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Soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ reduced grain cadmium concentration in Polish wheat (*Triticum polonicum* L.)

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Abstract

Background Wheat is one of major sources of human cadmium (Cd) intake. Reducing the grain Cd concentrations in wheat is urgently required to ensure food security and human health. In this study, we performed a field experiment at Wenjiang experimental field of Sichuan Agricultural University (Chengdu, China) to reveal the effects of $FeCl_3$ and $Fe_2(SO_4)_3$ on reducing grain Cd concentrations in dwarf Polish wheat (*Triticum polonicum* L., 2n = 4x = 28, AABB).

Results Soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ (0.04 M Fe^{3+}/m^2) significantly reduced grain Cd concentration in DPW at maturity by 19.04% and 33.33%, respectively. They did not reduce Cd uptake or root-to-shoot Cd translocation, but increased Cd distribution in lower leaves, lower internodes, and glumes. Meanwhile, application of $FeCl_3$ and $Fe_2(SO_4)_3$ up-regulated the expression of *TpNRAMP5*, *TpNRAMP2* and *TpYSL15* in roots, and *TpYSL15* and *TpZIP3* in shoots; they also downregulated the expression of *TpZIP1* and *TpZIP3* in roots, and *TpIRT1* and *TpNRAMP5* in shoots.

Conclusions The reduction in grain Cd concentration caused by application of $FeCl_3$ and $Fe_2(SO_4)_3$ was resulted from changes in shoot Cd distribution via regulating the expression of some metal transporter genes. Overall, this study reports the physiological pathways of soil applied Fe fertilizer on grain Cd concentration in wheat, suggests a strategy for reducing grain Cd concentration by altering shoot Cd distribution.

Keywords Wheat, Heavy metal, Cd stress, Fe fertilizer, Shoot Cd distribution

Introduction

Cadmium (Cd) is one of the most toxic metals and the primary heavy metal pollutant in arable soils [1]. Moreover, Cd is readily mobile and absorbed by plant roots and inhibits plant growth and development by impairing nutrient uptake, transpiration, and photosynthesis [2–4]. In crops, absorbed Cd is subsequently translocated into shoots and accumulates in edible parts [5, 6]. In China, each year, the Cd level in approximately 1.46 million tons of agricultural products exceeds the national standard (0.10 mg/kg, GB2762-2022), posing a potential risk to human health [7].

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Wheat is a staple food for more than 50% of the world's population. The incidence of arable soils contaminated by Cd in wheat-producing areas (GB/T 41685−2022) has been increasing [8, 9]. Meanwhile, wheat has a strong tendency to accumulate Cd in grains. Increasing of wheat grains accumulate Cd exceeding the maximum level of 0.1 mg/kg in China [10, 11], and even 0.20 mg/kg in European countries and the United States [12, 13]. Thus, wheat is a major source of human Cd uptake in many countries and regions [14]. Reducing Cd concentration in wheat grains is urgently required to ensure food security and human health.

Grain Cd concentration in wheat is mainly mediated by Cd uptake in roots, root-to-shoot translocation, and shoot-to-grain remobilization [8, 11, 15–19]. These processes are depending on wheat genotype and controlled by genetic factors [11]. Cd uptake and transport in plants depend on essential metal transporters, such as the IRT (iron-regulated transporter), NRAMP (natural resistance-associated macrophage protein), ZIP (zinc transporter), HMA (P_{1B}-ATPase-Heavy metal associated protein), and YSL (yellow stripe-like transporters) families [20–28]. The expression levels of genes encoding metal transporters are easily regulated by environmental factors, such as essential nutrients, light and temperature [11, 14]. Cd uptake in roots is also influenced by the rhizosphere soil's properties, such as pH and Cd bioavailability [29]. Thus, the grain Cd accumulation in wheat is mediated by environmental factors [11]; and agronomic practices, such as the application of iron (Fe) fertilizer, could be used to reduce grain Cd accumulation in wheat.

Fe (II) fertilizers such as $FeSO_4$ and EDTA-Na_2Fe have been used to mediate grain Cd accumulation in rice [30]. However, the synergistic/antagonistic relationship between Fe fertilizers and Cd developed on the application strategy and forms of Fe fertilizers. For example, soil application of EDTA-Na_2Fe reduced grain Cd concentrations in rice; while, foliar application of EDTA-Na_2Fe, $FeSO_4$, or soil application of $FeSO_4$ increased grain Cd concentrations [30]. Fe(III) fertilizers $FeCl_3$ and $Fe_2(SO_4)_3$ can enhance the mobility of Cd in contaminated soils by extracting Cd from soil in the form of Cd^{2+} and $CdCl^{+}$complex [31]. Our previous hydroponic experiment found that $FeCl_3$ and $Fe_2(SO_4)_3$ differentially reduced root Cd uptake and promoted root-to-shoot Cd translocation in dwarf Polish wheat (DPW; *Triticum polonicum* L., 2n=4x=28, AABB) seedlings [32]. Notably, Cd concentration in wheat grains is positively correlated with Cd uptake and root-to-shoot translocation [33]. Thus, we hypothesized that soil application of $FeCl_3$ or $Fe_2(SO_4)_3$ may influence Cd uptake and transport in wheat, finally affecting grain Cd concentration.

Our previous hydroponic experiment also showed that $FeCl_3$ and $Fe_2(SO_4)_3$ differentially regulated the expression levels of metal transporter genes, such as *TpIRT1* and *TpYSL15* [32]. However, whether soil application of $FeCl_3$ or $Fe_2(SO_4)_3$ can regulate the expression levels of metal transporter genes (e.g., *TpIRT1* and *TpYSL15*) to alter Cd uptake and grain Cd concentration in DPW remains unclear.

