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RESEARCH ARTICLE



Effects of vanillin on the community structures and abundances of *Fusarium* and *Trichoderma* spp. in cucumber seedling rhizosphere

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ABSTRACT

Soil microbial communities are crucial to the functioning of agricultural systems but little information is available on the effects of allelochemicals on soil microorganisms in vivo. Cucumber seedlings grown in soil were treated with different concentrations of vanillin (0.02–0.2 $\mu\text{mol/g}$ soil), a phenolic compound with autotoxic activity. The community structures and abundances of *Fusarium* and *Trichoderma* spp. in cucumber rhizosphere were analyzed by polymerase chain reaction (PCR)-denaturing gradient gel electrophoresis and quantitative PCR, respectively. Results showed that vanillin changed the community structures of *Fusarium* and *Trichoderma* spp. Vanillin decreased the number of bands of *Fusarium* spp., but increased the number of bands, Shannon–Wiener and evenness indices of *Trichoderma* spp. ($p < .05$). Vanillin at all concentrations promoted the abundances of *Fusarium* and *Trichoderma* spp. ($p < .05$), and this stimulating effects increased with increasing concentration of vanillin. Overall, this study provided primary evidence that vanillin changed the community structures and abundances of *Fusarium* and *Trichoderma* spp., and that these two microbial groups showed different responses to vanillin.

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Autotoxicity; *Cucumis sativus* L.; *Fusarium* spp.; *Trichoderma* spp.; vanillin

Introduction

In agricultural ecosystems, continuous monocropping of the same crop in the same land usually negatively affect crop growth, a phenomenon known as ‘soil sickness’ (Bever et al. 2012; Huang et al. 2013; Trezzi et al. 2016). Several economically important crops, such as rice (*Oryza sativa* L.) (Kreye et al. 2009), corn (*Zea mays* L.) (Gentry et al. 2013), cucumber (*Cucumis sativus* L.) (Zhou et al. 2011; Zhou, Liu, et al. 2017) and Jerusalem artichoke (*Helianthus tuberosus* L.) (Zhou et al. 2016; Zhou, Zhang, et al. 2017) were reported to suffer from the yield penalty caused by soil sickness. Possible factors contributing to soil sickness include build-up of soil-borne pathogens, deterioration of soil physico-chemical characters and accumulation of allelochemicals (Yu et al. 2000; Zhou et al. 2012). However, little is currently known about the interactions among these contributing factors.

Soil microorganisms are vital to the functioning and sustainability of agroecosystems and are sensitive to land management practices, such as cropping system, tillage, irrigation and fertilization (Mendes et al. 2011; Zhou et al. 2011; Zhou, Liu, et al. 2017). It has been shown that crop monocropping could negatively affect soil microbial communities, such as decreasing the activity and diversity of soil microbial communities, changing the composition of soil microbial communities and promoting soil-borne pathogens (Singh et al. 1999; Huang et al. 2013). Phenolic compounds, which are detected in root exudates and decomposing plant debris, are a type of allelochemical that could exert detrimental effects on plant growth (Inderjit and Duke 2003). Recent studies also indicated that phenolic compounds could act as specific substrates or signaling molecules for a large group of microbial species in the soil (Badri et al. 2013). However,

how phenolic compounds affect soil microbial communities are still not well understood.

Fusarium and *Trichoderma* spp. are filamentous ascomycete fungi that contain many species of environmental, agricultural and human health importance (Harman et al. 2004; Ma et al. 2013). Many species of *Fusarium* spp. are phytopathogenic fungi, which can infect a wide range of crop plants and cause vascular wilt diseases (Ma et al. 2013). *Trichoderma* spp. are opportunistic, avirulent plant symbionts, as well as being parasites of other fungi and have the ability to control plant pathogenic fungi and promote plant growth and development (Harman 2006). Cucumber, one of the most popular vegetables throughout the world, is commonly continuously cropped in the greenhouse. Phenolic compounds are proposed to account for the autotoxicity of cucumber (Yu et al. 2000). Previously, we reported that vanillin accumulated in the soil after continuous monocropping of cucumber (Zhou et al. 2012), and exogenous vanillin changed the whole fungal community structure (Zhou et al. 2015). This study aimed to further evaluate the effects of externally added vanillin on the community structures and abundances of *Fusarium* and *Trichoderma* spp. in cucumber rhizosphere with polymerase chain reaction (PCR)-denaturing gradient gel electrophoresis (DGGE) and quantitative PCR, respectively.

