Available online at www.sciencedirect.com
ScienceDirect
Journal of Environmental Sciences 2012, 24(3) 396–401
JOURNAL OF ENVIRONMENTAL SCIENCES
ISSN 1001-0742
CN 11-2629/X
www.jesc.ac.cn

Plant species coexistence alleviates the impacts of lead on *Zea mays* L.

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Received 10 February 2011; revised 29 March 2011; accepted 08 June 2011

Abstract

Whether plant coexistence can reduce the impacts of lead (Pb) on crops in agroecosystems has not been well understood. We conducted a factorial experiment to investigate the effects of weeds coexisting with maize (*Zea mays* L.) on Pb accumulation in maize and soil microbes at two Pb levels (ambient and 300 mg/kg). Elevated Pb tended to increase the Pb concentration in maize and decreased soil microbial activity (indicated by the average well color development, AWCD), functional group diversity, as well as arbuscular mycorrhizal (AM) colonization and vesicle number of maize. Compared to the monoculture, weeds coexisting with maize reduced the Pb concentrations in the root, leaf, sheath and stem of maize at both seedling and mature stages. In maize-weed mixtures, soil microbial activity and functional group diversity tended to increase for both Pb treatments relative to the monoculture. Furthermore, principal component analysis revealed that the soil microbial community structure changed with the introduction of weeds. The highest Pb accumulation in weeds occurred for the elevated Pb treatment in a three species mixture. The results suggest that multiple plant species coexistence could reduce lead accumulation in crop plants and alleviate the negative impacts on soil microbes in polluted land, thereby highlighting the significance of plant diversity in agroecosystems.

Key words: lead; plant coexistence; functional group diversity; *Zea mays* L.

DOI: 10.1016/S1001-0742(11)60721-3

Introduction

Recent concerns about the dramatic decline in ecological complexity, especially in intensive agricultural systems, and its potential consequences in a changing environment have ignited a renewed interest in the role of biodiversity in agroecosystems (Zhu et al., 2000; Chen et al., 2005; Franke et al., 2009). Previous studies showed that the coexistence of multiple plant species in agroecosystems could provide a variety of ecosystem services such as natural enemy protection, pathogen control, pollination, soil conservation, nutrient cycling promotion and system equilibrium maintenance (Hajjar et al., 2008; Quijas et al., 2010; Haaland et al., 2011). When non-production areas around farmlands in the United States were used to create diverse and heterogeneous habitats through manipulating plant diversity, water regulation and carbon storage were notably promoted (Smukler et al., 2010). Similarly, native weeds retained in an orchard ecosystem in southeastern China significantly increased soil microbial biomass carbon (MBC), microbial biomass nitrogen (MBN) and spore numbers of arbuscular mycorrhizal fungi (Chen et al., 2004). In our previous study we found that plant coexistence not only increased the microbial functional group diversity and urease activity under different levels of Pb pollution, but also changed the microbial community structure compared to monocultures (Yang et al., 2007). Despite the long-standing debates on the relationship between plant diversity and ecosystem function or stability, coexistence of multiple plants did show a positive effect on crop yield in agroecosystems even without chemical fertilizer and pesticide input (Cameron, 2002; Smith et al., 2008). However, whether plant coexistence can alleviate the detrimental effects of soil heavy metal pollution on crops is not well known.

Removing heavy metals from contaminated soils and reducing heavy metal accumulation in crops using crop-weed mixtures in agroecosystems was considered as an alternative strategy recently (Wu et al., 2007). As a result of long-term natural selection, weeds possess the characteristics of high stress resistance and extensive adaptability compared to crops. Water hyacinth (*Eichhornia crassipe* (Mart.) Solms.), redroot amaranth (*Amaranthus retroflexus* L.) and maidenstears (*Silene vulgaris* (Moench) Garcke) showed a strong uptake of Cu, Zn and Cr in heavy metal-polluted soil (Wang et al., 2002). The aquatic weeds *Limnocharis flava* L. and *Ipomonea aquatica* Forsk were found to be potential candidates to remediate Cd-contaminated wastewater (Wang et al., 2008; Abhilash et al., 2009). Wei and Zhou (2004) conducted a field-

