

Advances in the studies on symbiotic arbuscular mycorrhizal fungi of traditional Chinese medicinal plants

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Abstract: Arbuscular mycorrhizal (AM) fungi reside in the rhizosphere and form mutualistic associations with plant roots. They promote photosynthesis, improve stress resistance, and induce secondary metabolite biosynthesis in host medicinal plants. The AM fungi that are symbiotic with medicinal plants comprise a wide array of species and have abundant germplasm resources. Though research on the AM fungi in medicinal plants began relatively recently, it has nonetheless become an investigative hot spot. Several scholars have explored the diversity and the growth-promoting effects of mycorrhizal fungi in hundreds of medicinal plants. Current research on symbiotic AM fungi in medicinal plants has focused mainly on the effects of inoculating host plants with symbiotic mycorrhizal fungi. However, research on the symbiotic AM fungi in medicinal plants continues to expand, and further study is required to determine the mechanisms by which AM fungi interact with host plants. This paper introduces the diversity of symbiotic AM fungi of medicinal plants and the effects of AM fungi on rhizosphere soil of medicinal plants, including soil structure, microbiota, enzyme activities, etc. This review focuses on the effects of AM fungi on medicinal plants, including antioxidant enzyme systems, drought resistance, nutrient absorption profiles of macro- and micronutrients, accumulation of secondary metabolites such as terpenes, phenolic compounds, and nitrogenous compounds, and prevention of diseases. This review is expected to provide a reference for the application of AM fungi in medicinal plant cultivation, biological control, resource conservation, and the sustainable development of the traditional Chinese medicine industry.

Introduction

Market demand for medicinal plants has increased over recent years. However, wild medicinal plant resources have become scarce or even endangered. Primitive, incompatible artificial cultivation technology has degraded germplasms, lowered the quality of medicinal herbs, destabilized their medicinal properties, and limited the development of the traditional Chinese medicine (TCM) industry. Studies have shown that arbuscular mycorrhizal (AM) fungi use hyphae and other structures to expand the nutrient absorption range of plants, help medicinal plants acquire water from the soil and improve plant drought resistance and alleviate stress (Li and Chen, 2012; Xing *et al.*, 2019a). AM fungi can optimize soil structure and microbiota, such as soil fungi, bacteria, and actinomycetes (Ou *et al.*, 2016; Wei *et al.*, 2021). AM fungi play an important role in improving soil fertility (Li

and Zhao, 2005; Liu *et al.*, 2012; Ye *et al.*, 2013), increasing soil protease, urease, phosphatase, and invertase activities (Ou *et al.*, 2016; Jia *et al.*, 2020; Wei *et al.*, 2021), and promoting the absorption and transportation of macronutrient and micronutrient profiles such as C, N, P, Fe, Cu, and Zn in plants (Qi *et al.*, 2006; Shi *et al.*, 2016; Wang and Liu, 2017). AM fungi also regulate the plant antioxidant enzyme system, including superoxide dismutase, catalase, and peroxidase steady-states (Lanfranco *et al.*, 2005; Zhang *et al.*, 2016; Zhang *et al.*, 2019a). AM fungi can improve the yield and quality of active ingredients of medicinal plants, including terpenes, phenolic compounds, and nitrogenous compounds (Mandal *et al.*, 2015a; Xie *et al.*, 2020). In terms of diseases control, AM fungi can improve plant defense enzyme activities, regulate host defense gene expression, combat infectious and non-infectious diseases (Xiao *et al.*, 2011; Zhang *et al.*, 2013a), and improve plant disease resistance and enhance plant adaptability to adverse environments (Zhao and Cheng, 2001; Zhu *et al.*, 2011). AM fungi have shown great

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potential in promoting medicinal plant growth. Elucidating the relationship between AM fungi and medicinal plants is fundamental for improving the quality of the latter, maintaining biodiversity, and promoting the development of the TCM industry (Zeng et al., 2007). This review introduces the diversity of symbiotic AM fungi of medicinal plants and the effects of AM fungi on rhizosphere soil of medicinal plants, including soil structure, soil microbiota, enzyme activities, fertility, etc. This review also focuses on the effects of AM fungi on medicinal plants, including antioxidant enzyme system, drought resistance, nutrient absorption, transportation of macronutrient and micronutrient profiles, accumulation of secondary metabolites such as terpenes, phenolic compounds, and nitrogenous compounds, and the prevention and control of infectious diseases and non-infectious diseases of medicinal plants. The review provides comprehensive information about the application of AM fungi in medicinal plant cultivation, biological control, resource conservation, and sustainable development of the TCM industry.

Diversity of symbiotic AM fungi in medicinal plants

The AM fungi of the *Glomeromycota* comprise one class, four orders, 12 families, and 34 genera (Mi et al., 2020). Over 300 AM fungal species have been isolated worldwide (Wang and Liu, 2017). Global research on the diversity of symbiotic AM fungi associated with medicinal plants began relatively recently but has nonetheless become a priority. There are abundant AM fungi resources in the rhizospheres of medicinal plants (Table 1). Parmita et al. (2008) examined the rates of AM fungus infection in 40 medicinal plants, including *Andrographis paniculata* (Burm.f) Nees, *Rauwolfia serpentina* (L.) Benth.ex Kurz., and *Mentha arvensis* Linn. from Rajshahi University Campus in Bangladesh. Thirty-five medicinal plants were colonized by AM fungi at rates ranging from 13.3% to 100%. Zubek and Błaszczowski (2009) isolated 30 AM fungi from the rhizospheres of 31 medicinal plants, including *Artemisia dracuncululus* L., *Calendula officinalis* L., and *Hypericum perforatum* L. collected from the garden of Medicinal Plants of the Faculty of Pharmacy, Jagiellonian University, Collegium Medicum, Kraków, Poland. Piszczek et al. (2019) found that 35 of the 40 medicinal plant species collected from the Institute of Pharmacology of the Polish Academy of Sciences in Kraków were associated with 22 species of AM fungi. Later, Radhika and Rodrigues (2010) studied AM fungal diversity among 25 families and 36 species of cultivated or wild medicinal plants, including *Aloe vera* L., *Azadirachta indica* A Juss., and *Eclipta alba* (L.) Hassk., collected from various sites in North and South Goa, Western Ghats, Goa Region, India. They detected 30 species of medicinal plants that could form associations with AM fungi and isolated 42 species of AM fungi from five medicinal plant genera.

Chinese scholars have investigated rhizosphere AM fungal germplasm resources and diversity and their growth-promoting effects on hundreds of medicinal plants, including *Pinellia ternata* (Thunb.) Breit (Shi et al., 2017), *Polygonum multiflorum* Thunb. (Luo et al., 2013), *Broussonetia papyrifera* (L.) L'Hert (He et al., 2007), *Angelica dahurica* (Fisch. ex Hoffm.) Benth. et Hook. f. ex Franch. e (Zhao and He, 2011), *Atractylodes lancea*

