2+} 通过质外体途径进入根中^[23]。外部环境因素能够改变外皮层的发育速度,研究发现 Cd^{2+} 会刺激外皮层使其发育加快,从而减少根系对镉的吸收量^[24]。

1.4 Cd^{2+} 在植物体内的转运与沉积

镉胁迫下植物的耐受机理主要包括解毒和转运体系,其中,对镉的解毒涉及到抗氧化防卫机制、镉的螯合隔离以及外排机制等^[25-26];对镉的转运过程包括:根际活化吸附、经质外体途径和共质体途径的短距离运输、

经木质部及韧皮部装载的长距离运输^[24]。大多数植物根中 Cd^{2+} 的浓度高于茎叶,受根际 Cd^{2+} 浓度的影响,根中镉含量可能达到地上部分的 10 倍^[27]。研究发现,根内镉含量受土壤 Cd^{2+} 浓度、镉的有效性和镉胁迫持续时间等因素的影响^[28]。根际 Cd^{2+} 浓度较低时,吸收的 Cd^{2+} 主要向地上部分转运,随着镉浓度进一步升高,根内 Cd^{2+} 浓度迅速增加直至与外部达到平衡^[29]。

根中的镉浓度从外皮层薄壁组织到外皮层逐渐降低,中柱鞘中 Cd^{2+} 的累积量很少,推测是 Cd^{2+} 向不断生长的侧根转移所致^[30-31]。在维管束中镉主要累积在传导养分和水分的部位及其邻近的薄壁细胞,表明 Cd^{2+} 在长途运输中不断沉积^[32]。值得注意的是在内皮层与木质部之间的薄壁细胞,其镉含量高于邻近维管束的薄壁细胞,这种结构可能与内皮层的细胞通道有关,相比于内皮层的凯氏带,镉更容易透过内皮层的细胞膜^[29]。研究发现,高浓度镉胁迫条件下 Cd^{2+} 大量集中在根的中柱鞘和维管束组织,对主根的生长和侧根的分生具有明显的抑制作用^[33]。

对于大多数植物,根中质外体通道含镉最多,主要位于表皮、细胞壁和皮层细胞上,而细胞内的 Cd 含量很少,主要集中在液泡和细胞核内,有时也出现在细胞质和叶绿体中^[34-35]。镉敏感的植物较耐镉植物其细胞壁中的镉含量低而液泡中镉含量高^[36]。研究发现,大麦 (*Hordeum vulgare*) 根中 36% 的 Cd^{2+} 存在于细胞壁中,51% 的 Cd^{2+} 存在于细胞质中,后者 34-50% 的 Cd^{2+} 以螯合肽复合物的形式存在^[37],然而,在重金属超累积植物东南景天 (*Sedum alfredii*) 和遏蓝菜 (*Thlaspi caerulescens*) 中,70—90% 的 Cd^{2+} 集中在细胞壁/质外体通道而不是细胞质/液泡中^[38]。

研究发现,植物受镉胁迫后细胞壁阳离子交换能力加强^[39-40],透射电子显微观察显示棉花 (*Gossypium hirsutum*) 和遏蓝菜中镉颗粒出现在外层根组织细胞壁和细胞膜之间,维管束中少有分布^[41-42]。也有研究发现,镉颗粒主要出现在内皮层与木质部之间的质外体通道^[29]以及内皮层与中柱鞘细胞的中间壳层^[43]。通常,液泡中镉颗粒聚集并形成大的沉淀物,其数量和大小随镉浓度的增加而增加^[33],成熟的根内镉沉积在分生组织或外皮层薄壁细胞液泡中^[29]。内皮层细胞中镉则被隔离在液泡中或其大颗粒沉淀分布在靠近细胞壁的细胞质中,而维管束的镉沉积发生在内皮层和木质部之间的薄壁细胞^[42],沉积在筛管和韧皮部细胞中的镉进一步证明了植物对镉向地上部分转运的限制^[29]。

2 植物抗镉性的解剖结构基础

根部外皮层由分裂成多层细胞的表皮构成,剩余外围组织称为皮质,内皮层将皮质与中柱鞘隔开,中柱鞘决定性的控制着溶质向地上部分的转运,而形成凯氏带的木栓质是影响中柱鞘细胞壁渗透性的主要物质^[29, 44]。木栓质是构成凯氏带的基本材料,其在成熟的内皮层细胞壁上呈线状横向分布,这些物质占满内皮层细胞间的空隙,在细胞壁之间紧密连接,和质膜共同构成了根的质外体屏障,阻止溶质通过质外体途径进入

