

Review

Rhizosphere microbial markers (micro-markers): A new physical examination indicator for traditional Chinese medicines

Kailin Yang^{a,b}, Yaping Zheng^{a,b}, Kangmeng Sun^{a,b}, Xinyan Wu^{a,b}, Zheng Zhang^a, Chunnian He^{a,b,*}, Peigen Xiao^{a,b,*}

^aInstitute of Medicinal Plant Development, Chinese Academy of Medical Sciences & Peking Union Medical College, Beijing 100193, China

^bKey Laboratory of Bioactive Substances and Resources Utilization of Chinese Herbal Medicine, Ministry of Education, Beijing 100193, China

ARTICLE INFO

Article history:

Received 20 June 2023

Revised 17 September 2023

Accepted 18 November 2023

Available online 24 February 2024

Keywords:

physical examination indicator

quality evaluation

quality formation of medicinal plants

rhizosphere microorganisms

rhizosphere microbial markers

ABSTRACT

Rhizosphere microorganisms, as one of the most important components of the soil microbiota and plant holobiont, play a key role in the medicinal plant-soil ecosystem, which are closely related to the growth, adaptability, nutrient absorption, stress tolerance and pathogen resistance of host plants. In recent years, with the wide application of molecular biology and omics technologies, the outcomes of rhizosphere microorganisms on the health, biomass production and secondary metabolite biosynthesis of medicinal plants have received extensive attention. However, whether or to what extent rhizosphere microorganisms can contribute to the construction of the quality evaluation system of Chinese medicinal materials is still elusive. Based on the significant role of rhizosphere microbes in the survival and quality formation of medicinal plants, this paper proposed a new concept of rhizosphere microbial markers (micro-markers), expounded the relevant research methods and ideas of applying the new concept, highlighted the importance of micro-markers in the quality evaluation and control system of traditional Chinese medicines (TCMs), and introduced the potential value in soil environmental assessment, plant pest control and quality assessment of TCMs. It provides reference for developing ecological planting of TCMs and ensuring the production of high quality TCMs by regulating rhizosphere microbial communities.

© 2024 Tianjin Press of Chinese Herbal Medicines. Published by ELSEVIER B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Contents

1. Introduction	181
2. Research foundation of new concept “micro-markers”	181
2.1. Rhizosphere microorganisms promote survival of medicinal plants	181
2.1.1. Rhizosphere microorganisms enhance stress resistance of medicinal plants	181
2.1.2. Rhizosphere microorganisms prevent continuous cropping obstacle (CCO)	182
2.2. Rhizosphere microorganisms promote quality formation of medicinal plants	182
2.3. Rhizosphere microorganisms reflect habitat characteristics and plant quality	182
3. Determination principle of micro-markers	183
4. Determination and research method of micro-markers	183
4.1. Site selection and sampling of rhizosphere microorganisms	184
4.2. Identification of rhizosphere microorganisms	184
4.3. Establishment and application of micro-markers	185
5. Role and significance of micro-markers	185
5.1. Guaranteeing “safety” of medicinal plants	185
5.2. Safeguarding “effectiveness” of medicinal plants	185
5.3. Control of pests and diseases	186
5.4. Improving edaphic environment	186
5.5. Solving cultivation problem of endangered medicinal plants	186

* Corresponding authors.

E-mail addresses: cnhe@implad.ac.cn (C. He), pgxiao@implad.ac.cn (P. Xiao).

6. Summary and prospects	186
CRediT authorship contribution statement	187
Declaration of Competing Interest	187
Acknowledgments	187
References	187

1. Introduction

Medicinal plants, as the most important source of traditional Chinese medicines (TCMs), are the vital material basis for the prevention and treatment of diseases in traditional Chinese medicine, therefore their yield and quality have been widely concerned. However, with the transformation of medicinal plant sources from wild to artificial cultivation, many challenges have emerged, such as the quality degradation of cultivated varieties, serious pests and diseases, obstacles to continuous cropping, etc. The rational quality evaluation of medicinal plants is the key to ensure the safety, stability and effectiveness of TCMs (Xiao, Wang, & Yan, 2014). In the past, the quality evaluation of TCMs and medicinal plants focused on the chemical components contained therein, and a variety of quality evaluation methods were established, such as the content determination of active components, quantitative analysis of multi-components by single-marker (QAMS), chemical fingerprint, and others. Especially, the concept of Q-marker was proposed (Liu, Chen, Xiao, Zhang, & Liao, 2016), which effectively promoted the quality evaluation of TCMs. These methods are mainly applied to the post-harvest stage of medicinal plants, including medicinal materials, decoction pieces or proprietary Chinese medicine. Yet, there is a lack of effective evaluation and control of the quality formation process in the growth stage of medicinal plants.

The recent studies suggest that the quality formation of TCMs is not only influenced by genetics, environment, soil and climate, but also impacted by biological factors (Han, Liang, & Sai, 2024). Among many biotic factors, rhizosphere microbes, called the “second genome” of plants, have a great impact on the growth, nutrient absorption and stress resistance of plants (Compant, Samad, Faist, & Sessitsch, 2019; Huang, Li, & Huang, 2020; Jaramillo, Mendes, & Raaijmakers, 2015; Shao, Dong, Han, & Liang, 2021; C. Zhong et al., 2022; Y. Zhong et al., 2022). On the one hand, rhizosphere microbes can regulate the growth state of medicinal plants and the biosynthesis of active ingredients; on the other hand, the composition and abundance of specific rhizosphere microbes can provide some special needs for the growth process of medicinal plants, improving the growth environment to ensure the formation of medicinal quality. Therefore, rhizosphere microbes, as indispensable booster for the growth of medicinal plants, have the potential to be used as reasonable indicators in the quality evaluation of medicinal plants. In addition, with the development of molecular biology and omics technologies in recent years (Li et al., 2021), there is much progress in the research methods (Guo, Liu, Tang, Chen, & Pei, 2017), influencing factors (Xun, Shao, Shen, & Zhang, 2021) and interactions between medicinal plants and rhizosphere microbes (Xiao et al., 2013; Zhu et al., 2021). Accordingly, the upsurge of new technologies and the actual production requirements provide the basis for the establishment of rhizosphere microbial markers (micro-markers) of medicinal plants.

Based on the important effects of rhizosphere microorganisms on medicinal plants, this paper aims to establish rhizosphere microbial indexes that take into account both quality evaluation and production control. The concept of micro-markers is put forward for the first time by selecting appropriate microbial markers, establishing safe and effective evaluation standards for high-

quality, suitable origin and excellent variety of medicinal plants (Liu et al., 2020), and providing guidance for the existing problems and quality control in the growth process of medicinal plants. The establishment of micro-markers is of great significance for ensuring the safety and effectiveness of medicinal plants, monitoring the phytopathogens and pests of medicinal plants, understanding and improving the soil environment, as well as unearthing why endangered medicinal plants are in danger of extinction.

2. Research foundation of new concept “micro-markers

2.1. Rhizosphere microorganisms promote survival of medicinal plants

2.1.1. Rhizosphere microorganisms enhance stress resistance of medicinal plants

Survival is the first priority of plants, so the “resistance” is the first criterion for plants to consider. Abiotic stress, such as drought, salt, high temperature, low temperature and flood, and biotic stress, such as diseases, pests, weeds, affect the normal growth and development of plants, and even threaten the survival of plants (Waadt et al., 2022). Rhizosphere microorganisms of medicinal plants can promote the expression of defense genes of medicinal plants, activate the plant immune system, establish biofilms on the root surface, compete for ecological niche and nutrition, directly produce disease-resistant and insect-killing effects or indirectly secrete compounds that induce plant resistance, thereby increasing plant stress resistance and improving the survival rate of medicinal plants (Mohamed & Kamal, 2011; Yin et al., 2021). *Bacillus amylolyticus* TB6, an anti-fungal strain with 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, was isolated from the rhizosphere of *Panax ginseng* C. A. Mey. (Renshen in Chinese), which increased the expression of stress-inducing enzymes, such as polyphenol oxidase and catalase, thereby inducing resistance in plant systems (Tian et al., 2018). *Panax notoginseng* (Burk.) F. H. Chen (Sanqi in Chinese) rhizosphere bacteria *Bacillus cereus* NS-2 and *Bacillus velezensis* GJ-7 can form biofilm on the root surface of *P. notoginseng* and occupy ecological niche, effectively inhibiting nematode invasion (Wu et al., 2022). *Bacillus megaterium* reduces the infestation of *Meloidogyne incognita*, which was achieved by the competition, hyperparasitism, production of lytic enzymes, secondary metabolites, and induces systemic resistance (Gupta et al., 2015). Gu et al. (2020) proposed modifying the rhizosphere microbiome - pathogen interaction to enhance plant resistance through siderophore targeted therapy. *Bacillus pumilus* GZDF3, isolated from the rhizosphere soil of *Pinellia ternata* (Thunb.) Breit. (Banxia in Chinese), can produce antifungal components such as siderophore, which has a synergistic effect with the antibiotic amphotericin B, thus providing a basis for antifungal cultivation of *P. ternata* (Sheng et al., 2020).

Heavy metal stress is common in the cultivation of medicinal plants, which can affect plant morphology, photosynthesis and growth (Hu et al., 2023). The rhizosphere microorganisms can protect heavy metal-stressed plants by converting heavy metals into less toxic forms, absorbing heavy metals, forming protective films on the root surface, and producing plant hormones to increase plant heavy metal resistance. H_2S -producing *Desulfovibrio* sp. SRB1-1 could precipitate heavy metals as metal sulfides, immobilize Cd and Pb in the soil (Shan et al., 2019). Magnin, Gondrexon,

& Willison, 2014 proved the zinc biosorption potentialities of purple non-sulfur bacterium *Rhodobacter capsulatus*. Some bacteria, such as *Serratia*, *Achromobacter* promote the growth and heavy metal resistance of plants by producing indole acetic acid (IAA) (Tanwir, Abbas, Hussaan, Basit, & Alomrani, 2023), siderophores (Hesse et al., 2018; Rajkumar, Ae, Prasad, & Freitas, 2010), ACC deaminase (Sun et al., 2022), and arginine decarboxylase (Q. Wang, Zhang, He, & Sheng, 2018; X. Wang et al., 2018). In addition, increasing plant weight to reduce the relative content of heavy metals is also an approach of rhizosphere microorganisms to resist heavy metal stress (Zhou, Zhu, Ma, & Wang, 2017).

