2026, 66(10): 5009-5024
CSTR: 32112.14.j.AMS.20260194
DOI: 10.13343/j.cnki.wsxb.20260194

微生物学报
Acta Microbiologica Sinica
http://journals.im.ac.cn/actamicrocn

Research Article 研究报告

雪白睡莲内生促生真菌的分离鉴定及其对睡莲幼苗早期生长的促进作用

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邢玉伟, 刘聪, 刘阳, 王军. 雪白睡莲内生促生真菌的分离鉴定及其对睡莲幼苗早期生长的促进作用[J]. 微生物学报, 2026, 66(10): 5009-5024.
XING Yuwei, LIU Cong, LIU Yang, WANG Jun. An endophytic plant growth-promoting fungus from *Nymphaea candida*: isolation, identification, and evaluation of its promoting effects on early seedling growth[J]. Acta Microbiologica Sinica, 2026, 66(10): 5009-5024.

摘　要：雪白睡莲(*Nymphaea candida* C. Presl)是我国珍稀的睡莲品种，因其自然发芽率很低等因素而濒临灭绝，培育适用于人工繁育的健壮种苗成为了该物种保护的关键。【目的】通过分离和鉴定雪白睡莲根系内生促生真菌，评估其对雪白睡莲幼苗的促生作用，并初步解析其促生机制。【方法】从雪白睡莲根内分离得到了一株球毛壳菌(*Chaetomium globosum*)，并通过盆栽试验评估施加 *C. globosum* 后对雪白睡莲生长、土壤理化性质、根际微生物群落结构以及叶片基因表达量差异的影响。【结果】施加 *C. globosum* 后，雪白睡莲的叶长、叶宽、叶片个数和根系长度分别显著增加了 46.74%、96.08%、64.71% 和 130.13%，同时显著提高了土壤中有机质、碱解氮含量及蔗糖酶等活性。根际微生物群落分析表明，*C. globosum* 招募了 norank-p-*Cryptomycota*、norank-o-*Monhysterida*、*Surirella*、norank-p-*Aphelidea* 等有益微生物，改善了根际微生物群落结构。叶片转录组分析表明，施用 *C. globosum* 能够显著上调类固醇生物合成通路相关基因的表达。【结论】*C. globosum* 可通过改善根际微环境、招募有益微生物，以及调控叶片类固醇生物合成等途径有效促进雪白睡莲幼苗生长。该菌株有望为珍稀濒危植物雪白睡莲的种质资源保护提供可靠工具。

关键词：球毛壳菌；雪白睡莲；双菱藻属；类固醇生物合成通路

资助项目：新疆维吾尔自治区重点研发任务专项(2023B02037)
This work was supported by the Key Research and Development Program for Special Project of Xinjiang Uygur Autonomous Region (2023B02037).
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Received: 2026-03-10; Accepted: 2026-04-07; Published online: 2026-05-13

An endophytic plant growth-promoting fungus from *Nymphaea candida*: isolation, identification, and evaluation of its promoting effects on early seedling growth

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Abstract: *Nymphaea candida* C. Presl, a rare water lily species in China, is on the brink of extinction due to its extremely low natural germination rate. Obtaining robust seedlings suitable for artificial propagation has become a key for the conservation of this species. **[Objective]** To isolate and identify endophytic plant growth-promoting fungi from the roots of *N. candida* and evaluate their growth-promoting effects on seedlings. **[Methods]** Pot experiments were carried out with *Chaetomium globosum* isolated from *N. candida* to assess its effects on the growth of *N. candida*, soil physicochemical properties, rhizosphere microbial community structure, and leaf gene expression. **[Results]** The application of *C. globosum* significantly increased the leaf length, leaf width, number of leaves, and root length of *N. candida* by 46.74%, 96.08%, 64.71%, and 130.13%, respectively. Moreover, the application of *C. globosum* significantly increased soil organic matter, alkali-hydrolyzable nitrogen content, and sucrase activity. Rhizosphere microbial community analysis indicated that the application of *C. globosum* specifically enriched beneficial microorganisms, including norank-p-*Cryptomycota*, norank-o-*Monhysterida*, *Surirella*, and norank-p-*Aphelidea*. Leaf transcriptome analysis further revealed that *C. globosum* significantly upregulated the expression of the genes related to the steroid biosynthesis pathway. **[Conclusion]** *C. globosum* effectively promotes the growth of *N. candida* seedlings by improving the rhizosphere microenvironment, recruiting beneficial microorganisms, and regulating steroid biosynthesis in the leaves. Thus, the endophytic plant growth-promoting fungus *C. globosum* might be a reliable tool for the conservation of the endangered plant species *N. candida*.

Keywords: *Chaetomium globosum*; *Nymphaea candida*; *Surirella*; steroid biosynthesis pathway

睡莲(*Nymphaea*)为多年生水生草本植物，全球约有 50 种，中国原产 5 种，其中雪白睡莲(*Nymphaea candida* C. Presl)作为我国珍稀濒危品种仅分布在新疆地区[1]。雪白睡莲不仅具有较高的观赏价值，还是湿地生态系统健康状况的指示物种，在净化水质、提供野生动物栖息地等方面发挥重要生态功能[2]。雪白睡莲的种子被水禽大量捕食、自然发芽率很低，萌发过程易受病害干扰，导致其分布面积不断减少[3-4]。目前，雪白睡莲已被列入《世界自然保护联盟濒危物种红色名录》(IUCN red list of threatened species, IUCN Red List)和《国家重点保护野生植物名录》[2]。鉴于自然繁殖很难实现雪白睡莲的有效保护，亟需开展种苗的人工繁育工作。值得注

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意的是，在雪白睡莲幼苗人工繁育过程中常出现玻璃化现象，这一生理障碍严重影响根系发育与种苗移栽成活率[5]。因此，如何促进雪白睡莲早期生长，获得适于人工繁育的健壮种苗，成为该物种保护面临的关键问题。

近年来，接种具有固氮、溶磷和分泌植物激素能力的植物促生细菌成为促进水生植物生长的重要工具。例如，枯草芽孢杆菌(*Bacillus subtilis*)、荧光假单胞菌(*Pseudomonas fluorescens*)和贝莱斯芽孢杆菌(*Bacillus velezensis*)等细菌通过分泌生长激素加快根系发育，增加叶片叶绿素含量，促进植物生长，在水生植物促生方面表现出良好潜力[6-10]。在水生生态系统中，植物促生细菌会与植物竞争微量元素，pH 兼容性较差，并且某些固氮细菌会在水体中急剧死亡，限制了它们的应用[11-12]。相比之下，植物促生真菌，尤其是植物内生促生真菌具有更强的根系定殖、抑制病原菌和促进生物降解的能力，在促进植物生长和生物量积累方面发挥积极作用[13-16]。目前，研究较多的内生促生真菌包括木霉属(*Trichoderma*)、青霉属(*Penicillium*)、黄孢属(*Talaromyces*)和暗色有隔内生真菌等[17-18]。它们在提高植物生物量、产量及养分含量等方面起到重要作用[19-20]。例如，球毛壳菌(*Chaetomium globosum*)通过产生植物激素及抗菌活性物质促进拟南芥(*Arabidopsis thaliana*)的生长[21]。曲霉(*Aspergillus* spp.)通过溶解磷酸盐提高土壤养分有效性，促进木薯(*Manihot esculenta* Crantz)根系生长[22]。哈茨木霉(*Trichoderma harzianum*)和金龟子绿僵菌(*Metarhizium anisopliae*)分别能使水浮莲(*Pistia stratiotes*)鲜重增加 23.30% 和 10.30%[23]。我们推测从雪白睡莲体内分离的内生促生真菌具有促进幼苗生长、提高种苗繁育效率的潜力，可为雪白睡莲健壮种苗的培育提供可靠工具。

