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Relationships between root secretion of organic acids and lead uptake and translocation in different rice cultivars

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Abstract

To investigate some mechanisms causing the variations among rice cultivars in Pb uptake, translocation and accumulation, pot soil experiments were conducted with six rice cultivars under different soil Pb levels. Pb concentrations in rice plants and root secretions of low-molecular-weight organic acids (LMWOAs) were measured. The results showed that the variations among the rice cultivars in grain Pb concentrations were 114.29% -- 146.93%. Grain Pb concentrations correlated positively and significantly (P <0.05 or 0.01) with shoot Pb concentrations and the translocation factors (TFs) of Pb from roots to shoots. The variations among the rice cultivars in LMWOAs contents in the soils were 20.62% -- 37.30%. There were positive and significant (P <0.05 or 0.01) correlations between LMWOAs contents in the soils and Pb concentrations in rice shoots and the grains, and TFs of Pb from the roots to the shoots. The correlations between soil LMWOAs contents and root Pb concentrations were positive but mostly insignificant (P > 0.05). The results suggest that soil LMWOAs could promote root Pb uptake, and in a larger extent, enhanced the translocation of Pb form root to shoot. The effects would further influence Pb transfer to and accumulation in rice grain. In conclusion, the variations among rice cultivars in root LMWOAs secretion ought to be one of the main mechanisms that differentiate rice cultivars in Pb uptake, translocation and accumulation in rice grain.

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Introduction

Heavy metal contamination affects soil quality and plant growth. The pollution in agricultural soil also leads to bioaccumulation of heavy metals in the food chain, which will pose serious hazards to the health of humans and animals [1,2].

Lead (Pb) is a widespread and highly toxic metal pollutant, resulting from mining, disposal of wastewater and sewage sludge, road traffic, smelting activities, paints, etc [3,4]. Very high levels of Pb have been found in some agricultural soils in China. Pb concentration of 1486 mg kg^{-1} was reported in paddy field around a Pb/Zn mine in China. Pb concentrations as high as 419, 69.1, 13.2 and 4.67 mg kg^{-1}were found in rice root, straw, grain and brown rice respectively [5]. In Baoji of China, Pb concentrations even exceeded 25000 mg kg^{-1} in some urban soils [6].

Pb is highly dangerous to human body, specifically at early stages of human life. Prenatal and early postnatal exposure to Pb at the level 10–20 mg dl^{-1} (in blood) will result in damage to central nervous systems. The damage was characterized by diminished intelligence, shortened attention span, and slowed reaction time. The effects are irreversible, untreatable and lifelong [7]. It was reported that heavy metal contamination (Cd and Pb) in food crops grown around mine posed a great health risk to the local population [8]. Therefore, to develop the technology for preventing or diminishing Pb absorption by crops and the further transport to edible organs has attracted wide concern. Various physical and chemical cleanup techniques are available at present, but most of them are costly, labor intensive and cause soil disturbances [9].

The uptake of heavy metals by plant is mainly influenced by their bioavailability in the soils [10]. Though metal concentrations in some nature and contaminated soils are abundant, the bioavailability is often limited for some metals because of their low solubility in water and strong binding to soil particles. Metal mobility and plant availability in the rhizosphere are affected by rhizospheric environments and root exudates. Low-molecular-weight organic acids (LMWOAs) secreted by plant roots can form metal-LMWOA complexes in the rhizosphere, which may increase metal bioavailability and enhance metal uptake by plant roots and the transfer to aerial parts [11,12].

It was assumed that plant genotypes may play dominant role in the uptake and translocation of heavy metals by plants, and great genotypic differences have been reported [13-17]. Understanding the genetic mechanism of plants in metal uptake is important because it facilitates the approaches to improve plants for metal control, but the mechanisms are not well understood. It was reported that citric acid significantly facilitated Cd uptake by plant roots and improved the translocation from roots to shoots [18]. Our previous study also indicated that differences between rice cultivars in Cd accumulations were related to their differences in LMWOAs secretion by the roots [19]. But the differences among rice cultivars in root secretion of organic acids and the relationships with Pb uptake, translocation and the accumulation in rice grain were not reported.