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screening study on weed hyperaccumulators and found that dandelion (*Taraxacum mongolicum* Hand.-Mazz.), black nightshade (*Solanum nigrum* L.) and Canadian horseweed (*Conyza canadensis* (L.) Cronq) could strongly tolerate single Cd and Cd-Pb-Cu-Zn combined pollution, had high Cd-accumulative ability, and generally possessed the basic characteristics of hyperaccumulators. We hypothesized that coexisting with weed species can reduce the metal accumulation of crops in agroecosystems contaminated by heavy metals. We also thought that plant coexistence may facilitate the metabolic activities of soil microbes and arbuscular mycorrhizae. Here, we conducted a greenhouse experiment manipulating the plant coexistence of a crop (*Zea mays* L.) and two native weeds (*Digitaria ciliaris* and *Kummerowia striata*). Our specific objectives were to examine (1) the effects of plant coexistence on the Pb accumulative pattern of *Z. mays* and (2) whether plant coexistence can alleviate the adverse effects of Pb on soil microbes.

1 Materials and methods

1.1 Experimental design

The mesocosms (46.0 cm × 35.0 cm × 23.0 cm) used in this study were filled with 32.0 kg soil. The soil was gathered from a citrus orchard in Zhejiang Province, southeastern China situated at 28°54′N, 118°30′E. It is a clayey red soil, which is equivalent to *Ultisols* in U.S. soil taxonomy (Table 1). The ambient Pb concentration in the soil was 23.27 mg/kg. Two annual weeds (*D. ciliaris* and *K. striata*) and *Z. mays* were cultured in this experiment and species combinations are shown in Table 2. Two Pb levels (ambient and 300 mg/kg) were used in this study to simulate Pb pollution in the study site. Each treatment had 4 replicates and the number of mesocosms used in total was 24. Pb was applied as $Pb(NO_3)_2$ solution in the elevated Pb treatment, and NH_4NO_3 was added to the control soil to equalize the N concentrations. After being homogenized, the soil was watered to keep a constant water capacity equivalent to 60% of that in the field. The soil was stabilized for two weeks before plants were sown. No additional nutrients were added for the duration of the experiment in order to suppress the overgrowth of the weeds.

Table 1 Properties of the soil used in the greenhouse experiment

Properties	Values
Clay	70.57%
Silt	10.63%
Sand	18.7%
pH	4.59
Organic matter	34.39 g/kg
Total N	1.30 g/kg
Total P	0.95 g/kg
Extractable N	48.08 mg/kg
Extractable P	8.99 mg/kg
Extractable K	208.23 mg/kg

Table 2 Combinations of coexisting plant species

No.	Species combinations
1	Monoculture (*Zea mays*)
2	Two species (*Zea mays* and *Digitaria ciliaris*)
3	Three species (*Zea mays*, *Digitaria ciliaris* and *Kummerowia striata*)

1.2 Sampling and measurements

Maize was sampled at the juvenile (50 days) and mature stages (120 days), while the weeds sampled merely at maturity. Maize was divided into root, stem, leaf, sheath, spike and seed, while weeds were divided into root and shoot. Subsamples of fresh roots derived from maize and weeds were fixed in FAA (37% formaldehyde, glacial acetic acid, 50% ethanol, 9:0.5:0.5, *V*/*V*/*V*) for qualification of arbuscular mycorrhizal (AM) colonization and vesicle number. The fresh weight of total roots and of subsamples was measured. All remaining samples were oven-dried at 105°C for 30 min and subsequently 80°C to a constant weight. The water content of the tested roots and total root fresh weight were used to estimate the total root dry weight.

Dry samples were ground into fine powder and incinerated into ash at 600°C for 2 hr. The ash was dissolved in 1:1 (*V*/*V*) nitric acid (Bao, 2000). The Pb concentration was measured using the atomic absorption spectroscopy (AAS) method (AA6650, Shimadzu, Japan).

Root samples were stained with acid fuchsin in lactoglycerol, then mycorrhizal colonization and vesicle number were determined using the gridline intersect method (Giovannetti and Mosse, 1980).

