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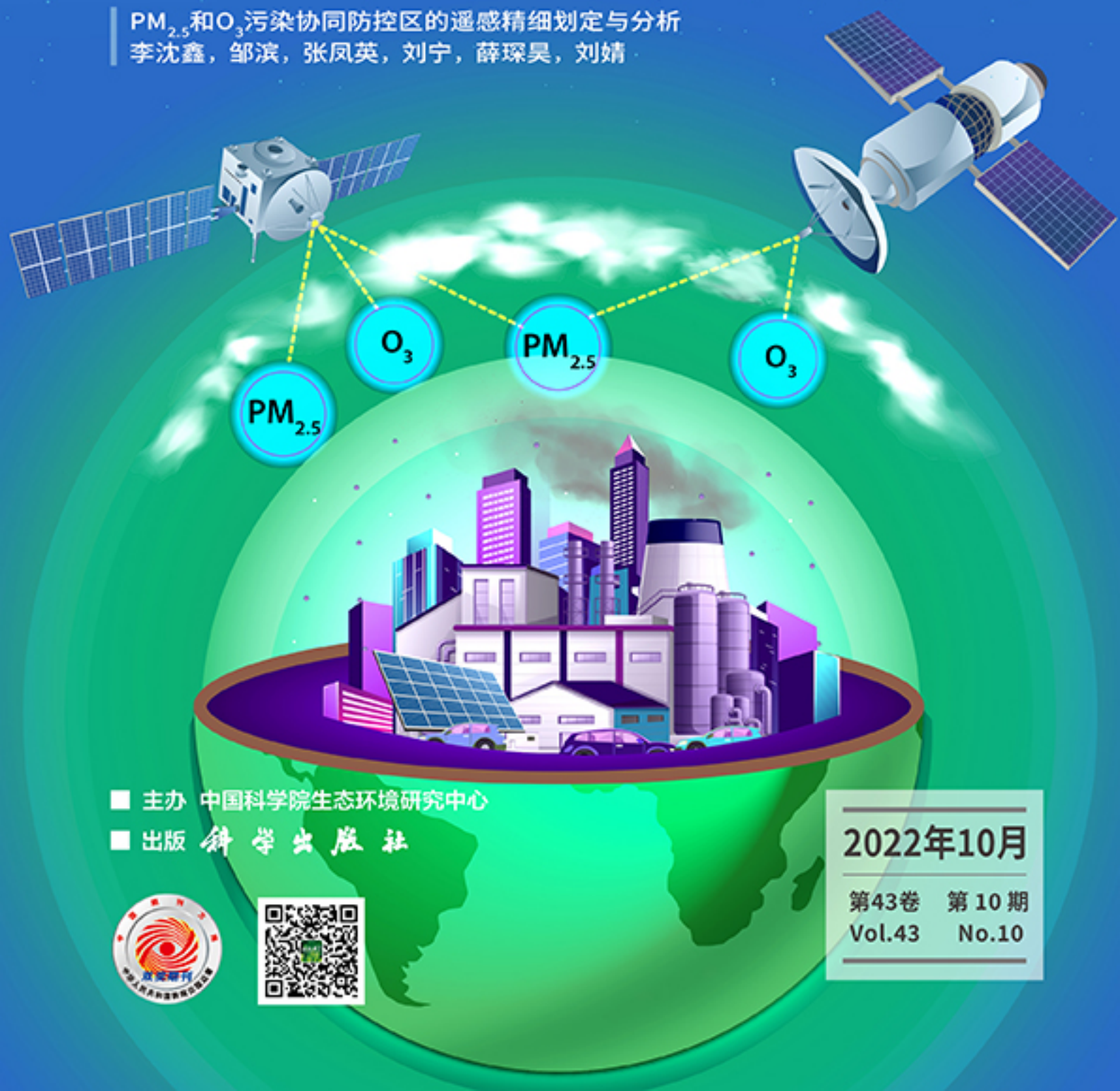
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HUANJING KEXUE

PM_{2.5}和O₃污染协同防控区的遥感精细划定与分析
李沈鑫, 邹滨, 张凤英, 刘宁, 薛琛昊, 刘婧



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低分子有机酸强化植物修复重金属污染土壤的作用与机制

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摘要: 植物修复是利用植物的物理、化学作用去除污染土壤中重金属的技术方法, 可以减少二次污染物的产生, 具有经济可行性。低分子有机酸(LMWOAs)具有生物降解性和环境友好性, 在重金属污染土壤植物修复中具有较强的应用潜力。综述了LMWOAs在植物修复中的作用机制, 主要包括: ①调控根茎叶发育, 增加植物生物量, 强化植物富集效果; ②增强光合作用, 提升植物抗性, 提高对重金属的耐受能力; ③改变根际土壤性质, 提高根际微生物活性, 促进对重金属的吸收; ④改变重金属形态, 减轻重金属毒性, 提高转运效率。最后阐述了LMWOAs强化植物修复重金属污染土壤的优缺点及应用, 提出了LMWOAs在重金属污染土壤植物修复中的研究方向, 这对LMWOAs在未来植物修复中的研究和应用具有科学意义。

