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Temporal dynamics of lead uptake in wheat: Identifying key growth stages for mitigation

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ABSTRACT

Given that atmospheric Pb has become the primary source of Pb in wheat grains, scientifically managing atmospheric Pb pollution is a notable global challenge. Identifying the critical periods for Pb absorption in straw and accumulation in grains was essential for developing targeted mitigation strategies, as the varying nutrient demands of wheat across different growth stages might have influenced Pb accumulation. To investigate this, a pot experiment using Pb exposure and isotope tracing was conducted. The results showed that wheat directly absorbed Pb through its aerial parts, with Pb content in both the straw and grains increasing with exposure duration. A clear coupling relationship was observed between Pb absorption in straw and its accumulation in grains. Grain filling stage (FS) is a critical period for Pb accumulation and pollution control in wheat straw and grains, contributing approximately 41.14–41.87 % to Pb absorption in straw and 56.21–58.16 % to Pb accumulation in grains. Furthermore, Pb accumulation during the greening, jointing, and booting stages contributed 40.62–42.61 % to the total Pb in grains, which reflects the redistribution of Pb stored in the shoots before FS to the grains. Further isotope tracing also revealed that FS contributed 51.06 % of Pb accumulation in the grains, whereas the redistribution of Pb absorbed by the straw before FS contributed approximately 44.33 % to grain Pb content. This study highlights the FS as a critical period for Pb accumulation in both wheat straw and grains, despite it accounting for only 13.89 % of the total growth period. This highlights the importance of enhancing atmospheric Pb contamination control at this this stage to ensure the quality and safety of wheat production.

1. Introduction

Wheat (*Triticum aestivum* L.), one of most important staple crops of the world, contains carbohydrates, proteins, vitamins, and minerals that are essential for human health [1,2]. However, heavy metal contamination, particularly lead (Pb), poses a considerable threat to wheat production [3]. Long-term consumption of wheat contaminated with Pb can lead to the biological accumulation of lead in the human body, thereby increasing the risk of health problems such as neurotoxicity, hypertension, and kidney damage, especially in sensitive populations such as children and pregnant women [4,5]. Research indicates that the majority of Pb in wheat grains originates from atmospheric deposition absorbed by the wheat shoot, rather than from soil uptake through the roots [6–8]. This finding further underscores the critical role of effectively managing atmospheric Pb exposure to control Pb contamination in wheat grains.

The accumulation of Pb within wheat plants does not occur uniformly throughout the growth cycle but is concentrated at specific growth stages. Numerous studies have indicated that the dynamics of heavy metal uptake by crops vary significantly across growth stages, which is crucial for informing Pb pollution control strategies [9,10]. For instance, in rice, 98 % of grain cadmium is absorbed by the roots during the grain filling stage (FS), while approximately 95 % of grain arsenic (As) is remobilized from As stored in the plant before FS [11,12]. In wheat, studies suggest that while Pb absorption by straw occurs throughout the growth cycle, Pb accumulation in grains is largely concentrated during the FS (approximately 25 days), aligning with the period of rapid grain mass increase [13,14]. This indicates that Pb

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absorbed in earlier stages may be temporarily stored in stems and leaves before being translocated to grains during the FS [15,16].

The nutrient and contaminant uptake capacity of crops varies across growth stages [16,17]. Research on wheat and other cereals has highlighted that the close link between Pb accumulation and atmospheric exposure at specific growth stages [6,18]. Given the relatively long growth period of wheat (approximately 180 days), managing atmospheric Pb accumulation poses a considerable challenge. This challenge underscores the need for targeted Pb management strategies during critical growth stages [12,18]. Reducing the risk of Pb contamination in wheat requires minimizing atmospheric Pb exposure during the green stage or applying heavy metal immobilization agents to inhibit Pb absorption during early growth [12,19–21]. The uptake of Pb by wheat at different growth stages is influenced by its physiological characteristics, metabolic activities, and nutrient demand. Pb accumulation in early stages may markedly affect Pb levels during the FS [9,10]. Although previous studies have examined the contribution of specific tissues (leaves (26.18 %) and spikes (55.47 %)) to grain Pb accumulation during the FS [15,18], studies on stage-specific contributions of Pb contamination to Pb accumulation in wheat grains and straw remain limited.

