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·研究报告·

单列毛壳菌通过促进秸秆降解并调控激素响应基因表达促进玉米生长

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摘要 为探究生防真菌单列毛壳菌(*Chaetomium uniseriatum*)对秸秆降解和玉米(*Zea mays*)生长的影响, 将单列毛壳菌接种到玉米盆栽土壤中, 其它条件不变, 以保证单一变量。于拔节期和抽雄期进行采样, 通过测定土壤有机碳、土壤可溶性碳/氮、微生物量碳/氮以及酶活性, 探究接种单列毛壳菌对土壤生物化学指标的影响。在抽雄期对秸秆降解率、地上部生物量、叶片SPAD值、玉米根系激素含量及根系转录组进行分析, 探究接种单列毛壳菌对秸秆降解和玉米植株生长发育的影响。结果表明, 接种单列毛壳菌后, 土壤养分含量未出现显著性变化, β-葡萄糖苷酶(β-GC)活性显著降低; 抽雄期玉米地上部生物量、叶片SPAD值以及秸秆降解率均显著高于对照组; 玉米根系生长激素(IAA)和玉米素(ZR)含量均显著低于对照组。不同处理下玉米根系转录组分析筛选得到990个差异表达基因(383个基因表达上调, 607个基因表达下调); 对差异基因进行GO富集分析, 得到5个植物激素相关的条目; KEGG富集分析得到1个与植物激素相关的通路(*P* value<0.05, *Q* value<0.05)。综上, 单列毛壳菌通过促进秸秆降解以及调控作物根系激素响应基因的表达, 进而促进玉米生长。

关键词 单列毛壳菌, 转录组, 植物激素, 秸秆降解, 土壤养分

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秸秆还田作为提升耕层土壤肥力的重要途径已广泛应用于生产实践中, 在改良土壤物理结构(Zhao et al., 2019)、提高土壤养分含量(Liu et al., 2019)、促进作物增产(Xu et al., 2019)以及优化土壤微生物群落结构(Yang et al., 2020)等方面均具有重要作用。秸秆在腐生真菌的作用下充分降解, 释放作物可利用的养分(Singh and Sharma, 2002; Berthane et al., 2020)。因此, 具有秸秆促腐能力的微生物备受关注。研究表明, 曲霉属(Chen et al., 2018)、青霉属(Pedraza-Zapata et al., 2017)和木霉属(Laothanachareon et al., 2015)等腐生真菌在秸秆刺激下可以分泌大量纤维素降解酶, 从而促进秸秆降解。同时, 腐生真菌还可通过产生植物生长激素相关代谢产物直接刺激作物生长(Ortiz et al., 2019)。此外, 优势真菌种类可通过优化土壤土著微生物结构, 改良根系微环境来间接促进作物的生长发育(Liu et al., 2015; Raza et al., 2017)。

毛壳属真菌是子囊菌门中重要的农业生物防治真菌之一。研究表明, 该属真菌可以产生纤维素酶、果胶酶和蛋白酶等胞外酶(Abdel-Azeem et al., 2016), 不仅有效促进土壤中秸秆降解(Shanthiyaa et al., 2013), 还可以促进土壤养分活化和作物生物量的增加(Zhao et al., 2016)。毛壳属真菌产生的毛壳素可以抑制病原真菌生长, 而毛壳素的分泌会受到秸秆添加的强烈刺激(Park et al., 2005; Jiang et al., 2017)。此外, 毛壳属真菌分泌的赤霉素和生长素, 有助于改善叶芽生长状况, 提高叶片中的叶绿素含量和植物生物量(Khan et al., 2012)。

根际微生物作为植物的第二基因组受到广泛重视(Berendsen et al., 2012)。根际促生细菌的研究已

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经非常广泛, 如根瘤菌、佩氏无色杆菌和多粘拟杆菌(Yang et al., 2009)。促生菌在植物生长和代谢过程中发挥至关重要的作用。根际促生微生物在促进植物生长、提高作物产量以及增强植株抗性等方面具有巨大的应用潜力(Kang et al., 2014; Liu et al., 2020)。然而, 已往研究多从养分转化的角度展开。例如, 丛枝真菌通过促进作物对氮和磷的吸收来刺激其生物量的累积(Wang et al., 2002), 对根际促生菌与植物根系基因互作的关注较少。本团队的最新研究表明, 稀有腐生真菌头被孢霉可通过下调次级代谢相关基因、上调初级代谢相关基因的表达促进玉米(*Zea mays*)生物量的增加(Li et al., 2020)。本研究以应用潜力巨大的生防真菌单列毛壳菌(*Chaetomium uniseriatum*)为研究对象, 通过盆栽单变量对照实验研究该菌的添加对秸秆降解和玉米生长的影响, 并利用转录组测序技术探究单列毛壳菌接种对玉米根系基因表达的影响, 可为进一步开发微生物肥料奠定基础。

1 材料与方法

1.1 真菌产生生长素验证

取马铃薯葡萄糖液体培养基中的菌丝球, 用无菌去离子水冲洗2–3次, 接种于50 mL改性Czapek-Dox液体培养基(CDM) (Jaroszuk-Ściseł et al., 2014) (3.0 g $NaNO_3$, 1.0 g K_2HPO_4, 0.50 g $MgSO_4$, 0.50 g KCl, 0.01 g $FeSO_4$, 溶于1 L蒸馏水, 调pH至7.0)中。分别于三角瓶中添加1、2和3 mL 3 mmol·L^{-1}的无菌色氨酸溶液, 以不添加色氨酸溶液为空白对照, 28°C、150 r·min^{-1}黑暗培养7天。