The carbon source utilization of soil microbial communities was examined using BIOLOG Ecoplate (Biolog Inc., USA). Moist soil equivalent to 10.0 g dry weight was extracted with 90 mL autoclaved 0.145 mol/L NaCl and shaken for 15 min. Then the original solution was diluted by 10^2 fold. Three replicates from one treatment were inoculated onto a BIOLOG EcoPlate. Each well was inoculated with 125 μL diluted soil extracts and the plates were incubated at 25°C in the dark for 156 hr. The color formation at 590 nm was measured every 12 hr for 7 days using an automatic plate reader (Bio-Tek Instruments Inc., USA). Absorbency from the control was subtracted from the wells containing substrates. The rate of color development over time was determined by calculating the average intensity of color on each plate at each reading time (Garland, 1996). The average well color development (AWCD) data at 96 hr was used for determining the functional group diversity of the soil microbial community. The functional group diversity of the microbial community was calculated for each sample by the Shannon-Weaver index (*H*) according to Yang et al. (2007) using the following equation:

$$H = -\sum_{i=1}^{m} P_i \ln P_i$$

where, P_i is the proportional color development of the *i*th well relative to the total color development of all wells on a plate (m = 95). This is comparable to the use of H in community ecology, where P_i is the relative abundance of species *i* in the total community.

1.3 Data analysis

The mycorrhizal colonization was arcsine transformed. The data were subjected to two-way ANOVA using the general linear model (GLM) design in SPSS 10.0 software (SPSS Inc., Chicago, USA). The independent variables were Pb concentrations and plant combinations. The difference due to Pb treatments within each plant combination was determined by independent-sample *t*-test. Principal component analysis (PCA) of the BIOLOG profile (96 hr) was performed to differentiate the structures of the soil microbial communities among Pb and plant combination treatments. Least significant difference (LSD) was performed for multiple comparisons of means derived from each treatment at a significance level of 0.05.

2 Results

2.1 Maize biomass

Neither Pb treatment, plant combination nor two-way interaction changed the maize biomass significantly at the juvenile stage ($p > 0.05$, Table 3). At the mature stage, however, maize biomass increased under the higher Pb treatment compared to the control except for the three species mixture ($p < 0.05$, Fig. 1). Coexistence with weeds tended to decrease maize biomass under higher Pb treatments ($p < 0.05$, Fig. 1).

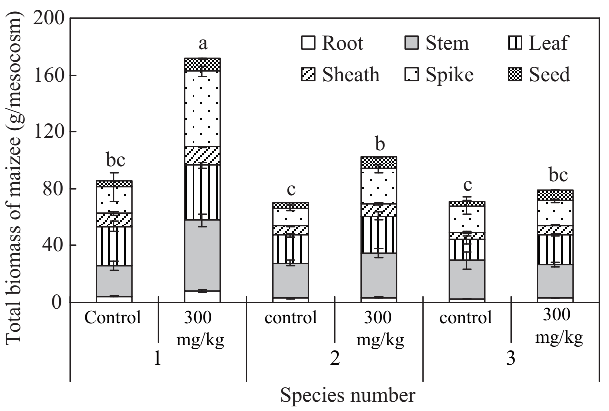

Fig. 1 Total biomass of maize grown in the monoculture and in mixtures for both Pb treatments. Values are means ± S.E. The means marked by the same letters are not significantly different according to the LSD test and independent-sample *t*-test at $p < 0.05$. Species number 1, 2, and 3 refers to Table 2.

2.2 Lead distribution in maize for different species combinations

Pb concentrations in the maize for the 300 mg/kg treatment were increased very significantly compared to the control ($p < 0.01$, Tables 3 and 4). Plant coexistence tended to reduce the Pb accumulation of maize relative to the monoculture, but the effectiveness depended on the sampling position, growth stage and Pb level as well. The most significant reduction occurred in the root and stem of maize under ambient Pb treatment at both juvenile and mature stages ($p < 0.05$, Tables 3 and 4). By contrast, plant coexistence merely offered marginally significant advantages to maize under the higher Pb treatment (Table 4). In the

