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Diversity of rhizosphere microbial communities and environmental variables in wild and cultivated *Scutellaria baicalensis* Georgi and their effect on flavonoid

Puyang Feng^{1,2}, Tao Qin^{1,2}, Weifeng Chen^{1,2}, Hong Yan^{1,2}, Yuxin Lu^{1,2}, Jianqiang Liang^{1,2} and Yani Bai^{1,2*} 

Abstract

Purpose *Scutellaria baicalensis* Georgi in Yaozhou District in Shaanxi Province is an important Dao-di Herb. However, little is known about the differences between wild and cultivated *S. baicalensis* rhizosphere microbial communities, and how the differences and environmental variables affect the accumulation of flavonoid active ingredients.

Methods We analyzed the interactions between rhizosphere microbial communities- environmental variables, environmental variables- flavonoid active ingredients of wild and cultivated *S. baicalensis* by high performance liquid chromatography, high-throughput sequencing and multianalytical approach.

Results Wild *S. baicalensis* contained a significantly higher content of scutellarin and baicalin compared to cultivated. Bacterial genera *Sphingomonas*, RB41 and fungal genera *Mortierella*, *Cordyceps*, *Phialophora* were higher in wild habitat than those of cultivated. The diversity of wild *S. baicalensis* rhizosphere fungal communities was higher, while the diversity and richness of cultivated rhizosphere bacterial communities were higher. The difference of rhizosphere microbial communities in wild and cultivated habitats may lead to differences in soil nitrogen, phosphorus and potassium nutrients. The KEGG pathways of rhizosphere bacterial communities were mainly enriched in global and overview maps. The relative abundance and species of functional species in the saprotroph in wild *S. baicalensis* were higher than those in cultivated. Soil SOM, TP, TK and altitude were significantly positively correlated with flavonoid contents ($P < 0.05$).

Conclusions Increasing the application of organic matter, TN: TP and TN: TK ratio was suggested in the future cultivation, meanwhile pH value of soil should be adjusted. Besides, it is speculated that *Sphingomonas* has potential application value in the cultivated *S. baicalensis*.

Keywords Rhizosphere microbial communities, Medicinal plants, Environmental variables, Accumulation in flavonoid active ingredients

Introduction

Scutellaria baicalensis Georgi with a history of more than 2000 years' application in medicine, has significant pharmacological properties like anti-bacterial, anti-inflammation, anti-viral, etc. (Wu et al. 2018; Xiang et al. 2022). Baicalin, a flavonoid, is among the main pharmaceutical active ingredients, and the Pharmacopoeia considers its content as the criterion for quality control of *S.*

*Correspondence:

Yani Bai

baiyn@xab.ac.cn

¹ Bio-Agriculture Institute of Shaanxi, Xi'an 710043, China

² Enzyme Engineering Research Center of Shaanxi Province, Xi'an 710600, China



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baicalensis (Committee 2020). In recent years, because of its medicinal values, there is an increasing market demand for *S. baicalensis*. Therefore, a large area of artificial cultivation was arranged by farmers (Bai et al. 2020). Nevertheless, in the course of cultivation, the urgent problem that needs to be resolved is how to keep the plant's quality intact and encourage the accumulation of active substances.

S. baicalensis in Yaozhou area (China) is defined as Dao-di Herbs, which means the medicine has better quality and efficacy, its quality is stable, and the herbs enjoy a high reputation (He et al. 2020). Yaozhou *S. baicalensis* produced in the bordering area of Guanzhong Plain and Weibei Plateau has become famous since the Tang and Song dynasties and has been certified as a national geographical indication of agricultural products. According to Huang et al. (2007), the development of geoherbism is attributed to the combined influence of genetic and environmental factors, including soil, climate, water quality, landform, and cultivation conditions. For medicinal plants, soil is the foundational effect factor influence rhizosphere microbiology (Butler et al. 2003). Medicinal plants' rhizosphere microorganisms play crucial roles. They can not only synthesize plant growth regulators and promote uptake of mineral nutrients such as P, Ca, Zn and N (He et al. 2020); but also enhance or endow medicinal plants with the characteristics of disease resistance, drought resistance, cold resistance and saline-alkali resistance (He et al. 2020; Lubna et al. 2018; Sturz and Matheson 1996). Meanwhile, they have impact on the growth, traits, chemical composition, metabolism and development of medicinal plants, eventually leading to the difference between Dao-di Herbs and non-Dao-di Herbs (Xiao et al. 2009). Therefore, it is highly significant to clarify and excavate the regional differentiation rules and causes of soil microorganisms (He et al. 2020), and to screen and utilize regional exclusive microbial resources for the cultivation of Dao-di Herbs.

Wild Yaozhou *S. baicalensis* had a higher baicalin content than cultivated ones. It has been reported that after 2 or 3 years of cultivation, *S. baicalensis* might suffer from soil-borne diseases and a decrease in quality. Zhang et al. (2010) suggested that it might be caused by infectious agents *Pythium ultimum* and *Rhizoctonia solani*. But it is reported that wild medicinal plants have strong

resistance in the natural environment, and although their biomass is lower than that of artificial cultivars, they can coexist harmoniously with nature for a long time (Wu and Lin 2020). This posed the question: are there differences in the root microorganisms between wild *S. baicalensis* and cultivated *S. baicalensis*? Will it have an impact on the accumulation of active ingredients in *S. baicalensis*? Until now, little is known about the differences between the rhizosphere microbial communities of wild and cultivated *S. baicalensis*. This study aimed to compare the differences of rhizosphere microbial communities and environmental variables between wild and cultivated *S. baicalensis*, analyzed the effects of rhizosphere microbial communities and environmental variables on the accumulation of flavonoid active ingredients in *S. baicalensis*, and provided improvement strategies for soil management of cultivated *S. baicalensis*.

Materials and methods

Samples collection

All *S. baicalensis* samples were collected from Yaozhou District, Tongchuan City, Shaanxi Province, China. The monthly basic statistics on climate of sampling sites are shown in Table 1. Annual average temperature is 11.7°C, highest temperature is 36.2°C, lowest temperature is −14.0°C. Annual precipitation is 517.8 mm. Annual sunshine hours are 2298.1 h. Mean wind speed is 2.4 m/s. Relative humidity is 68%. Frost-free period is 160 days. Pressure is 905.4 hPa (Shaanxi Provincial Bureau of Statistics).

Wild samples were collected at Caihe Village, Miaowan Town (W1), and at Koujiayuan Village, Shizhu Town (W2). Cultivated samples were collected from the Planting Demonstration Base (C1) and Baojian Village, Sunyuan Town (C2). As shown in Table 2, the sampling information of *S. baicalensis* habitat samples is presented.

