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Effects of intercropping of wheat on composition of cucumber seedling rhizosphere fungal community

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ABSTRACT

In pot experiments, we examined the effects of intercropping of wheat on composition of cucumber rhizosphere fungal community. Cucumber rhizosphere fungal composition was analyzed by high-throughput sequencing of total fungal ITS regions. Results showed that intercropping of wheat changed the cucumber seedling rhizosphere fungal community composition. However, cucumber seedlings fungal community alpha diversity was insensitive to intercropping. Compared with monocropped cucumber, intercropped cucumber had higher relative abundance of phylum *Ascomycota* but lower relative abundance of phylum *Zygomycota*. At the genus level, intercropping of wheat increased the relative abundances of *Humicola*, *Waitea*, *Preussia*, *Gibberella*, *Myrothecium* and *Cladorrhinum* spp. but decreased the relative abundances of *Mortierella*, *Chrysosporium*, *Ilyonectria*, *Thielavia* and *Metacordyceps* spp. in cucumber rhizosphere.

Key words: Cucumber, *Cucumis sativus*, fungal community, intercropping, monocropping, rhizosphere, *Triticum aestivum*, wheat

INTRODUCTION

In agricultural ecosystems, continuous monocropping on the same land negatively affects the crop growth and decreases the crop yield, a phenomenon known as ‘soil sickness’ (6,15,46). Soil sickness has been reported for several crops, [peanut (*Arachis hypogaea*) (14), corn (*Zea mays*) (10), Jerusalem artichoke (*Helianthus tuberosus*) (40,45), tea (*Camellia sinensis*) (16) and cucumber (*Cucumis sativus*) (41,44)]. The accumulation of autotoxic compounds, build-up of soil-borne pathogens, changes in soil microbial communities are major possible factors contributing to soil sickness (3,38).

Agricultural productivity relies on wide range of ecosystem services provided by soil microorganisms (8,24,39). Importantly, while some soil microorganisms are pathogenic to plants others can inhibit the soil pathogens and promotes plants growth (1,11,17,26). Also, one plant species can influence the performance of another by releasing secondary metabolites through root exudates and plant litter decomposition (6). These substances can directly affect the plant growth or indirectly through changing the soil microbial communities (6,38,46). For example, crop rotation induces changes in soil microbial communities that have positive effects on plants growth (38). *p*-Coumaric acid, a phenolic autotoxin of cucumber, changes the cucumber rhizosphere microbial communities, which exert negative effects on cucumber growth (46).

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Previous studies have shown that diversified cropping practices (intercropping, crop rotation and use of cover crop or green manure) can alleviate the soil sickness (2,13,22,34,38). For example, rotation of tomato-celery-cucumber-Chinese cabbage and intercropping of onion or garlic with cucumber could over comes the soil sickness of cucumber (38,44). Wheat is an annual crop with allelopathy potential (12,18). Previously, we found that leachates of decomposing wheat (*Triticum aestivum* L) straws inhibit the growth of *Fusarium oxysporum* f.sp. *cucumerinum* (FOC), the casual agent of the cucumber Fusarium wilt disease (32). Intercropping of wheat inhibited the cucumber Fusarium wilt disease and changed the cucumber rhizosphere bacterial community composition (unpublished data). However, the influence of intercropping of wheat on cucumber rhizosphere fungal communities is not clear. In the present study, we examined the cucumber rhizosphere fungal community composition as affected by intercropping of wheat by high-throughput Illumina sequencing of fungal ITS regions.

MATERIALS AND METHODS

Greenhouse experiment

Soil used in this study was collected from the upper soil layer (0-15 cms) of a greenhouse cultivated with cucumber in Experimental Station, Northeast Agricultural University, Harbin, China (45°41’N, 126°37’E). The soil was sandy loam, organic matter (3.51 %); inorganic N (NH_4^+-N and NO_3^--N), 146.60 mg/kg; Olsen P, 284.20 mg/kg; available K, 341.80 mg/kg; EC (1:2.5, w/v), 0.43 mS/cm; and pH (1:2.5, w/v), 7.64. Methods used to determine these soil parameters were described before (46). Soils were sieved (2 mm), hence, large stones and plant debris were removed.

