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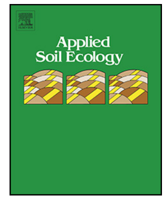

Interactions between arbuscular mycorrhizal fungi and fungivorous nematodes on the growth and arsenic uptake of tobacco in arsenic-contaminated soils

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ABSTRACT

The effects of inoculation with two AM fungi (M1, *Glomus caledonium*; M2, *Glomus* spp. and *Acaulospora* spp.) and a fungivorous nematode *Aphelenchoides* sp. on growth and arsenic (As) uptake of *Nicotiana tabacum* L. were investigated in soils contaminated with a range of As. The reproduction of *Aphelenchoides* sp. was triggered by the co-inoculation of AM fungi regardless of AM fungal isolates and As levels. Stimulative effects of *Aphelenchoides* sp. on the development of mycorrhiza, slightly different between two AM fungi, were found particularly at the lowest As level. Irrespective of mycorrhizal inoculi, increasing soil As level decreased plant growth, but increased plant As uptake. Co-inoculation of AM fungi and *Aphelenchoides* sp. led plants to achieving further growth and greater As accumulation at the lowest As level. Results showed that the interactions between AM fungi and fungivorous nematodes were important in plant As tolerance and phytoextraction at low level As-polluted soil.

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1. Introduction

Arbuscular mycorrhizal (AM) fungi are able to form a symbiotic association with approximately 80% of terrestrial plant species. In general, the growth of host plants will be improved through obtaining nutrients, especially phosphorus (P) via mycorrhizal hypha (Smith and Read, 2008). In addition, some AM fungi also play an important role in heavy metals uptake of host plants grown in contaminated soils (Gaur and Adholeya, 2004; Hildebrandt et al., 2007). For example, remarkable studies have found that mycorrhiza affected arsenic (As) uptake of plants since As transports across the plasma membrane via P transport systems (Li et al., 2013; Orlowska et al., 2012).

As the main soil microorganism in rhizosphere, AM fungi will interact with a wide range of other organisms, including bacteria, fungi, protozoa, arthropods and nematodes (Fitter and Garbaye, 1994). Some of these interactions have shown to be able to influence mycorrhizal behavior and function (Durán et al., 2013; Siddiky et al., 2012). Larsen et al. (2009) found that plant growth promoting species of *Paenibacillus* may have suppressive effects on AM fungi and growth of *Cucumis sativus*. Using ^{15}N and $^{13}CO_2$ labeling technology, Koller et al. (2013a,b) showed that both the root mycorrhizal colonization and the growth of *Plantago lanceolata* L. benefited from the presence of protozoa. As we know, soil nematodes are the most abundant multicellular animals on the planet. Some microbivorous nematodes could play important roles in the turnover of soil microbial biomass and availability of nutrients (Chen and Ferris, 2000; Mao et al., 2007). AM fungi producing substantial extraradical mycelium and spores are excellent feeding resource for fungivorous nematodes (Hussey and Roncadori, 1981). Today, many experiments have provided evidences that the presence of fungivorous nematodes could affect arbuscular mycorrhiza development and 'mycorrhiza effects' by grazing activity (Bakhtiar et al., 2001; Giannakis and Sanders, 1990; Ingham et al., 1985).

Despite the ubiquity of the interplay between AM fungi and other organisms and their importance for plant nutrition and growth, only few studies investigated their interactions on the growth and metal accumulation of plant grown in contaminated soils. Using AM fungal and earthworm cultures, Yu et al. (2005) observed that earthworms modified the functioning of AM fungus–plant symbiosis in Cd polluted soils. Inoculation of earthworms increased mycorrhizal infection rates of roots, shoot yield and Cd uptake of mycorrhizal ryegrass at 5 and 10 mg Cd kg^{-1} soils. Vivas

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et al. (2003) found that *Trifolium repens* dually inoculated with *Brevibacillus* sp. and AM fungi isolated from a Cd polluted soil attained further growth and nutrition and lower Cd concentration, particularly at 85.1 mg Cd kg^{-1} soil. However, few observations have been reported on the interaction between AM fungi and fungivorous nematodes on plant growth and As uptake.

In present study, we have investigated the effects of the inoculation with two isolates of AM fungi and a selected fungivorous nematode on the growth and As accumulation of tobacco plants (*Nicotiana tabacum* L.). AM fungi and nematodes were assayed in single or in co-inoculation in soils contaminated with a range of As. It is hypothesized that the interactions between AM fungi and fungivorous nematodes will stimulate the growth and As uptake of tobacco plants, and different fungal species and different soil As levels might induce differential outcomes.

2. Materials and methods

2.1. Soil and AM fungi and fungivorous nematodes inocula preparation

Soils were collected from agricultural fields near an As sulphide mine (29°39′N, 111°02′E), which has been exploited for more than 1500 years, in Shimen County, Hunan Province, China. This area has a North Asian subtropical maritime monsoon climate, with mean temperature 16.7 °C and average rainfall of about 1500 mm and more than 260 frost-free days.

Three sampling sites were selected: (1) an area at the foot of the mining area with high As content, later abbreviated as H; (2) a location about 2 km from the mining area, M; and (3) a site chosen about 8 km from the mining area, L. The land use in these areas was arable cropping. The dominant crop species was tobacco (*N. tabacum* L.). Soil samples were classified as Ali-Perudic Argosols, and the chemical properties are given in Table 1. All tested soils were air-dried and sieved with nylon mesh (4 mm) and then sterilized by ^{60}Co-irradiation (25 kGy) before a pot experiment.