2.1.2. Rhizosphere microorganisms prevent continuous cropping obstacle (CCO)

With the extension of planting years and release of root secretions to the soil, the diversity and uniformity of soil microorganisms in most medicinal plants are significantly reduced, the structure of bacterial community is degraded, the accumulation of pathogenic bacteria is increased, the activity of soil enzymes is decreased, and the stability of soil ecosystem is decreased, which may result in stunted plant growth and even dead seedlings (Li et al., 2020; Misra et al., 2019; Song, Pan, Li, Wu, & Wang, 2018; Zhang & Zhang, 2007; Zhang and He, 2011). For instance, the rhizosphere bacterial community structure of *Astragalus membranaceus* (Fisch.) Bge. var. *mongholicus* (Bge.) Hsiao (Huangqi in Chinese) (Li et al., 2021), *Sophora flavescens* Ait. (Kushen in Chinese) (Lei, Liu, Zhao, Hou, & Wang, 2020), *P. ginseng* (Tong, Liu, Liu, Xia, & Zhu, 2021), Cut Chrysanthemum (Wang et al., 2022) and other rhizosphere bacteria showed a decayed pattern with time under the influence of culture year, while the pathogenic fungal communities were enriched. Reasonable crop rotation and intercropping systems are common methods to solve CCOs, as they increase the diversity and richness of rhizosphere microbial communities and optimize community structure (Wang et al., 2022). Therefore, in theory, rhizosphere microorganisms can degrade allelopathic autotoxic substances, synthesize soil enzymes, improve soil physical and chemical properties, and thus alleviate CCOs. Recent research showed that *Klebsiella variicola* subsp. *Variicola* ZH07, isolated from peanut rhizosphere, can degrade autotoxic substances such as benzoic acid, *p*-hydroxybenzoic acid, salicylic acid, cinnamic acid, vanillic acid and coumaric acid produced during continuous cropping (Wang et al., 2022). *Streptomyces canus* GLY-P2, a strain obtained from cucumber rhizospheric soil, can significantly promote the activities of phosphatase, urease, sucrase, and catalase in rhizosphere soil, which can increase the resistance to stress of cucumber (Wu et al., 2019).

2.2. Rhizosphere microorganisms promote quality formation of medicinal plants

The interaction between root system and rhizosphere microorganisms of medicinal plants is essential for the yield increase and quality formation. Although the importance of rhizosphere microbial community to plant growth has been widely recognized, the understanding of rhizosphere microbes is still very limited. It is crucial to promote the high-quality growth of medicinal plants and understand the mechanism of rhizosphere microorganisms on the quality formation of medicinal plants (Mendes, Garbeva, & Raaijmakers, 2013).

Certain microorganisms contain gene pools involved in biosynthesis of bioactive ingredients, which provide additional metabolic capacity to the host plant, therefore specific plant–microbe interactions can promote the production of active ingredients in medicinal plant (Huang, Long, & Lam, 2018; Zhai et al., 2019). Zhong et al. (2022) found that the expressions of key genes involved in the biosynthesis of liquiritin and glycyrrhizic acid, such as *CYP72A154*,

CHI and *PAL*, were strongly negatively correlated with the abundance of *Lysobacter*. Regulating the communication between these rhizosphere growth-promoting bacteria and *Glycyrrhiza uralensis* Fisch. (Gancao in Chinese) by regulating the rhizosphere environment was conducive to promoting the biosynthesis of liquiritin and glycyrrhizic acid. The effect of rhizosphere microorganisms on the accumulation of liquiritin may even be greater than the growth time of *G. uralensis*. de Oliveira et al. (2019) believed that the rhizosphere colonization of arbuscular mycorrhizal fungi (AMF) in *Piper aduncum* L. (Hujiao in Chinese) could promote the expression of defense-related genes, thus promoting the production of volatile compounds (e.g. alcohol, ether and phenol), the potential signaling and defense molecules. Especially, AMF increased the content of sesquiterpene hydrocarbon, the main components of volatile oil of *P. aduncum*, and induced the production of 15 chemical components in plants.

Some rhizosphere microorganisms, especially plant rhizosphere growth-promoting bacteria (PGPR), can convert essential nutrients present in the soil into forms that are easily absorbed by plants for growth and development (Richard, Manuela, Antonella, Anna, & Stanislav, 2017). *Bacillus safensis* isolated from wheat rhizosphere has good plant growth promoting activity, which produced siderophore and indolelactic acid (IAA), dissolved zinc, potassium, inorganic phosphate, and is a safe biofertilizer. The Paneer-whey based bioformulation (P-WBF), developed from *Bacillus safensis*, can promote nutrient uptake, increase the fresh and dry weight of various parts of *Stevia rebaudiana* Bertoni (Tianyeju in Chinese) and content of the active ingredient stevioside (Prakash & Arora, 2019).

Plant rhizosphere microbiota may also affect the active components of medicinal plants by regulating plant metabolism through the production of plant hormones (Huang et al., 2018). *Stenotrophomonas* enrichment in the *A. membranaceus* rhizosphere can produce substances that regulate plant growth and promote the accumulation of bioactive ingredients, thereby promoting the growth of *A. membranaceus* and secretion of metabolites. The root exudates can in turn support the growth of *Stenotrophomonas* in the rhizosphere, thereby increasing the content of astragaloside (Li et al., 2021).

2.3. Rhizosphere microorganisms reflect habitat characteristics and plant quality

Some *Bacillus* species have good plant growth promoting activity, which can produce siderophore and IAA, dissolved zinc, potassium, inorganic phosphate, and are closely related to the high yield of many medicinal plants (Wang et al., 2022). *B.adius* and *B. firmus* can increase the biomass of above and below ground parts of licorice (Zhong et al., 2022). *B. amyloliquefaciens* can increase the activities of urease, catalase and phosphatase, and increased the fresh weight of roots of *P. ginseng* (Tian et al., 2018). *B. amyloliquefaciens* BF1 and *B. subtilis* Y37 treatment can increase the number of soil beneficial bacteria, antagonize pathogenic bacteria, improve soil physical and chemical properties, and upregulate glycolysis/gluconeogenesis pathways, thus improving the height, stem diameter, fresh weight, yield of *Lilium brownii* F. E. Brown var. *viridulum* Baker (Baihe in Chinese) (Tu et al., 2023).

Similar to *Fusarium*, a pathogen that causes root rot (Zhang et al., 2022), *Monographella* is likely to be a pathogen that causes continuous crop disorders (Yu, Jiang, Ren, Li, & Xu, 2018). With the growth of planting years, the relative abundance of *M. cucumerina* in *P. ginseng* and *P. notoginseng* was significantly increased, the abundance of beneficial bacteria was decreased significantly, and the pathogenicity of soil was increased (Luo et al., 2019; Tong, Liu, Liu, Xia, & Zhu, 2021). Also the abundance of *Monographella* in *Panax quinquefolius* L. (Xiyangshen in Chinese) with

root rot disease was significantly higher than that in healthy group (Yu, Jiang, Ren, Li, & Xu, 2018).

Some studies have found that the authenticity of Chinese medicinal materials may be related to the specificity of rhizosphere microorganisms. For example, six fungal genera, i.e., *Curvularia*, *Paraconiothyrium*, *Cylindrocarpon*, *Macrophomina*, *Xylaria* and *Otospora*, were present in Daodi areas, which were absent in non-Daodi areas (Zheng, Liu, Huang, & Hou, 2016).

3. Determination principle of micro-markers

Based on the above research background, we believe that similar to establishing physical examination criteria to detect physical conditions, micro-markers can be established to evaluate and monitor the growth state of medicinal plants. Micro-markers for medicinal plants are a type of key rhizosphere microorganisms in the planting process of medicinal plants, which is closely related to the safety and efficacy of medicinal plants, and can provide guidance for the high-quality cultivation of medicinal plants. It is not only an important index of quality evaluation, but also a chief index of problem diagnosis in the growth process of medicinal plants. Some potential micro-markers for medicinal plants are summarized in Table 1.

The identification of micro-markers are supposed to meet the following conditions: (1) Ideally, it is abundant in special stages, such as the planting stage of medicinal plants, the susceptibility period of plant diseases and pests or the harvest period; rhizosphere microorganisms unique to high quality medicinal plants or problematic medicinal plants could be considered as candidates,

so as to reflect the characteristics of high/low quality medicinal plants. (2) The unique and inherent rhizosphere microorganism of high-quality medicinal plants in genuine producing areas would be best. (3) The rhizosphere microorganisms that directly related to the content of medicinal or toxic components of medicinal plants might be suitable micro-markers. (4) The positive micro-markers can promote plant growth, while the negative micro-markers reflect the harmfulness of diseases, insects or heavy metals in medicinal plants, both of which have certain uniqueness and representativeness; it can be either the presence/absence of one or several microbes (which are relatively easy to identify) or the relative abundance range of a particular microorganism. (5) At the current stage, micro-markers could be defined at the genus level; in the future, more precise indicators will be available at the species level, depending on the available molecular biology technologies with the species level resolution. The selection, detection and application of micro-markers are summarized in Fig. 1.

4. Determination and research method of micro-markers

Safety is an important premise of rational drug use, and effectiveness is the primary goal of rational drug use. As an important index for quality evaluation and quality control of medicinal plants, micro-markers should take both safety and effectiveness into consideration. The standardized treatment method is an important premise to ensure the rationality, representativeness and repeatability of the evaluation of each batch of medicinal plants.

Table 1
Potential micro-markers for medicinal plants.

