SEL Soil Ecology Letters

REVIEW

The roles and performance of arbuscular mycorrhizal fungi in intercropping systems

Minghui Li[1], Junli Hu[1,2,*], Xiangui Lin[1]

1 State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, China
2 University of Chinese Academy of Sciences, Beijing 100049, China

HIGHLIGHTS

• Metabolic and non-metabolic benefits of AM fungi under intercropping were reviewed.
• Changes of AM fungi themselves respond to intercropping practices were summarized.
• Mechanistic understanding the synergy between intercropping and AM fungi is needed.
• It's valuable to harness AM fungal benefits for maximizing intercropping production.

GRAPHICAL ABSTRACT
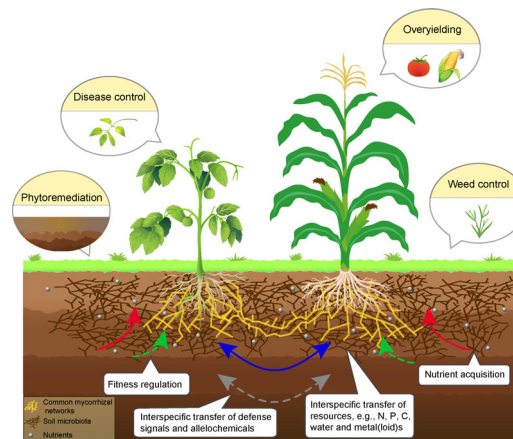
ABSTRACT

Intercropping, which gains productivity and ecological benefits through plant facilitative interactions, is a practice often associated with sustainable agriculture. In such systems, arbuscular mycorrhizal (AM) fungi and the hyphal networks play key roles in plant facilitation by promoting connectivity, mediating interplant transfer of metabolic resources, and managing weeds, pathogens, and contaminants. This review states that the symmetrically or unsymmetrically delivered resources via AM fungi are imperative to maintain facilitative interactions between intercrops. In addition, the responses of AM fungi to intercropping are also discussed, including changes in abundance, diversity, community composition and colonization level. Although general proliferations in AM fungi via intercropping have been shown, the plant hosts and neighbors may exert different influences on AM fungi. Therefore, further research is needed in quantifying the mediating role of AM fungi on outputs of intercropping systems, clarifying the driving forces, and exploring the causation between these processes and the changes in AM fungi themselves. To conclude, the integration with AM fungi extends the understanding of key soil biological processes driving plant facilitation and will guide efforts to optimizing intercropping systems.

1 Introduction

Agricultural productivity and food security need to be achieved in a more sustainable way in response to growing world population and climate change (Bruinsma, 2003; Wheeler and

* Corresponding author
E-mail address: jlhu@issas.ac.cn (J. Hu)

von Braun et al., 2013). Intercropping is the simultaneous cultivation of more than one crop cultivar (Vandermeer, 1989), mostly implemented in resource-limited and small-scale agriculture in tropical, subtropical and temperate areas in Africa, South Asia, and Central America (Brooker et al., 2015). Through processes such as niche complementarity and interspecific facilitation, intercropping systems have potential benefits in space and resource use, overall yield (Hauggaard-Nielsen and Jensen, 2005; Li et al., 2014), weed and disease control (Boudreau, 2013; Gurr et al., 2003), phytoremediation (Zeng et al., 2019), and soil quality improvement (Arantes et al., 2020), thereby holding great advantages for improving stability and sustainability of agroecosystems.

Intercropping can be considered as a practical application of ecological principles of natural ecosystem, taking the advantages of biodiversity to realize system productivity (Malezieux et al., 2009). For example, nitrogen (N)-fixing or phosphorus (P)-releasing species are commonly applied to intercropping systems to enhance soil fertility and growth of companion plants (Gunes et al., 2007; Li et al., 2007; Thilakarathna et al., 2016; Duchene et al., 2017). However, a more complex system means more difficulties for management and greater challenges to the techniques and concepts derived from monocropping systems (Malezieux et al., 2009). Thus, the agronomic and ecological advantages of intercropping should be further consolidated in order to providing effective support to smallholdings and being embraced by industrial farms, and a deeper understanding of the mechanisms driving these processes is definitely needed.

Soil microbial communities often positively respond to increased plant diversity (Montesinos-Navarro et al., 2012; He et al., 2013; Tang et al., 2014; Gong et al., 2019), in turn, which play crucial roles in soil nutrient cycling and regulation of plant-plant interactions. Among soil microbes, arbuscular mycorrhizal (AM) fungi are obligate biotrophs belonging to the phylum Glomeromycota, forming symbiotic associations with the majority of vascular plants, including most agricultural crops (Smith and Read, 2008; Brundrett and Tedersoo, 2018). In return for plant carbon (C), delivering nutrients (e.g., P and N) is the most important benefit of AM symbiosis for plant hosts (Smith and Read, 2008). There are also multiple ecological services provided by AM fungi, e.g., abiotic/biotic stress tolerance and soil structure improvement (Gianinazzi et al., 2010; Smith et al., 2010; Leifheit et al., 2014). While legume-based intercropping is widely used as an effective strategy for utilizing biologically fixed-N, AM fungi are essentially needed to alleviate the nutrient shortages and support the extra P need for N fixation (Barea et al., 2005).

In addition, the fungal mycelia simultaneously colonize and interconnect roots of the same or different plant species, forming so-called common mycorrhizal networks (CMNs). The CMNs allow direct and efficient pathways of resource transfers between intercrops, and closely bound to the outcomes of plant facilitative or competitive interactions (Montesinos-Navarro et al., 2016; Qiao et al., 2016; Dieng et al., 2017). Furthermore, AM fungi can provide a bunch of

services for plant adaptation under stressful environments (Gorzelak et al., 2015), facilitating the ecological functions and wider applications of intercropping (Ehrmann and Ritz, 2014). In turn, such roles of AM fungi under intercropping systems should be reflected in their quantity and diversity features. A diversified AM fungal community enables efficient exploitation of soil resources and functional compatibility between host plants, hence regulating plant facilitation and coexistence in field ecosystems (van der Heijden et al., 1998; Wagg et al., 2011; Montesinos-Navarro et al., 2012, 2019).

In the review provided by Bainard et al. (2011), the tree-based intercropping systems generally supported an abundant and diversified AM fungal community compared with conventional agricultural systems. However, an update of recent findings regarding how AM fungi respond to interactions between different intercrops, especially for crop species, is needed. In the current review, we set out to synthesize the roles and responses of AM fungi in a wider scope of planting systems, e.g., field crops, forages, trees, or a mixture thereof, where intercropping strategy has been applied. Such integration of intercropping and AM fungi is expected to enhance understanding of key soil biological processes driving plant-plant interactions, and bring novel insights into future developments of intercropping systems.

