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Influence of mixed phenolic acids on bacterial and fungal community in soils growing ginseng and maize

Y.M. Bi[1], G.L. Tian*[1,2], X.L. Jiao[1,3], X.X. Li[1] and W.W. Gao*[1]
School of Environmental and Municipal Engineering,
Tianjin Chengjian University, Tianjin, 300384, China,
E-mail: wwgao411@163.com, geilintian@126.com

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ABSTRACT

Nine phenolic acids (*p*-hydroxybenzoic, vanillic, syringic, *p*-coumaric, ferulic, benzoic, salicylic, cinnamic acids and vanillin) were found present in the soil after American ginseng cultivation. These were added to the soil for growing of American ginseng and maize according to their contents and proportions present in soil. These added phenolic acids were completely degraded by the soil microbes in 3 days. These soils microbial communities were studied by Illumina MiSeq sequencing technique. Results showed that the applied PAs (Phenolic acids) decreased the bacterial and fungal diversity in the rhizosphere soils of both ginseng and maize crops. The microbial diversity was greatly affected by the basic physical and chemical properties of soil. *Acidothermus* bacteria (population 6 %), dominated the bacterial genera while *Penicillium* fungi (population 15%) dominated the fungal genera. After adding the phenolic acids, the community structure of soil bacteria and fungi were changed and the pathogenic fungus *Ilyonectria*/*Rhizoctonia* disappeared or decreased. The microbial degradation rates of some PAs were significantly ($P < 0.05$) correlated with the increase in relative abundance of some specific microorganisms, indicating that the degradation of PAs was affected by the microbial communities concurrently in soil.

Key Words: American ginseng, bacteria, diversity, fungi, Illumina MiSeq sequencing technique, maize, phenolic acids, physico-chemical properties, soil.

INTRODUCTION

Phenolic acids are important allelochemicals in continuous cropping soil ecosystems (14,26,30) and influence the growth of plants (31,35). Phenolic acids detected in natural plant rhizosphere soil are produced from the degradation of plants residues (9), root secretions (10,15) and phenolic compounds acids transformations (28). The degradation includes microbial degradation (30) and non-biodegradation (13,16). The phenolic acids in soil allelopathically inhibit the microorganisms (29) and promote the pathogenic microorganisms (26). However, the concentration of some phenolic acids in crop rhizosphere soil is very low (33) or even undetectable (6), but these causes soil borne diseases in crops. The degradation of phenolic acids by microorganisms causes allelopathy (15,25). Such phenolic acids called "invisible phenolic acids" (25) are rapidly metabolized by microorganisms and play key role in disease management.

Plant rhizosphere soil microorganisms remains in the special soil microbial environment developed by plant root exudates (18,24). Various crops root exudates contains different kinds and concentration of phenolic acids, which have variable effects

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*Correspondence author, , [1]Institute of Medicinal Plant Development, Chinese Academy of Medical Sciences and Peking Union Medical College, Beijing, 100193, China, [2]College of Agricultural and Biological Engineering, Heze University, Heze, 274015, China, [3]Biomedicine School, Beijing City University, Beijing, 100094, China.

on the microorganisms in the crop rhizosphere (21). American ginseng (*Panax quinquefolius* L.) is highly valued perennial herb used in Chinese medicine, but the development of root rot diseases caused by soil-borne fungi during its growing period is a serious problem (20). In China, maize (*Zea mays* L.) is often used as rotation crop with American ginseng (8). Our previous studies have shown that the microbial degradation of phenolic acids in Maize and American ginseng rhizosphere soils was an efficient process, where, soil microbes completely degraded the phenolic acids within 3-days (3). However, the effects of these phenolic acids on the soil microorganism have not been studied.