关键词: 低分子有机酸(LMWOAs); 植物修复; 重金属污染; 植物生长调控; 作用机制

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Role and Mechanism of Low Molecular-Weight-Organic Acids in Enhanced Phytoremediation of Heavy Metal Contaminated Soil

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Abstract: Phytoremediation is an environmentally friendly technology to remove heavy metals from polluted soil by using the physical and chemical roles of plants. This can effectively reduce the production of secondary pollutants and is economically feasible. Low molecular-weight-organic acids (LMWOAs) are biodegradable and environmentally friendly and have strong application potential in the phytoremediation of heavy metal-contaminated soils. The role and mechanism of LMWOAs in phytoremediation was elaborated on in this study with the aim to: ① regulate the development of roots, stems, and leaves; increase plant biomass; and enhance plant enrichment of heavy metals; ② improve photosynthesis, enhance plant resistance, and promote tolerance to heavy metals; ③ change the properties of rhizosphere soil, improve rhizosphere microbial activity, and promote the absorption of heavy metals; and ④ change the form of heavy metals, reduce the toxicity of heavy metals, and improve transport efficiency. Moreover, the advantages, disadvantages, and application of LMWOAs in enhanced phytoremediation of heavy metal-contaminated soil were explored in this study. Finally, the research direction of LMWOAs in the phytoremediation of heavy metal-contaminated soils was proposed, which will have practical scientific significance for the research and application of LMWOAs in future phytoremediation.

Key words: low molecular-weight-organic acids (LMWOAs); phytoremediation; heavy metal contaminated; plant growth regulation; mechanism

由于采矿、电镀和冶炼等工业活动与农药化肥、杀虫剂和除草剂的使用等农业活动, 土壤环境中重金属污染越来越严重, 危害人类健康^[1]。植物修复是利用植物的物理和化学作用去除污染土壤中重金属的技术方法^[2,3], 与热脱附和土壤固化稳定化等方法相比, 可有效减少二次污染, 能有效改善污染土壤物理、化学和生物环境^[4]。植物强化修复技术能通过增加植物的生物量或提高植物体内重金属含量来获取更高的修复效率, 螯合剂能够改变植物的生长状态、生化特征和抗性机制等, 促进植物对污染土壤中重金属的吸收富集^[5,6]。因此, 植物-螯合剂联合修复技术被广泛用于重金属污染土壤的植物提取强化过程, 具有广阔的应用前景^[7]。

螯合剂是分子中含有2个及以上供电子基团的物质, 能与重金属发生配位螯合作用, 形成稳定的水溶性络合物^[8]。人工合成螯合剂如乙二胺四乙酸

(ethylene diamine tetraacetic acid, EDTA)、乙二醇双(2-氨基乙基醚)四乙酸[ethylene glycol bis(2-aminoethy) tetraacetate acid, EGTA]和二丙烯三胺(dipropylene triamine, DPTA)等, 因其具有环境持久性, 可生化性低, 易造成重金属浸出风险的缺点, 在实际应用中具有较大局限性^[8,9]。天然螯合剂主要是指低分子有机酸(low molecular-weight-organic acids, LMWOAs), 如柠檬酸、酒石酸和草酸等, 具有可生物降解性和环境友好性, 被认为在重金属污染土壤植物修复中具有较强的应用潜力^[10]。重点论述了LMWOAs强化植物修复重金属污染土壤的作用与机制, 阐述了LMWOAs在重金属污染土壤植物

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修复中的应用,并提出了 LMWOAs 在植物修复中的研究方向。

1 LMWOAs 的概念、种类和来源

LMWOAs 是指具有一个或多个羧基,带有特殊分子结构和荷电特性,呈弱酸性的小分子有机物,是土壤中可溶性有机物的重要组成部分^[11,12]。土壤中 LMWOAs 的种类与土壤类型、营养状况、土壤微生物数量和活性密切相关,并且处于合成和分解的动态变化过程中^[13]。LMWOAs 主要有:乙酸、乌头酸、醛酸、抗坏血酸、苯甲酸、丁酸、柠檬酸、甲酸、戊二酸、乙醇酸、乳酸、苹果酸、丙二酸、草酸、丙酸、丙酮酸和酒石酸等,还包括特殊的有机酸,如含羧基的植物生长调节剂(吡啶乙酸等)、氨基酸(天冬氨酸、甘氨酸、谷氨酸等)和糖酸(葡萄糖酸、葡萄糖醛酸、半乳糖醛酸、2-酮葡萄糖酸等)^[11]。

