◆健康保育与环境修复◆

环境胁迫下土壤–植物系统抵抗机制及抑制方法研究进展

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［摘　要］随着环境污染及生态破坏加剧，环境胁迫因子使土壤生态系统长期处于不断演变的过程，改变微生物群落的组成和稳态，导致植物的生理、生化和形态受损，进而影响其生长和发育。在介绍土壤环境胁迫相关概念的基础上，系统探究单一/复合胁迫下土壤植物、微生物的耐受机制；分析土壤生态系统中环境胁迫危害的抑制策略，通过磁场、电场作用可以调节土壤理化性质和微生物活性以减少环境胁迫带来的危害；基于上述土壤微生物、植物、外场加入对土壤生态系统环境胁迫的抵抗作用，分析生态脆弱区生态修复的策略。从土壤微生物、植物筛选、环境因子调控、外场介入等方面对土壤–植物系统生态恢复做出了展望，以期为环境胁迫下生态脆弱区的生态修复提供理论支撑。

［关键词］环境胁迫；土壤生态系统；生态修复；电场；磁场

［中图分类号］X53；S154.4　　［文献标志码］A　　［文章编号］ 2097–4566（2025）04–0100–13

Research progress on the resistance meachanisms of soil-plant system and inhibition methods under environmental stresses

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Abstract: With the increase of environmental pollution and ecological damage, environmental stresses make the soil ecosystem in a long-term process of continuous evolution, change the composition and homeostasis of microbial communities, and lead to the physiological, biochemical and morphological damage of plants, which affect their growth and development. First, based on the introduction of the concepts related to soil environmental stresses, the tolerance mechanisms of soil plants and microorganisms under single/complex stresses are systematically investigated; Subsequently, the suppression strategies of environmental stress hazards in soil ecosystems are analyzed, and the soil physicochemical properties and microbial activities can be regulated through the effects of magnetic and electric fields to reduce the hazards caused by environmental stresses; Based on the above mentioned roles of soil microorganisms, plants, and off-site accessions in resisting environmental stresses in soil ecosystems, strategies for ecological restoration of ecologically fragile zones are analyzed. An outlook on the ecological restoration of soil-plant system is made from the aspects of soil microorganisms, plant screening, environmental factor regulation and external field intervention, with a view to provide theoretical support for the ecological restoration of ecologically fragile areas under environmental stress.

Key words: environmental stress; soil ecosystem; ecological restoration; electric field; magnetic field

随着人类生产生活和工业不断发展，气候变化及资源枯竭等各种因素导致了日益加剧的环境胁迫。极端环境因素对生物体的生长、发育和繁殖产生不利影响，从而引发其生理、生化和行为的异常变化。环境胁迫因素可分为生物胁迫和非生物胁迫两大类，生物胁迫包括病原体、害虫和物种竞争等；非生物胁迫包括温度、水分、光照、土壤养分、盐碱化以及污染物等[1]。非生物胁迫影响植

［收稿日期］2024–12–20

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［基金项目］国家重点研发计划（2018YFC1900203）；云南省交通运输厅科技创新及示范项目（云交科教［2021］100号）

物、微生物和土壤状况，极端环境胁迫可能改变土壤、植物和微生物之间的相互作用，使得土壤生态系统长期处于不稳定的演替状态，严重削弱土壤生态系统的功能。

环境胁迫通常不是单一存在的，多种非生物胁迫可以同时发生，亟须研究植物及其微生物适应不利环境的机制，以维持生态系统平衡。然而，大部分研究侧重于单一环境胁迫条件对土壤生态系统的影响，缺乏复合环境胁迫下植物与微生物耐受机制的研究。此外，极端环境胁迫下土壤植物和微生物群落的代谢变化特征、对环境胁迫的响应机制以及抵抗作用有待进一步研究。同时，一定强度的外部物理场能有序调节植物和微生物的生命活动及功能，有助于改善土壤的理化性质和对污染物的阻隔能力，这一措施在重塑退化土壤生态结构和功能方面的作用有待进一步研究。

1　环境胁迫对土壤生态系统的影响

土壤生态系统在促进碳、氮、磷等元素的循环以及维持生物多样性方面发挥着重要作用[1–2]。土壤生态系统中的有机质分解、养分循环、生物生长，以及病菌、害虫防治等与土壤生物多样性密切相关，植物和根际微生物组成的复杂系统负责执行生化过程[3]。微生物和植物在土壤生态系统中驱动土壤养分的吸收和转化，促进土壤物质循环和能量流动。同时，土壤环境影响微生物的组成、生长和群落结构[4]，影响植物生长发育。土壤理化性质的变化可能改变植物和微生物的生态适应性，进而影响其在土壤中的分布、生长和相互作用方式。全球人口数量激增、气候变化、农业集约化和农用化学品滥用造成极端环境胁迫频发，导致土壤环境恶化，直接或间接影响植物和微生物的生存[5]。土壤生态系统面对的环境胁迫可分为生物胁迫和非生物胁迫（见图1）[6–8]，环境胁迫使土壤生态系统长期

图1　土壤生态系统在自然环境中面对的环境胁迫

Fig. 1　Environmental stresses faced by soil ecosystems in the natural environment

处于不断演变的过程，改变微生物群落的组成和稳态，导致植物的生理、生化和形态受损，进而影响其生长和发育[9–12]。干旱、温度和盐分是影响植物生产力和粮食安全的主要胁迫因素，抗逆性弱的植物会消耗更多的水分和肥料，对环境造成负担[13]。不同胁迫因子相互交织易导致极端的环境胁迫。现阶段，生态脆弱区面临生态修复工作开展难度大的问题，研究土壤、植物、微生物和非生物胁迫之间的相互作用对利用技术手段缓解生态脆弱区的环境胁迫极为重要。

2　复合环境胁迫对土壤生态系统的影响及生物体的抵抗机制

土壤、植物、微生物和非生物胁迫高度交织（见图2），在非生物胁迫期间，植物和微生物之间的相互作用动态且复杂[14]。土壤生态系统中，非生物胁迫的存在使得植物相关的微生物通过增强矿物质的溶解度来维持植物的健康生长，调节生长素、赤霉素和乙烯等植物激素的信号传导，直接供应养分以及减缓病原体的危害等。植物与土壤之间的相互作用影响非生物胁迫下根系微生物群落[15–16]以及植物生长[17–19]。

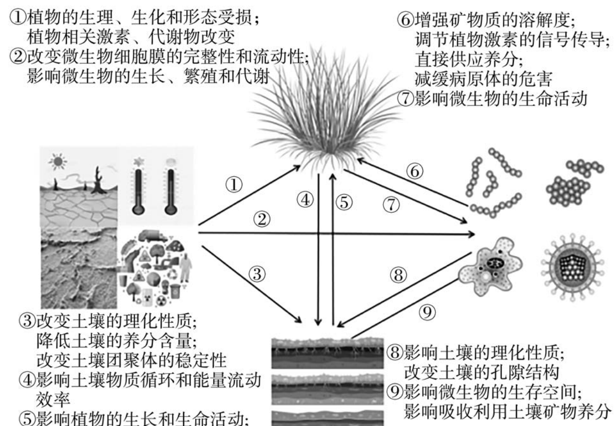

图2　土壤、植物、微生物和非生物胁迫的相互作用

Fig. 2　Interactions of soil, plant, microbial and abiotic stress

2.1　复合环境胁迫

干旱、温度或盐分等单一胁迫因子在较低强度时不会引起植物的初级生产力或整个生态系统的生产力显著下降。然而，如果同时受到另一个胁迫因子的影响，即使其强度较低也会导致整体生产力显著下降，多重胁迫的综合影响会造成生态系统的生物多样性减少以及生态系统功能下降[20–22]。复合环境胁迫通常呈现累积效应，常见的复合胁迫包括高温和盐胁迫[23–24]、干旱和盐胁迫[25–26]、干旱和热胁迫[27–28]、重金属和盐胁迫[29–30]。例如，某些地区高

温伴随着异常干旱，恶劣的条件使得该地区土壤生态失衡，土壤养分不足阻碍植物生长发育，严重降低植物的生产力[31]；植物同时面临高温和盐胁迫时，光合作用等生理过程会受到更严重的抑制[32-33]；细菌病原体和干旱胁迫同时发生比单独胁迫对植物生长的影响更大[34]；干旱和低温胁迫改变了植物光合作用和气体交换的正常速率，不利于植物光合器官的发育和光能的同化；干旱和热胁迫可能导致活性氧（ROS，如超氧化物和H_2O_2）过量产生[35]，造成蛋白质变性和过氧化脂质膜结构破坏，叶绿素含量降低[36]，进而降低光合作用和植物生产力[37-38]。