2 The contributions of AM fungi in intercropping systems

The CMNs allow intra- and inter-specific transfers of resources, either metabolic (including contaminants), e.g., N, P, C, water and metal(loid)s (Martins and Cruz, 1998; Yao et al., 2003; Egerton-Warburton et al., 2007; Meding and Zasoski, 2008; Ren et al., 2013), or non-metabolic, e.g., allelochemicals and defense signals (Barto et al., 2012). Therefore, we start by discussing the three major roles AM fungi play in intercropping systems: 1) mediation of plant interspecific transfer of C, N, P, and water resources and facilitative interactions; 2) control of parasitic weeds and plant pathogens; and 3) remediation of heavy metal(loid)-contaminated soil (Fig. 1).

2.1 The mediation of resource transfer and facilitation between intercrops via CMNs

The facilitative effect of AM fungi on N-fixation by legumes and subsequent N transfer to companion crops have been demonstrated by a number of studies using ^{15}N labeling. Ingraffia et al. (2019) showed that AM fungi accounted for 20% of increases in the N fixed by faba bean (*Vicia faba*) and also in the N transferred to the intercropped wheat (*Triticum turgidum*). Wahbi et al. (2016) reported the similar effect, but variation was shown due to different inoculation rates of AM fungi. Li et al. (2009) traced the bidirectional N transfer between mung bean (*Vigna radiata*) and rice (*Oryza sativa*),
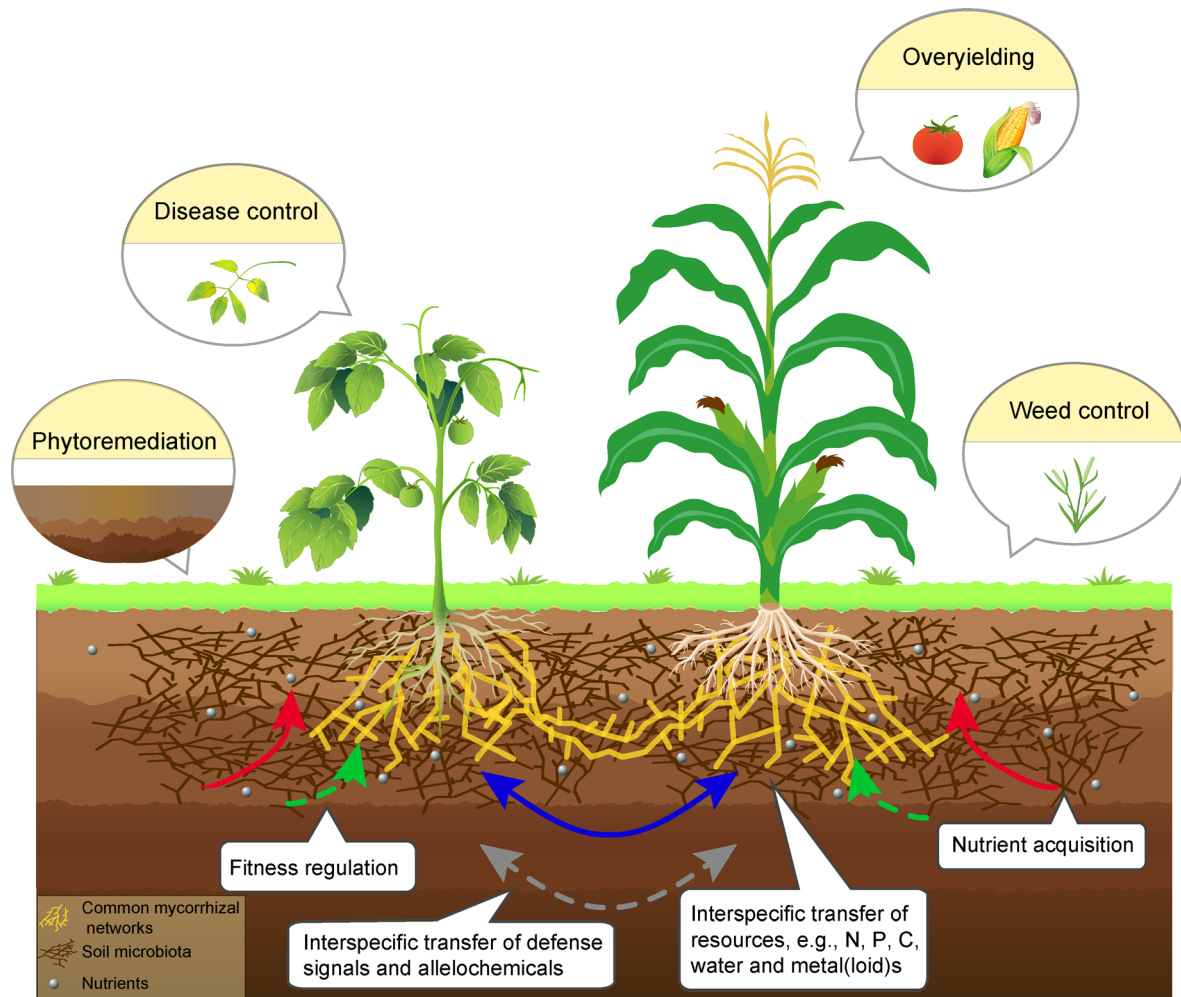
Fig. 1 The potential benefits of arbuscular mycorrhizal (AM) fungi in intercropping systems, e.g., overyielding, weed and disease control, and phytoremediation. Arrows and boxes show proposed mediation of AM fungi for uptake and/or interspecific transfer of metabolic resources, infochemicals and defense signals belowground.

the presence of AM fungi increased ^{15}N transfer from mung bean to rice from 5.4% to 15.7%, while only 2.7% of N was transferred from rice to mung bean. Zhang et al. (2020a) reported a more effective N transfer via CMNs than the indirect pathway via root exudation in an alfalfa (*Medicago sativa*) and maize (*Zea mays*) intercropping system without N fertilization. The dual inoculation of an AM fungal strain and a rhizobium strain led to significant increases of N uptake in co-cultivated soybean (*Glycine max*) and maize and the mycelium-derived N transfer from soybean to maize than any of single inoculation, suggesting the synergistic effect between AM fungi and rhizobia (Meng et al., 2015).