The method of collecting rhizosphere soil referred to the “shaking method” of Chen et al. (2022): After completely digging out fresh and healthy *S. baicalensis* with soil and shaking it gently, large chunks of bulk soil were removed. Subsequently, the rhizosphere soil that was still adhering to the root was gathered by a small sterilized fine brush. One portion was subsequently placed in sterile PE tubes and conserved in a −80 °C freezer, while another portion was dried in the open air to determine

Table 1 The monthly basic statistics on climate of sampling sites

	1	2	3	4	5	6	7	8	9	10	11	12
Monthly average temperature (°C)	−1.4	−0.6	9.2	13.2	16.6	23.5	23.9	24.0	17.5	10.9	6.3	−2.2
Monthly precipitation (mm)	17.0	7.1	34.8	21.0	22.9	54.1	161.9	88.0	19.1	65.2	22.8	3.9
Monthly sunshine hours (h)	144.4	183.7	169.3	203.7	250.0	293.4	235.2	195.9	166.5	123.9	121.3	210.8

Table 2 Sampling information of samples from *S. baicalensis* habitat

Samples	Longitude	Latitude	Altitude(m)
Caihe Village, Miaowan Town (W1)	108°48'19" E	35°8'53" N	1209
Koujiayuan Village, Shizhu Town (W2)	108°58'43" E	35°10'55" N	1242
Planting Demonstration Base (C1)	109°0'16" E	34°55'20" N	727
Baojian Village, Sunyuan Town (C2)	109°0'29" E	34°55'20" N	738

the soil’s physicochemical properties. At each sampling site, three replicate samples were collected (each replicate was the mixture of 10 samples), and a total of 12 soil samples were collected. Correspondingly, 12 samples of *S. baicalensis* were collected.

Phenotypic characteristics

The seeds of cultivated *S. baicalensis* were selected from wild populations by multi-generation single plant cooperative selection. For the wild samples, the underground dry weight was 20.61 ± 12.65 g, the root diameter was 14.94 ± 1.91 mm, the above ground length was 9.87 ± 2.16 cm. While for the cultivated samples, the underground dry weight was 14.06 ± 4.06 g, the root diameter was 11.81 ± 2.15 mm, and the above ground length was 18.54 ± 5.19 cm.

Management mode of the cultivated

When the height reached 8–10 cm, the plants were moved into the soil, with a distance of 8–15 cm among each other. No fertilizer was applied in the transplanting year. In the next year, when the plant height reached 10–15 cm, 75 kg/ha urea was applied; from the end of June to the beginning of July, 150 kg/ha potassium

sulphate and 150 kg/ha ammonium phosphate dibasic were applied. In the third year, after the rejuvenation of *S. baicalensis*, 300 kg/ha 12% calcium superphosphate, 75 kg/ha urea and 75 kg/ha potassium sulphate were applied. No extra watering was needed.

Measurement of the primary flavonoid active components in the roots

Employing high performance liquid chromatography techniques, we measured the concentrations of seven active components, namely scutellarin, baicalin, wogonoside, apigenin, baicalein, wogonin, and melaleuca A (Fig. 1). For each sample, firstly, the roots were dried and ground. And then 0.5 g root powder was measured. To extract the active ingredient, 50 mL of 70% ethanol was added into the powder and ultrasonic extraction (200 W, 40 kHz) was performed for 60 min. After that, the supernatant was filtered through a 0.45 μm filter membrane, so as to prepare it for HPLC analysis. Substances were examined using an Agilent Technologies 1200 Series (America) that had an Agilent ZORBAX Eclipse XDB-C8 column installed (4.6 × 150 mm, 5 μm). The mobile phase consisted of acetonitrile (A) and 0.1% formic acid (B), and the gradient elution was carried out with the following

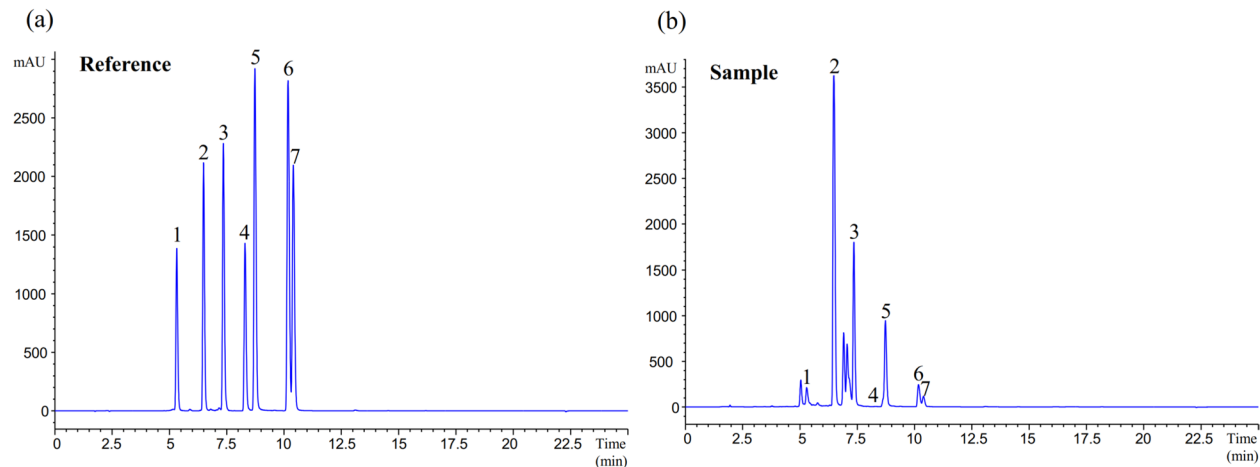


Fig. 1 The HPLC chromatograms for seven active ingredients in reference and samples. **a** The chromatograms of the standard samples. 1. scutellarin; 2. baicalin; 3. wogonoside; 4. apigenin; 5. baicalein; 6. wogonin; 7. melaleuca A. **b** The representative chromatograms of the sample. 1. scutellarin; 2. baicalin; 3. wogonoside; 4. apigenin; 5. baicalein; 6. wogonin; 7. melaleuca A

concentrations: 10% A (0 min); 100% A (15 min); 100% A (20 min); 10% A (21 min); 10% A (25 min). All separations occurred with the column temperature held steady at 28°C (wavelength: 274 nm, flow rate: 1.0 mL/min).

Soil physicochemical characteristics

Soil samples were air dried and ground passed through a 2 mm sieve at room temperature. Soil suspensions were made by combining soil and water in a 1:2.5 (w/w) ratio, and a pH meter (PHSJ-3E, INESA, China) was utilized to assess the pH values of these suspensions. Soil suspensions were formed by mixing soil and water at a 1:5 (w/w) ratio, a conductivity meter (DDS-307, LeiCi, China) was utilized to assess the electrical conductivity (EC) values of these suspensions. The Walkley and Black method was employed to measure the soil organic matter (SOM) (Huang et al. 2006). The contents of available nitrogen (AN), available phosphorous (AP), and available potassium (AK) in the soil samples were measured following the procedures outlined in “Soil and Agricultural Chemistry Analysis” (Bao 2000). After digestion with H₂SO₄, the Kjeldahl method was utilized to measure the total nitrogen (TN) content in soils (Huang et al. 2006). Once digested by H₂SO₄, HNO₃ and HClO₄, respectively, soil samples had their total phosphorus (TP) content determined according to the Murphy and Riley (1962) method, and the flame spectrometry method was used to determine the total potassium (TK) content.