In this study, rhizosphere soils of American ginseng and maize collected from two sites (Gejia Town, Zetou Town), Wendeng Dist., Weihai City, Shandong Province of China, were used and nine common phenolic acids (*p*-hydroxybenzoic, vanillic, syringic, *p*-coumaric, ferulic, benzoic, salicylic, cinnamic acids and vanillin) detected in American ginseng cultivated soils (5) were added to the above soils as described previously (3). Although the soil and experiment design were the same, in this study, we focussed on the influence of phenolic acids on soil microbial communities with high-throughput sequencing technology, to clarify the effects of various phenolic acids on the microbial diversity and composition of rhizosphere soil bacteria and fungi in both these test crops. Besides, we also analysed the correlation between the microbial degradation rate of phenolic acids and increment (or decrement) of relative abundance of bacterial or fungal genera. This study aimed to determine, how the phenolic acids added to soil influences the soil microorganisms, which may help to understand the role of phenolic acids in continuous cropping problem.

MATERIALS AND METHODS

The experimental soil was collected from crop fields of two sites: Gejia Town, Zetou Town (Table 1) in July of 2018 during the growth phase of American Ginseng and maize. The two sites were cultivated with American ginseng and maize since past 2-years. From each site in 1.0 m^2, 5-whole plants of 2-year-old American ginseng or maize were removed by digging and the soil adhering to roots was collected. The experiment design was the same as previously described by us (3). As all the nine phenolic acids were degraded in 3-days after addition, the soil samples were collected at the end of third day (72 h) for analysis.

Bacterial and fungal community analysis

We analysed the bacterial and fungal community of soil before adding phenolic acids (B) and soil collected at the end of the third day (72 h) i.e. after degradation of added phenolic acids (E) as shown in Table 1. The procedure included DNA extraction, PCR amplification, Illumina MiSeq sequencing and data processing as described previously (3). The boxes of alpha-diversity, beta-diversity and bar-tree at genera level of bacteria and fungi were plotted with *R.* Linear discriminant analysis (LDA). The effect of size (LEfSe) (http://huttenhower.sph.harvard.edu/lefse/) was used to characterize the features differentiate the bacterial and fungal communities in soils of B and E groups as previously described (23) at genera and phylum levels after removing those OTUs unidentified at genera level. The alpha value for the factorial Kruskal-Wallis test among classes was set to 0.05, the threshold on the logarithmic LDA score for discriminative features were set to 2.0, and the strategy for multi-class analysis was set as all-against-all.

Table 1. Informations about Treatments details and of soil samples collection sites for sequencing

Designation	Sterilization or not	Crop	Sampling sites	Longitude	Latitude	Altitude (m)
B.G-I	Before adding phenolic acids	American ginseng	Zetou Town	121°51’44”E	37°3’14”N	19
B.G-II	Before adding phenolic acids	American ginseng	Gejia Town	121°51’30”E	37°6’27”N	20
B.M-I	Before adding phenolic acids	Maize	Zetou Town	121°51’44”E	37°3’14”N	19
B.M-II	Before adding phenolic acids	Maize	Gejia Town	121°51’30”E	37°6’27”N	20
E.G-I	3- days after adding phenolic acids	American ginseng	Zetou Town	121°51’44”E	37°3’14”N	19
E.G-II	3- days after adding phenolic acids	American ginseng	Gejia Town	121°51’30”E	37°6’27”N	20
E.M-I	3-days after adding phenolic acids	Maize	Zetou Town	121°51’44”E	37°3’14”N	19
E.M-II	3-days after adding phenolic acids	Maize	Gejia Town	121°51’30”E	37°6’27”N	20

Statistical analysis

After LEfSe, microbial genera of high relative abundance (> 0.5 % for bacteria and > 0.05 % for fungi) were screened. The increase in relative abundance was calculated as under:

$$\Delta RA=RA(E)-RA(B)$$

Where, ΔRA: Variation of the relative abundance of specific microbial genera, $\Delta RA > 0$: Relative abundance of microbial genera increased after phenolic acids were degraded, $\Delta RA < 0$: decreased, RA(B): Relative abundance of microbial genera in soil before adding phenolic acids, RA(E): relative abundance of microbial genera in soil at the end of third day after adding phenolic acids.

Pearson correlation analysis between ΔRA and the microbial degradation rate of phenolic acids (MDA) (3) was done by SPSS software (version 19.0, SPSS Inc., Chicago, Il, USA). Correlation coefficient and significance was calculated and the significance level set at $P < 0.05$.

