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专论与综述

微生物调控小麦金属元素吸收与积累的研究进展

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摘 要：作为主粮，小麦对保障国家粮食安全和人民食品安全至关重要。金属矿质元素对植物生长和人类膳食健康都具有重要作用。小麦生产中，既面临土壤有害微量矿质元素过量胁迫植物生长的问题，也面临有益矿质元素积累不足的问题。作为主粮，小麦籽粒中有益微量矿质元素不足会导致人类严重的健康障碍，被称为“隐性饥饿”，是重要的营养问题。微生物能够环保高效地阻控或促进小麦吸收微量矿质元素，这为缓解矿质元素过量导致的非生物胁迫和可食部分积累不足导致的营养强化问题提供了绿色方案。一方面，本文从微生物-植物互作角度出发，以有害矿质元素(Cu, Cd)为例，总结了微生物阻抗小麦对这 2 种元素的吸收策略，以及缓解它们胁迫的分子机制。另一方面，本文分析了微生物对小麦吸收、转运和积累 2 种有益矿质元素(Fe, Zn)的调节作用。特别是解析了内生菌促进小麦富集铁和锌元素的机制，展望了其在绿色高效农业发展方面的前景，为微生物促进小麦高效生产和品质提升提供了理论参考和应用指导。
关键词：小麦；微生物；微量元素稳态；非生物胁迫；营养强化

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Research progress in microbial regulation of metal uptake and accumulation in wheat

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Abstract: As a staple food crop, wheat is of great significance to ensure national security and food supply. Minerals play an important role in plant growth and human health, exerting dual effects on wheat production. One is the abiotic stress caused by excessive heavy metals on plant growth. The other is insufficient acquisition of essential minerals due to low bioavailability and restricted uptake of minerals. Insufficient intake of beneficial trace minerals from wheat flour leads to serious health disorders, known as hidden hunger, which is an major nutritional problem worldwide. Microorganisms can modulate the homeostasis of trace minerals in wheat efficiently and environmentally friendly, which provides a green scheme for abiotic stress alleviation and nutrient enrichment. Therefore, on one hand, this paper summarizes the microbial regulation on the absorption of detrimental elements (Cu and Cd) and alleviation of their stress as well as the underlying molecular mechanisms from the perspective of microorganism-plant interactions. On the other hand, this paper analyzes the regulatory effects of microorganisms on the absorption, transport, and accumulation of two beneficial minerals (Fe and Zn) in wheat. In particular, the review focuses on the mechanism of endophytes in promoting Fe and Zn enrichment, which is promising for green and efficient sustainable agricultural development. This review aims to provide theoretical reference and practical guidance for the application of microorganisms in improving wheat production and quality.

Keywords: wheat; microorganisms; trace element homeostasis; abiotic stress; nutrient enrichment

小麦作为人类最主要的能量来源之一，其产量和品质直接关系到全球粮食安全与人类健康[1]。微量矿质元素对小麦生长与人类健康都至关重要,其合理供应有助于植物应对各种生物和非生物胁迫以及解决人类膳食营养问题[2]。首先，重金属胁迫严重影响小麦产量与品质，破坏农业绿色发展。例如，土壤铜胁迫大大降低种子发芽率及叶片光合效率，而镉胁迫抑制小麦对营养物质的吸收和运输，导致营养物质缺乏并危害人类健康[3-4]。其次，微量元素匮乏会导致人类膳食性营养问题[5]。例如，人类主要通过饮食长期摄入铁元素，小麦作为主粮之一，因其生长的土壤铁利用率低，籽粒中的铁含量远远不足，导致从饮食中摄入的铁不足，甚至引发缺铁性贫血[6]。而缺锌会导致贫血、运动和认知发育受损，甚至导致孕产妇死亡风险增加和早产等[7]。

近年来，随着生态农业理念的推广，微生物在绿色农业中的应用受到了越来越多的关注[8]。微生物不仅能改善土壤结构，而且能提高作物的营养品质和抗胁迫能力[9-10]。已有研究表明，利用微生物不仅可以有效缓解重金属对小麦生长的胁迫，而且可以显著促进有益矿质元素的吸收和积累[2]。这为利用微生物促进小麦生产

和改善营养品质提供了新手段。尽管已有不少涉及微生物调控小麦吸收微量元素的研究，但缺少系统分析与总结。因此，本文总结了微生物对小麦吸收微量矿质元素的调控策略，并深入解析了其分子机制，以期为微生物促进小麦高效生产和品质提升提供参考。

1 微生物对小麦吸收重金属元素(Cu, Cd)的影响

1.1 微生物阻抗小麦吸收重金属元素

小麦(*Triticum aestivum* L.)是全世界广泛栽培的主粮作物之一，其营养品质与人类健康紧密相关[11]。但随着金属矿物质的开采、冶炼与生产，土壤重金属污染情况愈发严重，尤其是铜、镉污染[12]。据报道，污染土壤中过量的重金属会严重影响小麦的产量与品质[13]。随着对植物微生物组的广泛认识，科学家们发现许多微生物都能保护植物免受生物和非生物胁迫(包括重金属胁迫)并促进植物生长。由于具有稳定、绿色、高效等特点，这些被称为植物促生菌(plant growth-promoting bacteria, PGPB)的微生物已被用作生物接种剂来增强包括小麦在内的主粮作物的重金属耐受性和抗病性等[14-15]。考虑到铜元素(Cu)广泛用于农药增效，而镉元素(Cd)具有剧毒，我们以这 2 种有害元素为例，讨论微生物对小麦吸收重金属元素的影响。

关于微生物阻抗小麦吸收铜和镉元素的报道较多，详见表 1。多个应用实例表明，微生物能够阻抗小麦对重金属元素的吸收[21]。Yue 等[3]分离的高地芽孢杆菌(*Bacillus altitudinis*) WR10 可耐受 2 mmol/L 的铜，发酵 24 h 后可清除培养基中约 74%的铜，并且在 50 μmol/L 铜条件下增加了小麦幼苗的根长和干重。联合施用可耐受并吸收高浓度铜的不动杆菌(*Acinetobacter* sp.) RG30 与恶臭假单胞菌(*Pseudomonas putida*) GN04 能促进玉米生长并提高叶绿素含量[22]。另外，据 Rizvi 等[20]的研究报道，多金属耐受性根际细菌铜绿假单胞菌(*Pseudomonas aeruginosa*) CPSB1 在镉和铜胁迫下，增加了小麦根的干生物量和谷物的产量。Han 等[23]通过将肠杆菌(*Enterobacter* sp.) TJ6 与粪肥联合施用，减少了小麦籽粒中镉的积累。Cheng 等[16]的田间试验表明，液化沙雷氏菌(*Serratia liquefaciens*) CL1 将小麦籽粒镉含量降低了 24%−27%。

表 1 微生物阻抗小麦吸收重金属元素 Cu 和 Cd 的报道

Table 1 Reports of microbial impeding the uptake of copper and cadmium in wheat

金属元素 Metal element	实验模型 Experimental model	菌种 Strain	生物功能 Biological function	参考文献 Reference
Cd	大田 Field experiment	液化沙雷氏菌 CL1 *Serratia liquefaciens* CL1	籽粒中 Cd 含量降低 24.0%−27.0% Cd content in grains reduced by 24.0%–27.0%	[16]
Cd	水培 Hydroponic	布甘多肠杆菌 TJ6 *Enterobacter bugandensis* TJ6	根和叶中 Cd 含量降低 44.7%−56.6% Cd content in roots and leaves reduced by 44.7%–56.6%	[17]
Cd	盆栽 Pot experiment	富养罗尔斯通氏菌 Q2-8 *Ralstonia eutropha* Q2-8	地上组织中 Cd 含量降低 37.0% Cd content in aboveground tissues reduced by 37.0%	[18]
Cd	盆栽 Pot experiment	布甘多肠杆菌 TJ6 *Enterobacter bugandensis* TJ6	籽粒和根中 Cd 含量降低 21.5%−77.8% Cd content in grains and roots reduced by 21.5%–77.8%	[19]
Cu	水培 Hydroponic	高地芽孢杆菌 WR10 *Bacillus altitudinis* WR10	提高根和叶的铜耐受性 Enhanced copper tolerance in roots and leaves	[3]
Cu, Cd	大田 Field experiment	铜绿假单胞菌 CPSB1 *Pseudomonas aeruginosa* CPSB1	提高 Cu 和 Cd 胁迫下的小麦产量 Improved wheat yield under combined Cu and Cd stress	[20]