本研究旨在为我国珍稀濒危植物雪白睡莲种苗的培育提供科学支撑。本研究拟对雪白睡莲根系的内生促生真菌进行分离与鉴定，测定其潜在促生性能。随后，将筛选出的内生真菌用于雪白睡莲幼苗的栽培，定期测定雪白睡莲幼苗叶长、叶宽和根长等指标，评估内生真菌对雪白睡莲幼苗生长的促进作用。进一步通过测定雪白睡莲幼苗根际土壤理化性质与酶活的变化，分析内生促生真菌对土壤营养成分的影响。最后，结合高通量测序技术分析内生促生真菌对雪白睡莲幼苗根际微生物群落结构和叶片转录组的影响，以期解析内生促生真菌促进雪白睡莲幼苗生长的潜在机制。

1 材料与方法

1.1 生物材料与试剂

雪白睡莲于 2024 年 4 月 25 日采自新疆维吾尔自治区博斯腾湖(41°56′−42°14′N, 86°40′−87°25′E)。内生真菌分离所用的马铃薯葡萄糖琼脂培养基(potato dextrose agar medium, PDA)与性能鉴定所用的解无机磷培养基(Pikovskaya’s agar medium, PVK)、解有机磷培养基(phosphate-solubilizing bacteria medium, OPM)、解钾培养基(potassium bacteria medium, PSM)及产铁载体培养基(chrome azurol S agar medium, CAS)购自上海阿拉丁生化科技股份有限公司。

1.2 内生真菌的分离、纯化与鉴定

将雪白睡莲植株带回实验室后，剪取 5−6 cm 的根系，用自来水冲洗 5−10 min，以去除表面污泥。将根系切成约 1 cm 的小段，依次经 75% 乙醇浸泡 10 s，无菌水冲洗，0.1% 氯化汞溶液浸泡 12 min，无菌水冲洗 5 次，完成表面消毒处理[24]。将处理后的组织样品接种于 PDA 培养基中，置于 28 ℃恒温培养箱中避光培养 3−5 d。待组织周围长出菌丝后，用接种针切取直径约 5 mm 的菌丝块，反扣于新的 PDA 培养基平板中央进行纯化培养。重复以上操作直至菌种完全纯化，观察菌落形态并拍照。将纯化后的菌株采用划线法接种于 PDA 斜面培养基中，待菌丝长满斜面后置于 4 ℃冰箱临时保存，用于后

续孢子收集[25]。用接种针将菌株切割成直径约5 mm的菌块，分别接种于PVK、OPM、PSM及CAS培养基平板中央，于28 ℃避光恒温培养箱中培养3−5 d，观察各菌株在不同功能培养基上的生长状况，评估内生真菌的促生潜能。

1.3 内生真菌分子鉴定及系统发育树构建

将纯化后的潜在内生促生真菌接种于PDA培养基平板上，于28 ℃培养48−96 h，观察菌落形态并拍照[26]。收集菌丝，经无菌玻璃珠研磨破碎后，使用Invitrogen Genomic DNA Extraction Kits [赛默飞世尔科技(中国)有限公司]提取菌株基因组DNA。采用上游引物NS1 (5′-GTAGTCATATGCTTGTCTC-3′)和下游引物NS6 (5′-GCATCACAGACCTGTTATTGCCTC-3′)对菌株18S rRNA基因进行PCR扩增。PCR反应体系：5×TransStart *FastPfu* 缓冲液4.0 μL，dNTPs (2.5 mmol/L) 2.0 μL，上、下游引物(5.0 μmol/L)各0.8 μL, TransStart *FastPfu* DNA聚合酶(5 U/μL) 0.4 μL，DNA模板10.0 ng，ddH_2O补充至20.0 μL。PCR反应条件：98 ℃ 30 s；98 ℃ 10 s，54 ℃ 30 s，72 ℃ 45 s，共32次循环；72 ℃ 10 min。扩增产物经1%琼脂糖凝胶电泳分析后，切胶回收目标条带，并使用纯化试剂盒进行纯化。纯化后的PCR产物送至生工生物工程(上海)股份有限公司进行Sanger测序。所得序列在美国国家生物技术信息中心(NCBI)数据库进行BLAST序列同源性比较，获得同源性序列，并选择相似性大于99%的菌株[27]。使用MEGA 7.0.14生物学软件对测试菌株和相关菌株进行多序列比对分析，并用邻接法(neighbor-joining method)构建系统发育树[26]。

1.4 内生真菌接种液的制备

将纯化后的内生真菌分别接种于PDA培养基平板上，于28 ℃下黑暗培养7 d。待菌株长满平板后用无菌接种铲刮取，用无菌水冲洗并用2层纱布过滤，除去菌丝。收集滤液中的孢子，用血细胞计数板计数，并以无菌水将孢子浓度调至1×10^8 spores/mL，用于后续实验接种液[28]。

1.5 内生真菌对雪白睡莲幼苗的促生作用

为探究内生真菌对雪白睡莲幼苗生长的影响，于2025年5月30日开展了为期60 d的盆栽试验。供试菌株为分离自雪白睡莲根系的潜在内生促生真菌球毛壳菌(*C. globosum*)。本研究设置2个处理：对照组(CK)和球毛壳菌(*C. globosum*)组，每个处理6个重复，共12盆(n=6)。种植土壤(草泥炭:淤泥=1:1)经高温高压灭菌处理后，均匀放置于12个塑料种植盒(长30 cm×宽20 cm×高12 cm)中，每盒铺设8 cm厚的种植土壤。将种植盒置于清水中静置48 h后，随机分成2组。移栽前，随机选取两叶一心且长势相同的雪白睡莲幼苗，将根部置于*C. globosum*接种液中浸泡20 min。随后，将其根茎顶端约5 cm插入种植盒的种植土壤中固定。每6个种植盒放入1个玻璃缸内，共设置2个玻璃缸。为减少光照强度变化引起的误差，每天随机改变种植盒的位置。在移栽后的第7、14和21天分别用无菌注射器向*C. globosum*组的水体中加入5 mL *C. globosum*的孢子悬液(1×10^8 spores/mL)。对照组则加入等体积的清水。在移栽后的第14、28、42和60天分别测定雪白睡莲的叶长、叶宽和叶片数。