土壤中 LMWOAs 主要来源于植物根系的分泌、有机残体的分解、微生物的合成和土壤中有机的分解等^[13]。土壤微生物在生命活动过程中能合成 LMWOAs,如细菌能够合成挥发性脂肪酸,真菌能够合成非挥发性有机酸^[14]。在植物生长过程中,为适应环境胁迫,植物根系会分泌无机离子和有机化合物^[15]。根系分泌物中的高分子(多糖、蛋白质)和低分子(氨基酸、有机酸、糖、酚)化合物都在根际过程中发挥着重要作用^[16]。其中,LMWOAs 最丰富也是参与重金属反应最多的物质,其分泌过程是植物适应外界环境重要的抗逆应答机制^[17]。白羽扇豆(*Lupinus albus* L.)对缺磷的适应性机制表现为加速须根的形成、柠檬酸的分泌和磷酸烯醇式丙酮酸羧化酶的表达与活性的提高^[18];铝胁迫能够诱导植物根系分泌柠檬酸、苹果酸和草酸等,分泌到胞外的有机酸通过螯合作用可有效缓解铝毒性^[19]。

2 LMWOAs 强化植物修复重金属污染土壤的作用与机制

2.1 调控根茎叶发育,增加植物生物量,强化植物富集效果

重金属胁迫下植物生物量减少是一种不可逆的植物生长抑制现象^[20]。根系是植物吸收土壤重金属的主要器官,重金属会对根系的细胞结构、细胞器及根尖产生危害作用^[21],使根系呼吸减弱,减少营养元素吸收和三磷酸腺苷(adenosine triphosphate, ATP)的产生,参与植物生长发育过程的过氧化物酶(peroxidase, POD)活性降低,导致植物生长受到抑制^[22]。LMWOAs 主要由植物根际释放,土壤微生物合成和植物凋落物降解所产生^[13],参与植物生长发

育过程^[23],能通过提供有效磷和有效铁化合物^[23],产生解聚腐殖质,激活生长素和减轻胁迫对光合器官的损害来促进植物生长^[24]。柠檬酸可以抵御生物和非生物胁迫,增强养分吸收以促进植物生长^[25];草酸和柠檬酸改善了苕麻(*Boehmeria nivea* L.)的生长特性,通过提高根系活力来增强呼吸作用,促进营养物质的吸收,低浓度柠檬酸的施加使植物鲜重和干重分别提高了 44.6% 和 74.4%^[26];酒石酸通过促进碳酸盐的溶解使东南景天(*Sedum alfredii*)的地上生物量增加了 15%^[27],草酸的施加使烟草(*Nicotiana tabacum* L.)地上生物量增加了 20%^[28,29],没食子酸的施用使印度芥菜(*Brassica juncea*)的地上生物量增加了 18%^[28];适当浓度马来酸的施加能够增加秋葵(*Abelmoschus esculentus* L.)根部和地上部干重^[30]。有研究表明,铬胁迫下外源施加 5 mmol·L⁻¹ 柠檬酸能使向日葵(*Helianthus annuus*)根、茎和叶的干重分别提高 31%、23% 和 42%,鲜重分别提高 21%、28% 和 32%^[25];铜胁迫下柠檬酸、酒石酸和草酸的施加均能显著促进蓖麻(*Ricinus communis* L.)的生长,提高植株生物量^[31];镉胁迫下外源柠檬酸盐和苹果酸盐的施加可使水稻(*Oryza sativa* L.)生物量提高 119.0%^[32]。然而,高浓度 LMWOAs 的施加,可使植物生物量呈显著下降趋势,施用过量柠檬酸可使东南景天的根部形态产生负面效应,使其根长、根茎和根体积减小^[33]。这可能是由于高浓度 LMWOAs 超过了植物耐受范围,损害了其良性生长状态,导致植物根尖附近的侧根发育受到抑制,甚至可能导致根尖细胞坏死^[34]。因此,施加不同种类和浓度的 LMWOAs 对植株生长发育及生物量的影响显著不同,重金属胁迫下科学施加 LMWOAs 能够有效调控植物根、茎和叶发育,显著提高植株生物量。