(Thunb.) DC. (Zhang et al., 2011), *Camptotheca acuminata* Decne. (Zhao et al., 2006), *Artemisia annua* L. (Huang et al., 2011), *Pogostemon cablin* (Blanco) Benth. (Liu, 2020), *Rheum palmatum* L. (Yang et al., 2018), *Fritillaria taipaiensis* P. Y. Li (Zhang et al., 2020), *Salvia miltiorrhiza* Bunge. (Yang, 2012), and *Paris polyphylla* var. *yunnanensis* (Franch.) Hand.-Mzt. (Huang et al., 2020). In Xiamen, China, Jiang (2012) isolated 63 AM fungal species from four genera in the rhizospheres of seven medicinal plant species, including *Camptotheca acuminata* Decne., *Houttuynia cordata* Thunb., and *Mirabilis jalapa* Linn. In Quanzhou, China, 56 species of AM fungi belonging to five genera were collected from the rhizospheres of 28 medicinal plants, including *Cyclobalanopsis chungii* (F. P. Metcalf) Y. C. Hsu et H. W. Jen ex Q. F. Zh, *Phyllanthus emblica* L., and *Lamium barbatum* Sieb. et Zucc. (Jiang, 2012). In Zhangzhou, China, 66 species of AM fungi belonging to five genera were isolated from the rhizospheres of 20 medicinal plants, including *Lygodium japonicum* (Thunb.) Sw., *Alpinia officinarum* Hance. and *Ardisia crenata* Sims. (Jiang, 2012). Shi et al. (2017) identified 20 AM fungi belonging to three genera in the rhizospheres of *Pinellia ternata* (Thunb.) Breit., collected from six locations in Zhejiang and Guizhou, China. *Glomus* was the dominant AM fungal taxon. In Hunyuan County, Shanxi Province, China, Liu et al. (2019b) isolated and identified 12 species of AM fungi belonging to three genera from the rhizospheres of wild *Astragalus membranaceus* (Fisch.) Bge. var. *Mongholicus* (Bge.) Hsiao. Six species of AM fungi belonging to three genera were gathered from the rhizospheres of growing *Astragalus membranaceus* (Fisch.) Bge., cultivated in Shanxi University of Chinese Medicine, Shanxi Province, China (Liu et al., 2019b). In the Karst region of China, Zhang et al. (2013a) detected 42 species and two genera of AM fungi in the rhizospheres of *Rosa laevigata* Michx and *Glomus* was the dominant AM fungal taxon. In Guiyang, China, Luo et al. (2013) found 55 species of AM fungi belonging to four genera in the rhizospheres of *Polygonum multiflorum* (Thunb.) Harald. Cao et al. (2020) used high-throughput sequencing analysis and identified three classes, four orders, eight families, and nine genera of AM fungi in the rhizospheres of *Atractylodes lancea* (Thunb.) DC in Chongqing (China). Ran et al. (2021) used staining microscopy and high-throughput sequencing technology to determine the rhizosphere AM fungi of *Panax quinquefolius* L. cultivated in Shandong Province, China, which included three genera, three families, three orders, one class, and one phylum. Yang et al. (2022) used Illumina MiSeq technology to detect 10 species of three genera of AM fungi in the rhizosphere soil of *Ophiopogon japonicus* (L. f.) Ker-Gawl. in cultivated and wild habitats. Song et al. (2019) identified AM fungi belonging to 14 genera and eight families in the rhizosphere soil of *Sophora flavescens* in Shanxi Province, China, using Illumina MiSeq technology. The foregoing studies generally indicated that most of the AM fungi in symbiotic association with medicinal plants were of *Glomus* spp. AM fungal identification has progressed from simple morphological to advanced high-throughput sequencing methods, which rapidly and accurately clarify AM fungal diversity in medicinal plants.

TABLE 1

Arbuscular mycorrhizal (AM) fungi diversity in medicinal plants

| Host plant | AM fungi species | Reference |
|--|---|-----------------------------|
| <i>Pinellia ternata</i> (Thunb.) Breit | <i>Acaulospora scrobiculata</i> , <i>Acaulospora excavata</i> , <i>Acaulospora laevis</i> , <i>Claroideoglomus claroideum</i> , <i>Diversispora eburnea</i> , <i>Funneliformis constrictus</i> , <i>F. mosseae</i> , <i>F. geosporus</i> , <i>Glomus hyderabadensis</i> , <i>Glomus melanosporum</i> , <i>Glomus sinuosum</i> , <i>Glomus clavisporea</i> , <i>Glomus multicaule</i> , <i>Glomus versiforme</i> , <i>Glomus intrardices</i> , <i>Rhizophagus clarus</i> , <i>Rhizophagus fasciculatus</i> , <i>Septoglomus deserticola</i> , <i>Scutellospora castania</i> | Shi <i>et al.</i> , 2017 |
| <i>Rosa laevigata</i> Michx | <i>Acaulospora sporocarpia</i> , <i>Acaulospora mellea</i> , <i>Acaulospora bireticulata</i> , <i>Acaulospora delicata</i> , <i>Acaulospora koskei</i> , <i>Acaulospora capcicula</i> , <i>Acaulospora morrowiae</i> , <i>Acaulospora rehmii</i> , <i>Acaulospora polonica</i> , <i>Acaulospora foveata</i> , <i>Acaulospora elegans</i> , <i>Acaulospora dilatata</i> , <i>Archaeospora undulata</i> , <i>Ambispora nicolsonii</i> , <i>C. etunicatum</i> , <i>C. claroideum</i> , <i>C. luteum</i> , <i>Diversispora gibbosa</i> , <i>F. constrictus</i> , <i>F. caledonius</i> , <i>F. badius</i> , <i>F. geosporus</i> , <i>Glomus liquidambaris</i> , <i>Glomus reticulatum</i> , <i>Glomus clavisporeum</i> , <i>Glomus glomerulatum</i> , <i>Glomus ambisporum</i> , <i>Glomus taiwanense</i> , <i>Glomus rubifome</i> , <i>Glomus tenebrosum</i> , <i>Glomus botryoides</i> , <i>Glomus magnicaule</i> , <i>Glomus multiforum</i> , <i>Glomus melanosporum</i> , <i>Paraglomus albidum</i> , <i>Rhizophagus clarus</i> , <i>Rhizophagus fasciculatus</i> , <i>Rhizophagus intraradices</i> , <i>Septoglomus deserticola</i> | Zhang <i>et al.</i> , 2013a |
| <i>Salvia miltiorrhiza</i> Bunge | <i>Acaulospora spinosa</i> , <i>Acaulospora dilatata</i> , <i>Acaulospora bireticulata</i> , <i>Acaulospora laevis</i> , <i>Acaulospora foveata</i> , <i>Acaulospora excavata</i> , <i>Acaulospora rugosa</i> , <i>Acaulospora tuberculata</i> , <i>Ambispora leptoticha</i> , <i>Ambispora gerdemannii</i> , <i>Ambispora appendicula</i> , <i>Ambispora nicolsonii</i> , <i>C. claroideum</i> , <i>F. geosporus</i> , <i>F. constrictus</i> , <i>F. verruculosus</i> , <i>Glomus ambisporum</i> , <i>Glomus reticulatum</i> , <i>Glomus formosanum</i> , <i>Glomus albidum</i> , <i>Glomus tenebrosum</i> , <i>Glomus monosporum</i> , <i>Glomus versiforme</i> , <i>Glomus dolichosporum</i> , <i>Rhizophagus manihotis</i> , <i>R. clarus</i> , <i>Pacispora chimonobambusae</i> | Liu <i>et al.</i> , 2017 |
| <i>Morus alba</i> L. | <i>Acaulospora rehmii</i> , <i>Acaulospora bireticulata</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora laevis</i> , <i>Acaulospora mellea</i> , <i>Acaulospora rugosa</i> , <i>Acaulospora foveata</i> , <i>Acaulospora excavata</i> , <i>Ambispora appendicula</i> , <i>Ambispora jimgerdemannii</i> , <i>Claroideoglomus walker</i> , <i>Dentiscutata nigra</i> , <i>Funneliformis constrictus</i> , <i>Glomus multiforum</i> , <i>Glomus hyderabadensis</i> , <i>Glomus reticulatum</i> , <i>Glomus multicaule</i> , <i>Glomus delhiense</i> , <i>Glomus versiforme</i> , <i>Glomus melanosporum</i> , <i>Glomus glomerulatum</i> , <i>Glomus coremioides</i> , <i>Rhizophagus intraradices</i> , <i>Rhizophagus aggregatus</i> , <i>Scutellospora cerradensis</i> , <i>Septoglomus deserticola</i> | Zheng, 2021 |
| <i>Dendranthema morifolium</i> | <i>Acaulospora bireticulata</i> , <i>Acaulospora excavata</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora foveata</i> , <i>C. claroideum</i> , <i>C. etunicatum</i> , <i>Dentiscutata reticulata</i> , <i>Diversispora spurca</i> , <i>F. mosseae</i> , <i>F. geosporus</i> , <i>Glomus versiforme</i> , <i>Glomus melanosporum</i> , <i>Glomus taiwanense</i> , <i>Glomus reticulatum</i> , <i>Glomus constrictumtrappe</i> , <i>Glomus multicaule</i> , <i>Oehlia diaphana</i> , <i>Rhizophagus clarus</i> , <i>Rhizophagus aggregatus</i> , <i>Rhizophagus microaggregatum</i> , <i>Septoglomus deserticola</i> , <i>Septoglomus viscosum</i> , <i>Sieverdingia tortuosa</i> | Wang, 2013 |
| Huangshan Magnolia (<i>Magnolia cylindrica</i> Wils.) | <i>Acaulospora denticulata</i> , <i>Acaulospora laevis</i> , <i>Acaulospora mellea</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora spinosa</i> , <i>Acaulospora tuberculata</i> , <i>C. claroideum</i> , <i>F. constrictus</i> , <i>F. verruculosus</i> , <i>F. geosporus</i> , <i>Glomus monosporum</i> , <i>Gigaspora gigantea</i> , <i>Rhizoglomus microaggregatum</i> , <i>Rhizophagus clarus</i> , <i>Scutellospora heterogana</i> , <i>Scutellospora verrucosa</i> | Yang <i>et al.</i> , 2011a |
| <i>Coptis deltoidea</i> C. Y. Cheng et Hsiao | <i>Acaulospora bireticulata</i> , <i>Acaulospora delicata</i> , <i>Acaulospora laevis</i> , <i>Acaulospora foveata</i> , <i>Acaulospora spinosa</i> , <i>Acaulospora polonica</i> , <i>Acaulospora rugosa</i> , <i>Acaulospora tuberculata</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora mellea</i> , <i>Acaulospora lacunosa</i> , <i>Acaulospora excavata</i> , <i>Acaulospora rehmii</i> , <i>Ambispora nicolsonii</i> , <i>Ambispora jimgerdemannii</i> , <i>Ambispora leptoticha</i> , <i>Ambispora gerdemannii</i> , <i>Archaeospora undulata</i> , <i>Archaeospora myriocarpa</i> , <i>C. etunicatum</i> , <i>Entrophospora infrequens</i> , <i>F. geosporus</i> , <i>Glomus ambisporum</i> , <i>Glomus dolichosporum</i> , <i>Glomus reticulatum</i> , <i>Gigaspora gigantea</i> , <i>Gigaspora albida</i> , <i>Paraglomus occultum</i> , <i>Septoglomus deserticola</i> | Huang <i>et al.</i> , 2012 |

