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转录组分析植物促生细菌缓解高粱微塑料和重金属复合污染胁迫机制

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摘要: 微塑料能成为其它环境污染物(比如重金属)潜在的转运营载体,因此微塑料与重金属的复合污染越来越受到研究者的重视. 为探究植物促生细菌 VY-1 缓解高粱微塑料和重金属复合污染胁迫机制,通过水培实验分析菌株接种对高粱生物量和重金属积累的影响,通过转录组学分析接菌对高粱基因表达的影响. 结果表明,聚乙烯(PE)和镉(Cd)复合污染相比单一 Cd 污染使高粱地上部和地下部干重分别下降 17.04% 和 10.36%,表现出复合污染对植物生长毒性效应增强的症状. 接种植物促生细菌 VY-1 能缓解 Cd-PE 复合污染的毒性,高粱地上部和地下部长度分别增加 33.83% 和 73.21%,干重分别增加 56.64% 和 33.44%. 转录组测序结果表明,接种 VY-1 后高粱根部有 904 个基因上调表达. 促生细菌 VY-1 接种能上调表达生长素、脱落酸、黄酮类和木质素生物合成通路中多个基因,促进了高粱在 Cd-PE 复合污染胁迫下的耐受能力,提高其抗性. 以上研究结果表明植物促生细菌在微塑料和重金属的复合污染中能通过调节植物基因表达缓解所受到的胁迫,为重金属与微塑料复合污染植物-微生物联合修复提供了参考.

关键词: 高粱; 镉(Cd); 聚乙烯(PE); 根际促生细菌; 转录组

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Transcriptome Analysis of Plant Growth-promoting Bacteria Alleviating Microplastic and Heavy Metal Combined Pollution Stress in Sorghum

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Abstract: Microplastics can become potential transport carriers of other environmental pollutants (such as heavy metals), so the combined pollution of microplastics and heavy metals has attracted increasing attention from researchers. To explore the mechanism of plant growth-promoting bacteria VY-1 alleviating the combined pollution stress of heavy metals and microplastics in sorghum, the effects of inoculation on biomass and accumulation of heavy metals in sorghum were analyzed using a hydroponics experiment, and the effects of inoculation on gene expression in sorghum were analyzed via transcriptomics. The results showed that the combined pollution of polyethylene (PE) and cadmium (Cd) decreased the dry weight of above-ground and underground parts by 17.04% and 10.36%, respectively, compared with that under the single Cd pollution, which showed that the combined toxicity effect of the combined pollution on plant growth was enhanced. The inoculation of plant growth-promoting bacteria VY-1 could alleviate the toxicity of Cd-PE combined pollution and increase the length of aboveground and underground parts by 33.83% and 73.21% and the dry weight by 56.64% and 33.44%, respectively. Transcriptome sequencing showed that 904 genes were up-regulated after inoculation with VY-1. Inoculation with growth-promoting bacteria VY-1 could up-regulate the expression of several genes in the auxin, abscisic acid, flavonoid synthesis, and lignin biosynthesis pathways, which promoted the response ability of sorghum under Cd-PE combined pollution stress and improved its resistance. The above results indicated that plant growth-promoting bacteria could alleviate the stress of heavy metal and microplastic combined pollution by regulating plant gene expression, which provided a reference for plant-microbial joint remediation of heavy metal and microplastic combined pollution.

Key words: sorghum; cadmium (Cd); polyethylene (PE); rhizosphere growth-promoting bacteria; transcriptome

由于不合理地采矿、工业发展和农用化学品过度使用等,大量的镉(Cd)等重金属进入土壤,造成土壤重金属含量超标^[1,2]. 调查表明,我国 Cd 污染耕地面积达 1 300 万 hm^2 ,这些土壤中 Cd 含量远高于背景值^[3]. Cd 在土壤中不能被微生物降解,随着土壤-植物系统进入到作物中,通过食物链进入到人体,严重威胁人类的健康^[4]. 微塑料(MPs)作为一种新的环境污染物,是指粒径为 0.1 μm ~5 mm 的塑料碎片/颗粒,调查表明其在水、土、气和沉积物等环境介质中广泛存在^[5]. 微塑料具有粒径小、来源广、易迁移和难消

除等特点,产生的生态环境风险越来越受到全球学者的关注^[6]. 微塑料具有复杂的表面特征及较大的比表面积,使其能够和其它环境污染物(比如重金属)

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相互作用并可能成为这些污染物潜在的转运载体^[7,8]。有研究表明,微塑料可以吸附 Pb、Cu 和 Cd 等重金属,从而带来更加复杂的生态风险^[9,10]。因此,微塑料与重金属的复合污染问题越来越受到人们的重视^[11]。