培养结束后, 取上清液, 菌丝过滤后烘干称重。按照Glickmann和Dessaux (1995)提出的方法配置改性试剂。按照1:1 (v/v)的比例将改性试剂添加到上清液中, 28°C黑暗静置培养30分钟, 待反应体系变为粉红色, 测定530 nm处的吸光值并计算单位质量单列毛壳菌所产生长素的量。

1.2 实验设计与样品收集

盆栽实验于河南省封丘农田生态系统国家试验站进行。设置2个处理: 接种单列毛壳菌(*Chaetomium uniseriatum*)处理组(T)和空白对照组(CK), 每处理重复4次。每盆装10.0 kg砂质潮土, 供试土壤基本养分状况: 有机碳含量7.830 g·kg^{-1}, 全氮含量0.680 g·kg^{-1}, 有效磷含量125.767 mg·kg^{-1}, 含水量15%。处理组土壤中均匀混合30 g单列毛壳菌菌丝体以及50 mL马铃薯葡萄糖液体培养基, 便于菌种在土壤中定植; 对照组加入等量液体培养基以保持单一变量。按照盆栽实验设置当地农民每公顷还田135 000 kg (每亩9 000 kg)当季新鲜秸秆进行等比例换算, 得出每盆添加10 g烘干恒重的秸秆, 为方便盆栽收获后收集秸秆和计算降解率, 将秸秆装在100目尼龙网袋内, 随后埋入盆栽中。同时, 对玉米(*Zea mays* L.)种子进行催芽后播种, 每盆3粒, 三叶期剔苗。实验在日光温室内进行, 培养条件为28°C光照14小时/15°C黑暗10小时, 相对湿度为60%–80%, 土壤含水量控制在田间最大持水量的20%。

拔节期用土钻小心采集0–15 cm土壤, 避免破坏植株根系和网袋。抽雄期破坏性采样, 采集玉米植株地上部分称重后装入信封, 然后采集土壤样品和玉米根系样品, 并小心取出网袋中的秸秆。

1.3 指标测定

采用氯仿熏蒸法测定土壤微生物碳(microbial biomass carbon, MBC)和氮(microbial biomass nitrogen, MBN)含量(Vance et al., 1987; Wu et al., 1990); 采用K_2SO_4浸提法测定土壤可溶性碳(dissolved organic carbon, DOC)和氮(dissolved organic nitrogen, DON)含量, 均用MultiN/C2100分析仪进行测定(Manirakiza et al., 2019)。采用$K_2Cr_2O_7$外加热法测定有机碳(soil organic carbon, SOC)含量(鲍士旦, 2000); 土壤N-乙酰-β,D-葡聚糖酶(N-acetyl-β,D-glucosaminidase, NAG)和土壤β-葡萄糖苷酶(β-glucosidase, β-GC)采用Saiya-Cork等(2002)的方法测定(酶活单位: 1分钟内反应1 μmol底物, 为1个酶活单位U)。SPAD仪是一种便携式测量仪器, 测定方法简单、快速, 已有研究证明SPAD值在一定程度上可以较好地反映植物叶片中叶绿素的浓度(Uddling et al., 2007), 因此采用SPAD值来表征玉米叶片中叶绿素的含量。将网袋内的秸秆烘干称重, 计算秸秆降解率(degradation rate, DR)。玉米根系生长素(indole-3-acetic acid, IAA)、赤霉素(gibberellic acid, GA)、脱落酸(abscisic acid, ABA)以及玉米素(zeatin riboside, ZR)含量均使用上海Mlbio公司的ELISA试剂盒测定。

1.4 玉米根系转录组测序

使用TRIzol试剂盒提取玉米总RNA，并用Nanodrop和Agilent 2100对RNA的纯度和完整度进行检测。检测合格后用带有Oligo(dT)的磁珠进行富集，再用fragmentation buffer将富集得到的mRNA打断成较短片段。随后，以mRNA为模板，用六碱基随机引物进行反转录合成第1链cDNA，加入缓冲液、dNTPs和DNA聚合酶I，以第1链cDNA为模板合成第2链cDNA，此时，碱基U已被碱基T替换，达到构建链特异性文库的目的。利用AMPure XP beads纯化cDNA，对cDNA片段的大小进行选择，然后通过PCR扩增以构建cDNA文库。使用Agilent 2100检测文库的插入片段大小，并通过Q-PCR方法对文库的有效浓度进行精确定量(Archer et al., 2014)。利用Illumina HiSeqTM 2500技术，采用PE150测序策略进行测序。去除原始序列中不确定碱基比例大于10%的序列同时对低质量碱基(Q≤20)含量大于50%的序列进行质量控制。选用STAR (Spliced Transcripts Alignments to a Reference)进行比较分析，参考基因组为玉米v4版本(http://ftp.ensemblgenomes.org/pub/plants/release-49/fasta/zea_mays/dna/Zea_mays.B73_RefGen_v4.dna.toplevel.fa.gz)。测序原始数据已上传至NCBI (National Center for Biotechnology Information Search Database)网站，编号为: PRJNA693635。

1.5 数据分析

利用IBM SPSS Statistics 26软件对土壤和植株理化指标进行独立样本T检验，利用GraphPad Prism 8软件实现图片可视化。使用HtSeq对各样品进行基因表达水平分析，模型为union，计算每百万Reads中来自某一基因每千碱基长度的Fragments数目，即FPKM (fragments per kilobase of exon model per million mapped reads)，将FPKM值为1作为判断基因是否表达的阈值。基因表达水平分析得到的readcount数据中有生物学重复的样品，采用Anders提出的基于R/Bioconductor的DESeq差异基因分析方法(Anders and Huber, 2010)对不同处理下的差异表达基因进行分析。GO (Gene Ontology)是国际标准化的基因功能分类体系，包括分子功能(molecular function)、生物学过程(biological process)和细胞组分(cellular component) 3个ontology (Ashburner et al., 2000)。KEGG (Kyoto Encyclopedia of Genes and Genomes)是系统分析基因功能和基因组信息数据库，为Pathway相关的主要公共数据库(Kanehisa et al., 2008)。采用基于R/Bioconductor中的clusterProfiler、topGO、Rgraphviz以及pathview进行GO和KEGG富集，采用ggplot2进行图片可视化。