RESULTS AND DISCUSSION

Alpha-diversity of microorganisms

Across all samples, using the 97 % sequence similarity cut off, 17252-98012 clean tags of 16S were obtained, grouped into 2682 bacterial OTUs and extracted to 2627 with 11573 final tags of each sample. Similarly, 36155-207206 clean tags of internal transcribed spacer (ITS) were obtained, grouped into 2243 fungal OTUs and extracted to 2039 with 35839 final tags of each sample. The coverage indices for bacteria and fungi were between a range of 96.0 % - 97.5 % and 99.4 % - 99.7 %, respectively, suggesting that sequencing capability was large enough to capture the majority of the diversity for all the samples. The Chao1 and Shannon diversity indices of soil bacteria and fungi were shown in Figure-1. Three days after adding phenolic acids, the bacterial Chao1 of G-I decreased, but the G-II, M-I and M-II did not change (Figure-1a). The bacterial Shannon of different groups, however, decreased drastically except for group M-II (Figure-1b).

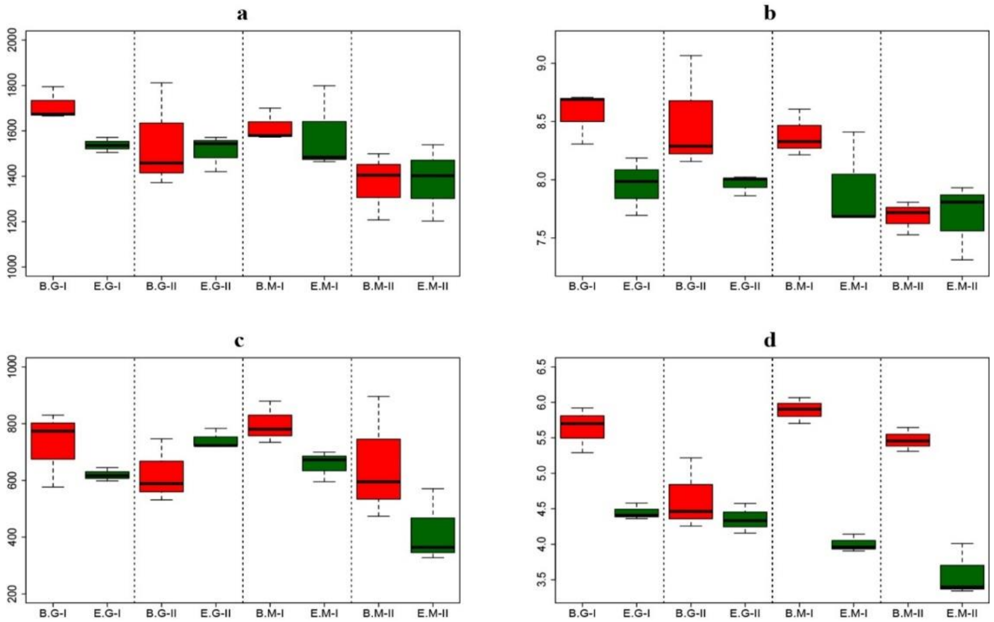


Figure 1. Alpha-diversity of microorganisms before and 3-days after adding phenolic acids to soil. Chao1 of bacteria (a), Shannon of bacteria (b), Chao 1 of fungi (c) and Shannon of fungi (d) in different soil samples. Thick horizontal bars show the median. The upper and lower "hinges" correspond to the 25th and 75th percentiles, and whiskers extend from the hinge to the highest (or lowest) value that is within 1.5 × interquartile range (IQR) of the hinge. B.G-I: Ginseng soil of Site I before adding phenolic acids, E.G-I: Ginseng soil of Site I at the end of the third day after adding phenolic acids, B.G-II: Ginseng soil of Site II before adding phenolic acids, E.G-II: Ginseng soil of Site II at the end of the third day after adding phenolic acids, B.M-I: Maize soil of Site I before adding phenolic acids, E.M-I: Maize soil of Site I at the end of the third day after adding phenolic acids, B.M-II: Maize soil of Site II before adding phenolic acids, E.M-II: Maize soil of Site II at the end of the third day after adding phenolic acids.