High-throughput sequencing of rhizosphere microbial communities

The total DNA of rhizosphere samples was extracted using the E.Z.N.A.[®] soil DNA Kit (Omega Bio-tek, Norcross, GA, USA). Then, a Scandrop200 (Analytik Jena AG, Jena, Germany) was used to measure the concentration of DNA. The specific primers for the 16S rRNA gene (Zeng et al. 2011) were 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'), and those for the fungal ITS region (Adams et al. 2013) were ITS1F (5'-CTTGGTCATTTA GAGGAAGTAA-3') and ITS2R (5'-GCTGCGTTCTTC ATCGATGC-3'). TransStartFastPfu PCR Supermix (AP221, TransGen Biotech, China) was used for the PCR reaction. The 20 µL reactions included 5×FastPfu buffer (4 µL), dNTPs (2.5 mM; 2 µL), forward primer (5 mM; 0.8 µL), reverse primer (5 mM; 0.8 µL), FastPfu polymerase (0.4 µL), BSA (0.2 µL), template DNA (10 ng), and then ddH₂O was used to add to 20 µL in total. An ABI GeneAmpv thermal cycler (9700, Thermo Fisher Scientific, USA) was used to perform the PCR reactions. For the 16S rRNA gene, the thermocycler program began with initial denaturation at 95°C for 3 min. This was followed by 27 cycles, each cycle consisting of 30 s at 95°C,

30 s at 55°C, and 45 s at 72°C. Finally, a final extension was carried out at 72°C for 10 min. The thermocycler protocol for the fungal ITS gene was configured with an initial denaturation step at 94°C for 5 min. This was followed by 35 cycles, each cycle consisting of 45 s at 94°C, 45 s at 55°C, and 1 min at 72°C. Finally, a final extension was conducted at 72°C for 10 min. The Quanti Fluor™—ST system (Promega, USA) was used to quantify the obtained amplicons, in order to pool in equimolar concentrations for samples. Finally, the pooled amplicons were subjected to paired-end sequencing on the Illumina MiSeq platform (Majorbio, Shanghai, China).

Statistical analysis

Fastp software (<https://github.com/OpenGene/fastp>, version 0.20.0) was used for the quality control of obtained raw sequences. Splicing of the raw sequences was conducted using FLASH software (<http://www.cbcb.umd.edu/software/flash>, version 1.2.7). Chimeras were removed using the UPARSE software (<http://drive5.com/uparse/>, version 7.1) with the 97% clustered similarity of OTUs as the basis. In detail, a 10-base-pair window was established to screen out bases at the terminal part of reads with a quality score lower than 20. When the mean quality score within the specified range fell below 20, the bases at the end of the read (backend) within that range were removed. Once the quality control procedure was completed, reads shorter than 50 base pairs were screened out, and reads with N-bases were eliminated. If the pairs of reads have an overlap length of at least 10 base pairs, the two sequences were combined into a single sequence. The splicing sequence's overlap region allowed a mismatch ratio of up to 0.2, and non-conforming sequences were filtered out. The orientation of the sequences was adjusted according to the barcodes and primers situated at either end. For barcode, the maximum mismatch number was 0; while for primer, the maximum mismatch number was 2. Taxonomic assignment was performed by comparing the categories in the database, bacteria: 16S silva138/16s_bacteria, fungus: ITS unite8.0/its_fungi. No normalizations were applied.

IBM SPSS Statistics 22 was used to conduct a One-way ANOVA for data analysis and post-hoc multiple comparison tests (including the least significant difference and Dunnett's tests) was used to assess the differences among treatments. Mothur software (<http://www.mothur.org/wiki/Calculators>) was utilized to compute the alpha diversity of microbial communities. Based on Euclidean distance algorithm, PCoA analysis (principal co-ordinate analysis) in R language (version 3.3.1) was applied to assess the resemblance of microbial community structure across samples. CCA and RDA analyses in R language (version 3.3.1) were conducted to calculate

the correlations between microbial communities and environmental variables. Spearman correlation analysis of the bacterial and fungal communities, environmental variables, and flavonoid active ingredient content was conducted using OriginPro 2023 software. Figures were created in OriginPro 2023 and Excel software.

Results

Concentrations of the key flavonoid bioactive components in the roots

The content of scutellarin and baicalin in wild *S. baicalensis* was significantly greater than that in cultivated ones. The content of baicalein, wogonin and melaleuca A in wild *S. baicalensis* was significantly less than that in cultivated ones. The content of wogonoside and apigenin did not show significant differences (Table 3).

Soil physicochemical properties

The statistical analysis of soil physicochemical properties in the current study indicated that the pH, TP, TK in wild habitats were significantly lower than those in cultivated habitat. On the contrary, the content of SOM, AN, TN in wild habitats were significantly higher than those in cultivated habitat (Table 4). And this finding suggested that the soil environment of wild and cultivated *S. baicalensis* differed significantly.

OTUs and α diversity analysis of microbial communities

The original data have been deposited on the NCBI website, with PRJNA991737 and PRJNA991750 assigned as the respective accession numbers.

On average, 58,000 bacterial 16S rDNA sequences and 51,000 fungal ITS1 sequences were obtained per sample. After screening, filtration and chimera removal, the sequences were clustered by 97% similarity of OTUs levels. Finally, we obtained 5338 OTUs for bacteria and 1799 OTUs for fungi separately. By annotation of OTUs, a total of 37 phyla, 111 classes, 266 orders, 420 families, 749 genera, and 1559 species of bacteria were obtained. While 14 phyla, 49 classes, 108 orders, 229 families, 444 genera, and 658 species of fungi were obtained.

Table 4 Basic physicochemical properties of soils

Samples	W1	W2	C1	C2
pH	8.12 ± 0.01b	7.83 ± 0.06c	8.34 ± 0.01a	8.30 ± 0.04a
EC (μS/cm)	138.93 ± 0.90a	79.57 ± 0.40d	120.61 ± 0.53b	111.50 ± 0.50c
SOM (g/kg)	18.13 ± 0.45b	41.52 ± 0.81a	11.31 ± 0.68d	12.64 ± 0.76c
AN (mg/kg)	103.33 ± 2.96b	147.11 ± 4.49a	43.82 ± 2.62c	46.25 ± 2.31c
AP (mg/kg)	2.47 ± 0.17d	10.80 ± 0.56b	19.43 ± 0.81a	5.77 ± 0.12c
AK (mg/kg)	223.33 ± 2.08b	185.67 ± 1.53c	161.00 ± 2.00d	237.67 ± 3.06a
TN (g/kg)	1.10 ± 0.02b	2.77 ± 0.11a	0.81 ± 0.04c	0.86 ± 0.01c
TP (g/kg)	0.49 ± 0.05b	0.47 ± 0.02b	0.71 ± 0.02a	0.76 ± 0.02a
TK (g/kg)	13.67 ± 0.15b	17.20 ± 0.56a	17.60 ± 0.46a	17.77 ± 0.45a

Significant differences within the same column are denoted by different letters ($P < 0.05$)

The species richness of the community is reflected by alpha diversity (Table 5). The bacterial community diversity of the cultivated group was greater than that of the wild group ($P < 0.05$), and the diversity of fungal communities in the cultivated group was lower than that of the wild group ($P < 0.05$). The Simpson index of the samples did not show any significant difference. The cultivated samples exhibited a significantly greater richness of the bacterial community compared to the wild samples ($P < 0.05$), while the fungal communities of the samples did not show significant differences.