Medicinal plants	Potential micro-markers	Functions	References
<i>Astragalus membranaceus</i>	<i>Stenotrophomonas</i>	Promote accumulation of astragaloside	Li et al., 2021
<i>Lycium barbarum</i>	<i>norank_f_Anaerolineaceae</i> , <i>norank_f_AKYG1722</i> , <i>norank_o_Gaiellales</i>	Promote accumulation of betaine and polysaccharide	Liu et al., 2022
<i>Artemisia annua</i>	<i>Trichoderma asperellum</i> ACCC30536	Promote accumulation of artemisinin	Zhai et al., 2019
<i>Glycyrrhiza uralensis</i>	<i>Bacillus badius</i> , <i>Bacillus firmus</i> , <i>Rhodoplanes</i> , <i>Lysobacter</i>	Promote yield, liquiritin and glycyrrhizic acid accumulation	Zhong et al., 2022
<i>Stevia rebaudiana</i>	<i>Bacillus safensis</i>	Promote yield and stevioside accumulation	Prakash & Arora, 2019
<i>Panax ginseng</i> <i>Bacopa monnieri</i>	<i>Bacillus amyloliquefaciens</i> <i>Bacillus megaterium</i> , <i>Trichoderma harzianum</i> ThU	Promote yield accumulation Promote the accumulation of bacoside	Tian et al., 2018 Gupta et al., 2015
<i>Panax ginseng</i> <i>Astragalus membranaceus</i> <i>Pseudostellaria heterophylla</i> <i>Paeonia lactiflora</i>	<i>Fusarium</i> <i>Rhizobiales</i> , <i>Sphingomonadales</i> , <i>Burkholderiales</i> <i>Trichoderma harzianum</i> <i>Alternaria</i>	Cause root rot Promote nodulation Predict CCOs Promote accumulation of paeoniflorin	Zhang et al., 2022 Li, 2019 Chen et al., 2021 Sun et al., 2022
<i>Paeonia suffruticosa</i>	<i>Curvularia</i> , <i>Paraconiothyrium</i> , <i>Cylindrocarpon</i> , <i>Macrophomina</i> , <i>Xylaria</i> , <i>Otospora</i>	Identification of high quality medicinal materials	Zheng, Liu, Huang, & Hou, 2016
<i>Alisma plantago-aquatica</i>	<i>Steroidobacter</i> , <i>Pseudolabrys</i> , <i>Nevskia</i> and <i>Nitrospira</i>	Identification of high quality medicinal materials	Wei et al., 2022
<i>Dendrobium nobile</i>	<i>Acidobacteriales</i> , <i>Pseudonocardiales</i> , <i>Pseudoalteromonas</i> , <i>Pseudomonadales</i>	Breed identification	Zuo, Zu, Liu, Song, & Yuan, 2021
<i>Ferula assa-foetida</i>	<i>Actinobacteria</i> , <i>Gemmatimonadetes</i> , <i>Bacteroidetes</i> , <i>Acidobacteria</i> , <i>Verrucomicrobia</i>	Reflects accumulation of volatile components	Q. Wang, Zhang, He, & Sheng, 2018; Wang et al., 2018
<i>Panax quinquefolius</i>	<i>Janthinobacterium</i> , <i>Nitrospira</i> , <i>Pedomicrobium</i> , <i>Mrakia</i> , <i>Paradendryphiella</i> , <i>Sporopachydermia</i> , <i>Myrothecium</i> , <i>Racocetra</i>	Reflect health status	Jiang et al., 2019
<i>Glycyrrhiza uralensis</i>	<i>Proteobacteria</i> , <i>Actinobacteria</i>	Identification of liquorice quality	Dong et al., 2021
<i>Panax notoginseng</i>	<i>Proteobacteria</i> , <i>Firmicutes</i> , <i>Actinobacteria</i>	Identify quality of <i>P. notoginseng</i>	Kui et al., 2021
<i>Solanum nigrum</i> , <i>Sedum alfredii</i> , <i>Noccaea caerulescens</i> , <i>Brassica juncea</i>	<i>Sphingomonas</i> , <i>Micrococcaceae</i>	Reflect accumulation of heavy metals	Luo et al., 2022

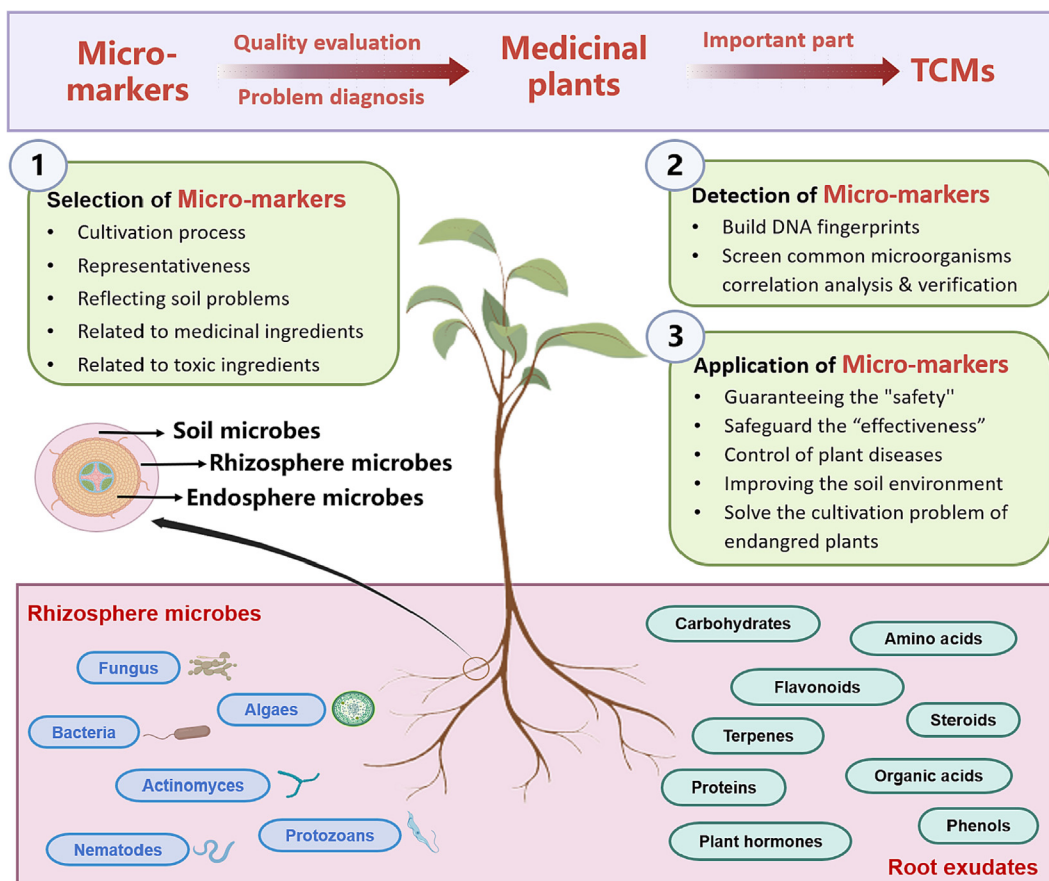


Fig. 1. Selection, detection and application of micro-markers. Micro-markers, which are closely related to the safety and effectiveness of medicinal plants, have been established by screening common microorganisms, analyzing their correlation with the traits of medicinal plants, and have been verified, and have important guiding significance for the cultivation of medicinal plants.

4.1. Site selection and sampling of rhizosphere microorganisms

In the stage of a certain medicinal plant susceptible to diseases and pests or the harvesting period, five-point sampling method (Liu et al., 2022; Xiao et al., 2017) is used to collect the complete root system of the characteristic medicinal plant; if it is a tree, the hairy roots about 1 m away from the tree in four directions can be harvested, and the depth is about 10–30 cm (Xu et al., 2018). The loosely bound non-rhizosphere soil was shaken off, and the roots with soil were eluted thrice with PBS for 15 s of each time. The eluent was combined, and DNA was extracted by centrifugation and precipitation for the rhizosphere microbial samples (Zhong et al., 2022).

4.2. Identification of rhizosphere microorganisms

The research methods of rhizosphere microorganisms mainly include traditional culture methods represented by plate culture method, biomarkers methods represented by phospholipid fatty acid (PLFA) and quinones profiling, and molecular biological methods based on PCR technology and probes technology. Huang, Li, & Huang, 2020 and Yan, Chen, Yan, Yin, & Zhao, 2008 made the detailed overview of research methods of rhizosphere microorganisms (Yan, Chen, Yan, Yin, & Zhao, 2008).

Since culturable microorganisms only account for 0.1 % to 10 % in the environment, the traditional culture methods have great limitations, and it is rarely used in the identification of rhizosphere microorganisms (Yan, Chen, Yan, Yin, & Zhao, 2008). Both respira-

tory quinone and PLFA are widely present in cell membranes. Although biomarkers methods do not rely on microbial culture, can reflect the composition and biomass of living cells, and are fast and reliable, the taxonomic level they can identify is limited. In addition, adapting to the environment can lead to altered fatty acid structure in the cell wall (Siliakus, van der Oost, & Kengen, 2017), archaeal cell walls have ether instead of ester bonds in their polar membrane lipids, and the PLFA patterns are similar in various soils, therefore PLFA is not suitable for the analysis of archaea, and is of no use in determining the microorganisms at the strain level (Borymski, Cycoń, Beckmann, Mur, & Piotrowska, 2018; Ling et al., 2020). Molecular biological method is mostly based on PCR amplification technology, such as PCR based molecular biological method and clone library method. In addition, there are studies based on probe-based identification techniques such as fluorescence in situ hybridization (FISH), micro-autoradiography, stable-isotope probing, and DNA microarray technologies (Yan, Chen, Yan, Yin, & Zhao, 2008). In the shotgun metagenome sequencing, the DNA of all microorganisms is extracted directly from environmental samples to construct a metagenome sequencing library for high throughput analysis. Molecular biology methods are no longer dependent on microbial culture, which can reveal the information of microorganisms in rhizosphere soil more comprehensively than microbial culture technology (Guo, Liu, Tang, Chen, & Pei, 2017). Among them, molecular fingerprinting technology based on PCR technology is rapid, easy to operate, and can simultaneously analyze multiple samples, which enables the establishment of micro-markers.