Materials and methods

Greenhouse experiment

The soil used in this experiment was collected from the upper soil layer (0–15 cm) of an open field in the experimental station of Northeast Agricultural University, Harbin, China (45°41'N, 126°37'E), which was covered with grasses and undisturbed for more than 15 years. The soil has a sandy

loam texture, contained organic matter, 3.67%; available N, 89.02 mg/kg; Olsen P, 63.36 mg/kg; available K, 119.15 mg/kg; EC (1:2.5, w/v), 0.33 mS/cm and pH (1:2.5, w/v), 7.78. Cucumber seedlings (cv. Jinlv 3) with two cotyledons were transplanted into pots, which contained 150 g soil. There was one cucumber seedling per pot. No fertilizer was added to the soil. Cucumber seedlings were maintained in a greenhouse (32°C day/22°C night, relative humidity of 60–80%, 16 h light/8 h dark).

Cucumber seedlings at the one-leaf stage were treated with different concentrations of vanillin (0.02, 0.05, 0.1, 0.2 µmol/g soil DW) every two days for five times. The final concentration added in each treatment was 0.1, 0.25, 0.5, and 1.0 µmol/g soil DW, respectively. The solution pH was adjusted to 7.0 with 0.1 M NaOH solution because the soil pH is widely accepted as a dominant factor that regulates soil microbial communities (Fierer and Jackson 2006). Cucumber seedlings treated with distilled water was served as the control. Soil water content was adjusted every two days with distilled water to maintain a constant weight of pots. There were five treatments (four concentrations of vanillin and one control) in total. Each treatment had five plants and was done in triplicate.

Rhizosphere soil sampling and DNA extraction

Ten days after the first application of vanillin, cucumber rhizosphere soil samples were collected from five plants in each replicate as described before (Zhou et al. 2011). Soil samples were stored at –70°C and total soil DNA was extracted with the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, USA) as per the manufacturer's instructions.

PCR–DGGE analysis

Community structures of *Fusarium* and *Trichoderma* spp. were analyzed by the PCR–DGGE method. Nested PCR protocols were used to amplify the *Fusarium* spp. *Ef1α* genes and *Trichoderma* spp. partial ITS regions. Primer sets of ITS1F/ITS4TrR and ITSTrF-GC/ITSTrR (Meincke et al. 2010) were used for *Trichoderma* ITS regions, EF-1/EF-2 (O'Donnell et al. 1998) and Alfie1-GC/Alfie2 (Yergeau et al. 2005) were used for *Fusarium* *Ef1α* genes in the first and second round of PCR amplifications, respectively.

DGGE analysis of *Trichoderma* spp. ITS regions was on a 6–9% (w/v) acrylamide gel with 30–60% denaturant gradient (Meincke et al. 2010), and *Fusarium* spp. *Ef1α* genes on a 6% (w/v) acrylamide gel with 40–60% denaturant gradient (Wakelin et al. 2008; Zhou and Wu 2012a). Gels were run in a 1 × TAE (Tris–acetate–EDTA) buffer for 12 h under conditions of 60°C and 80 V with a DCode universal mutation detection system (Bio-Rad Lab, LA, USA). After the electrophoresis, gels were stained with 1:3300 (v/v) GelRed (Biotium, USA) nucleic acid staining solution for 20 min. DGGE profiles were photographed with an AlphaImager HP imaging system (Alpha Innotech Corp., CA, USA) under UV light.

Quantitative PCR assay

Abundances of *Fusarium* and *Trichoderma* spp. were estimated by SYBR Green qPCR assays with an IQ5 real-time PCR system (Bio-Rad Lab, LA, USA). *Trichoderma* spp.

partial ITS regions were quantified with primer set of uTr/uTr (Hagn et al. 2007) as described before (Drigo et al. 2009; Zhou, Zhang, et al. 2017). For *Fusarium* spp., the *Ef1α* gene was nested amplified with EF-1/EF-2 (O'Donnell et al. 1998) and Alfie1/Alfie2 (Yergeau et al. 2005) in the first and second round of PCR amplifications, respectively, as described by Yergeau et al. (2005). Care was made to ensure that first-round PCR products were all in exponential amplification phase of the PCR (Wakelin et al. 2008). For *Trichoderma* spp., standard curves were created with 10-fold dilution series of plasmids containing the ITS regions from soil samples. Threshold cycle (*Ct*) values obtained for each sample were compared with the standard curve to determine the initial copy number of the target gene. The relative *Fusarium* spp. community abundance was calculated as describes by Wakelin et al. (2008) and then, all treatments were compared with the control soil and expressed as the percentage of the abundance in the control soil. Sterile water was used as a negative control to replace the template. All amplifications were performed in triplicate. The specificity of the products was confirmed by melting curve analysis and agarose gel electrophoresis.