Therefore, we hypothesized that different wheat growth stages, including the greening stage (GS), jointing stage (JS), booting stage (BS), FS, and maturity stage (MS), contribute to the Pb absorption and accumulation of Pb in wheat straw and grains. To address the challenges of Pb contamination and pollution control in wheat, Pb exposure experiments were conducted at individual growth stages, focusing on wheat shoots, to assess the relative importance of each growth stage in Pb accumulation. Additionally, the relationship between Pb accumulation and the grain filling rate (GFR) across these stages was investigated. The contribution of different growth stages to Pb accumulation in wheat straw and grains were quantified, and the contribution ratio of newly accumulated Pb (Pb absorbed during the FS) and pre-accumulated Pb (absorbed prior to filling and redistribution into the grain) during the wheat FS was refined. Finally, Pb isotope labeling was employed to accurately assess the relative impact of grain Pb accumulation across growth stages. These findings are expected to provide insights into the temporal dynamics of Pb accumulation, especially during the critical period; the relationship between Pb absorption in wheat straw and Pb accumulation in grains; and to establish a clear timeline for targeted intervention strategies aimed at reducing atmospheric Pb pollution in wheat and enhancing the safety of wheat grain production.

2. Materials and methods

2.1. Materials and experimental design

The experiments were performed in the experimental field of Zhengzhou University of Light Industry (34°48′27″N, 113°26′44″E), an experimental field with low atmospheric Pb exposure and good air quality, with no known history of heavy metal contamination. The experiments were performed using pot cultivation. The collected soil samples in the experimental field were air-dried, sieved through a 10-mesh sieve, and stored in barrels under ambient conditions for subsequent use. The soil texture was classified as clayey, with an organic matter content of 1.8 %, total nitrogen content of 1.29 g kg^{-1}, and a pH value of 7.12. Each treatment included five biological replicates, with all 60 plastic pots (5 L) filled with 4 kg of soil homogenously mixed with 5 g of basic fertilisers (urea at 0.15 g kg^{-1} N and potassium dihydrogen phosphate and potassium chloride at 0.03 g kg^{-1} P and 0.08 g kg^{-1} K). *T. aestivum* (AIKANG-58) seeds were selected for its dominance in the Huang-Huai Winter Wheat Region, high yield, stress resistance, and broad adaptability, kindly provided by the Henan Academy of Agriculture Sciences (China). Each pot contained 15 wheat plants to ensure consistent growth conditions and adequate biomass for the analysis.

Eleven Pb exposure treatments and one control group (CK) were established. Untreated Pb treatments (T1, T2, T3, T4, T5, T6) using untreated Pb solution ($PbNO_3$, sourced from Fu Chen (Tianjin) Chemical Reagent Co., Ltd) were applied at specific growth stages to ensure consistent Pb compounds and concentrations (T1–T5). Specifically, 10 mL of a 50 mg L^{-1} Pb solution was sprayed on each pot daily and continued for 7 days. This concentration reflects levels commonly found in contaminated atmospheric deposition, which could affect wheat growth and Pb accumulation. The T6 treatment, however, received continuous applications of the untreated Pb solution (Pb1) throughout the entire wheat growth period.

Isotopically modified Pb treatments (T1*, T2*, T3*, T4*, T5*) using a 50 mg L^{-1} Pb solution with an altered isotopic composition (Pb2, SRM 981, obtained from NIST, Gaithersburg, MD, USA) were applied at the corresponding growth stages to further analyze the contribution of Pb accumulation in wheat grains at different stages. During the intervals outside these specified stages, an untreated Pb solution (Pb1) was applied. The amount of Pb exposure at each growth stage was consistent across treatments to ensure comparability. To exclude soil contributions during foliar dosing, the pot surface was covered with a polyethylene film until leaves dried (approximately 10 min), and soil Pb remained at the homogenized baseline from pre-exposure (15.31 ± 0.22 mg kg^{-1}) to harvest across all treatments ($P > 0.05$; Table S1), confirming that observed effects arise from foliar deposition rather than soil inputs. Additionally, all plants were carefully monitored after application to ensure even distribution of the solution, with all leaves thoroughly wetted without dripping, and no areas left untreated. The treatment and CK were grown under identical light, temperature, humidity, and ventilation conditions. To ensure scientific rigor and experimental control, we provide detailed explanations of the key design elements and, in the Supplementary Materials, the specific measures used to minimize environmental variability. A schematic of the experimental design is shown in Fig. 1.