The aim of this study was to reveal the effects of soil application of $FeCl_3$ or $Fe_2(SO_4)_3$ on grain Cd concentration in DPW in the field. To achieve this objective, we evaluated the plant growth, photosynthetic parameters, and metal concentrations in tissues; calculated the parameters of Cd uptake, root-to-shoot translocation, and distribution in shoots; analyzed the expression levels of metal transporter genes, such as *TpIRT1* and *TpYSL15*. The findings may facilitate the reduction of grain Cd accumulation in wheat production by presenting a reasonable and effective agronomic strategy.

Materials and methods

Plant materials

Dwarf Polish wheat (DPW, *Triticum polonicum* L., 2n=4x=28, AABB) is a landrace of Turpan, Xinjiang Province, China, with a seed rate of approximately 75%. It shows high uptake and tolerance of Cd and carries other valuable genes, such as the long kernel gene *KL-PW* and dwarfing gene *Rht-B1b* [29, 34–36].

Field growth and treatments

During the wheat-growing season at 2018–2019, DPW seeds were sown in the Wenjiang experimental field of Sichuan Agricultural University (30°43′N; 103°52′E), Chengdu, China. The soil (0–15 cm depth) characteristics are presented in Supplemental Table S1. The total Cd concentration in the soil exceeded the safety threshold values (0.30 mg/kg, pH<6.5). Before sowing, N-P-K compound fertilizer ($N/P_2O_5/K_2O$=15:15:15, GB/T 15063−2009) was applied one-time with 600 kg/ha. The experiment was conducted in a randomized complete block design with three planted plots for each treatment; and all experiments were conducted at three different pieces of paddy field. Each plot contained 30 rows with twenty seeds planted in each row at 2 m intervals.

At the tillering stage, the 30 rows of each plot were randomly reclassified into three groups and treated with Fe(III) fertilizers. For group 1, the control (CK), Fe(III) fertilizer was not applied. For groups 2 and 3, $FeCl_3$ (0.04 M Fe^{3+}/m^2) and $Fe_2(SO_4)_3$ (0.04 M Fe^{3+}/m^2) were applied, respectively. Specifically, Fe(III) fertilizer was dissolved in 5 L distilled water and uniformly applied to the soil of each subgroup, and the CK soil was irrigated with 5 L distilled water.

At the grain filling (flowering after 15 d) stage and maturity, 30 plants were randomly sampled from each treatment of each plot (three plants each row) and then

divided into grains, glumes, rachises, node 1, internode 1, flag leaves, lower nodes, lower internodes, lower leaves, and roots. All samples were dried at 105 °C for 1 h and at 80 °C for 3 d and weighed.

Investigation of agronomic traits and photosynthetic parameters

Plant height, spike length, tiller number and dry weight of tissues were investigated at grain filling stage (on the 185th day after sowing) and maturity (on the 203th day after sowing). At the grain filling stage, photosynthetic parameters, including the assimilation rate, transportation rate, internal CO_2, stomatal conductance, vapor pressure deficit, and water use efficiency, were measured using a portable photosynthesis system (CIRAS-3, PP systems, Amesbury, USA). Monthly temperature, maximum temperature, minimum temperature, precipitation, wet days, and vapour pressure were obtained from the Climatic Research Unit (CRU TS version 4.08, https://crudata.uea.ac.uk/cru/data/hrg/).

Determination of metal concentrations

Concentrations of Cd and Fe in each sample were measured using the method described by Yao et al. (2023) [32]. In brief, each dried sample was ground to powder, and 0.20 g powder was digested using a mixture of acids (HNO_3/$HClO_4$; *v/v*, 4:1) at 280 °C. The digested solution was loaded onto an inductively coupled plasma mass spectrometer (ICP-MS; NexION, 2000; PerkinElmer, USA) to determine the concentrations of Cd and Fe. Reference standard solutions of Cd and Fe were purchased from the Guobiao Testing and Certification Company (Beijing, China).

Calculation of cd uptake, translocation and distribution

Cd uptake, root-to-shoot translocation and shoot distribution were calculated using the methods described by Shi et al. (2019) [37] and Cheng et al. (2021) [11].

(1) Tissue Cd content = Tissue Cd concentration × Tissue dry weight;

(2) Whole plant Cd content = ∑Cd content in each tissue;

(3) Cd uptake = Whole plant Cd content ÷ Whole plant dry weight;

(4) Shoot Cd content = Whole plant Cd content − Root Cd content;

(5) Cd translocation factor (TF) = Shoot Cd content ÷ whole plant Cd content;

(6) Cd distribution = Tissue Cd content ÷ whole plant Cd content;

(7) Continuous Cd uptake = Whole plant Cd content at maturity stage − Whole plant Cd content at early grain filling stage.

Total RNA extraction and RT-qPCR

At the grain filling stage, roots and shoots were sampled from each subgroup and frozen in liquid nitrogen for RNA isolation. Total RNA was isolated using the Total RNA Kit II (Omega, United States). cDNA was synthesized from 1 μg total RNA by using the M-MLV First Strand cDNA Synthesis Kit (Omega, United States). The expression levels of the metal transporter genes (*TpIRT1*, *TpYSL15*, *TpHMA2*, *TpNRAMP2*, *TpNRAMP5*, *TpZIP1*, *TpZIP3*, and *TpZIP5*) were normalized using the method Chai et al. (2022) described [36]. The specific primers we used are listed in Supplemental Table S2. *TpACTIN* and *TpGAPDH* were used as reference genes [38]. The software CFX Manager 3.1 (Bio-Rad, United States) and the $2^{\Delta\Delta Ct}$ method were used to calculate the relative expression level.

Statistical analysis

All data are reported as the mean values of three replicates with standard deviations. Statistical analyses were performed using a one-way analysis of variance (ANOVA) and Turkey's test using SPSS 20 (IBM Corporation, USA). Graphs were plotted using SigmaPlot (version 14.0; Systat Software Inc., USA).