Compared to N, less attention has been paid to plant interspecific P transfer via AM fungi. The CMNs allow bi-directional P transfer among different plant species (Martins and Read, 1996), and which plant is more benefited may depend on plant specific needs and mycorrhizal dependence. Ryegrass (*Lolium perenne*) showed a higher shoot P content than neighboring clover (*Trifolium pratense*), and a lower rate of P was transferred from ryegrass to clover than from clover

to ryegrass via CMNs (Yao et al., 2003). The interplant P transfer via CMNs accounted for more P acquisition in the obligately mycotrophic grass, i.e., indiangrass (*Sorghastrum nutans*, >50%) than the facultative grass, i.e., white sage-brush (*Artemisia ludoviciana*, 20%) (Wilson et al., 2006).

There are also evidences for the involvement of AM fungi in C and water allocation between intercropping plant species. With ^{14}C labeling in rice leaves, both enhanced ^{14}C activity in watermelon (*Citrullus lanatus*) leaves and increased P uptake and translocation in rice were shown, thus AM fungus mediated the C and P trade between intercrops (Ren et al., 2013). In a growth chamber $^{13}CO_2$-labeling experiment, inoculation with AM fungi increased ^{13}C content in maize shoots and decreased ^{13}C content in soybean roots, indicating that maize invested less C than soybean into the CMNs (Wang et al., 2016). Walnut (*Juglans nigra*) tree showed higher $\partial^{13}C$ ($^{13}C/^{12}C$ ratio) in leaves but lower $\partial^{13}C$ in root adjacent mycelium compared to the neighboring maize, suggesting the potential C transfer from walnut to maize via the CMNs (van Tuinen et al., 2020). Based on these

evidences, it is still not possible to conclude there is fungus-to-plant C transfer (Robinson and Fitter, 1999). Deep-rooted pigeon pea (*Cajanus cajan*) showed a 'bioirrigation' effect to shallow-rooted finger millet (*Eleusine coracana*) under drought and the enhanced facilitation by CMN was observed, however, pigeon pea showed competitive effect over finger millet at ambient water availability and the CMN also enhanced the competition (Singh et al., 2020).

Through mediating the N, P, C and water economy, symmetric benefits for both intercropped partners delivered by CMNs have been shown (Meng et al., 2015; Kumar et al., 2016). More frequently, AM fungi provide varying degree of benefits to different plant species. In legume-cereal intercropping systems, the preference by CMNs is important in maintaining the profits of legumes and enabling plant facilitation (Li et al., 2009; Xiao et al., 2010; Qiao et al., 2015; Bahadur et al., 2019). However, the opposite direction of CMNs derived benefits has also been reported. Wheat was more favored by CMNs with enhanced nutrient uptake rather than the neighboring annual medic (*Medicago scutellate*) and faba bean (Caruso et al., 2018; Ingraffia et al., 2019). Maize showed the preference by CMNs over the intercropped soybean (Hamel and Smith, 1991; Wang et al., 2019). When legumes are not included, pepper (*Capsicum annuum*) was the more beneficiary species of CMNs for enhanced P acquisition and fruit yield when intercropped with maize (Hu et al., 2019).

The effects of AM fungi on plant interspecific competition are related to specific plant mycorrhizal traits (Moora, 2014). The increased competitive ability of N-fixing forbs, the suppression in fibrous C_3 grasses, and unclear effects in C_4 grasses, non-fixing forbs and woody species have been shown (Lin et al., 2015). Soil properties such as pH and nutrient levels and aboveground factors such as planting density and shading also exert influences on the magnitudes and directions of AM fungal mediation (Chifflot et al., 2009; Menezes et al., 2016; Wang et al., 2016; Ren et al., 2017; Shukla et al., 2018; Zhang et al., 2020a). For intercropping patterns involving non-mycotrophic species, e.g., barley (*Hordeum vulgare*) and sugar beet (*Beta vulgaris*) (Hajiboland et al., 2020), and sesame (*Sesamum indicum*) and broccoli (*Brassica oleracea*) (Tong et al., 2015), AM fungal mycelium from the co-cultivated mycotrophic species induced changes in the defense parameters of non-host species, but evidence of reduced plant growth and fitness was not shown.

2.2 The potential of AM fungi in controlling weeds and diseases in intercropping systems

The AM fungi supported by intercropping trees enhanced the competitive strength of sorghum (*Sorghum bicolor*) against parasitic striga (*Striga hermonthica*) (Birhane et al., 2018). In the extreme case, a significant and negative correlation was observed between AM fungal spore density and colonization, and striga counts at the early stage of sorghum growth. In a facility shed, the suppression of pepper *Phytophthora* blight

by soil indigenous AM fungi was enhanced by intercropping with maize, which promoted the propagation of AM fungi and thereby colonization on pepper roots (Liu et al., 2021). Similarly, AM fungal inoculation induced a compensation for the negative effect of *Fusarium* wilt on the biomass of tomato (*Lycopersicon lycopersicum*) intercropped with leek (*Allium porrum*), which showed even a 20% higher mycorrhizal colonization rate than monocropped tomato, and thereby higher outcome of the bioprotective effects resulting from AM fungi (Hage-Ahmed et al., 2013).

In addition to nutritional compensation, CMNs also serve as potential 'superhighways' for transferring systemic allelochemicals and defense signals across plant species (Barto et al., 2012; Schuman and Baldwin, 2018). Experimental evidences indicated that AM fungal hyphae increased soil accumulation of allelochemicals, e.g., imazamox and thiophenes from signet marigold (*Tagetes tenuifolia*) (Barto et al., 2011) and juglone from walnut (Achatz and Rillig, 2014), thus triggering growth inhibition in the receiver plants, lettuce (*Lactuca sativa*) and tomato, respectively. Furthermore, belowground transportations of defense signals through CMNs between trifoliate orange (*Poncirus trifoliata*) seedlings (Zhang et al., 2018b), tomato (Song et al., 2010, 2015), and faba bean (Babikova et al., 2013) were also shown. However, it remains unclear whether communication between plants via CMNs can be maintained when scale up to diverse AM fungal communities and among multiple plant species under field conditions.