植物促生细菌(plant growth-promoting bacteria, PGPB)是指能够促进植物生长、提高植物抗性的一类有益细菌^[12]。PGPB 能在重金属胁迫条件下通过分泌生长素、溶磷、产 1-氨基环丙烷-1-羧酸(1-aminocyclopropane-1-carboxylic acid, ACC)脱氨酶和铁载体直接或间接地促进植物生长,在植物-微生物联合修复中得到广泛地应用^[13-15]。转录组测序(RNA-seq)利用高通量测序技术将细胞或组织中全部 RNA 进行测序分析,能系统、准确地探究从 DNA 向 RNA 转录这一复杂而精细的调控层次,在植物-微生物联合修复机制研究中具有重要的应用^[16,17]。

目前,植物促生细菌在微塑料和重金属复合污染中缓解植物胁迫的研究尚未开展。因此,本研究通过水培实验分析植物促生细菌对 Cd 和聚乙烯(PE)(Cd-PE)复合污染条件下高粱生长和重金属积累的影响,结合转录组学探究供试菌株提高高粱耐受 Cd-PE 复合污染的机制,以期重金属与微塑料复合污染的植物-微生物联合修复提供参考。

1 材料与方法

1.1 供试材料

供试高粱为京都铁杆 100,实验中所用重金属为硫酸镉 $3\text{CdSO}_4 \cdot 8\text{H}_2\text{O}$ (AR 分析纯),所用微塑料为聚乙烯(PE),粒径为 $13\ \mu\text{m}$ 。所用供试菌株为实验室保存菌株 VY-1 菌,经鉴定属于肠杆菌属(*Enterobacter* sp.),NCBI 数据库菌株保藏号为 ON320412。该菌株具有产 ACC 脱氨酶、产铁载体和产 IAA 等植物促生特性,产 IAA 能力为 $101.88\ \text{mg} \cdot \text{L}^{-1}$,对 Cd 具有较好耐受能力,最大耐受浓度为 $400\sim 500\ \text{mg} \cdot \text{L}^{-1}$ 。

1.2 实验方法

1.2.1 供试菌株发酵液制备

供试菌株接种于液体 LB 培养基中, 28°C , $150\ \text{r} \cdot \text{min}^{-1}$ 振荡培养至对数生长期,培养液 $4\ 800\ \text{r} \cdot \text{min}^{-1}$ 离心 20 min 收集菌体,菌体用无菌去离子水清洗两遍,重悬于无菌去离子水中,使菌体浓度达到 $1 \times 10^8\ \text{cfu} \cdot \text{mL}^{-1}$ 。

1.2.2 重金属及微塑料溶液配制

参考 Wu 等^[18]和 Liu 等^[19]的研究,通过预实验,确定水培实验方案为:以 Hoagland 营养液为基础进行溶液培养实验,添加 $3\text{CdSO}_4 \cdot 8\text{H}_2\text{O}$ 使其 $\omega(\text{Cd})$ 为 $3\ \text{mg} \cdot \text{L}^{-1}$,将微塑料 PE 添加到 300 mL 的 Hoagland 营

养液中,微波振荡以实现 MPs 固液比为 $\rho(\text{PE})0.05\ \text{mg} \cdot \text{mL}^{-1}$ 。

1.2.3 水培实验

选取籽粒饱满的高粱种子,75% 乙醇消毒 5 min 后用无菌去离子水冲洗, 28°C 催芽 24 h。选择 20 粒出芽种子移栽至双层塑料盆中,上层装有 200 g 石英砂,下层含有 300 mL Hoagland 营养液。实验处理设计见表 1。

表 1 实验设计¹⁾

Table 1 Design of experiments

实验分组	$\omega(\text{PE})$ / $\text{mg} \cdot \text{mL}^{-1}$	$\omega(\text{Cd})$ / $\text{mg} \cdot \text{L}^{-1}$	菌株 VY-1
未添加 Cd 和未接种对照组(CK)	0	0	—
单一 Cd 处理组(Cd)	0	3	—
Cd-PE 复合污染组(Cd-PE)	0.05	3	—
Cd-PE 复合污染接种菌株 VY-1 组(Cd-PE-VY-1)	0.05	3	+

1) “—”表示未接种供试菌株,“+”表示接种供试菌株。

每个处理设置 3 个重复。高粱幼苗培养 1 周后,添加 Cd 和 PE,同时接种菌株。供试菌株采用浸根的方式进行接种,即把高粱根放入到细菌菌悬液中浸泡 2 h。每周更换一次溶液。所有的植物都生长在组培室中,温室的室温保持在 $25^\circ\text{C} \pm 3^\circ\text{C}$ 。从第一次添加 Cd 和 PE 处理 30 d 后进行收获处理。

1.3 Cd 含量测定

植物样品的地上部与根部用清水洗净后浸泡在 $0.01\ \text{mol} \cdot \text{L}^{-1}$ 的 EDTA-2Na 缓冲液中 20 min,于烘箱中 80°C 烘干至恒重,用电子天平分别称取干重。用研钵将样品磨碎,精准称取 $0.1\ \text{g} (\pm 0.0002\ \text{g})$ 植物样品于聚四氟乙烯坩埚中,采用盐酸-硝酸-氢氟酸-高氯酸法进行微波消解,过滤后使用电感耦合等离子体发射光谱仪(ICP-OES)测 Cd 含量。