The composition of the microbial communities

As shown in Fig. 2, at the phylum level, for both wild and cultivated samples, Actinobacteriota (23.16%–37.67%), Proteobacteria (20.88%–32.51%), Acidobacteriota (11.11%–17.5%) and Chloroflexi (7.87%–13.33%) were dominant in the bacterial communities. At the genus level, the dominant genera of rhizosphere bacterial communities in the wild samples (abundance > 2%) included: *norank_f_norank_o_Vicinamibacterales* (4.81%), *norank_f_Vicinamibacteraceae* (3.77%), *norank_f_67-14* (3.21%), *Sphingomonas* (2.86%), *RB41* (2.50%), *norank_f_Xanthobacteraceae* (2.49%), *Gaiella* (2.39%), and *Solirubrobacter* (2.39%). The dominant genera (abundance > 2%) of rhizosphere bacterial communities in

Table 3 Contents of flavonoid active ingredients

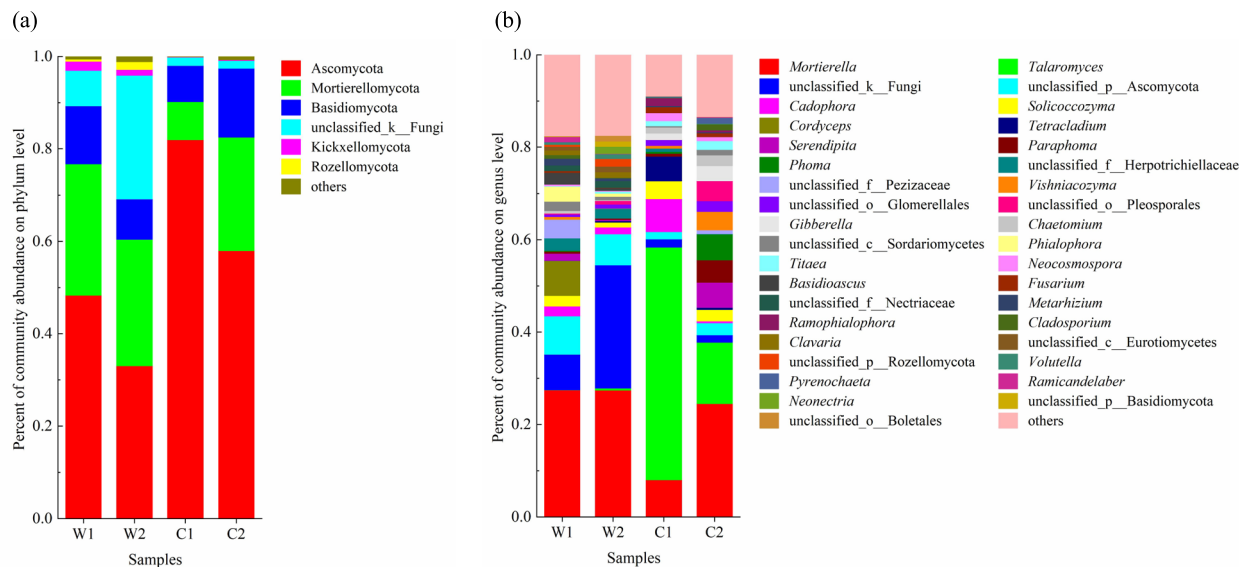
Samples	Contents of flavonoid active ingredients (Dry weight, %)						
	Scutellarin	Baicalin	Wogonoside	Apigenin	Baicalein	Wogonin	Melaleuca A
W1	0.79 ± 0.07a	13.22 ± 0.15a	4.55 ± 0.29a	0.03 ± 0.01a	1.71 ± 0.32b	0.26 ± 0.11b	0.18 ± 0.05b
W2	0.76 ± 0.09ab	12.85 ± 0.77a	4.22 ± 1.02a	0.07 ± 0.05a	2.28 ± 1.10b	0.35 ± 0.15b	0.27 ± 0.13b
C1	0.65 ± 0.05b	12.32 ± 0.67ab	4.21 ± 0.02a	0.04 ± 0.02a	1.80 ± 0.45b	0.39 ± 0.20b	0.31 ± 0.13ab
C2	0.64 ± 0.05b	11.54 ± 0.62b	3.56 ± 0.02a	0.03 ± 0.02a	3.81 ± 0.48a	0.71 ± 0.06a	0.50 ± 0.12a

Significant differences within the same column are denoted by different letters ($P < 0.05$)

Table 5 Alpha-diversity indexes of microbial communities in *S. baicalensis* rhizosphere soil

		Shannon index	Simpson index	Chao1 index	ACE index
Bacteria	W1	6.287±0.144b	0.005±0.002a	2783.179±158.368c	2789.131±166.812c
	W2	5.992±0.102c	0.006±0.001a	2523.584±101.149c	2531.550±139.134c
	C1	6.144±0.124bc	0.011±0.008a	3083.342±203.082b	3087.497±174.875b
	C2	6.545±0.091a	0.005±0.001a	3571.346±65.363a	3571.808±29.567a
Fungus	W1	3.526±0.575a	0.096±0.049a	325.787±118.965a	325.586±120.281a
	W2	4.299±0.276a	0.041±0.015a	424.576±34.101a	423.268±35.008a
	C1	2.375±1.030b	0.323±0.295a	345.232±28.590a	343.918±20.255a
	C2	3.721±0.090a	0.063±0.012a	446.202±50.736a	444.537±54.636a

Significant differences within the same column are denoted by different letters ($P < 0.05$)



(a) Relative abundance of fungi at the phylum level. (b) Relative abundance of fungi at the genus level.

