Analysis of Community Structure and Ecological Functions of Endophytic Fungi and Rhizosphere Soil Fungi in Black Tiger (Kadsura coccinea) Postprint

Authors: Liu Tao, Ma Nan, Jin Jifen, Peng Zhijun, Li Xingzhong, Wang Dekai

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Abstract

To investigate the composition and ecological functions of rhizosphere soil and tissue endophytic fungal communities in *Kadsura coccinea*, this study employed ITS high-throughput sequencing technology to analyze the community structure, diversity, and ecological functions of endophytic fungi from roots, stems, and leaves, as well as rhizosphere soil fungi in mature *Kadsura coccinea*. The results showed that: (1) A total of 2,241 operational taxonomic units (OTUs) were obtained from 12 samples, encompassing 10 phyla, 41 classes, 95 orders, 212 families, and 367 genera. The OTU numbers for root, stem, and leaf endophytic fungi, and rhizosphere soil fungi were 1,453, 386, 536, and 258, respectively, with 18 OTUs being shared among them. At the phylum level, Ascomycota and Basidiomycota were the dominant communities in both endophytic fungi and rhizosphere soil fungi of *Kadsura coccinea*, with Ascomycota accounting for as much as 96.99% and 95.37% in leaves and stems, respectively. At the genus level, the saprotrophic fungus *Mortierella* exhibited a relatively high proportion (13.5%) in rhizosphere soil fungi, whereas unclassified genera of Ascomycota and *Elsinoë* showed relatively high proportions in vigorously growing tissues such as leaves and stems. (2) Alpha diversity analysis indicated that the abundance and diversity of rhizosphere soil fungal communities in *Kadsura coccinea* were significantly higher than those of endophytic fungi; the abundance of endophytic fungi in stems was significantly higher than that in roots and leaves, while no significant differences in endophytic fungal diversity were observed among root, stem, and leaf tissues. PCoA results demonstrated that the fungal community structures of leaves and stems exhibited higher similarity. (3) Functional prediction analysis of *Kadsura coccinea* endophytic fungi and rhizosphere soil fungal communities using the FUNGuild database revealed that these communities contained numerous unclassified taxa. Among the functionally classified taxa,

pathotrophic functional groups accounted for a relatively high proportion in vigorously growing tissues. These findings provide a theoretical basis for screening and exploring excellent functional microorganisms in *Kadsura coccinea*.

Full Text

Composition and Ecological Function of Endophytic and Rhizosphere Soil Fungi in *Kadsura coccinea*

Liu Tao[1], Ma Nan[2], Jin Jifen[3], Peng Zhijun[1], Li Xinzhong[1], Wang Dekai[2]*

[1]Guizhou Institute of Fruit Tree Science, Guiyang 550006, China
[2]College of Life Sciences and Medicine, Zhejiang Sci-Tech University, Hangzhou 310018, China
[3]Institute of Crop Germplasm Resources, Guizhou Academy of Agricultural Sciences, Guiyang 550006, China

Abstract: To investigate the composition, diversity, and ecological functions of rhizosphere soil and endophytic fungal communities in *Kadsura coccinea*, we analyzed the endophytic fungal communities from roots, stems, and leaves, as well as rhizosphere soils of mature *K. coccinea* using high-throughput ITS sequencing. The results revealed: (1) A total of 2,241 operational taxonomic units (OTUs) were obtained from 12 samples, belonging to 10 phyla, 41 classes, 95 orders, 212 families, and 367 genera. The endophytic fungi from roots, stems, and leaves yielded 1,453, 386, 536, and 258 OTUs, respectively, with 18 OTUs shared among all samples. At the phylum level, the dominant fungal communities in both endophytic and rhizosphere soils were Ascomycota and Basidiomycota, with Ascomycota accounting for 96.99% and 95.37% of the communities in leaves and stems, respectively. At the genus level, the saprophytic fungus *Mortierella* showed high relative abundance (13.5%) in rhizosphere soil, whereas unclassified Ascomycota and *Elsinoe* were predominant in vigorously growing tissues such as leaves and stems. (2) Alpha diversity analysis indicated that the richness and diversity of rhizosphere soil fungal communities were significantly higher than those of endophytic fungi. The abundance of endophytic fungi in stems was significantly higher than in roots and leaves, while no significant differences in diversity were observed among root, stem, and leaf tissues. PCoA results demonstrated higher similarity in fungal community structure between leaves and stems. (3) Functional prediction using the FUNGuild database revealed that both rhizosphere soil fungi and endophytic fungi contained numerous unclassified taxa. Among the functionally classified groups, the pathotrophic functional guild showed higher proportions in vigorously growing tissues. These findings provide a theoretical basis for screening and exploring functional microorganisms in *K. coccinea*.