1.6 样品采集

在移植后第60天，分别从对照组和*C. globosum*组采集根际土壤样品。首先，使用无菌铲沿塑料种植盒边缘垂直挖至底部，小心取出完整的根土复合体，轻轻抖落松散附着的土壤，再用无菌刷收集紧密附着的根际土壤，保存于−80 ℃，用于18S rRNA和16S rRNA基因测序。同时，收集种植盒中的土壤，阴干保存，用于测定土壤理化指标。用直尺测定雪白睡莲根系长度，并将去除土壤后的雪白睡莲植株放入无菌采样袋中，保存于−80 ℃冰箱，用于叶片RNA提取和转录组测序[29]。

1.7 土壤理化指标测定

将种植盒中的土壤阴干后研磨，分别过 10 目和 100 目网筛[30]。将过 10 目筛的土壤与蒸馏水按照 1:2.5 的比例混合后，采用碱扩散法测定土壤碱解氮含量[31]。将过 100 目筛的土壤用重铬酸钾和硫酸的标准溶液在沸点氧化后，利用硫酸亚铁滴定法测定土壤有机质含量[32]。土壤蔗糖酶和土壤过氧化物酶的活性则使用试剂盒(北京索莱宝科技有限公司)进行测定。

1.8 根际土壤 DNA 提取和高通量测序

按照 FastDNA SPIN Kit for Soil (MP Biomedicals 公司)说明书提取总 DNA，利用 1% 琼脂糖凝胶电泳检测抽提的基因组 DNA。采用 16S rRNA 基因通用引物 27F (5′-AGRGTTYGATYMTGGCTCAG-3′)和 1492R (5′-RGYTACCTTGTTACGACTT-3′)、18S rRNA 基因通用引物 EukA (5′-AACCTGGTTGCTGCCAGTGCAGT-3′)和 EukB (5′-TGATCCTTGCAGGTTCACCTAC-3′)进行 PCR 扩增[33-34]。PCR 反应体系：5× TransStart *FastPfu* 缓冲液 4.0 μL，dNTPs (2.5 mmol/L) 2.0 μL，上、下游引物(5.0 μmol/L)各 0.8 μL，TransStart *FastPfu* DNA 聚合酶(5 U/μL) 0.4 μL，模板 DNA 10.0 ng，ddH_2O 补充体系至 20 μL。PCR 程序：98 ℃ 30 s；98 ℃ 10 s，54 ℃ 30 s，72 ℃ 45 s，共 32 次循环；72 ℃ 10 min。PCR 产物混合后用 2% 琼脂糖凝胶电泳检测，使用 AxyPrep DNA 凝胶回收试剂盒(Axygen 公司)切胶回收 PCR 产物，使用 2% 琼脂糖电泳检测[35]。双端测序在上海凌恩生物科技有限公司的 PacBio 平台上进行。通过 SMRT Link Analysis 软件(v11.0)获得高保真读取数据(hifi reads)，并使用 Lima (v2.6.99)进行 Barcode-CCS 序列识别。使用 QIIME 2 对原始读取数据进行修剪和质量控制，并使用 DADA2 去除嵌合体序列。将代表性扩增子序列变体(amplicon sequence variant, ASV)分配到 SILVA (v13.8)或 UNITE (v8.0)数据库。

1.9 雪白睡莲叶片 RNA 提取与转录组测序

从对照组和 *C. globosum* 组分别取大小相近的健康雪白睡莲叶片(n=6)，用无菌水冲洗干净后冷冻干燥，立即进行研磨，使用 TRIzol 试剂盒(ThermoFisher Scientific 公司)提取 RNA。分离的 RNA 样本使用 Agilent 2100 生物分析仪(Agilent 公司)和琼脂糖凝胶电泳进行数量和质量检查，以观察是否发生任何 RNA 降解。质检合格后，送至上海美吉生物医药科技有限公司进行 NovaSeq X Plus 平台上机测序。测序完成后，参照 Sharma 等[36]方法使用 Trinity 对所有样本 clean data 进行从头组装，并对组装结果进行优化评估与表达量分析。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，差异分析软件为 DESeq2，筛选阈值为：$|\log_2 \text{fold change}| \geq 1$ 且 $P<0.05$。

1.10 统计与分析

采用 Excel 软件对原始数据进行整理，计算各处理组数据的平均值与标准差。使用 IBM SPSS Statistics 22 软件进行统计分析，数据经 Shapiro-Wilk 正态性检验和 Levene’s 方差齐性检验后，采用 Duncan 事后检验进行单因素方差分析。显著性水平设为 $P<0.05$。采用多变量排列方差分析(permutational multivariate analysis of variance, PERMANOVA)分析群落结构的差异。使用 R 软件 DESeq2 包比较 ASV 相对丰度的差异。只有 $P<0.05$ (FDR-adjusted)和 $|\log_2 \text{fold change}|>2$ 被视为 ASV 有显著差异。用 GraphPad Prism 9.0.0.121 进行作图。通过线性判别分析(linear discriminant analysis effect size, LEfSe)分析获得不同试验组雪白睡莲根际土壤微生物标志物，其中筛选阈值设置为 LDA score>2.0。使用 R 语言(version 3.3.1)工具统计所有试验组中所共有和独有的物种数目，分析时选用相似水平为 97% 的 ASV 或其他分类学水平的样本表。用 R 软件 vegan 包(version 2.4.3)进行 RDA 分析和作图。根据每百万转录本读数(the transcripts per million reads, TPM)方法计算每个转录本的表达水平进

而鉴定 2 个不同样本之间的差异表达基因(differentially expressed genes, DEGs)。使用 RSEM 量化基因丰度，用 DESeq2 进行差异表达分析。KEGG 通路分析使用 Python scipy 软件进行。利用 Uparse 算法(Uparse v7.0.1001)对所有样本的全部 Effective Tags 进行聚类分析。数据可视化处理采用 Origin 2019 软件完成，以确保图片的规范性与可读性。

2 结果与分析

2.1 雪白睡莲内生真菌的分离与鉴定

从雪白睡莲的根系中分离获得 1 株内生真菌，菌落呈白色，表面不平整，菌种边缘均匀，菌丝较浅，与培养基结合松散，并且菌种表面无渗出物。该菌株具有产铁载体、溶解有机磷、溶解无机磷、解钾能力(图 1A)。18S rRNA 测序结果表明，该菌株与球毛壳菌(*Chaetomium globosum*)的同源性高达 99% 以上(图 1B)。结合形态学与分子生物学结果，将雪白睡莲根系分离的真菌鉴定为 *C. globosum*。