4.3. Establishment and application of micro-markers

The first thing to consider is the type of micro-markers. The micro-markers reflecting the growth state of medicinal plants are determined by two or more of the following aspects: content of medicinal ingredients, yield, heavy metal content, severity of diseases and pests, and accumulation of allergenic autotoxic substances in the environment (Zhang, 2017). Among them, the yield and medicinal component content are the common concerns of all medicinal plants, and the micro-markers about the yield and medicinal component content should be established for all medicinal plants. Micro-markers associated with other considerations are flexible depending on the characteristics of medicinal plants. For instance, some medicinal plants, such as *Solanum nigrum* L. (Wang et al., 2022), *Sedum alfredii* Hance (Ng, So, Wong, & Lau, 2023) and *Salvia miltiorrhiza* Bunge (Fu, Yuan, Liu, & Wang, 2023), are heavy metal hyperaccumulating plants, and establishing heavy metal micro-markers might be useful for them. Ginseng is susceptible to root rot (Ji et al., 2021), so establishing micro-markers of diseases and pests could be helpful in ginseng cultivation; the soil planted with *Rehmannia glutinosa* Libosch. (Guo et al., 2013) and *Ginseng* (Zhou et al., 2023) often had the accumulation of allelopathic self-toxic substances, and the micro-markers indicating the accumulation of these harmful compounds in the environment can be established.

A large number of experiments were conducted to screen the characteristic microorganisms of high quality medicinal materials, high yield medicinal materials, heavy metal contaminated medicinal materials, medicinal materials affected by diseases and pests, and medicinal materials in allelopathic and self-toxic soil. Representative high-quality medicinal plants, medicinal plants with excessive heavy metals or medicinal plants with serious diseases and pests were selected, and more than 30 batches of samples were investigated by denaturing gradient gel electrophoresis (DGGE), random amplified polymorphic DNA (RAPD), amplified ribosomal DNA restriction analysis (ARDRA), amplified fragment length polymorphism (AFLP), terminal restriction fragment length polymorphism (T-RFLP) (Duarte et al., 2019; Siqueira, Sakamoto, & Rosado, 2023; Vanechoutte et al., 1995) and other technologies to establish fingerprint profiling of rhizosphere microbes and screen the common microorganisms. Then, the correlations between common rhizosphere microorganisms and characteristic traits were analyzed (Chen et al., 2022). In addition, some easily miscible products, such as the plants in the genus of *Dendrobium* (Zuo, Zu, Liu, Song, & Yuan, 2021) and *Ferula* (Q. Wang, Zhang, He, & Sheng, 2018; X. Wang et al., 2018), can also be considered to establish relevant microbial standards for identification. Finally, the rhizosphere microorganisms were obtained by plate scribing method and verified by callus culture and cultivation experiments (Guo, Liu, Tang, Chen, & Pei, 2017; H.X. Xu et al., 2022; J. Xu et al., 2022).

In the application of micro-markers, their relative abundance can be determined by traditional culture method, biomarker method and molecular biology method (Das, Dash, Mangwani, Chakraborty, & Kumari, 2014).

5. Role and significance of micro-markers

5.1. Guaranteeing “safety” of medicinal plants

As the physical examination indicator of TCMs, micro-markers should first ensure the “physical health” of plants. Chen, Teng, Lu, Wang, & Wang, 2015 found that in seven southern provinces of China, e.g., Zhejiang, Jiangxi and Hunan, the average soil concentration of at least two heavy metals was higher than the first-level value of China’s soil environmental quality standards. The average concentrations of Cd, As and Ni in Guangxi and Guizhou provinces

of China were even higher than the secondary standards. In 37 kinds and 2427 batches of Chinese herbal medicines, the unqualified rates of heavy metals were 20.9% (Cd) > 5.8% (Pb) > 3.9% (Cu) > 3.5% (Hg) > 2.9% (As), and the percentage of unqualified parts were 97.3% (seed), 92.0% (fruit), 68.5% (flower), 53.2% (whole plant), 51.3% (leaf), respectively (Fei, Xiao, Wang, Zhu, & Nie, 2021). The content of heavy metals exceeded the standard in many medicinal plants, such as *Solanum nigrum* L. (Ldz et al., 2021), *Paeonia ostii* T. Hong & J. X. Zhang (Shen, Xu, Chen, & Zhang, 2017), *Portulaca oleracea* L. (Kale, Lokhande, & Ade, 2015) and *Lonicera japonica* Thunb. (Fan et al., 2020). In human, exposure to and ingestion of heavy metals via phytomedicine can lead to an increase in the risk of tumors, neurological disorders, diabetes, infertility, developmental disorders, kidney failure and cardiovascular diseases (Karri et al., 2018; Paithankar, Saini, Dwivedi, Sharma, & Chowdhuri, 2021; Yao et al., 2021). The growth period of most medicinal plants is longer than that of grain crops (Zhang et al., 2021), and more heavy metals or harmful elements could be accumulated in the former. Therefore, the planting soil of medicinal plants should have a special safety limit value for heavy metals.

The heavy metal stress can increase the number of special microorganisms such as heavy metal tolerant microorganisms, which can promote the increase of plant biomass (Yang, Dai, Skuza, & Wei, 2020), cell wall formation, phytochelatin synthesis, photosynthetic pigment synthesis, antioxidant defense system activation (Liu, Zhang, Zhang, & Chai, 2013) and organic acid secretion (Rehman, Rizwan, Ali, Ok, Ishaque, & Saifullah, 2017; Wang et al., 2022). Rhizosphere microorganisms can improve plant tolerance to heavy metals, and serve as an important indicator for heavy metal risk assessment in medicinal plants (Qian, Huang, Su, & Bao, 2022). Some studies found that *Sphingomonas* and *Micrococcaceae* are closely related to Cd accumulation in the roots of *Solanum nigrum*, *Sedum alfredii*, *Brassica juncea* and *Noccaea caerulea*, and *Micrococcaceae* was also related to Cd accumulation in the aboveground part (Luo et al., 2022), which may be potential micro-markers of these medicinal plants. In addition, rhizosphere microbial interactions can also promote the absorption of heavy metals by plants, and a micro-marker group could be established to monitor the safety of medicinal plants (Middleton, Yergeau, Monard, Combier, & Amrani, 2020). For example, the co-colonization of biocontrol microorganisms *Fusarium flocciferum* and *Delftia acidovorans* in the rhizosphere of *P. notoginseng* resulted in an increase of As concentration in the roots of *P. notoginseng* (Li et al., 2021), which may increase the potential risk of phytomedicine products.

5.2. Safeguarding “effectiveness” of medicinal plants

As the physical examination indicator of TCMs, micro-markers should then ensure the “physical fitness” of plants. Due to artificial breeding or changes in the living conditions of medicinal plants, such as climate change, the abuse of fertilizers and pesticides or environmental pollution, some medicinal plants have experienced the degradation of traits and qualities. For instance, the biosynthesis of ginsenosides and phyosterols in wild ginseng is higher than that in cultivated ginseng, as well as the ginsenoside diversity (Ma et al., 2023). By measuring and improving the relative abundance of rhizosphere microorganisms related to the biosynthesis of medicinal components, it is of great value to ensure the effectiveness of medicinal plants. Sun et al. (2023) found that the relative abundances of *Vicinamibacteriales* and *Rhizobiales* were significantly correlated with wogonoside, the active ingredient of *Scutellaria baicalensis* Georgi. The rhizosphere microorganisms *norank_f_Anaerolineaceae* in *Lycium barbarum* L. can promote the accumulation of betaine, while *norank_f_AKYG1722* and *no-*

rank_o_Gaiellales promoted the accumulation of polysaccharide (Liu et al., 2022). *Alternaria* is closely related to paeoniflorin accumulation in *Paeonia lactiflora* Pall. (Sun et al., 2022).

According to the pharmacophylogeny theory, the closely related medicinal plants tend to have the same or similar chemical compositions and pharmacological activities (Xiao, Li, Hao, & He, 2021); for example, the leaves of *Malus* species generally contain phlorizin and other polyphenols (Li, Shen, Bi, He, & Xiao, 2018), whereas the plants of *Acer tataricum* subsp. *ginnala* (Maximowicz) Wesm. contain abundant ginnalin (Bi et al., 2016). Some studies suggested that some rhizosphere microbes can promote the synthesis and accumulation of medicinal ingredients by regulating the expression of biosynthetic genes (Zhong et al., 2022). Thus, the phylogenetically related medicinal species with similar chemical components could be associated with similar rhizosphere microorganisms or core microbiome in the cultivated soil. This may provide a basis for the screening of micro-markers for the biosynthesis of key secondary metabolites of medicinal plants.

5.3. Control of pests and diseases

As the physical examination indicators of TCMs, micro-markers should also help plants find “health hidden trouble”. Planting a single variety on a large scale for a long time will reduce the stability of the ecological environment, and increase the risk of large-scale diseases and pests. Rhizosphere microbial diversity can be used as a biological index of disease susceptibility of medicinal plants, and has potential value in monitoring, evaluating and improving the health status of medicinal plants (Wu et al., 2015). Gu et al. (2022) found that plants tend to have a binary outcome, complete health or severe disease, when challenged by soilborne pathogens, which is caused by the early differentiation of rhizosphere microbiome, and subtle changes in the rhizosphere microbiome composition can predict plant health earlier than the traditional method of pathogen abundance detection. Shang et al. (2016) found that the rhizosphere-related bacteria diversity of healthy Lanzhou lilies was lower than that of diseased Lanzhou lilies, while fungi showed the opposite trend. Moreover, the relative abundance of *Fusarium*, *Rhizoctonia*, *Verticillium*, *Penicillium* and *Ilyonectria* (*Neonectria*) in diseased plants was relatively high, which may also be the cause of plant root rot. There were significant differences in rhizosphere microorganisms between healthy and root-rotting *P. quinquefolius*; *Rhodoplanes* and *Kaistobacter* were the dominant genera of healthy *P. quinquefolius*, while *Sphingobium* was the dominant genus of root rot one. Moreover, the content of *Monographella* in root rot samples (23.13%) was significantly higher than that in healthy samples (2.90%) (Jiang et al., 2019). It is of great significance to establish relevant standards for the species and quantity of rhizosphere microorganisms of medicinal plants, so as to understand the growth state of medicinal plants and promote the standardized production of Chinese herbal medicines. Based on the rhizosphere microorganisms of *A. membranaceus*, Li et al. (2021) constructed a consortia consisting of *Stenotrophomonas* sp., *Rhizobium* sp., *Ochrobactrum* sp. and *Advenella* sp., which can inhibit the growth of pathogenic fungi and active plant induced systemic resistance (ISR) synergies to protect plants. The rhizosphere microbiota can be a factor determining the ideal traits of plants, and how the plant genotypes interact with the rhizosphere microbiota can be evaluated to form an excellent host phenotype (Walters et al., 2018), so as to modify the plant phenotype in actual production; however, there are few reports on medicinal plants in this aspect.