2.3 The function of AM fungi for soil remediation in intercropping systems

Another applicable area of intercropping is phytoremediation, e.g., using metal(loid)-accumulating companion plants to ensure crop safety in contaminated soils, where AM fungi may play a crucial part either by mediating metal(loid) transfer between plants, or alleviating toxicities in plants. For example, AM fungal inoculation enhanced cadmium (Cd) acquisition by Alfred stonecrop (*Sedum alfredii*) over the neighboring upland kangkong (*Ipomoea aquatica*), increased soil P availability through activating phosphatase activity, and reduced soil available Cd concentrations via elevating soil pH (Hu et al., 2013a, 2013b). In a recent study reported by Yang et al. (2021), AM fungal inoculation also reduced Cd concentration in upland rice through regulating Cd transporter genes in rice, increasing the root surface area and Cd acquisition of the intercropped black nightshade (*Solanum nigrum)*, and modulating root exudation and rhizosphere pH to decrease Cd availability for rice and increase that for nightshade. In a heavy metal-polluted soil, AM fungal inoculation alleviated the toxicity level and increased the yield of garlic chives (*Allium tubersosum*) intercropped with sunflower (*Helianthus annuus*) via enhancing soil phosphatase activity and plant P acquisition, along with increased availabilities of heavy metals in soil and acquisitions by sunflower (Zhang et al., 2019). Through mediating plant P nutrient, AM fungi were also involved in the

adaptations of the mix-cropped ryegrass and clover, and alfafa (*Medicago sativa*) and pepperweed (*Lepidium apetalum*), to arsenic (As) contamination (Dong et al., 2008; Zhang et al., 2018a).

3 The responses of AM fungi to intercropping

The colonization level and abundance of AM fungi are important indicators reflecting plant growth performance and soil nutrient activation. With the diversified C resources and spatial patterns of soil properties under agroforestry management (Thevathasan and Gordon, 2004), increases of root colonization and soil sporulation of AM fungi were shown in intercropping systems of sorghum and ana tree (*Faidherbia albida*), and soybean and peacock flower (*Albizia gummifera*) or broad-leaved croton (*Croton macrostachyus*) (Birhane et al., 2018; Hailemariam et al., 2013). Mycorrhizal colonization of both seedling and mature tree roots of grandis gum (*Eucalyptus grandis*) was stimulated through intercropping with Buddha belly tree (*Acacia mangium*) (Bini et al., 2018; Pereira et al., 2018). Referring to mixtures of field crop, there were increases of mycorrhizal colonization for wheat and maize intercropped with faba bean (Wahbi et al., 2016) and soybean (Meng et al., 2015), respectively. With different combinations of pigeon pea, cowpea (*Vigna unguicularta*), and maize, there was no difference in mycorrhizal colonization level among crops in the growing season, whereas increased mycorrhizal colonization of maize in the following year was shown (Njira et al., 2017). However, factors such as soil nutrient conditions, aboveground management, and plant characteristics all can affect AM fungi in intercropping systems. The survey of 23 tree, crop and vegetable species of Ethiopia agroforestry systems showed that colonization and spore density of AM fungi favored moderate to low P and N levels (Dobo et al., 2018). The seeding density of neighboring palisade grass (*Urochloa brizantha*) negatively affected maize root colonization and soil population of AM fungi (de Freitas et al., 2018). Mycorrhizal colonization of tomato either increased, not changed, or decreased when intercropped with leek, cucumber/basil, and fennel, respectively (Hage-Ahmed et al., 2013), indicating a neighbor effect on plant-fungal interactions.

With interactions between intercrops, changes in the diversity and community composition of AM fungi have been demonstrated. Bainard et al. (2012) showed that intercropping with trees increased AM fungal diversity in a maize-planted soil, while tree species exerted different neighboring effects on the community composition. There were decreases of soil spore density and shifts in root and rhizosphere AM fungal community composition of oriental arborvitae (*Platycladus orientalis*) via neighboring with the leguminous tree, i.e., black locust (*Robinia pseudoacacia*); while neighboring oriental arborvitae only had influence on the rhizosphere AM fungal community composition of black locust (Chen et al., 2018). Gao et al. (2020) reported corresponding responses of soil

AM fungal abundance to intercropping derived asymmetric effects on tomato and potato onion (*Allium cepa* var. aggregatum) growth, while the community composition of AM fungi only shifted in the rhizosphere of potato onion. According to Zhang et al. (2020b), intercropping increased soil AM fungal diversity in the rhizosphere of soybean, whereas no such effect was shown in the neighboring maize. Also, there were opposite trends of change in the relative abundance of dominant genus (*Glomus*) between soybean and maize with increasing level of N application. However, a number of other studies suggested no guarantee for higher AM fungal diversity or shifted community composition through intercropping (Rajeshkumar et al., 2015; Menezes et al., 2016; Furze et al., 2017).

4 Conclusion and prospects

The roles of AM fungi for plant interspecific resource transfer and facilitative interactions in intercropping systems have been thoroughly summarized in the current review. Despite of accumulating evidences of AM fungi-mediated N, P, C, and water allocations between intercrops, there are still doubts about the significance of such mycelia-derived resource flows and whether resources are directly transferred through CMNs or indirectly through soil, and further developments of tracing and modeling methods are still needed (Simard and Durall, 2004). There are either symmetric or unsymmetric benefits provided by AM fungi, enhancing facilitative or sometimes competitive interactions between intercropped species. The underlying mechanisms driving plant interspecific facilitation and AM fungal mediation in intercropping systems need to be better understood. On the other hand, the identified plant and environmental factors worth further consolidation, which are crucial in defining the application scopes of intercropping and AM fungi.

Besides metabolic regulation, the contributions of AM fungi for the ecological/environmental applications of intercropping, e.g., weed and pathogen control and soil remediation, were discussed in this review. There are also possible roles of AM fungi in coping with insects via transferring herbivore-induced signals between plants (Babikova et al., 2013) and dissipating organic pollutants via a synergistic effect by intercropping, AM fungi, and soil bacteria (Shan et al., 2018). Intercropping approaches need to show enough advantages to offset the costs of sophisticated managements and technical developments, and these non-metabolic prospects can provide significant argument to intercropping. While a better understanding of the mechanisms driving plant-plant communications and exchanges via CMNs is needed. Further focuses should also be given to the cooperation among intercropping, AM fungi, and organic amendments, which hold great potential in solving soil depletion, contamination, and continuous cropping obstacles (Hu et al., 2014; Kumar et al., 2016; Liu et al., 2020).

The general proliferations in AM fungal abundance and

diversity have been suggested by studies of intercropping systems, while AM fungi may show different responses to intercropped species depending on the strengths of neighboring effects and relative changes in soil environment (Chen et al., 2018; Gao et al., 2020). However, current information about intercropping-induced changes in AM fungal community is very limited and it is difficult to link such changes with interactions between plant species. Also, further investigations on the relationship between the changes within AM fungi and their nutritional and ecological functions in intercropping systems are needed.