2.2 内生促生真菌对雪白睡莲叶片和根系生长的影响

与对照组相比，施加 *C. globosum* 60 d 后，雪白睡莲的叶长、叶宽和叶片数分别显著提高了 (46.74±0.55)% 、(96.08±0.51)% 和 (64.71±

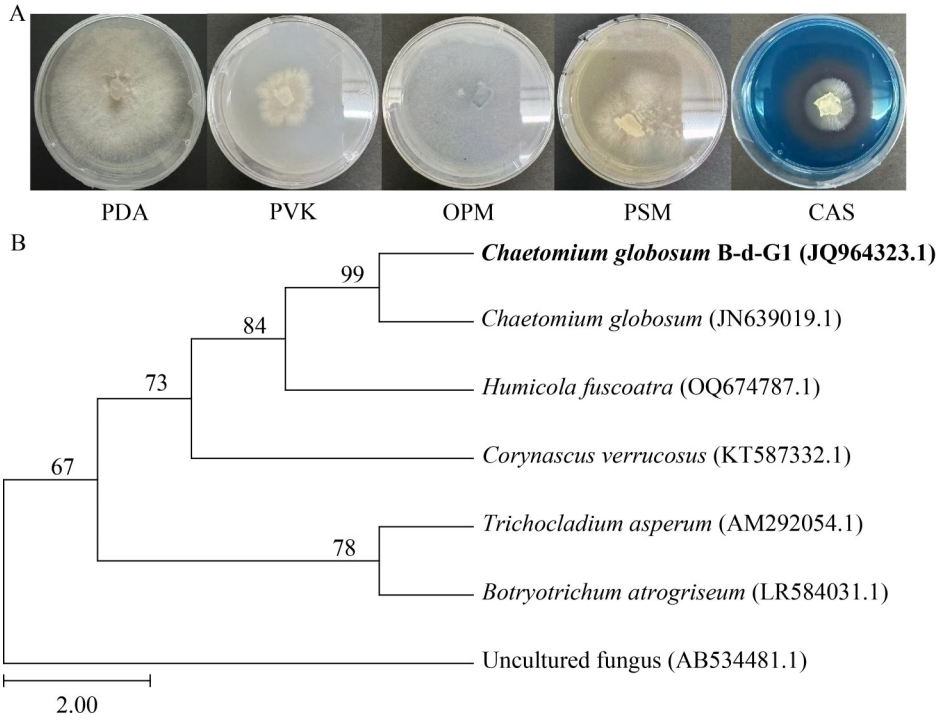


图1 雪白睡莲内生促生真菌的形态学鉴定和分子学鉴定结果

Figure 1 Morphological and molecular identification of endophytic growth-promoting fungi isolated from *Nymphaea candida* C. Presl. A: Colony morphology of *Chaetomium globosum* on PDA, inorganic phosphorus-solubilizing, organic phosphorus-solubilizing, potassium-solubilizing, and siderophore-producing media; B: Neighbor-joining phylogenetic tree based on 18S rRNA gene sequences of the endophytic growth-promoting fungus *Chaetomium globosum* obtained in this study. Species names and strain numbers in bold indicate the isolates obtained in this study; the species name represents the molecularly identified species, and B-d-G1 is the strain number. GenBank accession numbers are shown in parentheses. Bootstrap analysis was performed with 1 000 replicates; The scale bar represents 0.05 nucleotide substitutions per site.

3.31)% (P<0.05；图 2A、2C−2E)。值得注意的是，*C. globosum* 组的雪白睡莲根系长度较对照组提高了 1.31 倍(P<0.05；图 2B、2F)。

2.3 内生促生真菌对雪白睡莲栽培土壤理化指标的影响

施加 *C. globosum* 后，土壤中的有机质含量、碱解氮含量、蔗糖酶和过氧化物酶活性分别显著提高了(3.40±0.64)%、(15.53±0.90)%、(10.22±0.06)%和(36.68±0.06)% (图 3A−3D)。

2.4 内生促生真菌对雪白睡莲根际土壤中原核微生物群落的影响

施加 *C. globosum* 后，雪白睡莲根际土壤原

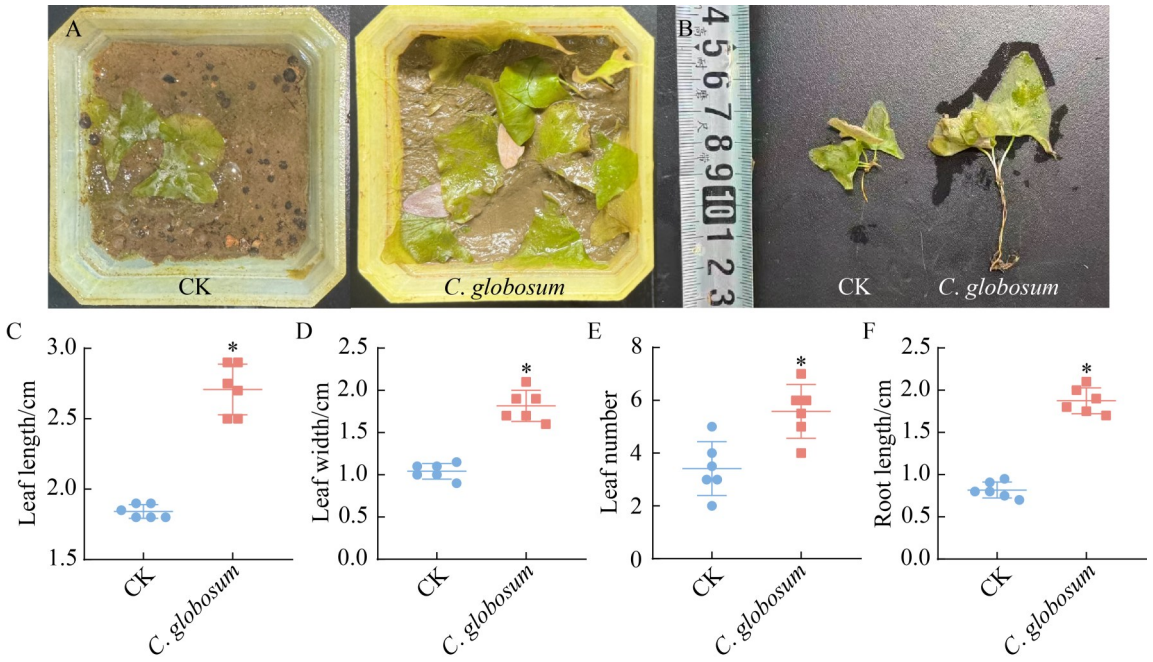


图2 *Chaetomium globosum*对雪白睡莲叶片和根系生长的影响

Figure 2 Effects of *Chaetomium globosum* on leaf and root growth of *Nymphaea candida* C. Presl. A: Leaf morphology; B: Root morphology; C: Leaf length; D: Leaf width; E: Number of leaves; F: Root length. All treatments were replicated six times, and data are presented as mean±SD (n=6). *: 0.01<P<0.05.

