

植物抗重金属胁迫研究进展

王若男, 乜兰春*, 张双双, 崔 强, 贾明飞

(河北农业大学园艺学院/河北省蔬菜种质创新与利用重点实验室/河北省蔬菜产业协同创新中心, 河北保定 071001)

摘 要: 土壤重金属污染导致植物重金属积累量增加, 重金属对植物产生毒害的同时, 植物也会通过避性和耐性机制抵抗重金属的毒害。从根系分泌物、亚细胞结构、螯合作用、渗透调节、抗氧化系统等方面综述了植物抵抗重金属胁迫的研究进展, 以期为该领域的深入研究提供参考。

关键词: 重金属胁迫; 根系分泌物; 亚细胞结构; 螯合作用; 渗透调节; 抗氧化系统

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Research Progress on Plant Resistance to Heavy Metal Stress

WANG Ruonan, NIE Lanchun*, ZHANG Shuangshuang, CUI Qiang, and JIA Mingfei

(College of Horticulture, Key Laboratory for Vegetable Germplasm Enhancement and Utilization of Hebei, Collaborative Innovation Center of Vegetable Industry in Hebei, Agricultural University of Hebei, Baoding, Hebei 071001, China)

Abstract: Heavy metal contamination in agricultural soil could cause the accumulation of heavy metals in plants. While plants suffer from toxicity of heavy metals, they could also operate avoidance and tolerance mechanisms to resist heavy metal poisoning. This paper reviewed the research progress on plant resistance to heavy metal stress in terms of root exudates, subcellular structures, chelation, osmoregulation, and antioxidant systems, aiming to provide reference for further research in this field.

Keywords: heavy metal stress; root exudates; subcellular structure; chelation; osmoregulation; antioxidant system

园艺作物和农作物生产中, 有机肥、化肥和农药大量使用, 加之污水灌溉、固体垃圾堆积及大气沉降等原因造成不同程度土壤重金属污染(黄绍文 等, 2016, 2017; Liu et al., 2018; Shen et al., 2018)。一部分重金属为植物生长非必需元素, 如镉、铅、铬、砷、汞等, 即使是较低浓度也会导致产品安全品质下降, 浓度较高时则会对植株产生毒害作用(Patra et al., 2004; Rizwan et al., 2016; Xie et al., 2018); 另一部分为植物生长必需元素, 浓度过高时也会对植物产生毒害作用, 包括铁、锰、锌、铜、镍等(Müller et al., 2017; Bhatti et al., 2018; Erdemir et al., 2018; Xie et al., 2018; Hattab et al., 2019)。

重金属通过 4 种途径[(1) 改变质膜透性, (2) 与蛋白质巯基反应, (3) 与 ADP/ATP 活性基团和磷酸基团结合, (4) 置换体内阳离子(主要包括 K、Ca、P)]破坏植物体内的膜系统和抗氧化系统, 致使染色体发生畸变, 影响金属离子稳态, 从而导致植株生长发育不良, 产量和品质下降,

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* 通信作者 Author for correspondence (E-mail: 13784960296@139.com)

严重时导致全株死亡 (Patra et al., 2004; Rizwan et al., 2016; Xie et al., 2018)。多数植物长期在重金属胁迫环境中逐渐形成了避性机制和耐性机制。避性机制包括植物通过根系分泌物影响重金属的移动性及微生物活性, 减少重金属进入植物体内 (Javed et al., 2017; Fu et al., 2018), 以及细胞壁、细胞膜和液泡的隔离和区化作用 (Kupper et al., 2000; Wang et al., 2015)。耐性机制指植物自身具有减轻体内重金属毒害的机制, 包括螯合作用、渗透调节、抗氧化系统等 (Anjum et al., 2015; Liu et al., 2016; Rizwan et al., 2016; Kováčik et al., 2017)。

