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PGPR调控植物响应逆境胁迫的作用机制

伍国强*，于祖隆，魏明
（兰州理工大学生命科学与工程学院，甘肃 兰州 730050）

摘要：盐碱、干旱等非生物胁迫是限制植物生长和产量的重要环境因子。植物根际促生菌（PGPR）是一类定殖于植物根系的有益微生物，利用其生物学功能制成的生物菌剂具有低成本、高效和环保等优点，不仅可促进植物生长与作物产量，还能提高植物对非生物胁迫的耐受性。本研究对PGPR定义和种类、生物学功能及其在植物响应盐碱、干旱、高低温及重金属等非生物胁迫中的作用加以综述，并对其未来研究方向进行展望，以期为今后PGPR介导植物抗逆性的研究与生物菌剂的开发和应用提供理论支撑。

关键词：植物根际促生菌；固氮菌；溶磷菌；植物激素；非生物胁迫；抗逆性

The mechanism of PGPR regulating plant response to abiotic stress

WU Guo-qiang*，YU Zu-long，WEI Ming
School of Life Science and Engineering，*Lanzhou University of Technology*，*Lanzhou* 730050，*China*

Abstract：Salt alkali，drought and other abiotic stresses are important environmental factors that limit plant growth and yield. Plant growth promoting rhizobacteria（PGPR），as beneficial microorganisms colonizing plant roots，have been shown to have a capacity for use as biological agents，thereby harnessing their functions for human benefit. This methodology has advantages compared to traditional agricultural chemicals，including low cost，high efficiency，and environmental protection. PGPR have been documented to not only promote plant growth and crop yield，but also to significantly improve the tolerance of plants to abiotic stress. In this study，the definition and types of PGPR，their biological functions and their role in plant response to abiotic stress such as salinity，drought，high and low temperature，and heavy metals were reviewed，and future research directions were also explored. The results from this study provide a foundation for further research on PGPR mediated plant stress resistance and the development and application of these biological agents.

Key words：plant growth promoting rhizobacteria；nitrogen-fixing bacteria；phosphate-solubilizing bacteria；phytohormone；abiotic stress；stress resistance

盐碱、干旱、极端温度和重金属等非生物胁迫是影响植物生长和作物产量的主要环境因素[1]。这些非生物胁迫限制了全球对耕地的利用，并对作物的生产产生了负面影响。气候变化模型预测这些非生物胁迫的发生率将持续增加，导致水稻（*Oryza sativa*）、小麦（*Triticum aestivum*）和玉米（*Zea mays*）等主要作物的产量下降，从而危及人类的粮食安全[2]。随着全球气候变暖、温室气体排放增加以及人类活动增强，全球盐碱和干旱区域的面积在

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作者简介：伍国强(1976－)，男，甘肃通渭人，教授，博士。E-mail：gqwu@lut. edu. cn
*通信作者 Corresponding author. E-mail：gqwu@lut. edu. cn

不断增加。在过去10年中,全球因干旱造成的农作物减产约300亿美元,预计到2050年,农业用水需求可能翻一番,而由于气候变化,淡水的可用性预计将下降50%[3]。我国是水资源匮乏的国家之一,并且农业耗水约占全国总耗水量的70%,由于不同生态种植区的降水量分布以及水资源丰缺不一导致季节性干旱频发,导致作物产量严重下降,持续性严重干旱还会导致作物的大面积死亡。土壤盐碱化同样严重制约植物的生长,全球盐碱地面积超过10亿 hm^2,而我国是世界上盐渍化最为严重的国家之一,受影响土地近1亿 hm^2,约占全国可耕地面积的25%,并且由于不合理的灌溉,农业区的次生盐渍化问题日益严峻,严重威胁粮食生产的可持续发展[4]。土壤高浓度盐分对植物造成渗透胁迫、离子毒害和氧化损伤,致使作物减产,甚至导致死亡[5]。为应对盐碱、干旱等各种环境胁迫,植物本身进化出诸如离子平衡、渗透调节、抗氧化系统、抗逆基因表达和各种激素信号途径等抗逆机制[6]。我国作为农业大国,农业的发展对国民经济的影响举足轻重,虽然化肥和农药的大规模使用在一定程度上提高了作物的产量,但长期施用对土壤健康和环境也会造成多种伤害,难以维持农业实践的可持续进行,为不断增长的世界人口提供粮食安全仍然是一项挑战[7]。因此,亟须制定具有低成本、高效益和环境友好的策略来解决这些农业问题。一些土壤微生物可在改良土壤环境、促进植物生长与发育和增强植物抗逆性方面发挥重要作用[8]。植物根际土壤中蕴藏着大量微生物菌群,且多数有益微生物能定殖于植物根系后与其形成共生体,进而通过多种作用机制对土壤结构与理化性质、植物生长和非生物胁迫响应等产生有益作用[9]。

Lorenz Hiltner在描述豆科植物根系与细菌相互关系时首次提出了"根际(rhizosphere)"一词,即根部附近理化和生物学性质与土壤存在微小差异的地域,并发现根际有益微生物对植物的生长具有促进作用[10]。植物根际存在细菌、真菌、放线菌、古生菌及病毒等各种微生物,其中细菌是土壤生态系统中最为丰富的一类微生物菌群[11]。研究表明,对植物生长或逆境适应等有直接或间接促进作用的有益细菌占根际微生物菌群的比例为2%~5%[12]。此类对植物有显著促生作用且能对植物响应非生物胁迫有直接和间接的积极作用的一类有益细菌被称为植物根际促生菌(plant growth promoting rhizobacteria, PGPR)[13]。当PGPR定殖于植物根际时,会供给植物所需的矿质元素与营养物质,并分泌植物激素和次生代谢物以促进植物生长和响应逆境胁迫[14]。如沙雷氏菌(*Serratia*)CDP-13具有固氮、溶解磷酸盐、产生铁载体和吲哚乙酸并能提高1-氨基环丙烷-1-羧酸(1-aminocyclopropane-1-carboxylicacid, ACC)脱氨酶活性的能力,在盐胁迫下起渗透保护剂的作用从而有效促进小麦的生长[15]。微生物肥料是将环境中发现的一种或多种有益微生物通过人工培养与量化生产后制成的一种高效、低成本和绿色无污染的新型生物肥料[16]。PGPR被认为是高效且环保的微生物肥料来源,可以减少化学农药和化肥的使用[17]。Wang等[18]研究发现,枯草芽孢杆菌(*Bacillus subtilis*)具有调节土壤酸碱平衡、提高土壤可溶性物质含量及改善土壤有益微生物菌群活性的作用,施加该菌肥能有效促进油菜(*Brassica chinensis*)的生长和生物量。由此表明,微生物菌肥在减少化肥使用、保护生态环境和促进农业可持续发展方面具有巨大潜力。本研究系统分析了PGPR种类、生物学功能及其在植物响应逆境胁迫中的作用,对该领域存在问题及其未来研究前景进行展望,以期为生物菌剂的制备和农业可持续发展提供新的视角。