Materials and methods

Soil preparation

The soil for the study was fetched from an unpolluted paddy field. The soil was air-dried and sieved with a 2 mm screen, and tested the following properties: particle size, pH, Organic Matter (OM) content and cation exchange capacity (CEC). Pb concentration of the soil was determined with AAS after a digesting procedure with H_2O_2-HF-HNO_3-$HClO_4$. The soil texture is a sandy loam (sand : silt : clay = 53.6% : 26.2% : 20.2%), with pH 6.6, OM 26.9 g kg^{-1}, CEC 12.9 cmol kg^{-1}, and Pb content 35.2 mg kg^{-1}.

The dried and sieved soil was put into pots (diameter 18 cm, height 20 cm, four kilogram for each pot) for rice cultivation. Two soil Pb levels were designed, e.g. 500 and 1000 mg Pb kg^{-1} soil (moderate and heavy pollution). $PbCl_2$ solution was added into the pot soils with prompt stirring to get the Pb levels. The soils without adding Pb served as control. The prepared pot soils were submerged in water (2-3 cm under water surface) for more than a month before the transplant of rice seedlings.

Experimental design

Six rice cultivars differing in grain Pb accumulations were selected for this research, according to our previous studies [20]. The cultivars were Liangyoupeijiu (high Pb accumulator, abbr. C01), Shanyou 63 (high Pb accumulator, C02), CV6 (moderate Pb accumulator, C03), Yangdao 6 (moderate Pb accumulator, C04), Wuyunjing 7 (low Pb accumulator, C05) and Yu 44 (low Pb accumulator, C06). Rice seeds were submerged in water for 48 h, germinated for 30 h, and then the sprouted seeds were sowed into unpolluted soil. After 30 days' growth, similar seedlings were selected and transplanted into the prepared pots (three seedlings for each pot). During the growth period of rice plants, the pot soils were submerged with water (2-3 cm under water surface). The pots were placed in the open air with a randomized arrangement and six replicates.

Determination of Pb concentrations in rice plants

At the 40^{th} day after seedling transplant (tillering stage), rice plants were sampled in three replicated pots for testing Pb concentrations in the roots and shoots. Grain samples were collected at maturity for Pb concentration testing. The samples were washed with tap water and deionized water, and oven-dried at 70°C to constant weights. The dry samples were ground with a grinder, and sieved with a 100-mesh screen. Pb concentrations of samples were tested with AAS after a digesting procedure with HNO_3-$HClO_4$ [21]. Certified reference materials and reagent blanks were run synchronously for the control of testing quality.

Determination of LMWOAs in the soils

At tillering stage of rice growth (the 40^{th} day after seedling transplant), pot soils were sampled , and LMWOAs in the samples were extracted and purified with reference to the procedure reported by Baziramakenga et al [22]. The soil samples (about 15 g, wet weight) were extracted with 100 mM NaOH for 12 h, filtered through Whatman No. 42, and centrifuged at 15,000 g for 15 min. In order to precipitate humic substances, the supernatants were acidified to pH 2.5 with 1M HCl. The mixtures were centrifuged at 15,000 g for 15 min after 16 h of standing. The supernatants were extracted for 3 times, with10 ml of ethyl acetate for 5 min each time. The extracts were evaporated to dryness in a rotary evaporator at 60^0C. LMWOAs were obtained by re-dissolving the residue in 3 ml distilled water.

It was reported that there were seven main kinds of LMWOAs excreted by crop roots, including formic acid, acetic acid, propionic acid, malic acid, tartaric acid, oxalic acid and citric acid [23]. Therefore, the seven kinds of LMWOAs were determined with an ion chromatograph (Dionex Dx 500, Dionex Corp.) in the soil extracts. The instrument was equipped with a U6K injector, a GP40 pump and a CD20 conductivity detector and a ASRS-ULTRA anion micromembrane suppressor. Columns were purchased from Dionex Corp. The LMWOAs were separated with an IonPac AS-11ion-exchange column (4×250 mm), an IonPac AG-11guard column (4×50 mm) and an IonPac ATC-3 anion-trap column (9×24 mm). The organic acid standards were purchased from Sigma Chemical Company.