(Continued)

Table 1 (continued)

| Host plant | AM fungi species | Reference |
|---|---|------------------|
| <i>Pteris vittata</i> L. | <i>C. claroideum</i> , <i>Dentiscutata nigra</i> , <i>Funneliformis constrictum</i> , <i>Glomus deserticola</i> , <i>Glomus flavisporum</i> , <i>Glomus glomerulatum</i> , <i>Glomus reticulatum</i> , <i>Glomus versiforme</i> , <i>Paraglomus albidum</i> , <i>Rhizophagus aggregatus</i> | Cai et al., 2020 |
| <i>Paeonia suffruticosa</i> Andr. | <i>Acaulospora tuberculata</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora foveata</i> , <i>Acaulospora spinosa</i> , <i>Acaulospora deniculata</i> , <i>Acaulospora rehmi</i> , <i>Acaulospora laevis</i> , <i>C. claroideum</i> , <i>C. etunicatum</i> , <i>Entrophospora infrequens</i> , <i>F. constrictus</i> , <i>F. mosseae</i> , <i>F. verruculosus</i> , <i>F. caledonius</i> , <i>F. geosporus</i> , <i>Glomus pansihelos</i> , <i>Glomus multicanle</i> , <i>Glomus manibotis</i> , <i>Glomus dipphanum</i> , <i>Glomus rubiformis</i> , <i>Glomus ambisporum</i> , <i>Glomus microcarpum</i> , <i>Gigaspora candida</i> , <i>Paraglomus albidum</i> , <i>Rhizophagus aggregatus</i> , <i>Rhizophagus intraradices</i> , <i>Rhizophagus microaggregatum</i> , <i>Rhizophagus clarus</i> , <i>Rhizophagus fasciculatus</i> , <i>Septoglomus deserticola</i> , <i>Scutellospora cerradensis</i> , <i>Scutellospora dipapillosa</i> , <i>Scutellospora gregaria</i> | Wei, 2010 |
| <i>Scutellaria baicalensis</i> Georgi | <i>Acaulospora bireticulata</i> , <i>Acaulospora excavata</i> , <i>Acaulospora foveata</i> , <i>Acaulospora laevis</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora spinosa</i> , <i>Acaulospora tuberculata</i> , <i>Acaulospora</i> sp., <i>C. claroideum</i> , <i>Dentiscutata reticulata</i> , <i>Entrophospora infrequens</i> , <i>F. mosseae</i> , <i>F. geosporus</i> , <i>Glomus constrictumtrappe</i> , <i>Glomus dolichosporum</i> , <i>Glomus glomerulatum</i> , <i>Glomus melanosporum</i> , <i>Glomus multicaule</i> , <i>Glomus multiformum</i> , <i>Glomus pustulatum</i> , <i>Glomus reticulatum</i> , <i>Glomus versiforme</i> , <i>Oehlia diaphana</i> , <i>Rhizophagus aggregatus</i> , <i>Rhizophagus clarus</i> , <i>Rhizophagus fasciculatus</i> , <i>Septoglomus deserticola</i> , <i>Septoglomus viscosum</i> , <i>Scutellospora calospora</i> , <i>Scutellospora erythropha</i> | Xu, 2012 |
| <i>Taxus chinensis</i> var. <i>mairei</i> | <i>Acaulospora tuberculata</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora rugosa</i> , <i>Acaulospora rehmi</i> , <i>Acaulospora laevis</i> , <i>Acaulospora cavernata</i> , <i>Acaulospora excavata</i> , <i>Acaulospora colossica</i> , <i>Acaulospora morrowiae</i> , <i>Acaulospora foveata</i> , <i>Acaulospora lacunosa</i> , <i>Acaulospora bireticulata</i> , <i>Ambispora jimgerdemannii</i> , <i>C. lamellosum</i> , <i>C. etunicatum</i> , <i>Dentiscutata erythropus</i> , <i>Dentiscutata nigra</i> , <i>Funneliformis constrictus</i> , <i>F. caledonius</i> , <i>F. coronatus</i> , <i>F. mosseae</i> , <i>F. geosporus</i> , <i>Halonatospora pansihalos</i> , <i>Glomus taiwanense</i> , <i>Glomus coremioides</i> , <i>Glomus multiformum</i> , <i>Glomus multicaule</i> , <i>Glomus melanosporum</i> , <i>Glomus convolutum</i> , <i>Glomus reticulatum</i> , <i>Glomus dolichosporum</i> , <i>Glomus</i> sp., <i>Rhizophagus clarus</i> , <i>Rhizophagus aggregatus</i> , <i>Scutellospora calospora</i> , <i>Septoglomus deserticola</i> | Fu, 2017 |
| <i>Angelica dahurica</i> (Fisch. ex Hoffm.) Benth. et Hook. f. ex Franch. e | <i>Acaulospora rehmi</i> , <i>Acaulospora lacunosa</i> , <i>C. claroideum</i> , <i>Diversispora spurca</i> , <i>Funneliformis mosseae</i> , <i>F. constrictus</i> , <i>F. verruculosus</i> , <i>F. geosporus</i> , <i>Glomus melanosporum</i> , <i>Glomus reticulatum</i> , <i>Scutellospora erythropus</i> | Cao, 2008 |