Statistical analysis

Banding patterns of the DGGE profiles were analyzed using Quantity One V4.5 (Bio-Rad Lab, LA, USA). The position and intensity of each band were determined automatically. The density value of each band was divided by the average band density of the lane in order to minimize the influence of loaded DNA concentrations among samples (Zhou et al. 2011). Principal component analysis (PCA) was used to compare the banding patterns between samples with normalized data using Canoco for Windows 4.5 software (Plant Research International, Wageningen, the Netherlands) as described before (Zhou et al. 2011, 2016). Analysis of similarities (ANOSIM) was used to test the overall effect of treatment on microbial community structures with normalized data using the Vegan package in 'R' (Oksanen et al. 2014). The microbial community diversity indices, including a number of bands (*S*), Shannon–Wiener index (*H*) and evenness index (*E*), were calculated as described before (Zhou et al. 2011, 2016). Data were analyzed following analysis of variance and mean comparison between treatments was performed based on the Tukey's honestly significant difference test at 0.05 probability level. Linear regressions were used to test the relationships between cucumber seedling dry biomass, which was reported before (Zhou et al. 2015), and rhizosphere microbial community abundances and diversity indices in 'R'.

Results

Community structure of *Fusarium* spp.

Visual inspection found that banding patterns of *Fusarium* spp. DGGE profiles in cucumber rhizosphere were broadly similar in triplicate samples of each treatment but were different among treatments, especially for the upper part of the profiles (Figure 1(a)). In total, 22 unique DGGE banding positions were identified for the *Fusarium* spp. Compared with cucumber rhizosphere treated with water, cucumber rhizosphere treated with vanillin had a higher number of bands

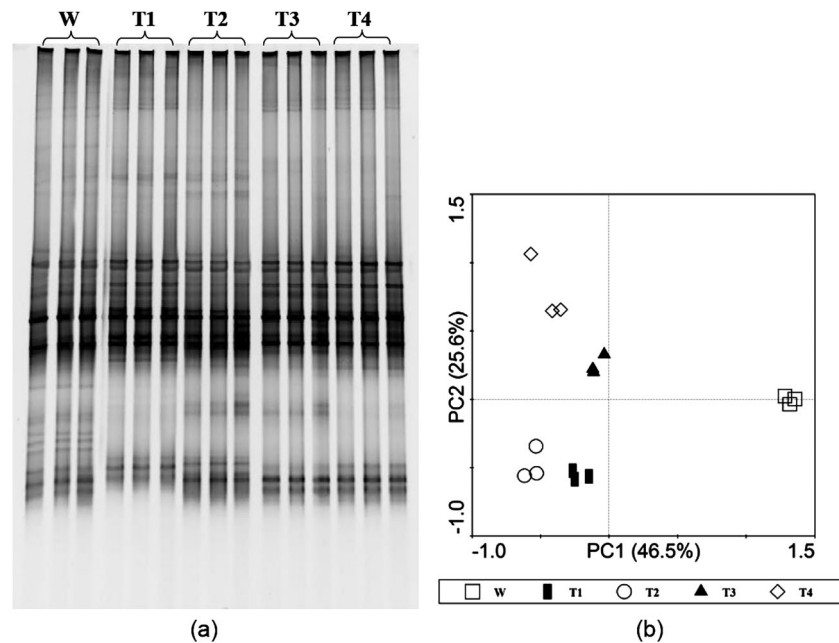


Figure 1. PCR–DGGE profile (a) and PCA analysis (b) of *Fusarium* spp. in cucumber rhizosphere treated with water (W) and vanillin (T). T1, T2, T3 and T4 represent samples treated with vanillin at 0.02, 0.05, 0.1 and 0.2 $\mu\text{mol/g}$ soil DW concentrations, respectively.

($p < .05$) (Figure 2(a)). However, Shannon–Wiener and evenness indices did not differ among treatments (Figure 2(b,c)).

