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硒阻控作物吸收重金属机制研究进展

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摘要　重金属污染对粮食安全及人体健康造成巨大威胁，目前已开发出许多农田重金属污染修复方法。硒的补充显著降低作物对重金属的吸收，同时促进作物在重金属污染土壤中的生长，施硒已成为阻控作物吸收重金属的新途径。本文对施硒阻控作物吸收重金属的5种机制即硒改变土壤重金属的生物有效性、硒与重金属竞争植物摄取通道、硒促进植物根系铁膜形成、硒诱导植物根系形态及结构变化、硒调控植物重金属螯合和转运基因表达等研究进展进行了综述，同时对施硒阻控作物吸收重金属潜在风险及未来研究重点进行展望，以期为将来利用硒作为重金属阻控剂提供参考。

关键词　重金属；硒；农作物；土壤修复；铁膜；植物根系

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矿山的开采、过度使用化肥和杀虫剂以及污水灌溉等人为活动会导致农田土壤严重的重金属及类金属污染[1-2]，其中，As、Cd、Hg、Sb、Zn、Cu、Cr、Pb等重金属的污染对粮食安全及人体健康造成极大的威胁[3-6]。目前已开发出多种重金属污染修复方式，包括利用超富集植物蜈蚣草（*Pteris vittata* L.）和东南景天（*Sedum alfredii* Hance）等对重金属进行吸收提取、利用生物炭或有机肥对土壤重金属进行吸附和钝化、通过重金属转化微生物对其进行解毒及固定等途径[7-9]。硒（Se）是人体和动物必需的微量元素，作为30多种硒蛋白及硒酶的重要活性中心，在维持人体抗氧化、抗癌及免疫调节中发挥重要作用[10-11]。长期的硒摄入不足可能会引发克山病、大骨节病等疾病[11-12]。膳食中的硒摄入是人体主要的硒补充方式，因此，农作物的硒生物强化受到广泛的关注[13-14]。研究表明，作为一种硒强化措施，叶面施硒或施加含硒肥料等方式不仅能促进作物富硒、提高作物产量和品质，还能显著降低蔬菜和谷物中As、Cd、Pb、Hg、Cr、Sb和Cu等重金属的积累。硒已被广泛认为是一种新型高效的作物吸收重金属阻控剂[15-18]。本文主要介绍在土壤-植物系统中由硒介导的重金属的迁移及转化，并阐释硒介导的阻控植物重金属吸收的潜在机制，以期为施用硒肥阻控作物重金属积累提供一定科学依据。

1　硒阻控作物吸收重金属机制

1.1　硒改变土壤重金属的生物有效性

施加到土壤中的硒会与土壤重金属发生复杂的相互作用，从而改变土壤重金属的生物有效性[18]。硒在土壤中的生物有效性及钝化重金属的效果受到pH值、Eh值、有机质及土壤微生物等土壤特性的影响[19]（图1）。土壤pH值的变化直接影响土壤中重金属的溶解性和土壤颗粒对重金属的吸附能力。土壤pH值的增加会提高土壤颗粒表面负电荷含量，从而增加As、Sb、Se等类金属含氧阴离子的流动性，但降低Cd、Pb、Cu、Hg等重金属阳离子的生物有效性[20-22]。研究发现，提高土壤pH值可以增强Se阻控水稻Cd吸收的效果[23]。此外，Huang等[24]报道向稻田土壤中施加1 mg/kg的亚硒酸钠（强碱弱酸盐）可显著增加根际和非根际土壤的pH值，从而降低稻田土壤中Cd的流动性和水稻中Cd的含量。然而，土壤pH类金属的提高同时会导致As、Sb等类金属的活化，因此，在利用硒处理As和Cd等重金属复合污染时需要综合考虑土壤pH对修复效果的影响。