1.2 微生物调节小麦吸收重金属元素的机制

微生物对小麦吸收有害重金属元素的调节机制主要有 3 个方面。首先，部分微生物可以吸附、固化、转化土壤中的重金属，降低其生物利用度。其次，一些微生物可以直接或间接地调控小麦介导重金属元素吸收和积累功能相关基因的表达，降低根的吸收并提高耐受能力。再次，微生物可以缓解重金属对小麦的毒害作用，有效减缓生理胁迫，增强小麦的抗逆性能，包括对抗氧化系统、激素信号通路的调节[24]。关于微生物调节小麦吸收重金属胁迫的机制详见图 1。

1.2.1 微生物降低重金属元素的生物利用度

微生物能够通过其细胞表面的特性吸附重金属离子。细胞表面的官能团，如巯基、羧基、羟基、磺酸根、胺基和酰胺基等能够与重金属离子结合，形成复合物或有效屏障，从而降低重金属的生物利用度。其次，细菌胞外多糖可以作为生物吸附剂捕获有毒的重金属离子。例如，盆栽试验表明，细菌 ZC3-2-1 通过生物吸附和细菌胞外多糖(extracellular polymeric

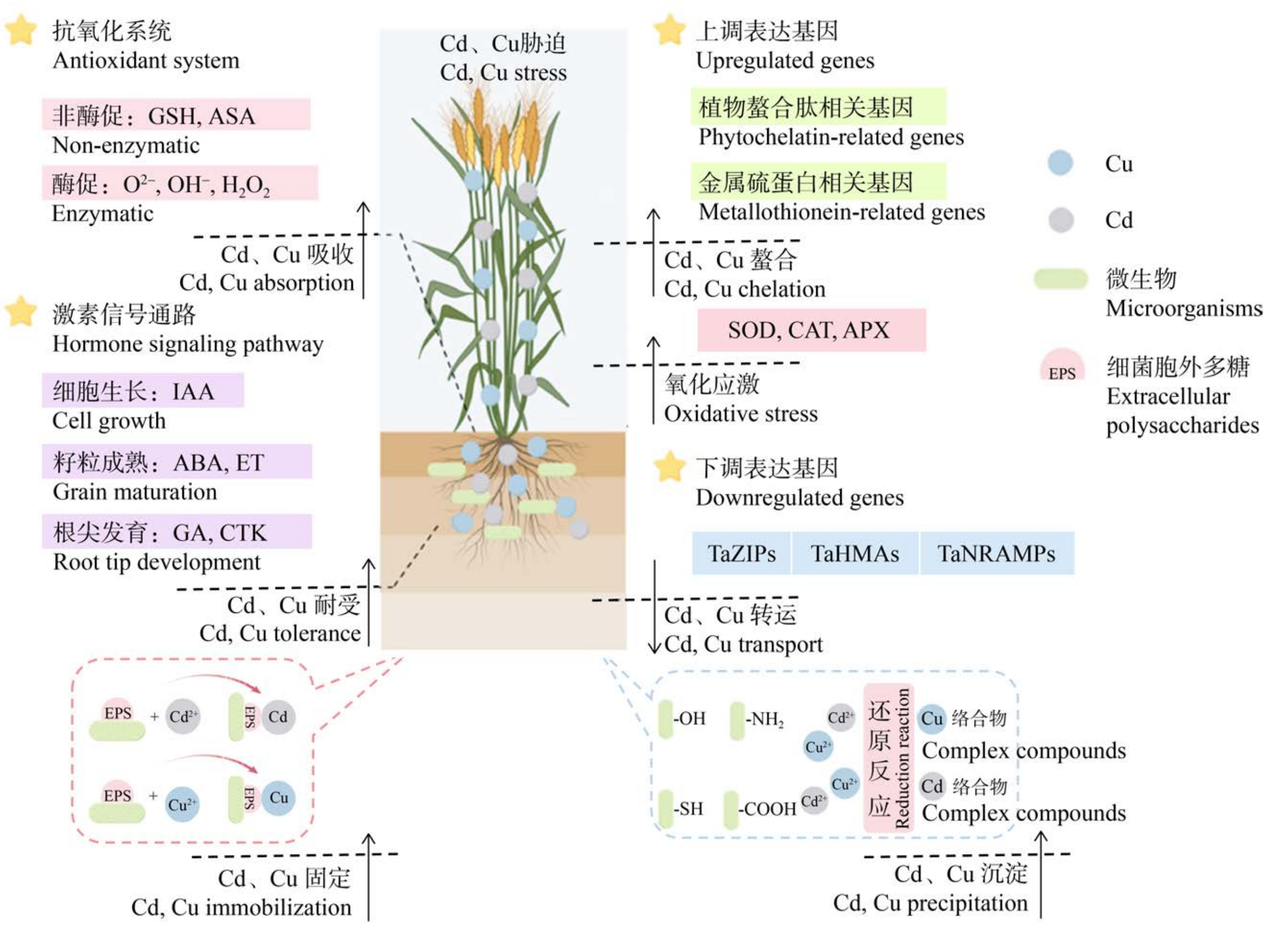

图 1 微生物调节小麦吸收重金属元素机制模式图 GSH：谷胱甘肽；ASA：抗坏血酸；IAA：吲哚乙酸；ABA：脱落酸；ET：乙烯；GA：赤霉素；CTK：细胞分裂素；SOD：超氧化物歧化酶；CAT：过氧化氢酶；APX：抗坏血酸过氧化物酶。

Figure 1 Model of mechanism of microbial regulation of heavy metal uptake in wheat. GSH: Glutathione; ASA: Ascorbic acid; IAA: Indoleacetic acid; ABA: Abscisic acid; ET: Ethylene; GA: Gibberellin; CTK: Cytokinin; SOD: Superoxide dismutase; CAT: Catalase; APX: Ascorbate peroxidase.

substances, EPS)的产生促进了土壤中镉的固定化，进而降低土壤中镉元素的生物可利用度[25]。另外，一些微生物还可以通过氧化还原过程促进有毒重金属的沉淀。总之，通过一系列的吸附、沉淀和固化过程，土壤中的有毒重金属生物可利用度有效降低，减少了其对生态系统和人类健康的潜在危害。

1.2.2 微生物缓解重金属元素对小麦的生理胁迫

重金属胁迫不仅会导致农作物严重减产，还会带来健康风险[26]。当受到重金属胁迫时，小麦组织中的金属积累会引起氧化应激[27]。氧化应激反过来影响细胞稳态并对生长发育产生不利影响[28]。微生物通过调节小麦的抗氧化系统来降低重金属毒性的负面影响[29]。首先，铜和镉胁迫会导致小麦体内产生大量的活性氧(reactive oxygen species, ROS)，如超氧阴离子(O_2^-)、过氧化氢(H_2O_2)等，对小麦细胞造成氧化损伤[12]。微生物能够通过调节小麦体内抗氧化酶(如过氧化氢酶、超氧化物歧化酶)的活性来降低 ROS 的水平，增强小麦的抗氧化能力，缓解铜和镉胁迫[30]。同时，微生物还可以调节小麦体内非酶促抗氧化系统的活性，如谷胱甘肽(glutathione, GSH)、抗坏血酸(ascorbic acid, ASA)等，增强小麦的抗氧化能力，降低氧化损伤。最近的研究报道指出，极端微生物耐辐射奇异球菌(*Deinococcus radiodurans*)将其胞内抗氧化相关分子释放到培养基中并改善了 Cd/Pb 诱导的氧化应激，降低了水稻中 ROS 水平并提高了抗氧化酶的活性[31]。另外，重金属耐受菌通过提高蒸腾速率、净光合作用和气孔导度、相对含水量和膜稳定性指数，抑制了酶促抗氧化剂的活性，并提高了植物对重金属镉胁迫的耐受性[32]。