Keywords: *Kadsura coccinea*; high-throughput sequencing; ITS; endophytic fungi; rhizosphere fungi; diversity; FUNGuild

Kadsura coccinea, also known as "Lengfantuan," "Choufantuan," or "Bufeina," is a plant belonging to the family Schisandraceae (Lin & Yang, 2007). It is primarily distributed in Hunan, Guizhou, Yunnan, Fujian, Guangxi, Sichuan, and Jiangxi provinces of China (Zeng, 1996). The roots and stems are used medicinally for promoting blood circulation, reducing swelling, and relieving pain (Wang et al., 2012). Modern pharmacological studies have demonstrated that *K. coccinea* extracts possess antioxidant, anti-aging, antiviral, hepatoprotective, and anticancer properties (Sun et al., 2009; Zhao et al., 2014; Zhao et al., 2021). The fruits are rich in lignans, amino acids, anthocyanins, and other trace elements (Shu et al., 2012; Zhao & Liang, 2019), and have gained recognition as an emerging fruit crop in recent years, particularly in poverty alleviation programs in southeastern Guizhou, Hunan, and Hubei (Liu et al., 2009; Gao et al., 2022).

Endophytic microorganisms colonize plant tissues and organs, establishing long-term symbiotic relationships and coevolving with their host plants (Rodriguez et al., 2009; Porras-Alfaro & Bayman, 2009). Endophytic fungi can promote plant growth and development, enhance resistance to abiotic stress, and increase host disease resistance. Some endophytic fungi from medicinal plants can produce secondary metabolites similar to those of their hosts, with applications in medicine, agriculture, industry, and biotechnology (Khan et al., 2012; Liu et al., 2018; Jurić et al., 2020). Endophytes have been extensively studied in various medicinal plants, including *Eucommia ulmoides* (Yang et al., 2019), *Paris polyphylla* (Wang et al., 2019), *Rheum palmatum* (Chen et al., 2021), and *Polygonatum sibiricum* (Fan et al., 2021). Research indicates that Schisandraceae plants harbor abundant endophytic fungi with diverse functions, including antioxidant activity (Zhao et al., 2015), antagonism against plant pathogens (Pan et al., 2007; Zhang et al., 2021), inhibition of tumor cell growth (Song et al., 2021), and production or biotransformation of host secondary metabolites such as lignans (Wang et al., 2017; Mao & Dou, 2019; Qin et al., 2019, 2020). Additionally, long-term cultivation of Schisandraceae plants alters soil microbial communities. Jiang et al. (2020) used high-throughput sequencing to analyze changes in rhizosphere soil chemistry and fungal communities in *Schisandra sphenanthera* after 3 and 6 years of cultivation, revealing significant alterations in nutrient status and fungal community composition after 6 years. While these studies provide valuable insights into endophytic and rhizosphere fungi in Schisandraceae, research specifically on *K. coccinea* remains limited.

Given the current state of knowledge, this study employed Illumina high-throughput sequencing to investigate the fungal community composition, diversity, and functional predictions in mature, perennial *K. coccinea* plants. Our objectives were to: (1) characterize the differences in community composition and dominant taxa between endophytic and rhizosphere soil fungi, and (2) explore the functional differences and underlying mechanisms between these fungal groups. This research provides a foundation for further investigation

and utilization of functional microbial communities in *K. coccinea*.

1.1 Sample Processing

Rhizosphere soil, roots, stems, and leaves of *K. coccinea* were collected from the experimental base of the Guizhou Institute of Fruit Tree Science (variety resource code: GZ1), from plants over 5 years old. In November 2021, after fruit harvest, mature roots, stems, and leaves from plants with consistent growth were selected. Samples from three plants were pooled as one replicate, with three replicates per tissue type. Root samples with adhering soil were placed in cold-chain containers and transported immediately to the laboratory. Rhizosphere soil was collected by shaking roots and retaining the soil that remained tightly attached, then stored in sterile PE tubes. Root samples were labeled RT1, RT2, and RT3; stem samples as ST1, ST2, and ST3; and leaf samples as LF1, LF2, and LF3. Following the surface sterilization method described by Wang et al. (2019), root, stem, and leaf samples were rinsed with running tap water to remove excess rhizosphere soil, then treated with 75% ethanol for 2 minutes, followed by 5% sodium hypochlorite for 3 minutes, and finally washed three times with sterile water to obtain surface-sterilized samples. Due to the fleshy nature of *K. coccinea* leaves, which makes DNA extraction difficult, surface-sterilized leaves were placed in sterile mesh bags, dried in silica gel for 24 hours, then snap-frozen in liquid nitrogen for subsequent DNA extraction.