Cucumber seeds (cv. Jinyan 4) were soaked in water at 55°C for 30 min and then germinated in sand in growth chamber at 25°C. After emergence, cucumber seedlings with two cotyledons were transplanted into plastic pots (20 cms dia, 17 cms height) containing 2.5 kg fresh powdered soil. Three seedlings were transplanted per pot. Three days later, cucumber seedlings were thinned to one plant per pot. Ten days after transplanting of cucumber, wheat seeds (PZ25) were directly sown into pots on one side of cucumber seedlings. There were 20 wheat seeds in each pot and the distance between wheat and cucumber seedlings was about 7 cms. Five days after wheat sowing, wheat seedlings were thinned to 15 plants per pot. There were two treatments in this study, cucumber monocropping and cucumber intercropped with wheat. There were five pots per treatment and the experiment was repeated thrice. All pots were randomly placed in greenhouse (32°C day/22°C night, relative humidity: 60-80%, 16 h light/8 h dark). Soil water content was maintained at about 65 % water holding capacity.

Rhizosphere soil sampling and DNA extraction

Thirty days after transplanting, cucumber rhizosphere soil samples were collected from five plants in each replicate as described before (46). Total soil DNA was extracted with the Power Soil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, USA) as per the manufacturer’s instructions**.**

Illumina Miseq sequencing and data processing

The ITS1 regions of the fungal rRNA gene were amplified with primer sets of ITS1F/ITS2 as described before (38). Both the forward and reverse primers also had a 6-

bp barcode unique to each sample. Each soil sample was independently amplified. Three technically replicated PCR reactions were performed for each soil DNA as suggested before (28,29). The products of the triplicate PCR reactions were pooled and purified using the agarose Gel DNA purification kit (TaKaRa). Then, purified amplicons were quantified by a TBS-380 micro fluorometer with Picogreen reagent (Invitrogen, USA) and mixed accordingly to achieve the equal concentration in the final mixture. The mixture was then paired-end sequenced (2×300) on an Illumina Miseq platform at Majorbio Bio-Pharm Technology Co., Ltd., Shanghai, China.

Raw sequence reads were de-multiplexed, quality-filtered and processed using FLASH as described before (38). Chimeric sequences were identified and removed using USEARCH 6.1 in QIIME. Sequences were binned to Operational taxonomic units (OTUs) at 97% sequence similarity with USEARCH using an agglomerative clustering algorithm. Then, a representative sequence of each OTU was taxonomically classified through BLAST against the Unite database.

Statistical analysis

To avoid potential bias caused by sequencing depth, a random subsampling effort of 30,735 ITS gene sequences per sample was performed. The defined OTUs were used to calculate taxon accumulation curves with the ‘vegan’ package in ‘R’ (Version 3.3.1). For alpha diversity analysis, Chao, ACE and Shannon index were calculated with the 'phyloseq' package in ‘R’ (Version 3.3.1). For beta diversity, principal coordinates analysis (PCoA) was performed to determine differences in microbial community structures based on Bray-Curtis distances with the ‘vegan’ package in ‘R’ (Version 3.3.1). Differences in alpha diversity indices and relative abundances of microbial taxa between treatments were analyzed using Welch’s *t* test in ‘R’ (Version 3.3.1).

RESULTS AND DISCUSSION

Illumina Miseq sequencing data

Across all soil samples, Illumina Miseq sequencing yielded 224,054 quality fungal sequences, with 31,026-42,665 fungal sequences per sample. The average read length of the ITS1 regions s was 260 bp. A total of 416 OTUs were identified at 97% sequence similarity. Rarefaction curves of OTUs at 97% sequence similarity of all samples tended to approach the saturation plateau (Fig. 1a). The Good’s coverage of each sample, which reflects the captured diversity, was 99.80±0.03% (Fig. 1b). Therefore, our Illumina Miseq sequencing data were enough for community analysis.

Taxonomic characteristics of fungal communities

Across all samples, three fungal phyla were detected and 1.11% sequences were unclassified at this level (Fig. 2a). *Ascomycota* and *Zygomycota* were the dominant phyla, which accounted for 83.80% and 13.86% of the total fungal sequences, respectively. Compared with monocropped cucumber, intercropped cucumber had higher relative abundance of *Ascomycota* but lower relative abundance of *Zygomycota* ($P<0.05$).

At the class level, *Sordariomycetes*, *Pezizomycetes* and *Zygomycetes* were the dominant classes (average relative abundance >10%) (Fig. 2b). These four classes accounted for more than 92.21% of the total fungal sequences. *Ascomycota Incertae sedis*, *Eurotiomycetes*, *Tremellomycetes*, *Agaricomycetes* and *Dothideomycetes* were also