PCA analysis of *Fusarium* spp. DGGE banding patterns explained 46.5% and 25.6% of the variation in the first two axes. On the PCA plot, all treatments could be separated from each other, indicating the community structures of *Fusarium* spp. were different among treatments (Figure 1 (b)). Moreover, the treatments of 0.02 and 0.05 $\mu\text{mol/g}$ soil

DW vanillin were closer to each other, and the treatments of 0.1 and 0.2 $\mu\text{mol/g}$ soil DW vanillin were closer to each other. ANOSIM analysis also showed that the community structure of *Fusarium* spp. significantly differed among treatments ($R = 0.984$, $p = .001$).

Community structure of *Trichoderma* spp.

For cucumber rhizosphere *Trichoderma* spp., DGGE banding patterns of triplicate samples per treatment were highly consistent (Figure 3(a)). However, there were differences between treatments, both in terms of the presence/absence of individual DGGE bands and the intensity of co-migrating DGGE bands. A total of 13 unique DNA bands with various intensities were detected in DGGE profiles for the *Trichoderma* spp. The number of bands, Shannon–Wiener and evenness indices were significantly higher in samples treated with vanillin than in samples treated with water ($p < .05$) (Figure 2). Meanwhile, treatments of 0.1 and 0.2 $\mu\text{mol/g}$ soil DW vanillin had higher number of bands, Shannon–Wiener and evenness indices than treatments of 0.02 and 0.05 $\mu\text{mol/g}$ soil DW vanillin ($p < .05$).

PCA analysis of DGGE profiles of *Trichoderma* spp. clearly separated all treatments from each other (Figure 3b). The PC1 and PC2 components together accounted for 72.9% of the variation. ANOSIM analysis confirmed that the community structure of *Trichoderma* spp. significantly differed among treatments ($R = 0.999$, $p = .001$).

Abundances of *Fusarium* and *Trichoderma* spp.

Quantitative PCR showed that all concentrations of vanillin significantly increased the abundances of *Fusarium* and *Trichoderma* spp. in cucumber rhizosphere ($p < .05$) (Figure 4 (a)). Generally, both the abundances of *Fusarium* and *Trichoderma* spp. increased with increasing concentration of vanillin. The abundance of *Fusarium* spp. was similar in cucumber rhizosphere treated with 0.02 and 0.05 $\mu\text{mol/g}$ soil DW vanillin. Cucumber rhizosphere treated with 0.2 $\mu\text{mol/g}$ soil DW

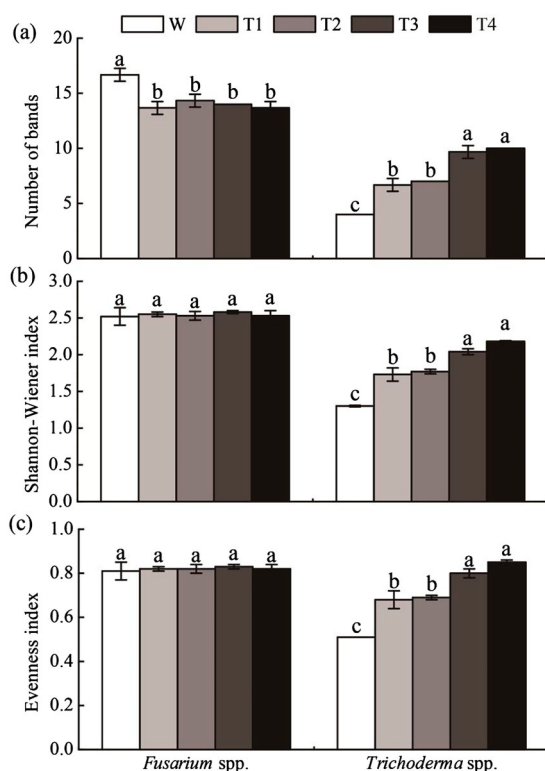


Figure 2. Number of visible bands (a), Shannon–Wiener (b) and evenness indices (c) based on DGGE analysis of *Fusarium* and *Trichoderma* spp. in cucumber rhizosphere. T1, T2, T3 and T4 represent samples treated with vanillin at 0.02, 0.05, 0.1 and 0.2 $\mu\text{mol/g}$ soil DW concentrations, respectively; W represents samples treated with water. Values (mean \pm standard error) with letters are significantly different ($p < .05$, Tukey's HSD test).