Chao1 represents richness, while Shannon represents richness and evenness (4), so we can conclude that phenolic acids influence the bacterial evenness more easily than richness. In fungi, the Chao1 increased for G-II, and decreased for other groups after degradation of phenolic acids (Figure-1c), while Shannon decreased for all the four groups (Figure-1d) indicating that phenolic acids inhibit fungal diversity and fungal richness of maize cultivated soil but did not show same trend of American ginseng cultivated soil fungal richness and diversity. The result that phenolic acids decreased the microbial diversity is consistent with Zhou *et al*. (34), who found that the number of visible bands, Shannon diversity index and evenness index of bacterial communities were significantly smaller in the phenolics-added soil (34). As is known, the soil microbial diversity is very important indicator of soil health (12,22,27) and from this respect, the mixed phenolic acids continuously secreted into the soil by plants may be harmful to soil health.

Changes in microbial Community Composition

Bacteria : According to average abundance, the top 20 genera (include unidentified genera) of bacteria and fungi are shown in Figure-2. For bacteria, the identified composition account for 41.1-70.9 % of all taxa (Figure-2a). According to the average relative abundance of all the sample of specific genera, *Acidothermus*, accounting for 6 %, was dominant in all samples. *Rhodanobacter*, *Mizugakiibacter* and *Burkholderia-Paraburkholderia* were the next three genera, whose relative abundance exceeded 2 %, and then followed *Bacillus, Rhizomicrobium*, *Acidibacter*, *Jatrophihabitans*, *Sphingomonas*, *Bryobacter*, *Actinospica* and *Streptomyces*, whose relative abundances were > 1 %. The rest genera had low relative abundances which were < 1 %. According to the bar tree in genera level, the samples of B.G-I, B.G-II and B.M-I were clustered together, E.G-I, E.G-II and E.M-I were clustered together, while E.M-II and B.M-II, were clustered together. The cluster results indicated that the effects of phenolic acids on bacterial composition were more strong in American ginseng soil than maize soil.

Fungi : The identified fungi composition accounted for 66.0-70.2 % for all the taxa in E.G-I group and 13.4-49.5 % in other groups (Figure-2b). According to the average relative abundance of all samples of specific genera, *Penicillium*, accounting for 15 % was dominant in all samples. *Mortierella, Trichoderma* and *Humicola* were the next 3-genera whose relative abundance exceeded 8 %, then followed by *Talaromyces, Solicoccozyma, Chaetomium, Chaetomidium,* and *Saitozyma,* whose relative abundance were more than 1-8 %. While the other genera had low relative abundances (< 1 %). According to the bar tree at genera level, the samples of E.G-I and E.G-II were clustered together, B.G-I, B.M-I and B.M-II were clustered together firstly, and then clustered with B.G-II, while the cluster of E.M-I and E.M-II differed in composition than rest groups. Besides, the applied phenolic acids increased the distance between the fungi of American ginseng soil and the fungi of maize by enhancing the effects of crops on fungal communities.

The differences in microbial communities between American ginseng and maize cultivated soils before and 3-days after adding phenolic acids were estimated, respectively, based on unweighted Unifrac distance matrix of 6 (3 replicates × 2 sampling sites) maize soil samples and likewise 6 American ginseng soil samples (Figure-3). It is evident that the phenolic acids decreased the differences in bacterial communities (Figure-3a), while increased the differences in fungal communities between American ginseng and maize cultivated soil (Figure-3b). These results were consistent with Figure-2, indicating that phenolic acids enhanced the effects of crops on fungal communities.