5.4. Improving edaphic environment

As the physical examination indicators of TCMs, micro-markers should also help plants “prevent disease”. Land degradation is the

loss of physical, chemical, or biological properties of soil by natural or anthropogenic processes and the reduction or disappearance of important ecosystem functions (Coban, De Deyn, & van der Ploeg, 2022). The continuous cultivation of many medicinal plants in the same plot can lead to deterioration of basic physical and chemical properties of soil, changes in soil microbial community structure, accumulation of autotoxic substances, slow plant growth, aggravation of soil microbial community and other problems (Chen et al., 2022). For example, the abundance of common soil-borne pathogens (e.g. *Monographella cucumerina*, *Ilyonectria morspanacis*, *Ilyonectria robusta*, *Fusarium solani* and *Nectria ramulariae*) of *P. ginseng* increased with the increase of cultivation years (Tong, Liu, Liu, Xia, & Zhu, 2021). With the increase of cultivation years, pathogenic fungi such as *Plectosphaerellaceae*, *Fusarium* and *Cladosporium* were also enriched in the rhizosphere of four cut chrysanthemums (Wang et al., 2022). The composition of soil compounds is roughly similar, and the amount of root exudates is very small, so it is not convenient to analyze plant pests and diseases by identifying soil chemical components. In contrast, microorganisms have high sensitivity to the changes of soil physical and chemical properties (Hermans, Buckley, Case, Curran, & Lear, 2020). Norris et al. (2020) believe that it is theoretically possible to link the microbial communities that are abundant and easily detected to soil function and health, so as to establish microbial standards for evaluating soil health. Micro-markers, as microorganisms recruited by plants from soil, can be used to evaluate soil health. They can be used to timely detect the deterioration of soil conditions. In addition, the microbial fertilizer developed from plant growth-promoting bacteria can effectively alleviate soil acidification and soil fertility decline, increase soil available potassium and organic matter content, and promote nitrate reductase activity in rhizosphere soil (Lai et al., 2023). Therefore, the core rhizosphere microorganisms of healthy medicinal plants can be transferred to diseased medicinal plants, which could improve soil rhizosphere microecology and protect the environment; such an approach is of great value for green development (Yu et al., 2023).

5.5. Solving cultivation problem of endangered medicinal plants

As the physical examination indicator of TCMs, micro-markers should also help plants find the “cause of physical problems”. The microbiome can dramatically alter the performance of individual plants and is fundamental to the persistence of endangered plant populations (David et al., 2019). Micro-marker, as the abundant microorganism in plant rhizosphere, is closely related to the growth and quality formation of medicinal plants. Exploring the common rhizosphere microorganisms of medicinal plants is of great value for solving the cultivation problems of endangered plants. The imbalance in the regulation of canopy density and soil pH-bacterial diversity might exacerbate the endangered status of *Scutellaria tsinyunensis* C. Y. Wu & S. Chow (Xu et al., 2022). Furthermore, it was revealed that *Haliangium* and *Candidatus Koribacter* are important genera for the protection of *S. tsinyunensis*, which are of great significance for promoting the growth of *S. tsinyunensis* and protecting the endangered plants.

6. Summary and prospects

Micro-markers can be divided into two types: one is for the quality monitoring of medicinal plants in special stage, such as high incidence period of medicinal plant diseases and pests, as well as soil health status, etc.; the other is useful in evaluating the quality of medicinal plants in the harvest period, such as those associated with the content of index components and heavy metal content of medicinal plants. In the past, most standards can only

be evaluated from the single aspect of TCMs or environment. The establishment of micro-markers would help analyzing the complex relationship between “environment - rhizosphere microorganisms - quality and health of medicinal plants”, discovering risks and intervening the growth state of medicinal plants in advance, improving the evaluation standard system of high-quality medicinal materials, and revealing the causes of high-quality medicinal materials. At present, there are also some challenges in the improvement of micro-markers. The existing rhizosphere microbiological research methods are costly, difficult to operate, of too large workload, time consuming and lacking complete database, which make it very difficult to establish and popularize micro-markers. The sampling and preservation of rhizosphere microorganisms require a low temperature environment, which brings inconvenience to the application of micro-marker in the field. Also, “rhizosphere” is a relatively vague concept, and the composition and abundance of rhizosphere microorganisms of medicinal plants are affected by many factors and are in a dynamic changing process with high complexity, which make it difficult to select micro-markers. Rhizosphere microorganisms, as the sensitive index, can help prevent and control plant diseases, understand soil health status, evaluate the quality of medicinal plants, and ensure the safety and reliability of clinical drugs. It is of great significance to alleviate the serious threats of diseases, pests and continuous cropping, improve non-uniform quality and decrease excessive heavy metals in the production of medicinal plants. Micro-markers can also work in the quality control of medicinal plants from the source and provide guidance for the cultivation of quality medicinal plants, and its unique significance in pharmacophylogeny awaits further investigations.

CRedit authorship contribution statement

Kailin Yang: Writing – original draft. **Yaping Zheng:** Writing – review & editing. **Kangmeng Sun:** Writing – review & editing. **Xinyan Wu:** Visualization. **Zheng Zhang:** Supervision. **Chunlian He:** Conceptualization, Supervision, Writing – review & editing. **Peigen Xiao:** Conceptualization.

Declaration of Competing 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.

Acknowledgments

This research was funded by Innovation Team and Talents Cultivation Program of National Administration of Traditional Chinese Medicine (No. ZYYCXTD-D-202005), the CAMS Innovation Fund for Medical Sciences (CIFMS) (ID: 2021-I2M-1-071 and 2022-I2M-2-001).

References

Bi, W., Shen, J., Gao, Y., He, C. N., Peng, Y., & Xiao, P. G. (2016). Ku-jin tea (*Acer tataricum* subsp. *ginnala* or *A. tataricum* subsp. *theiferum*), an underestimated functional beverage rich in antioxidant phenolics. *Journal of Functional Foods*, 24, 75–84.

Borymski, S., Cycoń, M., Beckmann, M., Mur, L. A. J., & Piotrowska, S. Z. (2018). Plant species and heavy metals affect biodiversity of microbial communities associated with metal-tolerant plants in metalliferous soils. *Frontiers in Microbiology*, 9, 1425–1442.

Chen, C. Y., Zhong, C. F., Gao, X., Tan, C. Y., Bai, H., & Ning, K. (2022). *Glycyrrhiza uralensis* Fisch. root-associated microbiota: The multifaceted hubs associated with environmental factors, growth status and accumulation of secondary metabolites. *Environmental Microbiome*, 17(1), 23–36.

Chen, H. Y., Teng, Y. G., Lu, S. J., Wang, Y. Y., & Wang, J. S. (2015). Contamination features and health risk of soil heavy metals in China. *Science of the Total Environment*, 512(513), 143–153.

Chen, J., Zhou, L. T., Din, I. U., Arafat, Y., Li, Q., Wang, J. Y., ... Lin, W. X. (2021). Antagonistic activity of *Trichoderma* spp. against *Fusarium oxysporum* in rhizosphere of radish *Pseudostellariae* triggers the expression of host defense genes and improves its growth under long-term monoculture system. *Frontiers in Microbiology*, 12, 579920–579931.

Chen, Y., Du, J. F., Li, Y., Tang, H., Yin, Z. Y., Yang, L., & Ding, X. H. (2022). Evolutions and managements of soil microbial community structure drove by continuous cropping. *Frontiers in Microbiology*, 13, 839494–839504.

Coban, O., De Deyn, G. B., & van der Ploeg, M. (2022). Soil microbiota as game-changers in restoration of degraded lands. *Science*, 375(6584), abe0725–abe735.

Compant, S., Samad, A., Faist, H., & Sessitsch, A. (2019). A review on the plant microbiome: Ecology, functions, and emerging trends in microbial application. *Journal of Advanced Research*, 19, 29–37.

Das, S., Dash, H. R., Mangwani, N., Chakraborty, J., & Kumari, S. (2014). Understanding molecular identification and polyphasic taxonomic approaches for genetic relatedness and phylogenetic relationships of microorganisms. *Journal of Microbiological Methods*, 103, 80–100.

David, A. S., Quintana, A. P. F., Menges, E. S., Thapa, M. K. B., Afkhami, M. E., & Searcy, C. A. (2019). Soil microbiomes underlie population persistence of an endangered plant species. *American Naturalist*, 194(4), 488–494.

de Oliveira, J. S. F., Xavier, L. P., Lins, A., Andrade, E. H. A., Maia, J. G. S., de Mello, A. H., ... da Silva, J. K. R. (2019). Effects of inoculation by arbuscular mycorrhizal fungi on the composition of the essential oil, plant growth, and lipoxygenase activity of *Piper aduncum* L. *AMB Express*, 9(1), 29–40.

Dong, Z. Y., Rao, M. P. N., Liao, T. J., Li, L., Liu, Y. H., Xiao, M., ... Li, W. J. (2021). Diversity and function of rhizosphere microorganisms between wild and cultivated medicinal plant *Glycyrrhiza uralensis* Fisch under different soil conditions. *Archives of Microbiology*, 203(6), 3657–3665.

Duarte, F. R., Černáková, L., Kadam, S., Kaushik, K. S., Salehi, B., Bevilacqua, A., ... Rodrigues, C. F. (2019). Advances in chemical and biological methods to identify microorganisms—from past to present. *Microorganisms*, 7(5), 130–161.

