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Bacterial community structure in tobacco rhizosphere soil at different altitudes in Hubei Province, China

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Abstract

Altitude is a comprehensive ecological factor, along with temperature, humidity, light, etc., that has an important effect on the growth and development of tobacco. This study was carried out in the typical mountainous tobacco-growing areas of Enshi Prefecture, Hubei Province, China. To understand the effects of different altitudes on the microbial community diversity in tobacco rhizosphere soil, we analyzed the differences in bacterial community structure in tobacco rhizosphere soil at high (>1300 m), medium (800–1300 m), and low altitudes (<800 m) using high-throughput sequencing technology. The results showed that as altitude increased, the number of soil bacterial operational taxonomic units (OTUs) across taxonomic levels decreased, and species richness also declined. At the phylum level, the relative abundance of Proteobacteria was the highest at low altitudes, and that of Actinobacteria and Acidobacteria was the highest at high altitudes. At the genus level, the abundance of *Sphingomonas* and *Subgroup_6* was relatively higher at low altitudes than at medium and high altitudes. The relative abundance of other species in the tobacco rhizosphere soil was lower at different altitudes. The abundances of Firmicutes (phylum level) and *Chujaibacter* (genus level) were relatively higher at medium altitudes than those at low and high altitudes. In conclusion, there were significant differences in the bacterial species of the tobacco rhizosphere soil among the three altitudes. The difference in species composition was greatest at low altitudes, whereas bacterial species composition was similar at medium and high altitudes.

1. Introduction

Soil microorganisms are the main components of soil ecosystems and play an important role in the transformation of soil materials and energy (Schloter et al., 2003; Butler et al., 2003). The structure and diversity of soil microbial communities are closely related to soil quality and are important indicators of soil health (Yao et al., 2000; Bartelt-Ryser et al., 2005). Rhizosphere soil is an important soil interface for various processes of plant metabolism. A large number of microorganisms inhabit plant rhizosphere soil; their number is much higher in rhizosphere soil than that in non-rhizosphere soil, and they interact with plants and form various associations (Xu et al., 2018; Lynch, 2007; Jousset et al., 2008; Yang, et al. 2013). Previous studies have shown that the species composition and abundance of microorganisms in rhizosphere soil vary under different ecological conditions, leading plant roots to exhibit specific rhizosphere effects (Waldrop and Firestone, 2006; Puissant, 2015). Altitude is a comprehensive ecological factor which includes temperature, humidity, light, and other environmental factors. Differences in the ecological environment across altitudes significantly affect soil microbial community composition (Ma et al., 2004; Bryant et al., 2008; Gong et al., 2024; Jin et al., 2024).

Tobacco is one of the most important economic crops in China. Its planting area has a large altitude span and a wide distribution range. Different ecological conditions, such as light, temperature, and precipitation, at different altitudes lead to pronounced regional differences in tobacco growth and development (Mangora et al., 2005; Yang et al., 2018; Yamori et al., 2010). Therefore, altitude has been used as a key indicator for evaluating the quality characteristics of tobacco (Shen et al., 2013; Yu et al., 2010; Tang et al., 2020). Rhizosphere microorganisms play

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an important role in the growth, development, and quality of tobacco. The difference in microbial diversity among tobacco-planting soil at different altitudes has received increasing attention in recent years (Wang et al., 2019; Zhang et al., 2018; Ding et al., 2021). The aim of this study is to investigate the differences in bacterial community structure among tobacco rhizosphere soil at high, medium, and low altitudes using high-throughput sequencing technology. Given that tobacco is a unique economic crop with nicotine primarily synthesized in its roots, and its root exudates significantly influence the rhizosphere soil microbial community, we hypothesize that there are distinct differences in microbial diversity across different altitudes due to varying ecological conditions such as light, temperature, and precipitation. While recent studies have begun to explore the microbial diversity in tobacco-planting soils at different altitudes, comprehensive analyses of bacterial community structure in this context remain limited. Our research fills this gap by providing a detailed investigation of how altitude affects the composition of bacterial communities in tobacco rhizosphere soil. The novelty of this study lies in its in-depth analysis of bacterial diversity across a wide altitude range, which has not been extensively reported. Our findings are expected to contribute significantly to the existing knowledge by offering new insights into the relationship between altitude and rhizosphere microbial diversity in tobacco. Furthermore, the results will provide theoretical support for regulating tobacco rhizosphere microecological health and the development and application of related microbial products, thereby advancing the understanding and practical applications of microbial ecology in agricultural practices.

2. Materials and methods

2.1. Site description

The sampling site was located in the high-quality tobacco-planting area of Enshi Tujia and Miao Autonomous Prefecture of Hubei Province, China, with the altitude ranging from 500–1400 m. The climate type of the sampling area is a mid-subtropical monsoon mountain humid climate, characterized by distinct seasons, abundant rainfall, and moderate temperatures, which are favorable for tobacco cultivation. During the flue-cured tobacco growing period, the average temperature is around 24.8°C, with the most suitable temperature range for tobacco growth being 25–28°C. The total precipitation during this period is approximately 400–600 mm, with higher rainfall in the later stages of growth. The region also receives adequate sunlight, with a total of around 500–700 h of sunshine during the growing season, which is beneficial for tobacco growth. The flue-cured tobacco variety planted in the area is Yunyan 87, which is well-adapted to local conditions. In terms of tobacco growing conditions, the region typically employs integrated pest management practices to protect against pathogens, ensuring the health and quality of the tobacco crops. The soil type in the sampling area is Luvisols (according to the FAO World Reference Base for Soil Resources classification).

