Fungal Community in Rotting Yam Tubers Based on FUNGuild and Isolation and Identification of Potential Pathogenic Fungi: Postprint

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Abstract

To investigate the characteristics of fungal communities and main pathogens in rotten yam tubers, this study employed ITS amplicon sequencing technology and FUNGuild analysis to elucidate the fungal community composition, network characteristics, and ecological functional groups, and conducted isolation and identification of potential pathogenic fungi. The results showed that: (1) The dominant fungal phylum in rotten yam tubers was Ascomycota, with dominant genera including Penicillium, Colletotrichum, Fusarium, Talaromyces, and Clonostachys, among others. The fungal ecological network displayed significant modularity and a high proportion of positive correlation edges (99.33%), with fungi demonstrating a strong tendency toward positive cooperation. (2) FUNGuild analysis revealed that ten fungal ecological functional groups were highly correlated with yam tuber rot. Among them, the relative abundances of dung saprotroph-undefined saprotroph-wood saprotroph and endophyte-plant pathogen reached 33.74% and 23.64%, respectively, with Penicillium and Colletotrichum as their representative genera. In addition, there were three ecological functional groups simultaneously associated with plant pathogens and wood saprotrophs, with a total relative abundance of 13.67%, and Fusarium as the representative genus. Further Trait analysis indicated that seven fungal genera, including Penicillium and Fusarium, were likely closely associated with yam tuber rot. (3) A total of 22 fungal strains were isolated and identified, belonging to six genera, including Fusarium (9 strains), Penicillium (5 strains), and Aspergillus (4 strains), among others. These research results provide a valuable reference for elucidating the disease occurrence patterns of yam tuber rot, targeted pesticide application, and screening of biocontrol agents.

Full Text

FUNGuild-Based Study of Fungal Community, and Isolation and Identification of Potential Pathogenic Fungi in Yam (Dioscorea polystachya) Rotting Tubers

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Abstract

To investigate the characteristics of the fungal community and identify potential key pathogens in rotting yam tubers, this study employed ITS rDNA gene amplicon sequencing technology and FUNGuild analysis to characterize fungal community composition, network features, and ecological functional groups, followed by isolation and identification of potential pathogenic fungi. The results revealed: (1) *Ascomycota* was the dominant phylum in rotting yam tubers, with prevalent genera including *Penicillium*, *Colletotrichum*, *Fusarium*, *Talaromyces*, and *Clonostachys*. The fungal molecular ecological network exhibited a clear modular structure with a high proportion of positive correlation edges (99.33%), indicating strong positive cooperation among fungal taxa. (2) FUNGuild analysis identified ten fungal ecological functional guilds highly correlated with yam tuber rot. Among these, the relative abundances of dung saprotroph-undefined saprotroph-wood saprotroph and endophyte-plant pathogen guilds reached 33.74% and 23.64%, respectively, with *Penicillium* and *Colletotrichum* as representative genera. Additionally, three guilds simultaneously associated with plant pathogens and wood saprotrophs accounted for a combined relative abundance of 13.67%, with *Fusarium* as the representative genus. Further trait analysis suggested that seven genera, including *Penicillium* and *Fusarium*, were likely closely associated with yam tuber rot. (3) A total of 22 fungal strains were isolated and identified, belonging to six genera: *Fusarium* (9 strains), *Penicillium* (5 strains), *Aspergillus* (4 strains), *Talaromyces* (1 strain), *Trichoderma* (2 strains), and *Cladosporium* (1 strain). These findings provide valuable insights into the pathogenesis of yam tuber rot and offer important references for targeted pesticide application and biocontrol agent screening.