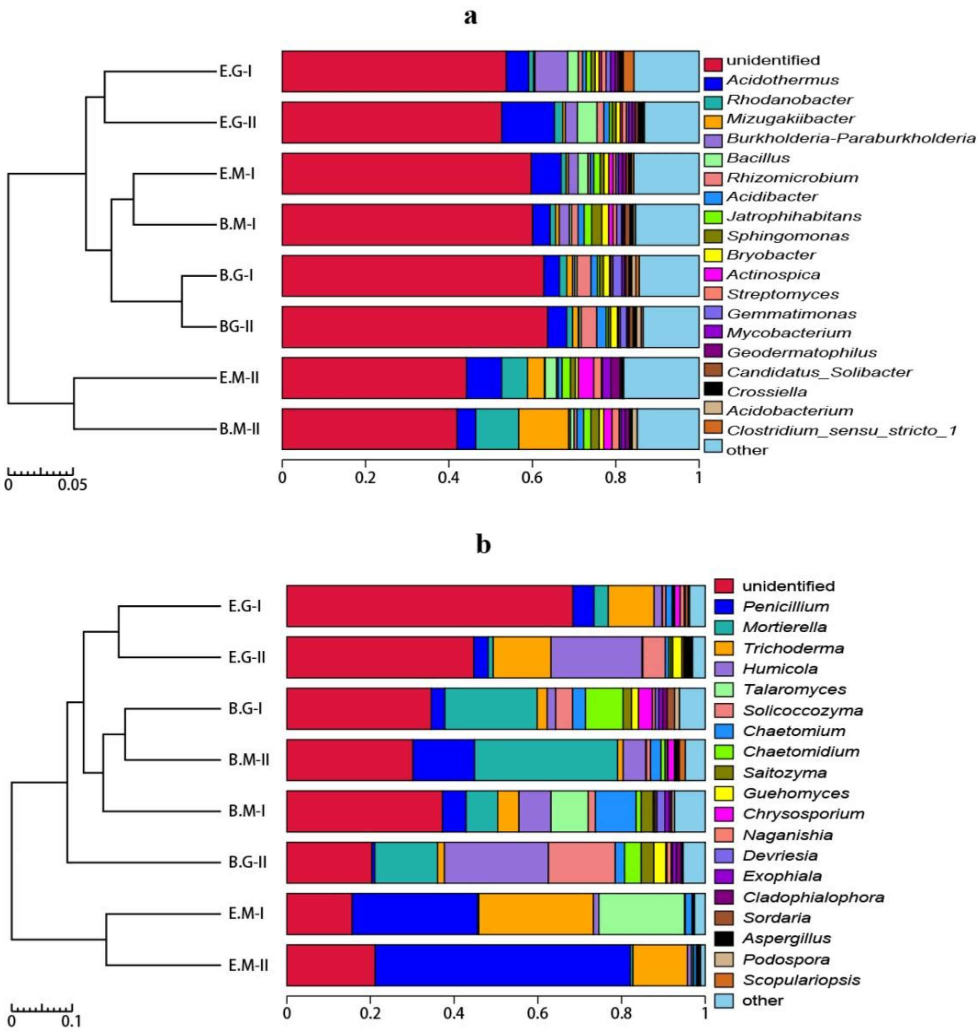


Figure 2. Changes in microbial communities after phenolic acids were degraded. Clustering on the axis is based on the bacterial (a) and fungal (b) composition at genera level of different soil samples. B.G-I: Ginseng soil of Site I before adding phenolic acids, E.G-I: Ginseng soil of Site I at the end of the third day after adding phenolic acids, B.G-II: Ginseng soil of Site II before adding phenolic acids, E.G-II: Ginseng soil of Site II at the end of the third day after adding phenolic acids, B.M-I: Maize soil of Site I before adding phenolic acids, E.M-I: Maize soil of Site I at the end of the third day after adding phenolic acids, B.M-II: Maize soil of Site II before adding phenolic acids, E.M-II: Maize soil of Site II at the end of the third day after adding phenolic acids.