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水稻种植涉及淹水及排水2种水分管理方式，稻田土壤的Eh变化对硒及土壤重金属的生物有效性有着重要影响[20-21]（图1）。长期淹水后的土壤Eh降低，当土壤Eh降低至－200 mV以下时，四或六价硫及硒的含氧阴离子被还原为负二价硫或负二价硒，二价镉阳离子会优先与负二价硫形成硫化镉，此外也能与负二价硒形成硒化镉沉淀，从而降低镉的流动性及镉在植物中的含量[25-26]。与之相反，土壤长期淹水不利于硒阻控植物对As等类金属阴离子的吸收。稻田淹水产生的厌氧环境会促进As(Ⅴ)还原为As(Ⅲ)并导致Fe/Mn氧化物的还原从而促进砷的解吸附，最终提高砷的流动性和毒性[20]。同时，淹水厌氧的环境导致Se(Ⅳ)还原为不溶的单质硒沉淀，降低生物有效性硒的含量，从而极大降低硒拮抗植物砷吸收的效果[18,26]。Wan等[27]发现，在有氧条件下施加硒可降低水稻对As的吸收，但在淹水条件下施加硒反而促进砷在水稻中的积累。因此，利用施硒阻控作物重金属吸收时应根据土壤污染情况调整土壤淹水状况，以保证最佳的修复效果。

除土壤pH、Eh等理化性质外，土壤微生物可通过对硒及土壤重金属的转化介导形成不溶性硒化物沉淀，最终降低重金属的生物有效性（图1）。Wang等[28]报道稻田土壤中施加硫酸盐及亚硒酸盐可通过形成HgS或HgSe沉淀，从而降低水稻中甲基汞的含量。由于Se对Hg的结合亲和力大于S，施加亚硒酸盐对汞污染修复效果优于施加硫酸盐[29]。He等[30]构建的活性污泥反应器通过微生物介导的HgSe生物矿化，实现Hg与Se的共去除。亚硒酸盐可在土壤微生物转化作用下与Cd反应生成CdSe沉淀，从而降低Cd的流动性和迁移率[31]。土壤中生物有效性Se及Cd的比例直接影响土壤难溶性CdSe的形成[31-32]。Zhang等[31]发现，当土壤中硒和镉的生物有效物质的量比大于0.7时，增加的生物有效性硒才能将酸性土壤中的Se(Ⅳ)还原为Se(－Ⅱ)，随后形成难溶性CdSe，最终显著降低玉米中Cd的含量。然而，当硒和镉物质的量比低于0.7时，Se和Cd可能以$CdSeO_3$和$CdSeO_4$的形式更高效地被根部吸收，导致玉米中镉的积累[31]。Guo等[32]在水培试验中发现，外源硒或镉的施加会降低水稻对另一种金属的吸收和转运。当Se/Cd物质的量比大于1时，水稻各部位Cd的浓度和转移因子同时达到最低值，硒与镉的相互拮抗吸收可能与CdSe形成相关。与Cd类似，研究指出Cu可在希瓦氏菌的转化下与硒形成CuSe沉淀进而实现共解毒[33]。除了直接介导硒与重金属不溶硒化物的合成外，某些硒氧化细菌可通过对土壤难利用态硒的溶解及低价态硒的氧化作用，将低生物可利用度的低价态硒转化为流动性更高的高价态硒，从而提升土壤硒的生物有效性。An等[34]通过施加硒氧化农杆菌T3F4提高土壤硒的流动性，从而促进小白菜对硒的吸收并降低砷的积累。Guo等[35]报道数株硒氧化细菌可活化土壤中的硒，最终提高小白菜的硒含量同时阻控镉的吸收。

图1　硒改变土壤重金属的生物有效性

Fig.1　Selenium alters the bioavailability of heavy metals in soil

1.2　硒与砷锑等类金属竞争植物摄取通道

除了直接改变土壤重金属的生物有效性之外，硒还可以通过与砷等类金属竞争离子摄取通道从而降低作物中类金属的含量[34,36]（图2）。水稻根部通过硅转运蛋白非特异性的摄取As(Ⅲ)离子，它属于水通道蛋白亚家族中的类NOD26膜内在蛋白[37]。