2 结果与讨论

2.1 单列毛壳菌产生生长素能力

在用马铃薯葡萄糖液体培养基培养单列毛壳菌的同时，添加生长素合成前体物质色氨酸。结果发现，随着色氨酸量的增加，单位质量的菌丝产生生长素的量随之增加(图1)。当在50 mL培养基中添加3 mL 3 mmol·L^{-1}色氨酸溶液时，产生的生长素量最多，且显著高于添加1和2 mL色氨酸溶液的处理。

2.2 添加单列毛壳菌后盆栽土壤和植株理化性质变化

分别于拔节期和抽雄期采集土壤样品，测定土壤可溶性碳/氮、微生物量碳/氮、土壤酶活性以及土壤有机碳含量。以相应阶段的对照组为参照，对数据进行归一化后作图，反映了不同时期各指标相对于对照的变

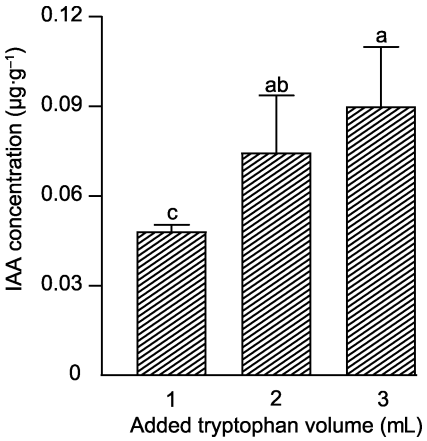

图1 不同浓度色氨酸条件下单列毛壳菌产生生长素(IAA)的浓度

不同小写字母表示在5%水平差异显著(n=4)。

Figure 1 The concentration of indole-3-acetic acid (IAA) produced by *Chaetomium uniseriatum* with different concentrations of tryptophan

Different lowercase letters indicate significant differences at 5% level (n=4).

化倍数(图2)。结果表明, 添加单列毛壳菌后, 拔节期土壤DOC、DON、SOC以及NAG含量高于对照组, 分别增加了1.07、1.03、1.02及1.04倍; 而MBC、MBN以及β-GC则低于对照组, 其中β-GC表现出显著性差异。到抽雄期后, 土壤微生物量碳/氮以及NAG活性均高于对照组, 分别增高了1.30、1.01以及0.99倍; DOC、SOC和β-GC则低于对照组, 其中β-GC表现出显著性差异。

接种单列毛壳菌后玉米根系IAA (图3A)、ABA (图3B)及ZR (图3D)含量有所降低, GA (图3C)含量则略微升高。其中, IAA和ZR含量分别显著降低了12.83%和10.09%。单列毛壳菌处理的玉米地上部干重(图3E)、盆栽内秸秆降解率(图3F)以及叶片SPAD (图3G)分别显著增加了19.37%、10.21%和16.45%。

2.3 差异表达基因的功能注释及GO富集分析

8个样品产生的reads总数为243 904 286, 总raw bases为36.55 G, 过滤后的clean reads数量为234 146 455, 总clean bases为35.13 G。对质控后的数据进行后续分析, 基因表达水平用FPKM值表征。采用R软件的DESeq包分析得到玉米根系中的差异表达基因共990个(图4A), 其中607个差异基因表达水平下调, 包括植物抗病性相关基因(*Zm00001d-032724*)和吲哚-3-乙酸酰胺合成酶基因(*Zm00001-d022017*); 383个差异基因表达水平上调, 包括生长素应答蛋白IAA26基因(*Zm00001d010360*)。

通过GO将差异表达基因进行功能分类注释, 得到*P* value<0.05的GO分类条目共87个。在生物学过程、细胞组分和分子功能中所占的比例分别为65.52% (57个)、4.60% (4个)和29.89% (26个)。图4B展示条目为GO富集的其中9个条目, 包括激素的响应(GO:0009725)、激素介导的信号通路(GO:0009755)、生长激素的信号通路(GO:0009734)、生长素的响应(GO:0071365, GO:0009733)、有机物响应(GO:007-1310)、光合作用(GO:0009768)、胡萝卜素代谢(GO:0016119)以及生物合成正调控(GO: 0009891), 其中与植物激素相关的条目共5个。

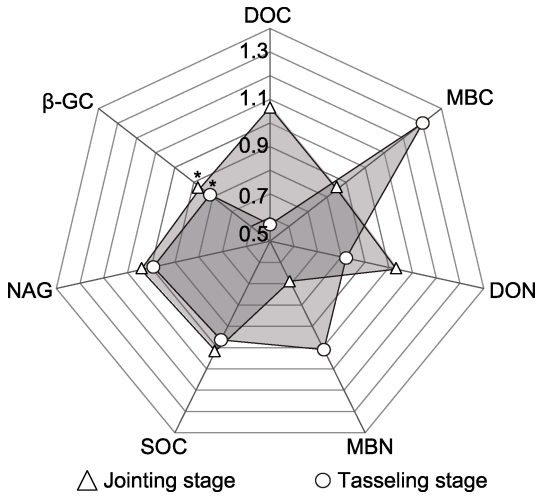

图2 不同时期土壤性质相对于对照的变化倍数

图中数值为土壤性质相对于对照的变化倍数, * 表示在5%水平差异显著。DOC: 可溶性碳; MBC: 微生物量碳; DON: 可溶性氮; MBN: 微生物量氮; NAG: N-乙酰-β,D-氨基葡萄糖苷酶; β-GC: β-葡萄糖苷酶; SOC: 土壤有机碳