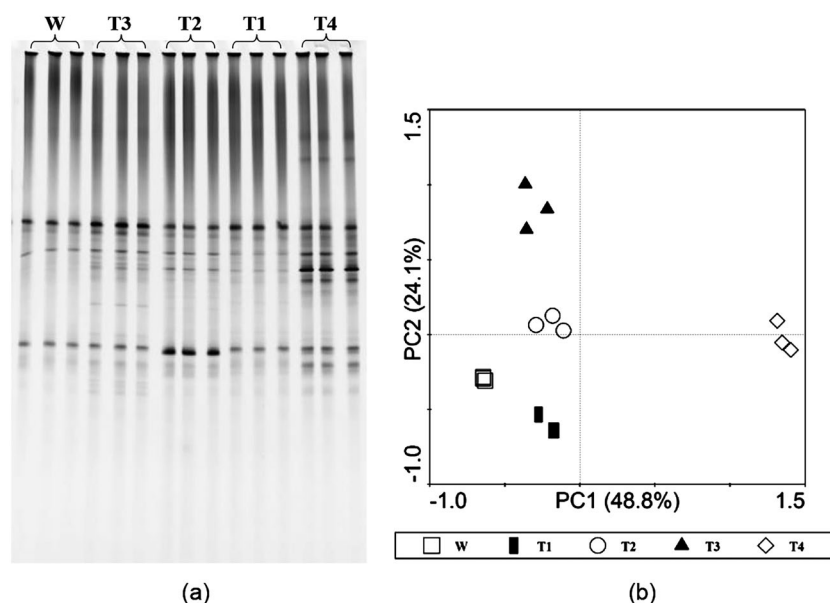


Figure 3. PCR–DGGE profile (a) and PCA analysis (b) of *Trichoderma* spp. in cucumber rhizosphere treated with water (W) and vanillin (T). T1, T2, T3 and T4 represent samples treated with vanillin at 0.02, 0.05, 0.1, 0.2 μmol/g soil DW concentrations, respectively.

vanillin had the highest relative abundance of *Fusarium* spp., which was about 8.98 times of the treatment received water. Cucumber rhizosphere treated with 0.02 and 0.05 μmol/g soil DW vanillin had similar abundance of *Trichoderma* spp., which were lower than soils treated with 0.1 and 0.2 μmol/g soil DW vanillin.

Relationships between cucumber seedling growth and *Fusarium* and *Trichoderma* spp

Linear regression analysis showed that cucumber seedling dry biomass was negatively related to the abundances of *Fusarium* and *Trichoderma* spp. in cucumber rhizosphere ($p < .05$) (Figure 5(a,b)). Moreover, cucumber seedling dry biomass was positively related to the number of visible bands of *Fusarium* spp. ($p < .05$) (Figure 5(c)) but was negatively related to the number of visible bands (c), Shannon–Wiener (b) and evenness indices (c) of *Trichoderma* spp. ($p < .05$) (Figure 5(d–f)).

Discussion

Accumulation of autotoxins has been suggested as an important factor contributing to the stunted growth and increased diseases in monoculture systems (Singh et al. 1999). Phenolic

compounds were shown to have detrimental effects on plant growth by influencing gene expression, cell division and elongation, nutrient uptake, enzyme activities, plant photosynthesis and respiration (Inderjit and Duke 2003; Chi et al. 2013). This study stressed the effects of phenolic compounds on soil microbial communities, which is a key determinant of plant productivity and health in agroecosystems. Our results revealed that vanillin at the concentrations tested (0.02–0.2 μmol/g soil DW) changed the community structures of *Fusarium* and *Trichoderma* spp in cucumber rhizosphere. In particular, vanillin decreased the number of bands in DGGE profile of *Fusarium* spp., but increased the number of visible bands, Shannon–Wiener and evenness indices of *Trichoderma* spp. Therefore, at the whole community level, *Fusarium* and *Trichoderma* spp. responded differently to vanillin.

Quantitative PCR found that vanillin stimulated the abundance of *Fusarium* spp. in cucumber rhizosphere, which were in line with former observations that some species of *Fusarium* spp. can use phenolic compounds as carbon resources (Dao 1987; DeRito and Madsen 2009). Continuous monocropping of cucumber could promote the proliferation of soil-borne pathogen *F. oxysporum* f.sp. *cucumerinum* (FOC), the causing agent of cucumber Fusarium wilt disease (Zhou, Liu, et al. 2017). Zhou and Wu (2012b) found that exogenous phenolic acid promoted the growth of FOC in soil. Michielse et al. (2012) revealed that the ability to metabolize phenolic compounds was required for pathogenicity of the tomato wilt pathogen *F. oxysporum* f. sp. *lycopersici* (FOL). Therefore, accumulated phenolic compounds may be linked to the increased soil-borne diseases in crop continuous monocropping systems.