1.4 转录组测序

为了分析植物促生细菌接种对重金属和微塑料复合污染条件下植物基因表达的影响,选取实验设计中 Cd-PE 和 Cd-PE-VY-1 处理进行转录组测序分析。转录组测序基于 Illumina NovaSeq 6000 测序平台进行测序,采用 Illumina TruSeq TM RNA sample prep Kit 方法进行文库构建,测序工作由上海美吉生物医药科技有限公司完成。

从高粱根部组织样品中提取 total RNA,利用 Nanodrop 2000 对所提 RNA 的浓度和纯度进行检测,琼脂糖凝胶电泳检测 RNA 完整性,Agilent 2100 测定 RIN 值。单次建库要求 RNA 总量 $\geq 1\ \mu\text{g}$,浓度 $\geq 35\ \text{ng} \cdot \mu\text{L}^{-1}$, $D_{260}/D_{280} \geq 1.8$, $D_{260}/D_{230} \geq 1.0$ 。利用带有 Oligo(dT)的磁珠与 ploy A 进行 A-T 碱基配对,可以

从总 RNA 中分离出 mRNA,用于分析转录组信息. 加入 fragmentation buffer,可以将 mRNA 随机断裂,通过磁珠筛选分离出 300 bp 左右的小片段. 在逆转录酶的作用下,加入六碱基随机引物(random hexamers),以 mRNA 为模板反转合成一链 cDNA,随后进行二链合成,形成稳定的双链结构. 加入 End Repair Mix 将其补成平末端,随后在 3' 末端加上一“A”碱基,用于连接 Y 字形的接头. 然后利用 Illumina NovaSeq 6000 平台进行转录组测序. 经质量控制后得到高质量的 Clean Reads,将其采用 HISATA2 软件与 *Sorghum bicolor* 的参考基因组进行序列比对,得到 Mapped Reads. 基于所选参考基因组序列,使用 String Tie 对 Mapped Reads 进行拼接,将基因与 GO、Swiss-Prot、COG、NR、KEGG 和 KOG 等六大数据库进行比对,获得基因的注释信息并对各数据库注释情况进行统计,分别对基因的表达水

平进行定量分析.

1.5 数据处理与分析

所有处理设置 3 次重复,使用 SPSS 23.0 进行统计分析,采用单因素方差分析中的 LSD 多重比较检验不同处理间的结果差异显著性,统计显著性设为 $P < 0.05$.

2 结果与分析

2.1 不同处理条件对高粱生长的影响

由表 2 可以看出,相比 CK,在 Cd 胁迫下高粱的地上部和地下部长度分别降低 28.05% 和 18.42%. 相较于单一 Cd 胁迫,Cd-PE 的复合处理组中地上部和地下部长度显著降低,分别降低 24.86% 和 39.78%. 在 Cd-PE-VY-1 处理中,供试菌株 VY-1 的接种显著提高地上部和地下部的长度,相较 Cd-PE 处理分别增加 33.83% 和 73.21%.

表 2 不同处理下高粱长度和生物量¹⁾

Table 2 Sorghum length and biomass under different treatments

处理	地上部长/cm	根长/cm	地上部鲜重/g	地上部干重/g	地下部鲜重/g	地下部干重/g
CK	41 ± 0.5a	19 ± 0a	3.23 ± 0.32a	0.8 ± 0.04bc	1.1 ± 0.09b	0.12 ± 0.01b
Cd	29.5 ± 4c	15.5 ± 4.33a	2.68 ± 0.64a	0.44 ± 0.11bc	0.97 ± 0.32a	0.12 ± 0.03a
Cd-PE	22.17 ± 1.76b	9.33 ± 0.58b	1.67 ± 0.17b	0.37 ± 0.04c	0.73 ± 0.13ab	0.11 ± 0.02a
Cd-PE-VY-1	29.67 ± 2.08c	16.17 ± 3.18a	3.16 ± 0.18a	0.57 ± 0.04a	1.05 ± 0.08a	0.14 ± 0.02a

1)不同小写字母表示同一列内处理之间有显著差异 $P < 0.05$

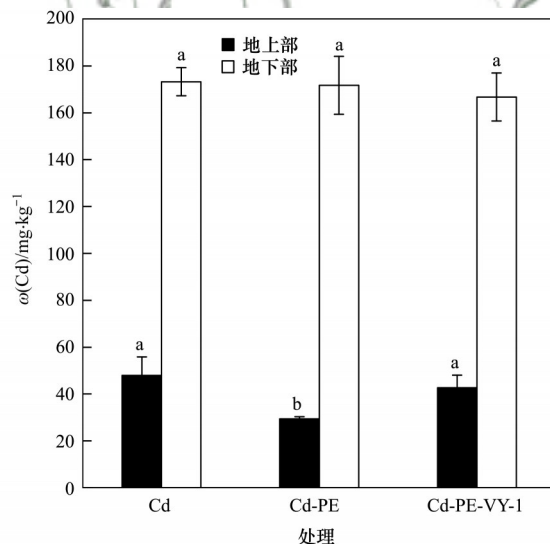
高粱生物量结果与长度结果相似,相比 CK,在 Cd 胁迫下高粱的地上部鲜重和干重分别降低 58.55% 和 45.21%,地下部鲜重和干重分别降低 11.76% 和 0.83%. 相较于单一 Cd 胁迫,Cd-PE 的复合处理组中地上部鲜重和干重分别降低 37.76% 和 17.04%,地下部鲜重和干重分别降低 24.64% 和 10.36%. 在 Cd-PE-VY-1 处理中,供试菌株 VY-1 的接种提高地上部和地下部的干重,相较 Cd-PE 分别增加 56.64% 和 33.44%.