Table 3 Significance levels of effects of different factors and factor interaction on variables based on two-way analysis of variance (ANOVA)

Sampling stage	Independent variable	Total biomass	Pb concentration						AWCD	Functional group diversity	Colonization rate	Vesicle number
			Root	Stem	Leaf	Sheath	Spike	Seed				
Seedling	Pb	ns	**	**	**	**						
	Species	ns	**	**	**	**						
	Pb × species	ns	ns	*	ns	*						
Maturity	Pb	**	**	**	**	**	**	**	ns	**	**	**
	Species	**	*	**	ns	ns	ns	*	ns	**	*	**
	Pb × species	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

* $p < 0.05$; ** $p < 0.01$; ns: $p > 0.05$.
AWCD: average well color development.

Table 4 Pb concentrations in different organs of maize sampled at seedling and mature stages

Sampling stage	Pb treatment	Species number	Pb concentration (mg/kg)					
			Root	Stem	Leaf	Sheath	Spike	Seed
Seedling	Control	1	27.97 ± 0.73 c	7.96 ± 1.04 c	16.60 ± 1.30 c	0.74 ± 0.14 c		
		2	23.40 ± 0.67 d	3.84 ± 0.55 d	14.37 ± 0.53 d	0.44 ± 0.02 d		
		3	17.68 ± 1.24 e	2.17 ± 0.76 e	12.76 ± 1.31 d	0.19 ± 0.04 e		
	300 mg/kg	1	41.69 ± 0.91 a	20.19 ± 2.12 a	28.25 ± 2.63 a	12.97 ± 0.40 a		
		2	45.54 ± 10.07 a	20.17± 2.20 a	24.80 ± 1.70 a	11.62 ± 0.42 b		
		3	31.89 ± 0.56 b	14.83 ± 0.41 b	21.38 ± 1.69 b	11.22 ± 0.61 b		
Maturity	Control	1	76.85 ± 1.72 c	13.49 ± 0.60 c	16.94 ± 0.92 b	2.49 ± 1.36 b	8.49 ± 0.79 b	4.62 ± 0.23 b
		2	70.26 ± 4.19 d	11.46 ± 0.47 d	14.00 ± 3.58 b	1.24 ± 0.07 b	7.47 ± 0.62 b	3.10 ± 0.27 c
		3	69.97 ± 1.15 d	10.67 ± 0.18 e	13.23 ± 0.48 b	1.27 ± 0.11 b	7.24 ± 1.15 b	2.33 ± 0.23 d
	300 mg/kg	1	100.82 ± 2.63 a	102.43 ± 4.80 a	95.78 ± 2.63 a	27.30 ± 1.35 a	87.98 ± 2.32 a	21.10 ± 2.18 a
		2	97.50 ± 4.95 ab	95.97 ± 1.12 b	94.86 ± 1.85 a	26.27 ± 0.55 a	85.33 ± 4.47 a	20.64 ± 0.22 a
		3	93.01 ± 4.97 b	93.38 ± 2.56 b	93.66 ± 1.29 a	25.51 ± 1.71 a	83.09 ± 4.42 a	20.35 ± 0.36 a

Values are means ± S.E. For each treatment, means marked by different letters indicate significant differences according to the LSD test and independent-sample *t*-test at the 0.05 level. The comparisons are only performed within each sampling stage.

case of leaf and sheath, however, the benefit from multiple plant coexistence could only be found at the juvenile stage ($p < 0.01$, Tables 3 and 4). In terms of sampling position, the spike was the only organ that showed no reduction of Pb accumulation due to plant coexistence ($p > 0.05$, Table 4). Our results showed that maize seed tended to accumulate less Pb when it coexisted with weeds under the ambient Pb treatment ($p < 0.05$, Table 4). With regard to Pb distribution, the highest concentration occurred in the maize root, followed by leaf, stem, spike, seed and sheath, which was consistent with our previous study (Li et al., 2010).

The Pb allocation of different parts of maize showed very significant responses to Pb, plant combination and two-way interaction ($p < 0.01$, data not shown). The highest Pb allocation occurred for the elevated Pb treatment under monoculture and followed the order of stem, spike, leaf, root, sheath and seed.