从根系分泌物、亚细胞结构、重金属螯合物质、渗透调节、抗氧化系统等方面综述了植物对重金属避性和耐性机制的最新研究进展, 以期在这方面更深入研究提供参考。

1 根系分泌物

1.1 有机酸

在重金属胁迫下, 根系草酸、柠檬酸、苹果酸、酒石酸和琥珀酸等有机酸的分泌量增加。有机酸具有一个或多个羧基, 可与重金属发生螯合作用形成无毒化合物, 避免其进入植株体内 (Javed et al., 2017; Fu et al., 2018)。Chen 等 (2016) 的研究表明, 毛竹根系分泌的有机酸可提高土壤磷酸盐活性, 磷酸根离子可与铅形成沉淀, 将铅固定在土壤中, 避免根系吸收。钱莲文等 (2018) 的研究表明, 草酸和柠檬酸是杨树根系分泌物抵抗铝毒害的主要有机酸组分。镉胁迫下耐镉水稻根系有机酸分泌总量为镉敏感型品种的 1.76 ~ 2.43 倍 (Fu et al., 2018)。辣椒耐镉品种根系酒石酸、草酸和乙酸分泌量显著高于镉敏感品种 (Xin et al., 2014)。在镉胁迫下, 水稻根部 2'-脱氧麦根酸分泌量显著增加, 可降低植株对镉的吸收 (Banakar et al., 2017; 高蕾, 2018)。高蕾 (2018) 的研究表明, 外源施加 2'-脱氧麦根酸促进水稻根系吸收大量的铁离子, 聚积在根部细胞壁, 与果胶结合形成根表铁膜保护机制, 避免镉离子进入细胞。此外, 根系分泌的有机酸还可为微生物提供碳源, 增强枯草芽孢杆菌和固氮螺旋菌等微生物活性, 可有效降低拟南芥根系对镉的吸收 (Xu et al., 2018; Yuan et al., 2018)。

1.2 氨基酸

重金属胁迫下, 植物根系氨基酸的分泌量显著增加。如水稻根系蛋氨酸、赖氨酸和组氨酸分泌量随着镉胁迫浓度的增加显著增加 (Fu et al., 2018)。根系氨基酸分泌物可为细菌、真菌、酵母菌和硫细菌等根际微生物提供营养源, 其中细菌和真菌利用其分泌物和代谢物抑制植物根系对重金属的吸收 (苑亚茹 等, 2011; Wang et al., 2018); 酵母菌细胞壁上的多糖可对铜、镉和镍产生不同程度的吸附; 硫细菌也可与重金属反应形成硫化物沉淀, 避免重金属进入植物体 (Elsamad et al., 2011; Sallah-Ud-Din et al., 2017)。根系氨基酸分泌物也可直接与重金属发生螯合作用, 缓解重金属的毒害作用 (Xie et al., 2013; 钱莲文 等, 2018)。

1.3 可溶性糖及多糖类物质

根系可溶性糖分泌量与植物抵抗重金属胁迫密切相关, 400 $\mu\text{mol} \cdot \text{L}^{-1}$ 镉处理下, 东南景天根系可溶性糖分泌量显著高于 100 和 200 $\mu\text{mol} \cdot \text{L}^{-1}$ 镉处理 (李雪莲, 2011)。Zu 等 (2015) 研究证实, 随着铅浓度的增加圆叶无心菜根系分泌物中可溶性糖逐渐增加。冬小麦根系可溶性糖分泌量与土壤中真菌、细菌和亚硝化菌数量均为正相关关系, 可溶性糖通过影响根际微生物群落和微生物活性降

低重金属对根系的毒害(贾夏 等, 2012; Zu et al., 2015; Wang et al., 2017, 2018)。Wang 等(2017, 2018)报道, 根际细菌可固定森林植物根际土壤镉和砷。欧洲赤松外生菌根的真菌可显著促进铅、镉和砷形成螯合物(Johansson et al., 2008; Yuan et al., 2018)。此外, 也有研究表明, 根系分泌的可溶性糖还可直接与铅形成无毒化合物(Weigel & Jager, 1980)。植物根系分泌物中还存在多糖和多糖醛(Marschner & Römhild, 1994), 可通过竞争性结合的方式将铅、铜、镉等金属离子螯合体固定在土壤中, 从而有效限制重金属离子被植物根吸收(Cunningham et al., 1995)。