Consequently, a mutually beneficial relationship between intercropping and AM fungi is suggested, AM fungi are necessarily involved in interspecific facilitation and ecological services of intercropping systems, and intercropping leads to improvements of mycorrhizal colonization and development of AM fungal community. Understanding the inextricable links between intercropping and AM fungi will guide the optimization in productivity and broader-scale applications of intercropping.

Acknowledgments

Conflict of interest

All authors declare that they have no conflict of interest.

References

Achatz, M., Rillig, M.C., 2014. Arbuscular mycorrhizal fungal hyphae enhance transport of the allelochemical juglone in the field. Soil Biology & Biochemistry 78, 76–82.

Arantes, A.C.C., Cotta, S.R., da Conceicao, P.M., Meneghin, S.P., Martinelli, R., Prospero, A.G., Boaretto, R.M., Andreote, F.D., Mattos, D., de Azevedo, F.A., 2020. Implication of *Urochloa* spp. intercropping and conservation agriculture on soil microbiological quality and yield of Tahiti acid lime in long term orchard experiment. Agriculture 10, 491.

Babikova, Z., Gilbert, L., Bruce, T.J.A., Birkett, M., Caulfield, J.C., Woodcock, C., Pickett, J.A., Johnson, D., 2013. Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. Ecology Letters 16, 835–843.

Bahadur, A., Jin, Z., Long, X., Jiang, S., Zhang, Q., Pan, J., Liu, Y., Feng, H., 2019. Arbuscular mycorrhizal fungi alter plant interspecific interaction under nitrogen fertilization. European Journal of Soil Biology 93, 103094.

Bainard, L.D., Klironomos, J.N., Gordon, A.M., 2011. Arbuscular mycorrhizal fungi in tree-based intercropping systems: A review of their abundance and diversity. Pedobiologia 54, 57–61.

Bainard, L.D., Koch, A.M., Gordon, A.M., Klironomos, J.N., 2012.

Temporal and compositional differences of arbuscular mycorrhizal fungal communities in conventional monocropping and tree-based intercropping systems. Soil Biology & Biochemistry 45, 172–180.

Barea, J.M., Werner, D., Azcon-Guilar, C., Azcon, R., 2005. Interactions of arbuscular mycorrhiza and nitrogen- fixing symbiosis in sustainable agriculture. In: Werner, D., Newton, W.E. (eds.), Nitrogen Fixation in Agriculture, Forestry, Ecology, and the Environment. Dordrecht: Springer, 199–222.

Barto, E.K., Hilker, M., Muller, F., Mohney, B.K., Weidenhamer, J.D., Rillig, M.C., 2011. The fungal fast lane: Common mycorrhizal networks extend bioactive zones of allelochemicals in soils. PLoS One 6, e27195.

Barto, E.K., Weidenhamer, J.D., Cipollini, D., Rillig, M.C., 2012. Fungal superhighways: do common mycorrhizal networks enhance below ground communication? Trends in Plant Science 17, 633–637.

Bini, D., dos Santos, C.A., da Silva, M.C.P., Bonfim, J.A., Cardoso, E., 2018. Intercropping *Acacia mangium* stimulates AMF colonization and soil phosphatase activity in *Eucalyptus grandis*. Scientia Agricola 75, 102–110.

Birhane, E., Gebremeskel, K., Taddesse, T., Hailemariam, M., Hadgu, K.M., Norgrove, L., Negussie, A., 2018. Integrating *Faidherbia albida* trees into a sorghum field reduces striga infestation and improves mycorrhiza spore density and colonization. Agroforestry Systems 92, 643–653.

Boudreau, M.A., 2013. Diseases in intercropping systems. Annual Review of Phytopathology 51, 499–519.

Brooker, R.W., Bennett, A.E., Cong, W.F., Daniell, T.J., George, T.S., Hallett, P.D., Hawes, C., Iannetta, P.P.M., Jones, H.G., Karley, A.J., Li, L., McKenzie, B.M., Pakeman, R.J., Paterson, E., Schob, C., Shen, J., Squire, G., Watson, C.A., Zhang, C., Zhang, F., Zhang, J., White, P.J., 2015. Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. New Phytologist 206, 107–117.

Bruinsma, J., 2003. World Agriculture: Towards 2015/2030: An FAO Perspective. Landon: Earthscan.

Brundrett, M.C., Tedersoo, L., 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytologist 220, 1108–1115.

Caruso, C., Maucieri, C., Cavallaro, V., Borin, M., Barbera, A.C., 2018. Olive mill wastewater spreading and AMF inoculation effects in a low-input semi-arid Mediterranean crop succession. Archives of Agronomy and Soil Science 64, 2060–2074.

Chen, X., Tang, M., Zhang, X., Hamel, C., Liu, S., Huo, Y., Sheng, M., 2018. Effects of plant neighborhood on arbuscular mycorrhizal fungal attributes in afforested zones. Forest Ecology and Management 422, 253–262.

Chifflot, V., Rivest, D., Olivier, A., Cogliastro, A., Khasa, D., 2009. Molecular analysis of arbuscular mycorrhizal community structure and spores distribution in tree-based intercropping and forest systems. Agriculture, Ecosystems & Environment 131, 32–39.

de Freitas, M.A.M., Silva, D.V., Guimaraes, F.R., Leal, P.L., Moreira, F.M.D., da Silva, A.A., Souza, M.D., 2018. Biological attributes of soil cultivated with corn intercropped with *Urochloa brizantha* in different plant arrangements with and without herbicide application. Agriculture, Ecosystems & Environment 254, 35–40.

Dieng, A., Duponnois, R., Ndoye, I., Baudoin, E., 2017. Positive feedback with mycorrhizal fungi alleviates negative effects of intercropping the energy crop *Jatropha curcas* with *Crotalaria retusa*. Symbiosis 73, 107–116.

Dobo, B., Asefa, F., Asfaw, Z., 2018. Diversity and abundance of arbuscular mycorrhizal fungi under different plant and soil properties in Sidama, southern Ethiopia. Agroforestry Systems 92, 91–101.

Dong, Y., Zhu, Y., Smith, F.A., Wang, Y., Chen, B., 2008. Arbuscular mycorrhiza enhanced arsenic resistance of both white clover (*Trifolium repens* Linn.) and ryegrass (*Lolium perenne* L.) plants in an arsenic- contaminated soil. Environmental Pollution 155, 174–181.

Duchene, O., Vian, J.F., Celette, F., 2017. Intercropping with legume for agroecological cropping systems: Complementarity and facilitation processes and the importance of soil microorganisms. A review. Agriculture, Ecosystems & Environment 240, 148–161.