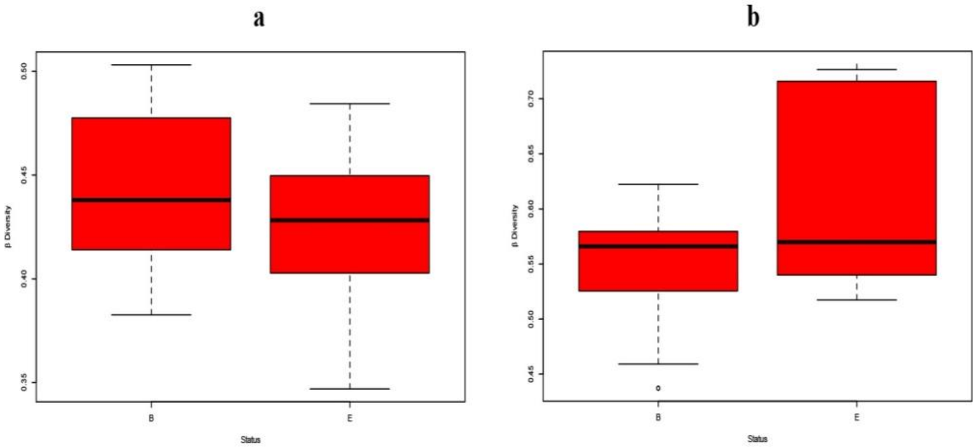


Figure 3. Differences in beta-diversity of bacteria(a) and fungi(b) between samples before and 3-days after adding phenolic acids. Beta-diversity were estimated based on unweighted Unifrac distance matrix of 6 maize soil samples and 6 American ginseng soil samples, including 36 data points for each group, B: before adding phenolic acids, E: at the end of the third day after adding phenolic acids.

Microbial communities can be affected by cultivated crops (2,11) and soil physical and chemical properties (12,19). So, the soils from the same sites or cultivated by same crops can be easily clustered together. The added phenolic acids during 3-days of incubation affected the microbial communities and changed the clusters based on the bacterial (Figure-2a) and fungal composition (Figure-2b). Consequently, the beta-diversity of bacteria based on unweighted Unifrac distance matrix of maize and American ginseng soil samples decreased. On the contrary, phenolic acids increased the distance of fungal community between American ginseng and maize cultivated soil. The different effects of phenolic acids on bacterial and fungal community may be due to higher dispersion of fungal communities, as previously reported by Jiao *et al.* (7). Besides, the effects of phenolic acids on fungal community were stronger in American ginseng soil than in maize soil. One explanation could be that the kinds, concentrations and property of phenolic acids added to soil in our experiment referred to the real condition of American ginseng soil (3).

Influence of phenolic acids on specific bacteria and fungi

To identify those microbial taxa responsible for community differentiation between the samples before (B) and 3-days after adding phenolic acids (E), we used LEfSe to determine the biomarkers at genera level and phylum level of B and E (Figure 4). For bacteria, phylum Verrucomicrobia, Nitrospirae and Bacteroidetes decreased, while, Firmicutes increased 3-days after adding phenolic acids. In general, phenolic acids decreased 15 taxa while increased 12 taxa (Figure-4a). For fungi, phylum Glomeromycota, Chytridiomycota and Rozellomycota were decreased, while, Mortierellomycota was increased 3-days after adding the phenolic acids. At genera level, the biomarkers for

Table 2. Correlation between MDA of phenolic acids and increase of relative abundance of bacterial genera

	SYA	V	FA	SA	PA	PHA	VA	BA	CA
Bacillus	-0.058	0.091	-0.092	0.197	0.236	0.089	-0.135	-0.561	-0.025
Sphingomonas	0.087	**0.758****	-0.086	0.539	0.494	-0.085	0.413	-0.06	-0.267
Geodermatophilus	-0.385	-0.214	-0.403	-0.317	-0.327	-0.142	0.025	0.286	0.109
Acidobacterium	0.333	-0.004	0.392	0.128	0.022	0.028	-0.376	-0.294	-0.028
Sporosarcina	0.087	-0.381	0.219	-0.317	-0.223	-0.025	-0.442	0.173	0.175
Arthrobacter	0.047	0.448	-0.008	0.334	0.154	0.081	-0.107	-0.15	-0.089
Aciditerrimonas	0.42	0.231	0.281	0.478	0.062	-0.001	0.297	-0.312	-0.051