由高粱长度和生物量可知,相对于 Cd 单一污染,Cd-PE 复合污染毒性更强,表现出复合毒性增强的现象,供试菌株 VY-1 能有效地缓解 Cd-PE 复合污染的胁迫.

2.2 不同处理条件下对高粱 Cd 含量、积累量的影响

Cd-PE 处理组地上部和地下部 Cd 含量相较于 Cd 组整体下降,地上部和地下部 Cd 含量分别降低 38.60% 和 0.87%. 相较 Cd-PE 处理组,Cd-PE-VY-1 处理中供试菌株 VY-1 的接种能提高地上部 Cd 含量,比例为 45.29%,降低地下部 Cd 含量,比例为 2.91%(图 1).

在不同部位 Cd 积累量方面,Cd-PE 处理组地上

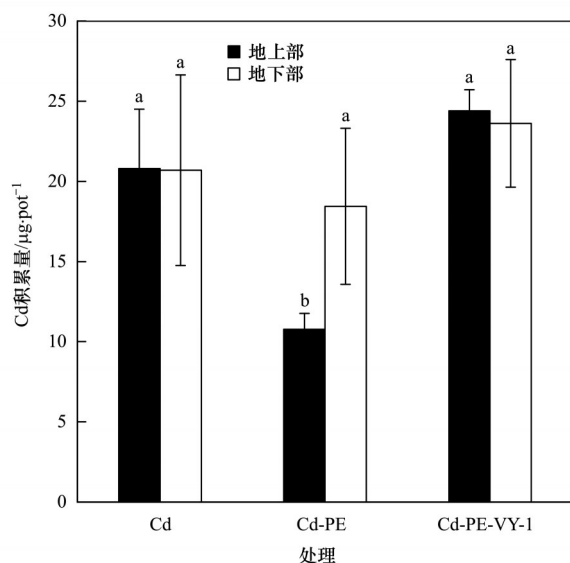


不同小写字母表示同一列内处理之间有显著差异 $P < 0.05$

图 1 高粱地上部和地下部 Cd 含量

Fig. 1 Cd content in aboveground and underground parts of sorghum

部和地下部 Cd 积累量相较于 Cd 组整体下降,分别降低 48.23% 和 10.92%. 相较 Cd-PE 处理组,Cd-PE-VY-1 处理中供试菌株 VY-1 的接种能提高地上部和地下部的 Cd 积累量,比例为 126.47% 和 28.08%(图 2).



不同小写字母表示同一列内处理之间有显著差异 $P < 0.05$

图2 高粱地上部分和地下部分Cd积累量

Fig. 2 Cd accumulation in aboveground and underground parts of sorghum

2.3 接菌对Cd-PE复合污染胁迫下高粱转录组表达的影响

通过转录组测序,共获得 90.77 Gb Clean Data.

分析共检测到表达基因 28 967 个、表达转录本共 57 880 个。基于表达量定量结果,进行组间差异基因分析,获得两组间发生差异表达的基因,在 Cd-PE 复合污染条件下接菌处理组 (Cd-PE-VY-1) 与对照组 (Cd-PE) 相比,上调基因为 904 个,下调基因为 2 041 个。

2.4 差异表达基因的GO富集分析

基于Nr蛋白数据库注释,使用GO和KEGG对预测的单基因的功能进行了分类,在GO功能分类中,注释的基因主要分为3个功能组:生物过程 (biological process)、细胞成分 (cellular component) 和分子功能 (molecular function) (图3)。在丰度排名前20的GO二级功能分类中,属于生物过程簇的占9种 (占比为 29.85%),细胞成分的占7种 (占比为 41.06%),分子功能的占4种 (占比为 29.09%)。在生物过程中,基因主要分布在代谢过程 (metabolic process) 和细胞代谢过程 (cellular process) 两种分类中;在分子功能中,基因主要分布在催化活性 (catalytic activity) 和链接 (binding) 两种分类中;在细胞成分中,基因主要分布在细胞器 (organelle)、膜元件 (membrane part) 和细胞区域 (cell part) 上。