Egerton-Warburton, L.M., Querejeta, J.I., Allen, M.F., 2007. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. Journal of Experimental Botany 58, 1473–1483.

Ehrmann, J., Ritz, K., 2014. Plant: soil interactions in temperate multi-cropping production systems. Plant and Soil 376, 1–29.

Furze, J.R., Martin, A.R., Nasielski, J., Thevathasan, N.V., Gordon, A.M., Isaac, M.E., 2017. Resistance and resilience of root fungal communities to water limitation in a temperate agroecosystem. Ecology and Evolution 7, 3443–3454.

Gao, D., Pan, X., Zhou, X., Wei, Z., Li, N., Wu, F., 2020. Phosphorus fertilization and intercropping interactively affect tomato and potato onion growth and rhizosphere arbuscular mycorrhizal fungal community. Archives of Agronomy and Soil Science, 1–15.

Gianinazzi, S., Gollotte, A., Binet, M.N., van Tuinen, D., Redecker, D., Wipf, D., 2010. Agroecology: the key role of arbuscular mycorrhizas in ecosystem services. Mycorrhiza 20, 519–530.

Gong, X., Liu, C., Li, J., Luo, Y., Yang, Q., Zhang, W., Yang, P., Feng, B., 2019. Responses of rhizosphere soil properties, enzyme activities and microbial diversity to intercropping patterns on the Loess Plateau of China. Soil & Tillage Research 195, 104355.

Gorzelak, M.A., Asay, A.K., Pickles, B.J., Simard, S.W., 2015. Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. AoB Plants 7, plv050.

Gunes, A., Bagci, E.G., Inal, A., 2007. Interspecific facilitative root interactions and rhizosphere effects on phosphorus and iron nutrition between mixed grown chickpea and barley. Journal of Plant Nutrition 30, 1455–1469.

Gurr, G.M., Wratten, S.D., Luna, J.M., 2003. Multi-function agricultural biodiversity: pest management and other benefits. Basic and Applied Ecology 4, 107–116.

Hage-Ahmed, K., Krammer, J., Steinkellner, S., 2013. The intercropping partner affects arbuscular mycorrhizal fungi and *Fusarium oxysporum* f. sp. *lycopersici* interactions in tomato. Mycorrhiza 23, 543–550.

Hailemariam, M., Birhane, E., Asfaw, Z., Zewdie, S., 2013. Arbuscular mycorrhizal association of indigenous agroforestry tree species and their infective potential with maize in the rift valley, Ethiopia.

Agroforestry Systems 87, 1261–1272.

Hajiboland, R., Sadeghzadeh, N., Moradtalab, N., Aliasgharzad, N., Schweikert, K., Poschenrieder, C., 2020. The arbuscular mycorrhizal mycelium from barley differentially influences various defense parameters in the non-host sugar beet under co-cultivation. Mycorrhiza 30, 647–661.

Hamel, C., Smith, D.L., 1991. Interspecific N-transfer and plant development in a mycorrhizal field-grown mixture. Soil Biology & Biochemistry 23, 661–665.

Hauggaard-Nielsen, H., Jensen, E.S., 2005. Facilitative root interactions in intercrops. Plant and Soil 274, 237–250.

He, Y., Ding, N., Shi, J., Wu, M., Liao, H., Xu, J., 2013. Profiling of microbial PLFAs: Implications for interspecific interactions due to intercropping which increase phosphorus uptake in phosphorus limited acidic soils. Soil Biology & Biochemistry 57, 625–634.

Hu, J., Chan, P.T., Wu, F., Wu, S., Zhang, J., Lin, X., Wong, M.H., 2013a. Arbuscular mycorrhizal fungi induce differential Cd and P acquisition by Alfred stonecrop (*Sedum alfredii* Hance) and upland kangkong (*Ipomoea aquatica* Forsk.) in an intercropping system. Applied Soil Ecology 63, 29–35.

Hu, J., Li, J., Wu, F., Wu, S., Ye, Z., Lin, X., Wong, M.H., 2013b. Arbuscular mycorrhizal fungi induced differential Cd and P phytoavailability via intercropping of upland kangkong (*Ipomoea aquatica* Forsk.) with Alfred stonecrop (*Sedum alfredii* Hance): post-harvest study. Environmental Science and Pollution Research 20, 8457–8463.

Hu, J., Li, M., Liu, H., Zhao, Q., Lin, X., 2019. Intercropping with sweet corn (*Zea mays* L. var. *rugosa* Bonaf.) expands P acquisition channels of chili pepper (*Capsicum annuum* L.) via arbuscular mycorrhizal hyphal networks. Journal of Soils and Sediments 16, 1632–1639.

Hu, J., Wu, F., Wu, S., Lam, C.L., Lin, X., Wong, M.H., 2014. Biochar and *Glomus caledonium* influence Cd accumulation of upland kangkong (*Ipomoea aquatica* Forsk.) intercropped with Alfred stonecrop (*Sedum alfredii* Hance). Scientific Reports 4, 4671.

Ingraffia, R., Amato, G., Frenda, A.S., Giambalvo, D., 2019. Impacts of arbuscular mycorrhizal fungi on nutrient uptake, N_2 fixation, N transfer, and growth in a wheat/faba bean intercropping system. PLoS One 14, e0213672.

Kumar, A., Choudhary, A.K., Suri, V.K., Rana, K.S., 2016. AM fungi lead to fertilizer phosphorus economy and enhanced system productivity and profitability in okra (*Abelmoschus esculentus* L.)-pea (*Pisum sativum* L.) cropping system in Himalayan acid Alfisol. Journal of Plant Nutrition 39, 1380–1390.

Leifheit, E.F., Veresoglou, S.D., Lehmann, A., Morris, E.K., Rillig, M.C., 2014. Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation-a meta-analysis. Plant and Soil 374, 523–537.

Li, L., Sun, S., Sun, J., Zhou, L., Bao, X., Zhang, H., Zhang, F., 2007. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. Proceedings of the National Academy of Sciences of the United States of America 104, 11192–11196.

Li, L., Tilman, D., Lambers, H., Zhang, F., 2014. Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. New Phytologist 203, 63–69.

Li, Y., Ran, W., Zhang, R., Sun, S., Xu, G., 2009. Facilitated legume nodulation, phosphate uptake and nitrogen transfer by arbuscular inoculation in an upland rice and mung bean intercropping system. Plant and Soil 315, 285–296.