Effects of AM fungi on medicinal plant rhizospheres

AM fungi exist as spores in the soil, which grow into hyphae under appropriate conditions (Shang et al., 2011). In the absence of a host, AM fungi can sustain for 2–4 weeks by utilizing their own energy sources such as triacylglycerides (Requena et al., 2000, 2007) and retract the hyphal cytoplasm into the spores (Bécard et al., 2004; Tang, 2016). After invading the host plant, AM fungi mainly colonize root cortex cells, intercellular spaces, and the root surface. Structures like hyphae, vesicles, clumps, and spores can be observed after staining (Zhang et al., 2019b). Mycelia produce glomalin-related soil protein (GRSP), a class of glycoproteins that are insoluble in water, extremely stable under natural conditions, and contain metal ions (Xing et al., 2019a). GRSP is distributed on the mycelial surface; it falls onto the soil to become carbon source (Kong, 2013) and acts as a soil structure engineer. The super glue function of adhering soil particles is 3–10 times stronger than that of other soil carbohydrates (Xing et al., 2019b). On the one hand, GRSP blocks the extraradical hyphae of AM fungi in rhizosphere soil, which helps plants to utilize

hyphae to acquire soil moisture and prevent other microbial disturbances (Li and Zhao, 2005; Liu et al., 2012; Ye et al., 2013). On the other hand, GRSP enters the soil concomitantly with the degradation of hyphae, thus improving the soil microenvironment and structural stability (Li and Zhao, 2005; Liu et al., 2012; Ye et al., 2013).

GRSP is synthesized and secreted by symbiotic AM fungi in medicinal plants. It optimizes the structure, regulates the microbiota, improves the activity of enzymes, enhances fertility, and improves the matrices of soils. These effects are conducive to medicinal plant growth (Li and Zhao, 2005; Liu et al., 2012; Ye et al., 2013). Zhou et al. (2020) conducted a greenhouse pot experiment and showed that inoculation with various AM fungi increased the content of easily extractable GRSP (e-GRSP) and total GRSP (t-GRSP) and was an important source of organic carbon in the rhizosphere of *Paris polyphylla* var. *yunnanensis* (Franch.) Hand.-Mzt. Li et al. (2017) showed that e-GRSP and t-GRSP are significantly positively correlated with available soil phosphorus (P) and alkaline phosphatase activity. AM fungi adhere to soil particles by secreting GRSP and forming

microaggregates composed of polyvalent ion bridges and polysaccharides (Xing *et al.*, 2019b). Microaggregates combine with fungal hyphae and plant roots to form large, stable soil aggregates (Xing *et al.*, 2019b). Hyphal networks and aggregate structures provide gas exchange channels and space for root expansion, promote dry-wet circulation, and improve soil water infiltration, tillage, and fertility (Xing *et al.*, 2019b).

AM fungi increase soil invertase, urease, and catalase activities and help plants metabolize, transform, and utilize carbon, nitrogen (N), and P, and K phytotoxic peroxide decomposition. Jia *et al.* (2020) showed that single strains of *Glomus tenebrosum* and *Glomus formosanum* most effectively improved invertase and phosphatase activities and urease activity, respectively, in the rhizosphere of *Salvia miltiorrhiza* Bunge. Wei *et al.* (2021) found that inoculation with mixed AM fungi increased protease, phosphatase, invertase, and catalase activities in the rhizosphere of *Saussurea costus* (Falc.) Lipsch. Ou *et al.* (2016), Huang *et al.* (2020), and Zhou *et al.* (2020) found that inoculation with mixed AM fungi increased protease, urease, phosphatase, invertase, and catalase activities in the rhizosphere of *Paris polyphylla* var. *yunnanensis*. Therefore, AM fungi play a key role in promoting soil enzyme activities.

AM fungi can optimize soil microbial structure and support plant growth and development by regulating soil fertility and microbial abundance and diversity in the rhizosphere. The field experiment of Huang *et al.* (2020), the greenhouse pot experiment of Zhou *et al.* (2020), and the investigation of Ou *et al.* (2016) on 28 types of AM fungi infecting *Paris polyphylla* Smith var. *yunnanensis* (Franch.) Hand.-Mazz. showed that the symbionts increased the numbers of bacteria, actinomycetes, and other microorganisms in host plant rhizospheres, improved microbial diversity, and augmented soil fertility. Wei *et al.* (2021) found that the inoculation of an AM fungal mixture increased the numbers of actinomycetes and bacteria without changing the pH of the *Saussurea costus* (Falc.) Lipsch. rhizosphere. Actinomycete and bacterial growth rates surpassed those of the fungi, and their numbers were significantly positively correlated. Whereas AM fungi regulate the numbers of soil microorganisms, the latter use mycorrhizal hypha and spores as nutrient sources for their own growth and development. Hence, they facilitate nutrient utilization (Liu *et al.*, 2012; Ye *et al.*, 2013). Gu *et al.* (2020) showed that the available P and available potassium (K) contents in the rhizosphere of *Paris polyphylla* var. *yunnanensis* seedlings are increased by inoculation with nine AM fungi treatment groups, including treatment group S1 (*Gigaspora rosea*, *Gigaspora albida*, *Gigaspora margarita*, and *Gigaspora gigantea*), and treatment group S2 (*Scutellospora calospora*, *Cetranspora pellucida*, *Scutellospora coralloidea*, and *Dentiscutata erythropus*). Huang *et al.* (2020) showed that when the inoculation of exogenous AM fungi in treatment groups S1 (*Scutellospora coralloidea*, *Scutellospora calospora*, *Cetranspora pellucida*, and *Dentiscutata erythropus*) and S2 (*Scutellospora calospora*, *Cetranspora pellucida*, *Gigaspora margarita*, *Gigaspora gigantea*, *Septoglomus deserticola*, and *Claroideoglomus claroideum*) did not significantly alter soil

pH, both treatment groups significantly increased available N, P, and K in the rhizosphere of *Paris polyphylla* var. *yunnanensis* (Franch.) Hand.-Mzt., promoted soil N, P, and K accumulation, and enhanced the soil nutrient-holding capacity and matrix. In summary, AM fungi are of great importance to soil microbial quantity and soil fertility regulation.