Results

Wheat growth at grain filling and maturity

During the entire growth stage, all plants were very healthy. At the grain filling stage, soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ significantly enhanced photosynthetic parameters, including assimilation rate, transportation rate, and stomatal conductance, but did not change internal CO_2 concentration and water use efficiency when compared with CK (Table 1). Moreover, they did not change the plant height, spike length, and tiller

Table 1 Photosynthetic parameters of DPW under Fe fertilizers treatments at grain filling stage

Treatments	Assimilation rate (μ mol m^{-2} s^{-1})	Transpiration rate (m mol m^{-2} s^{-1})	Internal CO_2 (ppm)	Stomatal conductance (m mol m^{-2} s^{-1})	Vapour pressure deficit (mb)	Water use efficiency (%)
CK	17.20 ± 0.17 b	5.73 ± 0.35 b	293.33 ± 3.33 a	303.33 ± 2.03 b	2.03 ± 0.03 a	3.17 ± 0.13 a
$FeCl_3$	21.27 ± 0.50 a	7.33 ± 0.33 a	295.67 ± 1.20 a	453.67 ± 12.41 a	1.90 ± 0.06 a	2.90 ± 0.06 a
$Fe_2(SO_4)_3$	20.05 ± 1.25 a	7.25 ± 0.15 a	305.00 ± 7.00 a	435.00 ± 12.00 a	1.90 ± 0.01 a	2.80 ± 0.20 a

Values are presented as means ± standard deviation ($n = 3$); different lowercase indicated significant differences in photosynthetic parameters between treatments at the grain filing stage ($P \leq 0.05$).

Table 2 Dry weight of DPW under Fe fertilizers treatments at grain filling and maturity stages

Tissues	Grain filling stage			Maturity stage		
	CK	$FeCl_3$	$Fe_2(SO_4)_3$	CK	$FeCl_3$	$Fe_2(SO_4)_3$
Grains	1.47 ± 0.07 b	1.46 ± 0.11 b	2.23 ± 0.30 a	3.75 ± 0.14 B	4.38 ± 0.12 A	4.33 ± 0.24 A
Rachises	1.25 ± 0.26 a	1.39 ± 0.17 a	1.32 ± 0.05 a	2.02 ± 0.03 A	1.88 ± 0.18 A	2.55 ± 0.34 A
Glumes	6.69 ± 0.72 a	7.56 ± 0.23 a	7.28 ± 0.57 a	6.25 ± 0.30 B	5.91 ± 0.59 B	8.52 ± 0.46 A
Node 1	0.29 ± 0.07 a	0.32 ± 0.03 a	0.29 ± 0.06 a	0.59 ± 0.02 A	0.59 ± 0.03 A	0.58 ± 0.02 A
Internode 1	4.38 ± 0.76 a	3.99 ± 0.68 a	4.26 ± 1.17 a	5.16 ± 0.28 A	4.64 ± 0.18 A	4.96 ± 0.21 A
Flag leaves	5.53 ± 0.58 a	6.91 ± 1.10 a	6.27 ± 0.62 a	5.45 ± 0.24 AB	4.72 ± 0.87 B	6.37 ± 0.44 A
Lower nodes	1.22 ± 0.25 a	1.15 ± 0.08 a	0.93 ± 0.08 a	1.72 ± 0.09 C	1.90 ± 0.04 B	2.14 ± 0.07 A
Lower internodes	5.87 ± 0.44 a	6.33 ± 0.46 a	5.70 ± 1.10 a	6.19 ± 0.71 B	6.93 ± 0.24 AB	7.44 ± 0.24 A
Lower leaves	9.56 ± 1.03 a	10.80 ± 0.33 a	10.40 ± 0.81 a	10.37 ± 0.54 AB	8.66 ± 0.80 B	10.60 ± 0.83 A
Roots	2.37 ± 0.44 a	2.00 ± 0.04 ab	1.69 ± 0.02 b	1.93 ± 0.04 A	1.91 ± 0.04 A	1.31 ± 0.08 B
Whole plant	38.63 ± 1.77 a	41.90 ± 2.36 a	40.38 ± 3.10 a	43.44 ± 1.07 B	41.53 ± 1.90 B	48.49 ± 1.50 A

Values are presented as means ± standard deviation ($n = 3$); different lowercase and uppercase letters indicate the significant differences in tissue dry weights among treatments at grain filling and maturity stages, respectively ($P \le 0.05$).