1 PGPR的种类

PGPR在促进植物生长作用中的优势及其作为微生物肥料的潜力,已日益成为国际研究热点。目前发现的PGPR有20多种,最常见的主要包括芽孢杆菌属(*Bacillus*)、假单胞菌属(*Pseudomonas*)、肠杆菌属(*Enterobacter*)、克雷伯菌属(*Klebsiella*)、伯克霍尔德氏菌属(*Burkhoolderia*)和沙雷氏菌属(*Serratia*)等(表1)。

其中,芽孢杆菌属是最主要的植物生长促进细菌,它们能在不同的生物和非生物环境胁迫下通过改变胁迫响应基因、蛋白质、植物激素和相关代谢产物来刺激植物抵抗胁迫[36]。

2 PGPR的生物学功能

PGPR通过直接或间接的作用改良土壤环境、促进植物生长以及介导植物抗逆[14](图1)。直接作用是某些PGPR合成或调控植物激素,或经生物固氮、溶磷和解钾等方式增加土壤矿质营养的利用率,可直接对植物产生促生和减轻植物胁迫等有益作用[37]。间接作用是指某些PGPR能够诱导宿主体内的系统性抗性或产生一些化学物质(如铁载体)及一些其他的作用机制间接地促进植物生长和抗逆[38]。

表 1 PGPR 种类及其功能

Table 1 Types and functions of PGPR

属 Genus	种 Species	功能 Function	参考文献 References
芽孢杆菌属 *Bacillus*	枯草芽孢杆菌 *B. subtilis*	诱导植物抗性,调节植物激素。Induce plant resistance, and regulate plant hormone.	[19]
假单胞菌属 *Pseudomonas*	固氮假单胞菌 *Pseudomonas azotoformans*	产胞外多糖、吲哚乙酸和可溶性磷酸三钙。Production of extracellular polysaccharides, indoleacetic acid and soluble tricalcium phosphate.	[20]
固氮螺旋菌属 *Azospirillum*	巴西固氮螺菌 *Azospirillum brasilense*	固氮,产铁载体、胞外多糖、ACC 脱氨酶、吲哚乙酸和水解酶。Nitrogen fixation, production of iron carrier, extracellular polysaccharide, ACC deaminase, indoleacetic acid and hydrolase.	[21]
固氮菌属 *Azotobacter*	贝氏固氮菌 *Azotobacter beijerinckii*	固氮,改良土壤,产生长素。Nitrogen fixation, soil improvement, and production of auxin.	[22]
克雷伯菌属 *Klebsiella*	肺炎克雷伯菌 *Klebsiella pneumoniae*	固氮,产氨、铁载体和吲哚乙酸。Nitrogen fixation, production of ammonia, iron carrier and indole acetic acid.	[23]
肠杆菌属 *Enterobacter*	气肠杆菌 *Enterobacter aerogenes*	固氮、溶磷,产生长素、ACC 脱氨酶和铁载体。Nitrogen fixation, phosphorus dissolution, production of auxin, ACC deaminase, and iron carrier.	[24]
节杆菌属 *Arthrobacter*	滋养节杆菌 *Arthrobacter pascens*	合成吲哚乙酸。Synthesis of indole acetic acid.	[25]
伯克霍尔德氏菌属 *Burkhoolderia*	越南伯克霍尔德菌 *Burkholderia vietnamiensis*	固氮。Nitrogen fixation.	[26]
类芽孢杆菌属 *Paenibacillus*	胶质类芽孢杆菌 *Paenibacillus mucilaginosus*	形成生物膜、溶磷和产生长素。Forming biofilm, phosphorus dissolution and production of auxin.	[27]
沙雷氏菌属 *Serratia*	格氏沙雷氏菌 *Serratia grimesii*	固氮、溶磷、产铁载体和生长素。Nitrogen fixation, phosphorus dissolution, production of iron carrier and auxin.	[17]
无色杆菌属 *Achromobacter*	木糖无色杆菌 *Achromobacter xylosoxidans*	产 ACC 脱氨酶。Production of ACC deaminase.	[28]
根瘤菌属 *Rhizobia*	阿拉米根瘤菌 *Rhizobium alamii*	产胞外多糖。Production of extracellular polysaccharide.	[29]
不动杆菌属 *Acinetobacter*	约氏不动杆菌 *Acinetobacter johnsonii*	调节土壤酶活性,改善土壤。Regulating soil enzyme activity and improving soil quality.	[30]
产碱杆菌属 *Alcaligenes*	粪产碱杆菌 *Alcaligenes faecalis*	产生长素,溶磷,改善营养吸收。Production of auxin, phosphorus dissolution, and improve nutrient absorption.	[31]
链霉菌属 *Streptomyces*	微黄链霉菌 *Streptomyces microflavus*	提高养分吸收。Improve nutrient absorption.	[32]
气单胞菌属 *Aeromonas*	豚鼠气单胞菌 *Aeromonas caviae*	改良土壤,促进营养吸收。Improve soil and promote nutrient absorption.	[33]
泛菌属 *Pantoea*	成团泛菌 *Pantoea agglomerans*	固氮、溶磷、产生长素。Nitrogen fixation, phosphorus dissolution, and production of auxin.	[34]
微球菌属 *Micrococcus*	云南微球菌 *Micrococcus yunnanensis*	提高营养元素的吸收。Improve the absorption of nutrients.	[35]