2 亚细胞结构

2.1 细胞壁

细胞壁由纤维素、半纤维素、果胶及蛋白质等构成, 其表面具有羧基、羟基、氨基和醛基等官能团, 可与金属离子结合, 限制重金属的跨膜运输(Kupper et al., 2000; Chai et al., 2018)。在铅胁迫下, 萝卜侧根细胞壁铅含量占侧根总铅量的 71.08%~80.40%(Wang et al., 2015)。去除普通白菜、叶用莴苣、辣椒、番茄和水稻等根细胞壁中的半纤维素, 发现根系细胞壁中锌积累量显著下降而地上部积累量增加, 表明半纤维素是根细胞壁中束缚锌离子的主要成分(陈世宝 等, 2012); 拟南芥根细胞壁中的果胶和纤维素可与锌离子结合, 将其区隔在细胞壁, 避免向上运输(Kupper et al., 2000)。此外, 水稻根细胞壁中还存在富含半胱氨酸的蛋白, 可将铅固定(Xiong et al., 2009)。外源施用氮氧化物通过增加根细胞壁中半纤维素及果胶含量, 提高水稻和秋茄对镉的耐受能力(Douchiche et al., 2010; Chai et al., 2018)。

2.2 细胞膜

植物细胞膜上存在许多转运蛋白, 其中与重金属转运相关的蛋白主要包括: 重金属 ATP 酶(heavy metal ATPase, P-ATPase)、三磷酸结合转运蛋白(ATP-binding cassette transporter, ABC)和阳离子转运促进蛋白(cation diffusion facilitator, CDF)。Sasaki 等(2014)的研究表明, P-ATPase 的一个亚类 HMA 家族成员中 *OsHMA3* 过表达增强了水稻根系对镉的耐受性。但 *NtHMA3a* 和 *NtHMA3b* 过表达并没有提高烟草对汞的耐受性, 而 ABC 转运蛋白在烟草响应汞毒害中具有重要作用(Chang & Shu, 2015)。Sun 等(2018)的研究表明, *PtABCC1* 过表达增强了拟南芥和杨树对汞的耐受性。拟南芥幼苗中 *AtABCC3* 过表达可参与转运 PC-Cd 复合物, 增强植株的耐镉性(Brunetti et al., 2015)。ABC 家族中 AtMRP 和 AtPDR 的表达直接受镉和铅的调节, 其中 *AtMRP3* 作为细胞膜上的镉转运子将镉转运至液泡储存, *AtPDR12* 可作为铅的外排泵, 将铅复合物排出细胞(Bovet et al., 2003; Zhu et al., 2013)。CDF 家族成员可将金属离子排出到质外体或内质网等特定细胞器, 或隔离在液泡中(Tsunemitsu et al., 2018)。Zhang 等(2018a)在甜橙中发现了 CDF 家族成员 MTPs (Metal tolerance proteins) 金属耐受蛋白, 包括 CitMTP1、CitMTP3 到 CitMTP12; 在锌、锰、铜和镉胁迫下, *CitMTP* 在根系和叶片中表达量上调。

2.3 液泡

重金属胁迫下, 液泡通过储集大量金属离子, 降低细胞质中金属离子浓度, 提高植物对重金属的耐受性。如洋葱根部液泡可以固定大量的铬, 遏兰菜表皮细胞液泡也可积累大量的锌离子(Saier, 2000; Thomine et al., 2003)。此外, 拟南芥、大麦、水稻和萝卜液泡膜上还存在阳离子转运促进

蛋白 (CDF) 中金属耐受蛋白 (MTPs) 家族中的成员, 可转运锌、钴、铁、镉等, 降低细胞质中金属离子的浓度, 维持金属离子稳态。萝卜 *BrrMTPs* 基因也可能参与了镁、铜、锰金属离子稳态平衡 (Kawachi et al., 2008; Menguer et al., 2013; Li et al., 2018)。Tsunemitsu 等 (2018) 发现 *MTP8.1* 将锰离子隔离在液泡中, 是水稻耐锰胁迫的重要原因之一。液泡膜上还存在参与重金属吸收转运相关的巨噬细胞蛋白 (natural resistance associated macrophage protein, Nramp) 家族成员 (Thomine et al., 2000; Peng et al., 2018)。在缺锰的条件下, 根系中 *AtNramp3* 过表达不仅平衡锰离子还提高对镉的耐受性 (Thomine et al., 2000; Lanquar et al., 2010)。*Nramp2* 和 *Nramp3* 在番茄根系中过表达会增强其对镉的耐受性 (Zhao et al., 2015)。另外, 将小麦中 *Narmp5* 转入拟南芥中可提高拟南芥对镉、锰和钴的耐受性 (Peng et al., 2018)。拟南芥液泡膜上的 HMA 家族成员 *AtHMA3* 及锌内流转运体 MHX 都参与液泡对镉和锌的隔离和区化作用 (Elnaz et al., 2006; Morel et al., 2009; Takahashi et al., 2012)。