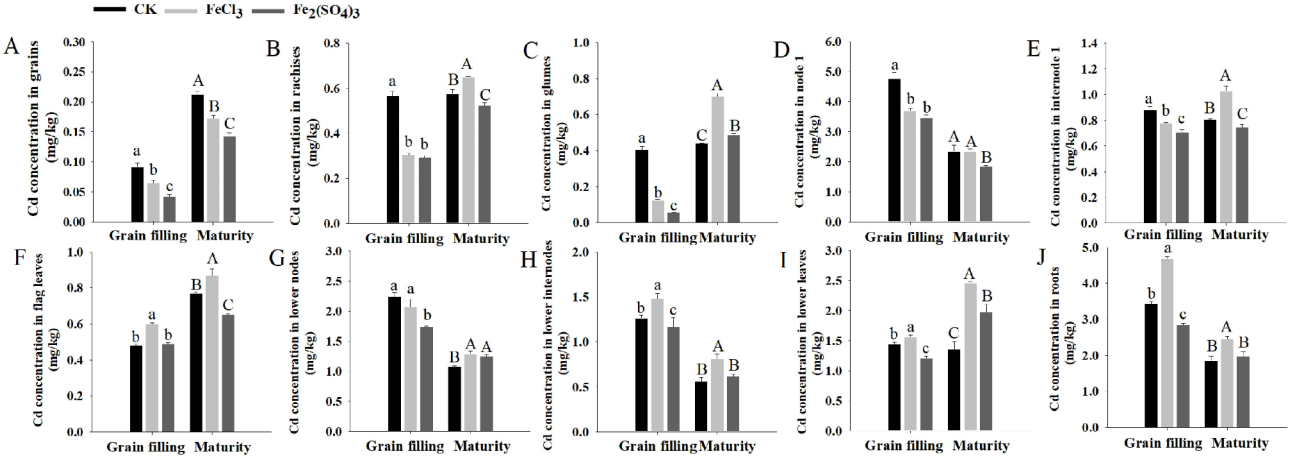

Fig. 1 Tissue Cd concentration of DPW at grain filling and maturity stages

A-**J**: Grains, rachises, glumes, node 1, internode 1, flag leaves, lower nodes, lower internodes, lower leaves and roots, respectively. Values are presented as means ± standard deviation ($n = 3$); lowercase and uppercase letters indicate the significant differences in Cd concentrations among treatments at grain filling and maturity stages, respectively ($P \le 0.05$)

numbers of DPW (Supplemental Figure S1), but differentially changed the dry weight of several tissues per plant. For example, $FeCl_3$ application did not changed the dry weight of all tissues of DPW at the grain filling stage, but significantly increased dry weight of grain by 16.80% and dry weight of lower nodes by 0.10% at maturity. $Fe_2(SO_4)_3$ application significantly increased dry weight of grain by 51.70% and decreased dry weight of root by 28.69% at the grain filling stage, and increased dry weight of grain by 15.47% and dry weights of glumes, lower nodes, lower internodes, and whole plants at maturity when compared with those of the CK (Table 2).

Tissue Cd and Fe concentrations at the grain filling and maturity stages

For the CK, the grain Cd concentrations of DPW were 0.09 mg/kg and 0.21 mg/kg at the grain filling and mature stages, respectively. Soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ dramatically reduced the grain Cd concentrations to 0.07 mg/kg and 0.04 mg/kg at the grain filling stage, and 0.17 mg/kg (reduced ratio of 19.04%) and 0.14 mg/kg (reduced ratio of 33.33%) at maturity, respectively (Fig. 1A). To reveal the underlying mechanisms, we investigated Cd concentrations in other tissues. At the grain filling stage, $Fe_2(SO_4)_3$ application significantly reduced the Cd concentrations of all tissues (except flag leaves) with the decreased ranges from 7.86% (lower internodes) to 85.78% (glumes) when compared with the CK; while, $FeCl_3$ application only reduced the Cd concentrations of rachis (46.12%), glumes (70.01%), node 1 (22.20%), and internodes 1 (11.95%), but increased the Cd concentrations of flag leaves (24.89%), lower internodes (17.11%), lower leaves (8.29%), and roots (36.35%) (Fig. 1B and J). At maturity, different results were observed. Compared with the CK, the application of $Fe_2(SO_4)_3$ decreased the Cd concentrations of rachis

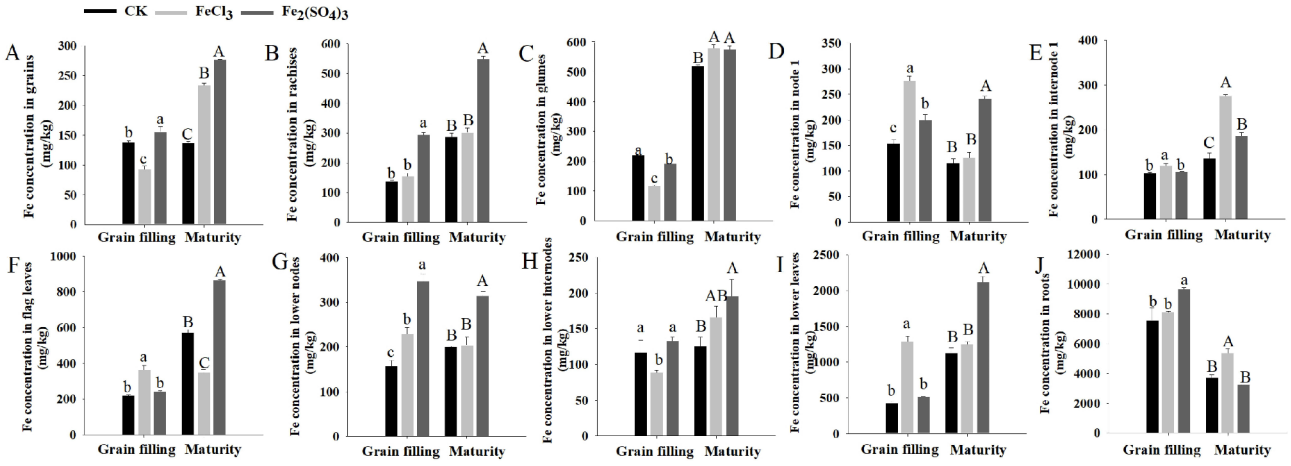

Fig. 2 Tissue Fe concentration of DPW at grain filling and maturity stages

A-J: Grains, rachises, glumes, node 1, internode 1, flag leaves, lower nodes, lower internodes, lower leaves and roots, respectively. Values are presented as ± standard deviation ($n = 3$); lowercase and uppercase letters indicate the significant differences in Fe concentrations among treatments at grain filling and maturity stages, respectively ($P \leq 0.05$)