2.2. Soil sampling

In the high-quality tobacco-planting area, three representative altitudes of tobacco fields were selected: low altitude (<800 m, H1), medium altitude (800–1300 m, H2), and high altitude (>1300 m, H3). These altitudes were chosen to reflect the diverse environmental conditions that may affect tobacco growth and soil properties across the region. Each tobacco field had an area of 0.20 hectares. Within each field, three tobacco plants with consistent growth were randomly selected. The plants were collected during the mature period of tobacco growth (July 30) to ensure that the rhizosphere soil samples reflected the soil conditions during the critical growth stage. Mix the rhizosphere soil of 3 tobacco plants collected from each tobacco field into a composite sample, obtaining a total of 15 soil samples, each weighing approximately 500 grams. The rhizosphere soil sampling method was as follows: we dug out the roots of tobacco plants with a sterilized sampling shovel, shook off the loose soil from the roots, and brushed off the soil that was closely attached to the roots using a small brush and placed it into a sterilized self-sealed bag. The rhizosphere soil samples were immediately transported to the laboratory in plastic bags using a portable refrigerator. Plant residues and other organic debris were carefully removed using forceps. The samples were kept moist and stored at −40°C for more than one month until the analysis of microbial community structure.

The soil characteristics for each altitude are described as follows:

- Low altitude (H1): The soil at low altitude had an alkaline nitrogen content of 107.61 $mg \cdot kg^{-1}$, available phosphorus of 15.09 $mg \cdot kg^{-1}$, and available potassium of 280.20 $mg \cdot kg^{-1}$. The soil pH was 6.50, indicating a slightly acidic to neutral condition. The total nitrogen content was 1.49 $g \cdot kg^{-1}$, and the organic carbon content was 12.78 $g \cdot kg^{-1}$.
- Medium altitude (H2): The soil at medium altitude had an alkaline nitrogen content of 115.80 $mg \cdot kg^{-1}$, available phosphorus of 20.95 $mg \cdot kg^{-1}$, and available potassium of 298.92 $mg \cdot kg^{-1}$. The soil pH was 6.15, which is slightly acidic. The total nitrogen content was 1.58 $g \cdot kg^{-1}$, and the organic carbon content was 15.06 $g \cdot kg^{-1}$.
- High altitude (H3): The soil at high altitude had the highest alkaline nitrogen content at 170.90 $mg \cdot kg^{-1}$, available phosphorus of 21.78 $mg \cdot kg^{-1}$, and available potassium of 256.50 $mg \cdot kg^{-1}$. The soil pH was 6.18, also slightly acidic. The total nitrogen content was 1.67 $g \cdot kg^{-1}$, and the organic carbon content was 15.37 $g \cdot kg^{-1}$.

The soil physicochemical properties were determined using standard soil agrochemical analysis methods. Soil pH was measured with a pH meter (water-to-soil ratio = 2.5:1). Alkaline nitrogen was determined by the alkali-hydrolyzed diffusion method. Available phosphorus was extracted with 0.5 mol/L $NaHCO_3$ and measured by the molybdenum blue colorimetric method. Available potassium was extracted with 1 mol/L NH_4OAc and determined by flame photometry. Total nitrogen was measured using the Kjeldahl method, and organic carbon was determined by the potassium dichromate oxidation-external heating method.

2.3. DNA extraction and PCR amplification

Total genomic DNA was extracted from soil samples using the QIAamp PowerFecal Pro DNA Kit (51804) (Qiagen, Germany) with three biological replicates and three technical replicates for each sample, following the manufacturer's instructions, and the extracted DNA was stored at –20°C prior to further analysis. The quantity and quality of extracted DNAs were measured using a NanoDrop NC2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and agarose gel electrophoresis, respectively.

PCR amplification of the bacterial 16S rRNA genes V3–V4 region was performed using the forward primer 338F (5'-ACTCCTACGGGAGGCAGCA-3') and the reverse primer 806R (5'-GGACTACHVGGGTWTCTAAT-3') (Fadrosh et al., 2014). The PCR components contained 5 µl of buffer (5×), 0.25 µl of Fast pfu DNA Polymerase (5U/µl), 2 µl (2.5 mM) of dNTPs, 1 µl (10 uM) of each Forward and Reverse primer, 1 µl of DNA Template, and 14.75 µl of ddH_2O. Thermal cycling consisted of initial denaturation at 98°C for 5 min, followed by 25 cycles consisting of denaturation at 98°C for 30 s, annealing at 53°C for 30 s, and extension at 72°C for 45 s, with a final extension of 5 min at 72°C. PCR amplicons were purified with Vazyme VAHTSTM DNA Clean Beads (Vazyme, Nanjing, China) and quantified using the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). And then sequencing libraries were constructed using KAPA DNA HyperPlus kit (KAPA,KK8514). After the individual quantification step, amplicons were pooled in equal amounts, and pair-end 2×250 bp sequencing was performed using the Illlumina NovaSeq platform.

2.4. Library preparation and sequencing

Sequencing libraries were generated using a NEB Next® Ultra™ DNA Library Prep Kit for Illumina (New England Biolabs, Ipswich, MA, USA) following the manufacturer's instructions, and index codes were added. The Qubit 4 quantitative library was utilized, and the PCR-enriched fragments were subjected to quality control using the Agilent 2100 to verify the fragment size and distribution of the DNA library. The libraries were then sequenced on an Illumina MiSeq platform, and 250–300 bp paired-end reads were generated.

2.5. Data analysis

Microbiome bioinformatics were performed with QIIME2 (2022.11) and R software (4.2.0). Sequences were then quality filtered, denoised, merged and chimera removed using the DADA2 plugin. Non-singleton amplicon sequence variants (ASVs) were aligned with mafft and used to construct a phylogeny with fasttree2. Then, operational taxonomic unit (OTU) clustering was performed on the obtained high-quality sequences based on a 97% similarity level, and species annotation was performed using the Greengenes database(http://greengenes.secondgenome.com/). According to the results of the OTU cluster analysis, Mothur was used to calculate alpha diversity of the samples, and R was used to analyze the bacterial diversity, after which histograms and Venn charts were prepared. LefSe (Linear discriminant analysis Effect Size) was used to analyze the differences in the microbial community composition at each classification level.