Keywords: *Dioscorea* sp.; amplicon sequencing; fungal community; FUNGuild; ecological functional groups; plant pathogenic fungi

Yam (*Dioscorea* sp.) is a herbaceous vine belonging to the Dioscoreaceae family, whose underground tubers are rich in bioactive compounds including polysac-

charides, amino acids, diosgenin, allantoin, and polyphenols. Traditionally used as both food and medicine, yam offers benefits such as strengthening the spleen, nourishing the lungs, and reinforcing kidney function. In recent years, growing recognition of traditional Chinese medicine and therapeutic diets has dramatically increased market demand, leading to expanded cultivation. Globally, yam is cultivated on approximately 156 million hectares with annual production reaching 88.257 million tons (FAOSTAT, 2022). However, fungal diseases causing tuber rot pose serious challenges, severely impacting both yield and quality (Li et al., 2005; Yang et al., 2021).

Previous research has demonstrated close relationships between plant disease development and shifts in microbial community composition, diversity, and ecological functional groups. High-throughput sequencing has become the standard method for analyzing these relationships. For instance, Li et al. (2023) reported that *Fusarium solani* infection significantly reduced the scale of the tobacco rhizosphere microbial ecological network, with stronger positive associations among fungi compared to healthy plants and increased abundance of several genera including *Scutellinia nigrohirtula*. Liu et al. (2022) found that brown root disease in trees markedly decreased rhizosphere fungal diversity, with *Phellinus noxius* showing significant positive correlation with *Cosmospora*, while six fungal classes including Agaricomycetes, Sordariomycetes, and Dothideomycetes exhibited negative correlations. Shu et al. (2019) observed that during avocado root rot, pathogenic fungi such as *Macrophomina* increased in abundance while beneficial fungi like *Rhizophagus* and *Cenococcum* decreased. However, these high-throughput sequencing studies could only analyze community composition and diversity, not predict ecological functions or comprehensively assess plant disease-fungal community relationships.

The development of the FUNGuild database and associated analytical tools has effectively addressed this limitation. By integrating FUNGuild analysis with high-throughput sequencing, researchers can not only compare fungal functions but also analyze trophic modes, ecological guilds, and pathogenic characteristics, thereby elucidating associations between plant physiological status and fungal functional groups. For example, Li et al. (2019) combined high-throughput sequencing with FUNGuild to reveal that pathotrophic fungi dominated the rhizosphere of tobacco with Fusarium root rot, accounting for 54.64% of the community, with *Fusarium* being absolutely dominant. Liu (2022) found that in diseased *Rosa roxburghii* leaves, the main functional groups of endophytic and phyllosphere fungi were saprotrophic and plant pathogenic, accounting for 63.16% and 32.26%, respectively. Guo et al. (2023) predicted functional characteristics of watermelon rhizosphere microbial communities under continuous cropping, finding that pathotrophic fungi were significantly enriched after six cropping cycles, with increased abundance of plant pathogenic guilds potentially damaging host cells to obtain nutrients and causing fungal diseases. Thus, combining high-throughput sequencing with FUNGuild analysis represents an effective strategy for clarifying plant disease-fungal community relationships.

Confirmed pathogens associated with yam tuber rot primarily include *Fusarium*, *Penicillium*, and *Aspergillus* (Li et al., 2023; Uy et al., 2022; Popoola et al., 2019). Additional reported pathogens include *Lasiodiplodia theobromae*, *Sclerotium rolfsii*, and *Pythium myriotylum* (Dania et al., 2016; Dania et al., 2019; Zhang et al., 2018). However, existing studies have focused solely on pathogen isolation and identification, without comprehensive evaluation of fungal community composition, ecological functional groups, and potential pathogens in rotting yam tubers.

This study integrated Illumina MiSeq high-throughput sequencing, FUNGuild analysis, and tissue isolation culture techniques to address three questions: (1) What are the fungal community composition and ecological network characteristics in rotting yam tubers? (2) What are the fungal ecological functional guilds, representative species, and their pathogenic traits? (3) Which potential pathogenic fungi can be isolated and identified? This research will deepen understanding of fungal community ecological functions in rotting yam tubers and provide valuable references for elucidating pathogenesis, targeted pesticide application, and biocontrol agent screening.