Statistical analysis

Data were analyzed with the statistical package SPSS 16.0. The differences among the rice cultivars in Pb concentrations, Pb translocation factors (TFs), and soil LMWOAs concentrations were compared through one-way ANOVA using Tukey's test at the level of $p < 0.05$. The relationships between LMWOAs concentrations in the soils and Pb concentrations in different parts of rice plants, and the TFs of Pb from roots to shoots were analyzed with Pearson correlations (linear model) at two significant levels of $p < 0.05$ and 0.01.

TFs of Pb from root to shoot = Pb concentrations in the shoots / Pb concentrations in the roots.

Results

Variation among rice cultivars in Pb uptake, translocation and accumulation in the grain

There were significant ($P < 0.05$) differences among six rice cultivars in plant Pb concentrations, but the magnitudes of variations differed with the parts of plants and soil Pb levels (Table 1).

Table 1: Pb concentrations in different parts of different rice cultivars at tillering stage (mg kg^{-1})

Rice cultivars	Control		Pb500 [a]		Pb1000 [b]	
	Root	Shoot	Root	Shoot	Root	Shoot
C01	24.29	5.93	1746.38	51.28	3856.48	77.84
C02	26.83	6.65	1988.26	60.92	4073.16	90.25
C03	24.66	5.21	1896.13	46.27	4182.34	71.63
C04	22.97	4.88	1658.42	48.10	3885.66	73.30
C05	23.02	4.24	1622.31	39.88	3815.73	67.05
C06	22.40	4.16	1639.64	36.31	3564.62	51.59
Average	24.03	5.18	1758.52	47.13	3896.33	71.94
$LSD_{0.05}$	2.34	0.80	201.94	3.06	397.82	3.47

[a] Soil Pb treatments of 500 mg kg^{-1}
[b] Soil Pb treatments of 1000 mg kg^{-1}.

The variations in roots were 17.33-22.56% [(the value of the highest cultivar − the value of the lowest cultivar)/the value of the lowest cultivar × 100%] under different soil Pb levels. The variations in shoots were larger and increased with the rise of soil Pb levels, and they were 59.86%, 67.78% and 74.94% for the control, 500 and 1000 mg kg^{-1} soil Pb treatments.

The translocation factors (TFs) of Pb from roots to shoots also varied largely among rice cultivars (Table 2). The magnitudes of variations were also in the order: control (33.49%) < 500 mg kg^{-1} soil Pb treatment (38.46%) < 1000 mg kg^{-1} soil Pb treatment (53.10%).

Table 2: Translocation factors (TFs) of Pb from roots to shoots at tillering stage

Rice cultivars	Control	Pb500	Pb1000
C01	0.2441	0.0294	0.0202
C02	0.2479	0.0306	0.0222
C03	0.2113	0.0244	0.0171
C04	0.2125	0.0290	0.0189
C05	0.1842	0.0246	0.0176
C06	0.1857	0.0221	0.0145
Average	0.2143	0.0267	0.0184
$LSD_{0.05}$	0.0252	0.0043	0.0025

Table 3: Pb concentrations in the grains of different rice cultivars at maturity (mg kg^{-1})

Rice cultivars	Control	Pb500	Pb1000
C01	0.45	3.04	4.47
C02	0.43	3.71	5.63
C03	0.33	2.36	3.61
C04	0.27	2.53	3.79
C05	0.18	1.70	2.74
C06	0.21	1.55	2.28
Average	0.31	2.48	3.75
$LSD_{0.05}$	0.05	0.47	0.71

The variations among the rice cultivars in grain Pb concentrations were larger than those in roots and shoots Pb concentrations, and they were all higher than 100% (Table 3). The variations also increased with the rise of soil Pb levels, and they were 114.29%, 139.35% and 146.93% for the control, 500 and 1000 mg kg^{-1} soil Pb treatments.

Correlation analysis indicate that grain Pb concentrations correlated positively and significantly (P <0.05 or 0.01) with shoot Pb concentrations and the TFs of Pb from roots to shoots, but insignificantly (P > 0.05) with root Pb concentrations (Table 4).