3 螯合作用

3.1 金属硫蛋白

植物体内参与重金属螯合作用的主要有两大类化合物: 一类是硫醇源化合物, 指金属硫蛋白、植物螯合肽和还原型谷胱甘肽; 另一类是非硫醇源化合物, 主要包括有机酸、氨基酸和烟酰胺 (Anjum et al., 2015)。

金属硫蛋白 (metallothionein, MTs) 是一类富含半胱氨酸的低分子量诱导性蛋白, 在维持金属离子稳态和氧化还原水平方面起关键作用, 其最基本的功能是与重金属离子结合, 降低植株体损伤 (Pan et al., 2018; Yu et al., 2018)。金属硫蛋白有 7 个以上半胱氨酸残基位点, 可直接结合金属离子 (Ryvolova et al., 2011)。金属硫蛋白分为 4 种类型: MT1 (亚型 a, b, c), 其基因表达在根中高于芽; MT2 (亚型 a, b, c, d), 其基因表达主要发生在芽; MT3 (亚型 a, b, c), 在肉质水果成熟时具有其转录物的特异性积累; MT4, 其基因表达仅存在于萌芽种子 (Teixeira et al., 2013)。Pan 等 (2018) 研究表明, 砷诱导 16 种 *BnaMTs* 蛋白表达, 大部分分布在子叶、根系和下胚轴中, 其中 *BnaMT3c* 在甘蓝型油菜抵抗砷胁迫中发挥重要作用。锌、铜、汞、铅、镉和铬等可诱导金属硫蛋白合成, 进而形成金属螯合剂, 降低对植株体的毒害作用 (Ryvolova et al., 2011; Teixeira et al., 2013; Duan et al., 2018)。玉米 *ZmMT1* 与镉形成螯合剂能力最强, 其次是铅和锌 (Duan et al., 2018)。三价铬诱导龙葵根和芽 *MT2a* 相关转录物合成及根中 *MT1* 和 *MT2d* 相关转录物合成; 六价铬则在较高浓度下诱导 *MT2a* 和 *MT2d* 及枝条中 *MT2c* 相关转录物的积累 (Teixeira et al., 2013)。将海桑根系 *SaMT3* 基因转入大肠杆菌中, 增强了细胞对铜和铅的抵抗能力 (Niu et al., 2018)。

3.2 植物螯合肽

植物螯合肽 (phytochelatins, PC) 是由半胱氨酸、谷氨酸和甘氨酸组成的分子量较小的多肽家族, 其巯基含量较高, 对重金属亲和力较强 (Jacquart et al., 2017)。镉、铜、汞、铅、锌、银、铋、金、锡、镍、砷和硒均可诱导玉米和小麦等产生植物螯合肽。不同重金属对植物螯合肽的结合力不同, 其中镉与植物螯合肽的结合能力最强, 依次为铅、锌、铋、银、汞、砷、铜、锡、金和铋 (Grill et al., 1987; Jacquart et al., 2017)。镉、铅、铬和镍胁迫下, 水稻植株体内产生大量植物螯合肽, 复合胁迫下, 植物螯合肽含量显著高于单独处理 (Gupta & Singh, 2017; Yu et al., 2018)。

重金属胁迫下耐性植物中 γ -谷氨酰半胱氨酸合成酶、谷胱甘肽还原酶、植物络合素酶等与植物螯合肽合成相关酶表达量均显著提高 (Gupta & Singh, 2017; Zhou et al., 2017)。将小麦植株体内的植物螯合肽合成酶基因 *TaPCSI* 转入烟草, 可显著提高其对锌的耐受性 (Martinez et al., 2006); 将箭筈豌豆 *VsPCSI* 基因转入苜蓿中, 镉胁迫时该基因在其根细胞质中表达, 在根中形成无毒复合物, 完成镉的解毒作用 (Zhang et al., 2018b)。