Fig. 3 Fungal community structures at phylum and genus level in samples

Table 6 The rhizosphere’s proportion of potential pathogenic fungi at the genus level

Samples	Relative abundance (%)					
	<i>Mortierella</i>	<i>Talaromyces</i>	<i>Cadophora</i>	<i>Cordyceps</i>	<i>Phoma</i>	<i>Gibberella</i>
W1	26.05 ± 8.54a	0.04 ± 0.04b	1.90 ± 1.21a	10.68 ± 17.97a	0.17 ± 0.26b	0.07 ± 0.01c
W2	26.97 ± 6.16a	0.48 ± 0.71b	1.42 ± 0.59a	0.09 ± 0.12a	0.01 ± 0.02b	0.05 ± 0.07c
C1	8.10 ± 4.58a	50.05 ± 28.60a	7.11 ± 7.39a	0.001 ± 0.002a	0.38 ± 0.26b	1.42 ± 0.61b
C2	26.65 ± 12.52b	11.7 ± 9.36b	0.31 ± 0.49a	0.002 ± 0.004a	5.24 ± 2.81a	2.98 ± 1.23a

Significant differences within the same column are denoted by different letters ($P < 0.05$)

Principal co-ordinates analysis of the microbial communities

Each group of bacterial communities (Fig. 4(a)) principal component 1 (PC1) and principal component 2 (PC2) explained a total of 54.76% difference. PC1 clearly distinguished bacterial communities from wild and artificial groups. The PC1 and PC2 of each group of fungal communities (Fig. 4(b)) explained a total of 44.52% difference. PC1 clearly distinguished the fungal communities of the wild and artificial groups as well. For both bacteria and fungi, the wild soil samples (W1 and W2) and the cultivation soil samples (C1 and C2) were located on the positive and negative half—axes of the PC1 axis respectively, and were quite distant from each other. It means that there were differences in the structure of bacterial communities and fungal communities in the rhizosphere soil of wild and cultivated *S. baicalensis*.

Correlations between microbial communities and environmental variables

Firstly, the OTUs table (species—sample data with 97% similarity of samples) was used for DCA analysis, and then the specific model was chosen according to the axis-lengths value in the DCA1 analysis results. If the axis-length value is less than 3.5, the RDA model is used; otherwise, if it is greater than or equal to 3.5, the CCA model is used. Figure 5(a) has an Axis-lengths value of 1.8977 and Fig. 5(b) has an Axis-lengths value of 4.0486. Therefore, RDA analysis was chosen for bacterial community analysis, while CCA analysis was chosen for fungal community analysis. Figure 5 showed the relationship between bacterial and fungal communities and environmental variables at the OTU level. RDA explained the total variance of 76.88% of bacterial communities, and soil pH, SOM, AN had significant effect on bacterial communities ($P = 0.001$). CCA explained the total variance of 34.87% of fungal communities, and

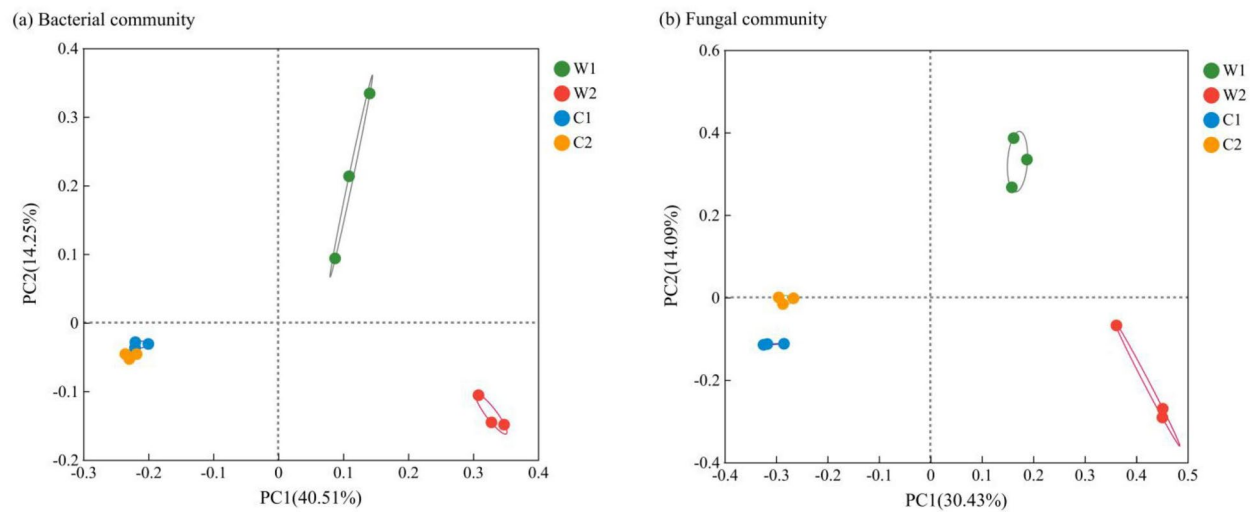


Fig. 4 PCoA of microbial communities in samples

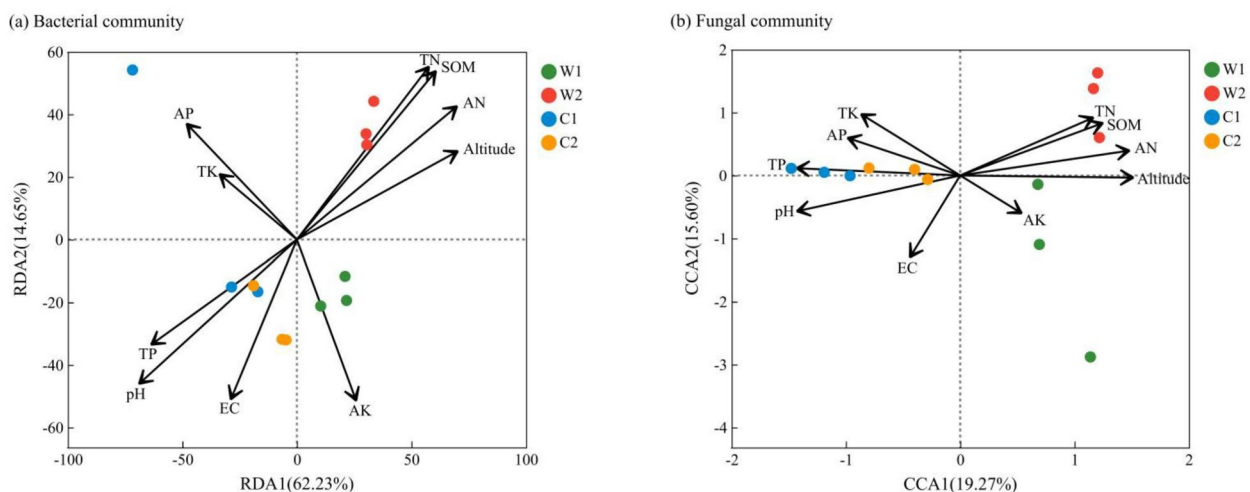


Fig. 5 CCA and RDA analysis of microbial communities and environmental variables

soil pH, SOM and altitude significantly influenced fungal communities ($P=0.001$).

Functional prediction analysis

Based on the high-throughput sequencing of microbial communities, PICRUSt2 functional prediction revealed that the KEGG pathways of rhizosphere bacterial communities in both wild and cultivated *S. baicalensis* were predominantly enriched in metabolism (relative abundance: 0.787), followed by genetic information processing (0.064), environmental information processing (0.052), cellular processes (0.043), human diseases (0.035), and organismal systems (0.018) (Fig. 6).