2.1 PGPR 促进氮的转化

氮(nitrogen,N)是植物生长过程中最重要的必需营养元素,对植物生长发育、产量和品质等具有极为显著的影响[39]。土壤中的 N 含量一般不能够满足植物的需求,空气中 N 元素含量虽高,但均以氮气(N_2)分子形式存在,也不能被植物直接吸收利用[40]。植物所需氮源最重要的来源途径之一是生物固氮(biological nitrogen fixation,BNF),即将大气中的 N_2 转化为简单可溶的无毒形式(主要是 NH_4^+)的自然过程,并被植物细胞用于合成各种生物分子[41]。具有固氮且能对植物起促生作用的根际微生物主要有固氮菌属(*Azotobacter*)、布克氏菌属(*Burkholderia*)、固氮螺旋菌属(*Azospirillum*)和根瘤菌属(*Rhizobia*)等,其中根瘤菌的固氮过程与其他固氮菌不同,其通过海藻糖-6-磷酸合酶(trehalose-6-phosphate synthase)基因 *otsA*、热休克蛋白(heat shock protein)基因 *groEL*、伴侣蛋白(chaperone)基因 *clpB* 及转录调节因子(transcriptional regulator)基因 *rpoH* 等应激反应基因在固

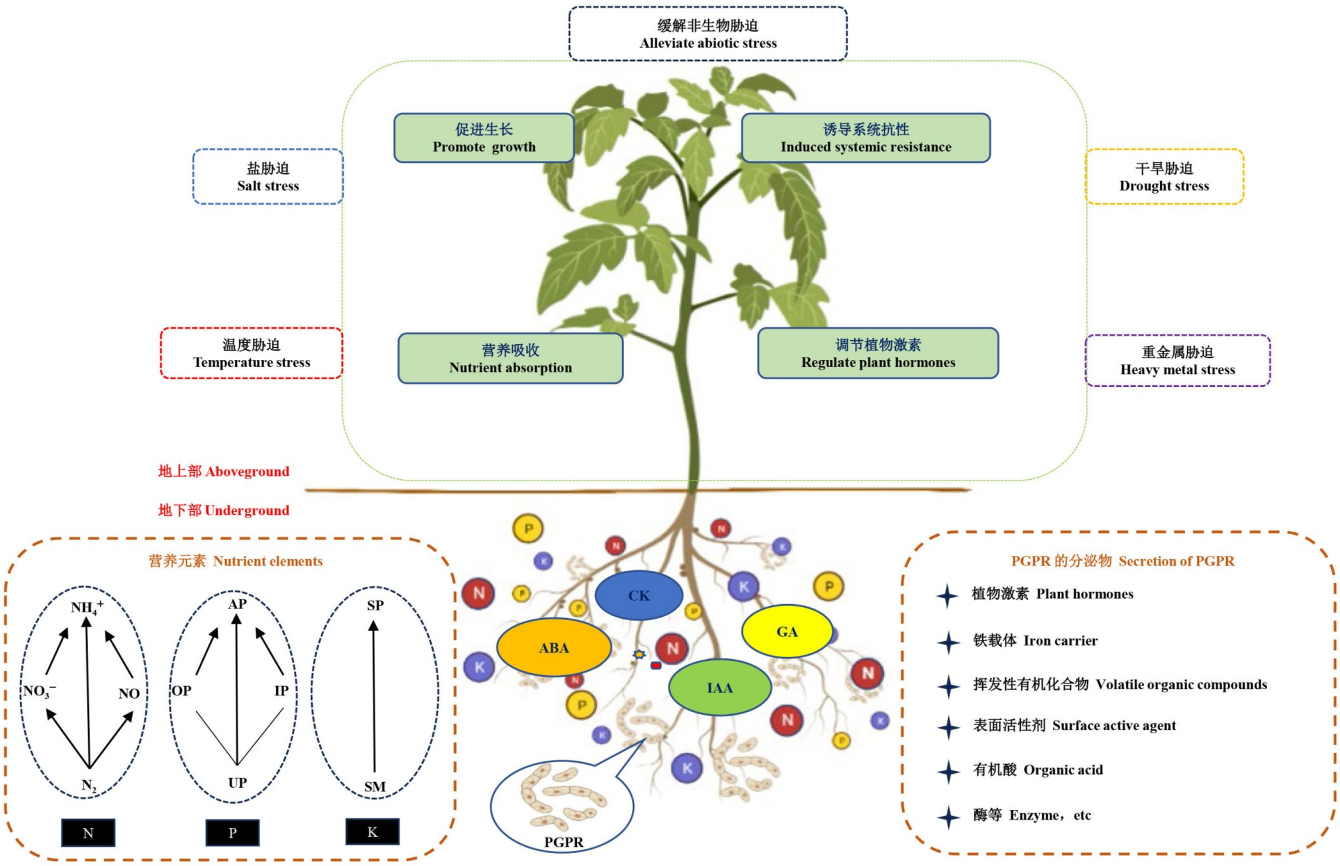

图1　PGPR生物学功能

Fig. 1　PGPR biological functions

UP:无效磷 Ineffective phosphorus; OP:有机磷 Organic phosphorus; IP:无机磷 Inorganic phosphorus; AP:有效磷 Available phosphorus; SM:土壤矿物质 Soil minerals; SP:可溶性钾 Soluble potassium; NO:有机氮氧化物 Organic nitrogen oxides; IAA:生长素 Indole-3-acetic acid; CK:细胞分裂素 Cytokinin; GA:赤霉素 Gibberellin; ABA:脱落酸 Abscisic acid.