3.3 还原型谷胱甘肽

谷胱甘肽 (reduced glutathione, GSH) 是由谷氨酸 (Glu)、半胱氨酸 (Cys) 和甘氨酸 (Gly) 所组成氨基酸衍生物, 半胱氨酸上的巯基是其活性位点, 可作为配体与重金属产生螯合作用, 降低重金属的毒害 (Geng et al., 2018; 张腾国 等, 2018)。水稻幼苗中 GSH 在砷胁迫时含量增加 (Geng et al., 2018); 外源施用 GSH 可促进石竹幼苗和杨树中植物螯合肽的形成, 与镉形成无毒螯合物缓解对植株的毒害 (丁继军 等, 2014; Ding et al., 2017)。

3.4 有机酸和氨基酸

植物体内对重金属起螯合作用的有机酸主要包括: 柠檬酸、苹果酸、草酸和酒石酸等。有研究认为有机酸作为配体的解毒作用大于氨基酸 (吴佳文, 2014)。在铜、铅、镉和镍等重金属胁迫下, 冰草植株分泌大量有机酸, 与重金属形成无毒复合物 (Yang et al., 2001)。镉胁迫下番茄和黄瓜幼苗中草酸、柠檬酸和苹果酸含量增加。柠檬酸不仅与重金属结合形成无毒复合物, 也可通过促进植株生长和提高抗氧化酶活性等途径减轻重金属对植物的毒害作用 (Morita et al., 2004; Sallah-Ud-Din et al., 2017)。

重金属胁迫下, 含羧基、氨基、巯基和酚基的氨基酸不仅参与植物螯合素和谷胱甘肽的合成, 还可直接与金属离子结合形成螯合物, 降低重金属的毒害作用 (Elsamad et al., 2011; Dave et al., 2013)。野苘蒿对镉的耐受性与植株体内谷氨酰胺和天冬酰胺积累相关 (Zhu et al., 2018)。李薇 (2010) 的研究表明, 镉胁迫下秋茄幼苗组织内积累大量的氨基酸, 其中半胱氨酸、组氨酸和甲硫氨酸与镉、铜、砷和镍二价金属离子亲和力较强。镉胁迫下, 拟南芥植株体内半胱氨酸含量显著增加 (Dominguez-Solis et al., 2004), 在其根系中发现 9 种铜结合蛋白化合物中均含有半胱氨酸、组氨酸和甲硫氨酸 (Opella et al., 2002; Kung et al., 2006)。

3.5 烟酰胺

重金属胁迫下, 植株体内烟酰胺 (nicotianamine, NA) 含量显著提高 (Ghssein et al., 2016; Gupta & Singh, 2017)。NA 由烟酰胺合成酶 (nicotianamine synthase, NAS) 和烟酰胺氨基转移酶 (nicotianamine aminotransferase, NAAT) 催化 *S*-腺苷甲硫氨酸 (*S*-adenosyl methionine, SAM) 而产生 (Higuchi et al., 1994)。Banakar 等 (2017) 研究表明, 水稻胚乳通过烟酰胺维持铁和锌离子稳态平衡, 与镉发生竞争结合, 从而抑制镉吸收。Han 等 (2018) 从苹果细胞质膜上分离出 NAS 基因 *MdNAS1*, 转入烟草中发现 *MdNAS1* 过表达可增强植株对过量铁的耐受性。*MdNAS1* 基因通过调节 NAS 和 NA 的合成平衡植株体内铁含量, 缓解铁胁迫。缺铁时, NA 可吸收和转运铁离子维持植株体内铁含量; 铁、镉、铅、镍过量时, NA 与植株体内多余的重金属发生螯合作用形成无毒化合物 (Deinlein et al., 2012; Banakar et al., 2017; Gupta & Singh, 2017)。

4 抗氧化系统

4.1 酶促系统

4.1.1 抗氧化酶

抗氧化酶主要包括超氧化物歧化酶(SOD)、过氧化氢酶(CAT)、过氧化物酶(POD)和抗坏血酸过氧化物酶(APX),在植物受到重金属胁迫时,抗氧化酶活性显著提高。在镉胁迫下,芥菜和玉米中的SOD、POD和APX活性上升,且耐镉型芥菜的APX和CAT活性较镉敏感型品种显著提高(Bauehdh & Singh, 2011; Maiti et al., 2012)。抗氧化酶活性随着重金属胁迫浓度的增加呈现逐渐上升的趋势,但胁迫浓度过高时,保护酶系统受到破坏,酶活性下降(Dixit et al., 2001; Liu et al., 2016; Chaabene et al., 2018)。抗氧化酶抵抗重金属胁迫是一个复杂的生理变化过程,受植物种类、重金属浓度和性质等多方面影响。如镉胁迫下,小麦叶片POX和APX含量显著提高,但SOD含量没有变化(Ozfıdan-Konakci et al., 2018)。敲除拟南芥中*APX1*基因,则铅胁迫下CAT酶活性显著增强,同时还增加了谷胱甘肽和植物螯合素相关基因的表达及ABC转运蛋白AtPDR相关基因的表达(Li et al., 2017)。