Two AM fungal isolates were used in this study, *Glomus caledonium* (represented as M1) isolated from an unpolluted agricultural soil in Henan Province, and an indigenous combined inoculum of *Glomus* spp. and *Acaulospora* spp. (represented as M2), wet-sieved from an As-polluted soil in Shimen County, Hunan Province (Bai et al., 2008). These AM fungal species were identified morphologically according to current taxonomic criteria (Schenck and Perez, 1990) and internet information by INVAM (http://invam.caf.wvu.edu). Fungal inocula were propagated on clover (*Trifolium subterraneum* L.) grown in an autoclaved substrate with successive propagation cycle, for 4 months in a greenhouse of the Institute of Soil Science, Chinese Academy of Sciences. Inocula were air-dried and sieved (≤2 mm), and consisted of thoroughly mixed rhizosphere samples containing spores, hyphae and mycorrhizal root fragments.

Fungivorous nematode *Aphelenchoides* sp. was used as a model species. It is eudominant in L, M and H soils with the presence ranging from 11.4% to 36.2% (Hua et al., 2009), and tolerant to As evidenced by a 10 mg L^{-1} As solution test. Worms were collected by cotton wool (Oostenbrink, 1960; Townshend, 1963) from M soil and cultured in petri dishes on Potato Dextrose Agar (PDA) with *Botrytis cinerea* Pers. at 25 ± 0.5 °C. They were collected by the cotton-wool filter method and washed twice with sterile distilled water before use in the experiments (Mao et al., 2007).

2.2. Experimental design

The experiment was designed 3 × 2 × 3 factorial with the following factors: (1) mycorrhizal treatments including assay with two AMF isolates (M1 and M2) and one non-inoculated control treatment; (2) addition or not of fungivorous nematodes; and (3) three levels of As polluted soils, referred to as L, M and H.

Tobacco (*N. tabacum* L.) was seeded into sterilized peat-based seeding substrate on August 4, 2011. At cross stage, the plantlets were carefully transplanted into 3 L plastic pots (one plant per pot) filled with 3.0 kg of dry soil. Each mycorrhizal treatment received 50 g AM fungi inocula at sowing stage. All non-mycorrhizal treatments were treated with the same amount of inocula that had been autoclaved twice at 121 °C for 30 min together with about 20 mL filtrate (<20 μm) of 50 g AM fungi inocula to provide a general microbial population free of AM propagules (Vivas et al., 2003). One week after transplanting, each nematode-added treatment received 2000 *Aphelenchoides* sp. Pots were arranged in randomized complete block design with three replicates per treatment. Plants were grown in a sunlit greenhouse with natural light, a day/night temperature 33/22 °C and relative humidity 40–60%. Plants were watered to maintain soil moisture at 60–70% of water holding capacity by adding deionised water during the experimental period. All plants did not receive any fertilizers during the study period.

2.3. Harvest and measurements

Heights of tobacco plants were recorded, and then roots and shoots were harvested separately after 13 weeks. Sub-samples of fresh roots were taken to assess mycorrhizal colonization. Fresh weights of total roots and of sub-samples were measured. Shoots and remaining roots were first rinsed with tap water and then rinsed with deionised water. Tissues were then weighed after oven drying at 60 °C for 72 h and then ground to <0.25 mm in a stainless steel mill. The water content (%) of remaining roots and total fresh weights of roots were used to estimate dry weights of roots.

Root mycorrhizal colonization was evaluated after clearing and staining (Koske and Gemma, 1989), using the grid-line intersect method (Giovannetti and Mosse, 1980). The length of extraradical mycelium (ERM) in soil was estimated using a modified membrane filtration technique (Jakobsen et al., 1992). A sub-sample of 30 g moist soil was used to determine total numbers of spores at the end of the experiment, using the wet sieving and centrifugation technique (Bakhtiar et al., 2001). *Aphelenchoides* sp. was extracted from 100 g fresh soil of each sample with a cotton-wool filter method. At the same time, water content (%) of each soil sample was determined. After 48 h extraction at room temperature, total numbers of *Aphelenchoides* sp. were counted, and their populations were expressed as the number of individuals per 100 g dry weight soil.

Table 1
Chemical properties of the soils with different As concentrations.

As level	Total As (mg kg^{-1})	pH (H_2O)	Organic C (g kg^{-1})	Total N (g kg^{-1})	Olsen P (mg kg^{-1})	Available K (mg kg^{-1})
L	12.7 ± 0.31	5.98 ± 0.05	31.0 ± 1.03	1.55 ± 0.11	49.5 ± 5.30	373 ± 25.2
M	36.8 ± 0.52	6.57 ± 0.07	28.2 ± 0.75	1.46 ± 0.08	39.8 ± 2.62	353 ± 26.1
H	148 ± 4.01	5.18 ± 0.02	19.6 ± 0.63	0.88 ± 0.09	22.1 ± 1.62	140 ± 19.4

Data presented are means ± standard deviation (n = 3). L, soil low in As level; M, soil medium in As level; H, soil high in As level.

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