1.1 Materials

Test samples were collected in November 2021 from a yam germplasm resource nursery in Wenxian County, Jiaozuo City, Henan Province (112°98'22'' N, 34°94'68'' E). The planting area was divided into six equal zones, and rotting yam tubers were collected from each zone as shown in [Figure 1: see original paper]. Rotting tubers were placed in sterile ziplock bags, stored in ice boxes, transported to the laboratory, and stored at 4 °C for subsequent analysis.

1.2 Soil Physicochemical Property Determination

Soil pH (6.63), total phosphorus (213.254 $mg \cdot kg^{-1}$), total organic matter (410.00 $mg \cdot kg^{-1}$), available phosphorus (13.88 $mg \cdot kg^{-1}$), and available potassium (300.28 $mg \cdot kg^{-1}$) were determined according to Bao (2000). Ammonia nitrogen (110.24 $mg \cdot kg^{-1}$), nitrate nitrogen (54.72 $mg \cdot kg^{-1}$), and nitrite nitrogen (3.12 $mg \cdot kg^{-1}$) were measured following the method of Zhou et al. (2021) for straw-mulched soil.

1.3 Sample Processing

Yam tubers were rinsed with running water, and 0.5 cm × 0.5 cm tissue blocks were excised from the junction between diseased and healthy tissue. Surface sterilization was performed by immersing blocks in 75% ethanol for 30 s, then in 0.1% mercuric chloride for 4–5 min, followed by three to four rinses with sterile water. To confirm complete surface sterilization, 100 L of the final rinse water was plated on PDA medium. After confirmation, tissue blocks were placed in sterile EP tubes and sent to Shanghai Majorbio Bio-Pharm Technology Co.,

Ltd. for DNA extraction and quality assessment. Illumina MiSeq platform was used for ITS amplicon sequencing with primers ITS1F (CTTGGTCATTTA-GAGGAAGTAA) and ITS2R (GCTGCGTTCTTCATCGATGC).

1.4 Bioinformatics Analysis of High-Throughput Sequencing Data

High-throughput data analysis and processing were performed using the Shanghai Majorbio Bio-Pharm Technology Co., Ltd. cloud platform (https://cloud.majorbio.com/). Raw data were quality-filtered, assembled, and optimized using FLASH 1.2.11, QIIME 1.9.1, and UCHIME 8.1. Amplicon sequence variants (ASVs) were clustered at 98% similarity with 100% coverage after error sequence removal (Tipton et al., 2021). Fungal species annotation was performed using the UNITE fungal database. Fungal community correlations were calculated using the psych and microecoR packages. Data visualization was conducted using gephi 0.10.1, ggClusterNet, WGCNA, and other R packages. The FUNGuild database (http://stbates.org/funguild_{db}.php) was integrated with R Studio to predict the ecological functional structure of fungi in rotting yam tubers.

1.5 Isolation and Purification of Fungi from Rotting Yam

After complete sterilization, 0.5 cm × 0.5 cm tissue blocks from the disease-healthy junction were crushed in a sterile mortar and suspended in 5 mL sterile water. Ten-fold serial dilutions were prepared, and four dilutions (original, 10^{-1}, 10^{-2}, and 10^{-3}) were plated on PDA medium. Plates were incubated at 28 °C in darkness for 5–7 days. Colonies with distinct morphologies and colors were selected and purified by streak plating until single colonies were obtained. Purified isolates were preserved and used for DNA extraction.