4.1.2 抗坏血酸—谷胱甘肽循环相关酶

谷胱甘肽和抗坏血酸循环相关酶主要包括脱氢抗坏血酸还原酶(DHAR)、单脱氢抗坏血酸还原酶(MDHAR)、谷胱甘肽转硫酶(GST)、谷胱甘肽还原酶(GR)、谷胱甘肽过氧化物酶(GPX)。镉胁迫下,旱柳根系和叶片中MDHAR和DHAR酶活性显著提高,可抑制单脱氢抗坏血酸(MDHA)歧化作用或促进MDHA与DHA合成为AsA,保证植物体内的AsA含量(杨卫东等, 2014)。但不同重金属胁迫,AsA-GSH中相关酶表达水平会有所差别,铅胁迫下,大麦植株体内MDHAR、DHAR和APX酶活性显著高于汞胁迫下表达量(Ullah et al., 2016)。黑藻中GR活性在锌胁迫下显著提高,该酶以NADPH作为电子供体,可催化氧化型谷胱甘肽(GSSG)还原成还原型谷胱甘肽(GSH),调节AsA-GSH有效地清除活性氧(Wang et al., 2009)。镉胁迫提高豌豆植株体中GST活性,清除由活性氧自由基引起脂或核酸分解产物,同时可催化GSH和亲电底物共价结合形成共轭物隔离在液泡或转移到质外体,减轻重金属的毒害作用(Dixit et al., 2001; Lyubenova et al., 2009)。

4.2 非酶促清除系统

非酶促清除系统主要包括抗坏血酸(AsA)、还原型谷胱甘肽(GSH)、类胡萝卜素、甘露醇、类黄酮和 α -生育酚等抗氧化剂(Dixit et al., 2001; Adrees et al., 2015; Rady & Hemida, 2015, 2016; Ferrer et al., 2018)。锌和镉胁迫下,植物体内的AsA和GSH含量显著提高(Wang et al., 2009; Ding et al., 2017)。AsA可改善铜胁迫下胶球藻缺钾现象;缓解镉对大麦的毒害;外源施用AsA也可有效缓解汞和铅对胶球藻的毒害作用(Ullah et al., 2016; Kováčová et al., 2017)。GSH可直接将活性氧还原,自身发生氧化反应形成GSSH, GSSH通过GR作用可以再次形成GSH,这样的循环可有效清除植株体内的活性氧自由基(Ding et al., 2017)。Ding等(2017)研究发现外源施用GSH,可提高杨树体内*MTPI*、*ABCC3*和*NRAMP1.3*的表达量,将镉隔离在根部液泡,增强杨树对镉的耐受性。铬胁迫下李氏禾中类黄酮化合物含量显著提高,可抑制或清除活性氧自由基(黄斌等, 2012; Muszyńska et al., 2018)。此外,甘露醇、类胡萝卜素、 α -生育酚等在清除植物体内活性氧自由基中均起着重要作用(Rucinska-Sobkowiak & Pukacki, 2006; Adrees et al., 2015; Ferrer et al., 2018)。

5 渗透调节

5.1 脯氨酸

重金属毒害导致植物体内水分平衡失调, 诱导脯氨酸大量增加, 参与细胞的渗透调节 (Clemens, 2006; Rady & Hemida, 2015)。镉和铅胁迫下, 水稻和油菜植株体内脯氨酸含量随着金属胁迫浓度的增加而增加 (Gohari et al., 2012; Majumdar et al., 2018)。Semida 等 (2018) 发现用脯氨酸浸泡黄瓜种子可提高植株对镉的耐受性。Mishra 和 Dubey (2006) 的研究表明, 脯氨酸还可作为金属螯合剂和蛋白质稳定剂, 抵抗重金属对细胞膜和蛋白质的毒害。外源增施脯氨酸可与铜、镉和锌形成螯合物, 缓解重金属胁迫对硝酸还原酶的抑制作用 (Hayat et al., 2012)。