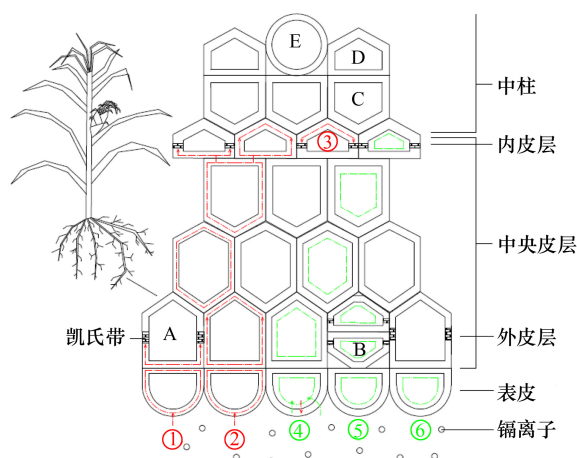


图1 玉米根中 Cd^{2+} 的质外体 (红色) 和共质体 (绿色) 转运途径示意图

Fig. 1 Diagram of apoplastic (red) and symplastic (green) pathways to transport Cd^{2+} in *Zea mays*

A 长细胞; B 短细胞; C 中柱鞘; D 木质部薄壁细胞; E 管胞。①根具有成熟的外皮层: Cd^{2+} 以质外体途径进入表皮细胞壁后,受到正常发育的外皮层凯氏带的阻碍; ②根缺少成熟的外皮层,但具有成熟的内皮层: Cd^{2+} 以质外体途径进入表皮层,之后通过中央皮层细胞壁的传递到达内皮层,正常发育的内皮层凯氏带会阻碍 Cd^{2+} 在细胞壁中进一步的传输,内皮层不具有凯氏带时 Cd^{2+} 可以顺利通过内皮层,到达维管束; ③中柱中的 Cd^{2+} 以质外体途径向中央皮层回流时会受到内皮层凯氏带的阻碍; ④根缺少成熟的外皮层: Cd^{2+} 通过共质体途径能够轻松穿过没有凯氏带的外皮层而进入维管束; ⑤根具有成熟的外皮层,但外皮层细胞较短小: Cd^{2+} 首先进入外皮层和中央皮层细胞壁,进而穿过外皮层和中央皮层细胞膜进入表皮细胞的细胞质,细胞间通过胞间连丝传递 Cd^{2+} ,使 Cd^{2+} 进入维管束; ⑥根具有成熟的外皮层,且外皮层细胞较长: Cd^{2+} 通过共质体途径无法进入成熟的外皮层长细胞,不能到达维管束

木质部与韧皮部^[45]。

2.1 Cd²⁺在植物根系内部转运的屏障

凯氏带的形成代表根内皮层细胞发育的最初阶段,是非常关键的时期^[46]。凯氏带的存在使水分和离子不能以质外体途径穿过内皮层,只能通过内皮层细胞具有选择性的质膜以共质体途径向木质部转运。根部内皮层细胞壁表面片状木栓质的沉积过程,是内皮层发育的第二阶段^[45]。该阶段内皮层表现出对质外体转运的屏障作用,根尖以后的成熟区域严格控制水和溶质以质外体通道向木质部的流动^[47]。栓质化能够增强细胞对镉胁迫的耐性,木栓质是栓质化过程的产物,其在根细胞壁中的含量影响着水和离子的流动。研究发现,拟南芥突变体由于内皮层木栓质的数量增加,显著降低了水分进入木质部的流通性和地上部分Ca²⁺、Mn²⁺、Zn²⁺的富集量^[48]。但是,木栓质在根中的数量差异可能不是唯一影响水分和溶质通过质外体途径向木质部转移的因素,其化学性质和沉积的微观位置尚需深入研究^[49]。此外,植物的周皮组织能够抑制水、离子、气体和病原菌的活动,对Cd²⁺的转运也具有限制作用^[50]。