土壤中重金属的生物有效性、超级累积植物的生长速率和生物量等显著影响着植物修复技术的应用和发展^[35],植物修复中生物富集因子(bioconcentration factor, BCF)、转运因子(translocation factor, TF)和去除效率(removal efficiency, RE)的高低与植株生物量密切相关^[36]。施加柠檬酸后东南景天地上部镉的 BCF 提高了 54.51%,根系镉的 BCF 降低了 62.53%,铅的 TF 提高了 66.67%,锌的 TF 提高了 73%,显著提高了东南景天对重金属提取效率^[32];外源施加 5 mmol·kg⁻¹ 的苹果酸,青葙(*Celosia argentea* L.)的 BCF、RE 和 TF 分别提高 3、2 和 1 倍^[37];喷施 10 mmol·kg⁻¹ 柠檬酸,龙葵(*Solanum nigrum* L.)的 BCF、RE 和 TF 分别提高了 19.7%、23.3% 和

0.3%^[38]; 柠檬酸的施加使高羊茅 (*Festuca arundinacea*) 根部和枝条对镉的吸收和积累分别提高了 3 倍和 2.3 倍^[35]; 外源施用 $1 \text{ mmol} \cdot \text{kg}^{-1}$ 乙酸时, 能显著提高甘蓝型油菜 (*Brassica napus* L.) 根部镉的含量, 增强其对镉的富集效果^[39]. 因此, 科学施加 LMWOAs, 能够促进植物对重金属的吸收, 强化植物富集效果.

2.2 增强光合作用, 提升植物抗性, 提高对重金属的耐受能力

植物光合作用对外界的环境胁迫非常敏感, 重金属等任何对植物生长造成影响的因素都可能降低光合作用速率, 会对光合作用产生抑制作用^[40,41]. 重金属进入植物体之后与硫醇基团结合, 破坏叶绿素酶的代谢, 抑制叶绿素的合成^[40], 通过降低相关基因 *psbA*、*psab* 和 *rbcL* 的转录来抑制光合作用^[42]. 植物根系分泌的内源 LMWOAs 在光合作用中发挥着关键的作用^[43], 外源 LMWOAs 也可以减轻重金属的诱导毒性, 缓解重金属胁迫下叶绿体和类囊体的损伤, 促进叶绿素合成, 增强植物光合作用^[44]. LMWOAs 如草酸、柠檬酸和苹果酸等在植物光合作用、呼吸作用、营养元素吸收和金属解毒等方面起着重要作用^[45]. 柠檬酸施加可提高高商陆 (*Phytolacca acinosa*)^[46] 和芥菜 (*Brassica juncea*) 的叶绿素和类胡萝卜素水平^[47], 因为柠檬酸抑制了叶绿素分解代谢酶 (Chlase) 的表达, 促进了邻菲罗烯合成酶 (PSY) 的表达, 从而提高了体内叶绿素含量^[48]. 施用 $2 \text{ mmol} \cdot \text{kg}^{-1}$ 柠檬酸可以分别提高喜盐鸢尾 (*Iris halophila* Pall) 地上部生物量、根系生物量、叶绿素 a 和耐受性指数 42.8%、51.6%、5.1% 和 11%^[49]. 在叶绿素荧光参数中, 初始荧光产量 (F_0) 和最大荧光产量 (F_m) 的增加表明镉对 PSII 反应中心造成不可逆的伤害, 外源 LMWOAs 施加能够减缓这种伤害; 镉胁迫下柠檬酸、苹果酸和酒石酸的施用能不同程度减轻秋华柳 (*Salix variegata* Franch) 叶绿体损伤, 且柠檬酸处理叶绿体膜结构的清晰度和类囊体排列的均匀性均优于苹果酸和酒石酸^[48]; 外源苹果酸的施加能够提高甘蔗 (*Saccharum officinarum*) 叶片 PSII 反应中心的最大光能转化效率^[50].

土壤中重金属水平的增加会刺激植物抗氧化系统, 激活参与三羧酸循环的酶, 导致植物体内的氧化应激效应, 从而刺激细胞中 LMWOAs 的产生. 当培养基中有铝存在时, 黑麦草 (*Lolium perenne* L.) *ScALMT1* 基因表达上调, Al³⁺ 位点编码一个铝激活的有机酸转运基因, 可以提高铝敏感植物的耐铝性^[51]. 重金属胁迫会引起植物体内脂质过氧化物