Fan, L. X., Chen, L., Cui, W. Y., Dong, Y. J., Yuan, X. X., Wang, L., ... Zhao, S. C. (2020). Analysis of heavy metal content in edible honeysuckle (*Lonicera japonica* Thunb.) from China and health risk assessment. *Journal of Environmental Health*, 55(10), 921–928.

Fei, Y. Q., Xiao, L., Wang, B., Zhu, H. L., & Nie, J. (2021). Residue analysis and risk assessment of heavy metals and harmful elements in 37 plant/medicinal materials. *Chinese Journal of Pharmaceutical Analysis*, 41(6), 1000–1008.

Fu, H. H., Yuan, J., Liu, R. P., & Wang, X. Y. (2023). Effects of cadmium on the synthesis of active ingredients in *Salvia miltiorrhiza*. *Open Life Sciences*, 18(1), 20220603–20220618.

Gu, S., Wei, Z., Shao, Z., Friman, V. P., Cao, K., Yang, T., ... Jousset, A. (2020). Competition for iron drives phytopathogen control by natural rhizosphere microbiomes. *Nature Microbiology*, 5(8), 1002–1010.

Gu, Y., Banerjee, S., Dini, A. F., Xu, Y., Shen, Q., Jousset, A., & Wei, Z. (2022). Small changes in rhizosphere microbiome composition predict disease outcomes earlier than pathogen density variations. *The ISME Journal*, 16(10), 2448–2456.

Guo, F. X., Liu, Y., Tang, L., Chen, C. C., & Pei, D. N. (2017). Research status and prospect on rhizosphere microbiome of medicinal plants. *Journal of Agricultural Science and Technology*, 19(5), 12–21.

Guo, G. Y., Li, M. J., Wang, P. F., Wang, F. Q., Li, J., Zheng, H. Y., ... Zhang, Z. Y. (2013). Abnormal change of calcium signal system on consecutive monoculture problem of *Rehmannia glutinosa*. *China Journal of Chinese Materia Medica*, 38(10), 1471–1478.

Gupta, R., Tiwari, S., Saikia, S. K., Shukla, V., Singh, R., Singh, S. P., ... Pandey, R. (2015). Exploitation of microbes for enhancing bacoside content and reduction of *Meloidogyne incognita* infestation in *Bacopa monnieri* L. *Protoplasma*, 252(1), 53–61.

Han, Z. C., Liang, Y. J., & Sai, C. M. (2024). Research progress on influencing factors of quality formation of *Scutellariae radix*. *Chinese Traditional and Herbal Drugs*, 55(1), 320–331.

Hermans, S. M., Buckley, H. L., Case, B. S., Curran, C. F., & Lear, G. J. M. (2020). Using soil bacterial communities to predict physico-chemical variables and soil quality. *Microbiome*, 8(1), 79–91.

Hesse, E., O'Brien, S., Tromas, N., Bayer, F., Luján, A. M., van Veen, E. M., ... Buckley, A. (2018). Ecological selection of siderophore-producing microbial taxa in response to heavy metal contamination. *Ecology Letters*, 21(1), 117–127.

Hu, Z., Zhao, C., Li, Q., Feng, Y., Zhang, X., Lu, Y., ... Ji, W. (2023). Heavy metals can affect plant morphology and limit plant growth and photosynthesis processes. *Agronomy*, 13(10), 2601–2615.

Huang, F. F., Li, Q., & Huang, J. A. (2020). Research progress of tea rhizosphere microorganisms. *Journal of Tea Science*, 40(6), 715–723.

Huang, W., Long, C., & Lam, E. (2018). Roles of plant-associated microbiota in traditional herbal medicine. *Trends in Plant Science*, 23(7), 559–562.

Jaramillo, J. P., Mendes, R., & Raaijmakers, J. M. (2015). Impact of plant domestication on rhizosphere microbiome assembly and functions. *Plant Molecular Biology*, 90(6), 635–644.

Ji, L., Nasir, F., Tian, L., Chang, J., Sun, Y., Zhang, J., ... Tian, C. (2021). Outbreaks of root rot disease in different aged American Ginseng plants are associated with field microbial dynamics. *Frontiers in Microbiology*, 12, 676880–676892.

Jiang, J. L., Yu, M., Hou, R. P., Li, L., Ren, X. M., Jiao, C. J., ... Xu, H. (2019). Changes in the soil microbial community are associated with the occurrence of *Panax quinquefolius* L. root rot diseases. *Plant and Soil*, 438(1–2), 143–156.