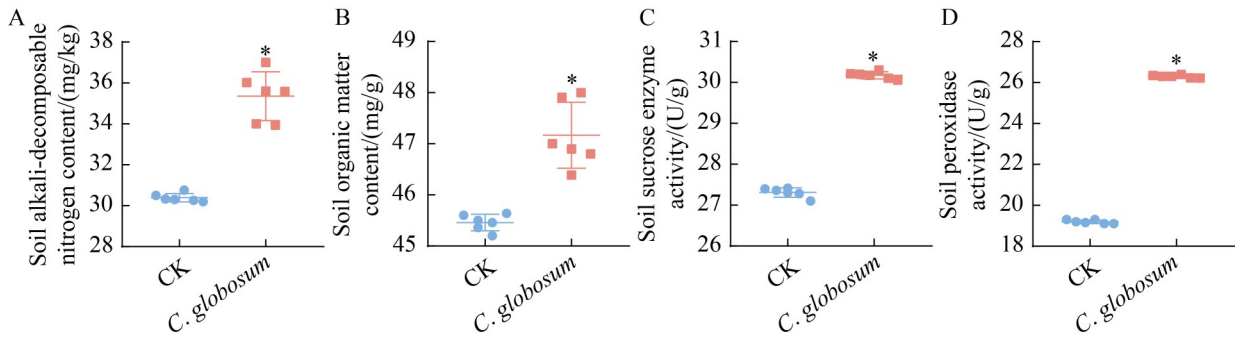


图3 *Chaetomium globosum*对雪白睡莲种植盒内土壤理化指标的影响

Figure 3 Effects of *Chaetomium globosum* on soil physicochemical properties in planting containers of *Nymphaea candida* C. Presl. A: Alkali-hydrolyzable nitrogen content; B: Organic matter content; C: Sucrose enzyme activity; D: Peroxidase activity. All treatments were replicated six times, and data are presented as mean±SD (n=6). *: 0.01<P<0.05.

核微生物的 α 和 β 多样性均无显著差异(P<0.05；图 4A、4B)。冗余分析(RDA)结果表明，施加 *C. globosum* 后，雪白睡莲根际原核微生物群落结构与土壤中过氧化物酶活性呈显著正相关关系(图 4C)。另外，施加 *C. globosum* 后 *Ellin*6067 和苍黄杆菌属 *Luteolibacter* 的相对丰度分别显著增加了 0.49 倍和 5.04 倍(P<0.05；图 4D)，而瞬时型原核微生物群落相对丰度降低至 13.90%，中间型原核微生物群落的相对丰度增加至 36.08% (图 4E)。施用 *C. globosum* 还使雪白睡莲根际原核微生物共现网络的图密度、模块化和加权平均度分别增加了 5.79%、8.25% 和 5.70% (图 4F)。

2.5 内生促生真菌对雪白睡莲根际土壤中真核微生物群落的影响

施加 *C. globosum* 后雪白睡莲根际土壤真核微生物的 α 和 β 多样性无显著差异(P<0.05；图 5A、5B)。RDA 结果表明，施用 *C. globosum* 能够使雪白睡莲根际真核微生物群落结构与土壤中有机质含量、碱解氮含量和蔗糖酶活性呈显著正相关关系(图 5C)，使 norank-p-*Cryptomycota*、norank-o-*Monhysterida*、*Surirella*、norank-p-*Aphelidea* 的相对丰度分别显著增加了 3.72、4.47、1.21、10.84 倍(P<0.05；图 5D)。施加 *C. globosum* 后，瞬时型和中间型真核微生物群落相对丰度分别增加至 7.63%、30.83% (图 5E)。此外，施加 *C. globosum* 使雪白睡莲根际真核微生物共现网络的图密度、模块化和加权平均度分别增加了 6.63%、64.95% 和 11.27% (图 5F)。

2.6 内生促生真菌对雪白睡莲叶片基因表达的影响

与对照组相比，*C. globosum* 组的雪白睡莲叶片有 4 839 个基因上调，8 758 个基因下调(图 6A)。聚类分析结果显示，CK 组和 *C. globosum* 组的 Unigenes 分别独立为一簇，所有 Unigenes 整体可划分为 Cluster Ⅰ 和 Cluster Ⅱ 两大簇，平行样本之间的重复性高，数据可用于进一步分析(图 6D)。KEGG 通路结果显示，施加 *C. globosum* 后显著富集的代谢途径主要包括“核糖体” “光合作用-天线蛋白” “光合作用”和“类固醇生物合成” (图 6B)。差异基因通路分析显示，施加 *C. globosum* 后，在类固醇生物合成途径中编码角鲨烯单加氧酶(SQLE)的基因(*DN2 027-c1-g1*) TPM 值显著增加了(63.83±0.02)%，编码甾醇 14α-去甲基酶(CYP51)的基因(*DN29 316-c0-g1*) TPM 值显著增加了 2.86 倍。与此同时，编码甲基甾醇单加氧酶(MESO1)的基因(*DN116 365-c0-g1*) TPM 值显著增加了 12.57 倍(图 6C、6E)。

3 讨论与结论

本研究发现，从雪白睡莲根系分离的内生促生真菌 *C. globosum* 具有产铁载体、溶解有机磷、溶解无机磷、解钾能力。施加 *C. globosum* 后能显著增加雪白睡莲叶长、叶宽、叶片数和根系长度。此前有研究表明，*C. globosum* 能够通过产生抗菌活性物质、促进植物生长、诱导植物抗性等多种机制发挥生防促生作用[21]。本研究发现从水生植物体内分离的内生植物促生真菌 *C. globosum* 能够显著促进水生植物雪白睡莲幼苗的生长(图 7)。

植物地上部分和地下部分生长相对协调，叶片性状的改善可能归因于雪白睡莲根系长度的增加[37-38]。*C. globosum* 被认为是具有植物生长促进潜力的内生真菌，尤其在促进植物叶片生长和根系伸长方面表现突出，这一特性与丛枝菌根真菌作用相近[39]。研究表明，施加哈茨木霉 (*T. harzianum*) 使番茄根长显著增加 42.70%[40]。相比之下，本研究中 *C. globosum* 对雪白睡莲叶片和根系均具有促进作用，并且在促进根系伸长方面表现出更强的优势，这为其作为高效内生促生菌的应用潜力提供了直接证据。*C. globosum* 对雪白睡莲生长的促进作用可能归因于其改善土壤理化性质的能力。接种 *C. globosum* 后雪白睡莲种植土壤中有机质含量显著提高 3.40%，碱解氮含量提高 15.53%，蔗