(lipid peroxidation, LPO) 和活性氧 (reactive oxygen species, ROS) 的积累, 导致严重的氧化胁迫, 甚至细胞失活等严重损伤^[52]. 植物主要通过释放多种抗氧化物质, 激活抗氧化系统, 抵御 ROS 对植物的损害^[52,53]. 有研究表明, 外源 LMWOAs 的科学施用能够有效提高植物抗性, 柠檬酸提高了甘蓝型油菜超氧化物歧化酶 (superoxide dismutase, SOD)、过氧化氢酶 (catalase, CAT) 和过氧化物酶的活性^[46,54], 这可能是因为外源 LMWOAs 可以促进 Cu/Zn-SOD、POD1、GR1、GPX1 和 GST1 等抗氧化酶基因的表达, 从而提高植物体内抗氧化酶和非酶类抗氧化剂的含量^[50]. 这些抗氧化剂与过氧化氢 (H_2O_2) 相互作用, 减缓 ROS 胁迫, 保护细胞免受氧化损伤, 还能抑制 $\text{O}_2^{\cdot -}$ 的产生, 减弱了细胞膜脂质过氧化作用, 增强植物抗逆性. 外源苹果酸能够诱导芒 (*Miscanthus sinensis*) 的 Cu/Zn-SOD、POD1、GR1、GPX1、GST1 和 DHAR 等抗氧化酶基因的表达, 缓解镉引起的毒性和氧化损伤^[50]; 镉胁迫下施加苹果酸可以通过调节荻 (*Triarrhena sacchariflora*) 的酶和非酶类抗氧化剂的活性和基因表达来缓解镉诱导的氧化损伤; 水杨酸通过提高植物 SOD、POD、谷胱甘肽还原酶 (glutathione reductase, GR)、抗坏血酸过氧化物酶 (ascorbate peroxidase, APX)、愈创木酚过氧化物酶 (guaiacol peroxidase, GPX) 和降低 CAT 的活性来抵御氧化应激和减缓 ROS 的产生^[55]; 铜胁迫下琥珀酸施加能增强玉米 (*Zea mays* L.) 的抗性机制, 缓解氧化应激作用^[56]. 然而, 较高浓度外源 LMWOAs 的施加会抑制 SOD 和 H_2O_2 酶等保护机制, 导致丙二醛 (malondialdehyde, MDA) 等有害物质积累, 降低植株对重金属的耐受性^[34]. 因此, 适当外源 LMWOAs 的施加能提高抗氧化酶活性, 减轻 ROS 积累, 提高植物抗氧化性, 使其在重金属胁迫下保持良好的生长状态.

植物通常采用两步机制来解毒金属离子, 植物螯合蛋白与有毒离子相结合, 形成的植物螯合蛋白-金属复合物被隔离在液泡中^[57]. 巯基物质如谷胱甘肽 (glutathione, GSH) 和半胱氨酸 (cysteine, Cys) 对镉的螯合作用也是植物主要的解毒机制^[58], 巯基与镉有很强的亲和力, 螯合形成的无毒络合物可以存在于细胞质或运输到液泡, 有效降低镉在组织内的毒性和迁移^[58]. AtATM3 转基因在芥菜中的表达可诱导 GSH II (谷胱甘肽合成酶 II) 和 PCS1 (螯合肽合成酶 I) 的高效表达, 增强对镉和铅的耐受性^[59]. 研究发现, 镉胁迫下施加有机酸能显著提高秋华柳根系中 GSH 的含量, 并用于植物螯合肽 (phytochelatins, PC) 的生物合成和抗氧化剂的消

耗^[60]; 柠檬酸和酒石酸的施用能显著促进 MTP4 在根系中的表达, 增强根系对镉的吸收; 外源 LMWOAs 的施加能促进 HMA1、HMA3 和 HMA5 的表达, 提高秋华柳对镉的耐受能力^[60]; 柠檬酸的施用能够增强东南景天对重金属的耐受性^[33]。

2.3 改变根际土壤性质, 提高根际微生物活性, 促进对重金属的吸收

土壤中重金属的诱导胁迫, 可以破坏植物细胞液 pH 稳定, 导致根际土壤 LMWOAs 分泌增加, 降低植物根际酸碱度^[61,62]。植物分泌的 LMWOAs 主要以游离形式存在于细胞质中, 并以阴离子的形式释放到根际土壤中, 导致植物细胞质内的阴阳离子失衡。为了平衡这个过程, 氢离子以质子泵的形式从植物细胞排放到根际土壤中, 降低根际土壤 pH 值^[61,63], 促使重金属从土壤中释放出来, 提高重金属的溶解性, 增加重金属的移动性, 增强重金属的吸收和转移过程^[64]。外源 LMWOAs 的施加还能有效改变根际土壤性质, 促进土壤中不可利用矿物质的溶解^[65]。此外, 施加 LMWOAs 可以为土壤提供碳源和活化养分, 如速效磷和碱解氮等显著增加, 提高土壤的生产力^[29]。