土壤生态系统易受多种胁迫的影响，干旱与低温胁迫是常见的两种非生物胁迫[39]。干旱胁迫产生的ROS导致细胞损伤、光合色素漂白和类囊体膜降解。低温胁迫影响土壤微生物的群落结构、多样性和生物量，导致土壤养分降低[40]；低温胁迫下，微生物产生脯氨酸、甘氨酸、甜菜碱、糖醇等低分子量氮化合物作为低温保护剂[41]。复合胁迫的危害取决于胁迫持续时间和严重程度、植物的种类、生长阶段、土壤改良剂以及生长介质的类型[42]。为适应恶劣环境，植物和微生物已经进化出一系列耐受胁迫的机制，以减轻外界环境胁迫的干扰[43]。

2.2 复合环境胁迫下植物的耐受机制

植物在整个生命周期中会受到多种环境胁迫的影响，其通过根系定植于土壤中，无法逃离不利的环境，对非生物胁迫产生了一系列的适应性反应，形成了耐受机制，涉及生理、生化和分子层面的反应[44-45]。在高温、低温、干旱、盐碱和重金属等胁迫条件下，植物的多基因反应被激活，其产生的相关激素、初级和次级代谢物发挥关键作用，从而提高植物的抗逆性[41]（见图3）。

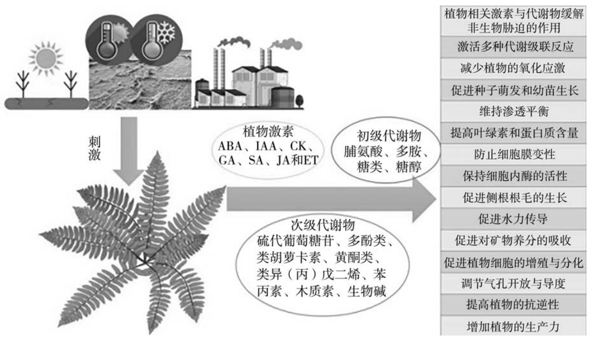

图3 植物激素、初级及次级代谢物在非生物胁迫中的作用

Fig. 3 Effect of phytohormones, primary and secondary metabolites in abiotic stresses

2.2.1 植物激素缓解复合胁迫的作用

复合胁迫之间的相互作用激活了多种反应机制及途径，影响植物在胁迫中产生的脱落酸(ABA)、吲哚-3-乙酸（IAA）、细胞分裂素（CK）、赤霉素（GA）、水杨酸（SA）、茉莉酸（JA）和乙烯（ET）等各种激素的功能，进而激活了多种代谢关联反应，表1总结了上述植物激素缓解植物所受环境胁迫的作用机制。

表1 植物激素缓解复合胁迫的作用机制

Table 1 Mechanisms of phytohormones in alleviating complex stress

植物激素	作用机制	适应环境胁迫类型	参考文献
ABA	控制由复合胁迫诱导的多数信号通路，控制气孔开放以降低蒸腾速率	干旱、重金属、草食动物和盐胁迫	[46-49]
IAA	促进根结瘤、细胞增殖和分化，增加根的表面积，降低乙烯浓度	干旱、低温和盐胁迫	[50]
CK	促进细胞分裂、种子萌发、顶端优势、叶绿素积累和延迟叶片衰老	干旱和盐胁迫	[51-52]
GA	促进叶片膨胀和茎伸长，提高酶活性、叶绿素含量，促进矿物质养分吸收	极端温度、干旱、重金属和盐胁迫	[53-54]
SA	促进植物的光合作用和生长发育，防止过氧化损伤	干旱、极端温度、重金属、养分缺乏和盐胁迫	[55-56]
JA	提高植物抗氧化防御酶的活性，调节植物的生长繁殖和养分运输	干旱、极端温度、重金属和盐胁迫	[57-59]
ET	控制植物种子萌发、开花和衰老，调节植物根系的生长发育	干旱、高温、养分缺乏和盐胁迫	[60-61]

2.2.2 植物初级代谢物缓解复合胁迫的作用

植物在遭受非生物胁迫时，会合成多种初级代谢物。脯氨酸是一种广泛分泌于干旱、盐渍和极端温度下的渗透物[62]，用于维持渗透平衡，清除ROS，稳定细胞膜和蛋白质。然而，脯氨酸过度积累将增加ROS和丙二醛的产生，并阻止ABA和ET的生物合成，导致胁迫耐受性降低[63]。多胺是一类带有正电荷的低分子量含氮化合物，可与带负电荷的化合物，如核酸、磷脂和蛋白质相互作用[64]，降低气孔孔径和蒸腾速率，提高植物在逆境下的耐受性[65]。大多数的糖类、糖醇也是重要的初级代谢物[66]。干旱胁迫下植物根部蔗糖、棉子糖、葡萄糖和果糖含量增多使根冠比增加，肌醇水平降低[67-68]。此外，遭受干旱胁迫的植物中积累了海藻糖等非还原性双糖，棉子糖和水苏糖等不提供能量的糖也会在遭受干旱、温度和盐胁迫的植物中积累，以保护其免受ROS的侵害[68-69]。海藻糖生物合成基因过表达的水稻可以降低ROS的损伤，改

善矿物质平衡，提高对干旱和盐胁迫的耐受性[70]。

2.2.3　植物的次级代谢物缓解复合胁迫的作用

复合胁迫的过程中，植物产生的次级代谢物通过激活各种信号通路和协调适应性反应来增强植物对环境胁迫的防御作用[71]。如硫代葡萄糖苷、多酚类和类胡萝卜素等，可促进植物细胞的增殖和健康[71]。黄酮类化合物可在非生物胁迫中保护植物免受紫外线辐射(UVB)，并作为抗氧化剂降低ROS的影响[72]。类异戊二烯在叶绿体中合成以应对非生物胁迫，由于其具有挥发性，可从植物组织中迅速蒸发到大气中。在干旱、UVB和热胁迫下，类异丙二烯合成生长素激活信号通路来控制植物生理过程和保护植物免受ROS侵害[8]。苯丙素是植物中的另一种次生代谢物，在UVB、干旱、寒冷和盐胁迫下合成。木质素积累有助于运输水分以及促进植物在逆境中发育和生长[73]。生物碱是含氮的次生代谢物，主要存在于维管植物中，在渗透、损伤、遗传毒性和热胁迫过程中，生物碱通过产生有毒物质来保护植物免受微生物感染和食草动物攻击[41]。

除了分泌激素、初级和次级代谢物外，植物具备一些适应策略和防御途径来抵抗环境胁迫。例如，高温和干旱胁迫同时发生时，植物可通过控制气孔的开闭，维持正常的蒸腾作用和保存水分[32]。因此，在面对复合环境胁迫时，为了提高植物的耐受性，有必要识别和分析在单个和多重胁迫下共同发挥作用的代谢途径和基因，研究可以抵御多种胁迫的植物种类[74–75]。此外，增强植物对复杂胁迫因素组合的耐受性需要提升植物的防御机制和创造有利的微环境。

2.3　复合环境胁迫下微生物的耐受机制

多数微生物可以在恶化的环境条件下生存，并且随着时间的推移，部分微生物对胁迫的耐受性可能会被诱导和增强。能够适应极端环境的微生物通常具备独特的代谢途径和功能，如化学异养、好氧异养、氮氧化、尿素分解代谢、硝酸盐还原、发酵、暗氢氧化和甲烷生成等[76]。

2.3.1　微生物抵御环境胁迫的方式

微生物自身抵御环境胁迫的方式包括维持细胞膜的完整性、流动性和通透性，调节转运体的活性来调节细胞的生理功能；通过调节转录因子的活性和特定的信号转导途径来控制基因表达以适应环境变化；调控微生物细胞的代谢，促进抗逆性保护因子和特异酶的形成；建立修复机制，保护大分子不受环境胁迫的影响[77–78]。

2.3.2　微生物缓解氧化应激、高渗应激、热胁迫、酸胁迫的机制

为保护细胞免受氧化应激的损伤，微生物已经发展出多种防御机制，例如抗氧化系统减少ROS的产生，降解和清除已产生的ROS，强化对目标物的攻击。铁蛋白、细菌铁蛋白和DNA结合蛋白是3种可用的铁储备蛋白，保护细胞免受芬顿反应产生的ROS的侵害。微生物抗氧化系统的谷胱甘肽也可保护菌株免受H_2O_2诱导的氧化损伤[79]。为保护细胞免受高渗应激，微生物发展出一系列感知、响应、调节和抵御高渗胁迫的机制，即渗透调节。例如，位于细胞膜上的ATP结合盒（ABC）转运体通过将过量离子运输出细胞而维持离子平衡[80]；一些特定的相容溶质，包括阳离子、糖、醇、氨基酸、甜菜碱和胆碱[81]的积累保证了细胞质酶在缺水下的活性，增加了内部渗透压以帮助微生物细胞适应高渗应激[82]。为保护细胞免受热胁迫，微生物已经发展出合成热休克蛋白、积累海藻糖、改变细胞膜结构等多种机制。热休克蛋白通过调节蛋白质翻译、维持蛋白质完整性、防止蛋白质变性、促进异常蛋白质降解、重新激活受损蛋白质等方式保护细胞免受热胁迫[83]；海藻糖通过稳定膜结构和氢键相互作用强度增强了微生物细胞的耐热性；分支和弯曲的甾醇在微生物细胞的耐热性发展中具有优势，通过调节甾醇种类和数量，增强细胞的耐热性[84–86]。为缓解酸胁迫，微生物细胞通过限制质子渗透[87]、增强质子泵和消耗细胞内质子维持pH稳态，以确保细胞生长和代谢[88–89]。微生物细胞也利用大分子的保护和修复机制来抵抗酸胁迫；酸引起的蛋白质聚集和变性可以被一些热休克蛋白修复[90–91]。