Though vanillin increased the abundance of *Fusarium* spp., vanillin did not affect the diversity (the Shannon–Wiener index) of the *Fusarium* spp. In *Fusarium* spp. DGGE profiles, some bands disappeared in vanillin-treated samples. These suggested that vanillin promoted some taxa in *Fusarium* spp. while inhibited others. Though *Fusarium* spp. contain phytopathogens, most species in *Fusarium* spp. are saprobes and some species even can protect plants by

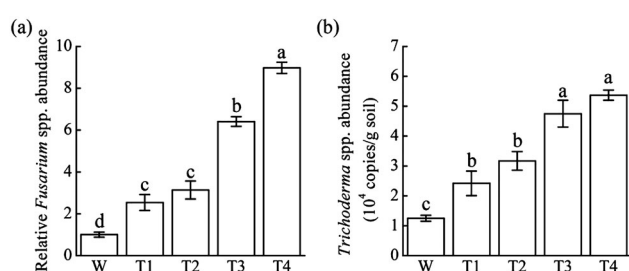


Figure 4. The abundances of *Fusarium* (a) and *Trichoderma* spp. (b) in cucumber rhizosphere treated with water (W) and vanillin (T). T1, T2, T3 and T4 represent samples treated with vanillin at 0.02, 0.05, 0.1 and 0.2 μmol/g soil DW concentrations, respectively. Values with different letters were significantly different between treatments ($P < 0.05$, Tukey's HSD test).