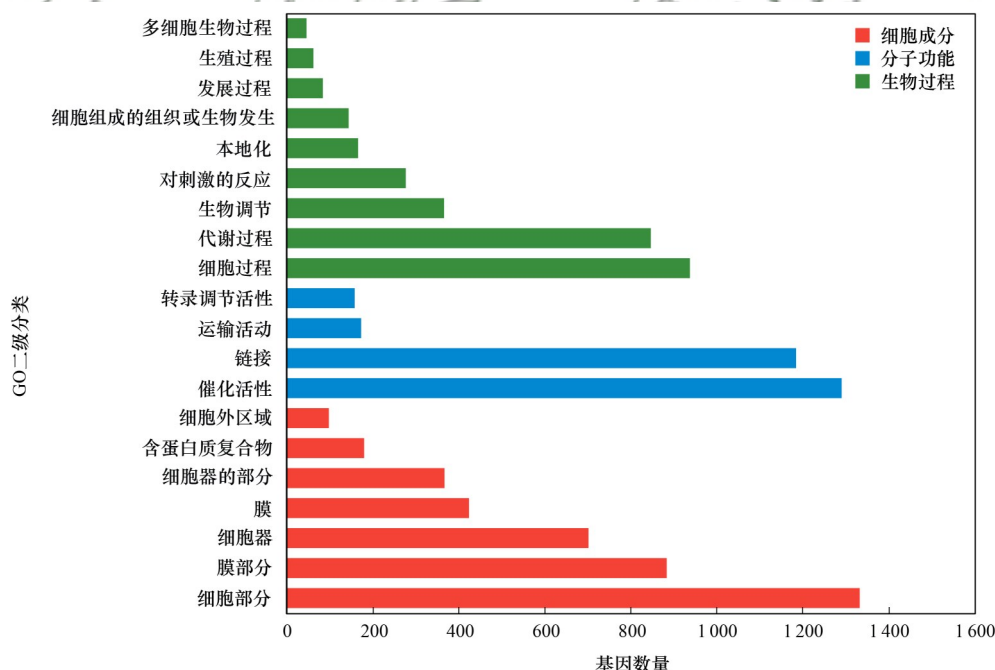


图3 GO分类统计

Fig. 3 GO classification statistics

2.5 差异表达基因的KEGG富集分析

在 Cd-PE 复合污染条件下接菌处理组 (Cd-PE-VY-1) 与对照组 (Cd-PE) 相比 KEGG 数据库中基因注释到 113 条通路,富集在五大类中。最丰富的途径是糖代谢 (carbohydrate metabolism), 其次是能量代谢 (energy metabolism) 和信号转导 (signal transduction)。

如图4所示,在 Cd-PE 复合污染条件下接菌处理组 (Cd-PE-VY-1) 与对照组 (Cd-PE) 相比,差异表达基因分析表明在植物激素信号转导 (plant hormone signal transduction)、苯基类丙烷生物合成 (phenylpropanoid biosynthesis) 和糖酵解/糖异生 (glycolysis/gluconeogenesis) 等方面富集程度最高。