Effects of AM fungi on drought resistance in medicinal plants
Under normal circumstances, the production and elimination of reactive oxygen species (ROS) in plants are in a dynamic balance to a certain extent. Drought stress results in the production and accumulation of ROS in plants (Wang *et al.*, 2019). Excessive accumulation of ROS and the depletion of antioxidant enzymes disrupt the steady-state of the plant antioxidant enzyme system (Wang *et al.*, 2019). Oxidative stress-mediated by elevated ROS levels will lead to harmful reactions such as peroxidation of plant biofilms and amino acid oxidation (Lushchak, 2011; Wang *et al.*, 2019). AM fungi play a key role in the plant antioxidant enzyme system. In *Poncirus trifoliata*, AM fungi regulate the expression of *PtFe-SOD*, *PtPOD*, *PtCAT1*, *PtADC*, *P5CS*, *PtPIPs*, *PtNIPs*, and plant antioxidant enzyme genes (Lanfranco *et al.*, 2005; Zhang *et al.*, 2019a), improve the activities of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and other enzymes in the plant antioxidant enzyme system (Lanfranco *et al.*, 2005; Zhang *et al.*, 2019a), increase the activity of proline dehydrogenase (ProDH), regulate transmembrane water transport between plant cells, and reduce drought-induced oxidative stress and subsequent damage in plants (Zhang *et al.*, 2016). AM fungi improve plant tolerance to alkaline soil by regulating NADPH oxidase and dehydrin genes, transmembrane transporter activity regulation pathway (GO: 0015077), and cell wall regulation pathway (GO: 0052386) (Ding, 2021). Zhang *et al.* (2019a) showed that AM fungi upregulate the expression of *PtFe-SOD*, *PtMn-SOD*, *PtPOD*, *PtCAT1*, *PtADC1*, and *PtADC2* genes of the host plant *Poncirus trifoliata* (L.) Raf. Sun (2014a) reported that AM fungi increase leaf water content and promote the removal of ROS in plants by upregulating the expression of *PtADC1* and *PtADC2* genes under drought conditions. In a pot experiment, Zhao and He (2011) inoculated AM fungi and observed significantly improved SOD and CAT activities in the leaves of *Angelica dahurica* (Fisch. ex Hoffm.) Benth. et Hook. f. ex Franch. e. Qi *et al.* (2006) found that inoculating AM fungi under drought conditions improved SOD and POD activities, reduced the malondialdehyde (MDA) content, and alleviated the adverse effects of drought stress in the leaves of *Diospyros lotus* L. Zhang *et al.* (2016) found that mycorrhizal fungi increased SOD and POD activities and mitigated physiological damage in *Cyclobalanopsis glauca* (Thunberg.) Oersted. seedlings under moderate drought stress. Zhang *et al.* (2020) found that inoculating AM fungi enhanced stress resistance in *Fritillaria taipaiensis* P. Y. Li by increasing POD, SOD, and CAT activities.

Drought resistance is also associated with the proline and soluble sugar levels in plant cells and tissues. Under drought conditions, plants synthesize abundant proline for osmotolerance and osmoregulation. Plants inoculated with

AM fungi maintain low proline levels to protect their enzyme function. Zou *et al.* (2013) found that AM fungi reduce the activity of $\Delta(1)$ -pyrroline-5-carboxylate synthetase (P5CS), increase the activity of proline dehydrogenase (ProDH), and decrease proline accumulation in the host plant trifoliolate orange. Zhao and He (2011) showed that the foliar proline and soluble sugar levels were lower and higher, respectively, in *Angelica dahurica* (Fisch. ex Hoffm.) Benth. et Hook. f. ex Franch. e inoculated with AM fungi than those in the leaves of uninoculated plants. Zhang *et al.* (2016) reported that mycorrhizal fungi promoted soluble sugar biosynthesis, lowered the osmotic potential, and improved water utilization in *Cyclobalanopsis glauca* (Thunberg.) Oersted. under drought stress. Also, the soluble sugar and soluble protein contents of *Fritillaria taipaiensis* P. Y. Li increased after inoculation with AM fungi compared with the control group (Zhang *et al.*, 2020).

AM fungal hyphae play an important role in water absorption by plants. AM fungal hyphae penetrate into the cortical cells of plant roots to form dendritic or cauliflower-like branched arbuscular structures, which act as convenient water transport channels for plants and also enhance the water holding capacity of the soil. Extra-root hyphae increase the length of plant roots and form a huge hyphal network in the soil, thereby enhancing the hydraulic conductivity of roots and promoting water absorption. AM fungi flexibly regulate water transport and redistribution and leaf transpiration rate in the host plant according to the water content and demand, thereby promoting a dry/wet cycle (Xing *et al.*, 2019a).

In addition to absorbing water via AM fungal hyphae, plants also rely on aquaporins (AQPs) to regulate transmembrane water transport between plant cells. Under drought stress, AM fungi regulate the gene expression of plasma membrane intrinsic proteins (PIPs) and vacuolar intrinsic proteins (TIPs) of host plant AQPs, mediate water absorption and efflux, regulate swelling pressure, osmotic pressure, and root water conductivity (Fotiadis *et al.*, 2001), promote water absorption and retention, improve water metabolism, and maintain water balance in plant cells (Li and Chen, 2012; Xing *et al.*, 2019a; Yu *et al.*, 2021). Porcel *et al.* (2006) found that inoculation with AM fungi reduces the influence of drought-induced stress on the transcription products of the aquaporin gene *GmPIP2*. Under drought stress, AM fungi downregulate the expression of seven *PtPIPs* and three *PtNIPs* in the roots of *Poncirus trifoliata* (L.) Raf. (Zou *et al.*, 2019). Under drought conditions, AM fungi upregulate *RpPIP2;1* and *RpTIP2;1* and downregulate *RpTIP1;1* and *RpPIP1;3* gene expression in *Robinia pseudoacacia* L. (He *et al.*, 2016). AM fungi upregulated the expression of *LbPIP2-1*, *LbTIP3-1*, and *Rir-AQP2* genes in host plants (Hu, 2017). In 200 mM NaCl, the expression of *RpPIP1;1*, *RpPIP2;1*, and *RpTIP1;1* aquaporin genes in plants harboring AM fungi was higher than in non-mycorrhizal plants (Chen *et al.*, 2017).

AM fungi use their hyphae (Zhang *et al.*, 2019b; Xing *et al.*, 2019a), channel proteins (Fotiadis *et al.*, 2001), and other structures to regulate the free and bound water levels (Yang and Liao, 2005; Li and Chen, 2012; Chen *et al.*, 2014) and proline and soluble sugar content, improve osmotic

pressure, root hydraulic conductivity, enzymatic clearance, and antioxidant systems, and water metabolism, attenuate drought stress, enhance water retention and photosynthesis, and strengthen drought resistance in host plants.

Effects of AM fungi on nutrient absorption in medicinal plants
Mycorrhizal fungi provide 90% of the nutrients to the host plants, which in return provide 30% of the photosynthetic carbon assimilation products to the mycorrhizal fungi, thus helping the fungi complete their life cycle while facilitating the redistribution of nutrients (Drigo *et al.*, 2010; Heijden *et al.*, 2015). During P deficiency, AM fungi help plants to obtain 50–75% of the P requirement (Mbodj *et al.*, 2018; Wang *et al.*, 2020). External hyphae absorb N and contribute 30% of the total nitrogen absorbed by the plants (Li and Zhang, 2008; Wang *et al.*, 2020). AM fungi promote the uptake of N, P, K, and other elements by upregulating the expression of *LbAMT1.1*, *LbNRT3.1*, *LbPT3*, and *LbKTI1* genes (Hu, 2017; Wang, 2020; Zhao, 2021).

AM fungi upregulate ammonium transport genes such as *LbAMT1.1* and nitrate transport genes such as *LbNRT2.4* and *LbNRT3.1* to promote N uptake in host plants (Zhao, 2021). Extracellular AM fungal hyphae and penetration of the high-affinity NH_4^+ transporter GintAMT1 in the intracellular hyphae of host plant root cortical cells were induced under low NH_4^+ and repressed under high NH_4^+ . By these mechanisms, N absorption was induced in host plants (Pérez-Tienda *et al.*, 2011; Vieira *et al.*, 2019; Shao *et al.*, 2021). The symbiosis between AM fungi and host plants stimulates the uptake of ammonium, nitrate, complex organic N, and other substances and their conversion into arginine in the extraradical hyphae. The arginine is then transported to the intraradical hyphae and converted to NH_4^+ , which regulates host plant N metabolism (Yang *et al.*, 2011b; Shirzad and Ahmad, 2020).

In the case of P deficiency, the expression of *GvPT*, *GiPT*, and *GmosPT* P-transporter genes in AM fungi was enhanced by extracellular hyphae, and P uptake by mycorrhizal fungi was promoted (Xu *et al.*, 2017; Xue *et al.*, 2019). Phosphate uptake mainly depends on phosphate transporter (Pht) (Wang *et al.*, 2020). AM fungi upregulate *Pht1* gene expression in the pre-branch site and promote P uptake when mycorrhizal fungi transport P to the arbuscular (Xue *et al.*, 2019; Wang *et al.*, 2020). Under short-term and long-term salt stress conditions, mycorrhizal symbiosis selectively regulates the expression of *ZjPHT1.1*, *ZjPHT1.4*, *ZjPHT1.11*, and *ZjPHT1.5* genes and affects plant P transport (Ma, 2020). AM fungi promote the gene expression of P transporters such as *LbPT3*, *LbPT4*, and *LbPT5*, thereby promoting P uptake by the host plants (Hu, 2017).