1.2 ITS Library Construction and High-Throughput Sequencing

Root, stem, and leaf tissues were ground in liquid nitrogen, and total DNA was extracted using the Plant Genomic DNA Kit (Tiangen Biotech, catalog no. DP305). Rhizosphere soil samples were ground in liquid nitrogen, and soil microbial DNA was extracted using the FastDNA SPIN Kit for Soil (MP Biomedicals, LLC, OH, catalog no. 116560200) according to the manufacturer' s instructions. The ITS2 region was amplified using universal primers fITS7 (5 -GTGARTCATCGARTCTTTG-3) and ITS4 (5 -TCCTCCGCTTATTGATATGC-3). PCR amplification was performed in a 25 L reaction containing 12.5 L 2×Phanta Max master mix (Vazyme Biotech, catalog no. P515-01), 2.5 L each of forward and reverse primers (1 $\mathrm{mol \cdot L^{-1}}$), and 50 ng template DNA. The PCR program consisted of initial denaturation at 95°C for 5 min, followed by 30 cycles of 95°C for 30 s, 50°C for 30 s, and 72°C for 40 s, with a final extension at 72°C for 7 min. PCR products were verified by 2% agarose gel electrophoresis, purified, and sequenced on the Illumina MiSeq PE300 platform (LC-Bio, Hangzhou).

1.3 Data Processing and Analysis

Raw sequencing data were processed by removing adapter sequences, merging paired-end reads using FLASH v1.2.7, and filtering low-quality bases using Trimmomatic v0.33. Chimeric reads were removed using Vsearch v2.3.4 to obtain

high-quality data. OTUs were clustered at 97% sequence similarity using UPARSE (http://drive5.com/uparse/) and annotated accordingly. Alpha and beta diversity analyses were performed using QIIME 2 (Bolyen et al., 2019). Variance analysis and multiple comparisons were conducted using SPSS 26.0. Figures were generated using R v3.5.2. The ecological functions of endophytic fungi were analyzed using the FUNGuild platform (Nguyen et al., 2016).

2.1 Sequencing Data Statistics for Endophytic and Rhizosphere Fungi in *K. coccinea*

High-throughput ITS sequencing of 12 samples from three different tissues and rhizosphere soil yielded 1,023,870 raw read pairs. After merging, quality control, and chimera filtering, 988,991 high-quality reads were obtained, with 78,302–84,135 reads per sample (average: 82,415). Valid data ranged from 94.79% to 98.4%, with Q20 scores above 98.98% for all samples (Table). Read lengths ranged from 1–500 bp, with the majority (90.6%) between 201–300 bp, indicating satisfactory sequencing quality. Rarefaction curves for both endophytic and rhizosphere fungi showed a rapid initial increase followed by plateauing, with library coverage exceeding 99.9% (Figure [Figure 1: see original paper]), suggesting that sequencing depth was sufficient to capture the majority of species. The rarefaction curves also indicated that rhizosphere soil fungal abundance was substantially higher than that of endophytic fungi, suggesting greater diversity in the rhizosphere.

2.2 OTU Analysis of Endophytic and Rhizosphere Fungal Communities in *K. coccinea*

Analysis and clustering of the 12 samples yielded 2,241 OTUs in total. Rhizosphere soil contained 1,453 OTUs, while root, stem, and leaf tissues contained 386, 536, and 258 OTUs, respectively. Venn diagram analysis revealed that only 18 OTUs were shared among all samples. Rhizosphere soil harbored the largest number of unique OTUs (1,192), while roots, stems, and leaves contained 151, 383, and 112 unique OTUs, respectively. The numbers of OTUs shared between rhizosphere soil and roots, stems, and leaves were 192, 65, and 52, respectively, while 40 OTUs were shared among the three plant tissues (Figure [Figure 2: see original paper]). These results indicate that despite the large number of detected OTUs, only 0.8% were shared across all sample types, suggesting that rhizosphere soil and plant tissues host relatively distinct fungal communities. The relatively high proportion of shared OTUs between rhizosphere soil and roots (8.8%) suggests potential interactions between root-associated fungi and the rhizosphere microbiome.