Lin, G., McCormack, M.L., Guo, D., 2015. Arbuscular mycorrhizal fungal effects on plant competition and community structure. Journal of Ecology 103, 1224–1232.

Liu, Y., Hou, S., Hu, J., Cai, P., Li, M., Wu, F., Lin, X., 2021. Intercropping with maize influences arbuscular mycorrhizal network formation and pepper *Phytophthora* blight suppression in facility sheds. Acta Pedologica Sinica DOI: 10.11766/trxb202102280112.

Liu, Y., Zhao, Q., Deng, X., Wang, B., Zhang, N., Zong, Q., Xia, Y., 2020. Effects of indigenous arbuscular mycorrhizal fungi and nitrogen forms on plant nitrogen utilization and the influencing factors in a pepper-common bean intercropping system. Chinese Journal of Eco-Agriculture 28, 245–254.

Malezieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., de Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: concepts, tools and models. A review. Agronomy for Sustainable Development 29, 43–62.

Martins, M.A., Cruz, A.F., 1998. The role of the external mycelial network of arbuscular mycorrhizal fungi: III. A study of nitrogen transfer between plants interconnected by a common mycelium. Revista de Microbiologia 29, 289–294.

Martins, M.A., Read, D.J., 1996. The role of the external mycelial network of arbuscular mycorrhizal (AM) fungi. 2. A study of phosphorous transfer between plants interconnected by a common mycelium. Revista de Microbiologia 27, 100–105.

Meding, S.M., Zasoski, R.J., 2008. Hyphal-mediated transfer of nitrate, arsenic, cesium, rubidium, and strontium between arbuscular mycorrhizal forbs and grasses from a California oak woodland. Soil Biology & Biochemistry 40, 126–134.

Menezes, K.M.S., Silva, D.K.A., Queiroz, M.A.A., Felix, W.P., Yano-Melon, A.M., 2016. Arbuscular mycorrhizal fungal communities in buffelgrass pasture under intercropping and shading systems in Brazilian semiarid conditions. Agriculture, Ecosystems & Environment 230, 55–67.

Meng, L., Zhang, A., Wang, F., Han, X., Wang, D., Li, S., 2015. Arbuscular mycorrhizal fungi and rhizobium facilitate nitrogen uptake and transfer in soybean/maize intercropping system. Frontiers in Plant Science 6, 339.

Montesinos-Navarro, A., Segarra-Moragues, J.G., Valiente-Banuet, A., Verdu, M., 2012. Plant facilitation occurs between species differing in their associated arbuscular mycorrhizal fungi. New Phytologist 196, 835–844.

Montesinos-Navarro, A., Valiente-Banuet, A., Verdu, M., 2019. Processes underlying the effect of mycorrhizal symbiosis on plant-plant interactions. Fungal Ecology 40, 98–106.

Montesinos-Navarro, A., Verdu, M., Querejetac, J.I., Sortibran, L., Valiente-Banuet, A., 2016. Soil fungi promote nitrogen transfer among plants involved in long-lasting facilitative interactions. Perspectives in Plant Ecology, Evolution and Systematics 18, 45–51.

Moora, M., 2014. Mycorrhizal traits and plant communities: perspec-tives for integration. Journal of Vegetation Science 25, 1126–1132.

Njira, K.O.W., Semu, E., Mrema, J.P., Nalivata, P.C., 2017. Pigeon pea and cowpea-based cropping systems improve vesicular arbuscular mycorrhizal fungal colonisation of subsequent maize on the alfisols in central Malawi. International Journal of Microbiology 2017, 2096314.

Pereira, A.P.D., Santana, M.C., Bonfim, J.A., Mescolotti, D.D., Cardoso, E., 2018. Digging deeper to study the distribution of mycorrhizal arbuscular fungi along the soil profile in pure and mixed *Eucalyptus grandis* and *Acacia mangium* plantations. Applied Soil Ecology 128, 1–11.

Qiao, X., Bei, S., Li, C., Dong, Y., Li, H., Christie, P., Zhang, F., Zhang, J., 2015. Enhancement of faba bean competitive ability by arbuscular mycorrhizal fungi is highly correlated with dynamic nutrient acquisition by competing wheat. Scientific Reports 5, 8122.

Qiao, X., Bei, S., Li, H., Christie, P., Zhang, F., Zhang, J., 2016. Arbuscular mycorrhizal fungi contribute to overyielding by enhancing crop biomass while suppressing weed biomass in intercropping systems. Plant and Soil 406, 173–185.

Rajeshkumar, P.P., Thomas, G.V., Gupta, A., Gopal, M., 2015. Diversity, richness and degree of colonization of arbuscular mycorrhizal fungi in coconut cultivated along with intercrops in high productive zone of Kerala, India. Symbiosis 65, 125–141.

Ren, H., Gao, T., Hu, J., Yang, G., 2017. The effects of arbuscular mycorrhizal fungi and root interaction on the competition between *Trifolium repens* and *Lolium perenne.* PeerJ 5, e4183.

Ren, L., Lou, Y., Zhang, N., Zhu, X., Hao, W., Sun, S., Shen, Q., Xu, G., 2013. Role of arbuscular mycorrhizal network in carbon and phosphorus transfer between plants. Biology and Fertility of Soils 49, 3–11.

Robinson, D., Fitter, A., 1999. The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. Journal of Experimental Botany 50, 9–13.

Schuman, M.C., Baldwin, I.T., 2018. Field studies reveal functions of chemical mediators in plant interactions. Chemical Society Reviews 47, 5338–5353.

Shan, M., Qin, H., Chen, J., Xu, Q., 2018. Effects of two different intercropping systems on arbuscular mycorrhizal fungal colonization and polychlorinated biphenyl (PCB) dissipation. Chinese Journal of Applied and Environmental Biology 24, 470–477.

Shukla, A., Kumar, A., Chaturvedi, O.P., Nagori, T., Kumar, N., Gupta, A., 2018. Efficacy of rhizobial and phosphate-solubilizing bacteria and arbuscular mycorrhizal fungi to ameliorate shade response on six pulse crops. Agroforestry Systems 92, 499–509.

Simard, S.W., Durall, D.M., 2004. Mycorrhizal networks: a review of their extent, function, and importance. Canadian Journal of Botany 82, 1140–1165.

Singh, D., Mathimaran, N., Boller, T., Kahmen, A., 2019. Bioirrigation: a common mycorrhizal network facilitates the water transfer from deep-rooted pigeon pea to shallow-rooted finger millet under drought. Plant and Soil 440, 277–292.