由于As(Ⅴ)与磷酸盐结构相似,植物根系可通过磷酸盐转运蛋白对As(Ⅴ)进行吸收[38]。与As(Ⅲ)类似,Se(Ⅳ)也被证实可以通过根系的硅转运通道而被植物非特异性吸收[39]。此外,Zhang等[40]发现水稻的磷酸盐转运蛋白OsPT2参与对亚硒酸盐的主动吸收。已有许多研究报道硒通过与砷竞争植物根系摄取通道从而拮抗砷的吸收。An等[34]在水培体系中加入10 μmol/L Se(Ⅳ)将小白菜对As(Ⅴ)的50%生长抑制浓度提高2倍,有效降低砷对植物的毒性,并显著降低植株地上部分砷的含量。然而,一些研究发现,在As(Ⅲ)暴露的水培水稻体系中加入Se(Ⅳ)仅阻控As从水稻根部向茎的转运,但会促进As在其根中的积累[36,41],说明硒阻控植物吸收砷不仅由竞争摄取通道介导,还存在其他机制。此外,多个研究发现硒的施加降低了锑对植物的毒性和植物中的锑积累[15,42]。已有研究报道,Sb(Ⅲ)与Se(Ⅳ)均可以被植物根系的水甘油通道蛋白进行非特异性摄取[43]。因此,竞争植物根部的硅酸盐摄取通道,也可能是硒降低锑毒性和吸收的重要途径。

1.3 硒促进植物根表铁膜形成

铁膜是水稻等水生植物根表由铁的氧化物或氢氧化物形成的铁斑块,对As、Cd、Hg、Sb、Zn及Cu等重金属均有较强吸附能力,已被广泛报道作为植物吸收重金属的屏障[44-50]。已有研究报道发现施加一定剂量的硒能改变水稻根表铁膜及其吸附重金属的含量(图2)。Zhou等[44]的研究发现,在水培体系中硒的施加能促进水稻根表铁膜中无机汞的积累进而降低茎中汞的含量。Huang等[48]的研究发现亚硒酸盐的施加刺激了水稻根系径向氧的释放,从而促进根系微环境亚铁离子的氧化,最终提高根表铁膜的含量和Cd的阻控效果。硒对植物根表铁膜的形成受到根系暴露的重金属的价态及其生物有效性浓度等诸多因素的影响。Liu等[51]的研究发现硒的施加仅能促进Sb(Ⅲ)而非Sb(Ⅴ)暴露下的水稻根表铁膜的形成。有研究报道,硒的施加仅在低镉污染土壤中通过促进水稻铁膜形成并阻控镉,而对高浓度镉污染土壤中水稻铁膜的形成无显著影响[52]。

除以上因素外,硒的施加剂量、价态及施加时机均会影响硒对植物根表铁膜形成及重金属阻控效果。Chang等[45]报道低剂量(1.0 mg/kg)的硒能够促进铁膜的形成从而降低水稻中Cd的含量,而高剂量(8.0 mg/kg)的硒抑制水稻根表铁膜的形成,说明硒对铁膜的形成影响具有剂量效应。最近的研究发现,Se(Ⅳ)和Se(Ⅵ)均能有效降低水稻茎叶中砷的积累,但Se(Ⅳ)会促进砷从铁膜中向根中的转运,而Se(Ⅵ)则显著降低铁膜中砷向根部的转移[49],表明硒的价态对铁膜的砷阻控至关重要,但其作用机制尚不明确。此外,施加硒的时期对铁膜阻控重金属的效果至关重要。Huang等[50]的研究发现,在分蘖期施加Se(Ⅳ)是降低糙米中镉含量的最佳时期,分蘖期施硒能刺激抽穗期的水稻根表产生大量的铁膜,最大程度地抑制了根系对镉的吸收和镉从根系向籽粒的转运。