Analysis using FUNGuild microecological tools revealed that saprotrophs represented a substantial proportion of the fungal community. Specifically, the relative abundances of saprotrophs labeled as W1, W2, C1, and C2 were 0.61, 0.60, 0.86, and 0.66 in the samples, respectively (Fig. 7(a)). Based on their utilization of environmental resources, saprotrophs were further categorized into ten functional guilds (Fig. 7(b)). Among wild *S. baicalensis* samples, fungal functional guilds with an average relative abundance exceeding 1% included Dung Saprotroph, Dung Saprotroph-Plant Saprotroph, Dung Saprotroph-Plant Saprotroph-Wood Saprotroph, Plant Saprotroph-Wood Saprotroph, Soil Saprotroph, Wood Saprotroph, and Undefined Saprotroph. In contrast, for

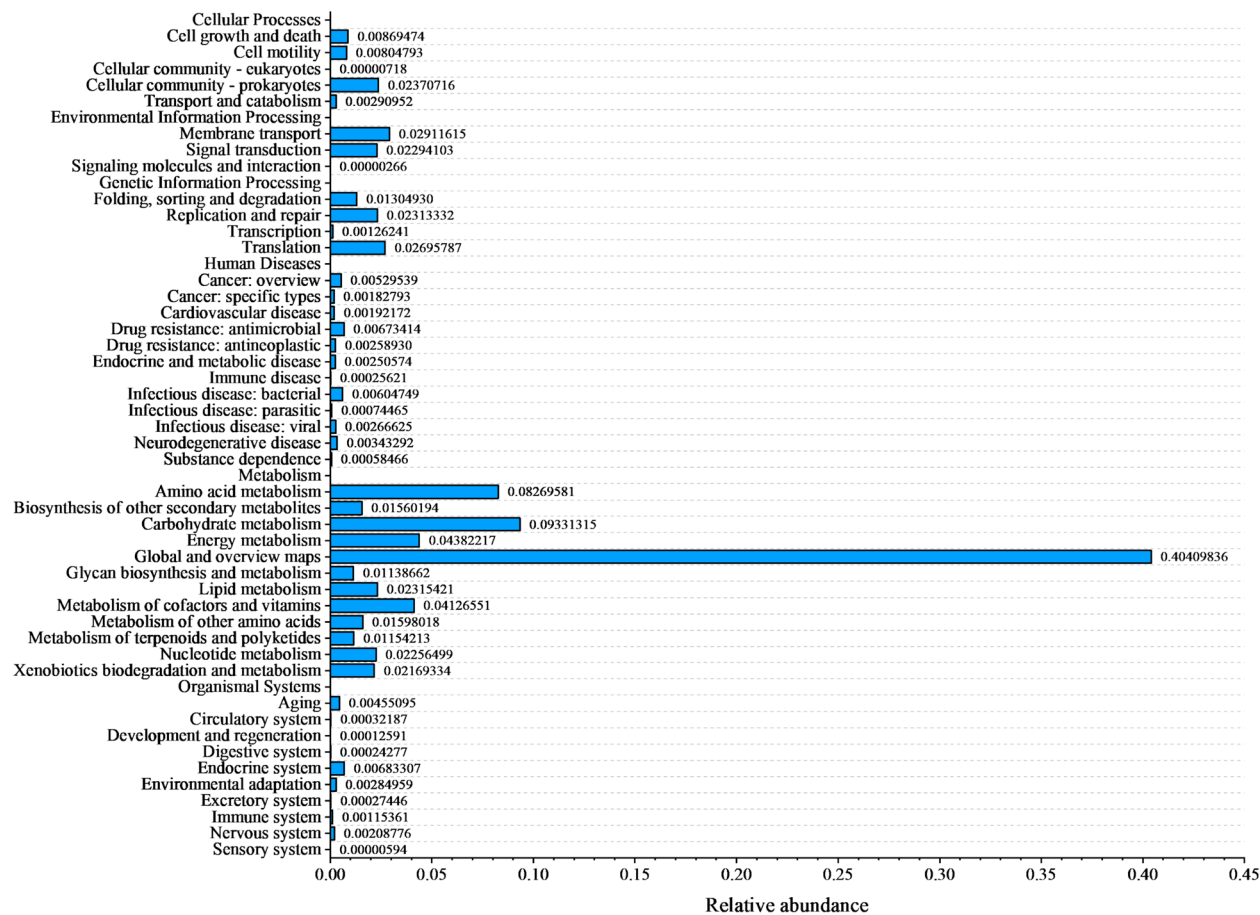
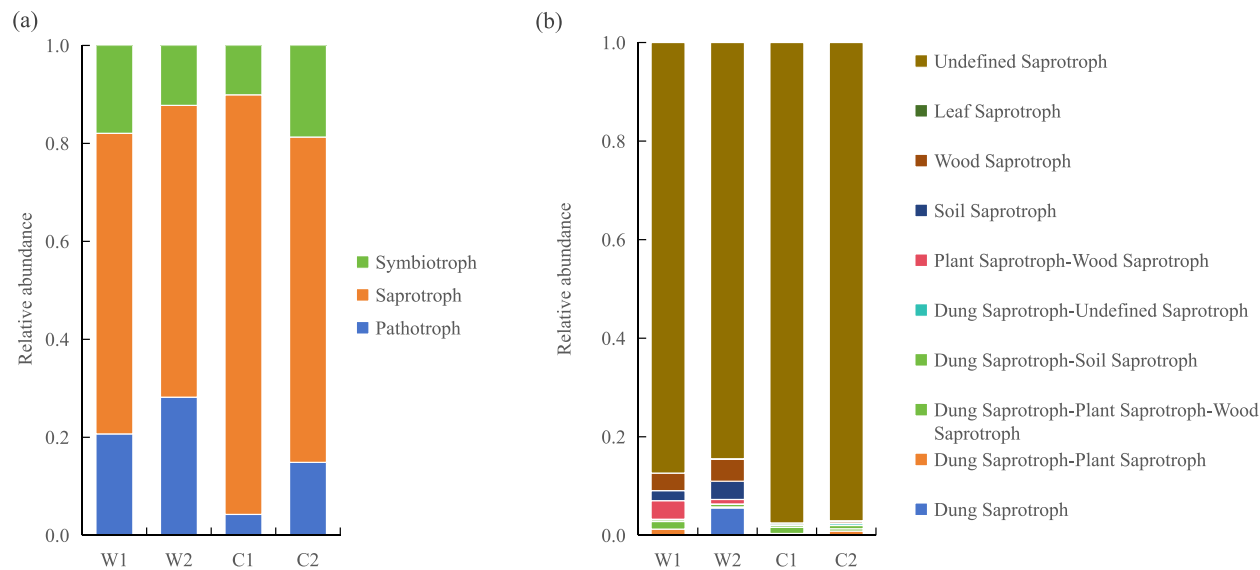


Fig. 6 KEGG pathway annotation of wild and cultivated *S. baicalensis* rhizosphere bacterial communities



(a) Classification of fungal communities. **(b)** Ten functional guilds of saprotrophs.
Fig. 7 Fungal functional group composition changes derived from FUNGuild analysis

cultivated *S. baicalensis* samples, the guilds with an average relative abundance greater than 1% were limited to Dung Saprotroph-Plant Saprotroph-Wood Saprotroph and Undefined Saprotroph. Notably, both the relative abundance and species of functional species in the saprotrophs were higher in wild *S. baicalensis* compared to their cultivated counterparts (Fig. 7(b)).