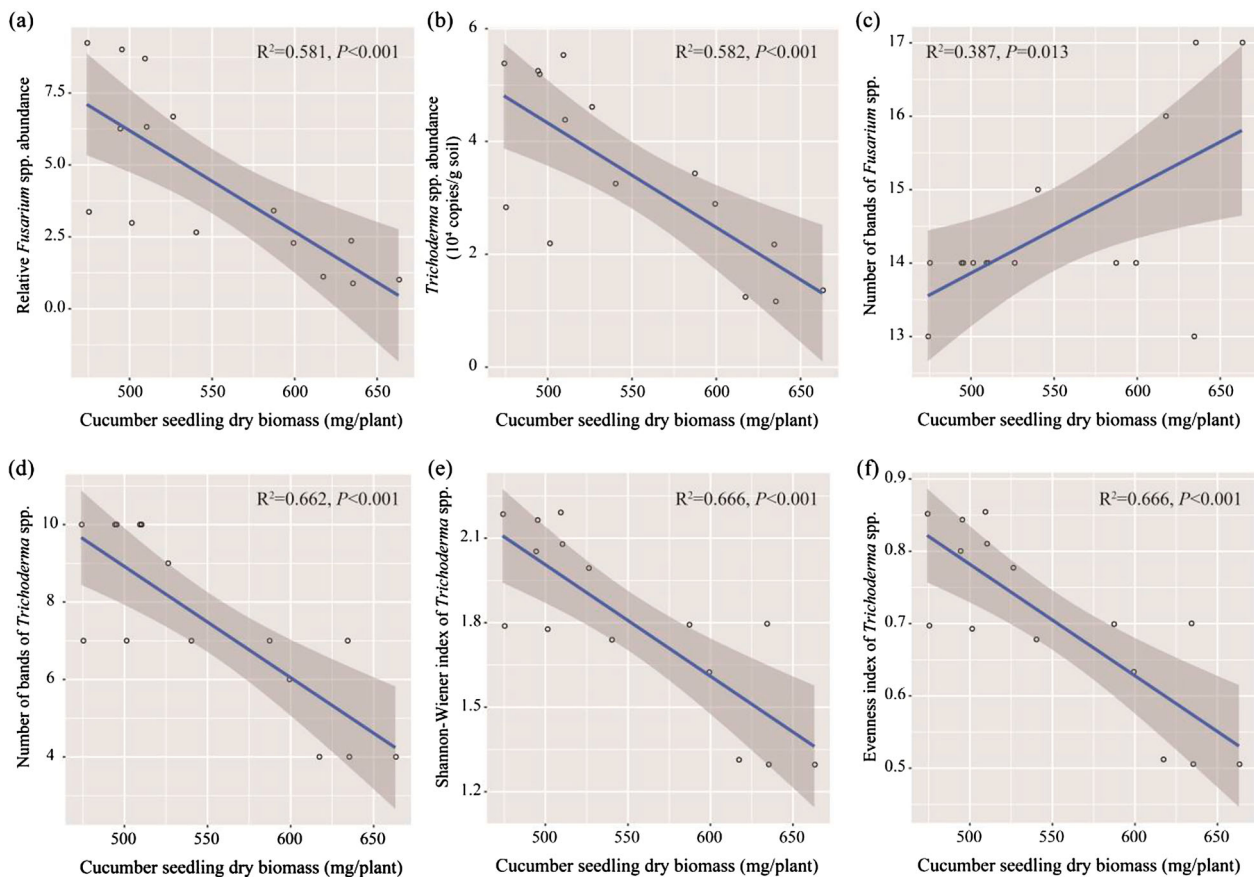


Figure 5. Scatterplots showing the relationships between cucumber seedling dry biomass and the abundances of *Fusarium* spp. (a) and *Trichoderma* spp. (b), number of visible bands of *Fusarium* spp. (c), number of visible bands (d), Shannon–Wiener (e) and evenness indices (f) of *Trichoderma* spp. in cucumber rhizosphere. The blue lines represent linear regression lines and the shaded areas represent 95% confidence intervals.

competing with phytopathogens for infection sites on the root surface and for nutrients and inducing systematic induce systemic resistance in plants (Fuchs et al. 1997). Our previous study found that vanillin significantly inhibited cucumber seedling growth at 0.1 and 0.2 $\mu\text{mol/g}$ soil DW (Zhou et al. 2015). Linear regression analysis showed that cucumber seedling dry biomass was negatively related to the abundance of *Fusarium* spp. but positively related to the number of visible bands of *Fusarium* spp. Therefore, it is possible that vanillin-stimulated taxa of *Fusarium* spp. with pathogenic activities, but inhibited others that are not harmful to cucumber. Our results also supported previous observations from in vitro studies showing that some species of *Fusarium* spp., such as *F. culmorum* and *F. graminearum* (Annelaure et al. 2010; Lanoue et al. 2010) were sensitive to the antimicrobial activity of phenolic compounds, while other pathogenic species, such as FOC and FOL (Michiels et al. 2012; Zhou and Wu 2012b), were able to degrade phenolic compounds.

For cucumber rhizosphere *Trichoderma* spp., vanillin promoted its abundance and Shannon–Wiener index, indicating vanillin selected for specific *Trichoderma* spp. groups in the soil. Some species of *Trichoderma* spp. were able to degrade phenolic compounds (DeRito and Madsen 2009). In particular, Chen et al. (2011) found that *Trichoderma harzianum* SQR-T037 could decompose phenolic compounds released by cucumber roots, thereby relieving the autotoxicity of cucumber. *Trichoderma* spp. are well known for their ability to inhibit plant pathogenic fungi, and enhance plant growth (Harman 2006). For example, previous studies observed that *Trichoderma* spp. were able to inhibit FOC, promote cucumber growth and induce systemic resistance in

cucumber (Shores et al. 2005; Alizadeh et al. 2013; Saravankumar et al. 2016). Linear regression analysis showed that cucumber seedling dry biomass was negatively related to the abundance and diversity of *Trichoderma* spp. These indicated that vanillin may inhibit taxa of *Trichoderma* spp. with plant-beneficial potentials in soil, which should be stressed in the future.

Overall, our results showed that exogenous vanillin, an autotoxin of cucumber, changed *Fusarium* and *Trichoderma* spp. in cucumber seedling rhizosphere. Vanillin changed the community structures of both *Fusarium* spp. and *Trichoderma* spp. Vanillin increased the number of bands, Shannon–Wiener and evenness indices of *Trichoderma* spp. and decreased the number of bands of *Fusarium* spp. ($p < .05$). Vanillin at all concentrations tested significantly promoted the abundances of *Fusarium* and *Trichoderma* spp. Rhizosphere microorganisms are important players in the terrestrial ecosystem and changes in microbial communities can influence the performance of plants (Bever et al. 2012). Therefore, changes in soil microbial communities induced by vanillin may exert feedback effects on cucumber growth, which should be further analyzed.

Disclosure statement

No potential conflict of interest was reported by the authors.

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