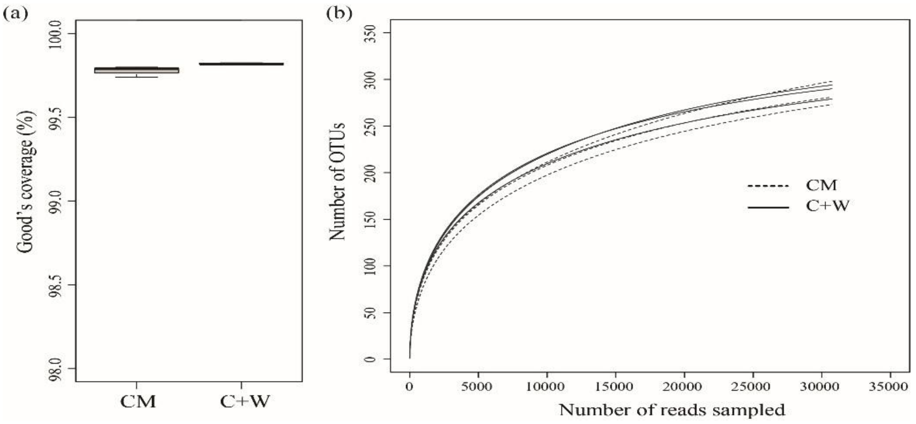

Figure 1. The Good's coverage (a) and rarefaction curves of the number of OTUs (b) of rhizosphere fungal community.
CM: Cucumber monocropping, C+W: Cucumber intercropped with wheat.

detected at relatively high abundances (average relative abundance >0.3%) (Fig. 2b). Compared with monocropped cucumber, intercropped cucumber had higher relative abundance of *Dothideomycetes* but lower relative abundance of *Zygomycota* (P<0.05).

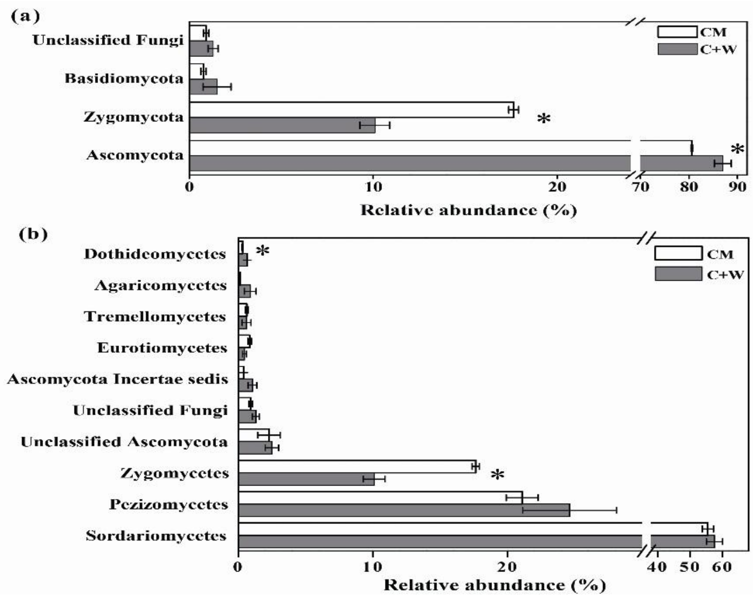

Figure 2. Relative abundances of fungal phyla (a) and main fungal classes (b, average relative abundances >0.3%). CM and C+W represent the treatments of cucumber monocropping and cucumber intercropped with wheat, respectively. Asterisks indicate significant difference between treatments based on Welch's *t* test (P<0.05).

More than 140 fungal genera were detected across all samples analyzed (data not shown). Among the classified genera, *Pseudallescheria*, *Mortierella*, *Fusarium*, *Pseudaleuria*, *Humicola*, *Kernia* and *Acremonium* spp. had mean relative abundances higher than 1.0% (Fig. 3a, b). Compared with monocropped cucumber, intercropped cucumber had higher relative abundances of *Humicola*, *Waitea*, *Preussia*, *Gibberella*, *Myrothecium* and *Cladorrhinum* spp. but lower relative abundances of *Mortierella*, *Chrysosporium*, *Ilyonectria*, *Thielavia* and *Metacordyceps* spp. ($P < 0.05$).