与许多植物盐胁迫加速根内皮层和外皮层的发育相似^[51],在含重金属的废弃矿渣上培育的玉米受到胁迫诱导内皮层细胞壁大范围增厚^[52]。因此,根外皮层和内皮层扮演着屏障的角色,限制Cd²⁺以质外体途径进入根部^[6]。当植物受到重金属镉胁迫时,质外体屏障受到感应,会在距离根尖很近的部位形成凯氏带。Vaculik 等^[53]观察在不含镉和含镉(5 μmol/L)的营养液中培养10 d的玉米幼苗,发现对照组发育形成的木栓质远离根尖,占总根长的10%,而镉处理组木栓质靠近根尖,占总根长的45%,表明镉的胁迫刺激增大了内皮层木栓质区域,促使木栓质化提前和内皮层成熟加快。进一步研究发现,镉胁迫不仅会导致玉米根内皮层木栓质和木质素含量增加,还会改变其化学构成^[54]。以上改变可能是植物为减少镉通过质外体途径进入木质部而做出的适应性反应。

2.2 Cd²⁺胁迫下植物根形态结构的抗逆变化

增加根际镉浓度不仅会加快内皮层和外皮层的发育速度,也会影响根的形态结构如根组织相对面积、尺寸和细胞类型^[6]。在玉米、萝卜(*Raphanus sativus*)、大麦和高粱(*Sorghum bicolor*)中研究发现,重金属镉抑制根的生长,增加靠近根尖处根毛的数量,表明Cd²⁺加快了这些植物根细胞的发育和成熟^[55]。然而,处于高浓度镉胁迫下的柳树(*Salix alba*)、白杨(*Populus euroamericana*)和萝卜,则会出现根毛数量减少、表皮溃烂和外皮层细胞衰变坏死的现象^[56]。玉米在镉胁迫环境中根系会变短、变粗,根尖转变为褐色,而中柱和维管组织的细胞尺寸不受镉的影响^[57],Maksimović等^[58]认为这归因于镉刺激改变了薄壁细胞的尺寸,进而增加了根直径,而扩大的皮层组织具有限制水分和溶质径向流动的功能。对耐镉与镉敏感柳树的对比观察发现,镉胁迫导致其表皮、外皮层和内皮层组织比例增大^[59]。另有研究发现,虽然镉胁迫环境中菜豆(*Phaseolus vulgaris*)根皮层上的薄壁细胞尺寸有所增大,但对其根径、根长和比表面积的影响较小^[60]。

Vitória 等^[56]在受0.5 mM镉胁迫的萝卜中观测到形成层细胞的减少,表明镉在促使根成熟的同时,也促进了中柱木质部的发育。与此研究一致,Schützendübel 等^[61]发现50 μmol/L的镉加速了欧洲赤松(*Pinus sylvestris*)根尖部位的木质化,而在大麦的根中也发现了同样的现象^[62]。Lunáčková 等^[63]观察到受镉胁迫后,在靠近根尖的部位形成活跃的侧根原基,表明镉促进了侧根的生长以躲避镉胁迫。与此相反,100 μmol/L镉处理下芦苇的根结构并没有发生显著的改变^[64]。

3 Cd²⁺在植物体内的转运调控

研究发现,许多植物的耐受性与液泡富集镉的能力相关,液泡能够大量富集镉,则植物对镉的耐受性强,反之则弱^[6]。目前,已鉴定克隆了H⁺/Cd²⁺逆向转运通道同源基因*AtCAX2*和*AtCAX4*^[65]、重金属转运酶P_{1B}同源基因*AtHMA3*和ABC转运同源基因*AtMRP3*^[18]。与此同时,研究还发现巨噬细胞蛋白(NRAMP, natural resistance-associated macrophage protein)可以从液泡向细胞质中转移镉,相同功能的转运蛋白还包括同源基因*AtNRAMP3*和*AtNRAMP4*的蛋白质^[66]。

许多植物感应到镉的侵入后,会产生螯合肽合成酶以促进螯合肽的形成,这些螯合肽能够捕获 Cd^{2+} 形成无毒螯合物,并将其隔离在液泡中^[5]。目前,植物螯合肽对镉的解毒作用已经得到证实,大多突变会增强植物螯合肽合成酶基因的表达,对镉的耐受性强于野生型,但也有突变会导致植物螯合肽合成酶产生缺陷,解毒性能降低,弱于野生型^[67]。然而,自然生态系统中许多植物对镉的耐受性和植物螯合肽合成酶的含量并不成正比,表明植物的抗镉性还存在其他机理^[68]。研究发现,镉胁迫诱导了小麦和水稻金属硫蛋白基因的表达,增加了植物中金属硫蛋白的含量,说明其对提高植物抗镉性和缓解镉毒害具有积极作用^[65,69]。