Data are correlation coefficient, value in bold means the MDA of phenolic acid in the row and the relative abundance of bacterial genera in the column were significantly correlated, * stands for P <0.05 and ** stands for P <0.01. PHA: *p*-Hydroxybenzoic acid, VA: Vanillic acid, SYA: Syringic acid, V: Vanillin, PA: *p*-Coumaric acid, FA: Ferulic acid, SA: Salicylic acid, BA: Bbenzoic acid, CA: Cinnamic acid

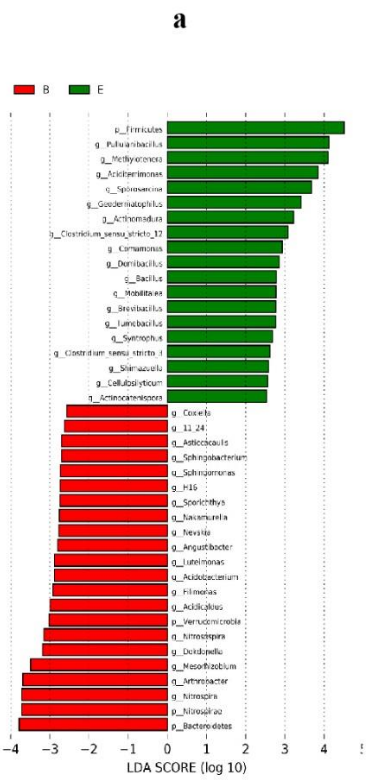
bacteria were much more than fungal biomarkers (Figure 4b). Although there were many biomarkers of bacteria and fungi, but most of the biomarkers accounted for very small proportion. So, we screened the high relative abundance of bacterial biomarkers (> 0.5 %, Top 7) and fungal biomarkers (> 0.05 %, Top 7) for further analysis. To reveal the effects of phenolic acids on specific microorganisms, correlations between the MDA (3) and ΔRA was analysed. The results showed significant positive correlation between MDA of vanillin and ΔRA of *Sphingomonas* (Table 2). In fungi, ΔRA of *Mortierella* was positively correlated with MDA of syringic acid, ΔRA of *Aleuria* was positively correlated with MDA of *p*-coumaric acid, ferulic acid and salicylic acid, while, ΔRA of *Holtermanniella* was negatively correlated with MDA of syringic, salicylic, vanillic acid and vanillin and ΔRA of *Epicoccum* was negatively correlated with MDA of ferulic acid (Table 3).

Table 3. Correlation between MDA of phenolic acids and increase of relative abundance of fungal genera

	SYA	V	FA	SA	PA	PHA	VA	BA	CA
Mortierella	**0.868****	0.302	**0.871****	**0.705***	0.51	0.4	0.267	-0.331	0.117
Chaetomidium	-0.409	-0.706	-0.314	-0.458	-0.368	0.435	-0.234	0.115	0.217
Holtermanniella	**-0.645***	**-0.781****	-0.463	**-0.814****	-0.54	0.35	**-0.629***	0.404	0.331
Epicoccum	-0.482	0.435	-0.615*	-0.024	0.04	-0.376	0.103	0.109	-0.304
Aleuria	0.523	0.207	0.518	0.482	**0.639***	0.348	0.478	0.032	0.5
Byssomerulius	-0.449	0.236	-0.518	-0.074	0.016	-0.266	-0.055	0.228	-0.212
Echria	-0.418	0.384	-0.451	-0.107	0.079	-0.311	-0.017	0.300	-0.263

Data are correlation coefficient, value in bold means the MDA of phenolic acid in the row and the relative abundance of fungal genera in the column were significantly correlated, * stands for P<0.05 and ** stands for P <0.01. PHA: *p*-Hydroxybenzoic acid, VA: Vanillic acid, SYA: Syringic acid, V: Vanillin, PA: *p*-Coumaric acid, FA: Ferulic acid, SA: Salicylic acid, BA: Bbenzoic acid, CA: Cinnamic acid