氮过程中发挥作用[42]。Mahmud等[43]发现PGPR与植物根系形成共生的根瘤后其固氮基因(*BNFnif*)通过酶促反应将较高价态的N_2还原为低价态氨(NH_3),从而使空气中的N_2为植物所利用。研究表明,在甘蔗(*Saccharum officinarum*)中接种固氮菌RB867515和RB92579可增加土壤和BNF中氮的积累[44]。PGPR还可通过反硝化作用将NO_3^-作为电子受体,转化为NO_x,并最终被还原为NH_4^+[45]。此外,PGPR还能减少矿物氮的损失和提高氮的有效性来促进植物对N的获取,但这些影响取决于N的形态和水平[46]。这些结果表明,根际PGPR通过生物固氮、酶促和反硝化等作用在植物氮循环中发挥着重要作用。

2.2　PGPR提高磷的利用

磷(phosphorus, P)是植物生长和发育所必需的仅次于氮的第二大营养元素,在植物代谢中起重要作用[47]。土壤中P较为丰富,但是有效P含量仍然很低,因为P会从土壤—植物循环系统中流失[48]。土壤中存在能将无效态P转化成可供植物吸收利用的正磷酸盐形式的溶磷细菌(phospate-solubilizing bacteria, PSB),其从不溶性磷酸盐中释放可溶性磷离子,包括无机磷酸盐和不溶性有机磷酸盐,根据P底物的不同,PSB菌株分为矿物(无机)溶磷菌和有机溶磷菌[49]。对于矿物PSB,低分子有机酸分泌被认为是磷酸盐增溶的主要机制[50]。研究表明,耐酪氨酸冢村菌(*Tsukamurella tyrosinosolvens*)能通过分泌乳酸、马来酸、草酸等多种有机酸来溶磷,从而促进花生(*Arachis hypogaea*)的生长[51]。有机磷的矿化是通过合成多种不同的磷酸酶,催化磷酸酯的水解而发生的[52]。Benbrik等[53]研究表明,联合接种假单胞菌DN13-01、鞘氨醇杆菌(*Sphingobacterium suaedae*)T47、短小芽孢杆菌(*Bacillus purnilus*)X22和蜡样芽孢杆菌(*Bacillus cereus*)263AG5可以通过产生酸性和碱性磷酸酶改良土壤肥力,

提高植物对土壤速效磷的吸收，促进缺 P 土壤中植物的生长。此外，假单胞菌、分枝杆菌、芽孢杆菌和伯克氏菌等也能采用不同的策略将不可用磷转化为可用的无机磷，促进植物 P 吸收[8]。研究表明，从枫香（*Liquidambar formosana*）根际土壤中分离出的溶磷菌，可显著提升枫香的茎粗与株高并显著提高其幼苗植株内的金属（钙、镁、锌）含量，增加幼苗的抗逆性，具有良好的促生效果[54]。

2.3　PGPR 增强钾的溶解

钾（potassium, K）是植物必需的大量元素，对植物的生长发育和应激反应相关生物过程至关重要[55]。土壤是植物获取 K 的主要来源，但是土壤中可被植物直接利用的 K 含量只有极少量，大部分的 K 被固定在长石、云母等矿质中而无法被植物吸收[56]。土壤中存在可将矿物 K 转化为可溶 K 的 PGPR，称为溶钾细菌（potassium-solubilizing bacteria，KSB），其能够将不溶形式的 K 转化为易溶形式供植物吸收利用的 K。KSB 的溶 K 机制是产生有机酸、降低土壤 pH 值、酸解、螯合、交换和络合反应[57−58]。Meena 等[59]对 K 溶解机制的研究表明，在废白云母和黑云母作为不溶钾矿物的唯一来源的培养期间，培养基 pH 值显著降低，K 释放增加。研究表明，在温室条件下接种 KSB 能改善番茄（*Solanum lycopersicu*）植株的生长参数，如株高、叶面积、总根长[60]。在缺钾区接种芽孢杆菌 MZ4、KM1 和短芽孢杆菌（*Brevibacilluse*）KM2 与不接种解钾菌相比，接种 MZ4、KM1 和 KM2 增加了拔节期、吐丝期玉米的株高、地上生物量、叶面积指数和叶绿素，接种 MZ4 和 KM2 可显著增加玉米产量[61]。

2.4　PGPR 调控激素稳态

植物激素（phytohormone）是影响植物生命几乎所有方面的主要信号成分，其构成了一个相互联系的沟通网络，以适应不断变化的环境，调节植物的生长和发育[62]。PGPR 可以通过直接分泌植物激素或者调节植物自身的激素合成，影响植物的生长[63]。植物激素主要有生长素（indole-3-acetic acid, IAA）、细胞分裂素（cytokinin, CTK）、赤霉素（gibberellin, GA）和脱落酸（abscisic acid, ABA）等。

IAA 是最主要的植物生长素类激素，可以调节各种植物的生长过程[64]。大多数 PGPR 都能通过不同的途径分泌或合成 IAA 参与植物的生长发育过程[65−68]。将高产 IAA 的 PGPR 菌株接种于紫花苜蓿（*Medicago sativa*）后增加了植株总 N、碳（C）、氨基酸、可溶性糖和有机酸的含量，并且显著提高了生物量[69]。PGPR 分泌的 IAA 会影响到植物内源 IAA 的合成，PGPR 与植物通过 IAA 可表现为互惠的关系，IAA 在低浓度下会刺激植物初生根的伸长，在较高浓度下会促进侧根和不定根的形成，增强植物根系对矿物质的吸收[70]。研究表明，在拟南芥（*Arabidopsis thaliana*）中接种无色杆菌 5B1 影响了 IAA 信号传导和再分配，改变了根的生长和分支模式，从而促进根的发育[71]。PGPR 分泌的 IAA 还能减缓胁迫条件对植物生长造成的影响。如阿氏芽孢杆菌（*Bacillus aryabhattai*）T61 可以合成 IAA 来促进水稻根的生长，并降低茎和叶中的丙二醛（malondialdehyde, MDA）含量和抗氧化酶活性，使水稻籽粒镉（cadmium, Cd）含量有明显的下降，从而缓解水稻 Cd 胁迫[72]。

CTK 是一种诱导细胞质分裂的植物激素，由于其对植物的形态发生、叶绿体发育、种子休眠、叶片衰老等多种生理过程的影响，在农业上具有相当大的价值[73]。PGPR 能影响 CTK 信号传导参与植物复杂功能的调控，还能减少植物患病。如接种荧光假单胞菌（*Pseudomonas fluorescens*）G20-18 能通过影响 CTK 的信号感知从而降低拟南芥被丁香假单胞菌（*Pseudomonas syringae*）感染的可能[74]。部分 PGPR 还能合成 CTK 来介导植物响应非生物胁迫。在干旱胁迫下，接种产 CTK 的枯草芽孢杆菌可增加侧柏（*Platycladus orientalis*）根和茎的干重，有效促进植物生长[75]。Park 等[76]把产 CTK 的阿氏芽孢杆菌 SRB02 接种于大豆（*Glycine max*），使得其耐热性有了明显的提升。