发生在根部外皮层的一些突变也与镉的转运调控有关,如图 1 中④、⑤所示,正常的外皮层细胞应由成熟的长细胞(图 1 中途径⑥中所示)构成,但发生突变后长细胞缺失凯氏带或变短小均会丧失对 Cd^{2+} 的抵抗能力^[59]。在根部缺少凯氏带的区域, Cd^{2+} 和镉的螯合物可能会唯一取道细胞外基质,以质外体途径进入木质部(如图 1 中途径②所示)^[70]。研究发现,阳离子通过质外体途径进入木质部的过程一般会受到根尖末端横向传输的限制^[71]。虽然共质体和质外体途径对传递 Cd 进入木质部的相对能力大小尚不清楚,但质外体途径随着根际溶液中 Cd^{2+} 浓度的升高而增加 Cd 的吸收量,与 Zn 和 Na 的吸收机制一致^[72]。支持质外体途径参与镉转运的观点认为根尖是根系中镉流通最活跃的区域,且镉的累积量与其根尖数成正比^[73]。相反的观点认为质外体途径对镉的运输影响不大,以遏蓝菜为材料的研究发现,24 h 内从根部吸收转运至地上部分的 Cd^{2+} 与质外体途径中的水流量呈负相关关系^[74],这与其他植物中蒸腾作用与镉吸收富集呈正相关的研究结论不一致^[75]。第三种观点认为以共质体途径传递镉进入木质部之前, Cd^{2+} 和其它阳离子的吸收存在竞争作用,遏蓝菜对 Cd 和 Zn 在地上部分的富集能力相差很大,表明植物对金属离子的转运具有选择性和专一性,表明共质体途径转运 Cd^{2+} 与蛋白质诱导有关^[74,76]。

4 展望

由于镉的共质体与质外体途径之间呈现紧密的联系和错综复杂的关系,迄今为止,关于镉诱导根中央部位组织和细胞发生改变的研究较少,今后应进一步关注 Cd^{2+} 以共质体和质外体途径进入木质部的转运过程,探析细胞间隙在镉转运过程中的作用。与此同时,木质部担负着调节 Cd^{2+} 向茎叶转运的重要作用,木质部在受到镉胁迫时会产生一定的应激反应,目前有关镉离子对木质部功能与形态的影响尚不清楚,通过研究这种应激反应的机制并促进反应发生,有可能为减少根中 Cd^{2+} 向地上部分转移提供依据^[77-78]。

进一步丰富植物耐镉突变体库,尝试定向诱导植物产生较强的外皮层和缺失功能的内皮层,并开展相应的细胞学、生理生化和分子调控机制研究,在抵御外部重金属镉侵袭的同时使根中 Cd^{2+} 容易进入木质部而向地上部分转运并收获移除,将为改造植物重金属超累积性能和实施重金属植物修复提供新思路。

综上所述,今后应进一步明晰植物共质体和质外体途径转运重金属镉的能力,深入探究镉胁迫下植物形态结构响应及其与抗镉性的关系,阐明共质体和质外体途径的分子调控机制,以增强根部耐受重金属胁迫并促进 Cd^{2+} 向植物地上部分转移为目的,培育适合我国生态环境治理的超富集植物,最终实现植物修复技术在镉污染土壤上的应用。

参考文献 (References):

- [1] Skórzyńska-Polit E, Drażkiewicz M, Krupa Z. Lipid peroxidation and antioxidative response in *Arabidopsis thaliana* exposed to cadmium and copper. *Acta Physiologiae Plantarum*, 2010, 32(1): 169-175.
- [2] Lin L, Zhou W, Dai H, Cao F, Zhang G, Wu F B. Selenium reduces cadmium uptake and mitigates cadmium toxicity in rice. *Journal of Hazardous Materials*, 2012, 235-236: 343-351.
- [3] Watanabe T, Broadley M R, Jansen S, White P J, Takada J, Satake K, Takamatsu T, Tuah S J, Osaki M. Evolutionary control of leaf element composition in plants. *New Phytologist*, 2007, 174(3): 516-523.
- [4] Liu F, Tang Y, Du R, Yang H, Wu Q, Qiu R. Root foraging for zinc and cadmium requirement in the Zn/Cd hyperaccumulator plant *Sedum alfredii*. *Plant and Soil*, 2010, 327(1-2): 365-375.
- [5] Clemens S. Toxic metal accumulation, responses to exposure and mechanisms of tolerance in plants. *Biochimie*, 2006, 88(11): 1707-1719.