1.4 硒诱导植物根系形态及结构变化

根系的形态及结构对植物抵御重金属的毒性和胁迫起着重要作用[53-54]。Huang等[53]研究表明,具有较大的表面积、较长的根长和较多根尖的辣椒品种具有更高Cd积累量,减少根毛、侧根数量和根的长度,有利于植物降低根系对重金属的摄取和吸收。在对水稻的研究中发现,单位根表面积更小、根孔隙度更大的水稻植株,其籽粒中镉积累量更低[54]。已有研究表明,硒能通过诱导植物根系形态及结构发生变化,从而降低植物对重金属的吸收和积累[55-58](图2)。Malheiros等[55]发现,施加Se(Ⅳ)可降低水稻生长素和乙烯的生物合成相关基因的表达量,从而抑制根系主根和侧根的生长。此外,Wu等[56]的研究发现,水培体系中加入0.5 mg/L的Se(Ⅳ)能调控植物生长素的运输及信号转导从而降低根的表面积和根尖数量,进而降低植物根系及地上部分对镉的吸收。Ding等[57]发现,硒能显著降低水稻根系须根的含量而促进主根的发育,从而降低根系对镉的吸收。施加硒可降低水稻植株在Sb(Ⅲ)暴露下的根叉及细根的数量,从而降低植物地上部的锑含量[17]。然而,也有研究发现硒的施加并未影响根系的形态,但小白菜地上部分的镉含量显著降低,说明不同植物存在不同的硒阻控镉吸收的机制[58]。

除了诱导植物根系形态或结构的改变外,硒还可通过改变根系细胞壁组成成分介导重金属的阻控。细胞壁主要由纤维素、半纤维素、果胶、木质素等物质组成,可通过与重金属的结合作用降低植物根系对重金属的吸收[59-60]。施硒可增加细胞壁中半纤维素、木质素和果胶等物质的合成来提高细胞壁的厚度和对重金属的螯合能力,从而有效降低植物根系对重金属的吸收[15,51]。Yang等[61]的研究发现,施加Se(Ⅵ)显著提高小白菜根中果胶和半纤维素的含量,并通过提升果胶甲基酯酶活性促进果胶的合

成，增强细胞壁对 Cd 的结合作用，从而降低植物地上部分镉的含量。此外，Wang 等[62]的研究发现，除了通过促进植物根细胞壁果胶、半纤维素和木质素的合成降低镉吸收外，硒的施加还可以促进根内皮层和外皮层凯氏带的沉积，从而阻断 Cd 的转运，并诱导细胞壁中羧基、羰基或酰胺基的释放而与 Cd 结合，最终阻控根系对镉的吸收。

1.5　硒调控植物重金属螯合和转运基因表达

除上述机制外，硒还可通过调控植物重金属螯合和转运相关基因的表达进而降低重金属的吸收和毒性(图 2)。Cui 等[63]的研究发现，Se(Ⅳ)的施加促进水稻参与镉向液泡转运的 *OsHMA3* 基因的表达，但降低了参与镉吸收基因 *OsNramp5* 和转运基因 *OsLCT1* 的表达量，从而将镉更多地固定在液泡中，同时降低根系对镉的摄入和向地上部分的转移。Huang 等[64]报道，Se(Ⅳ)诱导水稻根系中液泡镉转运 *OsNramp1* 和 *OsMHA3* 基因上调表达，促进镉在液泡中的隔离；同时，硒刺激水稻植物螯合素(PC)的合成，降低植物根系中镉的毒性和流动性。此外，纳米硒的施加使叶片及花序梗中的 *OsLCT1*，*OsCCX2* 和 *OsPCR1* 镉转运相关基因下调表达，从而降低镉向水稻籽粒的转移和积累[65]。叶面喷施 1 mg/L 的 Se(Ⅳ)可诱导油菜叶片细胞植物螯合素 PCS1 的合成，从而促进 PC-Cd 复合物的形成并将镉螯合物隔离在液泡中[66]。Se(Ⅳ)的施加可诱导小麦根系镉摄入转运蛋白 TaNramp5 的下调表达，同时刺激镉外排蛋白 TaTM20 和 TaHMA3 上调表达，从而降低植物对镉的吸收和积累[67]。也有研究发现，Se(Ⅵ)能提高砷暴露条件下水稻根系硝酸盐转运蛋白 NRT、磷酸盐转运蛋白 PHT、钾通道蛋白 KCP 的表达，进而促进植物对必需元素的吸收和利用来抵御砷的胁迫[68]。