一些微生物不仅能直接降低土壤中的重金属含量，还能通过促进生长提高小麦对重金属的耐受性[33]。这些微生物主要通过产生植物生长激素、改善养分吸收等策略增强植物的抗逆性[34]。脱落酸(abscisic acid, ABA)和乙烯(ethylene, ET)是重要的植物激素，在植物应对逆境胁迫中起着关键作用[35]。微生物可以通过激活小麦体内的激素信号通路，调节下游基因表达，增强小麦对重金属的耐受性[36]。例如，枯草芽孢杆菌(*Bacillus subtilis*) RT-3 和解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*) RT-5 通过产生水解酶和代谢物，有效抑制了重金属的毒害[37]。此外，微生物还能通过产生铁载体、金属硫蛋白和 1-氨基环丙烷-1-羧酸脱氨酶，促进小麦组织中激素的合成并维持内源激素的平衡，帮助提高小麦的解毒运输和重金属排放能力[38]。

1.2.3 微生物调节小麦金属离子转运和耐受基因表达

微生物可以通过调控小麦体内转录因子的表达，增强小麦的重金属耐受性[39]。例如，一些微生物可以诱导小麦体内 WRKY、MYB 等转录因子的表达，这些转录因子通过结合下游基因的启动子区域，调控其表达，从而增强小麦对铜和镉等有害矿质元素胁迫的耐受性[40]。另外，一些微生物能通过特定的重金属转运和抵抗基因来调节土壤中重金属的浓度。例如，蜡样芽孢杆菌(*Bacillus cereus*)能通过调节金属转运蛋白基因(*zips*, *nams*)和耐受基因(*hmas*, *mtps*)的表达来吸附不同的重金属，这不仅降低了土壤中的镉浓度，还抑制了小麦组织中的镉积累，从而保护小麦免受重金属毒害[41]。另外，微生物菌剂 TJ6 与羊粪的联合施用降低了小麦根系中镉转运蛋白编码基因的表达，从而抑制了小麦对镉的吸收[19]。

2 微生物对小麦吸收有益矿质元素(Fe, Zn)的影响

2.1 微生物促进小麦吸收有益矿质元素

有益微量矿质元素铁和锌是保证人类健康和维持植物生长发育的重要营养因子。土壤中以不溶性形式存在的铁和锌生物利用度低，导致小麦籽粒中的铁和锌积累不足，满足不了人

体每日膳食营养需求，最终造成的“隐性饥饿”严重影响人类健康[42]。近年来，微生物菌剂因在促进植物生长和可持续农业生产方面的巨大潜力成为研究热点[43]。这些微生物通过附生或共生关系，可以环保高效地促进小麦富集营养元素[44]。因此，利用微生物进行有益微量元素生物强化是解决膳食性营养缺乏症的高效策略[45]。我们总结了微生物促进小麦吸收铁和锌元素的实例(表 2)，以期为解决“隐性饥饿”问题提供新思路、新方法。

多个研究结果表明，微生物能够显著促进小麦等主粮作物吸收有益微量矿质元素。例如，田间应用产吲哚乙酸(indoleacetic acid, IAA)的内生芽孢杆菌 WR10 显著提高了小麦籽粒中的钾、氮和铁元素的含量[6]。从土壤中分离的枯草芽孢杆菌 CP4 和丛枝菌根真菌联合施用，在田间条件下具有较高的生物强化与增产能力[44]。Coccina 等[45]的研究表明，通过接种丛枝菌根真菌，小麦地上组织锌元素吸收总量提高 24.3%，大麦提高 12.7%。通过真菌施用，水稻植株对锌的吸收提高了约 2.5 倍[51]。另外，大田试验中联合施用固氮菌(*Azotobacter*)和纹状假单胞菌(*Pseudomonas striata*)分别提高了小麦籽粒(19.52%)和茎(15.76%)的锌含量[46]。总之，这些实例展示了微生物在提高小麦铁和锌元素吸收方面的潜力和实际应用，通过微生物发酵肥料、微生物接种以及合理耕作等方式，可以有效提升小麦的营养价值，对抗全球范围内的铁和锌营养不良问题。

2.2 微生物促进小麦吸收有益矿质元素的机制

铁和锌是几乎所有生物体中必不可少的微量元素，具有包括氧气运输与储存、DNA 合成、电子转移在内的多种重要生物功能[52-53]。微生物促进小麦吸收铁和锌元素的机制主要分为 3 个方面：(1) 微生物能够改变小麦的根系结构，提高其对铁和锌的吸收利用率；(2) 微生物可以调节金属代谢及小麦金属转运蛋白相关基因的表

表 2　微生物促进小麦吸收有益矿质元素 Fe 和 Zn 的报道

Table 2　Reports of microorganisms promote the absorption of Fe and Zn in wheat

金属元素 Metal element	实验模型 Experimental model	菌种 Strain	生物功能 Biological function	参考文献 Reference
Fe	大田 Field experiment	芽孢杆菌 WR10 *Bacillus altitudinis* WR10	根和籽粒 Fe 含量提高 20%−30% Root and grain Fe content increased by 20%−30%	[6]
Zn	大田 Field experiment	固氮菌、纹状假单胞菌 *Azotobacter* sp., *Pseudomonas striata*	籽粒和茎 Zn 含量分别提高 19.52%、15.76% Grain and stem Zn content increased by 19.52% and 15.76%, respectively	[46]
Zn	水培 Hydroponic	梨状孢子菌 *Piriformospora* sp.	提高地上组织 Zn 含量 Increased Zn content in aboveground tissues	[47]
Fe, Zn	盆栽 Pot experiment	梨状孢子菌、圆褐固氮菌 *Piriformospora* sp., *Azotobacter chroococcum*	籽粒 Fe、Zn 含量分别提高 1.33、3.12 倍 Grain Fe and Zn content increased by 1.33-fold and 3.12-fold, respectively	[48]
Fe, Zn	大田 Field experiment	微小杆菌 MS-ZT10 *Exiguobacterium* sp. MS-ZT10	籽粒 Zn、Fe 含量分别提高至 8.2 mg/L、24.6 mg/L Grain Zn and Fe content increased to 8.2 mg/L and 24.6 mg/L, respectively	[49]
Fe, Zn	盆栽 Pot experiment	枯草芽孢杆菌、节杆菌、肠球菌 *Bacillus subtilis* sp., *Arthrobacter* sp., *Enterococcus* sp.	籽粒 Fe、Zn 含量比膳食推荐剂量提高 75% Grain Fe and Zn content increased by 75% compared to dietary recommended levels	[50]

达，促进铁和锌的转运和积累；(3) 微生物还可以调控小麦转录因子及矿质元素分布，提高小麦籽粒营养品质[54]。关于微生物促进小麦吸收铁和锌元素的机制详见图 2。

2.2.1 微生物改变小麦根系结构和生理生化

微生物可以改变小麦根系结构，优化营养吸收。如通过增加侧根或根毛的数量，增加小麦对铁和锌等有益微量元素的吸收面积或吸收效率[55-56]。接种固氮菌能够改善小麦根系结构，增加根系微生物活性，从而提高小麦对磷、铁和锌等元素的吸收[57]。微生物通过与黏土矿物、腐殖质的吸附位点结合，减少金属离子的固化，提高小麦根对其的吸收率[58]。此外，微生物的代谢产物，如铁载体、酚类化合物等都能够促进小麦根系吸收利用铁和锌元素[59]。例如，内生芽孢杆菌 WR10 通过强化根系酚类物质合成，提高了铁的生物利用度和小麦对铁的吸收效率，同时还可以通过重塑根系结构并激活抗坏血酸-谷胱甘肽循环系统(ascorbic acid-glutathione, ASA-GSH)促进小麦吸收其他矿质元素[60-61]。某些微生物能够产生植物激素，特别是生长素，以此改变小麦的根系结构。微生物分泌的有机酸(草酸、乙酸、琥珀酸)能够将土壤中生物利用度低的铁和锌等有益矿质元素溶解成可利用的