- [6] Seregin I V, Kozhevnikova A D. Roles of root and shoot tissues in transport and accumulation of cadmium, lead, nickel, and strontium. *Russian Journal of Plant Physiology*, 2008, 55(1): 1-22.
- [7] Liu X Q, Peng K J, Wanga A G, Lian C L, Shen Z G. Cadmium accumulation and distribution in populations of *Phytolacca americana* L. and the role of transpiration. *Chemosphere*, 2010, 78(9): 1136-1141.
- [8] Peng K J, Luo C L, Chen Y H, Wang G P, Li X D, Shen Z G. Cadmium and other metal uptake by *Lobelia chinensis* and *Solanum nigrum* from contaminated soils. *Bulletin of Environmental Contamination and Toxicology*, 2009, 83(2): 260-264.
- [9] Conn S, Gilliam M. Comparative physiology of elemental distributions in plants. *Annals of Botany*, 2010, 105(7): 1081-1102.
- [10] Boyd R S. The defense hypothesis of elemental hyperaccumulation: status, challenges and new directions. *Plant and Soil*, 2007, 293(1-2): 153-176.
- [11] Clemens S, Aarts M G M, Thomine S, Verbruggen N. Plant science: the key to preventing slow cadmium poisoning. *Trends in Plant Science*, 2013, 18(2): 92-99.
- [12] Deinlein U, Weber M, Schmidt H, Rensch S, Trampeczynska A, Hansen T H, Husted S, Schjoerring J K, Talke I N, Krämer U, Clemens S. Elevated nicotianamine levels in *Arabidopsis halleri* roots play a key role in zinc hyperaccumulation. *The Plant Cell*, 2012, 24(2): 708-723.
- [13] Krämer U. Metal hyperaccumulation in plants. *Annual Review of Plant Biology*, 2010, 61: 517-534.
- [14] Mendoza-Cozatl D G, Jobe T O, Hauser F, Schroeder J I. Long-distance transport, vacuolar sequestration, tolerance, and transcriptional responses induced by cadmium and arsenic. *Current Opinion in Plant Biology*, 2011, 14(5): 554-562.
- [15] Yilmaz D D. Effects of salinity on growth and nickel accumulation capacity of *Lemna gibba* (Lemnaceae). *Journal of Hazardous Materials*, 2007, 147(1-2): 74-77.
- [16] Verbruggen N, Hermans C, Schat H. Mechanisms to cope with arsenic or cadmium excess in plants. *Current Opinion in Plant Biology*, 2009, 12(3): 364-372.
- [17] Curie C, Cassin G, Couch D, Divol F, Higuchi K, Le Jean M, Misson J, Schikora A, Czernic P, Mari S. Metal movement within the plant: contribution of nicotianamine and yellow stripe 1-like transporters. *Annals of Botany*, 2009, 103(1): 1-11.
- [18] DalCorso G, Farinati S, Maistri S, Furini A. How plants cope with cadmium: staking all on metabolism and gene expression. *Journal of Integrative Plant Biology*, 2008, 50(10): 1268-1280.
- [19] Arduini I, Godbold D L, Onnis A. Cadmium and copper uptake and distribution in Mediterranean tree seedlings. *Physiologia Plantarum*, 1996, 97(1): 111-117.
- [20] Seregin I V, Vooijs R, Kozhevnikova A D, Ivanov V B, Schat H. Effects of cadmium and lead on phytochelatin accumulation in maize shoots and different root parts. *Doklady Biological Sciences*, 2007, 415(1): 304-306.
- [21] Kim D Y, Bovet L, Maeshima M, Martinoia E, Lee Y. The ABC transporter *AtPDR8* is a cadmium extrusion pump conferring heavy metal resistance. *The Plant Journal*, 2007, 50(2): 207-218.
- [22] Enstone D E, Peterson C A, Ma F S. Root endodermis and exodermis: structure, function, and responses to the environment. *Journal of Plant Growth Regulation*, 2003, 21(4): 335-351.
- [23] Hose E, Clarkson D T, Steudle E, Schreiber L, Hartung W. The exodermis: a variable apoplastic barrier. *Journal of Experimental Botany*, 2001, 52(365): 2245-2264.
- [24] Zimmermann H M, Steudle E. Apoplastic transport across young maize roots; effect of the exodermis. *Planta*, 1998, 206(1): 7-19.
- [25] Parlak K U, Yilmaz D D. Ecophysiological tolerance of *Lemna gibba* L. exposed to cadmium. *Ecotoxicology and Environmental Safety*, 2013, 91(1): 79-85.
- [26] Shan S H, Liu F, Li C J, Wan S B. Effects of cadmium on growth, oxidative stress and antioxidant enzyme activities in peanut (*Arachis hypogaea* L.) seedlings. *Journal of Agricultural Science*, 2012, 4(6): 142-151.
- [27] Lukačová Z, Lux A. Silicon influence on maize, *Zea mays* L., hybrids exposed to cadmium treatment. *Bulletin of Environmental Contamination and Toxicology*, 2010, 85(3): 243-250.
- [28] Isaure M P, Fayard B, Sarret G, Pairis S, Bourguignon J. Localization and chemical forms of cadmium in plant samples by combining analytical electron microscopy and X-ray spectromicroscopy. *Spectrochimica Acta Part B: Atomic Spectroscopy*, 2006, 61(12): 1242-1252.
- [29] Van Bellegheem F V, Cuypers A, Semane B, Smeets K, Vangronsveld J, d'Haen J, Vaele R. Subcellular localization of cadmium in roots and leaves of *Arabidopsis thaliana*. *New Phytologist*, 2007, 173(3): 495-508.
- [30] Küpper H, Lombi E, Zhao F J, McGrath S P. Cellular compartmentation of cadmium and zinc in relation to other elements in the hyperaccumulator *Arabidopsis halleri*. *Planta*, 2000, 212(1): 75-84.
- [31] Seregin I V, Shpigun L K, Ivanov V B. Distribution and toxic effects of cadmium and lead on maize roots. *Russian Journal of Plant Physiology*, 2004, 51(4): 525-533.