- Kale, R. A., Lokhande, V. H., & Ade, A. B. (2015). Investigation of chromium phytoremediation and tolerance capacity of a weed, *Portulaca oleracea* L. in a hydroponic system. *Water Environment Journal*, 29(2), 236–242.
- Karri, V., Ramos, D., Martinez, J. B., Odena, A., Oliveira, E., Coort, S. L., ... Kumar, V. (2018). Differential protein expression of hippocampal cells associated with heavy metals (Pb, As, and MeHg) neurotoxicity: Deepening into the molecular mechanism of neurodegenerative diseases. *Journal of Proteomics*, 187, 106–125.
- Kui, L., Chen, B. Z., Chen, J., Sharifi, R., Dong, Y., Zhang, Z. J., & Miao, J. H. (2021). A comparative analysis on the structure and function of the *Panax notoginseng* rhizosphere microbiome. *Frontiers in Microbiology*, 12, 673512–673525.
- Lai, K. Y., Xiao, J. C., Wang, H. Y., Qiu, J. Z., Wan, X. F., Yan, B. B., ... Guo, L. P. (2023). Mechanism and application prospects of microbial fertilizers in regulating quality formation of medicinal plants. *China Journal of Chinese Materia Medica*.
- Ldz, A., Xiang, L., Myw, A., Zjg, A., Zzz, A., Chg, A., ... Hlz, A. (2021). Ammonium has stronger Cd detoxification ability than nitrate by reducing Cd influx and increasing Cd fixation in *Solanum nigrum* L. *Journal of Hazardous Materials*, 425, 127947.
- Lei, H. Y., Liu, A., Zhao, Q. S., Hou, Q. W., & Wang, Z. J. (2020). Diversity patterns of soil microbial communities in the *Sophora flavescens* rhizosphere in response to continuous monocropping. *BMC Microbiology*, 20(1), 272–283.
- Li, B. Z. (2019). Effects of continuous cropping and rotation on rhizosphere microorganism diversity and quality of *Astragalus membranaceus* (fisch) Bge. var. *mongholicus* (Bge.) Hsiao. *Inner Mongolia: Inner Mongolia University*. Thesis of Master Degree.
- Li, J. J., Yang, L., Miao, C. P., Teng, Y. J., Fu, Z. H., Cheng, C. L., ... Zhao, L. X. (2021). Impact of rhizosphere microorganisms on arsenic (As) transformation and accumulation in a traditional Chinese medicinal plant. *Environmental Science and Pollution Research*, 28(43), 60923–60934.
- Li, J. R., Chen, X. Z., Li, S. M., Zuo, Z. M., Zhan, R. T., & He, R. (2020). Variations of rhizospheric soil microbial communities in response to continuous *Andropogon paniculata* cropping practices. *Botanical Studies*, 61(1), 18–30.
- Li, P., Shen, J., Bi, W., He, C. N., & Xiao, P. G. (2018). Metabolomics analysis and quantitative determination of five components in *Malus* leaves. *Chinese Traditional Herbal Drugs*, 49(22), 5378–5387.
- Li, X., Wang, S., Fan, Y., Zhou, Z., Xu, S., Zhou, P., ... Wang, R. (2021). Peanut rotation and flooding induce rhizobacteriome variation with opposing influences on the growth and medicinal yield of *Corydalis yanhusuo*. *Frontiers in Plant Science*, 12, 779302–779314.
- Li, Y., Liu, Y., Zhang, H., Yang, Y., Wei, G., & Li, Z. (2021). The composition of root-associated bacteria and fungi of *Astragalus mongholicus* and their relationship with the bioactive ingredients. *Frontiers in Microbiology*, 12, 642730–642744.
- Li, Z., Bai, X., Jiao, S., Li, Y., Li, P., Yang, Y., ... Wei, G. (2021). A simplified synthetic community rescues *Astragalus mongholicus* from root rot disease by activating plant-induced systemic resistance. *Microbiome*, 9(1), 217–236.
- Ling, Y., Li, W., Tong, T., Li, Z., Li, Q., Bai, Z., ... Wang, Y. (2020). Assessing the microbial communities in four different daqus by using PCR-DGGE, PLFA, and biolig analyses. *Polish Journal of Microbiology*, 69(1), 1–11.
- Liu, C. X., Chen, S. L., Xiao, X. H., Zhang, T. J., & Liao, M. L. (2016). A new concept on quality marker of Chinese materia medica: Quality control for Chinese medicinal products. *Chinese Traditional Herbal Drugs*, 47(9), 1443–1457.
- Liu, J., Zhang, H., Zhang, Y., & Chai, T. (2013). Silicon attenuates cadmium toxicity in *Solanum nigrum* L. by reducing cadmium uptake and oxidative stress. *Plant Physiology and Biochemistry*, 68, 1–7.
- Liu, S. Y., Wang, Q. Q., Lei, Y. H., Wang, S. S., Chen, K. L., Li, Y., ... Sun, Y. F. (2022). Elucidating the interaction of rhizosphere bacteria and environmental factors in influencing active ingredient content of *Lycium barbarum* fruit in China. *Journal of Applied Microbiology*, 132(5), 3783–3796.
- Liu, X. D., Zhang, Y., Wu, M. H., Ma, Z. G., Huang, Z. H., Tian, F., ... Cao, H. (2020). The scientific elucidation of daodi medicinal materials. *Chinese Medicine*, 15, 86–96.
- Liu, Y., Li, D., Gao, H., Li, Y. H., Chen, W. M., Jiao, S., & Wei, G. H. (2022). Regulation of soil micro-foodies to root secondary metabolites in cultivated and wild licorice plants. *Science of the Total Environment*, 828, 154302–154314.
- Luo, J. P., Gu, S. H., Guo, X. Y., Liu, Y. K., Tao, Q., Zhao, H. P., ... Li, T. Q. (2022). Core microbiota in the rhizosphere of heavy metal accumulators and its contribution to plant performance. *Environmental Science & Technology*, 56(18), 12975–12987.
- Luo, L. F., Guo, C. W., Wang, L. T., Zhang, J. X., Deng, L. M., Luo, K. F., ... Yang, M. (2019). Negative plant-soil feedback driven by re-assembly of the rhizosphere microbiome with the growth of *Panax notoginseng*. *Frontiers in Microbiology*, 10, 1597–1609.
- Ma, R., Yang, P., Jing, C., Fu, B., Teng, X., Zhao, D., & Sun, L. (2023). Comparison of the metabolomic and proteomic profiles associated with triterpene and phytosterol accumulation between wild and cultivated ginseng. *Plant Physiology and Biochemistry*, 195, 288–299.
- Magnin, J. P., Gondrexon, N., & Willison, J. C. (2014). Zinc biosorption by the purple non-sulfur bacterium *rhodospirillum rubrum*. *Canadian Journal of Microbiology*, 60(12), 829–837.
- Mendes, R., Garbeva, P., & Raaijmakers, J. M. (2013). The rhizosphere microbiome: Significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiology Reviews*, 37(5), 634–663.
- Middleton, H., Yergeau, T., Monard, C., Combiere, J. P., & Amrani, A. E. (2020). Rhizospheric plant-microbe interactions: miRNAs as a key mediator. *Trends in Plant Science*, 26(2), 132–141.
- Misra, P., Maji, D., Awasthi, A., Pandey, S. S., Yadav, A., Pandey, A., ... Kalra, A. (2019). Vulnerability of soil microbiome to monocropping of medicinal and aromatic plants and its restoration through intercropping and organic amendments. *Frontiers in Microbiology*, 10, 2604–2618.
- Mohamed, H., & Kamal, A. E. K. (2011). Management of the root-knot nematode *Meloidogyne incognita* on tomato with combinations of different biocontrol organisms. *Crop Protection*, 30(3), 285–292.
- Ng, C. W. W., So, P. S., Wong, J. T. F., & Lau, S. Y. (2023). Intercropping of *Pinellia ternata* (herbal plant) with *Sedum alfredii* (Cd-hyperaccumulator) to reduce soil cadmium (Cd) absorption and improve yield. *Environmental Pollution*, 318, 120930.
- Norris, C. E., Bean, G. M., Cappellazzi, S. B., Cope, M., Greub, K. L. H., Liptzin, D., ... Honeycutt, C. W. (2020). Introducing the North American project to evaluate soil health measurements. *Agronomy Journal*, 112(4), 3195–3215.
- Paithankar, J. G., Saini, S., Dwivedi, S., Sharma, A., & Chowdhuri, D. K. (2021). Heavy metal associated health hazards: An interplay of oxidative stress and signal transduction. *Chemosphere*, 262, 128350.
- Prakash, J., & Arora, N. K. (2019). Development of *Bacillus safensis*-based liquid bioformulation to augment growth, stevioside content, and nutrient uptake in *Stevia rebaudiana*. *World Journal of Microbiology and Biotechnology*, 36(1), 8–20.
- Qian, F. H., Huang, X. J., Su, X. M., & Bao, Y. Y. (2022). Responses of microbial communities and metabolic profiles to the rhizosphere of *Tamarix ramosissima* in soils contaminated by multiple heavy metals. *Journal of Hazardous Materials*, 438, 129469.
- Rajkumar, M., Ae, N., Prasad, M. N. V., & Freitas, H. (2010). Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. *Trends in Biotechnology*, 28(3), 142–149.
- Rehman, M. Z. U., Rizwan, M., Ali, S., Ok, Y. S., Ishaque, W., Saifullah, N., ... Waqar, M. (2017). Remediation of heavy metal contaminated soils by using *Solanum nigrum*: A review. *Ecotoxicology and Environmental Safety*, 143, 236–248.
- Richard, J., Manuela, P., Antonella, S., Anna, K., & Stanislav, K. (2017). The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions. *Frontiers in Plant Science*, 8, 1617–1635.
- Shan, S. P., Guo, Z. H., Lei, P., Wang, Y. S., Li, Y. L., Cheng, W., ... Yi, H. W. (2019). Simultaneous mitigation of tissue cadmium and lead accumulation in rice via sulfate-reducing bacterium. *Ecotoxicology and Environmental Safety*, 169, 292–300.
- Shang, Q. H., Yang, G., Wang, Y., Wu, X. K., Zhao, X., Hao, H. T., ... Wang, R. Y. (2016). Illumina-based analysis of the rhizosphere microbial communities associated with healthy and wilted Lanzhou lily (*Lilium davidii* var. *unicolor*) plants grown in the field. *World Journal of Microbiology and Biotechnology*, 32(6), 95–109.
- Shao, Q. Y., Dong, C. B., Han, Y. F., & Liang, Z. Q. (2021). Research progress in the rhizosphere microbiome of plants. *Journal of Plant Nutrition and Fertilizer*, 27(1), 144–152.
- Shen, Z. J., Xu, D. C., Chen, Y. S., & Zhang, Z. (2017). Heavy metals translocation and accumulation from the rhizosphere soils to the edible parts of the medicinal plant *Paeonia ostii* grown on a metal mining area, China. *Ecotoxicology and Environmental Safety*, 143, 19–27.
- Sheng, M. M., Jia, H. K., Zhang, G. Y., Zeng, L. N., Zhang, T. T., Long, Y. H., ... Liu, H. M. (2020). Siderophore production by rhizosphere biological control bacteria *Brevibacillus brevis* GZDF3 of *Pinellia ternata* and its antifungal effects on *Candida albicans*. *Journal of Microbiology and Biotechnology*, 30(5), 689–699.
- Siliakus, M. F., van der Oost, J., & Kengen, S. W. M. (2017). Adaptations of archaeal and bacterial membranes to variations in temperature, pH and pressure. *Extremophiles*, 21(4), 651–670.
- Siqueira, J. F., Sakamoto, M., & Rosado, A. S. (2023). Microbial community profiling using terminal restriction fragment length polymorphism (T-RFLP) and denaturing gradient gel electrophoresis (DGGE). *Methods in Molecular Biology*, 2588, 91–104.
- Song, X., Pan, Y., Li, L., Wu, X., & Wang, Y. (2018). Composition and diversity of rhizosphere fungal community in *Coptis chinensis* Franch. Continuous cropping fields. *PLoS One*, 13(3), e0193811–e194024.
- Sun, L., Zhang, X., Ouyang, W., Yang, E., Cao, Y., & Sun, R. (2022). Lowered Cd toxicity, uptake and expression of metal transporter genes in maize plant by ACC deaminase-producing bacteria *Achromobacter* sp. *Journal of Hazardous Materials*, 423, 127036–127047.
- Sun, X., Zhang, X., Zhang, G., Miao, Y., Zeng, T., Zhang, M., ... Huang, L. (2022). Environmental response to root secondary metabolite accumulation in *Paeonia lactiflora*: Insights from rhizosphere metabolism and root-associated microbial communities. *Microbiology Spectrum*, 10(6), e0280022–e280041.
- Sun, Y., Liu, H., Peng, J., Shen, M., Hu, Y., Yu, D., ... Dong, Y. (2023). Rhizosphere microbes influence wogonoside accumulation in perennial *Scutellaria baicalensis*. *Pedosphere*, 33.
- Tanwir, K., Abbas, S., Hussaan, M., Basit, F., & Alomrani, S. O. (2023). Bio-inoculation with *Serratia* CP-13 enhances Cd detoxification via modulation of phytohormone, gas exchange attributes and nutrient acquisition in maize cultivars cultivated in Cd-stressed soil. *Plant Stress*, 10, 100290–100304.
- Tian, L., Shi, S. H., Ji, L., Nasir, F., Ma, L. N., & Tian, C. J. (2018). Effect of the biocontrol bacterium *Bacillus amyloliquefaciens* on the rhizosphere in ginseng plantings. *International Microbiology*, 21(3), 153–162.
- Tong, A. Z., Liu, W., Liu, Q., Xia, G. Q., & Zhu, J. Y. (2021). Diversity and composition of the *Panax ginseng* rhizosphere microbiome in various cultivation modes and ages. *BMC Microbiology*, 21(1), 18–30.