3. Results

3.1. OTU identification at different taxonomic levels

The OTU number of bacterial species in tobacco rhizosphere soil at different taxonomic levels was relatively lower at high altitudes than that at medium and low altitudes. With increasing altitude, the OTU number decreased at various taxonomic levels (Table 1). The total number of OTUs in tobacco rhizosphere soil at all three altitudes was 1777, and the number of unique OTUs in the tobacco rhizosphere soil was the highest at high altitudes (Fig. 1).

Table 1
Number of soil bacterial operational taxonomic units (OTUs) at different altitudes. H1, low altitude (<800 m); H2, medium altitude (800–1300 m); H3, high altitude (>1300 m)

Treatment	Phylum	Class	Order	Family	Genus	Species
H1	29.00a	85.00a	181.00a	285.00a	466.00a	144.00b
H2	27.00b	78.00a	171.00a	276.00a	468.00a	158.00a
H3	25.00b	68.00a	144.00b	224.00b	362.00b	123.00c

Different lowercase letters indicate significant differences between values at P<0.05.

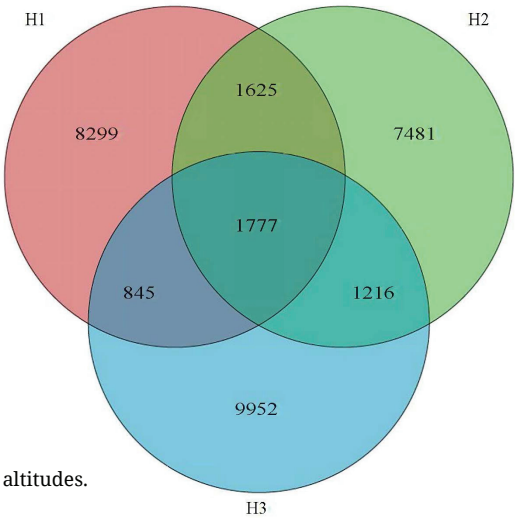


Fig. 1. Venn classification map of soil bacterial operational taxonomic units (OTUs) at different altitudes. H1, low altitude (<800 m); H2, medium altitude (800–1300 m); H3, high altitude (>1300 m)

3.2. Species abundances

At the phylum level, the predominant bacterial populations in tobacco rhizosphere soil across the three altitudes were Proteobacteria, Actinobacteria, and Acidobacteria. Specifically, the relative abundance of Proteobacteria was highest at low altitudes, while the relative abundance of Actinobacteria and Acidobacteria was highest at high altitudes (Fig. 2). Additionally, the relative abundance of Firmicutes was higher at medium altitudes compared to both lower and higher altitudes (Fig. 2). Other bacterial species detected in the tobacco rhizosphere soil samples had relatively low abundance across all three altitudes.

At the genus level, *Sphingomonas*, subgroup_6 (microbial groups that have not yet been clearly classified into specific genera), *Gemmatimonas*, and *Rhodanobacter* were the dominant bacterial species groups in the tobacco rhizosphere soil at different altitudes. Among them, the abundance of *Sphingomonas* and Subgroup_6 was relatively higher at low altitudes than at medium and high altitudes (Fig. 3). The relative abundance of other species detected in the tobacco rhizosphere soil samples at the three altitudes was low. However, the relative abundances of *Aquabacterium* was the highest at low altitudes, and that of *Chujaibacter* was the highest at medium altitudes (Fig. 3).

3.3. Alpha diversity

The Chao1 index of bacterial species in tobacco rhizosphere soil was higher at low and medium altitudes compared to high altitudes. Specifically, the Chao1 index values were 5472.46 and 5410.93 at low (H1) and medium (H2) altitudes, respectively, while it decreased to 5160.91 at high altitude (H3). This indicates a statistically significant reduction in bacterial species richness at the highest altitude (H3). In contrast, the Shannon index, which measures species diversity, did not show a significant change across different altitudes. The Shannon index values were 11.00, 10.88, and 10.86 for low (H1), medium (H2), and high (H3) altitudes, respectively. Therefore, while bacterial species richness decreased with increasing altitude, as indicated by the Chao1 index, the overall diversity of bacterial species, as measured by the Shannon index, remained relatively stable

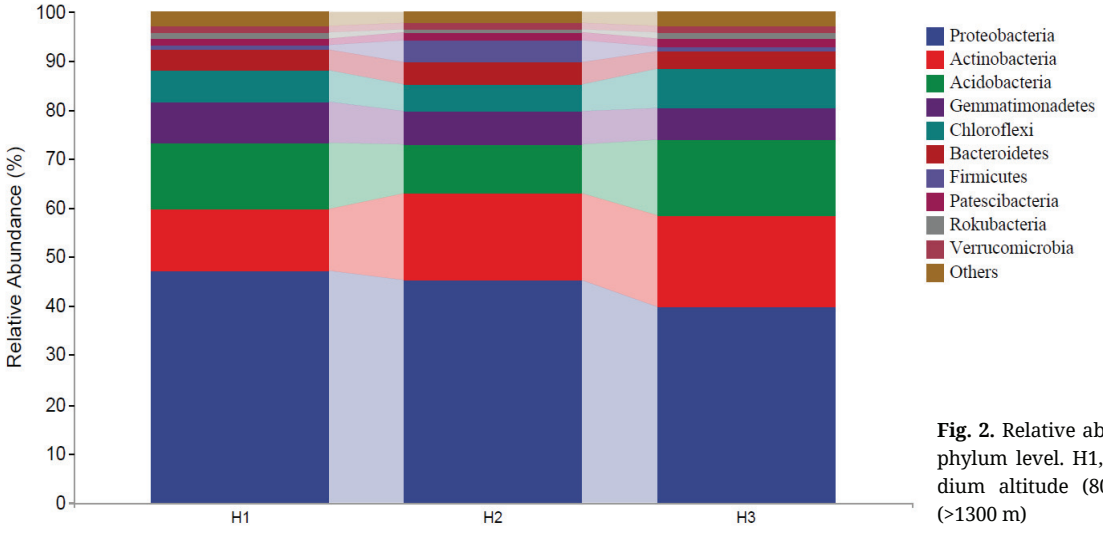


Fig. 2. Relative abundances of soil bacteria at the phylum level. H1, low altitude (<800 m); H2, medium altitude (800–1300 m); H3, high altitude (>1300 m)