- [32] Vázquez S, Fernandez-Pascual M, Sanchez-Pardo B, Carpena R O, Zornoza P. Subcellular compartmentalization of cadmium in white lupine determined by energy-dispersive X-ray microanalysis. *Journal of Plant Physiology*, 2007, 164(9): 1235-1238.
- [33] Solís-Domínguez F A, Gonzáles-Chávez M C, Carrillo-González R, Rodríguez-Vázquez R. Accumulation and localization of cadmium in *Echinochloa polystachya* grown within a hydroponic system. *Journal of Hazardous Materials*, 2007, 141(3): 630-636.
- [34] Wang J L, Yuan J G, Yang Z Y, Huang B F, Zhou Y H, Xin J L, Gong Y L, Yu H. Variation in cadmium accumulation among 30 cultivars and cadmium subcellular distribution in 2 selected cultivars of water spinach (*Ipomoea aquatica* Forsk.). *Journal of Agricultural and Food Chemistry*, 2009, 57(19): 8942-8949.
- [35] Liu D H, Kottke I. Subcellular localization of cadmium in the root cells of *Allium cepa* by electron energy loss spectroscopy and cytochemistry. *Journal of Biosciences*, 2004, 29(3): 329-335.
- [36] Uraguchi S, Kiyono M, Sakamoto T, Watanabe I, Kuno K. Contributions of apoplasmic cadmium accumulation, antioxidative enzymes and induction of phytochelatins in cadmium tolerance of the cadmium-accumulating cultivar of black oat (*Avena strigosa* Schreb.). *Planta*, 2009, 230(2): 267-276.
- [37] Wu F B, Dong J, Qian Q Q, Zhang G P. Subcellular distribution and chemical form of Cd and Cd-Zn interaction in different barley genotypes. *Chemosphere*, 2005, 60(10): 1437-1446.
- [38] Redjala T, Sterckeman T, Morel J L. Cadmium uptake by roots: contribution of apoplast and of high- and low-affinity membrane transport systems. *Environmental and Experimental Botany*, 2009, 67(1): 235-242.
- [39] Persson D P, Hansen T H, Holm P E, Schjoerring J K, Hansen H C B, Nielsen J, Cakmak I, Husted S. Multi-elemental speciation analysis of barley genotypes differing in tolerance to cadmium toxicity using SEC-ICP-MS and ESI-TOF-MS. *Journal of Analytical Atomic Spectrometry*, 2006, 21(10): 996-1005.
- [40] Nyquist J, Greger M. Response of two wetland plant species to Cd exposure at low and neutral pH. *Environmental and Experimental Botany*, 2009, 65(2-3): 417-424.
- [41] Daud M K, Sun Y Q, Dawood M, Hayat Y, Variath M T, Wu Y X, Raziuddin, Mishkat U, Salahuddin, Najeeb U, Zhu S J. Cadmium-induced functional and ultrastructural alterations in roots of two transgenic cotton cultivars. *Journal of Hazardous Materials*, 2009, 161(1): 463-473.
- [42] Wójcik M, Vangronsveld J, D'Haen J, Tukiendorf A. Cadmium tolerance in *Thlaspi caerulescens*. II. Localization of cadmium in *Thlaspi caerulescens*. *Environmental and Experimental Botany*, 2005, 53(2): 163-171.