Table 4: Correlation coefficients between grain Pb concentrations and Pb uptake and distribution in rice plants

		Grain Pb concentration (mg kg^{-1})		
		Control	Pb500	Pb1000
Pb concentration in roots (mg kg^{-1})	Control	0.7950		
	Pb500		0.7642	
	Pb1000			0.6425
Pb concentration in shoots (mg kg^{-1})	Control	0.9494**		
	Pb500		0.9919**	
	Pb1000			0.9604**
TFs of Pb from root to shoot	Control	0.9757**		
	Pb500		0.9046*	
	Pb1000			0.9465**

Variation among rice cultivars in organic acid concentrations in soils and the relationships with Pb uptake, translocation and accumulation in the grain

Six kinds of LMWOAs were detected in the pot soils of the six rice cultivars (propionic acid was not detected) (Table 5). The contents of the LMWOAs differed with rice cultivars, soil Pb levels and the kinds of LMWOAs.

On the composition of the LMWOAs, formic acid and acetic acid were dominant, and they occupied 96-98% of the total contents of six LMWOAs. There were significant ($P<0.05$) variations among six rice cultivars in the contents of six LMWOAs and in total contents of the LMWOAs. The magnitudes of variations differed with the kinds of LMWOAs and soil Pb levels. The variations were only 15.62-38.37% [(the value of the highest cultivar − the value of the lowest cultivar)/the value of the lowest cultivar × 100%] for formic acid and acetic acid, but relatively large (30.41-80.91%) for other four kinds of LMWOAs.

Table 5: LMWOAs concentrations in the soils of differences rice cultivars (μg g^{-1}, DW)

Rice cultivars	Organic acids						
	Formic cid	Acetic cid	Malic acid	Oxalic cid	Tartaric acid	Citric acid	Total contents
Control							
C01	70.39	63.52	1.737	1.327	0.993	0.145	138.11
C02	78.28	66.32	2.023	1.511	1.055	0.176	149.37
C03	66.85	60.81	1.615	1.344	0.864	0.130	131.61
C04	71.49	62.04	1.706	1.283	0.910	0.142	137.57
C05	62.47	57.74	1.549	1.146	0.816	0.121	123.84
C06	65.23	57.36	1.495	1.208	0.803	0.123	126.22
Average	69.12	61.30	1.688	1.303	0.907	0.140	134.45
$LSD_{0.05}$	6.64	3.05	0.189	0.116	0.070	0.018	8.23
500 mg kg^{-1} soil Pb treatment							
C01	75.41	64.77	1.684	1.574	1.362	0.162	144.96
C02	88.17	72.53	1.947	1.518	1.408	0.207	165.78
C03	67.23	58.65	1.597	1.481	1.270	0.153	130.38
C04	69.86	66.07	1.554	1.292	1.233	0.159	140.17
C05	64.35	59.76	1.203	1.207	1.168	0.136	127.82
C06	64.59	58.13	1.269	1.264	1.050	0.141	126.44
Average	71.60	63.32	1.542	1.389	1.249	0.160	139.26
$LSD_{0.05}$	5.22	4.93	0.181	0.089	0.091	0.020	9.75
1000 mg kg^{-1} soil Pb treatment							
C01	69.68	65.02	1.057	0.661	0.975	0.138	137.53
C02	79.45	67.66	1.232	0.713	0.980	0.145	150.18
C03	66.31	57.57	0.974	0.624	0.716	0.106	126.30
C04	67.98	60.87	0.937	0.572	0.749	0.112	131.22
C05	57.42	50.15	0.681	0.434	0.613	0.085	109.38
C06	60.72	51.20	0.767	0.487	0.637	0.088	113.90
Average	66.93	58.75	0.941	0.582	0.778	0.112	128.09
$LSD_{0.05}$	6.86	5.82	0.113	0.087	0.110	0.018	11.14

The magnitudes of variations among six rice cultivars in the contents of LMWOAs increased with the rise of soil Pb levels. The variations in the contents of six LMWOAs were 15.62-45.45%, 24.77-61.85% and 34.92-80.91% for the control, 500 and 1000 mg kg^{-1} soil Pb treatments, respectively. The variations in total contents of LMWOAs were 20.62%, 31.11% and 37.30% for the control, 500 and 1000 mg kg^{-1} soil Pb treatments, respectively.