1.6 DNA Extraction and Identification of Different Morphological Strains

DNA was extracted from different fungal morphotypes using the OMEGA BIO DNA extraction kit. The fungal universal primers ITS1 (TCCGTAGGTGAAC-CTGCGG) and ITS4 (TCCTCCGCTTATTGATATGC) were used to amplify the ITS region in a 25 L reaction system: 2X Master Mix 12.5 L, ddH_2O 9.9 L, forward primer 0.8 L, reverse primer 0.8 L, and template DNA 1 L. PCR amplification conditions were: 95 °C for 5 min; 35 cycles of 94 °C for 30 s, 54 °C for 30 s, and 72 °C for 60 s; final extension at 72 °C for 10 min. PCR products were quality-checked by 1.0% agarose gel electrophoresis and sequenced by Shanghai Sangon Biotech Co., Ltd. Sequences were subjected to BLAST alignment, multiple sequence alignment was performed using MEGA 11.0, and a maximum likelihood phylogenetic tree was constructed based on fungal ITS-rDNA sequences.

2.1 Fungal Community Structure Analysis in Rotting Yam Tubers

Illumina platform-based amplicon sequencing of the fungal ITS1 region yielded 382,426 effective sequences. Rarefaction curve analysis was performed by random subsampling five times, revealing that curves plateaued at this sequencing depth ([Figure 2: see original paper]), with coverage exceeding 99.9% for all samples, indicating sufficient depth to capture fungal community information in rotting yam tissues.

Further community structure analysis at the phylum level ([Figure 3: see original paper]A) showed that *Ascomycota* was the absolutely dominant phylum (91.75% relative abundance). *Basidiomycota*, *Rozellomycota*, *Mortierellomycota*, *Chytridiomycota*, and *Glomeromycota* were present at low abundances of 1.77%, 1.36%, 0.86%, 0.41%, and 0.02%, respectively. At the genus level ([Figure 3: see original paper]B), the most abundant fungi were *Penicillium* (32.65%), *Colletotrichum* (16.16%), *Fusarium* (8.13%), *Plectosphaerella* (7.30%), *Setophoma* (5.14%), *Sarocladium* (4.57%), *Fusicolla* (2.94%), unclassified *Nectriaceae* (2.53%), *Acremonium* (1.76%), *Talaromyces* (1.05%), and *Clonostachys* (1.01%).

Random and co-occurrence network node degree distributions were constructed using the R package igraph. The random network followed a Poisson distribution, while the co-occurrence network followed a power-law distribution ([Figure 4: see original paper]A), indicating that a few nodes possessed numerous connections and validating the network construction (Lin and Ji, 2024). *Talaromyces*, *Clonostachys*, and *Pseudeurotium* exhibited Hub values of 0.29, higher than other fungi, identifying them as keystone taxa in the network ([Figure 4: see original paper]B). The co-occurrence network ([Figure 4: see original paper]C) comprised 40 nodes and 151 edges, with an average degree of 7.415, average weighted degree of 22.20, network diameter of 6, graph density of 0.185, and average clustering coefficient of 99.33%. These results indicate that most fungi in the network tend to positively reinforce cooperative interactions and possess strong resistance to external disturbances, suggesting that ecological functional groups in rotting yam tubers likely converge and intensify.

2.2 FUNGuild Functional Guild Prediction in Rotting Yam Tubers

To further clarify ecological functional guilds, FUNGuild database analysis was performed on fungal trophic modes ([Figure 5: see original paper]A). Seven trophic types were identified: pathotroph (8.26%) and pathotroph-complex types [pathotroph-symbiotroph (23.64%), pathotroph-saprotroph (5.99%), and pathotroph-saprotroph-symbiotroph (15.57%)] collectively accounting for 53.56%; saprotroph (37.15%); symbiotroph (0.48%); and saprotroph-symbiotroph (1.06%).