2.3 Community Structure Composition of Endophytic and Rhizosphere Fungi in *K. coccinea*

Representative OTU sequences were analyzed at the phylum and genus levels. At the phylum level, Ascomycota and Basidiomycota dominated both endo-

phytic and rhizosphere fungal communities. Ascomycota was overwhelmingly dominant, comprising 57.26% and 58.76% of sequences in rhizosphere soil and roots, respectively, and reaching 96.99% and 95.37% in leaves and stems. Additional dominant phyla in roots included Basidiomycota (21.03%) and Glomeromycota (17.96%), whereas Glomeromycota represented only 0.044%, 0.004%, and 0.67% in stems, leaves, and rhizosphere soil, respectively. Zygomycota accounted for 13.84% in rhizosphere soil and 0.03–1.31% in plant tissues (Figure [Figure 3: see original paper]A). Unclassified OTUs represented 13.66% in rhizosphere soil and 0.19–0.93% in plant tissues.

At the genus level, endophytic and rhizosphere fungi were distributed across 367 genera. The top five genera in rhizosphere soil were unclassified fungi (13.7%), *Mortierella* (13.5%), *Plectosphaerella* (6.0%), *Subulicystidium* (4.5%), and *Neonectria* (4.3%). In roots, the most abundant genera were unclassified Sebacinales (19.7%), *Exophiala* (15.2%), unclassified Glomeromycota (12.1%), unclassified Chaetothyriales (8.8%), and *Fusarium* (8.0%). In stems, the dominant genera were unclassified Ascomycota (17.7%), unclassified Pleosporales (16.3%), unclassified Elsinoaceae (11.8%), *Strelitziana* (9.1%), and unclassified Trichomeriaceae (8.6%). In leaves, *Elsinoe* (21.5%), *Mycosphaerella* (18.2%), *Guignardia* (14.2%), *Diaporthe* (6.9%), and *Phialophora* (5.4%) were most abundant (Figure [Figure 3: see original paper]B). These results demonstrate tissue-specific fungal communities in *K. coccinea*, with distinct genera characteristic of rhizosphere soil and different plant tissues.

Heatmap analysis of the top 30 taxa at phylum and genus levels revealed that stems and leaves clustered together at the phylum level (Figure [Figure 4: see original paper]A). At the genus level, rhizosphere soil and root samples formed one cluster, while stem and leaf samples formed another (Figure [Figure 4: see original paper]B), indicating that root and rhizosphere fungal communities are more similar, possibly due to direct contact and reciprocal influence, whereas stem and leaf endophytic communities share more similar origins or interactions.

2.4 Diversity Analysis of Endophytic and Rhizosphere Fungal Communities in *K. coccinea*

Community richness (Chao1 and ACE indices) and diversity (Shannon and Simpson indices) were compared. Rhizosphere fungal communities exhibited significantly higher richness and diversity than endophytic fungi, with ACE, Chao1, and Shannon indices all significantly greater ($P < 0.05$). No significant differences in ACE or Chao1 indices were observed among roots, stems, and leaves ($P > 0.05$), except between stems and leaves ($P < 0.05$) (Table). While ACE and Chao1 indices reflect species richness, Shannon and Simpson indices reflect diversity. These results confirm that rhizosphere soil harbors greater fungal richness and diversity than plant tissues, with stem endophytes showing higher richness than leaf endophytes, but no significant differences in diversity among root, stem, and leaf tissues.

Principal Coordinates Analysis (PCoA) based on unweighted UniFrac distance matrices was performed to assess community differences. The first and second principal coordinates explained 32.44% and 16.11% of the variation in fungal community structure, respectively, cumulatively accounting for 48.55% (Figure [Figure 5: see original paper]). PCoA clearly separated different tissue types, with leaf and stem samples clustering together, indicating high similarity and potentially common origins. Despite direct contact between roots and rhizosphere soil, root endophytes remained distinct from rhizosphere fungi, suggesting different sources.

2.5 FUNGuild Functional Prediction of Endophytic and Rhizosphere Fungal Communities

FUNGuild analysis revealed that unassigned taxa represented substantial proportions in rhizosphere soil (31.5%), roots (37.3%), and stems (35.8%). Pathotrophic functional groups showed the highest proportions in vigorously growing tissues, following the order: leaves (62.9%) > stems (37.5%) > rhizosphere soil (16.7%) > roots (9.2%). In rhizosphere soil, other trophic modes exceeding 10% included saprotrophs (10.2%), pathotroph-saprotroph-symbiotrophs (12.7%), and saprotroph-symbiotrophs (13.9%). In roots, saprotroph-symbiotrophs (17.8%) and pathotroph-saprotrophs (17.2%) exceeded 10%. In stems and leaves, symbiotrophs (13.7%) and pathotroph-symbiotrophs (10.7%) were the only groups above 10%, respectively (Figure [Figure 6: see original paper]A).