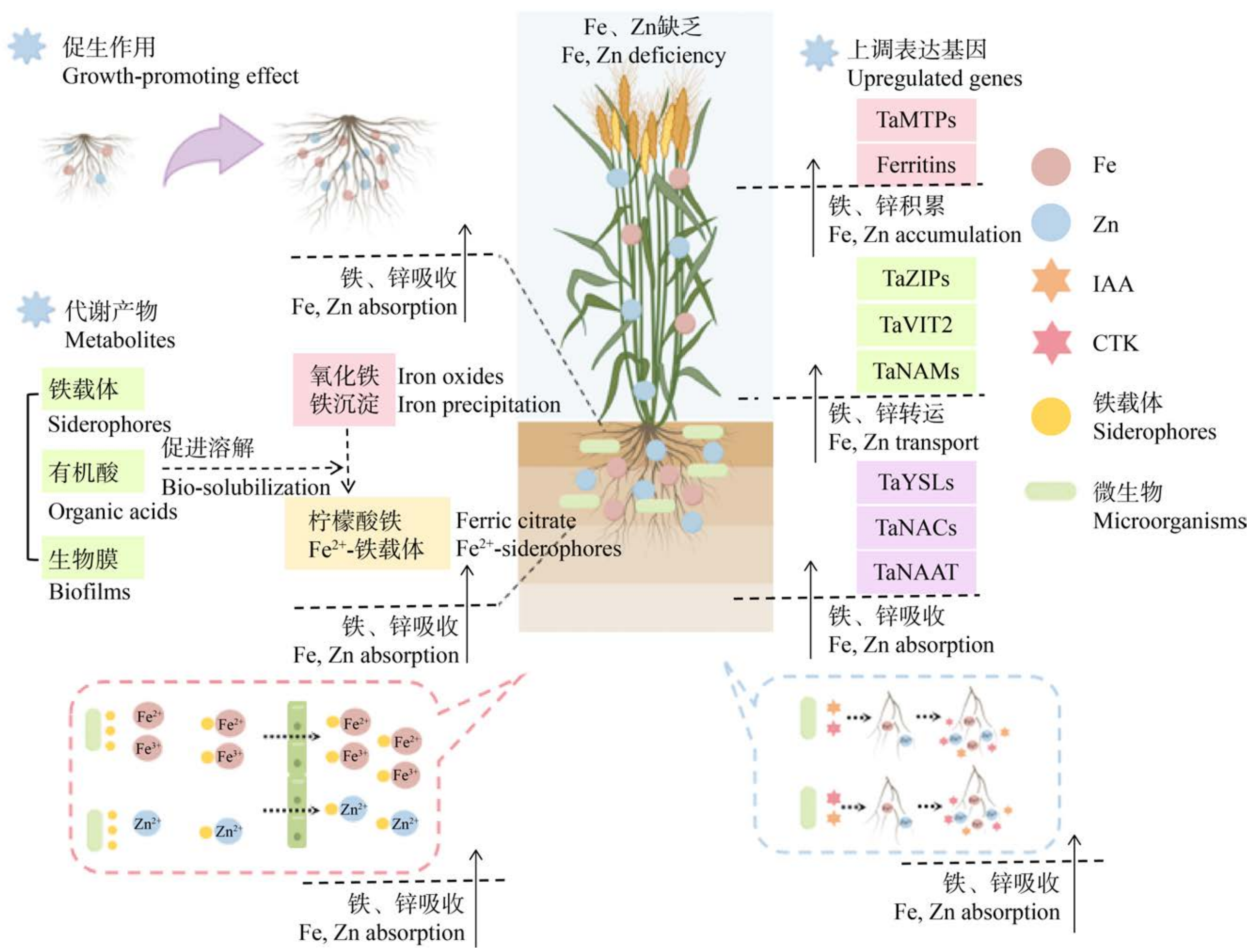

图 2 微生物促进小麦吸收有益矿质元素机制模式图 IAA：吲哚乙酸；CTK：细胞分裂素。

Figure 2 Model of mechanism of microbial regulation of heavy metal uptake in wheat. IAA: Indoleacetic acid; CTK: Cytokinin.

形式，从而促进小麦根系对其吸收和转运[62-63]。某些微生物还能够在小麦根系表面形成生物膜，这一物理屏障保护根系免受病原菌侵害的同时，还能保持根际水分，从而优化包括铁和锌在内的营养吸收[64]。

2.2.2 微生物调节小麦基因表达和金属代谢

微生物可以通过调节小麦基因表达和代谢途径影响矿质元素转运[65]。内生菌的代谢产物可以上调小麦铁吸收相关基因表达，如 *taysl*、*tanaat*[66]。有研究表明，接种植物内生真菌 Pi 和固氮菌 AzWR5 使 4 个 *zips* 转运蛋白基因表达数倍增加，显著改善了土壤中锌和铁的动员，增加了其在谷物中的浓度，并提高了作物产量[67]。其次，小麦中的伏氨酸转运体基因被认为是铁积累的关键调控因子，能够促进铁的有效运输和积累[68]。此外，内生芽孢杆菌 WR10 通过上调根中载铁蛋白编码的基因和生物浸出铁来增加小麦铁耐受和吸收[69]。

2.2.3 微生物影响小麦转录因子和矿质元素分布

微生物可以通过调控小麦体内转录因子的表达，促进小麦吸收铁和锌等有益微量矿质元素。例如，微生物通过调节 *nac* 转录因子家族成员 *idef2* 特异性结合缺铁应答顺式元件 *ide2*，调控铁吸收系统[70]。微生物也能促进小麦组织中的铁和锌向地上部分转运。例如，产吩嗪-1-羧酸的小麦根际微生物可以显著增加铁从根到茎的转运，而嗜铁内生菌可能因在器官之间转移可促进铁的转运[71]。微生物还可以促进籽粒积累铁和锌，将转运到籽粒中的铁和锌在糊粉层和胚乳中固定并存储下来，以提高其营养利用度[72]。

3 应用微生物调控小麦微量元素吸收与积累的挑战与解决途径

随着土壤恶化和人口增加，小麦中的有益微量元素匮乏和有害重金属胁迫等问题严重影响了人类可持续发展[73]。因具有环境友好、绿色高效等诸多优点，多种微生物已成功应用于促进小麦的微量元素稳态以及提高小麦产量中[74-75]。本文作者的研究结果显示，内生芽孢杆菌 WR10 不仅能缓解小麦铜胁迫，同时可以促进小麦籽粒中铁的生物强化[3,6]。Hagagy 等[76]的研究表明，古细菌 NARS9 通过显著增加糖代谢、有机酸和生物合成酶的水平，以此缓解小麦受到的钴胁迫，另外，NARS9 处理还可以增加矿质元素和抗氧化剂含量，从而提高小麦的营养价值。Berezhnaya 等[77]的研究表明，在小麦播种前施用固氮和溶磷微生物，显著提高了春小麦的产量(0.43 kg/m^2)。