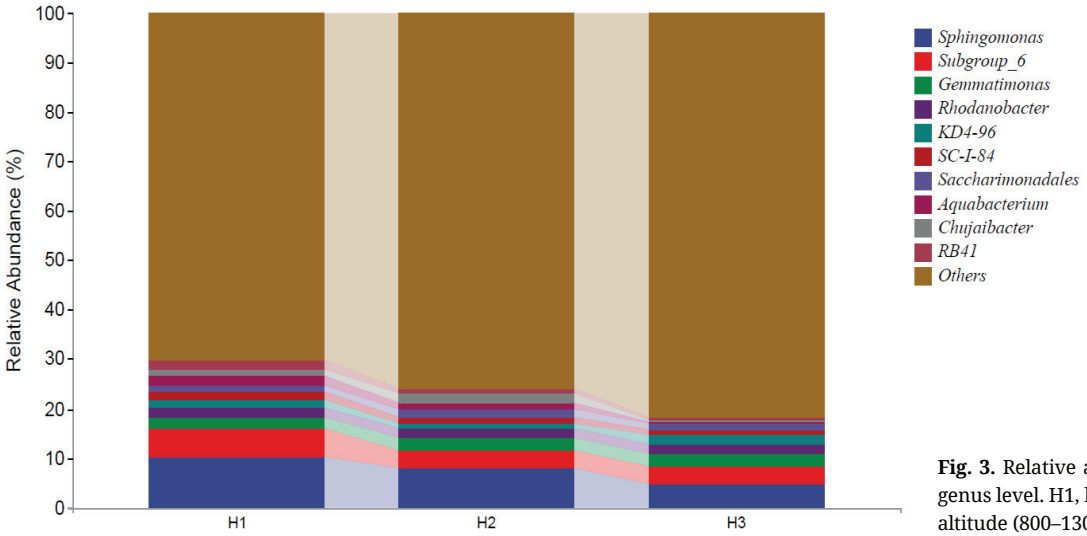


Fig. 3. Relative abundances of soil bacteria at the genus level. H1, low altitude (<800 m); H2, medium altitude (800–1300 m); H3, high altitude (>1300 m)

across the altitudes. Altitude had a strong influence on the richness of soil bacterial species (Table 2).

Table 2
Chao1 and Shannon indexes of soil bacterial community richness. H1, low altitude (<800 m); H2, medium altitude (800–1300 m); H3, high altitude (>1300 m)

Treatment	Chao1	Shannon
H1	5472.46a	11.00a
H2	5410.93a	10.88a
H3	5160.91b	10.86a

Different lowercase letters in the same column indicate significant differences at P<0.05.

3.4. Differences in bacterial community composition among different altitudes

The composition of the bacterial community (at the genus level) in tobacco rhizosphere soil at low altitudes was different among samples, whereas that at medium and high altitudes was similar (Fig. 4).

At different classification levels, there were significant species abundance differences in tobacco rhizosphere soil among the three altitudes; the species abundance differences at low altitudes were the most, followed by those at medium and high altitudes (Fig. 5). *Sphingomonas* was the most different bacterial genus in tobacco rhizosphere soil at low altitudes, and Myxococcales was the most different bacterial order at high altitudes (Fig. 5).

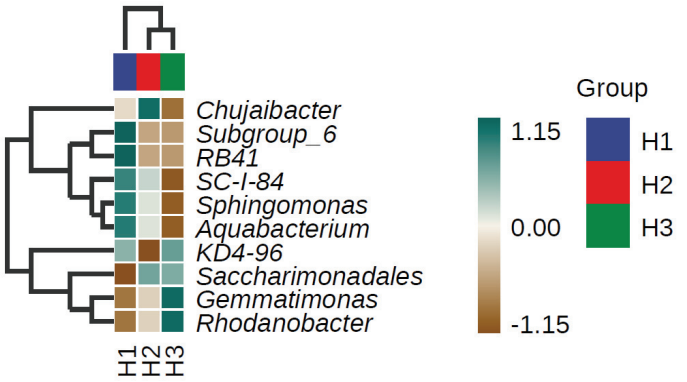


Fig. 4. Clustering diagram of soil bacterial species at the genus level at different altitudes. H1, low altitude (<800 m); H2, medium altitude (800–1300 m); H3, high altitude (>1300 m)