Figure 2 Fold change of soil properties relative to the control in different periods

The values in the figure are the change fold of soil properties relative to the control. * indicated significant differences at 5% level. DOC: Dissolved organic carbon; MBC: Microbial biomass carbon; DON: Dissolved organic nitrogen; MBN: Microbial biomass nitrogen; NAG: N-acetyl-β,D-glucosaminidase; β-GC: β-glucosidase; SOC: Soil organic carbon

2.4 差异表达基因的KEGG富集分析

依托KEGG系统基因组信息数据库, 对检测到的玉米差异表达基因所参与的代谢途径进行富集分析。结果表明, 这些差异基因分布于75个代谢通路中, 继续进行富集共发现7个*P* value<0.05的通路(图5), 分别为丙氨酸、天冬氨酸和谷氨酸代谢(alanine, aspartate and glutamate metabolism)通路、植物激素信号转导(plant hormone signal transduction)通路、苯丙酸生物合成(phenylpropanoid biosynthesis)通路、类胡萝卜素生物合成(carotenoid biosynthesis)通路、光合作用-触角蛋白(photosynthesis-antenna proteins)通路、MAPK信号通路(MAPK signaling pathway)、类黄酮生物合成(flavonoid biosynthesis)通路。其中, 丙氨酸、天冬氨酸和谷氨酸代谢及植物激素信号转导达到显著水平(*P* value<0.05且*Q* value<0.05)。

利用R软件的Pheatmap包对植物激素信号转导通路(plant hormone signal transduction)中的基因进行聚类分析(图6), 发现接种单列毛壳菌条件下植物激素合成的相关基因, 如AUX/IAA-转录因子基因(*Zm00001d033976*)和吲哚-3-乙酸酰胺合成酶基因

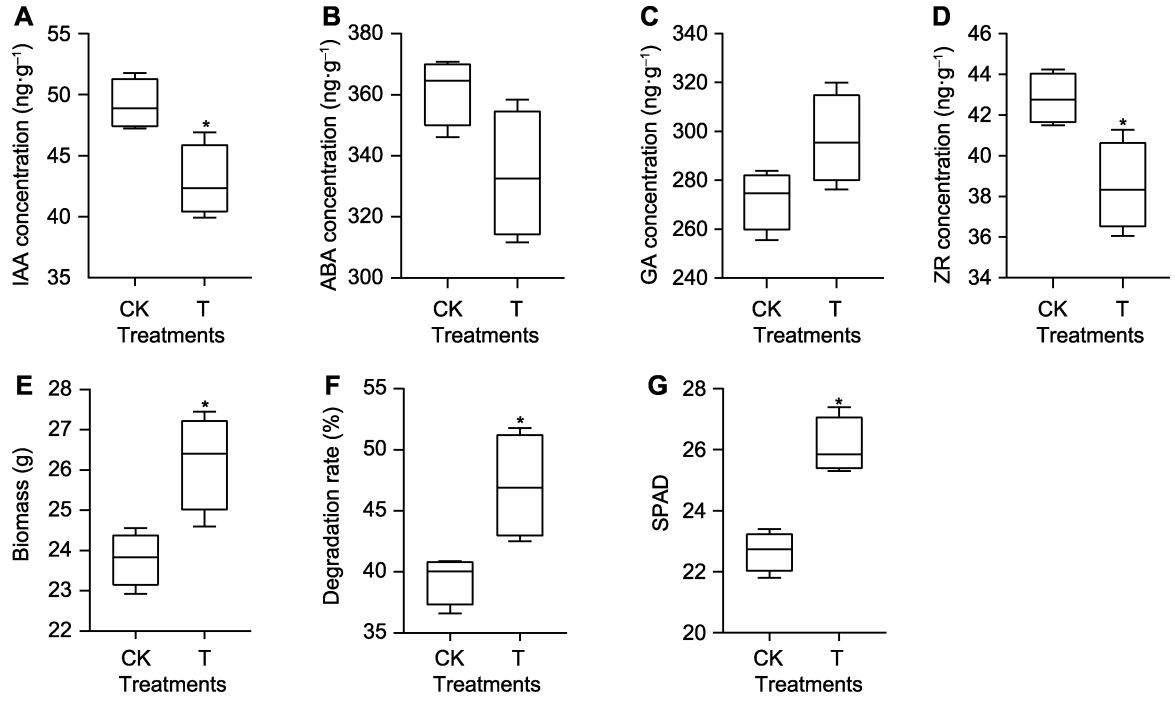

图3 接种单列毛壳菌对玉米生理特性的影响

(A) 玉米根系生长素(IAA)含量; **(B)** 玉米根系脱落酸(ABA)含量; **(C)** 玉米根系赤霉素(GA)含量; **(D)** 玉米根系玉米素(ZR)含量; **(E)** 玉米地上部生物量; **(F)** 网袋内秸秆降解率; **(G)** 玉米叶片SPAD值。* 表示5%水平差异显著(n=4)。CK表示对照处理; T表示接菌处理。

Figure 3 Effects of *Chaetomium uniseriatum* inoculation on maize physiological characteristics

(A) Auxin (IAA) content in maize roots; **(B)** Abscisic acid (ABA) content in maize roots; **(C)** Gibberellin (GA) content in maize roots; **(D)** Zeatin (ZR) content in maize roots; **(E)** Aboveground biomass of maize; **(F)** Degradation rate of straw in net bag; **(G)** SPAD value of maize leaves. * indicated significant differences at 5% level (n=4). CK represents the control treatment; T represents the inoculation treatment.