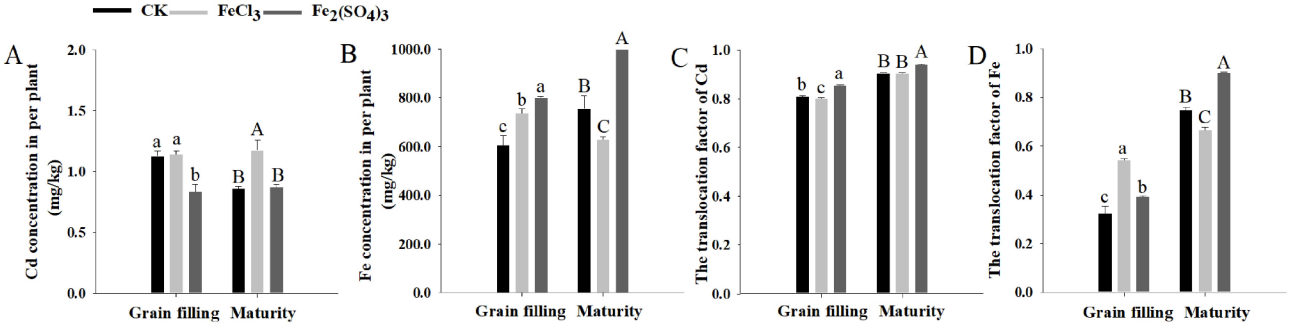

Fig. 3 Per plant concentration and TF of Cd and Fe in DPW

A: Cd concentration; **B**: Fe concentration; **C**: Cd TF; **D**: Fe TF. Values are presented as ± standard deviation ($n = 3$); lowercase and uppercase letters indicate significant differences in Cd and Fe concentration in per plant and TF among treatments at grain filling and maturity stages, respectively ($P \leq 0.05$)

(8.81%), node 1 (21.35%), internode 1 (7.41%) and flag leaves (15.45%) but increased the Cd concentrations of glumes (11.12%), lower nodes (15.91%), and lower leaves (23.08%). The application of $FeCl_3$ increased the Cd concentrations of all tissues (except node 1) with the increased range from 12.65% (flag leaves) to 67.67% (lower leaves) (Fig. 1B and J).

The grain Fe concentrations of DPW were similar at approximately of 137.83 mg/kg at both stages for the CK (Fig. 2A). Soil application of $FeCl_3$ significantly reduced grain Fe concentration to 92.79 mg/kg at the grain filling stage and increased it to 234.26 mg/kg at maturity; application of $Fe_2(SO_4)_3$ increased the grain Fe concentration to 156.22 mg/kg at the grain filling stage and to 276.48 mg/kg at maturity (Fig. 2A). Soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ also influenced the Fe concentrations of other tissues (Fig. 2B and J). Compared with the CK, application of $FeCl_3$ significantly reduced the Fe concentrations of glumes and lower internodes but increased those of node 1, internode 1, flag leaves, lower nodes, and lower leaves at the grain filling stage and increased the Fe concentrations of glumes, internode 1 and roots but reduced those of flag leaves at maturity (Fig. 2B and J). Application of $Fe_2(SO_4)_3$ increased the Fe concentrations of rachises, node 1, lower nodes, and roots but reduced those of glumes at the grain filling stage and increased the Fe concentrations of all tissues (except roots) at maturity (Fig. 2B and J).

Uptake and root-to-shoot translocation of Cd and Fe

For the CK, Cd concentration of the whole plant was 1.13 mg/kg at the grain filling stage and 0.86 mg/kg at maturity. Soil application of $FeCl_3$ did not alter the Cd concentration of the whole plant at the grain filling stage but increased it to 1.18 mg/kg at maturity, and the application of $Fe_2(SO_4)_3$ reduced the Cd concentration of the whole plant to 0.84 mg/kg at the grain filling stage but did not change that at maturity (Fig. 3A). For the CK, Fe concentration in the whole plant was 607.68 mg/kg at the grain filling stage and 756.05 mg/kg at maturity.

Application of $FeCl_3$ significantly increased the Fe concentration of the whole plant to 739.12 mg/kg at the grain filling stage, but that decreased to 628.54 mg/kg at maturity; the application of $Fe_2(SO_4)_3$ increased the Fe concentration of the whole plant to 802.24 mg/kg at the grain filling stage and 1007.39 mg/kg at maturity (Fig. 3B).

For the CK, root-to-shoot Cd translocation was 0.81 at the grain filling stage and 0.90 at maturity; root-to-shoot Fe translocation was 0.32 at the grain filling stage and 0.75 at maturity. Compared with the CK, the application of $FeCl_3$ significantly inhibited the root-to-shoot Cd translocation at the grain filling stage but did not influence that at maturity (Fig. 3C). It increased the root-to-shoot Fe translocation at the grain filling stage but reduced that at maturity (Fig. 3D). By contrast, the application of $Fe_2(SO_4)_3$ dramatically increased the root-to-shoot translocation of Cd and Fe at the grain filling stage or maturity (Fig. 3C and D).

Continuous absorption or efflux of Cd during grain filling

The change in the Cd content of the whole plant during grain filling represents the continuous absorption or efflux of Cd. During grain filling, Cd content of the whole plant was significantly reduced in the CK but increased with soil application of $Fe_2(SO_4)_3$ and did not change with soil application of $FeCl_3$. These results indicate that DPW showed a continuous Cd efflux under CK; however, soil application of $Fe_2(SO_4)_3$ promoted continuous Cd absorption (Supplemental Figure S2).

Distribution and shoot remobilization of Cd during grain filling

At the grain filling stage, Cd was mainly distributed in lower leaves (31.66%), followed by lower internodes (17.02%) and roots (18.73%), subsequently in internodes 1 (8.88%), lower nodes (6.29%), glumes (6.25%), flag leaves (6.10%), node 1 (3.13%), rachises (1.62%), and was the lowest in the grains for the CK (Table 3). Compared with the CK, soil application of $Fe_2(SO_4)_3$ and $FeCl_3$ significantly increased Cd distribution in the lower leaves, lower internodes, and flag leaves but decreased Cd distribution in the grains, rachis, glumes, and lower nodes (Table 3). At maturity, Cd was also mainly distributed in lower leaves (37.55%) and subsequently in flag leaves (11.24%), internodes 1 (11.15%), roots (9.57%), lower internodes (9.23%), glumes (7.37%), lower nodes (4.94%), node 1 (3.72%), rachises (3.11%) and grains (2.13%) for the CK (Table 3). Compared with the CK, soil application of $Fe_2(SO_4)_3$ and $FeCl_3$ also significantly increased Cd distribution in lower leaves, lower internodes, and glumes but reduced it in grains, internode 1, flag leaves, and node 1 (Table 3). Moreover, the Cd distribution ratios of the lower leaves, lower nodes, flag leaves, and glumes were significantly higher in the soil application of $Fe_2(SO_4)_3$ than $FeCl_3$.