GA 是促进生长的激素，在植物许多发育过程中有巨大的作用，包括器官生长和伸长[77]。至今已经发现 100 多种不同结构的 GA。有少数 PGPR 能产生 GA，对促进植物生长有一定的潜力[78]。Lee 等[79]发现，肠球菌（*Enterococcus faecium*）LKE12 可通过分泌多种结构的 GAs 来改善正常和矮生品种水稻芽的长度和生物量，还能改善甜瓜（*Cucumis melo*）的地上部和根长，同时增加鲜重和叶绿素含量。此外，PGPR 合成 GAs 也能缓解逆境对植物的影响。在高温胁迫下，特基拉芽孢杆菌（*Bacillus tequilensis*）SSB07 通过合成不同结构的 GAs 以促进白菜（*Brassica pekinensis*）幼苗生长[80]。

ABA是植物中最著名的胁迫信号分子，具有保护植物免受极端温度、干旱和盐胁迫影响，在植物生长发育过程保持正常生产力的作用[81]。PGPR通过合成调节植物中ABA的稳态，增强植物应对胁迫的能力，并促进植物生长。如解淀粉芽孢杆菌(*Bacillus amyloliquefaciens*)RWL-1通过合成ABA可显著提高水稻植株的生长属性，增强了水稻对盐胁迫的抗性[82]。PGPR产生ABA可介导植物气孔关闭和离子交换活性，减少水分散失，降低蒸腾速率。Cohen等[83]在拟南芥中接种产ABA的巴西固氮螺菌Sp245可改变根结构，增加拟南芥生物量，同时刺激光合和光保护色素，提高植物的耐旱性。

2.5 PGPR合成产铁载体

铁(iron, Fe)是植物生长发育过程中的必需元素，在各种细胞过程中起作用，包括呼吸、叶绿素的生物合成和光合作用等[84]。Fe通常以不溶性铁氢氧化物的形式存在于土壤中，因此植物无法获得[85]。PGPR能够合成对Fe具有高亲和力的低分子量铁载体来促进植物生长和营养吸收[86]。Fe载体(iron carrier)又称嗜铁素，是微生物通过非核糖体肽合成酶(non-ribosomal peptide synthetase，NRPS)途径和NRPS独立的铁载体合成酶(NRPS-independent siderophore，NIS)途径分泌的低分子量有机化合物[87]。Singh等[88]发现，伯克氏菌CSRS12通过产生铁载体显著增加了绿豆(*Vigna radiata*)的侧根数、根和茎长，并且增加了其生物量。有些PGPR还能在缺Fe情况下对植物吸收Fe起重要调节作用。如荧光假单胞菌和云南微球菌(*Microccucuce yunnanensis*)均能影响木瓜(*Pseudocydonia sinensis*)幼苗根部苯丙氨酸酶(phenylalaninammo-nialyase，PAL)活性、酚类化合物含量、柠檬酸浓度和高铁还原酶(ferric-chelate reductase，FCR)活性等生理生化参数，提高缺Fe条件下木瓜幼苗对Fe的利用效率[89]。此外，PGPR还能通过产生Fe载体增强植物抵抗非生物胁迫的能力。在盐胁迫下，接种产Fe载体的芽孢杆菌可增加番茄活性氧(reactive oxygen species，ROS)清除酶水平以及脯氨酸和可溶性糖的积累，降低MDA、Na^+和Cl^-的含量从而缓解盐胁迫对植株生长的影响并提高产量[90]。

2.6 PGPR作为生长促进剂

PGPR可作为植物生长促进剂或响应非生物胁迫因子的诱导剂，以改善植物生长和抗逆[91]。PGPR大量产生的次生代谢产物和挥发性有机化合物(volatile organic compounds, VOCs)可提高植物的抗逆性或促进植物的生长。如巨大芽孢杆菌(*Bacillus megaterium*)BOFC15能诱导拟南芥产生多胺，使其生物量增加，改变根系结构和提高光合能力并能在聚乙二醇(polyethylene glycol, PEG)诱导的干旱胁迫下表现出更高的耐旱性和ABA含量[92]。还有一些PGPR可以产生生物表面活性剂来促进植物生长和缓解非生物胁迫的影响。Ahmad等[93]共接种根瘤菌和假单胞菌可缓解盐胁迫对绿豆(*Vigna radiata*)相对含水量和二氧化碳(CO_2)同化速率的不利影响，从而提高光合速率、水分利用效率和叶绿素含量，改善离子平衡，提高产品质量。这些结果表明，PGPR可以有效地改善胁迫条件下植物的生长和品质。

3 PGPR在植物响应逆境胁迫中的作用

不利的气候变化引发了非生物胁迫，如高盐、干旱、极端温度和重金属毒性是对全球植物生长和作物生产力产生不利影响的最主要限制因素，导致全球农作物产量下降[94]。PGPR作为一类环境友好型细菌，其在改善植物生长和缓解非生物胁迫方面发挥着重要作用[95]。利用PGPR生物学功能与植物互作能够提高多种植物非生物胁迫的耐受性也已经被研究证明[96−98]。在非生物胁迫下每个PGPR的作用机制因寄主植物种类而异[99](表2)。

3.1 PGPR提高植物耐盐性

土壤过多盐分抑制了植物生理代谢，造成作物产量受损，甚至引起植物死亡[113]。在盐胁迫下，接种PGPR能诱导植物生长并改变植物代谢，如增加部分渗透物积累、养分获取、离子稳态和光合能力，降低MDA含量，从而增强植物抵抗盐胁迫的能力[114]。Shultana等[97]发现特基拉芽孢杆菌10b和阿氏芽孢杆菌B8W22可改善盐胁迫下水稻的生化特性和养分吸收。通过接种这两株菌株显著降低了盐胁迫下水稻MDA含量，提高了渗透保护剂(脯氨酸和总可溶性糖)和抗氧化酶活性。进一步研究表明，盐胁迫下水稻对N、P、K、Ca和Mg的吸收量增加了39.88%～276.47%。Din等[101]研究发现，甲基营养芽孢杆菌PM19通过胞外化合物[如胞外多糖(extracellular polysaccharides, EPS)]的产生作为化学信号诱导小麦在盐胁迫下的萌发和生长，PM19产生的EPS定殖在根系