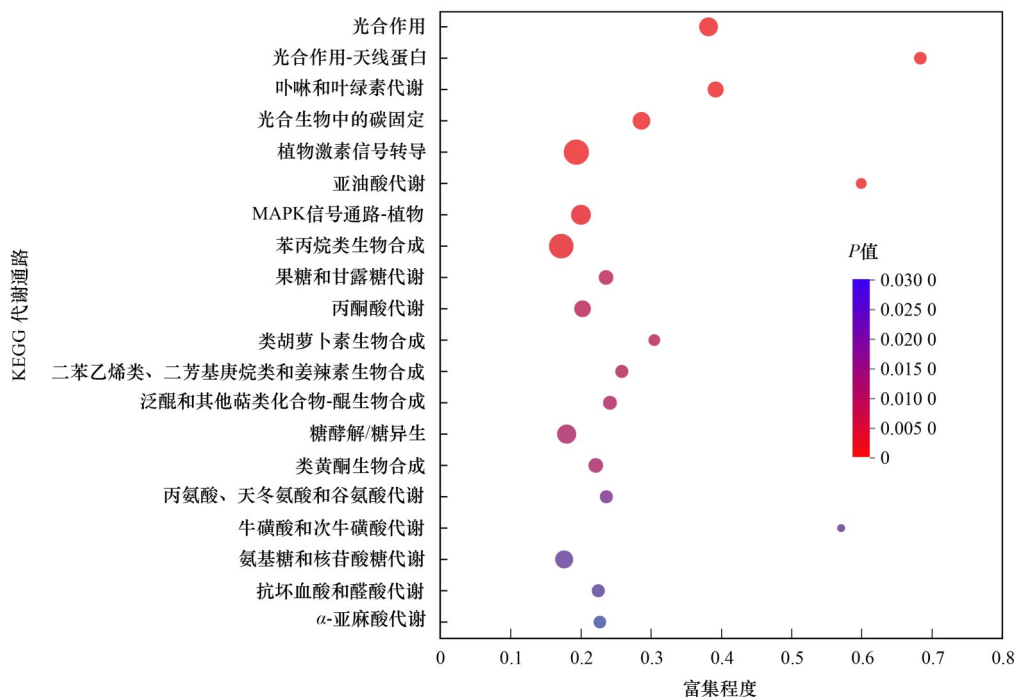


图 4 KEGG 富集分析气泡图
Fig. 4 KEGG enrichment analysis bubble chart

如图 5 所示,接菌处理组(Cd-PE-VY-1)与对照组(Cd-PE)相比,植物激素信号转导途径中差异主要是生长素途径和脱落酸途径.生长素转导途径中,生长素需要通过膜上蛋白 AUX1 传递给复合物 TIR1,然后信号进一步传递给生长素蛋白(AUX/IAA),影响 AUX/IAA 的关键基因 auxin-responsive protein IAA24 (gene-LOC8056625)、auxin-responsive protein IAA14 (gene-LOC8061165)和 auxin-responsive protein IAA9, transcript variant X1(gene-LOC8084668)全部上调.同时,probable indole-3-acetic acid-amido synthetase GH3.8(gene-LOC8059110)和 probable indole-3-acetic acid-amido synthetase GH3.2(gene-LOC8072113)上调表达影响 GH3 的表达,auxin-induced protein X10A (gene-LOC8054281)、auxin-induced protein 6B(gene-LOC8063834)和 auxin-responsive protein SAUR50 (gene-LOC8079823)作为影响 SAUR 的关键基因均上调表达.在脱落酸途径中脱落酸受体 PYR/PYL 家

族、蛋白磷酸酶 2C(PP2C)、丝氨酸/苏氨酸蛋白激酶 SRK2 和 ABA 响应元素结合因子(ABF)全部上调,其中影响 PYR/PYL 的基因 auxin-responsive protein SAUR50 (gene-LOC8081117),影响 PP2C 的 probable protein phosphatase 2C 51(gene-LOC8074621) probable protein phosphatase 2C 8 (gene-LOC8058260)和 probable protein phosphatase 2C 50(gene-LOC8061070)等 10 个关键基因上调表达.影响 SnRK2 的基因 serine/threonine-protein kinase SAPK1 (gene-LOC8077115)、serine/threonine-protein kinase SAPK4, transcript variant X1 (gene-LOC110433368)、serine/threonine-protein kinase SAPK7 (gene-LOC110436350)和 serine/threonine-protein kinase SAPK3 (gene-LOC110431683),影响 ABF 的基因 bZIP transcription factor TRAB1-like, transcript variant X1 (gene-LOC110437038)、G-box-binding factor 4 (gene-LOC8062379)、bZIP transcription factor 23 (gene-

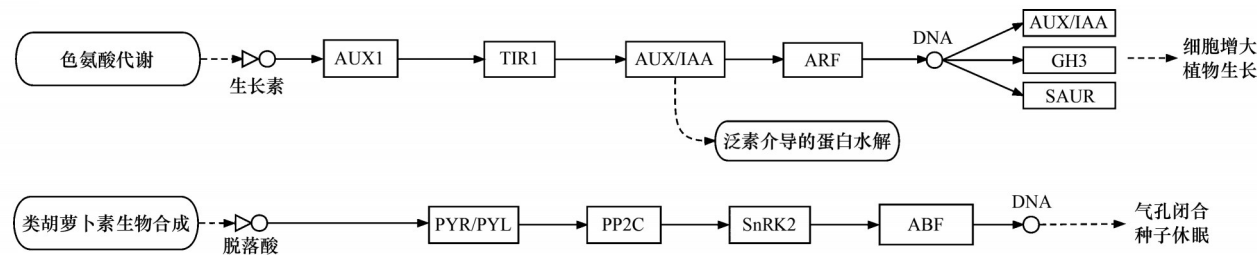


图 5 植物激素信号转导途径
Fig. 5 Plant hormone signal transduction pathway

LOC8077354) 和 bZIP transcription factor 23, transcript variant X1 (gene-LOC8075201) 都上调表达, 说明了菌株 VY-1 能提高脱落酸转导途径中基因的表达。

在苯基类丙烷生物合成通路中, 接菌处理组 (Cd-PE-VY-1) 与对照组 (Cd-PE) 相比多个关键基因上调 (图 6). 其中黄酮类的生物合成和木质素的合成 2 种合成通路是已报道的在抵御重金属伤害中起到重要作用. 在黄酮类合成通路中, phenylalanine/tyrosine ammonia-lyase (酶: 43.1.25, K13064, gene-LOC8074774)、trans-cinnamate 4-monooxygenase (酶: 1.14.14.91, K00487, gene-LOC8085395, gene-LOC8084483, gene-LOC8059757) 和 4-coumarate--CoA ligase (酶: 6.2.1.12, K01904, gene-LOC8079391, gene-

LOC8077870, gene-LOC8064652) 这 3 种关键酶基因呈上调表达。黄酮类化合物可以增强金属螯合过程, 有助于降低植物细胞中有害的羟基自由基的水平。在木质素生物合成中, 除了 phenylalanine/tyrosine ammonia-lyase、trans-cinnamate 4-monooxygenase 和 4-coumarate-CoA ligase 以外, cinnamoyl-CoA reductase (酶: 1. 2. 144, gene-LOC8076207)、cinnamyl-alcohol dehydrogenase (酶: 1. 1. 1. 195, gene-LOC8071179) 和 caffeoyl-CoA O-methyltransferase (酶: 2. 1. 104, gene-LOC8070884, gene-LOC8063763) 等上调表达。木质素生物合成中的中间产物能通过建立保护细胞免受重金属有害作用的物理屏障, 以及影响植物组织中金属离子的形态, 增加细胞壁的耐受力。