然而，微生物菌剂应用过程中往往面临着稳定性低、定殖能力差两大难题(图 3)。其中，微生物的稳定性主要指在特定环境下保证存活以及保持遗传、生长、功能、存储稳定的能力[78]。遗传生长稳定性与功能稳定性密切相关，共同影响着微生物菌剂的应用效果和质量。遗传生长稳定性确保微生物菌剂在繁殖过程中能够稳定地保持其优良的遗传特性与功能特性。同时，存储稳定性高的微生物菌剂在一定程度上能够降低农业生产的投入成本。因此，作为绿色农业投入品，微生物菌剂的稳定性决定了其能否持续高效地提高作物产量与营养品质。另外，微生物的定殖能力是指微生物在特定宿主或环境中建立并维持种群优势的能力，这是其能够在大田中持续地调节小麦微量元素的关键之一[79]。

考虑到以上两大问题，选择环境稳定性好、自身遗传稳定、生长迅速、在土壤中和植物上定殖力强的微生物菌种是解决问题的根本。同时，通过基因编辑改造和强化菌株，以及优选构建合成微生物组(SynCom)使其在存储、运输和施用过程中维持稳定性和竞争力，提高其定殖能力是更有力的技术手段。比如，Xu 等[80]的研究表明，通过 I 型 CRISPR-Cas 基因编辑技术提高微生物表面黏附蛋白编码基因的表达水平，可以达到提高定殖效果的目的；同时，调节群体感应相关基因的表达，能够增强菌株的

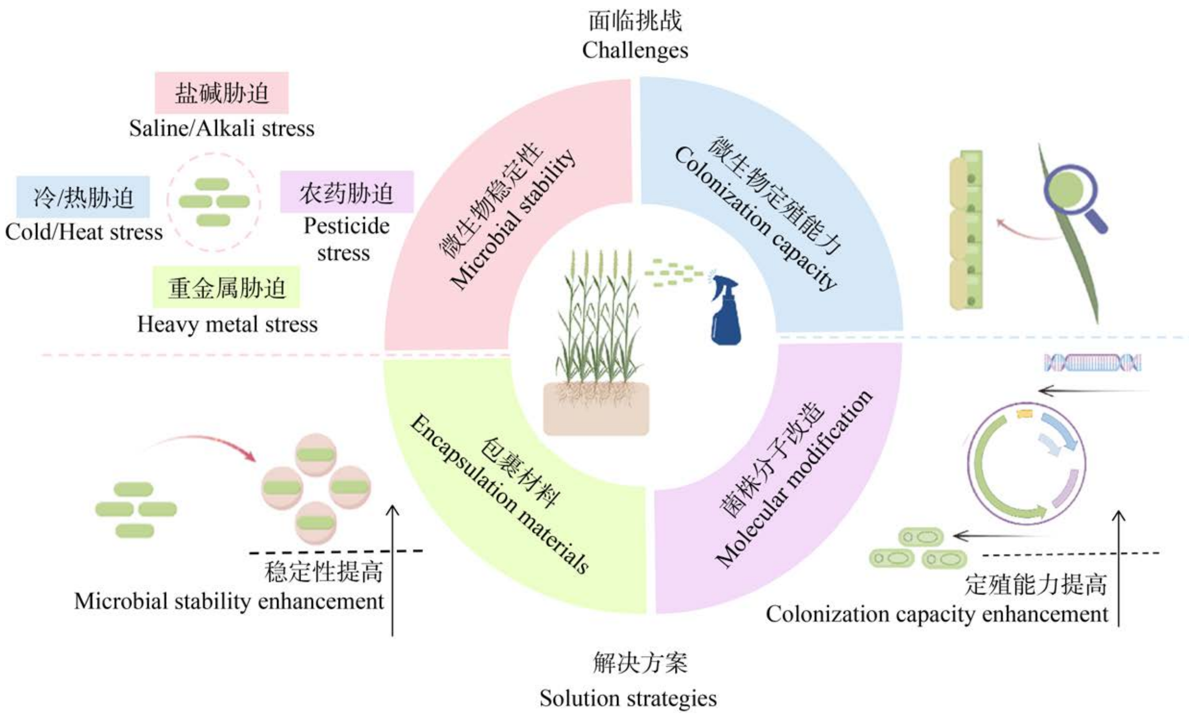

图 3　应用微生物调控小麦微量元素吸收的挑战与解决策略示意图　针对微生物稳定性低、定殖能力差的问题，可以参考加包裹材料以及菌株改造 2 种策略。

Figure 3　Schematic diagram of challenges and solutions for microbiological regulation of trace element absorption in wheat. Two major challenges are instability of the inoculant and low colonization ability. They can be partially solved by strain modification or enhancement and preparation techniques, such as wrapping with different materials.

群体感应能力，促进细菌之间的协作和生物膜的形成，进而提高定殖效果。

另外，开发新型的微生物制剂技术也能快速提升应用效果。例如，微胶囊技术可以将微生物包裹在微小的聚合物薄膜中，避免其直接接触外界环境，从而提高其稳定性[81]。Gong 等[82]采用乳化法和内凝胶法从海带中分离到了 1 株海洋细菌 DSM19842，用海藻酸钙对其进行了微胶囊化后存活率显著提高，同时其显著促进根系生长并缓解盐胁迫。而新型的生物保护剂 Etc-S 的核心成分为四氢嘧啶的衍生物，其与微生物的细胞膜相互作用，可增强细胞膜的稳定性，确保细胞在不利条件下仍能保持活性[83]。Fareez 等[84]的研究表明，壳聚糖包覆的海藻酸盐-黄原胶微珠封装技术，显著增强了植物乳杆菌(*Lactobacillus plantarum*) LAB12 的耐酸性与耐热性，这为植物乳杆菌的应用提供了重要突破。

总之，在微生物菌剂的应用中，无论是使用包裹材料，还是利用分子生物学手段进行菌株改造，均需考虑其作用的高效性、持续性以及安全性。毫无疑问，研发绿色、高效且经济实用的微生物制剂用于推动农业绿色发展需要多学科先进技术和手段的科学结合。

4　展望

由微量矿质元素失衡导致的作物减产、营养品质下降以及引起的人类膳食性营养缺乏症是重大的全球性问题。地理分布与土壤类型等诸多因素影响着小麦微量矿质元素的吸收、转化与积累。存在于土壤和植物根际的微生物是一个强大的“工程师”，在土壤矿物质的地球化学循环以及促进植物营养方面发挥着重要作

用。这些微生物还可以阻控有害元素、促进小麦中铁、锌等有益微量元素摄取以及转运相关基因的表达。因此，基于微生物缓解胁迫和生物强化作用，未来可以开发和利用微生物菌剂，用于增强粮食安全、消除“隐性饥饿”，助力农业的可持续发展。

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REFERENCES

[1] SHI Y, LI J, SUN ZK. Success to iron biofortification of wheat grain by combining both plant and microbial genetics[J]. Rhizosphere, 2020, 15: 100218.

[2] KAUR H, KAUR H, KAUR H, SRIVASTAVA S. The beneficial roles of trace and ultratrace elements in plants[J]. Plant Growth Regulation, 2023, 100(2): 219-236.

[3] YUE ZH, CHEN YJ, CHEN C, MA KS, TIAN EL, WANG Y, LIU HZ, SUN ZK. Endophytic *Bacillus altitudinis* WR10 alleviates Cu toxicity in wheat by augmenting reactive oxygen species scavenging and phenylpropanoid biosynthesis[J]. Journal of Hazardous Materials, 2021, 405: 124272.

[4] RASHEED A, AL-HUQAIL AA, ALI B, ALGHANEM SMS, ALI SHAH A, AZEEM F, RIZWAN M, AL-QTHANIN RN, SOUDY FA. Molecular characterization of genes involved in tolerance of cadmium in *Triticum aestivum* (L.) under Cd stress[J]. Journal of Hazardous Materials, 2024, 464: 132955.

[5] ZEMRANI B, BINES JE. Recent insights into trace element deficiencies: causes, recognition and correction[J]. Current Opinion in Gastroenterology, 2020, 36(2): 110-117.