3　生态系统中环境胁迫危害的抑制手段

除根际微生物可以缓解植物受到的非生物胁迫外，目前已经发现应用外场，如电场与磁场可以调控微生物和植物的生长。通过控制电磁场强度可促进种子萌发，提高植物产量，改变微生物的代谢模式，提高微生物、植物抵抗非生物胁迫的能力。

3.1　磁场对微生物和植物的作用

3.1.1　磁场对微生物的作用

磁场（MF）对微生物的影响取决于磁场类型、细菌种类和操作条件[92–93]。MF通过影响土壤的渗透性、膨胀性和团聚性等因素，改变土壤微生物群落的演替和物质循环过程[94]。微生物通过改变脂质组成来适应MF并保持适当的膜柔韧性[95–96]，提高膜通透性可促进营养物质的吸收[97]。MF也会

影响微生物的生长和代谢，例如通过调节跨膜蛋白和可溶性蛋白的构象，影响基因表达；提高细胞酶，如碱性磷酸盐酶、活性污泥脱氢酶、超氧化物歧化酶、α–蛋白酶的活性[98-99]；影响特定微生物的群落结构，并丰富具有特殊耐受性的微生物菌群[100]。LI等[101]的研究表明，暴露于MF的人工湿地中存在更多的微生物种类，且MF可以提高硝化细菌的丰度以及与硝化过程相关的酶的活性来促进硝化作用。DEAMICI等[102]研究表明某些情况下微生物短时间暴露在MF中更有效[103]。适当添加MF可以在一定范围内提高微生物的代谢效率，有利于微生物的富集[104]，从而促进土壤呼吸作用[105]。相反，高强度的MF可能抑制过氧化物酶和脲酶的活性[106]，从而抑制微生物的生长和繁殖，甚至导致微生物死亡[107]。

3.1.2 磁场对植物的作用

REINA等[108]提出MF的作用可能通过改变细胞内Ca^{2+}水平或跨细胞膜的离子浓度来影响植物的生长。此外，MF可以提高生物体内有机酸、激素和核酸的含量，有助于增强植物对外界不良环境的抵抗能力，MF的应用是一种促进植物生长和提高整体生产力的新方法。

不利的非生物胁迫，如干旱、盐渍、重金属、温度极端等会导致植物的分子和生理结构发生变化，从而降低种子发芽率，抑制植物生长[109]。MF处理可以减少植物在干旱胁迫下产生的ROS量，促进叶绿素和类胡萝卜素的合成[108]，提高植物对水和养分的吸收能力，以缓解干旱对植物的影响[110]。BAGHERI[111]发现采用3.7 mT的极低频磁场处理后，枸杞中超氧化物歧化酶（CAS）、过氧化氢酶（CAT）和抗坏血酸过氧化物酶（APX）活性和类黄酮含量均有提高，增强了枸杞的抗氧化能力。在盐胁迫下，MF预处理提高了种子的吸水率，以及α–淀粉酶和蛋白酶活性，促进了植物种子的萌发和生长[112-114]，植物的光合速率、气孔导度、蒸腾速率和内部CO_2浓度也有所提高[115-116]，生物碱、皂苷、类黄酮和黄酮醇等次生代谢物的积累量减少，可一定程度缓解盐胁迫[117]。在Cd胁迫下，经600 mT的MF处理的绿豆幼苗中H_2O_2、O_2^-和丙二醛（MDA）等活性氧水平较低，但碳氮浓度、总叶绿素、光合速率、气孔导度、蒸腾速率、胞间CO_2浓度和水分利用率较高[118]。此外，MF预处理调节植物细胞膜的离子流，改善种子萌发和生长，增加植物对As胁迫的耐受性[119-120]。植物生长受温度影响时，MF可以激活热休克蛋白的表达来减轻高温胁迫作用[121]。AFZAL等[122]证明MF处理可调节低温胁迫下玉米种子的膜透性和离子转运速率，加速了玉米植株在冷胁迫中的光合作用、蒸腾作用等初级代谢过程，从而缓解了低温胁迫。迄今为止，已经对MF影响种子萌发、激素变化、植物生长和产量进行了多项研究，适宜的磁场可改善植物生长已被证实，表2总结了磁场缓解植物所受非生物胁迫的作用。

表2 磁场缓解植物所受非生物胁迫的作用机制

Table 2 Mechanisms of magnetic fields in alleviating abiotic stresses on plants

非生物胁迫	植物	磁场参数	作用机制
干旱	西红柿	50 Hz，100 μT	叶片细胞膜的相对透性减小，抗病性在营养期明显增强[123]
干旱	小麦	14.3 Hz，3～180 μT	延迟生命活动过程中有害变化的发展，提高水分利用效率[124]
干旱	玉米	100 mT，2 h；200 mT，1 h	叶片水势、凝固势和水含量增加，光合作用、气孔导度和叶绿素含量增加[125]
盐	小麦	0.2～0.3 T	提高过氧化物酶活性，降低蒸腾速率与气孔导度，提高保水能力[126]
盐	鹰嘴豆	100 mT, 1h	提高种子的水吸收效率，蛋白酶和脱氢酶活性，进而提高种子发芽率和幼苗活力[127]
盐	大豆、玉米	200 mT 1 h	改变细胞膜的通透性，使水和能量进入细胞，从而增强代谢途径和水分吸收速率，提高α–淀粉酶、蛋白酶活性[128]
低温	玉米	150 mT，3 min	促进种子的离子转运，加速光合作用、蒸腾和气孔开闭等初级代谢过程[122]
Cd	绿豆	600 mT	降低活性氧，增加总叶绿素、光合速率、气孔导度、蒸腾速率、胞间CO_2浓度和水利用率[118]

选择适宜的磁场强度和处理时间对于改善植物的生长代谢和提高对极端环境的耐受性至关重要。目前，常用于处理植物种子或幼苗的磁场强度在0.2～0.5 T，处理时间范围较大，通常采用低磁场长时间或高磁场短时间的处理方式[129]。适当强度的磁场可以刺激碳水化合物和植物生长激素从合成部位向果实的运输[130]，加速植物体的代谢过程和呼吸速率，促进细胞内ATP的合成[131-132]，还可以提高植物体内POD、CAT和SOD等酶的活性，加速活性氧和自由基的清除速度，提高植物的抗逆性[133-134]。

3.2 电场对微生物和植物的作用

3.2.1 电场对微生物的作用

电场（EF）处理过程会引起土壤pH、水含量和

温度等环境因素的变化，影响微生物群落的结构、丰度、多样性和活性，对土壤生态影响显著[135]。EF的引入引起微生物代谢过程中电子迁移路径改变，导致微生物代谢途径的实质性改变[136]。直流电场促进土壤微生物的生长和繁殖，EF作用下土壤柱中微生物的迁移和分布取决于电泳、电渗析、养分流动等[137]。细菌表面带负电而具有负的电动势，由于静电吸引力细菌会向阳极移动[137]。MA等[138]发现阳极氧的产生可以提高土壤溶解氧含量，增强微生物的呼吸作用，间接提高土壤的氧化还原能力和土壤酶活性。EF作用下，土壤中的离子和水分通过电渗流向阴极迁移，为阴极附近的细菌生长提供了有利条件[138]。由于土壤中水的电解和土壤存在的欧姆电阻，土壤温度升高提高了微生物活性。LI等[135]研究发现2 V/cm的EF强度有利于微生物的生长和代谢，总微生物量和降解土壤中多环芳烃的活性最高。然而，较高的电场强度，例如3 V/cm可能会导致土壤温度较高，超过微生物最适宜生长的温度范围，抑制微生物的活动和代谢[139]。此外，电场处理后，土壤中的养分消耗和污染物浓度变化直接影响微生物的代谢状态[140]。适宜的EF强度驱动内生菌和外生菌在土壤原位选择性繁殖，根际菌群多样性和丰富性增加，产生更多有利于植物生长的维生素，并且可能促进植物根际的反硝化反应。