From the grain filling stage to maturity, Cd distribution in the lower internodes and roots was significantly reduced in all treatments (Table 3). Cd distribution in lower nodes was also reduced in the CK. The reduction in Cd distribution indicates that these tissues were sources

Table 3 Proportion of cd content in DPW at grain filling and maturity stages

Tissues	Grain filling			Maturity			Change value		
	CK	$FeCl_3$	$Fe_2(SO_4)_3$	CK	$FeCl_3$	$Fe_2(SO_4)_3$	CK	$FeCl_3$	$Fe_2(SO_4)_3$
Grains	0.31% ± 0.01 a	0.20% ± 0.02 c	0.28% ±0.01 b	2.13% ± 0.12 A	1.56% ± 0.21 B	1.46% ± 0.17 B	1.82%	1.36%	1.18%
Rachises	1.62% ± 0.12 a	0.89% ± 0.15 b	1.15% ± 0.11 b	3.11% ± 0.26 A	2.51% ± 0.14 B	2.78% ± 0.19 A	1.48%	1.62%	1.63%
Glumes	6.25% ± 0.54 a	1.93% ± 0.32 b	1.25% ± 0.25 c	7.37% ± 0.23 C	8.47% ± 0.19 B	9.82% ± 0.32 A	1.11%	6.54%	8.57%
Node 1	3.13% ± 0.17 a	2.45% ± 0.22 b	2.94% ± 0.12 a	3.72% ± 0.23 A	2.81% ± 0.43 B	2.53% ± 0.31 B	0.58%	0.36	-0.41%
Internode 1	8.88% ± 0.22 a	6.47% ± 0.32 b	8.95% ± 0.17 a	11.15% ± 0.16 A	9.78% ± 0.25 B	8.74% ± 0.31 C	2.27%	3.31%	-0.20%
Flag leaves	6.10% ± 0.12 b	8.67% ± 0.43 a	9.12% ± 0.37 a	11.24% ± 0.24 A	8.39% ± 0.35 C	9.79% ± 0.42 B	5.14	-0.28%	0.66%
Lower nodes	6.29% ± 0.31 a	4.97% ± 0.24 b	4.82% ± 0.18 b	4.94% ± 0.13 B	5.03% ± 0.11 B	6.28% ± 0.32 A	-1.35%	0.05%	1.46%
Lower internodes	17.02% ± 0.11 b	19.58% ± 0.32 a	19.81% ± 0.26 a	9.23% ± 0.17 B	11.46% ± 0.32 A	10.78% ± 0.43 A	-7.79	-8.12%	-9.03%
Lower leaves	31.66% ± 0.54 b	35.25% ± 0.39 a	37.36% ± 0.27 a	37.55% ± 0.65 B	40.35% ± 0.47 B	41.74% ± 0.28 A	5.89%	5.10%	4.38%
Roots	18.73% ± 0.76 a	19.59% ± 0.34 a	14.31% ± 0.46 b	9.57% ± 0.13 A	9.64% ± 0.22 A	6.07% ± 0.43 B	-9.16	-9.95%	-8.24%

Values are presented as means ± standard deviation ($n = 3$); different lowercase and uppercase letters indicate the significant differences in tissue proportion of Cd content

of Cd remobilization during grain filling. Cd distribution in the lower leaves, glumes, rachises, and grains was enhanced in all treatments (Table 3). Cd distributions in lower nodes in $Fe_2(SO_4)_3$ application, flag leaves and internode 1 in the CK, and internode 1 in $FeCl_3$ application also increased. The increase in Cd distribution indicates that these tissues were sinks for Cd remobilization.

Relative expression of metal transporter genes

Soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ also differentially regulated the expression of metal transporter genes, including *TpIRT1*, *TpYSL15*, *TpHMA2*, *TpNRAMP2*, *TpNRAMP5*, *TpZIP1*, *TpZIP3* and *TpZIP5*, in DPW roots and shoots at the filling stage (Fig. 4). *TpIRT1*, *TpNRAMP5*, *TpZIP3*, and *TpZIP5* were mainly expressed in the roots; *TpHMA2*, *TpYSL15*, and *TpZIP3* were mainly expressed in the roots and shoots; and *TpNRAMP2* was mainly expressed in the shoots.

In the roots, compared with the CK, soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ significantly upregulated the expression levels of *TpYSL15* and *TpNRAMP5* but downregulated the expression levels of *TpZIP1* and *TpZIP3* (Fig. 4A). The expression of *TpIRT1* and *TpHMA2* was upregulated by $FeCl_3$ and $Fe_2(SO_4)_3$ application (Fig. 4A). However, the expression level of *TpZIP5* was unchanged.

In shoots, compared with the CK, soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ significantly upregulated the expression levels of *TpYSL15* and *TpZIP3* but downregulated the expression levels of *TpNRAMP5* and *TpIRT1* (Fig. 4B). The expression levels of *TpHMA2* and *TpNRAMP2* were dramatically upregulated by $Fe_2(SO_4)_3$ application but downregulated by $FeCl_3$ application (Fig. 4B).