表 2 PGPR 缓解植物非生物胁迫的作用

Table 2 Role of PGPR in alleviating plant abiotic stress

非生物胁迫 Abiotic stress	植物根际促生菌 PGPR	植物种类 Plant species	PGPR 机制 PGPR mechanism	作用效果 Action effect	参考文献 References
盐胁迫 Salt stress	巴西固氮螺菌 *Azospirillum brasiliense* 褐球固氮菌 *Azotobacter chococcum*	香菜 *Coriandrum sativum*	调节抗氧化酶活性。Regulating antioxidant enzyme activity.	生物量增加，产量提高。Increase in biomass and yield.	[100]
	约氏不动杆菌 *A. johnsonii*	玉米 *Z. mays*	调节土壤酶活性。Regulating soil enzyme activity.	改良了土壤健康，养分吸收增加。Improved soil health and increased nutrient absorption.	[30]
	特基拉芽孢杆菌 *B. tequilensis* 阿氏芽孢杆菌 *B. aryabhattai*	水稻 *O. sativa*	维持渗透平衡。Maintain osmotic balance.	改善了生化特性和养分吸收。Improved biochemical characteristics and nutrient absorption.	[97]
	甲基营养芽孢杆菌 *Bacillus methyllotrophicus*	小麦 *T. aestivum*	产 IAA、ACC 脱氨酶和胞外多糖。Production of IAA, ACC deaminase and extracellular polysaccharides (EPS).	发芽率、根冠长、光合色素等均有显著增加。Significant increases in germination rate, root cap length, photosynthetic pigments, etc.	[101]
	巨大芽孢杆菌 *B. megaterium*	小麦 *T. aestivum*	产生 IAA。Production of IAA.	发芽率、根冠长等生长参数均有显著提高。The growth parameters such as germination rate and root cap length have significantly improved.	[102]
干旱胁迫 Drought stress	贝莱斯芽孢杆菌 *Bacillus velezensis* 解淀粉芽孢杆菌 *B. amyloliquefaciens*	胡桃 *Juglans regia*	产铁载体、氰化氢和 IAA。Production of iron carrier, hydrogen cyanide and IAA.	改善了抗逆机制。Improved stress resistance mechanism.	[103]
	枯草芽孢杆菌 *B. subtilis*	番茄 *S. lycopersicum*	产 ACC 脱氨酶，降低乙烯水平。Production of ACC deaminase and reduce ethylene (ET) levels.	脯氨酸含量升高，MDA 和 H_2O_2 含量降低。Proline content increases, MDA and H_2O_2 content decreases.	[104]
	恶臭假单胞菌 *Pseudomonas putida*	玉米 *Z. mays*	调节代谢、信号和应激反应基因。Regulating metabolism, signal and stress response gene.	超氧化物歧化酶、过氧化氢酶和 ET 表达均降低。The expression of superoxide dismutase, catalase and ET were reduced.	[105]
	固氮假单胞菌 *P. azotoformans*	小麦 *T. aestivum*	产生 EPS、IAA 和可溶性磷酸三钙。Production of EPS, IAA, and soluble tricalcium phosphate.	生长性状、光合色素效率等生理指标均有显著提高。Physiological indicators such as growth traits and photosynthetic pigment efficiency have significantly improved.	[20]
	阿拉米根瘤菌 *R. alamii*	油菜 *B. chinensis*	产 EPS。Production of EPS.	茎部生物量增加。Increased stem biomass.	[29]
	荧光假单胞菌 *P. fluorescens* 解淀粉芽孢杆菌 *B. amyloliquefaciens*	薄荷 *Mentha hyplocalyx*	调节酶活性。Regulating enzyme activity.	酶活性和总酚含量显著提高。Significant increase in enzyme activity and total phenolic content.	[106]
温度胁迫 Temperature stress	芥菜假单胞菌 *Pseudomonas brassicacearum*	小麦 *T. aestivum*	产生高分子量的耐热蛋白，调节植物抗氧化酶活性。Production of high molecular weight heat-resistant proteins to regulate plant antioxidant enzyme activity.	幼苗鲜重、抗氧化酶活性、脯氨酸和蛋白质含量显著提高。Significant increase in seedling fresh weight, antioxidant enzyme activity, proline and protein content.	[107]

续表 Continued Table

非生物胁迫 Abiotic stress	植物根际促生菌 PGPR	植物种类 Plant species	PGPR机制 PGPR mechanism	作用效果 Action effect	参考文献 References
温度胁迫 Temperature stress	特基拉芽孢杆菌 *B. tequilensis*	大豆 *G. max*	产IAA、ABA。Production of IAA and ABA.	植株茎长、生物量和光合色素含量显著提高。Significant increase in plant stem length, biomass, and photosynthetic pigment content.	[80]
	梭形芽孢杆菌 *Bacillus fusiformis* 球形芽孢杆菌 *Bacillus sphaericus*	玉米 *Z. mays*	溶磷,产生葡萄糖酸、植物激素、儿茶酚和铁载体。Dissolve phosphorus and production of gluconic acid, phytohormone, catechol and iron carrier.	渗透酶、酚类物质、植物激素和抗氧化酶均上调。Permeases, phenols, plant hormone and antioxidant enzymes were up-regulated.	[108]
	哈茨木霉菌 *Trichoderma harzianum* 木糖无色杆菌 *Achromobacter xylosoxidans*	圣罗勒 *Ocimum sanctum*	产ACC脱氨酶。Production of ACC deaminase.	营养吸收、光合作用、淀粉和脯氨酸积累增加,产量提高。Increased nutrient absorption, photosynthesis, starch and proline accumulation, resulting in increased yield.	[28]
重金属胁迫 Heavy metal stress	气肠杆菌 *E. aerogenes*	水稻 *O. sativa*	产生IAA、固氮、溶磷。Production of IAA, nitrogen fixation, and dissolved phosphorus.	光合作用增强。Enhanced photosynthesis.	[109]
	胶质类芽孢杆菌 *Paenibacillus mucilaginosus* 中华根瘤菌 *Sinorhizobium meliloti*	紫花苜蓿 *M. sativa*	降低MDA和ROS的积累。Reduce the accumulation of MDA and ROS.	提高植株的抗氧化能力,显著降低了氧化损伤。Improve the antioxidant capacity of plants and significantly reduce oxidative damage.	[110]
	不动杆菌 *Acinetobacter beijerinckii* 植生拉乌尔菌 *Raoultella planticola*	大豆 *G. max*	产IAA、水杨酸和代谢物。Production of IAA, salicylic acid (SA), and metabolites.	代谢物上调,氧化损伤减少。Up-regulation of metabolites and reduction of oxidative damage.	[111]
	荧光假单胞菌 *P. fluorescens* 假单胞菌 *Pseudomonas*	向日葵 *Helianthus annuus*	产生长素、铁载体、ACC脱氨酶,溶磷。Production of auxin, iron carrier, ACC deaminase, and dissolve phosphorus.	茎高和茎粗、叶绿素指数及生物量增加。Increase in stem height and stem diameter, chlorophyll index, and biomass.	[112]