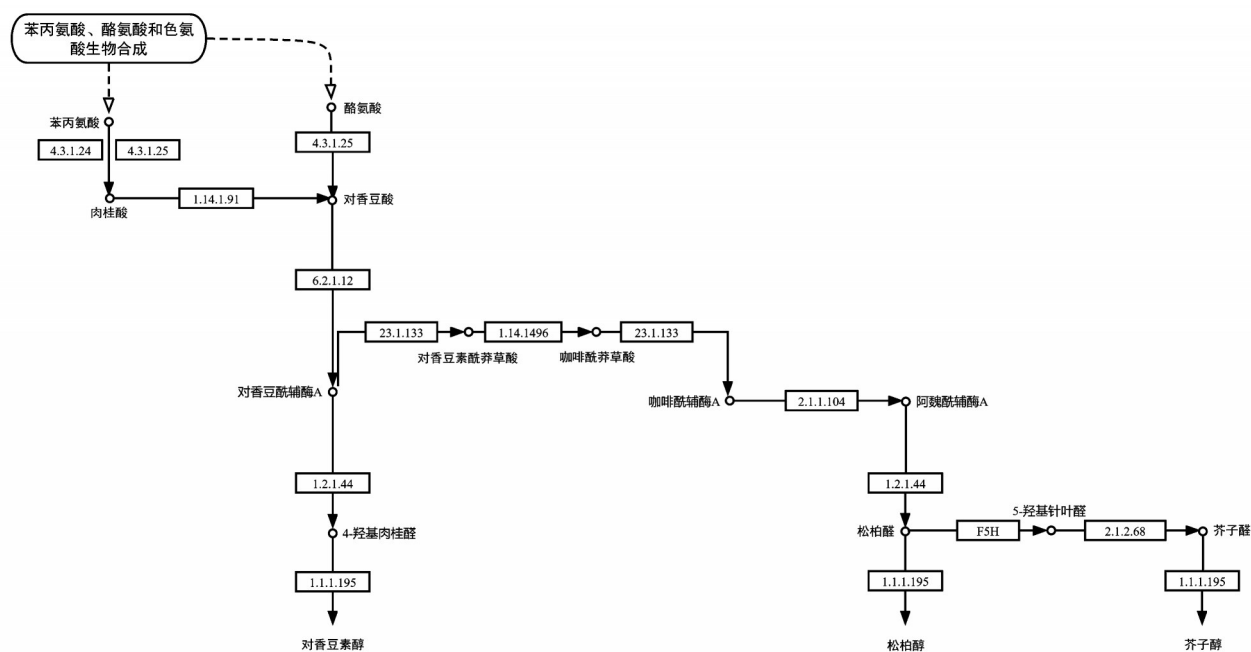


图6 苯基类丙烷生物合成通路

Fig. 6 Phenylpropanoid biosynthesis pathway

3 讨论

高粱作为高生物量能源植物,在重金属污染植物修复中得到广泛地应用^[20]. 本文结果表明,在 $\omega(\text{Cd})$ 为 $3 \text{ mg} \cdot \text{kg}^{-1}$ 水培的条件下高粱长度和生物量均有不同程度的下降,长度降低 $18.42\% \sim 28.05\%$,生物量降低 $0.83\% \sim 58.55\%$. 该结果与之前研究发现的Cd胁迫能导致高粱生物量降低,从而限制高粱修复重金属效率一致^[21,22]. 微塑料在水体和土壤等自然生态系统中与重金属共存时,能成为重金属潜在的转运载体,产生交互作用^[23,24]. 当微塑料与重金属共存时,吸附了重金属的微塑料被植物根系摄取很有可能提高重金属的生物毒性效应^[25]. Wang等^[26]探究了原始PVC微塑料与Cd对苦草 *Vallisneria spiralis* 的联

合毒性,发现PVC微塑料可以提高Cd对苦草的生长抑制。目前,关于微塑料与重金属复合污染对高粱生长和重金属积累的相关研究尚未开展。本实验表明,相较于单一Cd胁迫,Cd-PE的复合处理组中高粱长度降低24.86%~39.78%,生物量降低0.87%~38.60%,表现出微塑料和重金属协同抑制作用。联合毒性大于单一毒性在植物生长状态也得以验证,在水培过程中Cd-PE复合污染的处理组高粱生长明显出现叶片发黄现象,这与Khan等^[27]研究的微塑料PVC与Cr显著降低叶绿素含量等生理指标相一致。高粱不同部位对Cd-PE复合污染的响应有所差异,地下部鲜重和干重分别降低24.64%和10.36%,地上部鲜重和干重分别降低37.76%和17.04%,相比于高粱的地上部,地下部对Cd-PE复合污染更加敏感。这与