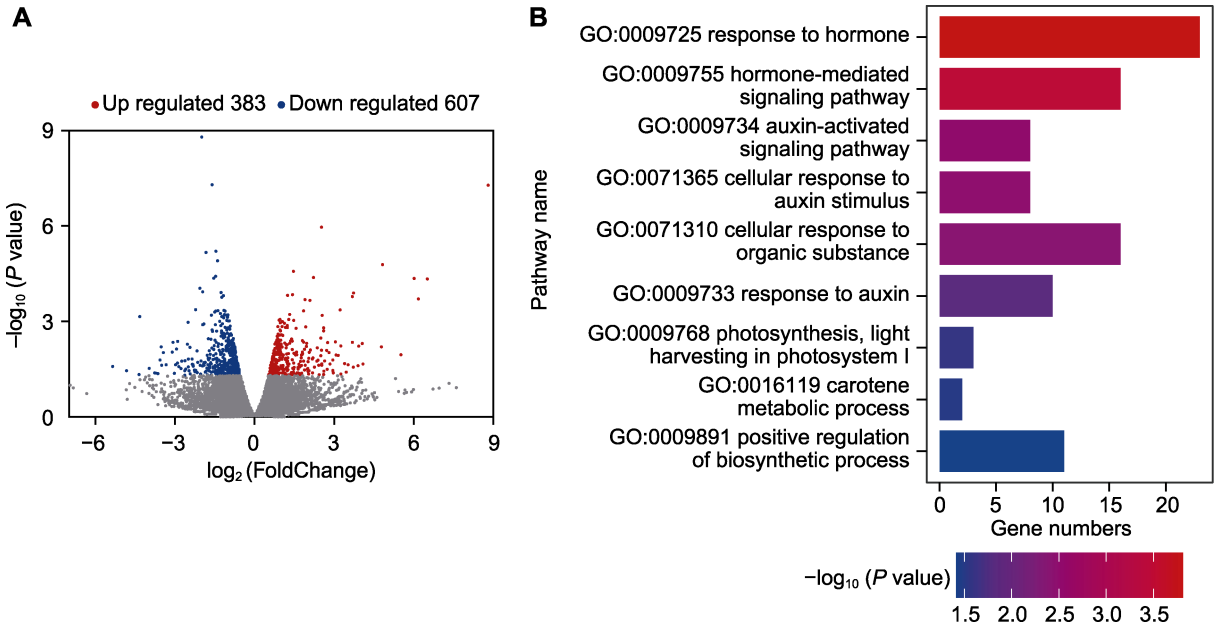

图4 接种单列毛壳菌后玉米差异表达基因分析

(A) 上调和下调基因的数量; **(B)** 差异表达基因的GO功能注释分类

Figure 4 Analysis of differentially expressed genes in maize after inoculation with *Chaetomium uniseriatum*
(A) The number of up-regulated/down-regulated genes; **(B)** The results of GO annotation on differentially expressed genes

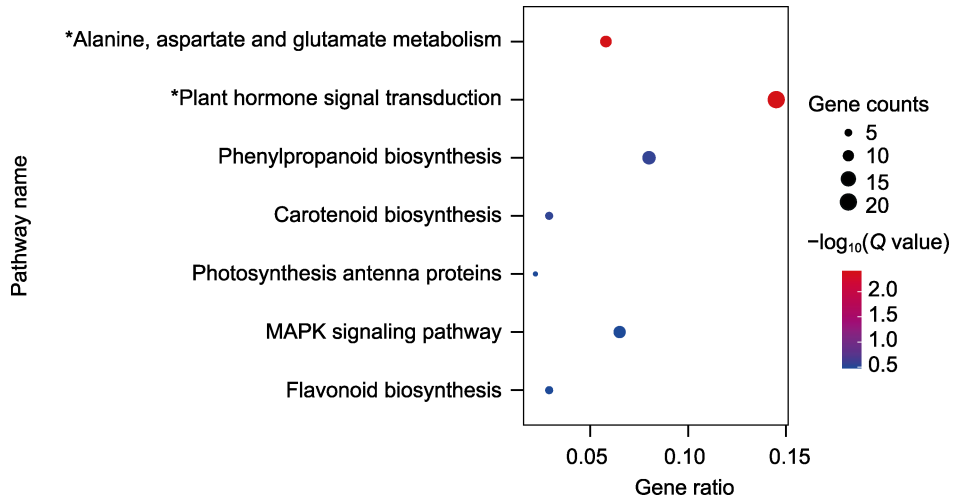

图5 差异表达基因的KEGG通路富集散点图
* 表示*P* value<0.05且*Q* value<0.05。

Figure 5 Scatter plot of KEGG enrichment of differentially expressed genes
* indicated *P* value<0.05 and *Q* value<0.05.