3.2.2 电场对植物的作用

电刺激可以增加植物体内酶的含量和提高酶活性，促使酶蛋白的构象改变，有利于植物的生长和代谢，增强基因表达的活性并且刺激植物对干旱、强光、寒冷和盐胁迫作出快速反应[141]。EF诱导植物细胞孔隙形成，增加了质膜的离子渗透性，导致Ca^{2+}进入细胞质，Ca^{2+}的流入增强或降低了一些细胞的膜电位，这可能导致渗透性的非特异性增加。Ca^{2+}影响细胞信号的各种酶级联反应，增加Ca^{2+}流入可以提高植株生长、发育和再生相关酶的代谢率[142–144]。暴露于电刺激下的黑麦、小麦、萝卜和大麦植株生长速度更快[145]。研究发现，在菠菜、羽衣甘蓝和生菜中，空气阴离子促进叶片气孔打开，促进光合作用、蒸腾作用和对矿物质的吸收，从而提高植物的产量[146–147]。LEE等[148]发现施加于羽衣甘蓝根际的电流促进了根毛形成和离子运输。EF影响植物次生代谢物的积累，电刺激增加了羽衣甘蓝、玉米、萝卜和大豆中类黄酮、花青素、木质素和植物甾醇的含量，其对植物的抗逆性至关重要[145]。OZUNA等[149]证明500 mA的EF可作为苋菜种子中的酚类物质和抗氧化酶合成的非生物激发剂；LEONG等[150]发现0.5 ~ 2.0 kV/m的EF刺激了小麦种子的新陈代谢，提高了抗氧化酶活性；VALLVERDUU – QUERALT等[151]发现1.2 kV/m的EF使收获的番茄果实中，总多酚含量和抗氧化能力提高44%，且在1 kV/m的EF下生物活性物质总体水平最高。已有研究证明，采用对种子及幼苗进行EF处理可以提高植物对干旱、盐度和极端温度等非生物胁迫的抗性。

表3总结了EF缓解植物所受非生物胁迫的作用机制。

表3 电场缓解植物所受非生物胁迫的作用机制

Table 3 Mechanisms of electric fields in alleviating abiotic stresses on plants

非生物胁迫	植物	电场条件	作用机制	参考文献
干旱	玉米	场强200 kV/m、脉宽80 ms、频率1 Hz的极低频脉冲电场	根细胞MDA含量降低，SOD活性增强，抗氧化活性增加	[152]
干旱	燕麦	99个单极矩形脉冲，每个脉冲持续10 μs，频率为13 Hz，电场强度为2 250 V/cm	促进根毛形成、水分吸收、抗氧化剂积累、呼吸作用、光合作用	[153]
干旱	油葵	3.0 kV/cm，15 min	提高SOD和POD的量，清除活性氧自由基，抑制膜内不饱和脂肪酸过氧化及其产物MDA的产量	[154]
干旱、高温	马铃薯	400 kV /m，12 min	提高马铃薯块茎种子的数量和质量	[155]
寒冷	菜豆、甘蓝	100 kV/m，50 Hz，10 min	提高抗氧化酶活性和组织活力，减少H_2O_2形成	[156]
养分缺乏	羽衣甘蓝	50 mA，3周	提高根的生物量，增加光合作用，促进矿物离子的吸收	[148]
Cd	玉米	0 ~ 4.5 V	提高光合速率，电场可以增加植物生物量	[157]

采用EF对植物进行处理通常分为：（1）低频电流处理，将植物种子或幼苗放在绝缘的容器中加水，容器两边放电极板，通入低频电流（200 V，50 Hz），处理时间和电流强度因植物种类而异，电流强度在0.1~1.0 A，处理时间为15 ~ 30 min[158]；（2）静电处理，将植物置于直流静电场中，正负电

场对植物的效应不同，因此需要根据植物的种类施加不同的电场[159]。图4展示了原位电场驱动微生物促进植物生长的机制。

图4　原位电场驱动微生物促进植物生长的作用

Fig. 4　In-situ electric field driven microorganisms promoting plant growth

4　生态脆弱区土壤生态系统修复

4.1　菌种和植物促进土壤生态系统修复

PSB、内生菌、PGPR和AMFs等微生物在缓解非生物胁迫、改善植物生长方面发挥重要作用，其可以促进植物生长，提高植物对生物和非生物胁迫的抵抗力。可以利用有益微生物配制合适的微生物配方或者菌剂以较低的成本帮助植物提高生产力。考虑到植物的生理和形态特性，可以采取上繁型草本植物和下繁型草本植物相结合的策略。上繁型草本植物的高大地上部分有助于提高植被的覆盖度，而下繁型草本植物的发达根系则可以提供良好的护坡作用。此外，灌木的根系十分发达，可以作为生态修复后期阶段主要的护坡植物。基于应用场景土壤生态系统的特点，在选择植物时，可以优先考虑禾本科和豆科植物的结合，因为它们具有丰富的植物资源，适应性强，且具有良好的生态功能。这样的组合不仅可以保证植被的多样性，还可以充分发挥植物自身的调节功能，提高生态修复的效果[160]。

4.2　调控环境因子促进植物生长

促进植物生长需要综合考虑温度、湿度、光照、二氧化碳浓度和土壤养分等环境因素。通过对这些因素的梯度分区，可以确定适宜的环境条件范围，从而优化植物生长环境。在减少化肥施用对土壤造成的污染方面，采用微生物接种剂和有机肥等方法增加生态脆弱区土壤的养分含量，并且有助于恢复土壤的肥力。生物肥料中含有多种细菌和真菌，可以与土壤中的其他微生物相互作用，促进土壤的营养循环，从而提高植物生长效率。适量的二氧化碳浓度可以促进光合作用和植物的生长。

4.3　外场增强生物体的抗逆性

外加物理场（电场、磁场、超声波、光、温度）已被确定是一种可定向调控植物、微生物生长发育与处理污染物的有效新兴手段，在一定强度的物理场作用下生物体可以预防病菌并提高对不良环境的耐受性。EF使功能微生物与有害物质富集在一起，微生物代谢过程中产生的多糖、蛋白质等与有害物质发生螯合反应，将有害物质转化为各种无毒沉淀物；添加适当强度的MF可提高微生物的代谢效率和种子活力，促进幼苗生长，提高作物产量；超声波使土壤形成较松散的结构，利于功能微生物的附着与富集；适度增加光照使光养微生物更好地生长和繁殖，控制微生物的代谢循环，提高植物的光合速率；温度可以筛选且促进对嗜冷、嗜温或超嗜热细菌的富集。然而，现在研究大多集中在单一物理场对生物体的影响上，多物理场耦合对微生物、植物在不利环境中生存的影响机制尚不明确。因此，探究外加交替或可变的多物理场对促进多重环境胁迫下的微生物代谢或提高微生物、植物对复杂污染物的降解速度，加速退化土壤的生态结构和功能重塑过程，促进土壤高质量发展至关重要。

5　结论与展望

各种环境胁迫下的土壤系统具有变异性、难处理性和未知性等特点。目前关于土壤微生物、植物抵抗环境胁迫取得了一系列进展，然而对植物、微生物同时遭受多种环境胁迫及其耐受机制的研究较少。针对复合型的环境胁迫，土壤生物体的生长代谢，微生物、植物在土壤生态系统中碳、氮、磷分解和养分循环以及结构稳定的驱动作用，以及外场调控技术研究显得尤为迫切，这对生态脆弱区土壤生态系统抵御环境胁迫危害、土壤生态修复具有重要意义。

未来的研究可着眼于：（1）构建土壤生态系统在环境胁迫下的演变模型，土壤生态系统长期处于演替的非平衡状态，急剧削弱土壤系统的生态功能，建立演变模型有助于了解植物、土壤、微生物和非生物胁迫的相互作用。（2）根据植物、微生物抵抗环境胁迫的机制筛选适合生态脆弱区生长的植物及菌种。基于植物与微生物的相互作用，将有益菌群接种植物或兼顾多种植物的优点搭配混种，减少农药、化肥的施用，发展绿色环保的修复方法。

（3）应用物理场对植物、微生物进行定向调控。单一物理场及多物理场耦合促进多重环境胁迫下的微生物代谢、提高微生物和植物对复合胁迫的抗逆性，加速退化土壤的生态结构和功能重塑，促进土壤高质量发展。

［参考文献］

[1] CHEN Z H, SOLTIS D E. Evolution of environmental stress responses in plants [J]. Plant Cell Environment, 2020,43(12): 2827–2831.

[2] NEZHAD M H, HUSSAIN M A, BRITZ M L. Stress responses in probiotic Lactobacillus casei [J]. Critical Reviews in Food Science Nutrition, 2015, 55(6):740–749.

[3] RUSYN I. Role of microbial community and plant species in performance of plant microbial fuel cells [J]. Renewable and Sustainable Energy Reviews, 2021, 152:111697.

[4] ISLAM W, NOMAN A, NAVEED H, et al. Role of environmental factors in shaping the soil microbiome [J]. Environmental Science Pollution Research International, 2020, 27(33):41225–41247.