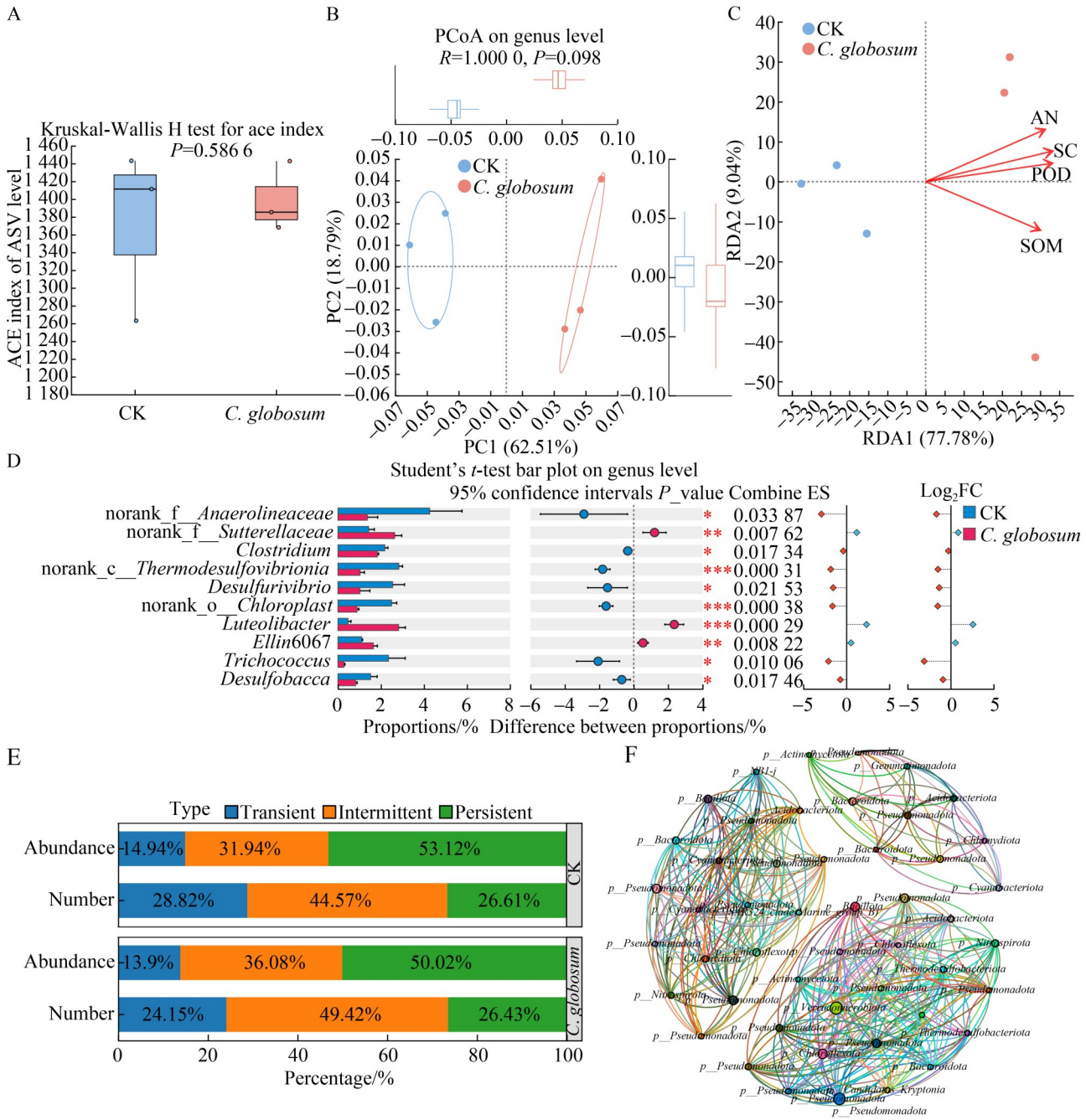


图4　施加*Chaetomium globosum*对雪白睡莲根际幼苗土壤中原核微生物群落结构的影响

Figure 4　Effects of *Chaetomium globosum* on the prokaryotic microbial community structure in the rhizosphere soil of *Nymphaea candida* C. Presl seedlings. A: Alpha diversity; B: PCoA analysis; C: RDA of soil physicochemical factors and rhizosphere soil prokaryotic microbial community; D: Histogram of species difference test; E: Stack plot showing the distribution of transient, intermediate, and persistent species; F: Co-occurrence network diagram of prokaryotic microorganisms in the rhizosphere soil of the *Chaetomium globosum* group. All treatments included three replicates. *: 0.01<*P*<0.05; **: 0.001<*P*<0.01; ***: *P*<0.001.