2.3 Lead accumulation in weeds

In order to illuminate the mechanisms underlying the effectiveness of plant coexistence on maize Pb accumulation, the Pb uptake by weeds was determined. The results revealed that the total Pb accumulated by weeds in the three species treatment was notably enhanced compared to the two species treatment regardless of Pb levels ($p < 0.05$, Fig. 2).

2.4 Average well color development and functional group diversity of soil microbes

Pb treatment significantly decreased the AWCD values of the two species treatment and functional group diversity of the soil microbial community compared to the control with the exception of the three species coexistence ($p < 0.05$, Fig. 3), which showed no difference between ambient and 300 mg/kg Pb treatments (specifically for AWCD values). The functional group diversity of soil microbes, however, consistently showed a positive response to plant species number no matter what the Pb status was ($p < 0.01$, Table 3 and Fig. 3). PCA analysis of the BIOLOG data (96 hr) indicated that plant coexistence altered the substrate utilization patterns of the microbial communities in both Pb treatments (Fig. 4). The first two principal components accounted for 37.54% (PC1 = 19.64%, PC2 = 17.90%) and 37.60% (PC1 = 21.03%, PC2 = 16.57%) of the total variances in the control and 300 mg/kg Pb treatments, respectively.

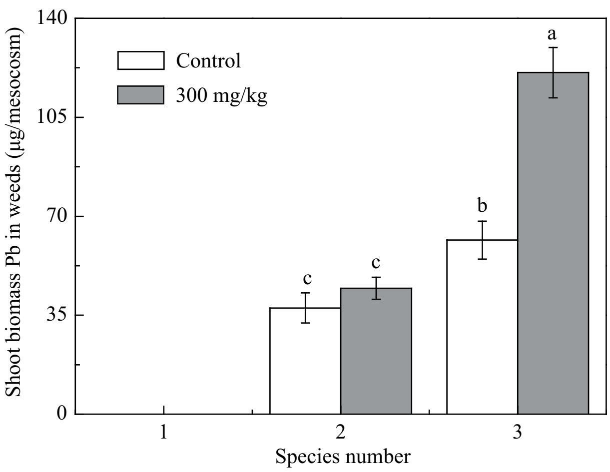

Fig. 2 Pb accumulation in aboveground biomass of weeds. Values are means ± S.E. The means marked by the same letters are not significantly different according to the independent-sample *t*-test at $p < 0.05$. Species number 1, 2, and 3 refers to Table 2.

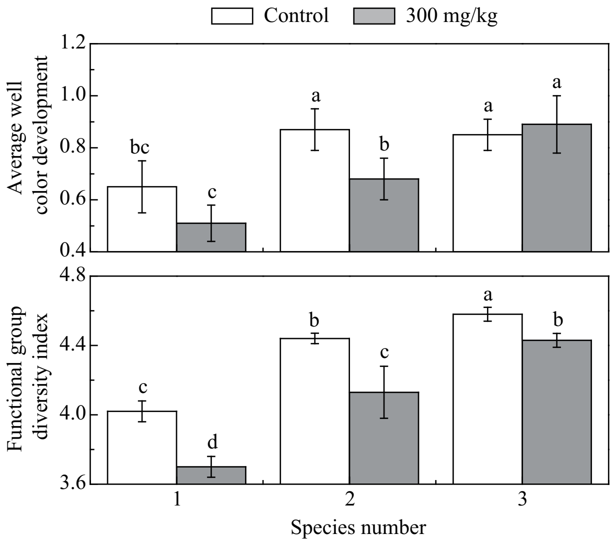

Fig. 3 Average well color development values and functional group diversity index at the reading time of 96 hr. The means marked by the same letters are not significantly different according to the LSD test and independent-sample *t*-test at $p < 0.05$. Species number 1, 2, and 3 refers to Table 2.

2.5 Arbuscular mycorrhizal colonization and vesicle number of maize

Both the AM colonization and vesicle number of maize decreased very significantly with the addition of Pb ($p < 0.01$, Table 3 and Fig. 5). However, only in the case of the three species mixture did plant coexistence show a positive effect on the AM colonization of maize.