LMWOAs 能够促进土壤中难溶性矿物质的溶解, 为微生物生长提供能源物质, 增加土壤微生物数量, 缓解重金属对微生物的毒害作用^[13,66], 以根系分泌物为营养的微生物可以产生更多的有机酸, 如柠檬酸、富马酸、苹果酸和草酸等^[67], 且外源 LMWOAs 施加对土壤微生物群落结构和多样性具有显著的影响, 能够维持微生物群落的生态平衡^[38]。外源 LMWOAs 的科学施用可以改善香菇 (*Lentinus edodes*) 修复重金属污染土壤的细菌群落结构和多样性, 显著提高了土壤微生物数量和酶活性, 改善土壤微生态, 提高真菌提取重金属的效率^[68]; LMWOAs 官能团通过形成有机酸-金属络合物, 防止重金属与酶的巯基结合, 进而维持土壤中酶的活性^[69]; 酒石酸的施加能显著提高铜污染土壤 CAT、脲酶 (Urease, URE) 和酸性磷酸酶 (acid phosphatase, ACP) 活性^[31]。此外, 二羧酸和三羧酸可溶解铝和铁氧化物上的难降解磷, 柠檬酸、苹果酸和草酸等可促进土壤中磷的转化, 提高磷生物有效性, 增加植物对土壤磷的吸收^[70,71]。因此, LMWOAs 可以增加沉积物中的可溶性养分, 用于微生物和植物的吸收利用, 促进根际微生物的增殖及土壤矿物质的溶解^[72]。

通过吸附和沉淀作用, LMWOAs 能与土壤固相发生较强的亲和作用, 促进植物对重金属的吸附作用, 降低土壤中重金属浓度^[73]。不同类型 LMWOAs

对不同重金属的吸附能力具有一定的选择性, 可以通过科学施加 LMWOAs 强化重金属污染土壤的植物修复作用。LMWOAs 与土壤因素 (有机阴离子、土壤类型、酸碱度和微生物等) 相互作用, 能使植物高效吸附污染土壤中的重金属^[74]。柠檬酸参与土壤吸附反应的羧基含量较高, 具有较高的吸附亲和力^[26]。有研究发现, 1-羟基亚乙基-1,1-二膦酸 (1-hydroxyethylidene-1,1-diphosphonic acid, HEPD) 和 D-葡萄糖醛酸 (D-glucuronic acid, D-GA) 的科学施加能促进龙葵对污染土壤中镉和铅的吸收^[38]。

2.4 改变重金属形态, 减轻重金属毒性, 提高转运效率

土壤中重金属具有高度持久性和不可生物降解性, 只能从一种化学状态转化为另一种化学状态^[8,75], 重金属的离子形式比络合物的毒性更强^[76]。重金属离子能够诱导植物分泌有机酸^[77], 通过螯合作用减轻植物体内游离活性重金属离子的毒性^[78], 有机酸作为植物体内重要的重金属配位体, 还参与重金属的吸收、运输和贮存等生理代谢过程^[79]。外源 LMWOAs 能够与镉整合, 形成可流动的和可溶性的有机酸-镉络合物, 可以穿透根细胞的脂膜, 这是玉米吸收镉的主要形式^[80]。由于土壤中重金属生物有效性较低, 植物提取效率会受到限制^[50], 外源 LMWOAs 的施加能够增加土壤和植物中交换态重金属的含量, 改变根际土壤中可交换态、碳酸盐结合态、铁锰氧化物结合态、有机物和硫化物结合态及残留重金属的分布情况^[81]。LMWOAs 的科学施用可提高美洲商陆 (*Phytolacca americana* L.) 根部-地上部镉的转运效率, 改变土壤中镉的形态分布, 提高活化效果, 强化植物体内镉的生物积累^[28]。

重金属进入植物细胞质后, 可以通过失活、螯合和区域化分布等机制进行解毒^[82]。LMWOAs 是重金属离子的潜在配体, 植物根系分泌 LMWOAs 被认为是植物抗逆应答的机制之一^[17], 其在解毒过程中发挥着重要作用。超积累植物中 ZIP、HMA、MATE、YSL 和 MTP 家族成员在驱动重金属吸收并转运到地上部, 在液泡或细胞壁封存过程中起决定性的作用^[83]。一方面, LMWOAs 能够促进重金属与细胞壁的结合。重金属与植物最先接触的细胞结构为细胞壁, 细胞壁被认为是重金属的主要储存场所^[79]。重金属胁迫下铅和镉的含量在获幼苗根细胞壁中含量很高, 分别为 63.98%~68.97% 和 3.81%~57.44%^[84]。植物细胞壁中的 LMWOAs 通过固定重金属, 将其与细胞壁结合, 从而限制重金属与植物其它重要组织的相互作用^[85,86]。重金属还能与植物