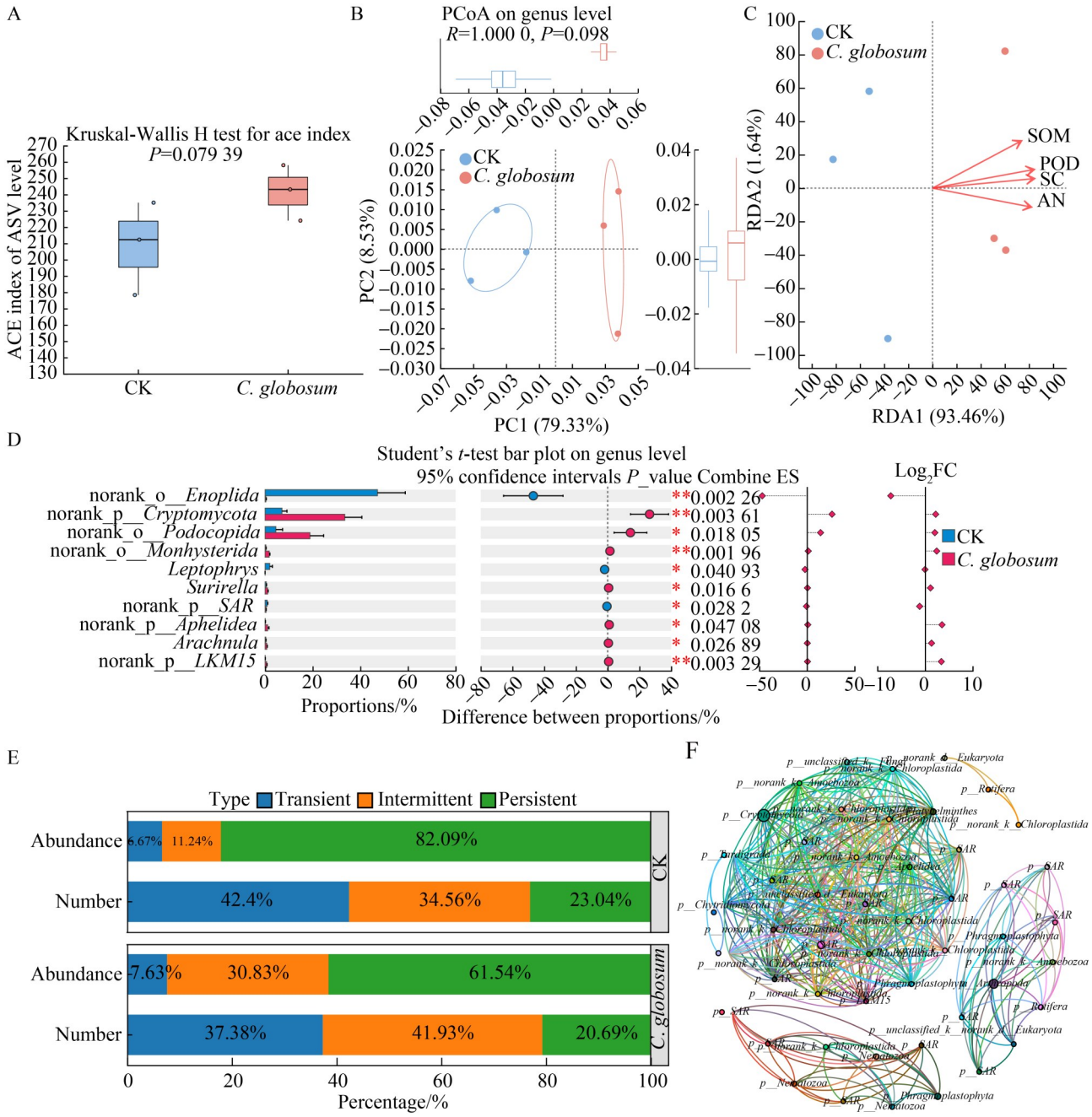


图5　施加*Chaetomium globosum*对雪白睡莲幼苗根际土壤中真核微生物群落结构的影响

Figure 5　Effects of *Chaetomium globosum* on the eukaryotic microbial community structure in the rhizosphere soil of *Nymphaea candida* C. Presl seedlings. A: Alpha diversity; B: PCoA analysis; C: RDA of soil physicochemical factors and rhizosphere soil eukaryotic microbial community; D: Histogram of species difference test; E: Stack plot showing the distribution of transient, intermediate, and persistent species; F: Co-occurrence network diagram of eukaryotic microorganisms in the rhizosphere soil of the *Chaetomium globosum* group. All treatments included three replicates. *: 0.01<*P*<0.05; **: 0.001<*P*<0.01; ***: *P*<0.001.

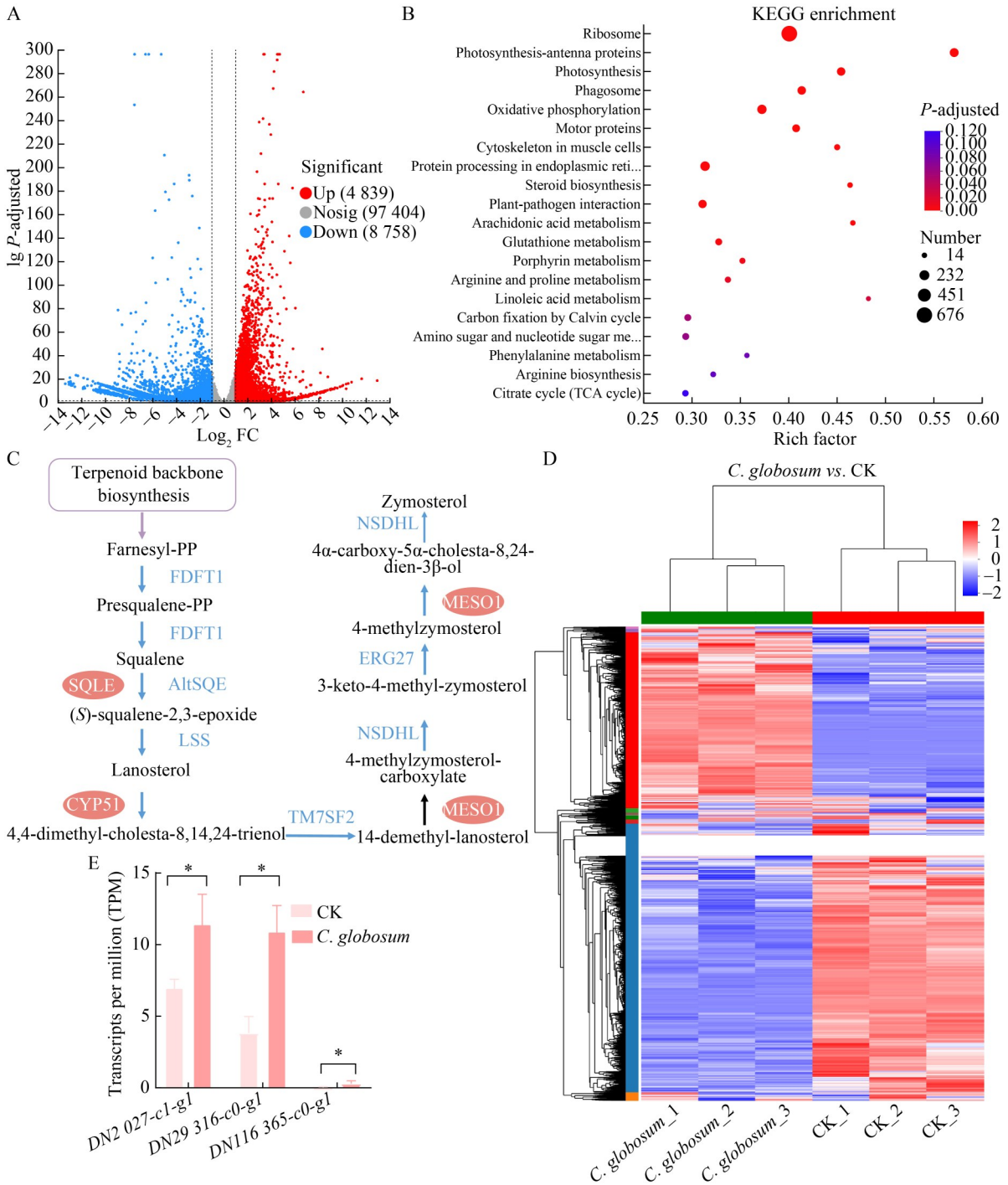


图6 *Chaetomium globosum*对雪白睡莲叶片转录组基因表达量的影响

Figure 6 Effects of *Chaetomium globosum* on gene expression in the leaf transcriptome of *Nymphaea candida* C. Presl. A: Volcano plot showing the distribution of differentially expressed genes in leaves of the *Chaetomium globosum* group; B: Top 20 KEGG enrichment pathways in the *Chaetomium globosum* group compared to the control group; C: Steroid biosynthesis pathway diagram in the *Chaetomium globosum* group; D: Cluster diagram of differentially expressed genes in *Nymphaea candida* C. Presl; E: Relative quantification of upregulated genes in relevant pathways in the *Chaetomium globosum* group. All treatments included three replicates. *: 0.01<*P*<0.05.