3 Discussion

Coexistence is a balanced mixture of species in a biotic community (Hart et al., 2003). When this term has been used in agroecosystems, however, it usually refers to the coexistence of multiple crops (Smith et al., 2008). Although weeds are unwanted species in agroecosystems because of their fast growing traits and competition with crops for light, space and nutrients, the functions of weeds have been increasingly recognized. Isaacs et al. (2009) found that it was essential to reintroduce native weed species into agroecosystems to provide habitats and shelters for pollinators, predators and parasitoids, which are critical for agricultural farming. Our results provide convincing evidence that the coexistence of crop and weeds significantly decreased the Pb accumulation in maize under ambient Pb treatment, especially in the root and stem, however, the effectiveness decreased for the mature stage and higher Pb treatment (Table 4). In other words, the results show both the potential and limits of this method in practical applications. Although leaf, sheath and spike only

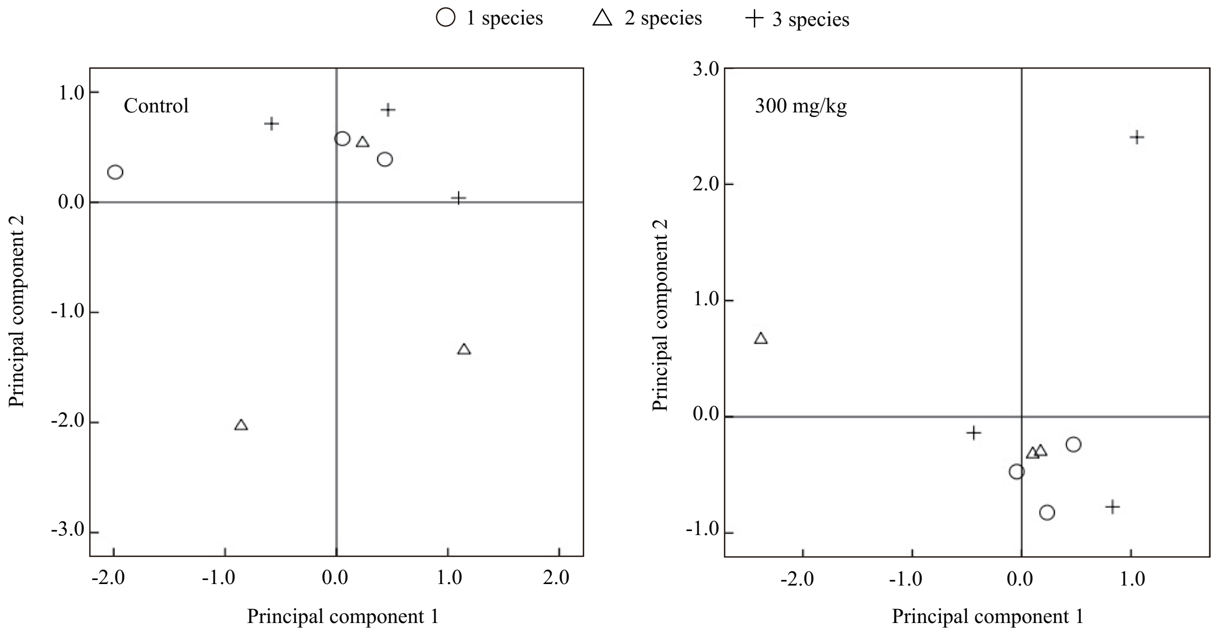

Fig. 4 Principal component analysis of the soil microbial metabolic profile under control and elevated Pb treatments.