[5] REN X W, YIN S, WANG L, et al. Microplastics in plant-microbes-soil system: A review on recent studies [J]. Science of the Total Environment, 2022, 816:151523.

[6] MIHIRI S, NISHANTA R, MUHAMMAD R, et al. Heavy metal-induced oxidative stress on seed germination and seedling development: a critical review [J]. Environmental Geochemistry and Health, 2019, 41(4):1813–1831.

[7] GUPTA S, YADAV B S, RAJ U, et al. Transcriptomic analysis of soil grown T. aestivum cv. root to reveal the changes in expression of genes in response to multiple nutrients deficiency [J]. Frontiers in Plant science,2017,8:1025.

[8] YADAV B S, LAHAV T, REUVENI E, et al. Multidimensional patterns of metabolic response in abiotic stress-induced growth of Arabidopsis thaliana [J]. Plant Molecular Biology, 2016, 92 (6):689–699.

[9] MALIK A A, SWENSON T, WEIHE C, et al. Drought and plant litter chemistry alter microbial gene expression and metabolite production[J]. The ISME Journal, 2020, 14 (9): 2236–2247.

[10] NGUYEN L T T, BROUGHTON K, OSANAI Y, et al. Effects of elevated temperature and elevated CO_2 on soil nitrification and ammonia-oxidizing microbial communities in field-grown crop [J]. Science of the total Environment, 2019, 675:81–89.

[11] HERNANDEZ D J, DAVID A S, MENGES E S, et al. Environmental stress destabilizes microbial networks [J]. The ISME Journal, 2021, 15(6):1722–1734.

[12] PICCARDI P, VESSMAN B, MITRI S. Toxicity drives facilitation between 4 bacterial species [J]. Proceedings of the National Academy of Sciences of the United States of America, 2019, 116(32):15979–15984.

[13] ZHU J K. Abiotic stress signaling and responses in plants [J]. Cell, 2016, 167(2):313–324.

[14] OMAE N, TSUDA K. Plant-microbiota interactions in abiotic stress environments [J]. Molecular Plant-Microbe Interactions: MPMI, 2022, 35(7):511–526.

[15] BHAT M A, KUMAR V, BHAT M A, et al. Mechanistic insights of the interaction of plant growth-promoting rhizobacteria (PGPR) with plant roots toward enhancing plant productivity by alleviating salinity stress [J]. Frontiers in Microbiology, 2020, 11:1952.

[16] DE VRIES F T, GRIFFITHS R I, KNIGHT C G, et al. Harnessing rhizosphere microbiomes for drought-resilient crop production [J]. Science, 2020, 368(6488):270–274.

[17] KOEVOETS I T, VENEMA J H, ELZENGA J T M, et al. Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance [J]. Phyto Keys, 2016, 7:1335.

[18] HARTMAN K, TRINGE S G. Interactions between plants and soil shaping the root microbiome under abiotic stress [J]. The Biochemical Journal, 2019, 476(19):2705–2724.

[19] DUAN D D, JIANG F F, LIN W H, et al. Effects of drought on the growth of Lespedeza davurica through the alteration of soil microbial communities and nutrient availability [J]. Journal of Fungi, 2022, 8(4):384.

[20] NAWAZ M, LI L, AZEEM F, et al. Insight of transcriptional regulators reveals the tolerance mechanism of carpet-grass (Axonopus compressus) against drought [J]. BMC Plant Biology, 2021, 21:71.

[21] NIU L J, LIAO W B. Hydrogen peroxide signaling in plant development and abiotic responses: crosstalk with nitric oxide and calcium [J]. Frontiers in Plant Science, 2016, 7(13):230.

[22] TABASSUM T, FAROOQ M, AHMAD R, et al. Terminal drought and seed priming improves drought tolerance in wheat [J]. Physiology and Molecular Biology of Plants, 2018, 24(5): 845–856.

[23] SHALABY T A, ABD-ALKARIM E, EL-AIDY F, et al. Nano-selenium, silicon and H_2O_2 boost growth and productivity of cucumber under combined salinity and heat stress [J]. Ecotoxicology and Environmental Safety, 2021, 212:111962.

[24] BAYOUMI Y, ABD ALKARIM E, EL RAMADY H, et al. Grafting improves fruit yield of cucumber plants grown under combined heat and soil salinity stresses [J]. Horticulturae, 2021, 7(3):61.

[25] SILAMBARASAN S, LOGESWARI P, CORNEJO P, et al. Simultaneous mitigation of aluminum, salinity and drought stress in Lactuca sativa growth via formulated plant growth promoting Rhodotorula mucilaginosa CAM4 [J]. Ecotoxicology and Environmental Safety, 2019, 180:63–72.

[26] ALAMRI S, HU Y B, MUKHERJEE S, et al. Silicon-induced postponement of leaf senescence is accompanied by modulation of antioxidative defense and ion homeostasis in mustard (Brassica juncea) seedlings exposed to salinity and drought stress [J]. Plant Physiology and Biochemistry, 2020, 157:47–59.

[27] DUC N H, CSINTALAN Z, POSTA K. Arbuscular mycorrhizal fungi mitigate negative effects of combined drought and heat stress on tomato plants [J]. Plant Physiology and

Biochemistry, 2018, 132:297-307.

[28] HOSSEINI S Z, ISMAILI A, NAZARIAN-FIROUZABADI F, et al. Dissecting the molecular responses of lentil to individual and combined drought and heat stresses by comparative transcriptomic analysis [J]. Genomics, 2021, 113(2):693-705.

[29] CHRYSARGYRIS A, PAPAKYRIAKOU E, PETROPOULOS S A, et al. The combined and single effect of salinity and copper stress on growth and quality of Mentha spicata plants [J]. Journal of Hazardous Materials, 2019, 368:584-593.

[30] EL-SAADONY M T, DESOKY E-S M, SAAD A M, et al. Biological silicon nanoparticles improve Phaseolus vulgaris L. yield and minimize its contaminant contents on a heavy metals-contaminated saline soil [J]. Journal of Environ mental Science, 2021, 106:1-14.

[31] MA L, ZHANG Z H, YAO B Q, et al. Effects of drought and heat on the productivity and photosynthetic characteristics of alpine meadow plants on the Qinghai-Tibetan Plateau [J]. Journal of Mountain Science, 2021, 18(8):2079-2093.

[32] FAHAD S, BAJWA A A, NAZIR U, et al. Crop production under drought and heat stress: plant responses and management options [J]. Frontiers in Plant Science, 2017, 8:1147.

[33] MA J, UR REHMAN M Z, SALEEM M H, et al. Effect of phosphorus sources on growth and cadmium accumulation in wheat under different soil moisture levels [J]. Environmental Pollution, 2022, 311:119977.

[34] PANDEY A, KHAN M K, HAKKI E E, et al. Combined boron toxicity and salinity stress—An insight into its interaction in plants [J]. Plants, 2019, 8(10):364.

[35] HUSSAIN S, RAO M J, ANJUM M A, et al. Oxidative stress and antioxidant defense in plants under drought conditions [J]. Plant Abiotic Stress Tolerance, 2019:207-219.

[36] AMIRI H, DOUSTY B, HOSSEINZEDEH S R. Water stress-induced changes of morphological, physiological and essential oil compounds in Thymus eriocalyx from Iran [J]. Journal of Essential Oil Bearing Plants, 2018, 21 (5): 1210-1223.

[37] CHOUKRI H, HEJJAOUI K, EL-BAOUCHI A, et al. Heat and drought stress impact on phenology, grain yield, and nutritional quality of lentil (Lens culinaris Medikus) [J]. Frontiers in Nutrition, 2020, 7:596307.

[38] SAHITHI B M, RAZI K, AL MURAD M, et al. Comparative physiological and proteomic analysis deciphering tolerance and homeostatic signaling pathways in chrysanthemum under drought stress [J]. Physiologia Plantarum, 2021, 172 (2): 289-2303.

[39] LI X Y, WANG Y, HOU X Y, et al. Flexible response and rapid recovery strategies of the plateau forage Poa crymophila to cold and drought [J]. Frontiers in Plant Science, 2022, 13: 970496.

[40] MUHAMMAD I, KHAN F, KHAN A, et al. Soil fertility in response to urea and farmyard manure incorporation under different tillage systems in Peshawar, Pakistan [J]. International Journal of Agriculture and Biology, 2018, 20(7): 1539-1547.

[41] SINGH A K, DHANAPAL S, YADAV B S. The dynamic responses of plant physiology and metabolism during environmental stress progression [J]. Molecular Biology Reports, 2020, 47(2):1459-1470.

[42] SHAHID M. Effect of soil amendments on trace element-mediated oxidative stress in plants: Meta-analysis and mechanistic interpretations [J]. Journal of Hazardous Materials, 2021, 407:124881.

[43] NAWAZ M, SUN J, SHABBIR S, et al. A review of plants strategies to resist biotic and abiotic environmental stressors [J]. The Science of the Total Environment, 2023,900:165832.