细胞壁中多聚半乳糖醛酸通过其羧酸形成金属-有机酸复合物,对重金属进行有效解毒^[19,87]. 锌胁迫下芥菜植株中主要以锌-多聚半乳糖醛酸的形式存在于植物根系中^[86],对东南景天进行¹³C 标记实验发现,根系分泌的酒石酸能有效地增溶镉,形成可溶性的镉-酒石酸络合物,促进东南景天对镉的积累^[27]. 有机酸参与金属从根到地上部的运输,以及参与金属在细胞水平的解毒. 细胞质中重金属与有机酸等有机配体的结合及其在液泡中的封存和固定被认为是植物耐受重金属的最重要机制之一^[88]. 柠檬酸在重金属的木质部运输中起着特殊作用^[89]. 柠檬酸在这些离子的木质部运输过程中起着螯合 Fe^{2+} 的作用,而 FRD3 则介导柠檬酸向根导管的外流,以维持铁向地上部的转移^[90]. 此外,LMWOAs 与重金属络合会改变根际环境的 pH 值,从而促进细胞壁对铅和镉的吸收和积累^[91]. 另一方面,液泡被认为是重金属积累和解毒的第二道屏障,也是最终的屏障位点^[91]. 细胞内的 LMWOAs 通过螯合作用与重金属在胞浆中形成无毒或毒性较小的络合物,并在液泡中将络合物连接起来,将重金属固定在液泡中^[92]. 重金属贮存前能被有机酸(柠檬酸、组氨酸)和螯合配体(PCs、MTs)解毒^[93]; AtMTP1、PtMTP1、CsMTP1、AtMTP3 和 CsMTP4 主要参与液泡锌和镉的运输和分离^[94],柠檬酸和酒石酸的施加显著促进了秋华柳 MTP4 在根系的表达,增强根系对镉的吸收^[60],这可在很大程度上减少游离重金属离子的含量,降低重金属对植物的生物利用度,从而起到积累和解毒重金属离子的作用^[73,95]. 镉胁迫下,负责分泌柠檬酸盐和苹果酸盐的转运体 AtALMT 和 AtMATE 的表达升高,促进细胞间隙中镉-柠檬酸的积累和沉淀^[96]. 柠檬酸和酒石酸的施加显著增加 NRAMP5 在根和叶片中的表达水平^[60]. 镉在获幼苗根部中主要以酸提取态镉(18.79%~50.50%)的形态存在,这说明铅和镉与不溶性磷酸盐/草酸盐形成络合物是获幼苗对铅和镉耐受性和解毒的重要机制^[84]; 外源柠檬酸通过提高蓖麻的生长和光合作用活性,减少 H_2O_2 产生和膜透性,降低蓖麻的铅毒害^[97]. 由此可知,重金属胁迫下 LMWOAs 能够降低重金属毒性,有助于耐受和储存重金属和维持细胞稳态^[95,98].

超积累植物吸收土壤中的重金属后,由木质部和韧皮部将重金属从根部向地上部运输^[99],这是决定茎叶中重金属积累水平的关键,木质部和韧皮部汁液中的 LMWOAs 能够显著提高重金属在植物体内的转运效率^[100]. 柠檬酸和乳酸的施加对芥菜吸收铀的实验发现,铀以磷酸铀酰形式在根部固定的

含量降低,以有机酸-铀络合物形式通过质外体途径转运到地上部的含量增加^[89]; 施加适当浓度的柠檬酸、苹果酸和酒石酸均能提高龙葵对镉的吸收能力及镉从根部向地上部的转运能力^[101]; 东南景天木质部镉和柠檬酸的联合运输增加了其在叶片中的转移和积累; ZIP 转运蛋白将镉、锰和锌等离子从根部运送到地上部,锌通过共生体进入细胞后,在木质部中以锌-烟碱/组氨酸/柠檬酸复合物的形式参与转运过程^[82],这是一种依赖于木质部负载的能量消耗,由重金属运输 ATP 酶 HMA3 促进的^[102]. 镉胁迫下, HMA3 的表达水平明显受到抑制,外源柠檬酸、苹果酸和酒石酸的施加能促进 HMA1、HMA3 和 HMA5 的表达,提高秋华柳对镉的转运效率^[60]. 由此可见,LMWOAs 的施加能够显著提高超积累植物的重金属转运效率.