Discussion

In this study, the soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ reduced the grain Cd concentration in DPW at maturity (Fig. 1A). This reduction did not result from plant growth or development because there was no change in plant height, spike length, or tiller number. However, we did not exclude the dilution effect of grain dry weight on the reduction in grain Cd concentration, although the increased ratios of grain dry weight per plant (16.80% and 15.47%) were significantly lower than the decreased ratios of grain Cd concentration (19.04% and 33.33%) (Fig. 1A). Grain weight is jointly regulated by pre-anthesis nutrient accumulation and photosynthesis during grain filling [39, 40]. Thus, the increase in grain dry weight might have resulted from the enhanced assimilation rate, transportation rate, and stomatal conductance at the grain filling stage caused by the soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ (Tables 1 and 2). The enhances may promote aboveground biomass accumulation and transport to grains, because they are closely and positively correlated [41].

Our previous hydroponic experiment showed that application of $FeCl_3$ and $Fe_2(SO_4)_3$ significantly reduced Cd uptake but promoted root-to-shoot Cd translocation in DPW seedlings [32]. In this study, soil application of $FeCl_3$ significantly enhanced Cd uptake but did not change root-to-shoot Cd translocation, and soil application of $Fe_2(SO_4)_3$ did not change Cd uptake but promoted

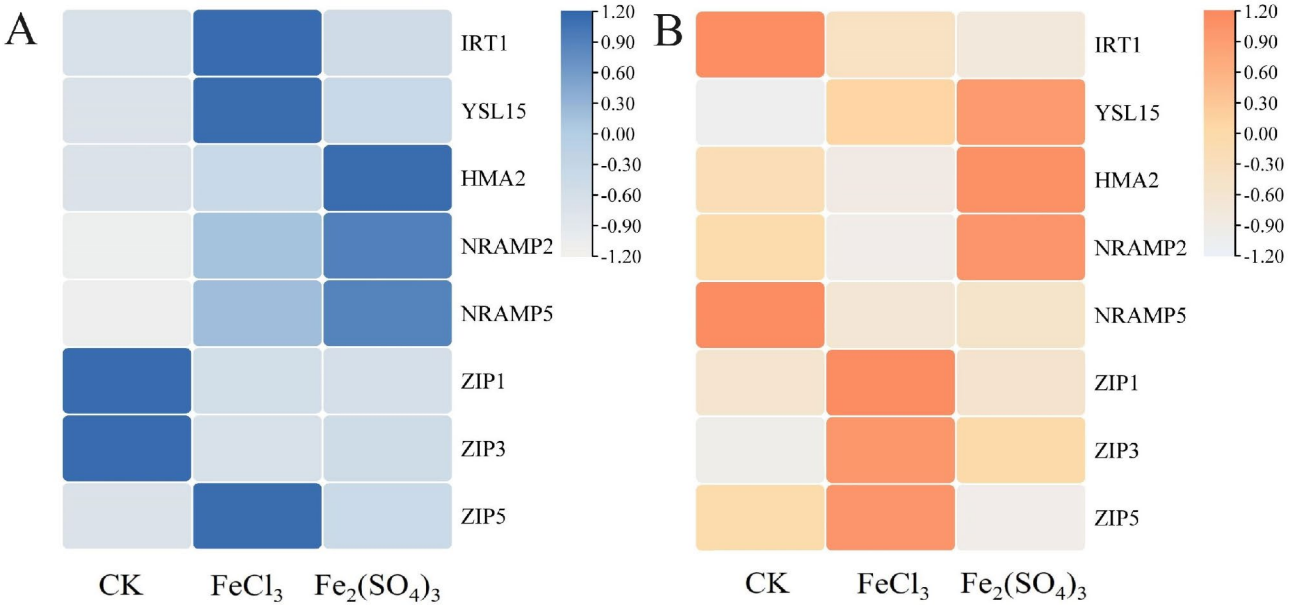

Fig. 4 Heatmap of metal transporter genes in root and shoot of DPW

A: Root; **B**: shoot. Values are presented as ± standard deviation ($n = 3$). Different expressions are performed in gradient ramp; the deeper the color, the higher gene expression.

root-to-shoot Cd translocation in DPW at maturity (Fig. 3A and C). These differences may be due to different growth conditions (hydroponic and field), external Cd concentration (80 μM and 0.30 mg/kg) and growth period (seedling and mature). The enhanced Cd uptake by $FeCl_3$ application probably resulted from the soil application of $FeCl_3$ (1) promoting Cd bioavailability [31], and (2) upregulating the expression level of a Cd absorber gene *TpIRT1* when compared with the CK (Fig. 4A; [27]). The potential reasons for the unchanged Cd uptake and enhanced root-to-shoot Cd translocation by $Fe_2(SO_4)_3$ were that soil application of $Fe_2(SO_4)_3$ (1) did not change Cd bioavailability [31], or (2) did not change the expression level of Cd absorber gene *TpIRT1* when compared with those of the CK (Fig. 4A), but (3) significantly upregulated the expression level of *TpHMA2*, whose homologous gene *OsHMA2* is responsible for root-to-shoot Cd translocation in rice [42]. Soil application of $Fe_2(SO_4)_3$ upregulated the expression level of Cd absorber gene *TpNRAMP5*, which potentially promoted the continuous absorption of Cd during grain filling (Table 3; [22]). This may also explain why $Fe_2(SO_4)_3$ application reduced Cd uptake at the grain filling stage but did not change that at maturity (Fig. 3A). *TpZIP1*, whose homologous gene *OsZIP1* encodes a Cd efflux transporter that limits excess Cd accumulation in rice [43], was highly expressed in the roots under CK (Fig. 4A), supporting that it was responsible for Cd efflux during grain filling (Table 3). Cd uptake, root-to-shoot Cd translocation, and Cd continuous absorption positively determine the grain Cd concentration in wheat [11, 15, 17–19]. Thus, the reduction in grain Cd concentration in the DPW caused by soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ was independent of Cd uptake, root-to-shoot Cd translocation, and continuous Cd absorption. These results differed from those of the soil application of EDTA-Na_2Fe, which reduced the grain Cd concentration in rice by reducing Cd uptake and root-to-shoot Cd translocation [30].