- [43] Wójcik M, Tukiendorf A. Cadmium uptake, localization and detoxification in *Zea mays*. *Biologia Plantarum*, 2005, 49(2): 237-245.
- [44] Franke R, Schreiber L. Suberin: a biopolyester forming apoplastic plant interfaces. *Current Opinion in Plant Biology*, 2007, 10(3): 252-259.
- [45] White P J. The pathways of calcium movement to the xylem. *Journal of Experimental Botany*, 2001, 52(358): 891-899.
- [46] Seago J L. The root cortex of the *Nymphaeaceae*, *Cabombaceae*, and *Nelumbonaceae*. *Journal of the Torrey Botanical Society*, 2002, 129(1): 1-9.
- [47] Steudle E, Peterson C A. How does water get through roots? *Journal of Experimental Botany*. 1998, 49(322): 775-788.
- [48] Baxter I, Hosmani P S, Rus A, Lahner B, Borevitz J O, Muthukumar B, Mickelbart M V, Schreiber L, Franke R B, Salt D E. Root suberin forms an extracellular barrier that affects water relations and mineral nutrition in *Arabidopsis*. *PLoS Genetics*, 2009, 5(5): e1000492.
- [49] Schreiber L, Franke R, Hartmann K D, Ranathunge K, Steudle E. The chemical composition of suberin in apoplastic barriers affects radial hydraulic conductivity differently in the roots of rice (*Oryza sativa* L. cv. IR64) and corn (*Zea mays* L. cv. Helix). *Journal of Experimental Botany*, 2005, 56(415): 1427-1436.
- [50] Lulai E C, Corsini D L. Differential deposition of suberin phenolic and aliphatic domains and their roles in resistance to infection during potato tuber (*Solanum tuberosum* L.) wound-healing. *Physiological and Molecular Plant Pathology*, 1998, 53(4): 209-222.
- [51] Karahara I, Ikeda A, Kondo T, Uetake Y. Development of the casparian strip in primary roots of maize under salt stress. *Planta*, 2004, 219(1): 41-47.
- [52] Degenhardt B, Gimmler H. Cell wall adaptations to multiple environmental stresses in maize roots. *Journal of Experimental Botany*, 2000, 51(344): 595-603.
- [53] Vaculík M, Lux A, Luxová M, Tanimoto E, Lichtscheidl I. Silicon mitigates cadmium inhibitory effects in young maize plants. *Environmental and Experimental Botany*, 2009, 67(1): 52-58.
- [54] Schreiber L, Hartmann K, Skrabs M, Zeier J. Apoplastic barriers in roots: chemical composition of endodermal and hypodermal cell walls. *Journal of Experimental Botany*, 1999, 50(337): 1267-1280.
- [55] Seregin I V, Ivanov V B. Physiological aspects of cadmium and lead toxic effects on higher plants. *Russian Journal of Plant Physiology*, 2001, 48(4): 523-544.
- [56] Vitória A P, Rodriguez A P M, Cunha M, Lea P J, Azevedo R A. Structural changes in radish seedlings exposed to cadmium. *Biologia Plantarum*, 2003, 47(4): 561-568.