Table 6: Correlations between Pb uptake, translocation in plants and organic acids in soils (n = 6)

	Soil treatments	Organic acids						
		Formic acid	Acetic acid	Malic acid	Oxalic acid	Tartaric acid	Citric acid	Total content
Pb concentration in roots (mg kg^{-1})	Control	0.7770	0.8464*	0.8806*	0.9293**	0.8230*	0.8528*	0.8189*
	Pb500	0.7494	0.5400	0.8486*	0.7707	0.7537	0.8064	0.6908
	Pb1000	0.5743	0.5415	0.6322	0.6629	0.4045	0.4933	0.5662
Pb concentration in shoots (mg kg^{-1})	Control	0.9478**	0.9663**	0.9276**	0.9371**	0.9662**	0.9177**	0.9266**
	Pb500	0.9300**	0.9123*	0.9669**	0.7564	0.9467**	0.9458**	0.9553**
	Pb1000	0.8594*	0.8771*	0.8554*	0.8145*	0.8255*	0.8700*	0.8790*
Pb transfer factor from root to shoot	Control	0.8630*	0.9656**	08775*	0.8713*	0.9737**	0.8757*	0.9151*
	Pb500	0.8253*	0.9229**	0.8151*	0.5810	0.8629*	0.7855	0.8789*
	Pb1000	0.8379*	0.8830*	0.8155*	0.7574	0.8663*	0.8894*	0.8704*
Pb concentration in grains (mg kg^{-1})	Control	0.7641	0.8976*	0.7800	0.8459*	0.9081*	0.7807	0.8275*
	Pb500	0.9492**	0.8989*	0.9750**	0.8083	0.9493**	0.9330**	0.9518**
	Pb1000	0.9596**	0.9592**	0.9568**	0.9178**	0.9249**	0.9603**	0.9720**

With regard to the relationships between the contents of LMWOAs and Pb uptake, translocation and accumulation in rice plants. The contents of six LMWOAs and the total contents of LMWOAs correlated positively and generally significantly (P <0.05 or 0.01) with shoot Pb concentrations (only one exceptional value) (table 6). The contents of LMWOAs correlated positively and mostly significantly (p <0.05 or 0.01) with TFs of Pb from roots to shoots (three exceptional values), and with grain Pb concentrations (four exceptional values). The correlations between the contents of LMWOAs and root Pb concentrations were also positive but mostly insignificant (p > 0.05).

Discussion

Due to drastically increased industrial operations and fast urban expansion, some soils in China were contaminated by heavy metals in varying degrees. According to a national soil pollution survey, cadmium, mercury, arsenic, lead, chromium and nickel were identified as the priority control metals due to their higher concentrations in soils or higher health risks posed to the public. Children and adult females were the relatively vulnerable populations for the non-carcinogenic and carcinogenic risks, respectively. Metal pollution in the soils in southern provinces of China is relatively higher than that in other provinces [24].

Earlier researches showed that the uptake and translocation of trace elements in plants vary greatly not only among plant species but also among cultivars of the same species [25,26]. However, limited information is available about the mechanisms of variations

As suggested by some reports, there are three transport processes that most likely mediate metal accumulation into plant shoots, and subsequently into the seeds: (1) uptake by roots, (2) xylem-loading-mediated translocation to shoots, and (3) further translocation to seeds via the phloem [27].

Our present research showed that the variations among rice cultivars in Pb accumulations differed with plant parts and soil Pb levels. The magnitudes of the variations in different plant parts were in the order: grains > shoots > roots. The magnitudes of the variations under different soil Pb levels were in the order: 1000 mg kg^{-1} (heavily Pb-polluted soil) > 500 mg kg^{-1} (moderately Pb-polluted soil) > control (non-Pb-polluted soil). The differences among rice cultivars in TFs of Pb from roots to shoots were also in the order shown above. Therefore, the diversities between rice cultivars in Pb uptake, translocation and accumulation would be aroused by soil Pb stress.