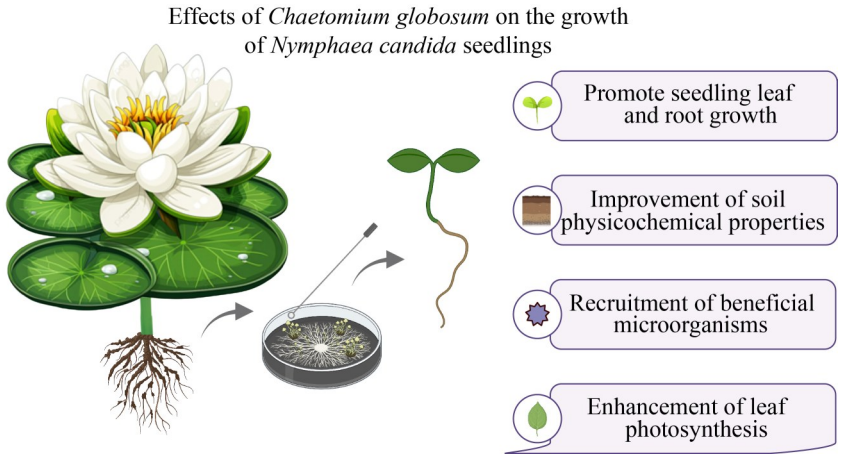


图7 *Chaetomium globosum*促进雪白睡莲幼苗生长的作用机制

Figure 7 *Chaetomium globosum*-mediated mechanism underlying the growth promotion of *Nymphaea candida* C. Presl seedlings.

糖酶和过氧化物酶活性均提高 10.22%。土壤酶活性是衡量土壤生物学活性和养分循环能力的重要指标[41]。蔗糖酶参与土壤有机碳分解和碳循环，其活性提升意味着土壤中有机物质的矿化速率增加，可为植物提供更多可利用的碳源和养分[42]。过氧化物酶则与土壤有机质的聚合和腐殖质形成密切相关，其活性提高有助于改善土壤结构[43]。可见，*C. globosum* 能够通过降解有机质、促进养分循环来改善土壤健康，进而促进雪白睡莲的生长[44]。

尽管根际微生物群落的 α 和 β 多样性未受影响，但 *C. globosum* 富集了不同的有益微生物，形成了特定的功能微生物群落。施加 *C. globosum* 后显著招募了 *Ellin*6067 和 *Luteolibacter*。*Ellin*6067 是一种氨氧化细菌，能将植物难以直接利用的氨(NH_3)转化为亚硝酸盐(NO_2^-)，进而促进植物光合作用[45]。*Luteolibacter* 则作为潜在植物促生菌，可促进植物生长[46]。此外，*C. globosum* 组雪白睡莲根际显著富集了 unclassified-p-*Cryptomycota*、norank-o-*Monhysterida*、*Surirella*、norank-p-*Aphelidea* 等真核微生物。其中，隐真菌门(*Cryptomycota*)作为真菌类群参与有机质分解过程，在碳循环过程中发挥重要作用，间接促进植物生长[47]。*Monhysterida* 能够摄食病原菌并促进养分循环，在抑制土传病害和维持土壤健康中发挥积极作用[48]。双菱藻属(*Surirella*)则能够分泌胞外聚合物，促进土壤团聚体形成，并参与微量元素活化，间接影响次生代谢产物的积累[49]。无褶菌目(*Aphelidea*)是一类专性寄生真菌，能附着于宿主真菌、侵入并利用宿主内容物进行繁殖，作为潜在的生物防治剂，能够自然控制镰刀菌等病原真菌的种群[50]。在本研究中，施加 *C. globosum* 降低了瞬时型微生物的相对丰度，增加了中间型微生物的相对丰度。瞬时型微生物相对丰度的降低，反映了根际微生物群落对环境变化的适应能力增强，有助于维持根际微生态的稳定性[51]。RDA 分析结果显示，雪白睡莲根际微生物群落与根际土壤中有机质含量、碱解氮含量、蔗糖酶活性、过氧化物酶活性呈显著正相关，进一步证实了 *C. globosum* 通过改良土壤微环境间接促进宿主生长[52]。共现网络分析表明，施加 *C. globosum* 显著增加了雪白睡莲根际原核和真核微生物群落的模块性，导致网络结构更加复杂，表明形成了更稳定的根际土壤微环境，有利于促进雪白

睡莲幼苗生长。

雪白睡莲叶片转录组分析显示，*C. globosum* 诱导的差异表达基因显著富集在“核糖体” “光合作用-天线蛋白” “光合作用”和“类固醇生物合成”等代谢途径。值得注意的是，在类固醇生物合成途径中角鲨烯单加氧酶编码基因(*SQLE*)表达量显著增加了 63.83%，甾醇 14α-去甲基酶的编码基因(*CYP51*)与甲基甾醇单加氧酶的编码基因(*MESO1*)表达量分别上调了 2.86 倍和 12.57 倍。研究表明，类固醇类物质(植物甾醇)是植物细胞膜的重要组分，也是油菜素内酯等植物激素合成的前体[53]。甾醇生物合成途径的激活会通过增加细胞膜稳定性，增强细胞分裂、促进油菜素内酯合成来促进植物生长[54]。此外，“光合作用-天线蛋白”通路的富集表明 *C. globosum* 可能通过增强光能捕获效率来促进光合作用，这与雪白睡莲叶片数显著增加的现象相互印证[55]。研究表明，*C. globosum* Cg-2 使番茄植株光合速率显著增加，*C. globosum* ND35 菌株则使黄瓜苯丙烷生物合成、植物激素信号转导和光合作用等通路显著富集[56-58]。据此推测，*C. globosum* 可通过招募有益微生物、改善土壤养分供应调控植物光合代谢多重通路协同促进雪白睡莲生长。本研究在球毛壳菌-雪白睡莲互作体系中发现了甾醇生物合成途径的显著激活，这为解析内生促生真菌促进水生植物生长的机制提供了新的思路。后续可以通过代谢组学验证甾醇合成通路的激活，并利用合成菌群构建方法探索 *C. globosum* 与其他功能微生物的协同促生潜力。

综上所述，*C. globosum* 通过改善根际微环境、招募有益微生物、调控叶片类固醇生物合成等多条途径有效促进雪白睡莲幼苗生长。因此，*C. globosum* 具备开发为雪白睡莲种苗繁育生物肥料的潜力，可为我国珍稀濒危水生植物雪白睡莲的种苗繁育与种群恢复提供新型生物资源。

作者贡献声明

邢玉伟：研究构思和设计、数据收集和处理、论文撰写和修改；刘聪：提供技术支持、协助实验操作、参与论文讨论；刘阳：提供技术支持、协助实验操作；王军：研究构思和设计、论文修改、提供技术支持。

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