Singh, D., Mathimaran, N., Boller, T., Kahmen, A., 2020. Deep-rooted pigeon pea promotes the water relations and survival of shallow-rooted finger millet during drought—Despite strong competitive interactions at ambient water availability. PLoS One 15, e0228993.

Smith, S.E., Facelli, E., Pope, S., Smith, F.A., 2010. Plant perfor-mance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. Plant and Soil 326, 3–20.

Smith, S.E., Read, D., 2008. Mycorrhizal Symbiosis, 3rd edition. Landon: Academic Press.

Song, Y., Chen, D., Lu, K., Sun, Z., Zeng, R., 2015. Enhanced tomato disease resistance primed by arbuscular mycorrhizal fungus. Frontiers in Plant Science 6, 786.

Song, Y.Y., Zeng, R.S., Xu, J.F., Li, J., Shen, X., Yihdego, W.G., 2010. Interplant communication of tomato plants through underground common mycorrhizal networks. PLoS One 5, e13324.

Tang, X., Bernard, L., Brauman, A., Daufresne, T., Deleporte, P., Desclaux, D., Souche, G., Placella, S.A., Hinsinger, P., 2014. Increase in microbial biomass and phosphorus availability in the rhizosphere of intercropped cereal and legumes under field conditions. Soil Biology & Biochemistry 75, 86–93.

Thevathasan, N.V., Gordon, A.M., 2004. Ecology of tree intercropping systems in the north temperate region: experiences from southern Ontario, Canada. Agroforestry Systems 61, 257–268.

Thilakarathna, M.S., McElroy, M.S., Chapagain, T., Papadopoulos, Y.A., Raizada, M.N., 2016. Belowground nitrogen transfer from legumes to non-legumes under managed herbaceous cropping systems. A review. Agronomy for Sustainable Development 36, 58.

Tong, Y., Gabriel-Neumann, E., Krumbein, A., Ngwene, B., George, E., Schreiner, M., 2015. Interactive effects of arbuscular mycor-rhizal fungi and intercropping with sesame (*Sesamum indicum*) on the glucosinolate profile in broccoli (*Brassica oleracea* var. Italica). Environmental and Experimental Botany 109, 288–295.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosys-tem variability and productivity. Nature 396, 69–72.

van Tuinen, D., Tranchand, E., Hirissou, F., Wipf, D., Courty, P.E., 2020. Carbon partitioning in a walnut-maize agroforestry system through arbuscular mycorrhizal fungi. Rhizosphere 15, 100230.

Vandermeer, J.H., 1989. The Ecology of Intercropping. UK: Cam-bridge University Press.

Wagg, C., Jansa, J., Stadler, M., Schmid, B., van der Heijden, M.G.A., 2011. Mycorrhizal fungal identity and diversity relaxes plant-plant competition. Ecology 92, 1303–1313.

Wahbi, S., Maghraoui, T., Hafidi, M., Sanguin, H., Oufdou, K., Prin, Y., Duponnois, R., Galiana, A., 2016. Enhanced transfer of biologi-cally fixed N from faba bean to intercropped wheat through mycorrhizal symbiosis. Applied Soil Ecology 107, 91–98.

Wang, G., Sheng, L., Zhao, D., Sheng, J., Wang, X., Liao, H., 2016. Allocation of nitrogen and carbon is regulated by nodulation and mycorrhizal networks in soybean/maize intercropping system. Frontiers in Plant Science 7, 1901.

Wang, G., Ye, C., Zhang, J., Koziol, L., Bever, J.D., Li, X., 2019. Asymmetric facilitation induced by inoculation with arbuscular mycorrhizal fungi leads to overyielding in maize/faba bean intercropping. Journal of Plant Interactions 14, 10–20.

Wheeler, T., von Braun, J., 2013. Climate change impacts on global food security. Science 341, 508–513.

Wilson, G.W.T., Hartnett, D.C., Rice, C.W., 2006. Mycorrhizal-mediated phosphorus transfer between tallgrass prairie plants *Sorghastrum nutans* and *Artemisia ludoviciana.* Functional Ecol-ogy 20, 427–435.

Xiao, T., Yang, Q., Ran, W., Xu, G., Shen, Q., 2010. Effect of inoculation with arbuscular mycorrhizal fungus on nitrogen and phosphorus utilization in upland rice-mungbean intercropping system. Agricultural Sciences in China 9, 528–535.

Yang, X., Qin, J., Li, J., Lai, Z., Li, H., 2021. Upland rice intercropping with *Solanum nigrum* inoculated with arbuscular mycorrhizal fungi reduces grain Cd while promoting phytoremediation of Cd-contaminated soil. Journal of Hazardous Materials 406, 124325.

Yao, Q., Li, X., Ai, W., Christie, P., 2003. Bi-directional transfer of phosphorus between red clover and perennial ryegrass via arbuscular mycorrhizal hyphal links. European Journal of Soil Biology 39, 47–54.

Zeng, P., Guo, Z., Xiao, X., Peng, C., 2019. Dynamic response of enzymatic activity and microbial community structure in metal (loid)-contaminated soil with tree-herb intercropping. Geoderma 345, 5–16.

Zhang, H., Wang, X., Gao, Y., Sun, B., 2020a. Short-term N transfer from alfalfa to maize is dependent more on arbuscular mycorrhizal fungi than root exudates in N deficient soil. Plant and Soil 466, 23–41.

Zhang, R., Mu, Y., Li, X., Li, S., Sang, P., Wang, X., Wu, H., Xu, N., 2020b. Response of the arbuscular mycorrhizal fungi diversity and community in maize and soybean rhizosphere soil and roots to intercropping systems with different nitrogen application rates. Science of the Total Environment 740, 139810.

Zhang, X., Ren, B., Wu, S., Sun, Y., Chen, B., Li, R., 2018a. Rhizophagus irregularis influences As and P uptake by alfafa and the neighboring non-host pepperweed growing in an As-contami-nated soil. Journal of Environmental Sciences 67, 36–44.

Zhang, Y., Hu, J., Bai, J., Qin, H., Wang, J., Wang, J., Lin, X., 2019. Intercropping with sunflower and inoculation with arbuscular mycorrhizal fungi promotes growth of garlic chive in metal-contaminated soil at a WEEE-recycling site. Ecotoxicology and Environmental Safety 167, 376–384.

Zhang, Y.C., Zou, Y.N., Liu, L.P., Wu, Q.S., 2018b. Common mycorrhizal networks activate salicylic acid defense responses of trifoliate orange (*Poncirus trifoliata*). Journal of Integrative Plant Biology 61, 1099–1111.