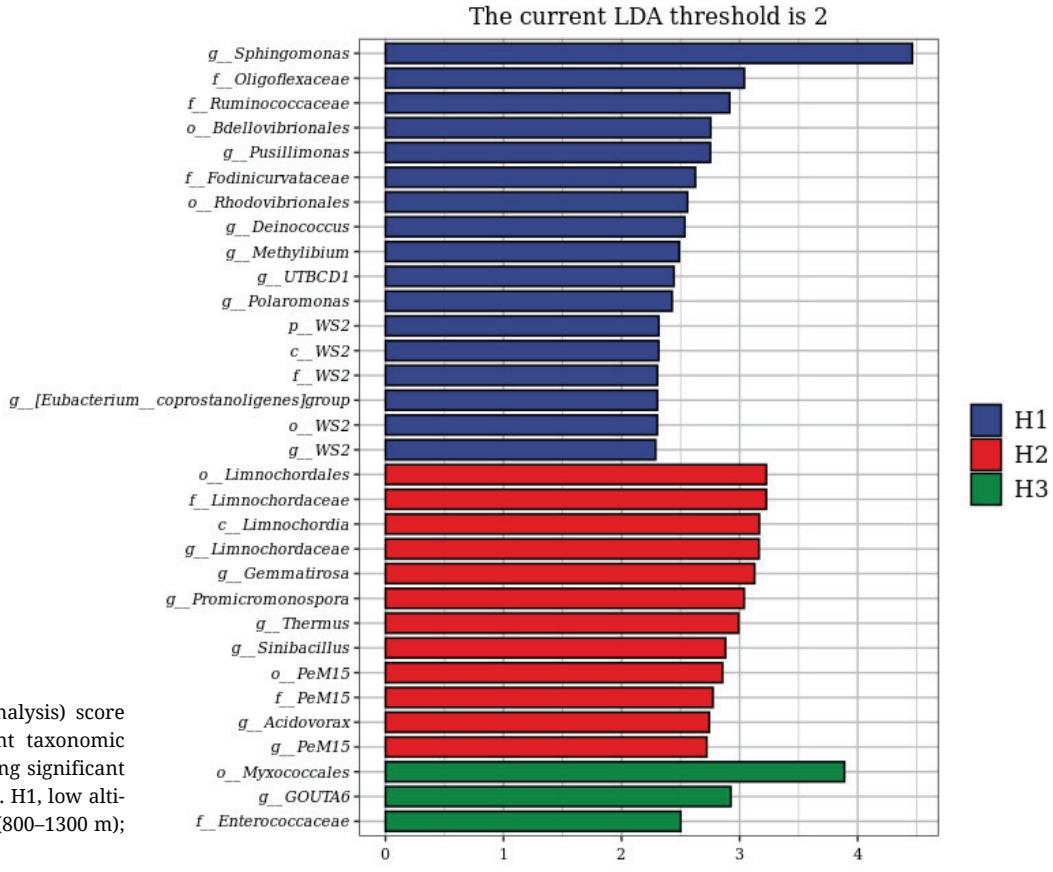


Fig. 5. LDA (Linear discriminant analysis) score of soil bacterial species at different taxonomic levels and different altitudes (showing significant differences in LefSe analysis results). H1, low altitude (<800 m); H2, medium altitude (800–1300 m); H3, high altitude (>1300 m)

4. Discussion

Soil microbial diversity is a key factor in maintaining soil quality (Kennedy et al., 1995). The difference in environmental conditions at different altitudes affect soil properties, which leads to changes in soil microbial diversity. In this study, we examined the characteristics of the tobacco rhizosphere soil microbial community across low, medium, and high altitudes. Our results showed that bacterial species richness decreased with increasing altitude (Table 2), consistent with previous studies (Bryant et al., 2008; Xu et al., 2023) that have found a general trend of declining microbial diversity in higher altitude soils. This trend may be attributed to the combined effects of soil pH, nutrient availability, and other abiotic factors that vary with altitude(Ma et al., 2004; Zhang et al., 2025). Differences in climate factors such as temperature and precipitation at different altitudes can have a large impact on the distribution of soil bacteria (Maron et al., 2011; Xun et al., 2015). In addition, low altitudes are conducive to the formation of soil humus, and adequate soil physical and chemical properties can promote the formation of the rhizosphere microbial community. With increasing altitude, soil quality and soil microbial diversity decrease (Ji et al., 2015; Kostenko, 2017; Ligia et al., 2020; Gao et al., 2022).

Furthermore, our results showed that there were significant differences in bacterial species abundance among tobacco rhizosphere soil at the three altitudes, and the differences were most obvious at low altitudes. The genus *Sphingomonas* was the most abundant in tobacco rhizosphere soil at low altitudes, and the order Myxococcales was the most abundant in tobacco rhizosphere soil at high altitudes (Fig. 5). Sphingomonas species are known for their strong ability to degrade aromatic pollutants and their robust survival capabilities (Supaka et al., 2001; He et al., 2017). Moreover, some Sphingomonas strains can enhance plant resistance to pathogens and promote plant growth (Chen et al., 2014; Khan et al., 2014). The prevalence of Sphingomonasat low altitudes may reflect its adaptation to the specific environmental conditions or anthropogenic influences prevalent in these areas, aligning with its documented metabolic versatility and stress tolerance. Myxobacteria, which belong to the order Myxococcales, are micropredators in the soil ecosystem. They can move cooperatively and forage, preying on a variety of bacteria and fungi for nutrition (Morgan et al., 2010; Bull et al., 2002). Some Myxobacteria strains have been used to control the spread of fungal plant pathogens in the soil (Dahm et al., 2015; Olanya et al., 2015). For instance, Ye et al. (2020) demonstrated that predatory Myxobacteria (Corallococcus sp.) can migrate to plant roots and regulate the soil microbial community to control cucumber fusarium wilt. In this study, we observed significant differences in the abundance of Myxococcales between high-altitude tobacco rhizosphere soil and that at low and medium altitudes (Fig. 5). At higher altitudes, tobacco plants are more susceptible to soil-borne rhizome diseases due to adverse climatic conditions (Campbell et al., 1980; Drake-Stowe et al., 2017). A higher abundance of Myxococcus species can inhibit the growth of pathogens. The soil characteristics at different altitudes revealed distinct patterns. Low-altitude soils had relatively high organic carbon content and a slightly acidic to neutral pH, which may favor the growth of certain microbial taxa such as Sphingomonas. These conditions are similar to those reported in agricultural soils with high organic matter content, where microbial communities are often dominated by copiotrophic bacteria that thrive in nutrient-rich environments. In contrast, high-altitude soils exhibited higher alkaline nitrogen content and slightly acidic pH, conditions that may support the dominance of Myxococcales. This is consistent with findings that Myxobacteria are prevalent in soils with specific nutrient profiles and pH conditions (Yoon et al., 2024).