表面,作为盐胁迫的保护屏障,减少植物吸收Na^+并增加持水能力,接种后小麦幼苗发芽率、根冠长、光合色素等均有显著增加。Shabaan等[30]研究表明,接种约氏不动杆菌SUA-14可通过促进必需营养物质(N、P和K)的吸收,抑制Na^+进入植株,与未接种相比,脲酶、酸性磷酸酶、碱性磷酸酶和脱氢酶活性显著提高,MDA含量及植株的氧化损伤显著降低,并改善了土壤酶活性和土壤健康,克服营养失衡,从而改善盐胁迫下植物的养分获取,赋予玉米应对盐胁迫的能力。Lee等[102]在200 $mmol\cdot L^{-1}$ NaCl下接种具有产IAA的巨大芽孢杆菌PN89,对小麦的生长有显著的影响,与未接种对照相比,PN89处理对小麦的发芽率、根冠长等生长参数均有显著提高,可见巨大芽孢杆菌PN89可用作生物肥料缓解盐胁迫。本课题组研究发现,在100 $mmol\cdot L^{-1}$ NaCl胁迫下,暹罗芽孢杆菌(*Bacillus siamensis*)可能通过固氮、溶磷、解钾和产铁载体改善植物生长和土壤健康,接种后能显著增加红豆草(*Onobrychis viciaefolia*)鲜重、株高和根长,提高可溶性糖、可溶性蛋白、脯氨酸和叶绿素的含量,降低叶片死亡率,减轻盐胁迫造成的不利影响(数据尚未发表)。这些结果表明,接种耐盐PGPR能够通过改变和调节植物内外离子浓度、植物激素信号、养分和水分吸收、土壤理化性质等多种方式直接或间接影响植物生理状态,提高植物应对盐胁迫的能力,另一方面还可通过改良土壤健康进一步缓解盐碱化的加剧。

3.2 PGPR提高植物耐旱性

干旱胁迫会对植物造成渗透胁迫,引起植物形态、生化和生理等各种损伤,从而影响植物生长、发育和产量形

成[115]。PGPR能通过溶磷、解钾、合成植物生长调节因子、降低乙烯(ethylene,ET)水平和诱导抗氧化防御系统等作用增强植物在干旱环境中的生存能力[116]。Rashid等[117]通过接种可溶磷和解钾的巨大芽孢杆菌可显著提高小麦植株的相对含水量、叶绿素a、b和类胡萝卜素、蛋白质以及脯氨酸含量,降低MDA含量,有效缓解干旱胁迫对小麦造成的不利影响。ACC脱氨酶可分解干旱胁迫下产生的乙烯。Gowtham等[104]利用产ACC脱氨酶的枯草芽孢杆菌SF 48降低番茄的ET水平,提高抗氧化酶活性,保护番茄植株免受干旱胁迫引起的氧化损伤,促进植株生长。接种后的番茄植株脯氨酸、SOD和抗坏血酸过氧化物酶(aseorbateperoxidase, APX)活性均有所提高,MDA含量和乙烯响应因子显著降低,含水量显著增加。Ansari等[20]发现固氮假单胞菌FAP5具有产生EPS、IAA和可溶性磷酸三钙的能力,并表现出ACC脱氨酶活性,在干旱胁迫条件下,FAP5的生物膜发育明显增强,能改善小麦的生长性状、光合色素效率等生理指标,有效缓解小麦的干旱胁迫,接种后的种子萌发率显著提高,植株的气孔导度、蒸腾速率、光合速率增加,总脯氨酸含量显著提高,CAT、SOD活性和MDA含量显著降低。此外,FAP5合成的EPS可增加土壤分子的聚集以改善土壤渗透性,并保持根周围较高的水势,从而增加干旱胁迫下植物的养分吸收。Chiappero等[106]研究发现,在干旱胁迫下接种荧光假单胞菌WCS417 r和解淀粉芽孢杆菌GB03可以改善薄荷植株抗氧化酶活性,提高植物总酚含量,避免ROS积累,从而促进植物生长。接种后薄荷植株的地上部鲜重、SOD活性和总酚含量增加,而MDA含量显著降低。这些结果表明,PGPR通过产生生长调节因子和增强抗氧化酶活性等作用机制,增强植物营养吸收和维持土壤较高含水量,从而改善植物生长和改良土壤健康,进一步增强植物应对干旱胁迫的能力。