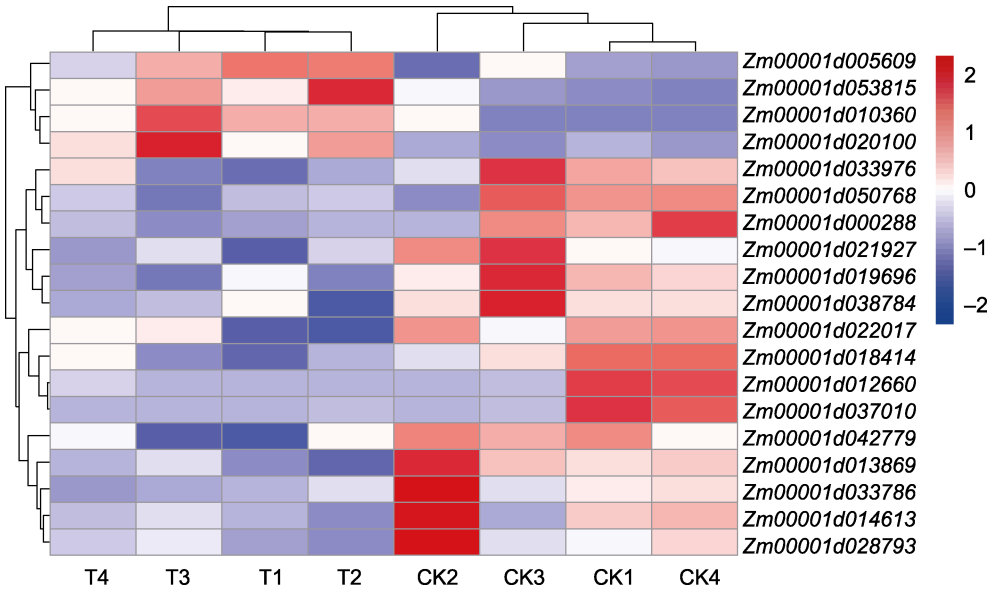

图6 植物激素信号转导通路相关基因聚类分析
CK1–CK4: 对照处理; T1–T4: 接菌处理

Figure 6 Cluster analysis of genes involved in plant hormone signal transduction pathway
CK1–CK4: Control; T1–T4: Inoculation treatment

(*Zm00001d022017*)表达下调，而植物激素应答的相关基因，如生长素应答蛋白SAUR71基因(*Zm00001d053815*)和生长素应答蛋白IAA26基因(*Zm00001d010360*)表达上调。

2.5 讨论

毛壳属真菌有较强的植物残基降解能力，接种后玉米秸秆降解率显著增加了19.37%。这可能是由于毛壳属真菌分泌的纤维素酶促进网袋内秸秆中纤维素的

降解(Jiang et al., 2020)。然而，本研究中并未发现土壤中养分的显著增高，可能与玉米根系的吸收转化有关。β-GC参与纤维素糖化过程的最后一步，与内切葡聚糖酶和纤维二糖水解酶协同作用，将纤维二糖降解为葡萄糖，是土壤有机碳循环的重要环节(Cañizares et al., 2011)。本研究中，接菌处理后β-GC活性显著降低，我们推测这与单列毛壳菌在秸秆降解过程中起主导作用的酶有关。纤维素酶是可以降解纤维素的复杂酶系，根据反应位点、底物以及产物的不同，可以分为内切β-葡聚糖酶、外切β-葡聚糖酶和β-葡萄糖苷酶(何芳芳等，2020)。内切β-葡聚糖酶随机作用于β-1,4-糖苷键，将长链纤维素分子截成大小不同的短链。存在于大多数丝状真菌中的外切β-葡聚糖酶作用于非还原性和还原性纤维素分子，得到纤维二糖或葡萄糖。β-葡萄糖苷酶能将纤维二糖彻底水解成葡萄糖(Yun et al., 2001)。有研究表明，毛壳属真菌可以产生较高活性的内切葡聚糖酶和外切葡聚糖酶(Shanthiyaa et al., 2013)。因此我们推测，单列毛壳菌在秸秆降解过程中主要依赖内切β-葡聚糖酶和外切β-葡聚糖酶，而不是β-GC。此外，单列毛壳菌通过分泌毛壳素等物质(Sato et al., 2016)，抑制其它依赖β-GC获取葡萄糖的微生物活性，以减少竞争者的数量，获得更多的养分，从而引起土壤中的β-GC活性下降。

IAA和ZR在玉米生长过程中发挥重要作用。本研究显示，接种单列毛壳菌的玉米地上部生物量和SPAD值分别显著增加了10.21%和15.13%，而IAA和ZR含量分别显著下降了12.83%和10.09%。与此类似，拟南芥(*Arabidopsis thaliana*)幼苗(Narukawa-Nara et al., 2016)和玉米(Li et al., 2018)表现出侧根和根毛增多以及生物量增加时，亦检测到内源性生长素水平呈下降趋势。造成这种矛盾现象的原因可能是玉米根系周围存在外源性激素。而外源生长素的添加会抑制植物根系内源性生长素的合成(Kang et al., 2014)。本研究证实了单列毛壳菌具有向环境中分泌生长素的能力。并且Fattorini等(2009)研究表明，植物同样能感知外源激素并做出响应。本研究中，GO富集分析发现5个与植物激素相关的信号条目(图4B)，KEGG富集得到1个激素相关通路(图5)。综上，玉米根系对单列毛壳菌产生的生长素及其它激素类似物作出响应，激素应答相关基因表达上调，最终表现为促进生长。

毛壳属真菌是在抑制土传病原菌生长和繁殖过程中发挥关键作用的生防菌(Siegel-Hertz et al., 2018)。其产生的毛壳素以及次级代谢产物chaetoviridin A和B (Sato et al., 2016)对马铃薯晚疫病(Shanthiyaa et al., 2013)、稻瘟病和小麦叶锈病(Park et al., 2005)等真菌病害的生物防治均有显著效果，可以有效减缓病原菌对作物的生物胁迫(Zhang et al., 2019)。本研究中，接种单列毛壳菌后玉米根系生长素含量降低，多个抗性相关基因表达下调，其中1个显著下调($|\log_2(\text{FoldChange})|\geq 1$, $P<0.05$) (表1)，表明接种单列毛壳菌对根际土壤环境具有很好的改良作用(Wang et al., 2017)，营造了低染病率的根际环境，可使作物在提高抗逆性方面分配更少的物质和能量，从而使作物将更多能量用于细胞组分合成及生长，整体表现为生物量增加(Kazan and Manners, 2009)。