- Tu, J., Zhao, X., Yang, Y., Yi, Y., Wang, H., Wei, B., & Zeng, L. (2023). Two *Bacillus* spp. strains improve the structure and diversity of the rhizosphere soil microbial community of *Lilium brownii* var. *viridulum*. *Microorganisms*, 11(5), 1229–1244.
- Vaneecoutte, M., Riegel, P., Briel, D. D., Monteil, H., Verschraegen, G., Rouck, A. D., & Claeys, G. (1995). Evaluation of the applicability of amplified rDNA-restriction analysis (ARDRA) to identification of species of the genus *Corynebacterium*. *Research in Microbiology*, 146(8), 633–641.
- Waadt, R., Seller, C. A., Hsu, P. K., Takahashi, Y., Munemasa, S., & Schroeder, J. I. (2022). Plant hormone regulation of abiotic stress responses. *Nature Reviews Molecular Cell Biology*, 23(10), 680–694.
- Walters, W. A., Jin, Z., Youngblut, N., Wallace, J. G., Sutter, J., Zhang, W., ... Ley, R. E. (2018). Large-scale replicated field study of maize rhizosphere identifies heritable microbes. *Proceedings of the National Academy of Sciences of the United States of America*, 115(28), 7368–7373.
- Wang, D., Sun, L., Yin, Z., Cui, S., Huang, W., & Xie, Z. (2022). Insights into genomic evolution and the potential genetic basis of *Klebsiella variicola* subsp. *variicola* ZH07 reveal its potential for plant growth promotion and autotoxin degradation. *Microbiology Spectrum*, 10(6), e0084622–e90037.
- Wang, F. Y., Zhang, X. M., Wei, M. T., Wang, Y., Liang, Z. S., & Xia, P. G. (2022). Appropriate crop rotation alleviates continuous cropping barriers by changing rhizosphere microorganisms in *Panax notoginseng*. *Rhizosphere*, 23, 100568.
- Wang, J., Chen, X., Chu, S., You, Y., Chi, Y., Wang, R., ... Zhou, P. (2022). Comparative cytology combined with transcriptomic and metabolomic analyses of *Solanum nigrum* L. in response to Cd toxicity. *Journal of Hazardous Materials*, 423, 127168–127182.
- Wang, Q., Zhang, W. J., He, L. Y., & Sheng, X. F. (2018). Increased biomass and quality and reduced heavy metal accumulation of edible tissues of vegetables in the presence of Cd-tolerant and immobilizing *Bacillus megaterium* H3. *Ecotoxicology and Environmental Safety*, 148, 269–274.
- Wang, T., Yang, K., Ma, Q., Jiang, X., Zhou, Y., Kong, D., ... Ruan, Z. (2022). Rhizosphere microbial community diversity and function analysis of cut chrysanthemum during continuous monocropping. *Frontiers in Microbiology*, 13, 801546–801561.
- Wang, X., Wang, Z., Jiang, P., He, Y., Mu, Y., Lv, X., & Zhuang, L. (2018). Bacterial diversity and community structure in the rhizosphere of four *Ferula* species. *Scientific Reports*, 8(1), 5345–5354.
- Wang, Z., Zhang, H., Liu, L., Li, S., Xie, J., Xue, X., & Jiang, Y. (2022). Screening of phosphate-solubilizing bacteria and their abilities of phosphorus solubilization and wheat growth promotion. *BMC Microbiology*, 22(1), 296–310.
- Wei, C. B., Gu, W., Tian, R., Xu, F., Han, Y., Ji, Y. Y., ... Wu, W. Q. (2022). Comparative analysis of the structure and function of rhizosphere microbiome of the Chinese medicinal herb *Alisma* in different regions. *Archives of Microbiology*, 204(7), 1–13.
- Wu, F., Shi, Q., Wang, X. J., Sun, Z. T., Wang, W., Li, X., ... Bai, J. G. (2019). *Streptomyces canus* GLY-P2 degrades ferulic and *p*-hydroxybenzoic acids in soil and affects cucumber antioxidant enzyme activity and rhizosphere bacterial community. *Plant and Soil*, 436(1–2), 71–89.
- Wu, W., Wang, J., Wang, Z., Guo, L., Zhu, S., Zhu, Y., ... He, X. (2022). Rhizosphere bacteria from *Panax notoginseng* against *Meloidogyne hapla* by rapid colonization and mediated resistance. *Frontiers in Microbiology*, 13, 877082–877091.
- Wu, Z. X., Hao, Z. P., Zeng, Y., Guo, L. P., Huang, L. Q., & Chen, B. D. (2015). Molecular characterization of microbial communities in the rhizosphere soils and roots of diseased and healthy *Panax notoginseng*. *Antonie van Leeuwenhoek*, 108(5), 1059–1074.
- Xiao, P. G., Li, M. H., Hao, D. C., He, C. N., & Xu, L. J. (2021). Theoretical innovation and application practice of pharmacophylogeny. *Modern Chinese Medicine*, 23(9), 1499–1505+1494.
- Xiao, X., Chen, W. M., Zong, L., Yang, J., Jiao, S., Lin, Y. B., ... Wei, G. H. (2017). Two cultivated legume plants reveal the enrichment process of the microbiome in the rhizocompartments. *Molecular Ecology*, 26(6), 1641–1651.
- Xiao, X. H., Wang, J. B., & Yan, D. (2014). Studies and application of biological evaluation in the quality standardization of Chinese medicines. *Modernization of Traditional Chinese Medicine and Materia Medica—World Science and Technology*, 16(3), 514–518.
- Xiao, Y. H., Li, J., Liu, Z. X., Li, Y. J., Li, G., & Long, H. (2013). Advances in studies on rhizospheric microorganism of medicinal plants. *Chinese Traditional and Herbal Drugs*, 44(4), 497–504.
- Xu, H. X., Yu, F. Q., Zuo, Y. W., Dai, Y. D., Deng, H. P., & Xie, J. P. (2022). Selected rhizosphere bacteria are associated with endangered species - *Scutellaria tsinyunensis* via comparative microbiome analysis. *Microbiological Research*, 258, 126917–126924.
- Xu, J., Shi, R., Cheng, Y., Xie, G., Zhu, Y., & Qin, M. (2022). Metabolomic association analysis reveals defense related secondary metabolic reprogramming in callus of *Scutellaria baicalensis* Georgi induced by endophytic *Pseudomonas* sp. 2B. *Industrial Crops and Products*, 187, 115409.
- Xu, J., Zhang, Y., Zhang, P., Trivedi, P., Riera, N., Wang, Y., ... Wang, N. (2018). The structure and function of the global citrus rhizosphere microbiome. *Nature Communications*, 9(1), 4894–4903.
- Xun, W. B., Shao, J. H., Shen, Q. R., & Zhang, R. F. (2021). Rhizosphere microbiome: Functional compensatory assembly for plant fitness. *Computational Structural Biotechnology Journal*, 19(4), 5487–5497.
- Yan, Y., Chen, J., Yan, C. J., Yin, X. J., & Zhao, Y. (2008). The method of identifying the edaphon using molecular biology techniques. *Journal of Northeast Agricultural University*, 39(3), 129–133.
- Yang, W., Dai, H. P., Skuza, L., & Wei, S. H. (2020). The front-heavy and back-light nitrogen application mode to increase stem and leaf biomass significantly improved cadmium accumulation in *Solanum nigrum* L. *Journal of Hazardous Materials*, 393, 122482–122489.
- Yao, X., Steven, X., Yang, Y. N., Zhu, Z., Zhu, Z., Tao, F. B., & Yuan, M. (2021). Stratification of population in based on exposure pattern of lead, cadmium, mercury, and arsenic and their association with cardiovascular, renal and respiratory outcomes. *Environment International*, 149, 106410–106419.
- Yin, N., Zhao, J. L., Liu, R., Li, Y., Ling, J., Yang, Y. H., ... Mao, Z. C. (2021). Biocontrol efficacy of *Bacillus cereus* strain Bc-cm103 against *Meloidogyne incognita*. *Plant Disease*, 105(8), 2061–2070.
- Yu, M., Jiang, J. L., Ren, X. M., Li, L., & Xu, H. (2018). Research on relationship between occurrence of root rot and changes of fungal communities in rhizosphere of *Panax quinquefolius*. *China Journal of Chinese Materia Medica*, 43(10), 2038–2047.
- Yu, X. Q., Zhang, Y. Z., Shen, M. C., Dong, S. Y., Zhang, F. J., Gao, Q., ... Bo, G. D. (2023). Soil conditioner affects tobacco rhizosphere soil microecology. *Microbial Ecology*, 86(1), 460–473.
- Zhai, T., Wang, Y., Liu, C., Liu, Z., Zhao, M., Chang, Y., & Zhang, R. (2019). *Trichoderma asperellum* ACCC30536 inoculation improves soil nutrition and leaf artemisinin production in *Artemisia annua*. *Acta Physiologiae Plantarum*, 41(4), 46–56.
- Zhang, A. C., Cao, H. B., Jiang, Y., Chen, X. F., Liu, J. W., Zhou, X., ... Li, J. (2021). Refining health risk assessment for determining arsenic and cadmium safety limits in an herbal medicine and its cultivation soils. *Journal of Cleaner Production*, 331(10), 129837.
- Zhang, J. X., Zhou, D. P., Yuan, X. Q., Xu, Y. H., Chen, C. B., & Zhao, L. (2022). Soil microbiome and metabolome analysis reveals beneficial effects of ginseng-celandine rotation on the rhizosphere soil of ginseng-used fields. *Rhizosphere*, 23, 100559–100567.
- Zhang, X. D., & He, W. (2011). Quantitative characteristics of soil microorganisms in *Scutellaria baicalensis* field during different planting years. *Shaanxi Journal of Agricultural Sciences*, 57(4), 3–4+8.
- Zhang, X. H., & Zhang, E. H. (2007). Variation of rhizosphere microflora of hops at different planting ages and its relationship with yield and quality. *Acta Prataculturae Sinica*, 16(5), 56–60.
- Zheng, Y., Liu, W., Huang, J. X., & Hou, Y. R. (2016). Rhizosphere microorganism evidence on geo-authentic features of traditional Chinese medicine from Moutan (*Paeonia suffruticosa*). *Acta Pharmaceutica Sinica*, 51(8), 1325–1333.
- Zhong, C., Chen, C., Gao, X., Tan, C., Bai, H., & Ning, K. (2022). Multi-omics profiling reveals comprehensive microbe-plant-metabolite regulation patterns for medicinal plant *Glycyrrhiza uralensis* Fisch. *Plant Biotechnology Journal*, 20(10), 1874–1887.
- Zhong, Y., Xun, W. B., Wang, X. H., Tian, S. W., Zhang, Y. C., Li, D. W., ... Shang, Y. (2022). Root-secreted bitter triterpene modulates the rhizosphere microbiota to improve plant fitness. *Nature Plants*, 8(8), 887–896.
- Zhou, C., Zhu, L., Ma, Z., & Wang, J. (2017). *Bacillus amyloliquefaciens* SAY09 increases cadmium resistance in plants by activation of auxin-mediated signaling pathways. *Genes (Basel)*, 8(7), 173–194.
- Zhou, T. T., Zhan, Y., Li, Q., Wang, E. P., Huang, X., & Chen, C. B. (2023). Research progress on the types and mechanism of allelochemicals in ginseng medicinal plant. *Special Wild Economic Animal and Plant Research*.
- Zhu, L., Yan, H., Liu, P., Zhang, Z. Y., Zhang, S., & Guo, S. (2021). Research progress on effects of rhizosphere microorganisms on quality formation of medicinal plants and their interaction mechanisms. *Chinese Traditional and Herbal Drugs*, 52(13), 4064–4073.
- Zuo, J. J., Zu, M. T., Liu, L., Song, X. M., & Yuan, Y. D. (2021). Composition and diversity of bacterial communities in the rhizosphere of the Chinese medicinal herb *dendrobium*. *BMC Plant Biology*, 21(1), 127–139.