Microorganisms play an important role in microbial degradation of phenolic acids (3). The present study showed that vanillin stimulated the abundance of Sphingomonas, which indicated that these bacteria use vanillin as source of carbon and energy and undergo rapid multiplication. Similarly, *Mortierella* may use syringic, ferulic and salicylic acids, while *Aleuria* may use *p*-coumaric acid as carbon resource. Previous studies also



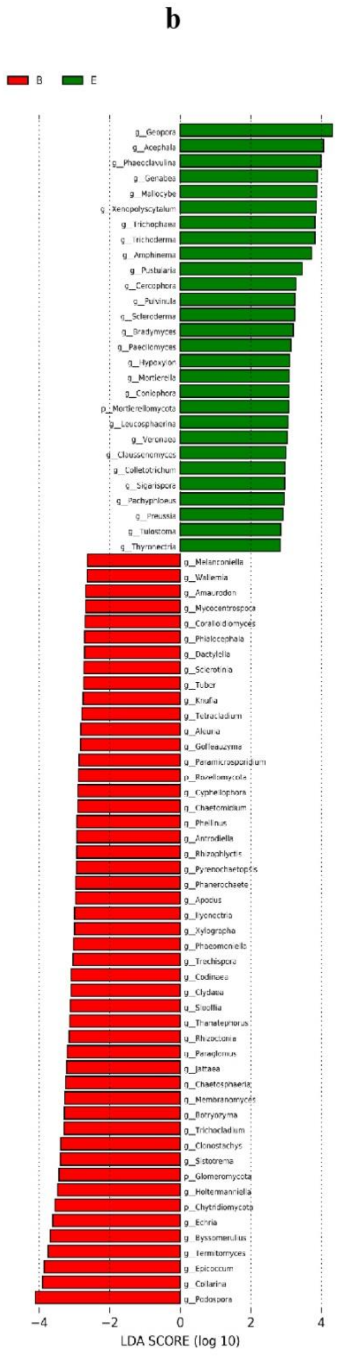


Figure 4. The biomarkers of bacteria (a) and fungi (b) in general and phylum level before and three days after adding phenolic acids. The markers are selected with Lefse and LDA value was set at 2. B: before adding phenolic acids, E: at the end of the third day after adding phenolic acids.

reported that the relationship between phenolic acids and some specific microbial genera. Liu *et al.* (15). found that 0.6 mmol g^{-1} soil benzoic acid reduced the relative abundance of *Mortierella* (15). While in our study, *Mortierella* increased with the degradation of phenolic acids, which may be due to the synthetic effects of mixed phenolic acids. Besides, ΔRA of *Mortierella* was positively correlated with MDA of syringic acid, supporting that different phenolic acids may have antagonistic effects (1). MDA reflects the degradation process of phenolic acid in soil, while ΔRA reflects the change processes in soil microorganisms, so the correlation between MDA and ΔRA indicated that the degradation of phenolic acids would affect the microbial communities concurrently. Considering that the imbalance of microbial community plays an important role in continuous cropping problem (17,32). Our studies have revealed that the presence of PAs influenced the soil microorganisms and their interaction and microbial degradation may help to understand the role of PAs in continuous cropping problem. The present study is unable to specify the effects of individual phenolic acid, as only the mixture of nine phenolic acids was used.

CONCLUSIONS

Our result demonstrated that in American ginseng and maize grown soils although the phenolic acids in soil are metabolized rapidly by soil microorganisms, but they decreased the bacterial diversity and changed the composition of microbial communities. Besides, the degradation of phenolic acids would affect the microbial communities concurrently in soil. This study revealed, how the degraded PAs influenced the soil microorganisms, which may help to understand the role of PAs in continuous cropping problem.

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DECLARATION

We declare that all authors of this Ms. have made substantial contributions. We have not excluded any author that substantially contributed to this Ms. We have followed our ethical norms established by our respective institutions.

CONFLICT OF INTEREST

The authors announce that they have no conflict of interest.

ETHICAL APPROVAL

The authors declare that the study was carried out following scientific ethics and conduct. However, this study did not involve any use of animals, hence no ethical approval has been obtained from the concerned committee.

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