In the uptake of K, upregulation of *Solanum lycopersicum* High-affinity Potassium Transporter10 (*SHAK10*) gene expression by AM fungi promotes K^+ uptake by plants (Liu *et al.*, 2019a). AM fungi promote plant K uptake and transport by increasing the expression levels of *LbKTI1* and *LbSKOR* (Zhang *et al.*, 2017a) and promote uptake of K by inducing the expression of *LbKAT3*, *LbHAK*, *LbKTI1*, and *LbSKOR* genes related to mediating K uptake, release and transport (Wang, 2020). Estrada *et al.* (2013) showed that *ZmAKT2*, *ZmSOS1* and *ZmSKOR* were related to Na^+ net

absorption and long-distance transportation, xylem and phloem K^+ transportation and release. Also, AM fungi maintained Na^+ and K^+ homeostasis in host plants by up-regulating the above gene expression (Estrada *et al.*, 2013).

AM fungi expand the nutrient type and content absorption via their hyphae and other structures. They play active roles in improving chlorophyll content, net photosynthetic rate, and plant nutrient absorption. The pot experiment of Zhao and He (2011) disclosed that AM fungi promoted photosynthesis by increasing the chlorophyll a, total chlorophyll, and carotenoid content in *Angelica dahurica* (Fisch. ex Hoffm.) Benth. et Hook. f. ex Franch. e leaves. Huang *et al.* (2011) indicated that inoculation with AM fungi increased the chlorophyll content and transpiration and net photosynthetic rates and promoted N, P, and K uptake in *Artemisia annua* L. Yang (2012) suggested that AM fungi promoted foliar Fe, Mn, Mg, and Ca absorption and root Cu, Mn, and Fe uptake in *Salvia miltiorrhiza* Bunge. Huang *et al.* (2020) found that inoculation with exogenous AM fungi cause the accumulation of N, P and K in *Paris polyphylla* var. *yunnanensis* (Franch.) Hand.-Mzt. Sun *et al.* (2013) proposed that inoculation with AM fungi promote N, P, and K absorption and utilization, inhibit Na uptake, and fortify saline-alkaline resistance in *Glycyrrhiza uralensis* Fisch.

Effects of AM fungi on secondary metabolite accumulation in medicinal plants

The active principle content is a quality criterion of medicinal plants. Active substances in medicinal plants include secondary metabolites such as terpenes (sesquiterpene, etc.), phenolic compounds (flavonoids, etc.), and nitrogenous compounds (alkaloids, etc.) (Zhang *et al.*, 2015). AM fungi are of great significance in regulating gene expression in medicinal plants, which improves the yield of secondary metabolites and the overall medicinal quality (Mandal *et al.*, 2015b; Xie *et al.*, 2020).

Terpenes. In plant terpenoid biosynthesis, the substrate isopentenyl pyrophosphate and its isomer dimethylallyl diphosphate are obtained via the 2-C-methyl-D-erythritol-4-phosphate pathway (MEP pathway) in plastids and mevalonate pathway (MVA pathway) in the cytoplasm (Wang *et al.*, 2013; Xie *et al.*, 2020). In the MEP pathway, 1-deoxy-D-xylulose 5-phosphate synthase (DXS) and 1-deoxy-D-xylulose 5-phosphate reductoisomerase (DXR) are the two key enzymes (Xie *et al.*, 2020), while 3-Hydroxy-3-methylglutaryl coenzyme A reductase (HMGR) is the key enzyme in MVA pathway (Chappell *et al.*, 1995). Huang *et al.* (2011) and Chaudhary *et al.* (2008) showed that inoculation of AM fungi increased the artemisinin (sesquiterpene) and essential oil content in *Artemisia annua* L. to varying degrees depending on the plant organ or tissue. It was also reported that AM fungi increased artemisinin accumulation in the host plant by upregulating key genes involved in artemisinin biosynthesis, including *ADS*, *DBR2*, and *ALDH1* (Mandal *et al.*, 2015b; Xie *et al.*, 2020). Maes *et al.* (2011) and Mandal *et al.* (2015b) demonstrated that jasmonic acid (JA) promotes glandular synthesis and upregulates the expression of artemisinin synthesis genes, causing artemisinin accumulation. AM fungi upregulate the

expression of *DXS* and *DXR* genes in the leaves of *Stevia rebaudiana* Bertoni and promote stevioside accumulation (Mandal *et al.*, 2015a). Relative *MtDXS2* expression and carotenoid content increased in *Ocimum basilicum* L. var. inoculated with AM fungi (Copetta *et al.*, 2006). AM fungi upregulate *HMGR* gene expression and promote alpha- and beta-amyrin accumulation in the roots of *Zea mays* L. (Gerlach *et al.*, 2015). Inoculation of AM fungi increased the auxin (indole-3-acetic acid), content and promoted the accumulation of organic matter and patchouli alcohol in *Pogostemon cablin* (Blanco.) Benth. (Liu, 2020). In a greenhouse pot experiment, the content and structure ratios of dehydrocostus lactone, costunolide, and other lactones were increased to varying degrees in *Saussurea costus* (Falc.) Lipsch treated with exogenous AM fungi (Zhang *et al.*, 2017b). The saponin content in *Panax notoginseng* (Bruk) F. H. Chen markedly increased in response to 20–30% AM fungi infection intensity (Zeng *et al.*, 2015). Li *et al.* (2021) found that AM fungi inoculation increased the content of polyphyllin, the active substance of *Paris polyphylla* var. *yunnanensis*, and this was related to the expression of *PpSE* and *PpHMGR* genes. *PkSS1*, *PkSS2*, *PkFPS1*, *PkCAS1*, and other genes coding for key enzymes of steroid saponin synthesis respond differently to AM fungi and P levels in different parts of *Polygonatum kingianum* Coll. et Hemsl. (Zhang, 2021). Under the interaction of AM fungi and P levels, the differentially expressed genes are mainly enriched in ribosomes, biosynthesis of secondary metabolites, and metabolic pathways (Zhang, 2021). AM fungal infection improved the content of fat-soluble tanshinone I and miltionone in the roots of *Salvia miltiorrhiza* Bunge (Yang, 2012). Zubek *et al.* (2010) reported that AM fungi significantly increased the thymol content in the roots of *Inula ensifolia* L.