[44] ÁLVAREZ S, ACOSTA-MOTOS J R. Miscellaneous Sets of Abiotic Stresses and Plant Strategies to Cope with Them [J]. Agronomy, 2022,12:2727.

[45] SAMEENA P P, PUTHUR J T. Heavy metal phytoremediation by bioenergy plants and associated tolerance mechanisms [J]. Soil and Sediment Contamination: An International Journal, 2021, 30(3):253-274.

[46] SONG Y S, ZHENG H X, SUI Y, et al. SbWRKY55 regulates sorghum response to saline environment by its dual role in abscisic acid signaling [J]. Theoretical Applied Genetics, 2022, 135(8):2609-2625.

[47] VOCCIANTE M, GRIFONI M, FUSINI D, et al. The role of plant growth-promoting rhizobacteria (PGPR) in mitigating plant's environmental stresses [J]. Applied Sciences, 2022, 12(3):1231.

[48] ASGHARI B, KHADEMIAN R, SEDAGHATI B. Plant growth promoting rhizobacteria (PGPR) confer drought resistance and stimulate biosynthesis of secondary metabolites in pennyroyal (Mentha pulegium L.) under water shortage condition [J]. Scientia Horticulturae, 2020, 263:109132.

[49] SHAHZAD R, KHAN A L, BILAL S, et al. Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in Oryza sativa [J]. Environmental and Experimental Botany, 2017, 136:68-77.

[50] ZHANG Z J, ZHOU W J, LI H Z. The role of GA, IAA and BAP in the regulation of in vitro shoot growth and microtuberization in potato [J]. Acta Physiologiae Plantarum, 2005, 27(3):363-369.

[51] ZWACK P J, RASHOTTE A M. Interactions between cytokinin signalling and abiotic stress responses [J]. Journal of Experimental Botany, 2015, 66(16):4863-4871.

[52] GOLAN Y, SHIRRON N, AVNI A, et al. Cytokinins induce transcriptional reprograming and improve Arabidopsis plant performance under drought and salt stress conditions [J]. Frontiers in Environmental Science, 2016, 4:63.

[53] KANG S-M, RADHAKRISHNAN R, KHAN A L, et al. Gibberellin secreting rhizobacterium, Pseudomonas putida H-2-3 modulates the hormonal and stress physiology of soybean to improve the plant growth under saline and drought conditions [J]. Plant Physiology and Biochemistry, 2014, 84: 115-124.

[54] SHAH S H, ISLAM S, MOHAMMAD F, et al. Gibberellic acid: A versatile regulator of plant growth, development and stress responses [J]. Journal of Plant Growth Regulation, 2023, 42(12):7352-7373.

[55] WANI A, CHADAR H, SINGH S, et al. Salicylic acid to decrease plant stress [J]. Environmental Chemistry Letters, 2017, 15(1):101-123.

[56] NADARAJAH K, ABDUL HAMID N W, ABDUL RAHMAN N S N. SA-mediated regulation and control of abiotic stress tolerance in rice [J]. International Journal of Molecular Science, 2021, 22(11):5591.

[57] YANG J, DUAN G H, LI C Q, et al. The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses [J]. Frontiers in Plant Science, 2019, 10:1349.

[58] PARK Y G, MUN B G, KANG S M, et al. Bacillus aryabhattai SRB02 tolerates oxidative and nitrosative stress and promotes the growth of soybean by modulating the production of phytohormones [J]. PLoS One, 2017, 12(3):e0173203.

[59] RAZA A, CHARAGH S, ZAHID Z, et al. Jasmonic acid: a key frontier in conferring abiotic stress tolerance in plants [J]. Plant Cell Reports, 2021, 40(8):1513-1541.

[60] BHARADWAJ P S, SANCHEZ L, LI D, et al. The plant hormone ethylene promotes abiotic stress tolerance in the liverwort Marchantia polymorpha [J]. Frontiers in Plant Science, 2022, 13:998267.

[61] QIN H, XIAO M G, LI Y X, et al. Ethylene Modulates Rice Root Plasticity under Abiotic Stresses [J]. Plants, 2024, 13(3):432.

[62] SZABADOS L, SAVOURÉ A. Proline: a multifunctional amino acid [J]. Trends in Plant Science, 2010, 15(2):89-97.

[63] GROPPA M D, BENAVIDES M P. Polyamines and abiotic stress: recent advances [J]. Amino Acids, 2008, 34(1): 35-45.

[64] FARRIOL M, SEGOVIA T, VENEREO Y, et al. Importance of the polyamines: review of the literature [J]. Nutricion Hospitalaria, 1999, 14(3):101-113.

[65] GILL S S, TUTEJA N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants [J]. Plant Physiology and Biochemistry, 2010, 48(12): 909-930.

[66] YU J J, LI R, FAN N L, et al. Metabolic pathways involved in carbon dioxide enhanced heat tolerance in Bermudagrass [J]. Frontiers in Plant Science, 2017, 8:1506.

[67] SICHER R C, TIMLIN D, BAILEY B. Responses of growth and primary metabolism of water-stressed barley roots to rehydration [J]. Journal of Plant Physiology, 2012, 169(7): 686-695.

[68] IORDACHESCU M, IMAI R. Trehalose biosynthesis in response to abiotic stresses [J]. Journal of Integrative Plant Biology, 2008, 50(10):1223-1229.

[69] MOLINARI H B C, MARUR C J, FILHO J C B, et al. Osmotic adjustment in transgenic citrus rootstock Carrizo citrange (Citrus sinensis Osb. x Poncirus trifoliata L. Raf.) overproducing proline [J]. Plant Science, 2004, 167(6): 1375-1381.

[70] GARG A K, KIM J-K, OWENS T G, et al. Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses [J]. Proceedings of the National Academy of Sciences of the United States of America, 2002, 99(25):15898-15903.

[71] KUMARI S, NAZIR F, MAHESHWARI C, et al. Plant hormones and secondary metabolites under environmental stresses: Enlightening defense molecules [J]. Plant Physiology and Biochemistry, 2024, 206:108238.

[72] KURUTAS E B. The importance of antioxidants which play the role in cellular response against oxidative/nitrosative stress: current state [J]. Nutrition Journal, 2015, 15(1):71.

[73] SOMSSICH M, KHAN G A, PERSSON S. Cell wall heterogeneity in root development of Arabidopsis [J]. Frontiers in Plant Science, 2016, 7:1242.

[74] GONZÁLEZ DE LEÓN S, BRIONES O, AGUIRRE A, et al. Germination of an invasive fern responds better than native ferns to water and light stress in a Mexican cloud forest [J]. Biological Invasions, 2021, 23(10):3187-3199.

[75] MONTESINOS D, GRAEBNER R C, CALLAWAY R M. Evidence for evolution of increased competitive ability for invasive Centaurea solstitialis, but not for naturalized C. calcitrapa [J]. Biological Invasions, 2019, 21(1):99-110.

[76] POLI A, FINORE I, ROMANO I, et al. Microbial diversity in extreme marine habitats and their biomolecules [J]. Microorganisms, 2017, 5(2):25.

[77] GUAN N Z, LI J H, SHIN H D, et al. Microbial response to environmental stresses: from fundamental mechanisms to practical applications [J]. Applied Microbiology and Biotechnology, 2017, 101(10):3991-4008.

[78] BLEOANCA I, BAHRIM G. Overview on brewing yeast stress factors [J]. Romanian Biotechnological Letters, 2013, 18(5): 8559-8572.

[79] LIANG G B, LIAO X Y, DU G C, et al. A new strategy to enhance glutathione production by multiple H_2O_2-induced oxidative stresses in Candida utilis [J]. Bioresource Technology, 2009, 100(1):350-355.

[80] ESMANN M, FEDOSOVA N U, MARSH D. Osmotic stress and viscous retardation of the Na, K-ATPase ion pump [J]. Biophysical Journal, 2008, 94(7):2767-2776.

[81] KIMURA Y, KAWASAKI S, YOSHIMOTO H, et al. Glycine betaine biosynthesized from glycine provides an osmolyte for cell growth and spore germination during osmotic stress in Myxococcus xanthus [J]. Journal of Bacteriology, 2010, 192(5):1467-1470.

[82] HELD C, SADOWSKI G. Compatible solutes: Thermodynamic properties relevant for effective protection against osmotic stress [J]. Fluid Phase Equilibria, 2016, 407:224-235.

[83] ANANTHAN J, GOLDBERG A L, VOELLMY R. Abnormal proteins serve as eukaryotic stress signals and trigger the activation of heat shock genes [J]. Science, 1986, 232(4749):522-524.

[84] CASPETA L, CHEN Y, GHIACI P, et al. Altered sterol composition renders yeast thermotolerant [J]. Science, 2014, 346(6205):75-78.