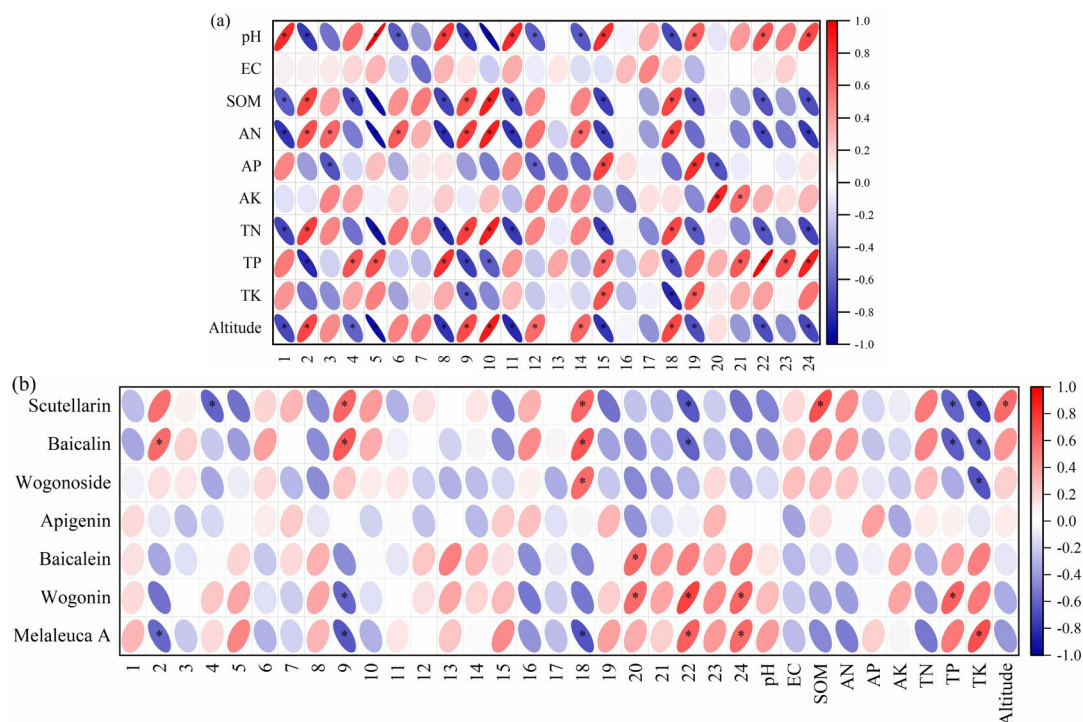
Correlations between dominant microbial taxa, environmental variables and flavonoid active ingredients content in *S. baicalensis*

Soil SOM exhibited a significant positive correlation with Proteobacteria, *Sphingomonas*, RB41 and *Cordyceps*. Soil nitrogen content exhibited a significant positive correlation with Proteobacteria, Acidobacteriota, *Gaiella*, *Sphingomonas*, RB41 and *Cordyceps*. Soil phosphorus content exhibited a significant positive correlation with Chloroflexi, *Arthrobacter*, *Blastococcus*, *Talaromyces*, *Tetracladium*, *Paraphoma*, *Phoma*, *Vishniacozyma* and *Gibberella*. Soil potassium content exhibited a significant positive correlation with *Talaromyces*, *Tetracladium*, *Serendipita* and *Paraphoma* (Fig. 8(a)).

The content of scutellarin exhibited a significant positive correlation with *Sphingomonas*, *Cordyceps*, SOM and altitude. Conversely, it was significantly negatively associated with Chloroflexi, *Phoma*, TP and TK. For baicalin, significant positive correlations were observed with Proteobacteria, *Sphingomonas* and *Cordyceps*, while significant negative correlations were found with *Phoma*, TP and TK. Wogonoside content was significantly positively correlated only with *Cordyceps*, but negatively correlated with TK. Baicalein content showed a significant positive correlation with *Serendipita*. Wogonin content was significantly positively correlated with *Serendipita*, *Phoma*, *Gibberella* and TP. Melaleuca A content was significantly positively correlated with *Phoma*, *Gibberella* and TK, yet significantly negatively correlated with Proteobacteria, *Sphingomonas* and *Cordyceps* (Fig. 8(b)).

Discussion

Dao-di herbs are closely related to ecological environment. The physicochemical properties of rhizosphere soil are influenced by root exudate, microbial activity, and environmental conditions. In the current study, correlation analysis showed that microorganism was correlated



* $P < 0.05$

Bacteria: 1. Actinobacteriota, 2. Proteobacteria, 3. Acidobacteriota, 4. Chloroflexi, 5. *Arthrobacter*, 6. *Gaiella*, 7. *Solirubrobacter*, 8. *Blastococcus*, 9. *Sphingomonas*, 10. RB41. Fungus: 11. Ascomycota, 12. Mortierellomycota, 13. Basidiomycota, 14. *Mortierella*, 15. *Talaromyces*, 16. *Cadophora*, 17. *Solicoccozyma*, 18. *Cordyceps*, 19. *Tetracladium*, 20. *Serendipita*, 21. *Paraphoma*, 22. *Phoma*, 23. *Vishniacozyma*, 24. *Gibberella*.

Fig. 8 Spearman correlations between dominant microbial taxa, environmental variables and contents of flavonoid active ingredients

with the environmental variables (Fig. 8(a)). Similar to our results, Zhang et al. (2023) found that the relative abundance of Proteobacteria was usually related to soil nitrogen content, this may be because Proteobacteria can dominate biological nitrogen fixation and ammonium oxidation processes (McCaig et al. 1999). The Chloroflexi was significantly positively correlated with phosphorus content, which was in line with the results of Ran et al. (2023). Furthermore, *Arthrobacter* was significantly positively correlated with phosphorus content. Sharma et al. (2013) believed that *Arthrobacter* could secrete a large amount of exopolysaccharide and showed strong phosphorus dissolution ability. *Sphingomonas* was significantly correlated with organic matter and nitrogen content, which may be due to the dual pathways of nitrogen fixation (Videira et al. 2009) and nitrogen mineralization (Sørensen et al. 2001) by *Sphingomonas* to improve soil nitrogen availability. The physicochemical properties of soil are directly or indirectly affected by the metabolic activities, decomposition and synthesis functions of bacteria. Therefore, the difference of rhizosphere bacterial communities in wild and cultivated habitats might be the main driving factor for the difference of nitrogen, phosphorus and potassium nutrients.