Detailed functional classification of taxa representing >1% revealed that plant pathogens were the primary identified ecological functional group across all samples, accounting for 15.4%, 9.1%, 37.5%, and 62.9% in rhizosphere soil, roots, stems, and leaves, respectively (Figure [Figure 6: see original paper]B). Among functional groups exceeding 10% abundance, rhizosphere soil was dominated by endophyte-litter saprotroph-soil saprotroph-undefined saprotrophs (13.6%), while roots contained animal pathogen-fungal parasite-undefined saprotrophs (17.1%) and arbuscular mycorrhizal fungi (17%). No other functional groups exceeded 10% in stems or leaves.

3 Discussion and Conclusion

Through long-term coevolution, fungi have established complex interactions with host plants, playing crucial roles in plant growth, pathogen defense, and abiotic stress tolerance, while some endophytes produce host-identical secondary metabolites. Traditional isolation techniques limit the discovery of unculturable endophytes. This high-throughput sequencing study of *K. coccinea* endophytic and rhizosphere fungi identified numerous unclassified OTUs, suggesting that: (1) high-throughput sequencing reveals greater fungal diversity than culture-dependent methods; (2) many fungal taxa in *K. coccinea* remain unclassified, possibly due to database limitations; and (3) many undiscovered taxa may be recalcitrant to cultivation, requiring improved isolation techniques.

Endophytic community composition is influenced by host genotype, environment, and tissue type (Fuchs et al., 2017). Our results show substantial differences in fungal communities among rhizosphere soil, roots, stems, and leaves. At the phylum level, Ascomycota and Basidiomycota dominated, with Ascomycota comprising >90% in leaves and stems, consistent with reports of Ascomycota as the predominant endophytic phylum in many plants, though proportions vary among species and tissues. At the genus level, *Mortierella*, a saprophytic genus important for straw decomposition and nutrient cycling (Ning et al., 2022), was abundant in rhizosphere soil. Unclassified Ascomycota and *Elsinoe*, primarily plant pathogens, were prevalent in metabolically active tissues like leaves and stems. Heatmap analysis revealed that root and rhizosphere communities were more similar, likely due to direct physical contact and microbial exchange (Ren et al., 2019), while stem and leaf communities clustered separately, possibly reflecting their similar developmental origins and limited soil contact.

Diversity analysis revealed rich fungal communities, with rhizosphere fungi showing significantly higher richness and diversity than endophytes, consistent with findings in other medicinal plants such as *Paris polyphylla* (Wang et al., 2019) and *Ageratina adenophora* (Zhou et al., 2019). Tissue-specific endophytic communities were observed, with stems showing higher richness than leaves, though diversity differences among tissues were not significant.

Kadsura coccinea is a traditional medicinal plant rich in lignans, triterpenoids, and anthocyanins (Shu et al., 2012), with fruits containing abundant phenolic acids, flavonoids, and amino acids (Yang et al., 2020). Few endophytes have been reported from *K. coccinea*, but related Schisandraceae species have yielded functional endophytes including *Umbelopsis* and *Penicillium* with antioxidant, antagonistic, and biotransformation capabilities (Wang et al., 2017; Mao & Dou, 2019; Qin et al., 2019; Song et al., 2021). These genera were detected in our study, suggesting that endophyte information from related species can guide the discovery of metabolically active fungi in *K. coccinea*.

FUNGuild predictions showed that leaves had relatively fewer unassigned taxa compared to rhizosphere soil, roots, and stems, indicating substantial unexplored functional diversity in these compartments. The high proportion of pathotrophs in *K. coccinea* tissues may reflect its evergreen habit and the nutrient-rich nature of stems and leaves, which favor pathogenic colonization (Qiao et al., 2018). The prevalence of saprotrophs and saprotroph-symbiotrophs in rhizosphere soil and roots likely reflects the abundance of organic matter and decomposition processes (Liang et al., 2003; Ning et al., 2021). The distinct functional guild distributions among tissues suggest that endophytes perform tissue-specific roles. As fungal functions continue to be elucidated, the ecological roles of *K. coccinea* endophytes and rhizosphere fungi will become increasingly clear.

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