结合植物激素含量测定结果、土壤和植株理化性质以及对玉米根系转录组结果进行分析，我们推测单列毛壳菌能通过生物合成生长素刺激作物生长，最终表现为生物量增加。为验证这一推测，我们通过实验室培养确定了单列毛壳菌合成生长素的能力。研究表明，植物组织中生长素的动力学和转运受生长素相关细胞信号通路的调节，生长素通过ARF-Aux/IAA信号通路影响基因表达(Leyser, 2005)。结合本研究结果，我们提出了添加单列毛壳菌促进玉米生长的推定机理(图7)。即单列毛壳菌利用土壤中的少量色氨酸合成生长素并分泌到根际，这些生长素被根系细胞膜上的生长素运输载体AUX1捕获，进一步运输至细胞内(Allen and Ptashnyk, 2020)。随后与生长素受体TIR1结合并在其帮助下穿过核膜进入细胞核内(滕青云等，2020)。泛素化作用将AUX1-IAA-TIR复合体水解，释放IAA。游离的生长素作用于生长素响应因子ARF (Guilfoyle et al., 1998)，使得ARF与DNA双螺旋结构上的生长素反应元件启动子结合，促使玉米根系基因的表达发生变化，并促进生长素信号转导因子SAUR (郭栋等，2019)的响应和生长素转运载体AUX/IAA (Leyser，2005)的生物合成。IAA在IAA酰胺合成酶CH3的作用下进行酰胺化，与丙氨酸、谷氨酸和天冬氨酸结合(Millevoi and Vagner, 2010)，使IAA可以在植物体中发挥作用。通过对差异表达基因进行检索发现，接种单列毛壳菌后玉米根系丙氨酸转运相关酶

表1 抗病相关基因表达情况

Table 1 Expression of genes associated with disease resistance

Gene	log_2(FoldChange)	*P* value	Gene description
*Zm00001d032724**	–1.541	0.000	Disease resistance RPP13-like protein 4
*Zm00001d035172**	–0.901	0.041	Disease resistance protein RPM1
Zm00001d030888	–0.327	0.227	Probable disease resistance protein
Zm00001d054090	–1.297	0.259	Protein enhanced disease resistance 2
Zm00001d041343	–0.278	0.307	Probable disease resistance protein
Zm00001d043197	–0.549	0.349	Probable disease resistance protein
Zm00001d052992	–0.251	0.368	Disease resistance protein RPM1
Zm00001d021491	–0.267	0.370	Disease resistance RPP13-like protein 4
Zm00001d041358	–1.208	0.394	NBS-LRR disease resistance protein-like
Zm00001d043233	–0.239	0.407	Disease resistance gene analog PIC21
Zm00001d031711	–0.529	0.435	Disease resistance gene analog PIC15
Zm00001d032510	–0.632	0.473	Putative disease resistance RPP13-like protein 1
Zm00001d006873	–0.329	0.517	Disease resistance response protein-like; protein
Zm00001d007776	–0.298	0.519	Disease resistance protein RGA2
Zm00001d024681	–0.599	0.547	Disease resistance protein RPM1
Zm00001d017954	–0.179	0.554	Disease resistance protein RPM1
Zm00001d049121	–0.296	0.582	Disease resistance protein RPM1
Zm00001d035973	–0.159	0.601	Protein enhanced disease resistance 2
Zm00001d048663	–0.180	0.611	Disease resistance protein RGA2
Zm00001d024977	–0.376	0.623	Disease resistance protein RPM1
Zm00001d014654	–0.130	0.651	Disease resistance protein RPM1
Zm00001d034555	–0.179	0.653	Disease resistance protein RPM1
Zm00001d006755	–0.260	0.658	Disease resistance RPP13-like protein 4
Zm00001d021564	–0.936	0.681	Disease resistance protein RPM1
Zm00001d014876	–0.104	0.726	Disease resistance RPP13-like protein 4
Zm00001d037648	–0.090	0.753	Disease resistance protein RPP13
Zm00001d024975	–0.111	0.756	Disease resistance protein RPM1
Zm00001d048639	–0.147	0.762	Disease resistance protein RPM1
Zm00001d007935	–0.593	0.781	Disease resistance response protein 206
Zm00001d007630	–0.051	0.844	Disease resistance protein RPS2
Zm00001d023923	–0.056	0.872	Disease resistance protein RPM1
Zm00001d045512	–0.177	0.886	Putative disease resistance RPP13-like protein 3
Zm00001d044172	–0.022	0.903	SGT1 disease resistance protein homolog1
Zm00001d045335	–0.027	0.916	Putative disease resistance RPP13-like protein 1
Zm00001d052389	–0.094	0.923	Disease resistance protein RPM1
Zm00001d048637	–0.062	0.950	Disease resistance RPP13-like protein 4
Zm00001d048635	–0.282	0.971	Disease resistance protein RPM1
Zm00001d032166	–0.016	0.975	Protein enhanced disease resistance 2
Zm00001d053244	–0.002	1.000	Disease resistance protein (TIR-NBS class)
Zm00001d048613	–0.031	1.000	Disease resistance protein RGA2