We also found that the abundance of Firmicutes in tobacco rhizosphere soil was higher at medium altitudes than at high and low altitudes (Fig. 5). Many Firmicutes species can produce spores to resist extreme conditions such as drought or low temperature, thereby reducing the impact of harsh climates on soil and maintaining soil structure and quality stability (Sevasti et al., 2016; Michael et al., 2013). Firmicutes are strongly correlated with soil pH and are prevalent in long-term continuously cropped soils (Li et al., 2020; Anderson et al., 2018). Therefore, the distinct microbial community compositions at each altitude underscore the complex interplay between abiotic and biotic factors in shaping soil ecosystems. Future research should further explore the functional roles of dominant microbial taxa in different altitude soils and investigate how these communities respond to environmental changes and management practices.

5. Conclusions

The main bacterial populations in the studied tobacco rhizosphere soil at different altitudes were Proteobacteria, Actinobacteria, and Acidobacteria (phylum level); and *Sphingomonas*, *Subgroup_6*, *Gemmatimonas*, and *Rhodanobacter* (genus level). Among them, the relative abundance of Proteobacteria, *Sphingomonas*, and *Subgroup_6* was the highest at low altitudes, that of Actinobacteria and Acidobacteria was the highest at high altitudes, and that of Firmicutes and *Chujaibacter* was the highest at medium altitudes. The relative abundances of other bacterial species was low. At different classification levels, there were significant differences in bacterial species abundance in tobacco rhizosphere soil among the three altitudes, and the most diverse species were found in tobacco rhizosphere soil at low altitudes. At the genus level, *Sphingomonas* was the most different in the tobacco rhizosphere soil at low altitudes. With increasing altitude, the bacterial species richness in tobacco rhizosphere soil decreased, and the bacterial species composition in tobacco rhizosphere soil was similar at medium and high altitudes.

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Conflict of interest

The authors declare no conflict of interest. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. This research did not involve human or animal subjects.

Author Contributions

Lin Gao – Conceptualization, Data curation, Investigation, Methodology, Visualization, Writing – original draft. **Jiaming Gao** – Investigation, Data curation. **Xiaohong Ren** – Investigation, Data curation. **Jun Fan** – Investigation, Data curation. **Yanbo Gao** – Investigation, Data curation. **Guanghua Huang** – Investigation, Validation. **Xiao Wang** – Investigation, Validation. **Changhe Cheng** – Conceptualization, Supervision, Writing – review & editing. **Weimin Wang** – Conceptualization, Supervision, Writing – review & editing. All authors read and approved the final manuscript.

References

Anderson, C.R., Peterson, M.E., Frampton, R.A., Bulman, S.R., Keenan, S., Curtin, D., 2018. Rapid increases in soil pH solubilize organic matter, dramatically increase denitrification potential and strongly stimulate microorganisms from the Firmicutes phylum. Peer J 6, e6090. https://doi.org/10.7717/peerj.6090

Bartelt-Ryser, J., Joshi, J., Schmid, B., Brandl, H., Balser, T., 2005. Soil feedbacks of plant diversity on soil microbial communities and subsequent plant growth. Perspectives in Plant Ecology Evolution Systematics 7, 27–49. https://doi.org/10.1016/j.ppees.2004.11.002

Bryant, J.A., Lamanna, C., Morlon, H., Kerkhoff, A.J., Enquist, B.J., Green, J.L., 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences of the United States of America 105, 11505–11511. https://doi.org/10.1073/pnas.0801920105

Bull, C.T., Shetty, K.G., Subbarao, K.V., 2002. Interactions between myxobacteria, plant pathogenic fungi, and biocontrol agents. Plant Disease 86(8), 889–96. https://doi.org/10.1094/PDIS.2002.86.8.889

Butler, J.L., Williams, M.A., Bottomley, P.J., Myrold, D.D., 2003. Microbial community dynamics associated with rhizosphere carbon flow. Applied and Environmental Microbiology 69, 6793–6800. https://doi.org/10.1128/AEM.69.11.6793-6800.2003

Campbell, C.L., Powell, N.T., Pennypacker, S.P., Madden, L.C., 1980. Progression of diseases induced by soilborne pathogens: tobacco black shank. Protection Ecology 2(3), 177–182.

Chen, B., Zhang, Y., Rafiq, M.T., Khan, K.Y., Pan, F., Yang, X., Feng, Y., 2014. Improvement of cadmium uptake and accumulation in Sedum alfredii by endophytic bacteria Sphingomonas SaMR12: Effects on plant growth and root exudates. Chemosphere 117, 367–373. https://doi.org/10.1016/j.chemosphere.2014.07.078

Dahm, H., Brzezińska, J., Wrótniak-Drzewiecka, W., Golińska, P., Rai, M., 2015. Myxobacteria as a potential biocontrol agent effective against pathogenic fungi of economically important forest trees. Dendrobiology 74, 13–24. https://doi.org/10.12657/denbio.074.002

Ding, Y.R., Chen, Y.L., Lin, Z.Q., Tuo, Y.Y., Li, H.L., Wang, Y., 2021. Differences in soil microbial community composition between suppressive and root rot-conducive in tobacco fields. Current Microbiology 78, 624–633. https://doi.org/10.1007/s00284-020-02318-3

Drake-Stowe, K., Bakaher, N., Goepfert, S., Philippon, B., Mark, R., Peterson, P.D., Lewis, R., 2017. Multiple disease resistance loci affect soilborne disease resistance in tobacco (Nicotiana tabacum). Phytopathology 107(9), 1055–1061. https://doi.org/10.1094/PHYTO-03-17-0118-R

Fadrosh, D.W., Ma, B., Gajer, P., Sengamalay, N., Ott, S., Brotman, R.M., Ravel, J., 2014. An improved dual-indexing approach for multiplexed 16S rRNA gene sequencing on the Illumina MiSeq platform. Microbiome 2(1), 6. https://doi.org/10.1186/2049-2618-2-6