[6] SUN ZK, YUE ZH, LIU HZ, MA KS, LI CW. Microbial-assisted wheat iron biofortification using endophytic *Bacillus altitudinis* WR10[J]. Frontiers in Nutrition, 2021, 8: 704030.

[7] KONG DY, KHAN SA, WU HL, LIU Y, LING HQ. Biofortification of iron and zinc in rice and wheat[J]. Journal of Integrative Plant Biology, 2022, 64(6): 1157-1167.

[8] NARTEY LK, PU Q, ZHU WJ, ZHANG SS, LI J, YAO YL, HU XF. Antagonistic and plant growth promotion effects of *Mucor moelleri*, a potential biocontrol agent[J]. Microbiological Research, 2022, 255: 126922.

[9] PRAJAPATI P, YADAV M, NISHAD JH, GAUTAM VS, KHARWAR RN. Salt tolerant fungal endophytes alleviate the growth and yield of saline-affected wheat genotype PBW-343[J]. Microbiological Research, 2024, 278: 127514.

[10] SHI HM, LU LX, YE JR, SHI LN. Effects of two *Bacillus velezensis* microbial inoculants on the growth and rhizosphere soil environment of *Prunus davidiana*[J]. International Journal of Molecular Sciences, 2022, 23(21): 13639.

[11] SUN ZK, ADELEKE BS, SHI YN, LI CW. The seed microbiomes of staple food crops[J]. Microbial Biotechnology, 2023, 16(12): 2236-2249.

[12] DHALIWAL SS, SHARMA V, KAUR J, SHUKLA AK, SINGH J, SINGH P. Cadmium phytoremediation potential of *Brassica genotypes* grown in Cd spiked Loamy sand soils: accumulation and tolerance[J]. Chemosphere, 2022, 302: 134842.

[13] BRAVIN MN, Le MERRER B, DENAIX L, SCHNEIDER A, HINSINGER P. Copper uptake kinetics in hydroponically-grown durum wheat (*Triticum turgidum* durum L.) as compared with soil's ability to supply copper[J]. Plant and Soil, 2010, 331(1): 91-104.

[14] MATSUMOTO H, FAN XY, WANG Y, KUSSTATSCHER P, DUAN J, WU SL, CHEN SL, QIAO K, WANG YL, MA B, ZHU GN, HASHIDOKO Y, BERG G, CERNAVA T, WANG MC. Bacterial seed endophyte shapes disease resistance in rice[J]. Nature Plants, 2021, 7(1): 60-72.

[15] MA Y, RAJKUMAR M, OLIVEIRA RS, ZHANG C, FREITAS H. Potential of plant beneficial bacteria and arbuscular mycorrhizal fungi in phytoremediation of metal-contaminated saline soils[J]. Journal of Hazardous Materials, 2019, 379: 120813.

[16] CHENG C, HAN H, WANG YP, WANG R, HE LY, SHENG XF. Biochar and metal-immobilizing *Serratia liquefaciens* CL-1 synergistically reduced metal accumulation in wheat grains in a metal-contaminated soil[J]. Science of The Total Environment, 2020, 740: 139972.

[17] HAN H, ZHANG H, QIN SM, ZHANG J, YAO LG, CHEN ZJ, YANG JJ. Mechanisms of *Enterobacter bugandensis* TJ6 immobilization of heavy metals and inhibition of Cd and Pb uptake by wheat based on metabolomics and proteomics[J]. Chemosphere, 2021, 276: 130157.

[18] WANG XH, WANG Q, NIE ZW, HE LY, SHENG XF. *Ralstonia eutropha* Q2-8 reduces wheat plant above-ground tissue cadmium and arsenic uptake and increases the expression of the plant root cell wall organization and biosynthesis-related proteins[J]. Environmental Pollution, 2018, 242: 1488-1499.

[19] HAN H, WU XJ, YAO LG, CHEN ZJ. Heavy metal-immobilizing bacteria combined with calcium polypeptides reduced the uptake of Cd in wheat and shifted the rhizosphere bacterial communities[J]. Environmental Pollution, 2020, 267: 115432.

[20] RIZVI A, KHAN MS. Biotoxic impact of heavy metals on growth, oxidative stress and morphological changes in root structure of wheat (*Triticum aestivum* L.) and stress alleviation by *Pseudomonas aeruginosa* strain