[85] CHEN Y Y, GÄNZLE M G. Influence of cyclopropane fatty acids on heat, high pressure, acid and oxidative resistance in

Escherichia coli [J]. International Journal of Food Microbiology, 2016, 222:16-22.
[86] DUFOURC E J. Sterols and membrane dynamics [J]. Journal of Chemical Biology, 2008, 1(1):63-77.
[87] MACALADY J, BANFIELD J F. Molecular geomicrobiology: genes and geochemical cycling [J]. Earth and Planetary Science Letters, 2003, 209(1-2):1-17.
[88] GUAN N Z, LIU L, SHIN H D, et al. Systems-level understanding of how Propionibacterium acidipropionici respond to propionic acid stress at the microenvironment levels: mechanism and application [J]. Journal of Biotechnology, 2013, 167(1):56-63.
[89] XIONG L F, TENG J L L, WATT R M, et al. Arginine deiminase pathway is far more important than urease for acid resistance and intracellular survival in Laribacter hongkongensis: a possible result of arc gene cassette duplication [J]. BMC Microbiology, 2014, 14(1):42.
[90] COX M M. The RecA protein as a recombinational repair system [J]. Mol Microbiol, 1991, 5(6):1295-1299.
[91] VEINGER L, DIAMANT S, BUCHNER J, et al. The small heat-shock protein IbpB from Escherichia coli stabilizes stress-denatured proteins for subsequent refolding by a multichaperone network [J]. Journal of Biological Chemistry, 1998, 273(18):11032-11037.
[92] LIU Q, WANG F C, LIU R, et al. Aboveground litter input alters the effects of understory vegetation removal on soil microbial communities and enzyme activities along a 60-cm profile in a subtropical plantation forest [J]. Applied Soil Ecology, 2022, 176:104489.
[93] XU Y B, HOU M Y, RUAN J J, et al. Effect of magnetic field on surface properties of Bacillus cereus CrA and its extracellular polymeric substances (EPS) [J]. Journal of Adhesion Science and Technology, 2014, 28(21):2196-2208.
[94] ZAIDI N S, SOHAILI J, MUDA K, et al. Magnetic field application and its potential in water and wastewater treatment systems [J]. Separation & Purification Reviews, 2014, 43(3): 206-240.
[95] MOUHOUB R B, EL MAY A, CHERAIEF I, et al. Influence of static magnetic field exposure on fatty acid composition in Salmonella Hadar [J]. Microbial Pathogenesis, 2017, 108: 13-20.
[96] MIHOUB M, EL MAY A, ALOUI A, et al. Effects of static magnetic fields on growth and membrane lipid composition of Salmonella typhimurium wild-type and dam mutant strains [J]. International Journal of Food Microbiology, 2012, 157(2): 259-266.
[97] CHEN S R, JIN Y M, YANG N, et al. Improving microbial production of value-added products through the intervention of magnetic fields [J]. Bioresource Technology, 2023, 393: 130087.
[98] ŁEBKOWSKA M, RUTKOWSKA-NAROŻNIAK A, PAJOR E, et al. Impact of a static magnetic field on biodegradation of wastewater compounds and bacteria recombination [J]. Environmental Science and Pollution Research International, 2018, 25(23):22571-22583.
[99] SINGH V, RAKSHIT K, RATHEE S, et al. Metallic/bimetallic magnetic nanoparticle functionalization for immobilization of α-amylase for enhanced reusability in bio-catalytic processes [J]. Bioresource Technology, 2016, 214: 528-533.
[100] NIU C, LIANG W H, REN H Q, et al. Enhancement of activated sludge activity by 10-50 mT static magnetic field intensity at low temperature [J]. Bioresource Technology, 2014, 159:48-54.
[101] LI M Q, ZHANG J, LIANG S, et al. Novel magnetic coupling constructed wetland for nitrogen removal: Enhancing performance and responses of plants and microbial communities [J]. The Science of the Total Environment, 2022, 819:152040.
[102] DEAMICI K M, CARDIAS B B, COSTA J A V, et al. Static magnetic fields in culture of Chlorella fusca: Bioeffects on growth and biomass composition [J]. Process Biochemistry, 2016, 51(7):912-916.
[103] BAUER L M, COSTA J A V, DA ROSA A P C, et al. Growth stimulation and synthesis of lipids, pigments and antioxidants with magnetic fields in Chlorella kessleri cultivations [J]. Bioresource Technology, 2017, 244: 1425-1432.
[104] AN T Y, CHANG Y F, XIE J X, et al. Deciphering physicochemical properties and enhanced microbial electron transfer capacity by magnetic biochar [J]. Bioresource Technology, 2022, 363:127894.
[105] YAN H J, CUI Y W, HAN S C. Promoting enrichment of sulfur-oxidizing autotrophic denitrifiers via static magnetic fields: Performance and mechanism of magnetic biological effects [J]. Bioresource Technology, 2022, 347:126388.
[106] FRANKL A L, MAXBAUER D P, SAVINA M E. Linkages between soil organic matter and magnetic mineral formation in agricultural fields in southeastern Minnesota, USA [J]. Geoderma, 2022, 406:115466.
[107] LI W, MA H L, HE R H, et al. Prospects and application of ultrasound and magnetic fields in the fermentation of rare edible fungi [J]. Ultrasonics Sonochemistry, 2021, 76: 105613.
[108] REINA F G, PASCUAL L A. Influence of a stationary magnetic field on water relations in lettuce seeds. Part I: Theoretical considerations [J]. Bioelectromagnetics, 2002, 22 (8):596-602.
[109] RADHAKRISHNAN R. Magnetic field regulates plant functions, growth and enhances tolerance against environmental stresses [J]. Physiology and Molecular Biology of Plants, 2019, 25(5):1107-1119.
[110] JAVED N, ASHRAF M, AKRAM N A, et al. Alleviation of adverse effects of drought stress on growth and some potential physiological attributes in maize (Zea mays L.) by seed electromagnetic treatment [J]. Photochemistry and Photobiology, 2011, 87(6):1354-1362.
[111] BAGHERI A E. Low frequency electromagnetic field induced oxidative stress in Lepidium sativum L [J]. Iranian Journal of Science and Technology, Transactions A: Science, 2018, 42

(3):1419-1426.

[112] CAKMAK T, DUMLUPINAR R, ERDAL S. Acceleration of germination and early growth of wheat and bean seedlings grown under various magnetic field and osmotic conditions [J]. Bioelectromagnetics, 2010, 31(2):120-129.

[113] RADHAKRISHNAN R, LEE I J. Regulation of salicylic acid, jasmonic acid and fatty acids in cucumber (Cucumis sativus L.) by spermidine promotes plant growth against salt stress [J]. Acta Physiologiae Plantarum, 2013, 35(12): 3315-3322.

[114] KARIMI S, ESHGHI S, KARIMI S, et al. Inducing salt tolerance in sweet corn by magnetic priming [J]. Acta Agriculturae Slovenica, 2017, 109(1):89-102.

[115] BAGHEL L, KATARIA S, GURUPRASAD K N. Static magnetic field treatment of seeds improves carbon and nitrogen metabolism under salinity stress in soybean [J]. Bioelectromagnetics, 2016, 37(7):455-470.

[116] RATHOD G R, ANAND A. Effect of seed magneto-priming on growth, yield and Na/K ratio in wheat (Triticum aestivum L.) under salt stress [J]. Indian Journal of Plant Physiology, 2016, 21(1):15-22.

[117] RADHAKRISHNAN R, KUMARI B D R. Pulsed magnetic field:A contemporary approach offers to enhance plant growth and yield of soybean [J]. Plant Physiology and Biochemistry, 2012, 51:139-144.

[118] CHEN Y P, LI R, HE J M. Magnetic field can alleviate toxicological effect induced by cadmium in mungbean seedlings [J]. Ecotoxicology, 2011, 20(4):760-769.

[119] GALLAND P, PAZUR A. Magnetoreception in plants [J]. Journal of Plant Research, 2005, 118(6):371-389.

[120] FLORES-TAVIZóN E, MOKGALAKA-MATLALA N S, ELIZALDE GALINDO J T, et al. Magnetic field effect on growth, arsenic uptake, and total amylolytic activity on mesquite (Prosopis juliflora x P. velutina) seeds [J]. Journal of Appllied Physics, 2012, 111:07B321(1-3).

[121] RUŽIČ R, JERMAN I. Weak magnetic field decreases heat stress in cress seedlings [J]. Electromagnetic Biology and Medicine, 2002, 21(1):69-80.

[122] AFZAL I, NOOR M, BAKHTAVAR M, et al. Improvement of spring maize performance through physical and physiological seed enhancements [J]. Seed Science and Technology, 2015, 43(2):238-249.

[123] 朱建楚,刘思春,陈建文,等. 磁环境条件下番茄抗逆性的初探[J]. 干旱地区农业研究, 2001,19(4):58-64.
ZHU J C, LIU S C, CHEN J W, et al. The effects of magnetic environment on tomato under drought and disease dress[J]. Agricultural Research in the Arid Areas, 2001, 19(4):58-64.