Gao, L., Gao, J.M., Wang, R., Ren, X.H., Fan, J., Shen, G.M., 2022. Effect of altitude on the release of metabolites in the tobacco rhizosphere soil. Eurasian Soil Science 55(12), 1786–1793. https://doi.org/10.1134/S106422932260097X

Gong, B., He, Y., Luo, Z.B. Peng, H.W., Cai, H.Q., Zhu, Y.N., Bin, J., Ding, M.J., 2024. Response of rhizosphere soil physicochemical properties and microbial community structure to continuous cultivation of tobacco. Annals of Microbiology 74, 4. https://doi.org/10.1186/s13213-023-01748-1

He, W.J., Zhang, L., Yi, S.Y., Tang, X.L., Yuan, Q.S., Guo, M.W., Wu, A.B., Qu, B., Li, H.P., Liao, Y.C., 2017. An aldo-keto reductase is responsible for Fusarium toxin-degrading activity in a soil Sphingomonas strain. Scientific Reports 7(1), 9549. https://doi.org/10.1038/s41598-017-08799-w

Puissant, J., Cécillon, L., Mills, R.T.E., Robroek, B.J.M., Gavazov, K., De Danieli, S., Spiegelberger, T., 2015. Seasonal influence of climate manipulation on microbial community structure and function in mountain soils. Soil Biology and Biochemistry 80, 296–305. https://doi.org/10.1016/j.soilbio.2014.10.013

Ji, H.B., Zhuang, S.Y., Zhu, Z.L., Zhong, Z.K., 2015. Soil organic carbon pool and its chemical composition in phyllostachy pubescens forests at two altitudes in Jian-ou city, China. PLOS ONE 10(12), e0146029. https://doi.org/10.1371/journal.pone.0146029

Jin, X.F., Yang, X.Q., Peng, S., Ma, E.D., Zhang, H., Lin, X.G., Wang, Y.M., Li, J.Y., 2024. Cropping rotation improved bacterial diversity and N-cycling genes in tobacco fields through a 19-year long-term experiment. Applied Soil Ecology 193, 105165. https://doi.org/10.1016/j.apsoil.2023.105165

Jousset, A., Scheu, S., Bonkowski, M., 2008. Secondary metabolite production facilitates establishment of rhizobacteria by reducing both protozoan predation and the competitive effects of indigenous bacteria. Functional Ecology 22,714–719. https://doi.org/10.1111/j.1365-2435.2008.01411.x

Kennedy, A.C., Smith, K.L., 1995. Soil microbial diversity and the sustainability of agricultural soils. Plant and Soil 170(1), 75–86. https://doi.org/10.1007/BF02183056

Khan, A.L., Waqas, M., Kang, S.M., Al-Harrasi, A., Al-Rawahi, A., Al-Khiziri, S., Ullah, I., Ali, L., Jung, H.Y., Lee, I.J., 2014. Bacterial endophyte Sphingomonas sp. LK11 produces gibberellins and IAA and promotes tomato plant growth. Journal of Microbiology 52(8), 689–695. https://doi.org/10.1007/s12275-014-4002-7

Kostenko, I.V., 2017. Relationships between parameters of the humus status of forest and meadow soils and their altitudinal position on the main Crimean range. Eurasian Soil Science 50(5), 515–525. https://doi.org/10.1134/S1064229317050088

Li, W., Zhang, Y., Mao, W., Wang, C., Yin, S., 2020. Functional potential differences between Firmicutes and Proteobacteria in response to manure amendment in a reclaimed soil. Canadian Journal of Microbiology 66(9), 689–697. https://doi.org/10.1139/cjm-2020-0143

Ligia, C.M.A., Fusaro, C., Mario, H.G., Luc, D., Arturo, E.T., Yendi, E.N.N., 2020. Soil microbial diversity drops with land-use change in a high mountain temperate forest: a metagenomics survey. Environmental Microbiology Reports 12(2), 185–194. https://doi.org/10.1111/1758-2229.12822

Lynch, J.M., 2007.The Rhizosphere. John Wiley & Sons: New York, NY, USA.

Ma, X., Chen, T., Zhang, G., Wang, R., 2004. Microbial community structure along an altitude gradient in three different localities. Folia Microbiologica 49(2), 105–111. https://doi.org/10.1007/BF02931382

Mangora, M.M., 2005. Ecological impact of tobacco farming in miombo woodlands of Urambo District, Tanzania. African Journal of Ecology 43(4), 385–391. https://doi.org/10.1111/j.1365-2028.2005.00603.x

Maron, P.A., Mougel, C., Ranjard, L., 2011. Soil microbial diversity: methodological strategy, spatial overview and functional interest. Comptes Rendus Biologies 334(5–6), 403–411. https://doi.org/10.1016/j.crvi.2010.12.003

Michael, Y.G., 2013. Genome diversity of spore-forming firmicutes. Microbiology Spectrum 1(2), TBS-0015-2012. https://doi.org/10.1128/microbiolspec.TBS-0015-2012

Morgan, A.D., Maclean, R.C., Hillesland, K.L., Velicer, G.J., 2010. Comparative analysis of Myxococcus predation on soil bacteria. Applied and Environmental Microbiology 76(20), 6920–6927. https://doi.org/10.1128/AEM.00414-10

Olanya, O.M., Lakshman, D.K., 2015. Potential of predatory bacteria as biocontrol agents for foodborne and plant pathogens. Journal of Plant Pathology, 97(3), 405–417.