3 LMWOAs 强化植物修复重金属污染土壤的优缺点及应用

植物修复重金属污染土壤,主要包括以下过程:

① 重金属的生物有效性和根系对重金属的吸收; ② 重金属从根部向地上部转运; ③ 重金属在细胞器(主要是液泡)中的隔离^[93]. LMWOAs 丰富土壤微生物群落结构和多样性^[66],提高土壤有机物生物可降解性,增加土壤养分,影响解吸动力学,提高土壤中有害物质的降解吸收^[103]; LMWOAs 与有机碳接触过程中,可提高生物炭的孔隙率,增加表面积,促进对矿物质的溶解^[104]; LMWOAs 使得根际土壤 pH 值降低,间接促进植物根系对磷素的吸收^[105]; LMWOAs 参与植物必需元素的吸收和重金属的解毒,可以螯合和隔离液泡中的金属离子^[23]; LMWOAs 能促进植株生长,增强抗氧化防御系统^[97],提高植物修复效率; LMWOAs 对环境更加友好,具有生物降解性好和无二次污染等优点^[46]. 然而,与 EDTA 等化学螯合剂相比,LMWOAs 的植物提取能力较弱^[106],在自然条件下,土壤中有机酸含量较低,且 LMWOAs 分解遵循 Michaelis-Menten 动力学规律^[107],因此外源 LMWOAs 的多次施加比单次效果好^[39].

LMWOAs 强化植物修复主要采用叶面喷施和土壤外源施加两种方式进行,后者能与土壤重金属络合并减轻毒性,提高生物有效性和植物修复效率^[108]. 外源施加 $5 \text{ mmol} \cdot \text{kg}^{-1}$ 的苹果酸提高龙葵对贵州黄壤区镉吸收和转移效率的效果最佳^[109]; $3 \text{ mmol} \cdot \text{kg}^{-1}$ 柠檬酸的施加能提高阔叶山麦冬 (*Liriope platyphylla* Wang et Tang) 对锌、铜、铅、镍和镉的修复指数 60%~187%^[110]; $2 \text{ mmol} \cdot \text{kg}^{-1}$ 柠

檬酸处理喜盐鸢尾促进了其地上部和地下部重金属积累,有机酸施加可作为修复铅尾矿以改善矿山环境^[49];柠檬酸施加可提高苧麻(*Boehmeria nivea* L. Gaud.)对镉的吸收和耐受能力,在中度镉污染场地植物修复中具有广阔的应用前景^[26];施加乙酸、草酸、柠檬酸、苹果酸和酒石酸均能增加甘蓝型油菜对镉吸收达100%以上^[39];施加10 mmol·kg⁻¹的柠檬酸能有效提高美洲商陆的镉迁移系数^[46],最大限度提高了博落回(*Macleaya cordata*)对铀的吸收^[111];柠檬酸和嗜根考克氏菌(*Kocuria rhizophila*)合施能促进大豆(*Glycine max* L.)对镉、铬、铜和镍的积累量分别增加40.63%、56.39%、59.1%和39.76%^[112]。LMWOAs与植物根际促生菌(plant growth promoting rhizobacteria, PGPR)联合应用是可行的植物提取技术,会对植物修复效率产生积极的影响^[113]。然而,工程项目实施条件复杂,可能导致LMWOAs在实际应用时强化效果有所不同,且不同植物适用的LMWOAs也不相同。因此,实际工程项目中,根据应用效果需不断完善外源施加LMWOAs的种类和浓度等关键因子。

4 结论与展望

(1)目前研究热点主要集中在LMWOAs的施加对植物生长和重金属富集转运的影响作用,忽略了LMWOAs对植物内源激素包括生长素、细胞分裂素和脱落酸等调控的影响和机制研究,应深入开展LMWOAs对植物内源激素调控机制的研究,为LMWOAs强化植物修复重金属污染土壤的应用提供更充分更科学的理论依据。

(2)重金属污染土壤植物修复中LMWOAs作为可生物降解螯合剂,其在土壤中的可持久性较低,这是LMWOAs施加不能高效提高植物提取效率的主要原因之一。外源LMWOAs可作为土壤微生物的碳源,可被土壤微生物降解,而内源LMWOAs又来源于微生物的合成和土壤中有机的分解,LMWOAs与土壤微生物的关系究竟如何?LMWOAs强化植物修复重金属污染土壤中,应重点探索土壤微生物的响应及作用机制。

(3)目前较多研究侧重于LMWOAs施加对植物的作用及其与重金属的螯合作用,忽略了LMWOAs施加对植物作用的分子机制研究,应深入开展重金属胁迫下LMWOAs与植物信号分子的响应、基因转录、信号传递等过程的研究,这对深层次掌握LMWOAs在植物修复中的作用有着重要意义。

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