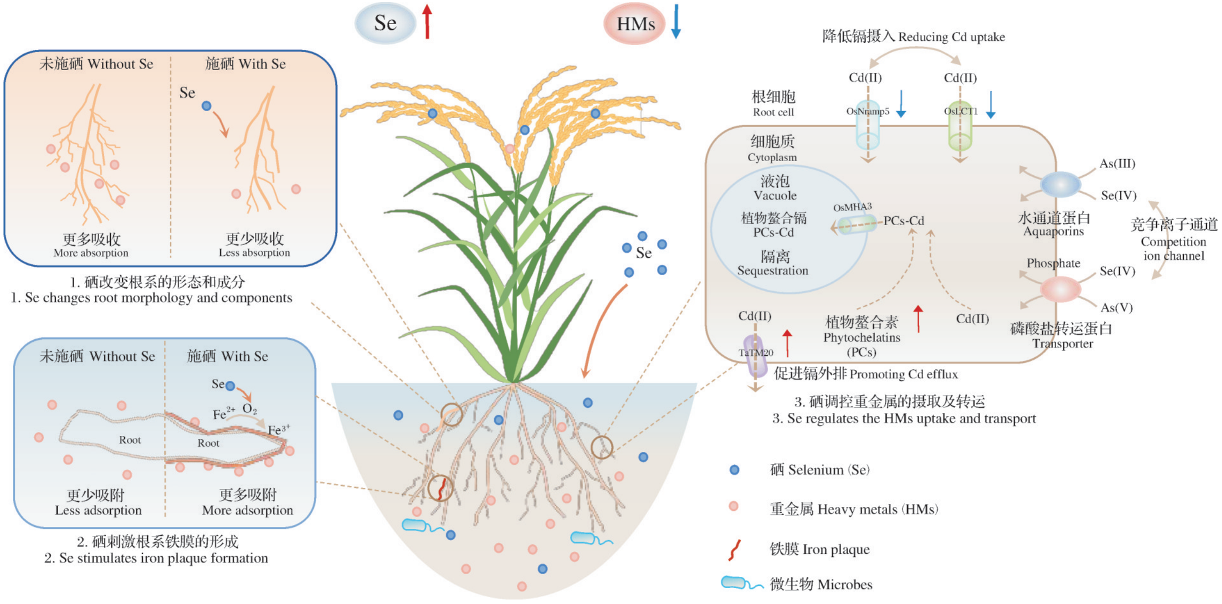

图 2　硒阻控作物吸收重金属的机制(改自文献[21])

Fig.2　Mechanism of selenium in mitigating heavy metal uptake by crops(modified form reference[21])

2　使用硒阻控作物中重金属吸收的潜在风险

尽管施加硒阻控植物吸收各种重金属的效果得到广泛的验证，以亚硒酸盐为主要成分的重金属叶面阻隔剂也得到一定的应用，但是使用硒修复重金属污染也存在潜在的风险[18,57]。硒的施用剂量、作物的种类、土壤的理化环境及土壤重金属的组成和浓度均可能影响硒对重金属的阻控效果[18]。重金属污染土壤中施加硒在保证阻控效果的前提下，需要尽可能降低硒的使用剂量，以防止土壤出现硒过量甚至硒污染的情况。硒污染会导致硒在植物体内过度积累，如果人体摄入过量的硒，会对人体健康产生危害[69]。不当的硒施加剂量可能起不到阻控重金属的作用，反而促进作物中重金属的积累。Ding 等[57]发现，给暴露于 12 mg/L Cd(Ⅱ)胁迫下的水稻施加 0.2 mg/L Se(Ⅳ)不能使水稻中镉含量降低，反而增强镉在水稻中的积累。此外，也有研究报道 Se(Ⅳ)虽能降低小白菜根系对镉的亲和力，但 Se(Ⅳ)含氧阴离子同时可通过电荷缓冲，降低 Cd(Ⅱ)阳离子转