Phenolic compounds. The synthesis of phenolic compounds is related to cascade signaling pathways of signal molecules H_2O_2 , salicylic acid (SA), and nitric oxide (NO) (Zhang *et al.*, 2013b; Zhang *et al.*, 2015). Signal molecule SA regulates the gene expression of systemic acquired resistance (SAR) in plants and induces the synthesis of phenolic compounds (Kogel and Langen, 2005; Zhang *et al.*, 2010). NO is involved in the regulation of chalcone synthase (*CHS*) expression, and an NO donor enhances H_2O_2 accumulation (Soheila *et al.*, 2001; Wang *et al.*, 2006). Under N deficiency conditions, H_2O_2 and NO jointly regulate the activity of phenylalanine ammonia-lyase (*PAL*) and the accumulation of phenolic substances in *Matricaria chamomilla* L. (Kováčik *et al.*, 2009). Zhang *et al.* (2010) speculated that the mechanism and pathway of phenolic synthesis induced by AM fungi as follows: after infecting plant roots with AM fungi, SA and H_2O_2 were induced *in-situ*, and the enzyme activity related to phenolic biosynthesis centered on *PAL* was stimulated, and the phenolic content in infected plant roots was increased. At the same time, SA and H_2O_2 can be used as signal molecules to transport to the sites not infected by AM fungi at a long distance in the plant transport tissues, induce the expression of *CHS*, *PAL*, and other genes, and promote the synthesis of phenolic compounds in roots not infected by

AM fungi in plants. (Zhang et al., 2010). Studies have shown that AM fungi increase the H₂O₂, SA, and NO contents in roots, and H₂O₂, SA, and NO signaling molecules activate PAL and participate in the synthesis of phenolic compounds in plant roots (Zhang et al., 2013b). AM fungi promote total flavonoid accumulation in *Clematis intricata* Bunge by up-regulating *CiCHS* expression (Liu, 2017). Through greenhouse experiments and field trials, Ceccarelli et al. (2010) found that inoculation with AM fungi increased the total phenolic content and anti-ROS capacity of artichoke (*Cynara cardunculus* L. var. *scolymus*). Jurkiewicz et al. (2010) showed that inoculation with AM fungi increased the phenolic acid content in the roots and buds of *Arnica montana* L. Zubek et al. (2012) demonstrated that inoculation with AM fungi, such as *Rhizophagus intraradices*, increased the levels of the anthraquinone derivatives hypericin and pseudohypericin in *Hypericum perforatum* L. Toussaint et al. (2007) disclosed that inoculation with AM fungi promoted the accumulation of the antioxidants rosmarinic and caffeic acid in *Ocimum basilicum* L. stems. Yang (2012) reported that inoculation with AM fungi increased the content of water-soluble salvianolic acid B and rosmarinic acid in *Salvia miltiorrhiza* Bunge. Inoculation with AM fungi promoted P uptake and enhanced the glycyrrhizin content in licorice (*Glycyrrhiza uralensis*) Fisch. leaves and roots, respectively (Liu et al., 2007).

Nitrogenous compounds. Studies have shown that the alkaloid biosynthetic pathway is similar to the terpene biosynthetic pathway, which can be synthesized by MVA or MEP pathways, such as *Dendrobium* alkaloids (Bai, 2019). MVA pathway is the main pathway to produce steroidal alkaloid backbones (Suzuki and Muranaka, 2007; Chen, 2019). HMGR is a key MVA pathway regulator (Chen, 2019). First, cycloartenol synthase (CAS) cyclizes 2,3-oxidosqualene to form an important precursor for the synthesis of *Fritillaria* alkaloids, namely cycloartenol (CA) and then forms various *Fritillaria* alkaloids through a series of complex reactions (Sun, 2014b; Chen, 2019). CAS is considered to be the key enzyme for the synthesis of *Fritillaria* alkaloids (Sun, 2014b; Chen, 2019). Chen (2019) cloned two genes related to alkaloid synthesis in *Fritillaria cirrhosa* D. Don, namely HMGR gene (*FcHMGR*) and CAS gene (*FcCAS*), and found that the increase of alkaloid content in *Fritillaria cirrhosa* D. Don with age may be positively correlated with the high expression of genes. Inoculation with *Claroideoglossum etunicatum* changed the accumulation of monoterpene indole alkaloids (MIAs) such as ajmalicine and serpentine in different parts of *Catharanthus roseus* (L.) G. Don, and the expression patterns of *TDC*, *STR*, *SGD*, *DAT*, *PRX1*, and other analytical genes of alkaloids (Andrade et al., 2013). The q-markers peimisine, onych-peimisine, and aethyl-peimisine were enhanced in *Fritillaria taipaiensis* P. Y. Li inoculated with AM fungi (Zhang et al., 2020). *Phellodendron amurense* Rupr. from three different provenances (including space breeding and Jilin, China, and Heihe, China) were infected with three different AM fungi: *Rhizophagus intraradices*, *Claroideoglossum etunicatum*, and *Funneliformis mosseae*. The levels of three alkaloids, including palmatine, berberine, and jatrorrhizine, increased in various plant

fractions (Zhou et al., 2015). Zhou et al. (2015) also showed that *Funneliformis mosseae* had the most significant effect on berberine and jatrorrhizine, and *Rhizophagus intraradices* had the most significant effect on palmatine. Fan et al. (2006) found that inoculation of *Funneliformis mosseae*, *Claroideoglossum etunicatum*, *Glomus versiforme*, and *Oehlia diaphana* increased the content of berberine, jatrorrhizine, and palmatine in *Phellodendron amurense* Rupr. Zhou and Fan (2007) found that AM fungi promoted the accumulation of berberine in *Phellodendron chinense* Schneid. through the greenhouse pot experiment of inoculating *Phellodendron chinense* Schneid. with seven AM fungi, including *Acaulospora laevis*, *Acaulospora mellea*, *Oehlia diaphana*, *Claroideoglossum etunicatum*, *Rhizophagus intraradices*, *Funneliformis mosseae*, and *Glomus versiforme*. Zhao et al. (2006) conducted greenhouse pot experiments on *Camptotheca acuminata* Decne. inoculated with *Oehlia diaphana* and *Acaulospora laevis*. Yu et al. (2012) infected *Camptotheca acuminata* Decne. with *Acaulospora mellea* and *Rhizophagus intraradices*. Both studies revealed that inoculation with AM fungi increased the camptothecin content in the host plant. Rojas-Andrade et al. (2003) indicated that in *Prosopis laevigata* (Willd.) M.C. Johnst. inoculated with *Gigaspora rosea*, the shoot pyridine alkaloid content remained constant while the root trigonelline content increased 1.8-fold compared with the uninoculated plants.

Effects of AM fungi on disease resistance in medicinal plants

Medicinal plant diseases may be infectious or non-infectious depending on the nature of the pathogenic factors (Xiao et al., 2011). Non-infectious diseases are caused by non-biological factors, such as the toxic effects of environmental pollutants, drought, and flooding caused by too much or too little soil moisture, burning or freezing caused by high or low temperatures, nutritional imbalances caused by excess or insufficient fertilizer, improper cultivation measures, and planting density and sowing time (Xiao et al., 2011). AM fungi alleviate non-infectious diseases by expanding the absorption range of plant roots with their hypha, promoting nutrient absorption, and improving plant stress resistance and survival rates (Xiao et al., 2011; Yang, 2012).

Diseases caused by fungi, bacteria, viruses, nematodes, and other contagious pathogens are called infectious diseases (Xiao et al., 2011). AM fungi resist infectious diseases by increasing defense enzyme activity and upregulating defense genes in the host and by improving the sensitivity of the plant defense system to pathogens (Xiao et al., 2011; Zhang et al., 2013a). Plants induce the expression of pathogenesis-related (PR) genes *PR1* and *PR5*, *PDF1*, and *Thi2.1* (Berrocal and Molina, 2007; Sukhada et al., 2011; Wang et al., 2012) through SA, JA, and NO signaling pathways (Spoel and Dong, 2008; Schmidt et al., 2008; Wang et al., 2012) to establish their own defense mechanisms against pathogen invasion. SA pathway induces the expression of PR genes (Ganesan and Thomas, 2001). Infection by AM fungi can enhance the cDNA expression of the main JA synthase allene oxide cyclase and increase the endogenous JA content in roots (Isayenkov et al., 2005). AM fungi improve JA levels and enhance plant defense by inducing the synthesis of key enzymes in the JA pathway,