Guild classification revealed 37 functional guilds, with ten exceeding 1% relative abundance ([Figure 5: see original paper]B). The dung saprotroph-undefined saprotroph-wood saprotroph guild (32.59%) was represented

exclusively by *Penicillium*. The endophyte-plant pathogen guild (23.64%) was primarily represented by *Colletotrichum* and *Plectosphaerella*. Three guilds associated with both plant pathogens and wood saprotrophs—animal pathogen-endophyte-fungal parasite-lichen parasite-plant pathogen-wood saprotroph (5.48%), animal pathogen-endophyte-lichen parasite-plant pathogen-soil saprotroph-wood saprotroph (4.24%), and animal pathogen-endophyte-plant pathogen-wood saprotroph (3.95%)—were predominantly represented by *Fusarium*. The animal pathogen guild (5.70%) was mainly represented by *Sarocladium*, while the fungal parasite-plant pathogen-plant saprotroph guild (5.69%) was exclusively represented by *Setophoma*. The undefined saprotroph guild (3.75%) was primarily represented by *Talaromyces*, and the plant pathogen guild (2.60%) by *Clonostachys*, *Botryosphaeria*, and *Tubakia*. The animal pathogen-endophyte-fungal parasite-plant pathogen-wood saprotroph guild (1.57%) was exclusively represented by *Acremonium*. These results demonstrate that pathogen- or saprotroph-associated guilds play crucial roles in yam tuber rot.

Trait pathogenicity analysis revealed that several guild members could cause plant soft rot, with varying abundances and confidence levels (). *Penicillium* (32.70%) and *Acremonium alternatum* (0.19%) were classified as "Highly probable" pathogens, while *Fusarium* (3.89%), *Xylaria* (0.13%), and *Trichoderma* (0.03%) were "Probable," and *Alternaria* (0.06%) and *Acremonium* (1.57%) were "Possible." All these potential pathogens belonged to saprotroph- or plant pathogen-associated guilds, likely playing significant roles in yam tuber rot.

2.3 Isolation and Identification of Potential Pathogenic Fungi

High-throughput sequencing and functional guild analyses indicated that plant pathogenic and saprotrophic fungi dominated rotting yam tubers. However, these results relied solely on DNA sequencing. To validate these findings, tissue isolation and culture experiments were conducted, yielding 135 fungal isolates. Twenty-two isolates with distinct colony morphologies were selected (designated RP1–RP22) ([Figure 6: see original paper]) for ITS-rDNA amplification and sequencing. BLAST alignment and phylogenetic tree construction using MEGA 11.0 revealed that these isolates belonged to six genera: *Fusarium* (9 isolates), *Penicillium* (5 isolates), *Aspergillus* (4 isolates), *Talaromyces* (1 isolate), *Trichoderma* (2 isolates), and *Cladosporium* (1 isolate) ([Figure 7: see original paper]). Notably, *Fusarium*, *Penicillium*, *Aspergillus*, and *Talaromyces* were among the most abundant genera detected by high-throughput sequencing ([Figure 3: see original paper]B), confirming their presence in rotting yam tubers.

Literature review of yam tuber pathogens revealed that *Penicillium*, *Fusarium*, and *Aspergillus* species are well-documented as primary causal agents of yam tuber rot. Other potential pathogens such as *Rhizoctonia solani*, *Lasiodiplodia theobromae*, and *Chaetomium* spp. have been occasionally reported (). The pathogens isolated in this study are largely consistent with previous reports, though differences in isolated taxa may be attributed to soil type, nutrient con-

ditions, temperature, humidity (Li et al., 2022), pathogen virulence characteristics (Geng et al., 2021; Zhang et al., 2013), and methodological limitations or biases in fungal cultivation (Xu et al., 2024). Notably, although *Colletotrichum* was not isolated, it exhibited high relative abundance (16.16%) in rotting tubers. *Colletotrichum* is recognized as a major foliar pathogen causing anthracnose with characteristic sunken lesions surrounded by yellow halos, ultimately leading to plant death. Some studies have shown that *Colletotrichum* leaf infection can indirectly reduce yam tuber fresh weight and size (Palaniyandi et al., 2016). However, direct root infection by *Colletotrichum* has not been reported. In potato anthracnose research, *Colletotrichum coccodes* has been isolated from underground necrotic tissues and confirmed to spread intercellularly in both stem and tuber tissues, causing stem necrosis and tuber rot (Wei et al., 2012; Cui, 2017). Future studies should investigate isolation conditions for *Colletotrichum* and determine whether it can directly infect yam tubers or colonize them via leaf-to-tuber transmission.