运的电荷屏障，从而显著提高根系对Cd（Ⅱ）吸收[70]。Wan等[27]报道，在淹水条件下施加低剂量的Se（Ⅳ）会增加水稻籽粒砷的浓度，而在有氧条件下硒的施加显著降低水稻的砷积累。因此，施硒修复重金属污染时需控制土壤水分，长期淹水可能影响其修复效果，甚至促进作物对重金属的吸收。

在某些条件下，硒可能改变植物吸收重金属元素的价态，因而影响硒对重金属的修复效果。有研究发现，尽管施加硒显著降低水稻籽粒中总砷的含量，但却提高了稻米中As（Ⅲ）的含量，而As（Ⅲ）的毒性远高于As（Ⅴ）[71]。此外，某些条件下，硒的施加可能降低植物对其他必需营养元素的吸收。Feng等[72]的研究发现，硒的施加显著降低水稻植株的锑含量，但同时降低了水稻植株地上部钾、锰及镁的含量。Sousa等[73]发现，尽管施加硒显著降低植物中砷的积累，但却降低植物茎和根中的铁锰及锌的含量。因此，在使用硒进行重金属污染修复时，需要对土壤的污染状况和土壤性质进行详细调研，确保修复措施既有效又安全，不会对环境和人体健康造成额外的风险[74]。

3 展望

施硒作为一种硒强化手段，不仅能促进作物富硒，提升作物品质，同时也在阻控作物重金属吸收方面展现出良好的应用前景。由于土壤-植物体系的复杂性，不同的作物及土壤的性质、重金属污染程度等因素均会影响硒对重金属的修复效果，硒降低植物重金属吸收机制的研究需要更深入的研究。未来的研究有以下几个重点：(1)需进一步明确土壤中不同形态的Se与重金属的互作机制，阐释多大剂量的Se能阻控作物重金属的积累；(2)进一步探究土壤pH、Eh、有机质等理化因子如何影响硒修复重金属的效果；(3)探究硒的施加量对不同作物吸收重金属的阻控效果，优化出阻控特定作物吸收重金属的安全硒施加剂量；(4)除Se（Ⅳ）及Se（Ⅵ）外，纳米硒毒性更小且容易被植物吸收，需开展更多纳米硒阻控植物吸收重金属的研究；(5)除镉之外，硒如何在基因水平调控植物摄入及转运其他重金属的机制尚不明确，有待进一步的阐释；(6)实际重金属复合污染土壤多为复合污染，硒对复合污染如砷镉共污染的修复效果的研究鲜有报道，需更多的研究；(7)施加硒对土壤微生物群落和重金属转化功能菌株的影响少有研究，硒对土壤生态平衡的影响尚不明确。通过对硒阻控植物吸收重金属机制的阐释，不仅能实现对毒性重金属精准高效阻控，同时能避免硒施加所带来的潜在风险。

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Mechanism of selenium in mitigating absorption of heavy metals by crops

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Abstract Pollution of heavy metals poses a huge threat to food security and human health, and many methods for repairing the pollution of heavy metals in farmland have been developed. The supplementation of selenium significantly reduces the absorption of heavy metals by crops, while promoting their growth in soils polluted by heavy metals. The application of selenium has become a new way to mitigate the absorption of heavy metals by crops. This article reviewed five mechanisms including the alteration of the bioavailability of heavy metals in soil, competition between selenium and heavy metals in plant uptake channels, the promotion of forming iron plaque in plant roots, the induction of morphological and structural changes in plant roots, the regulation of gene expression involved in the chelation and transport of heavy metals in plants by which selenium mitigates the absorption of heavy metals by crops. The potential risks and priorities of studying selenium in mitigating the absorption of heavy metals by crops in the future were prospected. It will provide insights and a scientific basis for the use of selenium as a highly efficient inhibitor of the absorption of heavy metals in agricultural practices.

Keywords heavy metals; selenium; crops; soil remediation; iron plaque; plant roots

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