CPSB1[J]. Chemosphere, 2017, 185: 942-952.
[21] MA Y, RAJKUMAR M, ZHANG C, FREITAS H. Inoculation of *Brassica oxyrrhina* with plant growth promoting bacteria for the improvement of heavy metal phytoremediation under drought conditions[J]. Journal of Hazardous Materials, 2016, 320: 36-44.
[22] LIU AR, WANG WJ, ZHENG XY, CHEN XC, FU WT, WANG G, JI J, JIN C, GUAN CF. Improvement of the Cd and Zn phytoremediation efficiency of rice (*Oryza sativa*) through the inoculation of a metal-resistant PGPR strain[J]. Chemosphere, 2022, 302: 134900.
[23] HAN H, WU XJ, BOLAN N, KIRKHAM MB, YANG JJ, CHEN ZJ. Inhibition of cadmium uptake by wheat with urease-producing bacteria combined with sheep manure under field conditions[J]. Chemosphere, 2022, 293: 133534.
[24] FENG D, WANG RX, SUN XA, LIU LN, LIU P, TANG JC, ZHANG CX, LIU H. Heavy metal stress in plants: ways to alleviate with exogenous substances[J]. Science of The Total Environment, 2023, 897: 165397.
[25] ROJAS-TAPIAS DF, BONILLA R, DUSSÁN J. Effect of inoculation and co-inoculation of *Acinetobacter* sp. RG30 and *Pseudomonas putida* GN04 on growth, fitness, and copper accumulation of maize (*Zea mays*)[J]. Water, Air, & Soil Pollution, 2014, 225(12): 2232.
[26] RAI PK, LEE SS, ZHANG M, TSANG YF, KIM KH. Heavy metals in food crops: health risks, fate, mechanisms, and management[J]. Environment International, 2019, 125: 365-385.
[27] TIWARI S, LATA CR. Heavy metal stress, signaling, and tolerance due to plant-associated microbes: an overview[J]. Frontiers in Plant Science, 2018, 9: 452.
[28] ZHOU M, ZHENG SG. Multi-omics uncover the mechanism of wheat under heavy metal stress[J]. International Journal of Molecular Sciences, 2022, 23(24): 15968.
[29] KOUR D, SHARMA B, NEGI R, KUMAR S, KAUR S, KAUR T, KHAN SS, KOUR H, RAMNIWAS S, RUSTEGI S, RAI AK, SINGH S, SHREAZ S, YADAV AN, AHLUWALIA AS. Microbial amelioration of heavy metal toxicity in plants for agro-environmental sustainability[J]. Water, Air, & Soil Pollution, 2024, 235(7): 431.
[30] ETESAMI H. Bacterial mediated alleviation of heavy metal stress and decreased accumulation of metals in plant tissues: mechanisms and future prospects[J]. Ecotoxicology and Environmental Safety, 2018, 147: 175-191.
[31] DAI S, CHEN Q, JIANG M, WANG BQ, XIE ZM, YU N, ZHOU YL, LI S, WANG LY, HUA YJ, TIAN B. Colonized extremophile *Deinococcus radiodurans* alleviates toxicity of cadmium and lead by suppressing heavy metal accumulation and improving antioxidant system in rice[J]. Environmental Pollution, 2021, 284: 117127.
[32] DESOKY EM, MERWAD AM, SEMIDA WM, IBRAHIM SA, EL-SAADONY MT, RADY MM. Heavy metals-resistant bacteria (HM-RB): potential bioremediators of heavy metals-stressed *Spinacia oleracea* plant[J]. Ecotoxicology and Environmental Safety, 2020, 198: 110685.
[33] YIN K, WANG QN, LYU M, CHEN LX. Microorganism remediation strategies towards heavy metals[J]. Chemical Engineering Journal, 2019, 360: 1553-1563.
[34] LAI HJ, DING XZ, CUI MJ, ZHENG JJ, CHEN ZB, PEI JL, ZHANG JW. Mechanisms and influencing factors of biomineralization based heavy metal remediation: a review[J]. Biogeotechnics, 2023, 1(3): 100039.
[35] GUL N, AHMAD WANI I, AHMAD MIR R, NOWSHEHRI JA, ASLAM S, GUPTA R, VERMA S, ASLAM S. Plant growth promoting microorganisms mediated abiotic stress tolerance in crop plants: a critical appraisal[J]. Plant Growth Regulation, 2023, 100(1): 7-24.
[36] JIN YY, LUAN YN, NING YC, WANG LY. Effects and mechanisms of microbial remediation of heavy metals in soil: a critical review[J]. Applied Sciences, 2018, 8(8): 1336.
[37] IMRAN M, SUN ZK, ABO-ELYOUSR KAM, ALI H, ALDAYEL MF, LI CW. One stone two birds: endophytes alleviating trace elements accumulation and suppressing soilborne pathogen by stimulating plant growth, photosynthetic potential and defense related gene expression[J]. Journal of Hazardous Materials, 2024, 476: 135084.
[38] ZHENG JD, XIE XG, LI CY, WANG HX, YU YR, HUANG BK. Regulation mechanism of plant response to heavy metal stress mediated by endophytic fungi[J]. International Journal of Phytoremediation, 2023, 25(12): 1596-1613.
[39] FU SL, IQBAL B, LI GL, ALABBOSH KF, KHAN KA, ZHAO X, RAHEEM A, DU DL. The role of microbial partners in heavy metal metabolism in plants: a review[J]. Plant Cell Reports, 2024, 43(4): 111.
[40] SAHA B, NAYAK J, SRIVASTAVA R, SAMAL S, KUMAR D, CHANWALA J, DEY N, GIRI MK. Unraveling the involvement of WRKY TFs in regulating plant disease defense signaling[J]. Planta, 2023, 259(1): 7.
[41] SINGH D, PRASANNA R. Potential of microbes in the biofortification of Zn and Fe in dietary food grains: a review[J]. Agronomy for Sustainable Development, 2020, 40(2): 15.
[42] CHOI BY, HONG DK, JEONG JH, LEE BE, KOH JY, SUH SW. Zinc transporter 3 modulates cell proliferation and neuronal differentiation in the adult hippocampus[J]. Stem Cells, 2020, 38(8): 994-1006.
[43] BALK J, CONNORTON JM, WAN Y, LOVEGROVE A, MOORE KL, UAUY C, SHARP PA, SHEWRY PR. Improving wheat as a source of iron and zinc for global nutrition[J]. Nutrition Bulletin, 2019, 44(1): 53-59.
[44] YADAV R, ROR P, RATHORE P, RAMAKRISHNA W. Bacteria from native soil in combination with arbuscular mycorrhizal fungi augment wheat yield and biofortification[J]. Plant Physiology and Biochemistry, 2020, 150: 222-233.
[45] COCCINA A, CAVAGNARO TR, PELLEGRINO E, ERCOLI L, McLAUGHLIN MJ, WATTS-WILLIAMS SJ. The mycorrhizal pathway of zinc uptake contributes to zinc accumulation in barley and wheat grain[J]. BMC Plant Biology, 2019, 19(1): 133.
[46] BAGMARE RR, ISMAIL S. Microbial biofortification of Zn by plant growth promoting microorganisms in wheat (*Triticum aestivum*)[J]. International Journal of

Plant & Soil Science, 2023, 35(17): 238-253.
[47] ABADI VAJM, SEPEHRI M. Effect of *Piriformospora indica* and *Azotobacter chroococcum* on mitigation of zinc deficiency stress in wheat (*Triticum aestivum* L.)[J]. Symbiosis, 2016, 69(1): 9-19.
[48] SINGH S, SAKSHI, ANNAPURNA K, SHRIVASTAVA N, VARMA A. Symbiotic interplay of *Piriformospora indica* and *Azotobacter chroococcum* augments crop productivity and biofortification of Zinc and Iron[J]. Microbiological Research, 2022, 262: 127075.
[49] SHAIKH S, SARAF M. Biofortification of *Triticum aestivum* through the inoculation of zinc solubilizing plant growth promoting rhizobacteria in field experiment[J]. Biocatalysis and Agricultural Biotechnology, 2017, 9: 120-126.
[50] SINGH D, GEAT N, RAJAWAT MVS, PRASANNA R, KAR A, SINGH AM, SAXENA AK. Prospecting endophytes from different Fe or Zn accumulating wheat genotypes for their influence as inoculants on plant growth, yield, and micronutrient content[J]. Annals of Microbiology, 2018, 68(12): 815-833.
[51] SENTHIL KUMAR CM, D'SILVA S, PRAVEENA R, KAPRAKKADEN A, ATHIRA KRISHNAN LR, BALAJI RAJKUMAR M, SRINIVASAN V, DINESH R. Zinc solubilization and organic acid production by the entomopathogenic fungus, *Metarhizium pingshaense* sheds light on its key ecological role in the environment[J]. Science of The Total Environment, 2024, 923: 171348.
[52] CUI FC, FAN RS, WANG DF, LI JR, LI TT. Research progress on iron uptake pathways and mechanisms of foodborne microorganisms and their application in the food sector[J]. Critical Reviews in Food Science and Nutrition, 2024, 64(24): 8892-8910.
[53] NOOR M, KIRAN A, SHAHBAZ M, SANAULLAH M, WAKEEL A. Root system architecture associated zinc variability in wheat (*Triticum aestivum* L.)[J]. Scientific Reports, 2024, 14: 1781.
[54] TRIVEDI P, LEACH JE, TRINGE SG, SA TM, SINGH BK. Plant-microbiome interactions: from community assembly to plant health[J]. Nature Reviews Microbiology, 2020, 18(11): 607-621.
[55] CHEN SM, WAGHMODE TR, SUN RB, KURAMAE EE, HU CS, LIU BB. Root-associated microbiomes of wheat under the combined effect of plant development and nitrogen fertilization[J]. Microbiome, 2019, 7(1): 136.
[56] SHAKEEL M, HAFEEZ FY, MALIK IR, RAUF A, JAN F, KHAN I, IJAZ I, ELSADEK MF, ALI MA, RASHID K, MUZAMMAL M, MUNIR M, KHAN NU, MOHIBULLAH M, YASIN M. Zinc solubilizing bacteria synergize the effect of zinc sulfate on growth, yield and grain zinc content of rice (*Oryza sativa*)[J]. Cereal Research Communications, 2024, 52(3): 961-971.
[57] LAMLOM SF, IRSHAD A, MOSA WFA. The biological and biochemical composition of wheat (*Triticum aestivum*) as affected by the bio and organic fertilizers[J]. BMC Plant Biology, 2023, 23(1): 111.
[58] LI GL, ZHOU CH, FIORE S, YU WH. Interactions between microorganisms and clay minerals: new insights and broader applications[J]. Applied Clay Science, 2019, 177: 91-113.
[59] YADAV R, ROR P, RATHORE P, KUMAR S, RAMAKRISHNA W. *Bacillus subtilis* CP4, isolated from native soil in combination with arbuscular mycorrhizal fungi promotes biofortification, yield and metabolite production in wheat under field conditions[J]. Journal of Applied Microbiology, 2021, 131(1): 339-359.
[60] YUE ZH, CHEN C, LIU YC, CHEN XM, CHEN YJ, HU CH, ZHENG MM, ZHANG J, HE L, MA KS, SUN ZK. Phosphorus solubilizing *Bacillus altitudinis* WR10 alleviates wheat phosphorus deficiency *via* remodeling root system architecture, enhancing phosphorus availability, and activating the ASA-GSH cycle[J]. Plant and Soil, 2023, 492(1): 367-379.
[61] YUE ZH, CHEN YJ, HAO YW, WANG CC, ZHANG ZF, CHEN C, LIU HZ, LIU YC, LI LL, SUN ZK. *Bacillus* sp. WR12 alleviates iron deficiency in wheat *via* enhancing siderophore- and phenol-mediated iron acquisition in roots[J]. Plant and Soil, 2022, 471(1): 247-260.
[62] KUMAR V, PANDITA S, SINGH SIDHU GP, SHARMA A, KHANNA K, KAUR P, BALI AS, SETIA R. Copper bioavailability, uptake, toxicity and tolerance in plants: a comprehensive review[J]. Chemosphere, 2021, 262: 127810.
[63] IFTIKHAR A, FAROOQ R, AKHTAR M, KHALID H, HUSSAIN N, ALI Q, MALOOK SU, ALI D. Ecological and sustainable implications of phosphorous-solubilizing microorganisms in soil[J]. Discover Applied Sciences, 2024, 6(2): 33.
[64] BROKATE O, PAPENBROCK J, TURCIOS AE. Biofilm-forming microorganisms in the rhizosphere to improve plant growth: coping with abiotic stress and environmental pollution[J]. Applied Soil Ecology, 2024, 202: 105591.
[65] YADAV RC, SHARMA SK, VARMA A, RAJAWAT MVS, KHAN MS, SHARMA PK, MALVIYA D, SINGH UB, RAI JP, SAXENA AK. Modulation in biofertilization and biofortification of wheat crop by inoculation of zinc-solubilizing rhizobacteria[J]. Frontiers in Plant Science, 2022, 13: 777771.
[66] MERINERO M, ALCUDIA A, BEGINES B, MARTÍNEZ G, MARTÍN-VALERO MJ, PÉREZ-ROMERO JA, MATEOS-NARANJO E, REDONDO-GÓMEZ S, NAVARRO-TORRE S, TORRES Y, MERCHÁN F, RODRÍGUEZ-LLORENTE ID, PAJUELO E. Assessing the biofortification of wheat plants by combining a plant growth-promoting rhizobacterium (PGPR) and polymeric Fe-nanoparticles: allies or enemies?[J]. Agronomy, 2022, 12(1): 228.
[67] SINGH S, BALODI R, MEENA PN, SINGHAL S. Biocontrol activity of *Trichoderma harzianum*, *Bacillus subtilis* and *Pseudomonas fluorescens* against *Meloidogyne incognita*, *Fusarium oxysporum* and *Rhizoctonia solani*[J]. Indian Phytopathology, 2021, 74(3): 703-714.
[68] ROY C, KUMAR S, RANJAN RD, KUMHAR SR, GOVINDAN V. Genomic approaches for improving grain zinc and iron content in wheat[J]. Frontiers in Genetics, 2022, 13: 1045955.
[69] SUN ZK, LIU K, ZHANG J, ZHANG Y, XU KD, YU DS, WANG J, HU LZ, CHEN L, LI CW. *IAA* producing *Bacillus altitudinis* alleviates iron stress in