Schloter, M., Dilly, O., Munch, J.C., 2003. Indicators for evaluating soil quality. Agriculture, Ecosystems and Environment 98(1), 255–262. https://doi.org/10.1016/S0167-8809(03)00085-9

Sevasti, F., Tina, W., Thomas, J., Nicole, J., Cristina, D., Veronica, M., Pilar, J., 2016. A combination of extreme environmental conditions favor the prevalence of endospore-forming firmicutes. Frontiers in Microbiology 7, 1707. https://doi.org/10.3389/fmicb.2016.01707

Shen, H., Zhou, J., Zhao, B., Li, Q., Song, S., Wang, S., Luo, H., 2013. Altitude adaptability of main tobacco cultivars in Baoshan of Yunnan. Acta Tabacaria Sinica 19(5), 43–49. https://doi.org/10.3969/j.issn.1004-5708.2013.05.008

Supaka, N., Pinphanichakarn, P., Pattaragulwanit, K., Thaniyavarn, S., Juntongjin, K., 2001. Isolation and characterization of a phenanthrene-degrading Sphingomonas sp. strain P2 and its ability to degrade fluoranthene and pyrene via cometabolism. Science Asia 27, 21–28. https://doi.org/10.2306/scienceasia1513-1874.2001.27.021

Tang, Z.X., Chen, L.L., Chen, Z.B., Fu, Y.L., Sun, X.L., Wang, B.B., Xia, T.Y., 2020. Climatic factors determine the yield and quality of Honghe fluecured tobacco. Scientific Reports 10, 19868. https://doi.org/10.1038/s41598-020-76919-0

Waldrop, M.P., Firestone, M.K., 2006. Response of microbial community composition and function to soil climate change. Microbial Ecology 52, 716–724. https://doi.org/10.1007/s00248-006-9103-3

Wang, Z.B., Yang, Y., Xia, Y.Z., Wu, T., Zhu, J., Yang, J.M., Li, Z.F., 2019. Time-course relationship between environmental factors and microbial diversity in tobacco soil. Scientific Reports 9(1), 19969. https://doi.org/10.1038/s41598-019-55859-4

Xu, J., Zhang, Y., Zhang, P., Pankaj, T., Nadia, R., Wang, Y.Y., 2018. The structure and function of the global citrus rhizosphere microbiome. Nature Communications 9, 4894. https://doi.org/10.1038/s41467-018-07343-2

Xu, S.J., Yuan, Y., Song, P.F., Cui, M.F., Zhao, R.S., Song, X.Y., Cao, M., Zhang, Y.Z., Yang, J., 2023. The spatial patterns of diversity and their relationships with environments in rhizosphere microorganisms and host plants differ along elevational gradients. Frontiers in Microbiology 14, 1079113. https://doi.org/10.3389/fmicb.2023.1079113

Xun, W.B., Huang, T., Zhao, J., Ran, W., Wang, B.R., Shen, Q.R., Zhang, R.F., 2015. Environmental conditions rather than microbial inoculum composition determine the bacterial composition, microbial biomass and enzymatic activity of reconstructed soil microbial communities. Soil Biology & Biochemistry 90, 10–18. https://doi.org/10.1016/j.soilbio.2015.07.018

Yamori, W., Evans, J.R., Von, C.S., 2010. Effects of growth and measurement light intensities on temperature dependence of CO_2 assimilation rate in tobacco leaves. Plant Cell and Environment 33(3), 332–343. https://doi.org/10.1111/j.1365-3040.2009.02067.x

Yang, L.Y., Yang, S.L., Li, J.Y., Ma, J.H., Pang, T., Zou, C.M., He, B., Gong, M., 2018. Effects of different growth temperatures on growth, development, and plastid pigments metabolism of tobacco (Nicotiana tabacum L.) plants. Botanical Studies 59(1), 5. https://doi.org/10.1186/s40529-018-0221-2

Yang, Q., Wang, X., Shen, Y., 2013. Comparison of soil microbial community catabolic diversity between rhizosphere and bulk soil induced by tillage or residue retention. Journal of soil science and plant nutrition 13, 187–199. https://doi.org/10.4067/S0718-95162013005000017

Yao, H., He, Z., Wilson, M.J., 2000. Microbial biomass and community structure in a sequence of soils with increasing fertility and changing land use. Microbial Ecology 40,223–237. https://doi.org/10.1007/s002480000053

Ye, X.F., Li, Z.K., Luo, X., Wang, W.H., Li, Y.K., Li, R., Zhang, B., Qiao, Y., Zhou, J., Fan, J.Q., Wang, H., Huang, Y., Cao, H., Cui, Z.L., Zhang, R.F., 2020. A predatory myxobacterium controls cucumber Fusarium wilt by regulating the soil microbial community. Microbiome 8, 49. https://doi.org/10.1186/s40168-020-00824-x

Yoon, J.H., Adhikari, M., Jeong, S.S., Lee, S.P.□Kim, H.S.□Lee, G.S.□Park, D.H.□Kim, H.□Yang, J.E., 2024. Microbial diversity of soils under different land use and chemical conditions. Applied Biological Chemistry 67(1), 111. https://doi.org/10.1186/s13765-024-00970-y

Yu, J.J., Wang, G.L., Ye, X.W., Yan, D., Wei, P.P., Feng, J., 2010. Effects of altitude on quality of tobacco in tobacco-planting areas. Hunan Agricultural Sciences 1, 38–41.

Zhang, S.T., Song, X.N., Li, N., Zhang, K., 2018. Influence of high-carbon basal fertiliser on the structure and composition of a soil microbial community under tobacco cultivation. Research in Microbiology 169(2), 115–126. https://doi.org/10.1016/j.resmic.2017.10.004

Zhang, Z.C., Xin, Y.K., Jiang, Z.R., Shi, X.D., Xing, L., Chai, Z.S., Jia Y., Huang Y., Xue F., Chen J.W., Guo S.D., Hu W.R., Lin Z.H., Hu Z.L., Zhao Y.F., Peng H.J., Ye L.F., Li D.L., 2025. Environmental conditions, but not host genotype, are significant factors controlling the rhizosphere bacteria community of tobacco (Nicotiana tabaccum). Cogent Food & Agriculture 11(1), 2565715. https://doi.org/10.1080/23311932.2025.2565715