Intrinsically, soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ reduced the grain Cd concentration by altering shoot Cd distribution or redistribution (Table 3). During grain filling in wheat, Cd remobilization from internodes and leaves mainly contributes to grain Cd concentration [11, 17, 18]. In this study, Cd was remobilized from lower internodes to grains and glumes in DPW, which was why soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ increased Cd distribution in glumes during grain filling (Table 3). Internodes store pre-anthesis reserves in their phloem parenchyma and play a critical role in grain yield formation [44, 45]. However, in this study, lower nodes played a distinct role in reducing the gain in Cd concentration. This node is a core site for the xylem-to-phloem transfer of Cd [28, 46], and the transfer of Cd to grains via the phloem is restricted to lower nodes of wheat [17]. Soil application of $FeCl_3$ and $Fe_2(SO_4)_3$ completely inhibited Cd remobilization from lower nodes and altered the sinks (Table 3). Thus, they limited the xylem-to-phloem transfer of Cd in lower nodes and then increased Cd distributions in lower internodes and lower leaves via the xylem when compared with the CK (Table 3; [15, 47], but decreased Cd distributions in grains, rachises, node 1, internode 1 and flag leaves (Table 3). Additionally, Cd distributions in the lower leaves, lower nodes, and glumes were significantly higher in the $Fe_2(SO_4)_3$ treatment than in the $FeCl_3$ treatment (Table 3), resulting in a lower grain Cd concentration in the former than in the latter (Fig. 1A). The changes in Cd distribution in these tissues did not correspond to the changes in dry weight (Tables 2 and 3). Thus, tissue senescence did not catalyze Cd distribution from vegetative tissues to grains during grain filling, similar to previous study in durum wheat [18].

Another reason for the distribution of Cd is the regulation of metal transporter genes.

In rice, knockout of *OsNRAMP2* and *OsHMA2* significantly limits Cd distribution to upper nodes and developing tissues [47, 48]. In this study, expression levels of *TpHMA2* and *TpNRAMP2* in DPW shoots were upregulated by $Fe_2(SO_4)_3$ application and downregulated by $FeCl_3$ application (Fig. 4B), which did not illustrate changes in Cd distribution. Thus, *TpHMA2* and *TpNRAMP2* were not responsible for the change in Cd distribution due to the soil application of $Fe_2(SO_4)_3$ and $FeCl_3$. We also found that soil application of $Fe_2(SO_4)_3$ and $FeCl_3$ regulated the expression of *TpIRT1* and *TpNRAMP5*, to affect Cd distribution in DPW shoots and grain Cd concentration. The reasons for this are as follows: (1) soil application of $Fe_2(SO_4)_3$ and $FeCl_3$ significantly downregulated the expression levels of *TpIRT1* and *TpRNRAMP5* in DPW shoots when compared with those of the CK (Fig. 4B), consistent with the increases in Cd distributions of lower leaves, lower internodes, and glumes (Table 3), and the decrease in Cd concentration of grains; (2) *TpIRT1* and *TpRNRAMP5* individually encode a Cd influx transporter because the expression of *TpIRT1* and *TpRNRAMP5* increased the Cd concentration in yeast (Peng et al., 2018; Jiang et al., 2021); (3) knockout of *OsNRAMP5*, the homologous genes of *TpNRAMP5* increased the metal accumulation in the lower leaves but reduced that in the shoot elongating zone and nodes [49] (Huang et al., 2024). Since O*sZIP3* is responsible for the preferential distribution of Zn to developing tissue in rice [50] (Sasaki et al., 2015); thus, soil application of $Fe_2(SO_4)_3$ and $FeCl_3$ via upregulating the expression of its homologous gene *TpZIP3* to increase grain Zn concentration in DPW.

Conclusion

In conclusion, the present study showed that soil application of $Fe_2(SO_4)_3$ and $FeCl_3$ (0.04 M Fe^{3+}/m^2) significantly reduced grain Cd concentration and increased grain yield per plant in DPW. Thus, applying appropriate concentrations of Fe fertilizer in agricultural production can promote the yield and protect the grain quality. The reductions in grain Cd concentration were independent of wheat plant growth and development, Cd uptake, root-to-shoot translocation, and root continuous absorption, and resulted from the increase in Cd distribution in the lower leaves, lower internodes, and glumes. Soil application of $Fe_2(SO_4)_3$ and $FeCl_3$ increased Cd distribution in these tissues by upregulating the expression levels of *TpYSL15* and *TpZIP3*, and downregulating the expression levels of *TpIRT1*, *TpNRAMP5* in shoots.

Abbreviations

Cd	cadmium
CK	the control
DPW	dwarf Polish wheat
HMA	p1B-ATPase-Heavy metal associated protein
ICP-MS	inductively coupled plasma mass spectrometry
IRT	iron regulated transporter
K	potassium
N	nitrogen
NRAMP	natural resistance-associated macrophage protein
P	phosphorus
RT-qPCR	quantitative reverse transcription polymerase chain reaction
TF	translocation factor
YSL	yellow stripe 1-like proteins
ZIP	Zinc regulated transporter/IRT-like protein

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

Supplementary Material 3

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Not applicable.

Author contributions

QY, YC and YW wrote the main manuscript text. QY, YY, JC and XL prepared Figs. 1, 2, 3 and 4. QY, MH and DL prepared Tables 1, 2 and 3. YC, YW, YZ, HK, JZ, DW, XF, LS and HZ discussed the results and commented on the paper. All authors reviewed the manuscript.

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Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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