[124] MSHENSKAYA N, GRINBERG M, KALYASOVA E, et al. The effect of an extremely low-frequency electromagnetic field on the drought sensitivity of wheat plants [J]. Plants, 2023, 12(4):826.

[125] ANAND A, NAGARAJAN S, VERMA A, et al. Pre-treatment of seeds with static magnetic field ameliorates soil water stress in seedlings of maize (Zea mays L.) [J]. Indian Journal of Biochemistry & Biophysics, 2012, 49(1): 63-70.

[126] XI G, FU Z D, LING J. Change of peroxidase activity in wheat seedlings induced by magnetic field and its response under dehydration condition [J]. Acta Botanica Sincia, 1994, 36:113-118.

[127] THOMAS S, ANAND A, CHINNUSAMY V, et al. Magnetopriming circumvents the effect of salinity stress on germination in chickpea seeds [J]. Acta Physiologiae Plantarum, 2013, 35:3401-3411.

[128] KATARIA S, BAGHEL L, GURUPRASAD K. Pre-treatment of seeds with static magnetic field improves germination and early growth characteristics under salt stress in maize and soybean [J]. Biocatalysis and Agricultural Biotechnology, 2017, 10:83-90.

[129] D E SOUZA T A, PORRAS L E, CASATE F R. Effect of magnetic treatment of tomato (Lycopersicon esculentum Mill) seeds on germination and seedling growth [J]. Investigation Agraria Production y Proteccion Vegetables, 1999, 14(3): 437-444.

[130] EŞITKEN A, TURAN M. Alternating magnetic field effects on yield and plant nutrient element composition of strawberry (Fragaria x ananassa cv. Camarosa) [J]. Acta Agriculturae Scandinavica, Section B:Soil & Plant Science, 2004, 54(3): 135-139.

[131] MARTINEZ E, CARBONELL M V, AMAYA J M. A static magnetic field of 125 mT stimulates the initial growth stages of barley (Hordeum vulgare L.) [J]. Electro-and Magnetobiology, 2000, 19(3):271-277.

[132] EŞİTKEN A. Effects of magnetic fields on yield and growth in strawberry 'Camarosa' [J]. The Journal of Horticultural Science and Biotechnology, 2003, 78(2):145-147.

[133] PIACENTINI M P, FRATERNALE D, PIATTI E, et al. Senescence delay and change of antioxidant enzyme levels in Cucumis sativus L. etiolated seedlings by ELF magnetic fields [J]. Plant Science, 2001, 161(1):45-53.

[134] 刘新成, 李秋祯. 磁场和Cu^{2+}对蚕豆幼根生长、细胞分裂和过氧化物酶同工酶谱的影响 [J]. 天津师范大学学报(自然科学版), 2003, 23(3):27-29.
LIU X C, LI Q Z. Effects of magnetic field and Cu^{2+} on root growth, peroxidase isoenzyme and cell division of broad bean [J]. Journal of Tianjin Normal University (Natural Science Edition), 2003, 23(3):27-29.

[135] LI F M, GUO S H, WANG S, et al. Changes of microbial community and activity under different electric fields during electro-bioremediation of PAH-contaminated soil [J]. Chemosphere, 2020, 254:126880.

[136] HE M J, WU F H, QU G F, et al. Harmless and resourceful utilization of solid waste: Multi physical field regulation in the microbiological treatment process of solid waste treatment [J]. Environmental Research, 2023,238(P1):117149.

[137] DONG Z Y, HUANG W H, XING D F, et al. Remediation of soil co-contaminated with petroleum and heavy metals by

the integration of electrokinetics and biostimulation [J]. Journal of Hazardous Materials, 2013, 260:399-408.

[138] MA J, ZHANG Q, CHEN F, et al. Remediation of resins-contaminated soil by the combination of electrokinetic and bioremediation processes [J]. Environmental Pollution, 2020, 260:114047.

[139] FAN R J, MA W P, ZHANG H L. Microbial community responses to soil parameters and their effects on petroleum degradation during bio-electrokinetic remediation [J]. Science of the Total Environment, 2020, 748:142463.

[140] KUBAR A A, JIN N N, CUI Y, et al. Magnetic/electric field intervention on oil-rich filamentous algae production in the application of acrylonitrile butadiene styrene based wastewater treatment [J]. Bioresource Technology, 2022, 356:127272.

[141] VOLKOV A G, SHTESSEL Y B. Electrical signal propagation within and between tomato plants [J]. Bioelectrochemistry, 2018, 124:195-205.

[142] MELIKOV K C, FROLOV V A, SHCHERBAKOV A, et al. Voltage-induced nonconductive pre-pores and metastable single pores in unmodified planar lipid bilayer [J]. Biophysical Journal, 2001, 80(4):1829-1836.

[143] NEUMANN E, ROSENHECK K. Permeability changes induced by electric impulses in vesicular membranes [J]. The Journal of membrane biology, 1972, 10(1):279-290.

[144] VOLKOV A G. Plant electrophysiology [M]. Berlin: Springer, 2006.

[145] LEE S, OH M-M. Electric field: a new environmental factor for controlling plant growth and development in agriculture [J]. Horticulture, Environment, and Biotechnology, 2023, 64(6):955-961.

[146] AN J I, LEE S, OH M. Air Anions Promote the Growth and Mineral Accumulation of Spinach (Spinacia oleracea) Cultivated in Greenhouses [J]. Horticultural Science & Technology, 2021,39(3):332-342.

[147] SONG M J, KANG T H, HAN C S, et al. Air anions enhance lettuce growth in plant factories [J]. Horticulture, Environment, and Biotechnology, 2014, 55(4):293-298.

[148] LEE S, OH M M. Electric stimulation promotes growth, mineral uptake, and antioxidant accumulation in kale (Brassica oleracea var. acephala) [J]. Bioelectrochemistry, 2021, 138:107727.

[149] OZUNA C, CERON-GARCIA A, ELENA SOSA-MORALES M, et al. Electrically induced changes in amaranth seed enzymatic activity and their effect on bioactive compounds content after germination [J]. Journal of Food Science and Technology, 2018, 55(2):648-657.

[150] LEONG S Y, BURRITT D J, OEY I. Electropriming of wheatgrass seeds using pulsed electric fields enhances antioxidant metabolism and the bioprotective capacity of wheatgrass shoots [J]. Scientific Reports, 2016, 6(1):25306.

[151] VALLVERDU-QUERALT A, OMS-OLIU G, ODRIOZOLA-SERRANO I, et al. Effects of Pulsed Electric Fields on the Bioactive Compound Content and Antioxidant Capacity of Tomato Fruit [J]. Journal of Agricultural and Food Chemistry, 2012, 60(12):3126-3134.

[152] HE R R, XI G, LIU K. Alleviating effect of extremely low frequency pulsed electric field on drought damage of maize seedling roots [J]. Journal of Luminescence, 2017, 188: 441-447.

[153] AL-KHAFAJI A H, KWAO S, GOMEZ GALINDO F, et al. Germination and stress tolerance of oats treated with pulsed electric field at different phases of seedling growth [J]. Bioelectrochemistry, 2024, 158:108692.

[154] HOU J, YANG L, YANG T, et al. Effect of electric field treatment of sunflower seeds on the drought resistance in the germination stage [J]. Acta Biophysica Sinica, 2003, 19(2): 193-197.

[155] CRAMARIUC R, DONESCU V, POPA M, et al. The biological effect of the electrical field treatment on the potato seed: agronomic evaluation [J]. Journal of Electrostatics, 2005, 63(6-10):837-846.

[156] CAKMAK T, DUMLUPINAR R, ERDAL S. Chilling Resistance of Phaseolus vulgaris and Brassica oleracea under a High-Intensity Electric Field [J]. Zeitschrift für Naturforschung, 2010, 65(5-6):380-386.

[157] ZHAO L F, LIU W T, LIAN J P, et al. Effects of electric fields on Cd accumulation and photosynthesis in Zea mays seedlings [J]. Journal of Environmental Management, 2020, 276:111328.

[158] VALBERG P A, RAFFERTY R K N. Can Low-Level 50/60 Hz Electric and Magnetic Fields Cause Biological Effects? [J]. Radiattion Research, 1997, 148(1):2-21.

[159] CARSTENSEN E L. Biological effects of power frequency electric fields [J]. Journal of Electrostatics, 1997, 39(3): 157-174.

[160] 王君武，张茂林，侯克锁，等. 高寒高海拔地区路域生态修复技术体系研究 [J]. 交通节能与环保，2018，14(1):34-36.
WANG J W, ZHANG M L, HOU K S, et al. Study on Ecological Restoration Technology System for Road Areas in Alpine Area at High-Altitude [J]. Energy Conservation & Environmental Protection in transportion, 2018, 14(1): 34-36.