Triticum aestivum L. seedling by both bioleaching of iron and up-regulation of genes encoding ferritins[J]. Plant and Soil, 2017, 419(1): 1-11.

[70] OGO Y, KOBAYASHI T, NAKANISHI ITAI R, NAKANISHI H, KAKEI Y, TAKAHASHI M, TOKI S, MORI S, NISHIZAWA NK. A novel *NAC* transcription factor, IDEF2 that recognizes the iron deficiency-responsive element 2 regulates the genes involved in iron homeostasis in plants[J]. Journal of Biological Chemistry, 2008, 283(19): 13407-13417.

[71] LeTOURNEAU MK, MARSHALL MJ, GRANT M, FREEZE PM, STRAWN DG, LAI B, DOHNALKOVA AC, HARSH JB, WELLER DM, THOMASHOW LS. Phenazine-1-carboxylic acid-producing bacteria enhance the reactivity of iron minerals in dryland and irrigated wheat rhizospheres[J]. Environmental Science & Technology, 2019, 53(24): 14273-14284.

[72] MISRA S, SEMWAL P, PANDEY DD, MISHRA SK, CHAUHAN PS. Siderophore-producing *Spinacia oleracea* bacterial endophytes enhance nutrient status and vegetative growth under iron-deficit conditions[J]. Journal of Plant Growth Regulation, 2024, 43(5): 1317-1330.

[73] LIU LY, ZHENG XQ, WEI XC, KAI Z, XU Y. Excessive application of chemical fertilizer and organophosphorus pesticides induced total phosphorus loss from planting causing surface water eutrophication[J]. Scientific Reports, 2021, 11: 23015.

[74] LIU YC, YUE ZH, SUN ZK, LI CW. Harnessing native *Bacillus* spp. for sustainable wheat production[J]. Applied and Environmental Microbiology, 2023, 89(2): e0124722.

[75] HE L, YUE ZH, CHEN C, LI CY, LI J, SUN ZK. Enhancing iron uptake and alleviating iron toxicity in wheat by plant growth-promoting bacteria: theories and practices[J]. International Journal of Agriculture and Biology, 2020, 23(1): 190-196.

[76] HAGAGY N, ABDEL-MAWGOUD M, AKHTAR N, SELIM S, AbdELGAWAD H. The new isolated Archaea strain improved grain yield, metabolism and quality of wheat plants under Co stress conditions[J]. Journal of Plant Physiology, 2023, 280: 153876.

[77] BEREZHNAYA VV, KLYKOV AG, SIDORENKO ML, SLEPTSOVA NA, TIMOFEEVA YO. Use of microbial strains to increase yields of spring soft wheat (*Triticum aestivum* L.)[J]. Russian Agricultural Sciences, 2021, 47(1): 1-5.

[78] HERNANDEZ DJ, DAVID AS, MENGES ES, SEARCY CA, AFKHAMI ME. Environmental stress destabilizes microbial networks[J]. The ISME Journal, 2021, 15(6): 1722-1734.

[79] CABALLERO-FLORES G, PICKARD JM, NÚÑEZ G. Microbiota-mediated colonization resistance: mechanisms and regulation[J]. Nature Reviews Microbiology, 2022, 21(6): 347-360.

[80] XU ZL, CHEN SZ, WU WY, WEN YQ, CAO HL. Type I CRISPR-Cas-mediated microbial gene editing and regulation[J]. AIMS Microbiology, 2023, 9(4): 780-800.

[81] VALDIVIA-RIVERA S, AYORA-TALAVERA T, LIZARDI-JIMÉNEZ MA, GARCÍA-CRUZ U, CUEVAS-BERNARDINO JC, PACHECO N. Encapsulation of microorganisms for bioremediation: techniques and carriers[J]. Reviews in Environmental Science and Bio/Technology, 2021, 20(3): 815-838.

[82] GONG M, HE JX, KONG M, HUO QY, JIANG YW, SONG JQ, HAN W, LV GH. A microencapsulation approach to design microbial seed coatings to boost wheat seed germination and seedling growth under salt stress[J]. Frontiers in Plant Science, 2023, 14: 1283590.

[83] HERMANN L, MAIS CN, CZECH L, SMITS SHJ, BANGE G, BREMER E. The ups and downs of ectoine: structural enzymology of a major microbial stress protectant and versatile nutrient[J]. Biological Chemistry, 2020, 401(12): 1443-1468.

[84] FAREEZ IM, LIM SM, MISHRA RK, RAMASAMY K. Chitosan coated alginate–xanthan gum bead enhanced pH and thermotolerance of *Lactobacillus plantarum* LAB12[J]. International Journal of Biological Macromolecules, 2015, 72: 1419-1428.