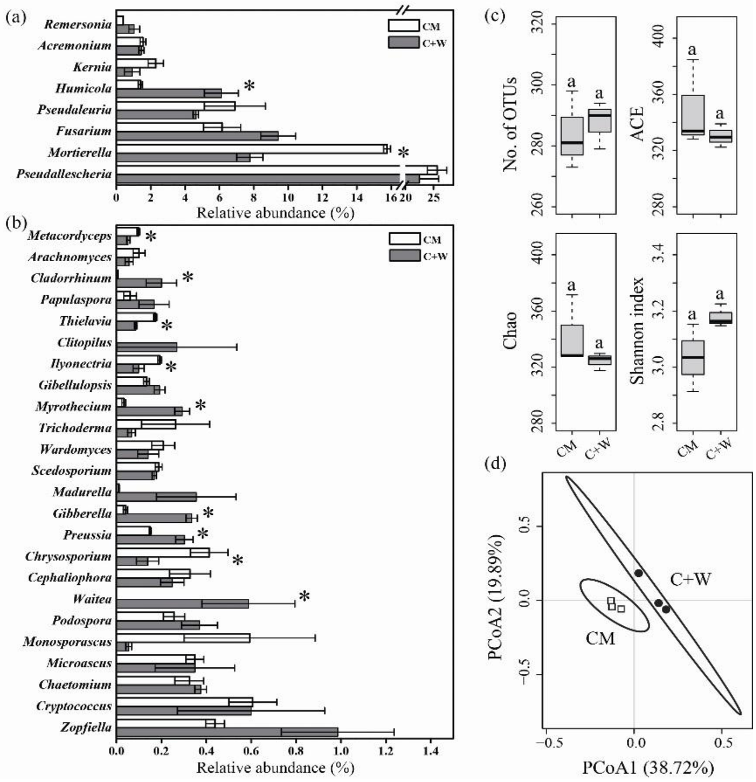

Figure 3. Relative abundances of main classified fungal genera (a, b), fungal community alpha (c) and beta diversities (d).

Fungal genera with average relative abundances >1.0% (a) and >0.1% (b) in at least one sample are shown. CM and C+W represent the treatments of cucumber monocropping and cucumber intercropped with wheat, respectively. Asterisks indicate significant difference between treatments based on Welch's *t* test ($P<0.05$).

Crop disease index and soil-borne pathogen abundances usually increase in continuous monocropping systems (20,38,44). For example, the abundance of FOC was higher in the cucumber monocropping system than in tomato-celery-cucumber-Chinese cabbage rotation system (38). In the present study, intercropping of wheat decreased the relative abundances of several fungal taxa that contained potential plant pathogens in cucumber rhizosphere, such as *Ilyonectria* (31) and *Thielavia* spp. (25) and increased the relative abundances of several fungal taxa with antifungal and plant-growth promoting potentials, such as *Waitea* (5), *Preussia* (23) and *Cladorrhinum* spp. (9). These changes in these fungal taxa may contribute to the suppression of cucumber Fusarium wilt disease by intercropping of wheat (unpublished data).

The accumulation of autotoxic compounds is one of the major possible factors contributing to soil sickness (3,38). In this study, we found that intercropping of wheat increased the relative abundances of several fungal taxa with phenolic compound-degrading capability in cucumber rhizosphere, such as *Humicola* (7), *Preussia* (30) and *Myrothecium* (27) spp. Previous studies demonstrated that phenolic autotoxins were able to change the cucumber rhizosphere microbial compositions and especially, decreased the abundances of plant-beneficial microorganisms (15,35-37,42,43,46,47). For example, autotoxic phenolic compound syringic acid decreased the *Preussia* spp. in cucumber rhizosphere (33). In this study, *Preussia* spp. in cucumber rhizosphere was stimulated by intercropping of wheat. It was demonstrated that interspecific plant interactions are able to change the plant secondary metabolism (4,19,21). Therefore, it is possible that intercropping of wheat could stimulate the phenolic compound-degrading microbes in cucumber rhizosphere and, thus, alleviate the autotoxicity of phenolic compounds. However, future research should be done to verify this by measuring phenolic compound contents in cucumber rhizosphere.

Alpha and beta diversities of fungal communities

For fungal community alpha diversity in cucumber rhizosphere, the number of OTUs, ACE, Chao and Shannon indices were similar between the treatments of monocropping and intercropping (Fig. 3c). For fungal community beta diversity, PCoA analysis, based on the Bray-Curtis distance dissimilarity, clearly separated the two treatments from each other (Fig. 3d). The first two axes together accounted for 58.61% of the variation.

Soil microbial community composition and its function are tightly linked and changes in soil microbial community composition may alter the functions performed by the community and thus have feedbacks on plant health and fitness (3,38,39). In agricultural ecosystems, diversified cropping practices can promote the crop growth through altering the soil microbial communities. For example, tomato-celery-cucumber-Chinese cabbage rotation changed the soil microbial community composition and enhanced the soil microbial community's function to support cucumber growth (38). Changes in cucumber rhizosphere fungal community composition induced by intercropping of wheat, may have functional consequences on cucumber, which should be further illustrated.

CONCLUSIONS

Intercropping of wheat changed the cucumber seedling rhizosphere fungal community composition but had no significant effects on cucumber seedling fungal community richness and diversity indices. Specifically, intercropping of wheat decreased the relative abundances of fungal taxa that contained potential plant pathogens in cucumber rhizosphere and increased the relative abundances of fungal taxa with antifungal and plant-growth promoting potentials taxa with phenolic compound-degrading capability in cucumber rhizosphere.

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