Besides, according to the results of the current study, the relative abundance and species of functional species in the wild *S. baicalensis* rhizosphere soil saprophytes were higher and more diverse (Fig. 7(b)), which could play a greater role in directly or indirectly affecting the physicochemical properties of the soil. When we collected samples, we found that there was a lot of litter surrounding the wild plants. By secreting lignin enzyme, cellulase and other extracellular enzymes, saprophytic bacteria decompose complex organic matter and convert macromolecular carbon into humus, soluble organic carbon and other small molecular compounds to improve soil fertility (Cao et al. 2022). At the same time, fungal metabolism and saprophytic decomposition of organic matter produce organic acids (Li et al. 2025), which affect soil pH. Goodell (2020) believed that lignin-degrading bacteria tended to release organic acids in forest soil, which reduced the soil pH. In addition, some fungi can fix ammonium nitrogen in the soil through assimilation to reduce nitrogen volatilization loss (Pellitier and Zak 2018); they can also convert organic nitrogen into ammonium nitrogen (NH_4^+) and nitrate nitrogen (NO_3^-) through mineralization (Liu et al. 2024), thus improving soil nitrogen availability. This may be one of the reasons for the low pH and high organic matter and N content in the rhizosphere soil of wild *S. baicalensis* (Table 4).

Soil physicochemical properties are the key factors affecting plant nutrient absorption. Soil pH significantly affects the nutrient absorption efficiency of plants by

changing the chemical form of nutrients (Liu et al. 2022). Soil organic matter is a reservoir of nutrients such as nitrogen, phosphorus and sulfur, which can supply nutrients slowly and continuously (Paul et al. 2013). Soil nitrogen content is closely related to plant photosynthesis and affects the synthesis of macromolecules such as chlorophyll and protein (Cruz et al. 2003). Soil phosphorus content affects the structural components of many macromolecules and important organic compounds in plants, and participates in many metabolic processes in plants (Prathap et al. 2022). Soil potassium content affects the biochemical and biophysical reactions of plants, which can promote energy conversion and assimilation product transport in plants (Regmi et al. 2002).

In the current study, correlation analysis showed that SOM, TP, TK and altitude were correlated with the accumulation of flavonoid active ingredients (Fig. 8(b)). Ren et al. (2016) found that physicochemical properties of soil affected 14 active ingredients of *Rheum palmatum* L., which were in consistent with our results. This may be because soil nutrients directly determine the absorption of mineral elements (such as N, P, K, trace elements) by plants, and mineral nutrition is the material basis of plant metabolism. Studies have shown that organic matter can promote photosynthesis and carbohydrate synthesis in the above-ground parts of *S. baicalensis*, and phosphorus and potassium are involved in a variety of metabolic processes in plants, providing more precursors such as phenylalanine for flavonoid synthesis. Nitrogen affects the synthesis and accumulation of alkaloids, non-protein amino acids, phenols, terpenes, flavonoids, and tannins in plants (Chen et al. 2010). Excessive nitrogen can reduce the activity of key enzymes involved in flavonoid synthesis, leading to competition with the large amount of proteins synthesized by growing plants for the precursor—phenylalanine, thereby inhibiting flavonoid synthesis (Chen et al. 2010).

In the sampling, we selected healthy *S. baicalensis*. We expected that through the study of healthy *S. baicalensis*, the complex interference caused by disease factors can be excluded, and the relationship between the flavonoid content and microorganisms can be more accurately analyzed in a relatively simple system. As we analyzed the makeup of the fungal community in the samples, we identified that the relative abundance of *Talaromyces*, *Phoma*, *Gibberella* in cultivated *S. baicalensis* was significantly greater than that in wild *S. baicalensis* ($P < 0.05$) (Table 6). Meanwhile, the content of wogonin and melaleuca A was significantly positively correlated with *Phoma* and *Gibberella* ($P < 0.05$). But the content of scutellarin and baicalin was significantly negatively correlated with *Phoma* ($P < 0.05$) (Fig. 8). This may be because when plants are infected by pathogens, the activity of

key flavonoid synthesis enzymes such as phenylalanine deaminase (PAL) and chalcone synthase (CHS) in plants may increase, thus promoting flavonoid synthesis. However, not all species in the above genera are pathogenic fungi, and the pathogenicity of microorganisms is also affected by many factors.

The differences in the microecological environment of wild and cultivated *S. baicalensis* roots and their effects on flavonoid content were compared. We found the content of baicalin was positively correlated with genus *Sphingomonas* (Fig. 8(b)). This may be because *Sphingomonas paucimobilis* ZJSH1 produces plant hormones. These hormones function as signaling agents in plants and are capable of modulating the expression of genes associated with flavonoid biosynthesis (Yang et al. 2015). Meanwhile, Wang et al. (2022) found *Sphingomonas* sp. Hbc-6 enhances photosynthesis of plants. The photosynthetic products provide carbon skeleton, energy and reducing agent for the biosynthesis of flavonoids (Li et al. 2023). This conclusion is based on reasonable speculation of correlation, reflecting statistical association rather than causal relationship. In the future, it is necessary to conduct comparative inoculation experiments, metagenomic and transcriptome data analysis to reveal the specific mechanism of action of *Sphingomonas* in flavonoid synthesis.

Mining rhizosphere soil microbial resources of medicinal plants can help develop effective and sustainable field management strategies. In the future, we should further strengthen the research on the growth-promoting mechanism of beneficial microorganisms in the rhizosphere of medicinal plants and accelerate the development of microbial inoculants. By studying how rhizosphere microorganisms influence the accumulation of active components in medicinal plants, we can explore the way to stimulate the synthesis of active components and promote the scientific, ecological and standardized development of artificial cultivation of Chinese medicinal materials.

Conclusions

Wild *S. baicalensis* contained a significantly greater content of scutellarin and baicalin compared to cultivated ones. Microorganisms were correlated with the environmental variables, the difference of rhizosphere bacterial communities in wild and cultivated habitats may be the main driving factor of the difference of nitrogen, phosphorus and potassium nutrients. Both the relative abundance and species of functional species in the saprotrophs were higher in wild *S. baicalensis*, and saprotroph can decompose organic matter to produce a large amount of humus and organic acids, which can reduce the pH value and increase the content of organic matter and N of

soil in wild habitat. Soil SOM, TP, TK and altitude were significantly positively correlated with flavonoid contents ($P < 0.05$). In the current study, the proposed improvement strategies for soil management of cultivated *S. baicalensis* are: increasing the application of organic matter and the ratio of TN:TP and TN:TK, paying attention to the pH value of the soil and to explore the potential application of genus *Sphingomonas*.

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Authors' contributions

PYF: Conceptualization, Funding acquisition, Methodology, Writing—original draft, Data curation, Visualization. YNB: Conceptualization, Funding acquisition, Project administration, Writing—review & editing, Validation. TQ: Investigation, Funding acquisition, Software. WFC: Investigation, Writing—review & editing, Formal analysis. HY and YXL: Investigation, Writing—review & editing. JQL: Review & editing. All authors read and approved the final manuscript.

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Data availability

The original data have been deposited on the NCBI website, with PRJNA991737 and PRJNA991750 assigned as the respective accession numbers.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

No competing interests.

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