**P* value<0.05

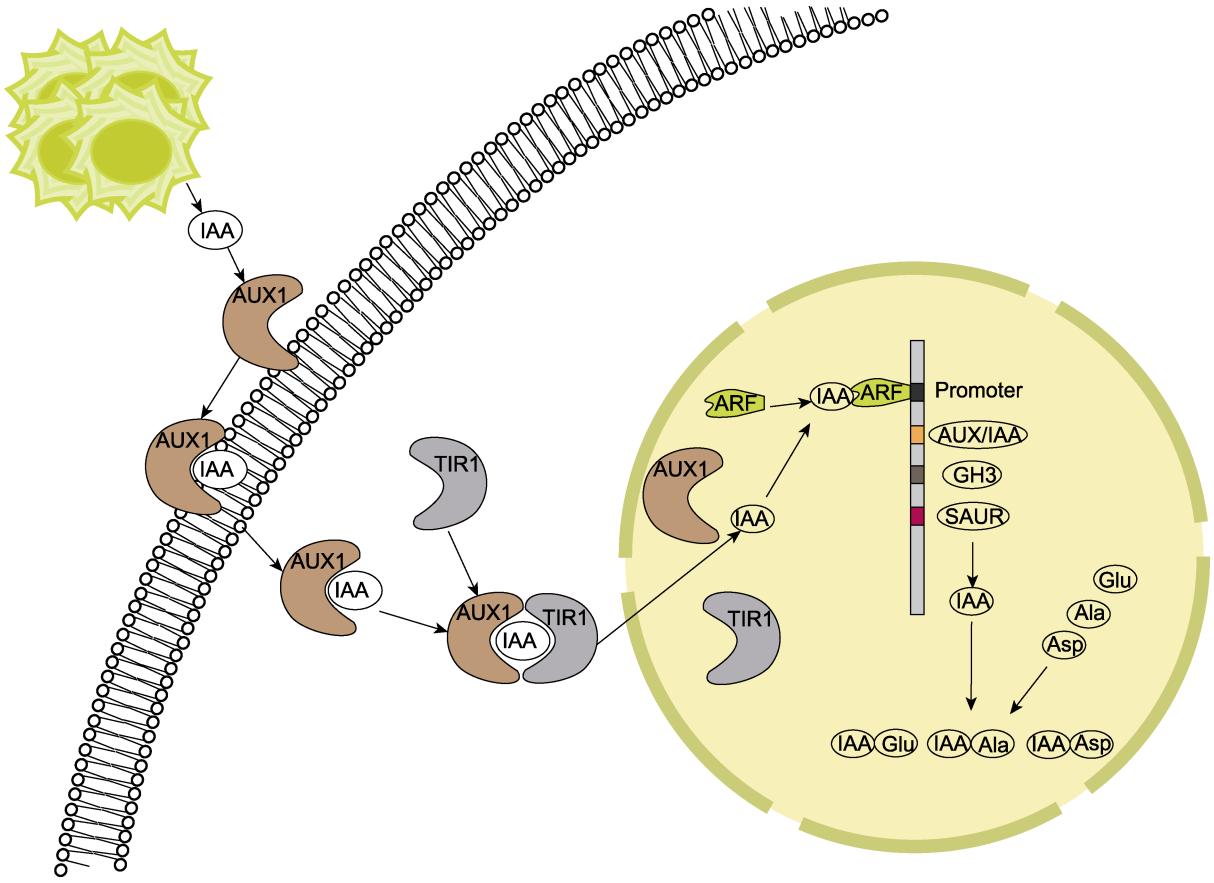

图7 单列毛壳菌促进玉米生长的机制
IAA: 生长素; Asp: 天冬氨酸; Ala: 丙氨酸; Glu: 谷氨酸

Figure 7 Mechanism of maize growth promotion by *Chaetomium uniseriatum*
IAA: Auxin; Asp: Aspartate; Ala: Alanine; Glu: Glutamate

及ARF转录因子差异表达。

3 结论

本研究表明，接种单列毛壳菌显著促进了土壤中秸秆的降解和作物生物量的增加。作为一种生防真菌，单列毛壳菌可通过改良土壤环境并优化根系基因表达来促进作物生长，表现出一定的促生潜力。

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Chaetomium uniseriatum Promotes Maize Growth by Accelerating Straw Degradation and Regulating the Expression of Hormone Responsive Genes

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Abstract To explore the effect of *Chaetomium uniseriatum* on straw degradation and maize growth, *C. uniseriatum* was inoculated into pots planted with maize, with other conditions unchanged to ensure a single variable. The soil organic carbon, microbial biomass C/N, dissolved organic C/N content and enzymes activities were measured to assess the response of soil biochemical properties to *C. uniseriatum* inoculation at jointing and tasseling stage. The degradation rate of straw, aboveground biomass, SPAD value of leaves, root hormones and root transcriptomes were investigated to verify the influence of *C. uniseriatum* on the growth of maize. The soil nutrients content did not change significantly in inoculated treatments, while the activity of β-glucosidase (β-GC) decreased significantly. At tasseling stage, the aboveground biomass, SPAD value of leaves and degradation rate of straw were significantly enhanced in inoculated treatments as compared with the control. The contents of auxin (IAA) and zeatin (ZR) in maize roots were significantly lower than those in control. Transcriptome analysis of maize roots revealed that there were 990 differentially expressed genes (607 down regulated and 383 up regulated) between the two treatments. Five GO terms associated with regulation of plant hormones were enriched, and one hormone related pathway was enriched significantly (P value<0.05, Q value<0.05) according to KEGG annotation. Our study revealed that *C. uniseriatum* could improve maize growth by accelerating straw degradation and regulating the expression of hormone response genes in roots.

Key words *Chaetomium uniseriatum*, transcriptome, phytohormone, straw degradation, soil nutrients

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