In our present results, grain Pb concentrations correlated positively and significantly (P <0.05 or 0.01) with shoot Pb concentrations and the TFs of Pb from roots to shoots, and positively but insignificantly (P > 0.05) with root Pb concentrations. The results indicate that grain Pb accumulation depends somewhat on root uptake, and to a larger extent, depends upon the transport of Pb from root to aerial parts.

It was assumed that the metals in soils and plants were likely bound to many kinds of ligands, such as organic acids, organic alkalis, proteins, etc [28]. But others thought that the association between the release of organic chelators from roots and the enhanced uptake and translocation of metals in plants was not proved by sufficient evidences [29].

This study presents that there were significant differences among the rice cultivars in the concentrations of six kinds of LMWOAs and the total contents of the LMWOAs in the soils. The magnitudes of the differences generally matched the variations of root and shoot Pb concentrations, and were all in the order: 1000 mg kg^{-1} soil Pb treatment > 500 mg kg^{-1} treatment > control. The rice cultivars reacted differently to soil Pb stress on LMWOAs secretion. Under 500 mg kg^{-1} soil Pb treatment (moderately polluted), the total contents of LMWOAs were significantly increased for high Pb-accumulating cultivars (such as Shanyou 63), compared to the control, but they were not changed for low Pb-accumulating cultivars (such as Yu 44). Under 1000 mg kg^{-1} soil Pb treatment (heavily polluted), the total LMWOAs contents were not significantly changed for high Pb-accumulating cultivars (such as Liangyoupeijiu and Shanyou

63), but they were significantly reduced for low Pb-accumulating cultivars (such as Wuyunjing 7 and Yu 44). The analyses on the relationships between the contents of LMWOAs and Pb uptake, translocation and accumulation in rice plants indicated that there were close (positive and significant) correlations between LMWOAs contents in the soils and Pb concentrations in the shoots. The correlations between soil LMWOAs contents and TFs of Pb from roots to shoots, and grain Pb concentrations were also positive and generally significant. The correlations between soil LMWOAs contents and root Pb concentrations were positive but mostly insignificant ($P > 0.05$). The results suggest that LMWOAs in the soils promoted root Pb uptake, and to a larger extent, enhanced the translocation of Pb form root to shoot. The effects would further influence Pb transfer to and accumulation in rice grain.

It was reported that a rapid root-to-shoot translocation and enhanced xylem loading capacity may be the crucial processes for high Zn density in rice grains [30]. In hydroponic conditions, application of citric acid alleviated Cd toxicity, and significantly increased Cd uptake and accumulation in the roots, stems and leaves of *Brassica napus* [31]. But in a phytoextraction experiment, the accumulation and total removal of Cd by shoots was not significantly changed by EDTA [32]. Uptake of Pb by plant roots may varies according to the type of chelators used. It was reported that EDTA was capable of dose-dependently increasing Pb uptake by *Vicia faba* roots, but citric acid was unable to enhance Pb accumulation by *V. faba* roots [33]. Therefore, the functions of different kinds of organic acids in Pb uptake, translocation and accumulation in rice plants need further investigation.

Conclusions

Our present research indicates that Pb accumulation in rice grain depends somewhat on root uptake, and to a larger extent, depends upon the transport from root to aerial parts. The rice cultivars varying significantly in grain Pb accumulations also differed greatly in the secretion of LMWOAs, and the rice cultivars reacted differently to soil Pb stress in the secretion of LMWOAs. As a consequence, the magnitudes of the variations among the cultivars in LMWOAs secretions increased with the rise of soil Pb levels. There were close (positive and significant) correlations between the secretion of LMWOAs and Pb concentrations in the shoots and in the grains, and TFs of Pb from roots to shoots. The correlations between LMWOAs secretions and root Pb concentrations were positive but mostly insignificant ($p > 0.05$). The results suggest that LMWOAs promotes root Pb uptake, and to a larger extent, enhance the translocation of Pb form root to shoot. The effects would further influence Pb transfer to and accumulation in rice grain. In conclusion, the variations among rice cultivars in root LMWOAs secretions ought to be one of the main mechanisms that differentiate rice cultivars in Pb uptake, translocation and accumulation in rice grain.

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