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3 Discussion and Conclusion

Fungal diseases severely threaten yam tuber health, substantially affecting yield and marketability. This study represents the first comprehensive analysis of the relationship between yam tuber rot and fungal functional communities using ITS amplicon sequencing, network analysis, and FUNGuild, combined with isolation and identification of potential pathogens.

Network structure and FUNGuild analyses revealed that plant pathogenic and saprotrophic fungi dominated the community in rotting yam tubers, forming a modular network with predominantly positive cooperation. This suggests functional synergy or superposition between pathogenic and saprotrophic fungi. Previous research indicates that plant diseases typically occur through two modes: single infection and mixed infection, with mixed infection being the predominant pattern for most fungal diseases (Wang et al., 2018). Co-infection by different fungi can dramatically increase disease severity (Lamichhane et al., 2015; Whitelaw et al., 2013; Lu et al., 2023). Primary pathogens can penetrate plant cells directly via appressoria and infection pegs or through natural openings (stomata, lenticels, and hydathodes), secrete toxins, and create wounds that facilitate secondary infection by other pathogens (Li, 2022). Mixed infections can synergistically alter host resistance and enhance fungal pathogenicity, ultimately exacerbating disease severity (Debray et al., 2022; Halliday et al., 2020). Additionally, invading pathogens can modify fungal community structure by providing nutrients for saprotrophs (Liu et al., 2022) or exerting selective pressure through secretion of specific amino acids (valine, leucine, isoleucine) and cofactors (pantothenic acid and coenzyme A) (Shu et al., 2019), thereby strengthening mutualistic interactions and accelerating disease development. Therefore, yam tuber rot likely results from initial invasion by highly virulent pathogens through epidermal cells or root tips, which create wounds and

produce attractants that recruit less virulent pathogens and saprotrophs with complementary or superimposed functions. This interaction alters tuber fungal community structure, driving functional guild convergence and ultimately allowing pathogenic and saprotrophic guilds to dominate.

All isolated potential pathogens belonged to saprotrophic or pathogen-saprotroph functional guilds, primarily *Penicillium*, *Fusarium*, and *Aspergillus*, consistent with previous studies (). These three genera should be prioritized in yam tuber rot prevention. While some studies have isolated additional pathogens such as *Rhizoctonia solani*, *Lasiodiplodia theobromae*, and *Chaetomium* spp., our study isolated *Talaromyces*, *Trichoderma*, and *Cladosporium* species. These differences likely reflect variations in soil type, nutrition, temperature, humidity (Li et al., 2022), pathogen characteristics (Geng et al., 2021; Zhang et al., 2013), and cultivation biases (Xu et al., 2024). Although *Colletotrichum* was not isolated, its high relative abundance (16.16%) warrants attention. While known as a foliar pathogen, *Colletotrichum* may also directly or indirectly infect tubers, as demonstrated in potato anthracnose (Wei et al., 2012; Cui, 2017). Future research should optimize isolation conditions for *Colletotrichum* and investigate its potential for direct or leaf-mediated tuber infection.

In summary, this study demonstrates that yam tuber rot likely results from synergistic interactions between plant pathogenic and saprotrophic fungal functional guilds. Members of *Fusarium* and *Penicillium* are primary pathogens causing underground tuber rot, likely exacerbating decay through interactions with other fungi. These findings provide valuable references for understanding yam tuber rot pathogenesis, guiding targeted pesticide use, and screening biocontrol agents.

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Note: Figure translations are in progress. See original paper for figures.