- [57] Scebbba F, Arduini I, Ercoli L, Sebastiani L. Cadmium effects on growth and antioxidant enzymes activities in *Miscanthus sinensis*. *Biologia Plantarum*, 2006, 50(4): 688-692.
- [58] Maksimović I, Kastori R, Krstić L, Luković J. Steady presence of cadmium and nickel affects roots anatomy, accumulation and distribution of essential ions in maize seedlings. *Biologia Plantarum*, 2007, 51(3): 589-592.
- [59] Lux A, Šottníková A, Opatrná J, Greger M. Differences in structure of adventitious roots in *Salix* clones with contrasting characteristics of cadmium accumulation and sensitivity. *Physiologia Plantarum*, 2004, 120(4): 537-545.
- [60] Vázquez M D, Poschenrieder C, Barceló J. Ultrastructural effects and localization of low cadmium concentrations in bean roots. *New Phytologist*, 1992, 120(2): 215-226.
- [61] Schützendübel A, Schwanz P, Teichmann T, Gross K, Langenfeld-Heyser R, Godbold D L, Polle A. Cadmium-induced changes in antioxidative systems, hydrogen peroxide content and differentiation in Scots pine roots. *Plant Physiology*, 2001, 127(3): 887-898.
- [62] Ďurčáková K, Huttová J, Mistrík I, Ollé M, Tamás L. Cadmium induces premature xylogenesis in barley roots. *Plant and Soil*, 2007, 290(1-2): 61-68.
- [63] Lunáčeková L, Šottníková A, Masarovicova E, Lux A, Stresko V. Comparison of cadmium effect on willow and poplar in response to different cultivation conditions. *Biologia Plantarum*, 2003, 47(3): 403-411.
- [64] Ederli L, Reale L, Ferrari F, Pasqualini S. Responses induced by high concentration of cadmium in *Phragmites australis* roots. *Physiologia Plantarum*, 2004, 121(1): 66-74.
- [65] Korenkov V, King B, Hirschi K, Wagner G J. Root-selective expression of *AtCAX4* and *AtCAX2* results in reduced lamina cadmium in field-grown *Nicotiana tabacum* L. *Plant Biotechnology Journal*, 2009, 7(3): 219-226.
- [66] Thomine S, Lelièvre F, Debarbieux E, Schroeder J I, Barbier-Brygoo H. *AtNRAMP3*, a multispecific vacuolar metal transporter involved in plant responses to iron deficiency. *The Plant Journal*, 2003, 34(5): 685-695.
- [67] Cobbett C S. Phytochelatin and their roles in heavy metal detoxification. *Plant Physiology*, 2000, 123(3): 825-832.
- [68] Schat H, Llugany M, Vooijs R, Hartley-Whitaker J, Bleeker P M. The role of phytochelatin in constitutive and adaptive heavy metal tolerance in hyperaccumulator and non-hyperaccumulator metallophytes. *Journal of Experimental Botany*, 2002, 53(379): 2381-2392.
- [69] Shim D, Hwang J U, Lee J, Lee S, Choi Y, An G, Martinoia E, Lee Y. Orthologues of the class A4 heat shock transcription factor *HsfA4a* confer cadmium tolerance in wheat and rice. *The Plant Cell*, 2009, 21(12): 4031-4043.
- [70] Berkelaar E J, Hale B A. Cadmium accumulation by durum wheat roots in ligand-buffered hydroponic culture: uptake of Cd-ligand complexes or enhanced diffusion? *Canadian Journal of Botany*, 2003, 81(7): 755-763.
- [71] Moore C A, Bowen H C, Scrase-Field S, Knight M R, White P J. The deposition of suberin lamellae determines the magnitude of cytosolic Ca^{2+} elevations in root endodermal cells subjected to cooling. *The Plant Journal*, 2002, 30(4): 457-466.
- [72] Plett D C, Møller I S. Na^{+} transport in glycophytic plants: what we know and would like to know. *Plant, Cell and Environment*, 2010, 33(4): 612-626.
- [73] Berkelaar E, Hale B A. The relationship between root morphology and cadmium accumulation in seedlings of two durum wheat cultivars. *Canadian Journal of Botany*, 2000, 78(3): 381-387.
- [74] Xing J P, Jiang R F, Ueno D, Ma J F, Schat H, McGrath S P, Zhao F J. Variation in root-to-shoot translocation of cadmium and zinc among different accessions of the hyperaccumulators *Thlaspi caerulescens* and *Thlaspi praecox*. *New Phytologist*, 2008, 178(2): 315-325.
- [75] Ingwersen J, Streck T. A regional-scale study on the crop uptake of cadmium from sandy soils: measurement and modeling. *Journal of Environmental Quality*, 2005, 34(3): 1026-1035.
- [76] Hart J J, Welch R M, Norvell W A, Kochian L V. Transport interactions between cadmium and zinc in roots of bread and durum wheat seedlings. *Physiologia Plantarum*, 2002, 116(1): 73-78.
- [77] Papayan A, Pineros M, Kochian L V. Plant Cd^{2+} and Zn^{2+} status effects on root and shoot heavy metal accumulation in *Thlaspi caerulescens*. *New Phytologist*, 2007, 175(1): 51-58.
- [78] Ueno D, Iwashita T, Zhao F J, Ma J F. Characterization of Cd translocation and identification of the Cd form in xylem sap of the Cd-hyperaccumulator *Arabidopsis halleri*. *Plant and Cell Physiology*, 2008, 49(4): 540-548.