3.3 PGPR提高植物对温度胁迫的耐受性

极端温度(高温和低温)是植物生长发育的重要限制因素,严重影响植物生理生化和分子过程[118]。高温可破坏植物细胞膜和胞内各种蛋白的活性,扰乱生物活性分子的合成与细胞代谢过程。低温也可减缓植物细胞代谢,造成细胞形成冰晶、脱水和电解质泄漏,从而导致细胞死亡[119]。PGPR能产生和调节各种植物激素、酶和代谢物,增加脯氨酸和可溶性糖含量以及光合作用和抗氧化酶的活性从而提高植物对极端温度的耐受性[120-121]。Kang等[80]发现,特基拉芽孢杆菌SSB07具有较强的产生GA、IAA、ABA的能力,可显著提高大豆植株的茎长、生物量、叶片发育和光合色素含量。在热胁迫下接种SSB07可显著提高大豆叶根圈内源茉莉酸(jasmonic acid, JA)和SA含量,显著下调应激响应ABA的产生,与未接种相比,大豆植株的茎长、生物量、叶面积和光合色素均有显著提高,可有效缓解高温胁迫产生的不利影响。Ashraf等[107]发现,在45 ℃高温胁迫下接种芥菜假单胞菌可通过产生高分子量的耐热蛋白,增强抗氧化酶活性,使得玉米幼苗具有更高的根和芽鲜重,脯氨酸和蛋白质含量,进一步有效缓解高温胁迫对玉米植株的影响,与未接种相比,玉米根和茎的长度及鲜重均有明显增加,叶片SOD、APX和CAT活性也显著增强。Jha等[108]发现在4 ℃条件下接种梭形芽孢杆菌YJ4和球形芽孢杆菌YJ5可通过产生渗透物(如脯氨酸、甘氨酸、甜菜碱和可溶性糖)、植物激素(如IAA、GA和ABA)、酚类物质和抗氧化酶(如PAL、SOD和CAT),提高玉米植株的生长和生物量,还可降低电解质水平和MDA含量,提高木质素含量,从而诱导玉米抵抗冷胁迫引起的渗透胁迫和氧化胁迫。在冷胁迫下接种嗜冷芽孢杆菌(*Psychrophilic bacillus*)也能正向调节植物激素的表达,通过调节ABA、脂质过氧化和脯氨酸积累途径,从而显著改善小麦在冷胁迫下的生长[122],与未接种相比,接种后植株鲜重和干重增加近一倍,并提高了植株的气孔导度和光合速率。这些结果表明,PGPR可以通过合成或调节植物激素、酶、代谢物和渗透物质等作用机制,增强植物抗氧化酶活性,从而有效缓解极端温度对植物的不利影响。

3.4 PGPR提高植物重金属胁迫耐受性

重金属,如铜(Cu)、铅(Pb)、镉(Cd)、铬(Cr)、汞(Hg)和砷(As)等造成的土壤污染被认为是世界上最大的环境问题之一,并对生态系统、农业可持续性和人类健康构成了永久性威胁[123]。重金属过量会直接影响植物的生长、代谢、生理和衰老[124]。PGPR可以通过影响植物体内根系呼吸和氧化应激以及植物营养参数减少重金属离子的积累,缓解各种重金属胁迫[112]。Pramanik等[125]分离到一株具有产IAA、固氮、溶磷、ACC脱氨酶活性等促生特性并有较强耐重金属能力的产气肠杆菌菌株K6。在3 $g\cdot L^{-1}$ Cd胁迫条件下,K6可提高水稻的α淀粉酶活性,

促进种子萌发;可控制蛋白质降解,通过活性蛋白酶维持蛋白质稳态;可提高叶绿素含量,通过增强光合作用保证养分利用率,降低了幼苗组织对Cd的吸收,显著促进了Cd胁迫下水稻幼苗的生长。Husna等[111]研究发现,在1200 $mg \cdot L^{-1}$重金属(铬酸盐和砷酸盐)胁迫下,不动杆菌C5和植生拉乌尔菌C9会释放出大量代谢物(酚类物质、类黄酮、脯氨酸、糖和蛋白质)和植物激素(IAA、SA和GA),并表现出溶解磷酸盐和释放铁载体的能力,接种后能促进大豆抗氧化剂的产生,通过清除应激下产生的过量ROS来减少氧化损伤,IAA和SA也均显著升高,进一步改善大豆的生理和代谢反应,使其能够更好地在Cr和As胁迫下良好生长。在Cu胁迫下接种具有产IAA、铁载体、ACC脱氨酶以及溶磷能力的荧光假单胞菌P22和假单胞菌Z6均对向日葵的生长有显著影响,与未接种相比,两株PGPR可显著提高向日葵的茎干重、茎长、茎粗和叶绿素含量,也显著提高了K、P、Ca、Fe和Zn等营养物质的吸收,进一步缓解了Cu胁迫对植物造成的离子毒害[112]。因此,PGPR能通过固氮、溶磷、分泌植物激素和代谢物等作用机制,改善植物生长及营养吸收,提高植物抗氧化酶活性和氧化应激,进一步增强植物对重金属胁迫的耐受性。

4 展望

PGPR的种类丰富且功能多样,在响应植物逆境胁迫,促进植物生长中发挥着重要作用,是实现农业可持续发展的有效途径之一,将在农业实践中有较好的应用前景。然而,目前学术界对PGPR的研究重点在于其分离、鉴定及其功能上,缺乏将现有菌株制成生物制剂在大田中的实际效果等方面的研究,使得PGPR在农业实践中的应用受到限制。人们对其调控机制的认识还很有限,如PGPR间的联合使用和相互协调的促生机制尚不清楚。另外,PGPR对不同作物在抗逆过程中的调控机制是否存在特异性,其通过何种特异性机制来促进植物生长及对抗逆性的影响有何特异性等问题,尚需深入研究。结合本课题组已有的研究成果,建议今后对PGPR的研究可以从以下3方面着手:1)利用高新技术对更多PGPR种类及其功能进行挖掘,以确定PGPR的促生机制及与其他PGPR间的相互协调关系;2)采用基因组、转录组和蛋白质组等组学手段进一步探索PGPR的调控机制,揭示其在不同作物中抗逆功能的特异性;3)以已知PGPR种类和功能为基础,选出具有高效抗逆性的单一PGPR菌株或组合PGPR菌株,以获得介导植物抗逆的最佳组合,制成促生菌剂或者生物肥料,或者通过胶囊化技术将优良PGPR微胶囊化,在保护促生菌活性的同时,也可较好地克服外界复杂的使用条件并应用到农业实践中。随着生物技术的发展,更多PGPR的种类和功能及响应逆境胁迫的作用机制将被阐明,有望为抵抗非生物胁迫研究提供新的参考,并为提高作物产量及对非生物胁迫耐受性提供新的思路和视角。

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