顾馨悦等^[23]研究的氯乙烯微塑料与Cd对小麦的联合毒性结果相一致,即根生长发育受到的抑制大于地上部,植物根系为直接摄取微塑料和重金属的部位,产生的胁迫较地上部更大。

植物促生细菌在重金属胁迫条件下植物生长和重金属积累方面起到重要作用,被广泛应用于强化植物对重金属的修复效果^[28]。重金属胁迫条件下植物促生细菌能通过多种植物促生特性缓解胁迫,提高高粱生物量和重金属积累量^[29]。Luo等^[30]研究表明具有产IAA和ACC脱氨酶的促生细菌*Bacillus* sp. SLS18,能提高Mn和Cd污染条件下高粱生物量37.0%~81%和重金属积累量18.6%~65.2%。微塑料与重金属共同存在的复合污染中,微塑料、重金属以及微塑料和重金属的交互均能对植物生长产生胁迫,影响植物的生长。该条件下植物促生细菌对植物生长影响的相关研究未见报道,本实验供试菌株VY-1具有多种植物促生特性,在Cd-PE复合污染中接种能显著提高地上部和地下部的长度,相较未接菌处理分别增加33.83%和73.21%。生物量结果与之类似,供试菌株VY-1的接种能提高Cd-PE复合污染中地上部和地下部干重,分别增加56.64%和33.44%。该结果与重金属-多环芳烃和重金属-盐碱等复合污染一致,植物促生细菌在复合污染条件下良好生存,通过直接或间接作用缓解复合污染导致的胁迫^[31-32]。相较于其他复合污染,微塑料具有较大的比表面积,能够为微生物提供附着点,在微塑料表面形成生物膜,植物促生细菌能否在微塑料表面定殖并形成生物膜以及细菌长期存在对微塑料的降解情况需要深入研究^[33]。

转录组测序在植物-微生物联合修复机制研究中具有广泛地应用^[34,35]。为了进一步解析促生细菌VY-1提高高粱耐受复合污染胁迫的机制,本实验采用转录组测序的方法分析了植物基因表达情况。在Cd-PE复合污染条件下接种促生细菌VY-1,高粱根部上调基因为904个。KEGG表达富集分析显示,这些DEGs在植物激素信号转导方面富集程度最高,差异的主体是生长素途径和脱落酸途径。有研究表明促生细菌能调节植物生长激素的变化来抵御外界重金属等的胁迫。Růžicka等^[36]研究表明在重金属胁迫条件下乙烯诱导生长素生物合成相关基因的表达,并刺激生长素向伸长区运输,从而使根伸长。Hu等^[37]研究发现植物激素脱落酸(ABA)在减轻植物重金属和类金属胁迫方面起着至关重要的作用。Cd-PE复合污染条件下促生细菌VY-1接种能上调表达生长素途径中的AUX/IAA基因、GH3基因和SAUR基因以及脱落酸途径中的PYR/PYL基因、PP2C基因、

SnRK2基因和ABF基因(图5),该结果表明菌株VY-1可能通过调节高粱生长素和脱落酸途径缓解Cd-PE复合污染导致的胁迫。苯基类丙烷生物合成通路也是差异基因中的组成(图6),苯丙烷是一大类植物的次级代谢产物,广泛分布于植物中,通过充当细胞壁的重要组成部分,在植物发育中发挥着至关重要的作用。植物对胁迫因子的常见反应包括PAL活性的增强和木质素含量的增加,经Cu或Cd处理的辣椒和大豆的木质素积累增加^[36-42]。Cd-PE复合污染条件下促生细菌VY-1接种能上调表达黄酮类合成通路中phenylalanine/tyrosine ammonialyas、transcinnamate 4-monooxygenase和4-coumarate-CoA ligase等多个基因以及木质素生物合成通路中cinnamoyl-CoA reductase、cinnamylalcohol dehydrogenase和caffeoyl-CoA O-methyltransferase等多个基因。重金属会增加活性氧(ROS)的水平,从而对植物细胞造成严重损害^[43]。有研究表明含过渡金属的类黄酮复合物具有超氧化物歧化酶活性,在缓解活性氧损伤中起到作用^[44]。以上结果表明菌株VY-1可能通过调节苯基类丙烷生物合成通路途径,缓解Cd-PE复合污染导致的胁迫。

4 结论

(1)相较于单一Cd胁迫,Cd-PE的复合处理组中高梁长度降低24.86%~39.78%,生物量降低0.87%~38.60%,表现出微塑料和重金属协同抑制作用。

(2)接种植物促生细菌VY-1能缓解Cd-PE复合污染的毒性,地上部和地下部长度分别增加33.83%和73.21%,干重分别增加56.64%和33.44%。植物促生细菌在微塑料和重金属复合污染环境缓解植物胁迫和提高修复效率中具有较好的应用前景。

(3)转录组测序分析表明,促生细菌VY-1能通过调节高粱生长素、脱落酸、黄酮类合成和木质素生物合成通路中多个基因表达,可能通过这些途径缓解Cd-PE复合污染导致的胁迫。

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