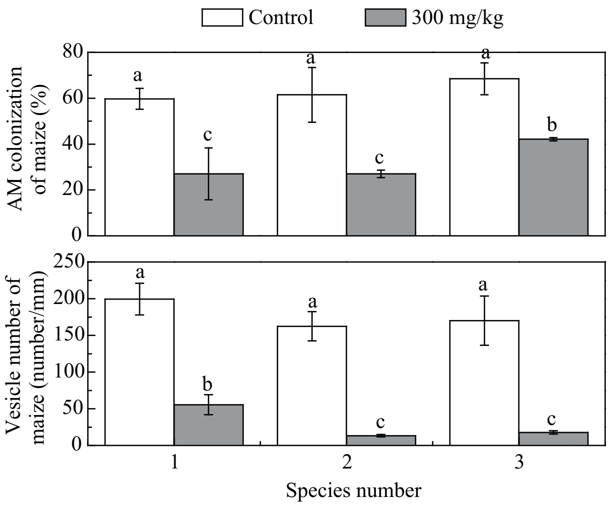

Fig. 5 Arbuscular mycorrhizal colonization and vesicle number of maize. Values are means ± S.E. The means marked by the same letters are not significantly different according to the LSD test and independent-sample *t*-test at $p < 0.05$. Species number 1, 2, and 3 refers to Table 2.

showed marginally significant or insignificant responses, our experiment found that crop-weed mixtures tended to decrease the Pb concentration of the edible part of maize (i.e., seed) at the mature stage under ambient pollution (Table 4). The minimum Pb concentration in seed (2.33 mg/kg) was still far beyond the hygienic standards for grains (⩽ 0.2 mg/kg, GB2715-2005). We checked the data in previous studies and found that the Pb concentration in maize seed under the control was barely detectable. Thus, the reason for the astonishingly high Pb concentrations in maize seed in this study still waits to be uncovered. The significance of this finding, however, cannot be ignored as it provides new insight into the importance of plant diversity maintenance in low-pollution agroecosytems and enhances our understanding of the linkages between diversity and ecosystem function.

The mechanism for this reduction may partially due to the "dilution effect" because in the mixtures, the Pb uptake in weeds increased significantly when the species number increased from 2 to 3 (Fig. 2). This implies that weeds tended to accumulate more Pb under coexistence and thereby decreased the amount of soil Pb available to maize. The "dilution effect" was, in a sense, one of the most useful and viable strategies that could protect the target species (*Z. mays*) at the expense of unwanted species (weeds). However, the tradeoff between production loss (Fig. 1) and Pb accumulation reduction of *Z. mays* should be taken into account as well. Furthermore, it was not always the case that plant coexistence would reduce crop metal accumulation as indicated by Liu et al. (2011).

Our study shows that the benefits of plant coexistence on crop plant include not only reduction in plant Pb accumulation, but also enhancement of soil microbes. In our experiment, higher Pb treatment increased the Pb concentration in maize and decreased the microbial activity (indicated by AWCD) and functional group diversity (Fig. 3). However, plant coexistence decreased the Pb accumulation of *Z. mays* and increased microbial activity and functional group diversity (Fig. 3) in both Pb treatments. Moreover, the introduction of weeds changed the soil microbial community structure compared to the monoculture (Fig. 4), which might have great importance for the adaptation of soil microbes to Pb contamination. The results indicate a positive and combined response of aboveground maize and belowground microbial community to plant coexistence. The facilitation of the belowground microbial community could be a result of stress conditions alleviation and diversified food resources like root exudates released by aboveground coexisting plants (Yang et al., 2007). In return, the microbial community showed a mutual feedback with plant fitness. Our experiment found that the mycorrhizal colonization of maize in the 3 species coexistence increased by 14.63% and 55.67% for ambient and elevated Pb treatments respectively compared to the monoculture (Fig. 5). The symbiotic association was found to be able to sequester or exclude heavy metal from the host root and more importantly, improve the mineral nutrient uptake of the host plants, especially P and N (Meharg and Cairney, 1999; Jamal et al., 2002).

4 Conclusions

Pb treatment induced higher Pb accumulations in maize and weeds, along with decreased soil microbial activity and functional group diversity. Plant coexistence reduced the Pb concentration in maize and increased soil microbial activity and functional group diversity under elevated Pb treatment. The results implied that plant species coexistence could alleviate the adverse effects of Pb on crops and soil microbes.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (No. 30970477), the Key Laboratory of Ministry of Agriculture, the People's Republic of China (No. KYJD09021), the Natural Science Foundation of Zhejiang Province (No. Y307418), the Science and Technology Department of Zhejiang Province (No. 2007C13063), and the Education Department of Zhejiang Province (No. Y200805536).

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