5.2 可溶性糖和可溶性蛋白

镉胁迫下, 刺槐、紫萍叶片可溶性糖含量显著增加 (Jia et al., 2017; Su et al., 2017)。可溶性糖可降低细胞内的渗透势, 保持细胞水势, 维持正常的代谢 (Abd et al., 2017; Zhang et al., 2018a)。张阿芳等 (2018) 研究表明, 镉胁迫下, 银灰杨根系和叶片可溶性蛋白含量显著提高。红菜薹体内可溶性蛋白随着镉胁迫浓度的增加呈先增加后降低的变化。低浓度镉胁迫时, 诱导镉结合蛋白和多肽的合成及表达, 缓解镉对植株的毒害和维持细胞水分平衡; 也有报道, 重金属影响蛋白水解酶和蛋白合成酶的活性, 使得蛋白分解或抑制蛋白合成, 使可溶性蛋白增加 (John et al., 2009; Shen et al., 2017)。

5.3 甜菜碱

重金属胁迫下, 植物细胞质中的甜菜碱积累量提高 (刘慧 等, 2017; Akhtar et al., 2018)。植物中甜菜碱合成底物主要是胆碱, 在胆碱单加氧酶 (choline monooxygenase, CMO) 的催化下生成甜菜碱醛, 再经甜菜碱醛脱氢酶 (betaine aldehyde dehydrogenase, BADH) 催化生成甜菜碱 (Chen & Murata, 2002)。Akhtar 等 (2018) 的研究表明, 随着镍胁迫浓度的增加, 香蒲植株体内的甜菜碱显著增加。通过外源增施硒肥提高番茄甜菜碱含量, 可降低镉对植株的毒害效应 (Alyemeni et al., 2018)。Farooq 等 (2016) 研究表明, 镉胁迫下, 外源增施甜菜碱可降低棉花过氧化氢和丙二醛含量, 减轻镉对植株的毒害作用。外源施用甜菜碱可通过提高 SOD、CAT 和 POD 酶的表达量, 提高细胞膜稳定性, 避免膜脂氧化作用的产生, 缓解镉对黑麦草的毒害作用 (Lou et al., 2015)。封鹏雯 (2018) 将甜菜碱醛脱氢酶基因 (*BADH*) 转入烟草中, 促使植株体内甜菜碱的合成, 有效维持细胞内钾离子含量, 抑制镉离子进入植株体内, 甜菜碱还可调节液泡膜上 HMA3、AtNramp3 和 AtNramp5 转运蛋白避免已储存在液泡的镉离子流出。

6 问题与展望

(1) 关于避性机制。根际环境中的重金属诱导根系分泌有机酸、氨基酸、糖类等物质, 这些物质一方面作为重金属配体直接与根际环境中重金属结合, 避免根系对重金属的吸收; 另一方面可为微生物提供营养物质, 增强细菌、真菌、酵母菌等微生物活性, 这些微生物可直接固定重金属或通过其代谢和分泌物与重金属结合。这一途径是减轻或避免重金属对植物的毒害和农产品污染最有效和安全的途径。但这方面的研究还远不够深入, 今后应加强对根际分泌物活性成分分离鉴定及根

际微生物在减轻或避免重金属毒害方面作用的研究,未来利用根系分泌物活性成分及根际有益微生物减轻或避免重金属对植物的毒害和农产品污染将具有广阔前景。

(2) 关于耐性机制。重金属从根部进入植物体后,可诱导植株亚细胞结构发生改变,如增加细胞壁多糖组分有利于结合重金属,避免向上运输;诱导细胞膜和液泡膜上金属转运子的过表达,将重金属固定在液泡等细胞器中,降低细胞质中重金属离子浓度;诱导植株体内螯合肽、金属硫蛋白、还原型谷胱甘肽、有机酸、氨基酸和烟酰胺的过表达,与重金属形成螯合物;同时植物体内抗氧化系统和渗透调节机制启动,防止重金属导致的自由基伤害和渗透失衡。关于重金属作为外源刺激信号是如何启动上述一系列应答反应目前尚不清楚,其分子机理有待研究。从分子水平揭示植物对重金属的耐性机制,将为开展分子辅助育种,定向选育对重金属耐性强、产品器官少富集或不富集的作物新品种奠定基础。

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