such as lipoxygenase, chitinase (Xie *et al.*, 2012), and allene oxide synthase (Mandal *et al.*, 2015b). Jasmonic acid carboxyl methyltransferase (JMT) catalyzes JA to form methyl jasmonate (MeJA) with strong volatility (Li *et al.*, 2019). The effect of MeJA varies on the expression levels of *GubAS*, *GubAO*, and *GuDOCS* genes in *Glycyrrhiza uralensis* Fisch. under different concentrations and different durations of treatment, thereby affecting plant chemical defense (Liang *et al.*, 2017; Li *et al.*, 2019). NO accumulation is partly dependent on the activities and functions of *DMI1*, *DMI2*, and *DMI3* (Wang *et al.*, 2012). Inoculation of AM fungi elicits high mRNA expression of extracellular *PR-1*, intracellular *GluBAS*, and *Chi9* in host plant mutants (Gao *et al.*, 2004, 2006; Wang *et al.*, 2012). Huang *et al.* (2007) found that AM fungi stimulate plant disease resistance mechanisms by upregulating the genes encoding the biosynthesis of secondary metabolites such as 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one. Yang (2012) found that inoculation with AM fungi and pathogens increased chitinase and β -1,3-glucanase activity, upregulated *PR10* and *PDF2.1*, and improved disease resistance in *Salvia miltiorrhiza* Bunge. In an earlier report, Li (2002) suggested that inoculation with AM fungi increased POD, PAL, and β -1,3-glucanase activity and regulated *PAL5*, *Chib1*, and *VCH3* expression at the transcriptional level in host plants. In this way, nematode infestations were inhibited. When AM fungus-inoculated host plants were reinfested with the soybean cyst nematode (SCN; *Heterodera glycines*) (infectious disease), their defense genes were upregulated. According to the statistics of Veresoglou and Rillig (2012), differences in the efficiency of nematode pathogens depend on the number of AM isolates. Carlsen *et al.* (2008) demonstrated that AM fungi reduced the biomass of *Pythium ultimum* (infectious disease) by modulating the flavonoid content in white clover (*Trifolium repens* L.). Compared with the control, replanted *Ginkgo biloba* L. inoculated with three AM fungi presented with lower leaf blight disease indices, enhanced growth, and successful continuous cropping (Qi *et al.*, 2002). The use of microorganisms to control plant pests and diseases is an important means of biological control (Huang *et al.*, 2011). AM fungi play vital roles in plant disease resistance. Nevertheless, their practical application in plant disease control remains to be developed. Small-scale application of AM fungi for biological control cannot completely replace conventional agrochemicals (Xiao *et al.*, 2011).

Prospects

Traditional methods of research on AM fungal diversity in medicinal plants have certain limitations. AM fungi are still identified mainly based on conventional physiological ecology, morphology, and histochemistry. However, the classification of AM fungi may be affected by certain discrepancies in morphological description resulting from examining different stages of plant development, using different sampling times and staining techniques, and human error (Chen *et al.*, 2011). With the development of molecular biological techniques, more precise means of identifying AM fungi currently employ second-generation

high-throughput sequencing (HTS), including Illumina (Solexa), Roche/454, and Applied Biosystems solid, among others (Chen *et al.*, 2011). Among them, Illumina (Solexa), which utilizes single-molecule arrays to bridge polymerase chain reactions on a minichip (flow cell) (Mardis, 2008; Du *et al.*, 2014), has gradually become a popular sequencing platform, being high throughput, accurate, sensitive, and low-cost technique (Du *et al.*, 2014; Tang, 2016). Nevertheless, the methods used to assess fungal symbiosis in agriculture and ecology are not fully transferable to symbiotic AM fungi in medicinal plants as the latter include a wide range of different taxa that occupy diverse and complex habitats. Hence, soil texture, microbial abundance and diversity, root morphology, and sampling time must be considered in the processes of isolating and identifying symbiotic AM fungi in medicinal plants (Chen *et al.*, 2011).

Most studies on the growth-promoting effects of AM fungi on medicinal plants were performed as pot experiments; little field research was conducted. Until now, studies have been reported on the use of AM fungi, including *Acaulospora laevis* (Zhou and Fan, 2007), *Oehlia diaphana* (Zhou and Fan, 2007), *Claroideoglossum etunicatum* (Andrade *et al.*, 2013), *Rhizophagus intraradices* (Zhou *et al.*, 2015), *Gigaspora rosea* (Gu *et al.*, 2020), *Gigaspora albida* (Gu *et al.*, 2020), *Scutellospora calospora* (Huang *et al.*, 2020), *Scutellospora coralloidea* (Huang *et al.*, 2020), and others to investigate the inoculation effect of medicinal plants. Most of these inoculation experiments were performed on potted plants raised in a greenhouse and/or under artificial interventions such as high-temperature, drought, or salt stress. Under the foregoing conditions, AM fungal inoculation is usually beneficial to the host plant. Nevertheless, soil volume and water and nutrient content differ between field and greenhouse pot experiments. Furthermore, in these reports, AM fungi were comparatively less efficacious in the field than in greenhouse-grown plants. High temperature accelerates evaporation and causes drought, which in turn results in salt accumulation on the soil surface and in plant roots. Hence, plants are often simultaneously subjected to multiple stressors. AM fungi improve plant resistance to a single controllable stress factor. It is not known whether they can also mitigate the negative impact of multiple adverse effects on commercial crops and medicinal plants. It also remains to be determined whether they can benefit host plants under multiple stressors, different soil types and field experiment designs, or long-term cultivation. Future research should also investigate whether medicinal plants can maintain good growth status even after they are no longer being inoculated with AM fungi.

Most prior studies focused on the effects of AM fungi on medicinal plant seedlings. AM fungi increased the terpene, phenolic, and nitrogenous secondary metabolite content of medicinal plants and improved their quality. Subsequent research must aim to elucidate the physiological effects of AM fungi on perennial plants, different plant growth stages, and various secondary metabolites. The impact of AM fungi on the expression of genes encoding secondary metabolites in different plant tissues and organs should also be explored. Moreover, the influences of various AM fungi infection

intensities on the host plant and environmental factors on the AM fungi merit further evaluation.

Research on the disease resistance effect of AM fungi on medicinal plants is still in the early stages. AM fungi help plants resist disease by regulating the expression of their defense genes and improving the sensitivity of their defense systems to pathogens. These services could greatly advance sustainable agriculture. Nevertheless, the application of AM fungus in plant disease control is still under development. Furthermore, small-scale application of AM fungi in biological control cannot completely replace conventional pesticides (Xiao *et al.*, 2011). Future investigations should examine plant defense-related enzyme activity, gene expression, and pathogen sensitivity. The signal transduction pathways among AM and pathogenic fungi, bacteria, and viruses in medicinal plants should also be explored. Other research focal points could include the relationships among root exudates, host genotype, soil microenvironment, biocontrol agents, and active and passive AM fungus defense mechanisms. The relationships among inoculant dosages, disease types, and AM fungal control agents also merit further research. The learnings from the foregoing studies might lay the foundation for improving the soil environment, yield, and quality of medicinal plants.

AM fungi-based fertilizer is promising for medicinal plant cultivation. Research on the diversity and growth promotion of symbiotic AM fungi in medicinal plants has increased in recent years. However, AM fungi are seldom practically applied to medicinal plant production. The isolation and identification of AM fungi by molecular methods and the development of novel, efficacious AM fungi-based fertilizer preparations may enhance the breeding and propagation of endangered wild medicinal plants. Newly discovered AM fungal strains could restore and promote medicinal plant growth, stimulate secondary metabolite biosynthesis, reduce chemical fertilizer and pesticide consumption, augment the therapeutic efficacy of medicinal plants, and increase the ecological and economic value of cultivating these crops. Techniques involving biochemistry, molecular ecology, metabolomics, proteomics, bioinformatics, genotyping, and phenotyping can be used to determine the heritability, germplasm resources, infection rates, diversity, and distribution of AM fungi at the transcriptional and translational levels. The effects of AM fungi colonization on energy distribution, photosynthesis, phytohormones, and secondary metabolites in medicinal plants should also be explored. Moreover, determination of the key roles of AM fungi in medicinal plant cultivation may eventually facilitate novel approaches towards biological control, environmental protection, and the sustainable development of TCM and other constituents of the economy.

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