2.2. Preparation of samples

Soil samples were collected before Pb exposure. With time expressed as days after sowing (DAS; sowing on October 25, 2021), wheat was sampled at GS (DAS = 133; March 7, 2022), JS (DAS = 162; April 5, 2022), BS (DAS = 177; April 20, 2022), at three grain filling windows:

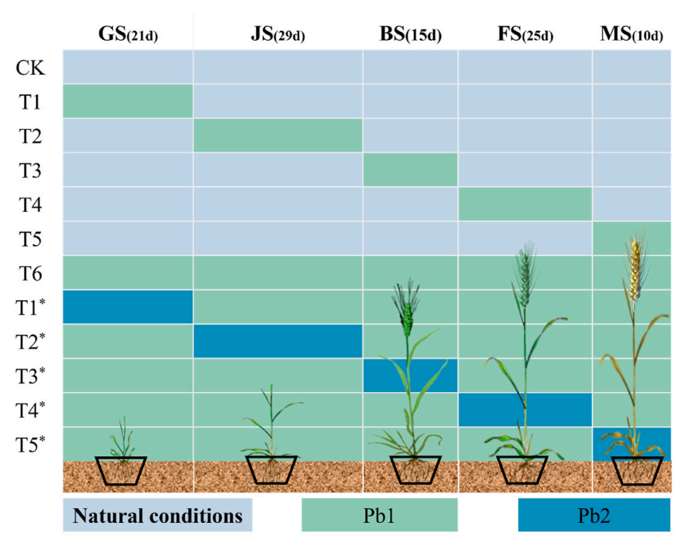

Fig. 1. A schematic diagram of different wheat treatments.
Note: The colors represent varying Pb treatments: green squares indicate Pb1 exposure ($PbNO_3$, Fu Chen (Tianjin) Chemical Reagent Co., Ltd), dark blue squares represent Pb2 exposure (SRM 981, NIST, Gaithersburg, MD, USA), and light blue squares show natural conditions with no Pb exposure. Growth stages include greening (GS), jointing (JS), booting (BS), filling (FS), and maturity (MS).

FS1 (early grain filling; DAS = 185; April 28, 2022), FS2 (middle grain filling; DAS = 193; May 6, 2022), FS3 (late grain filling; DAS = 202; May 15, 2022), and MS (DAS = 212; May 25, 2022). The wheat samples were washed several times with tap water, followed by three rinses with ultrapure water. Finally, the washed wheat samples were immediately placed in an oven at 105 °C for 30 min, followed by drying at 75 °C until a constant weight was achieved. To avoid cross-contamination, dried wheat samples were then manually separated into different tissues, including roots, stems, leaves, husks, and grains (when applicable). The separated samples were ground, placed in labelled bags, and stored for further analysis.

2.3. Pb content determination

Wheat tissue and soil samples were placed on a hot plate and acid-digested (wheat tissue: HNO_3-$HClO_4$-H_2O_2, Soil: HCl-HNO_3-HF-$HClO_4$) until a clear solution was obtained [15]. Sample digestion is described in detail in the Supplementary Material. Each sample was replicated three times for all analyses. The Pb concentration was analyzed using an atomic absorption spectrometer (ZEEnit-700P, Analytik Jena, Germany). Blank samples were analyzed for quality control, and reference materials for soil (GBW07454) and plants (GBW10046) certified by national authorities were used. The recovery rates of Pb in the standard plant samples met the national standards, with a range of 101.25 ± 0.56 % (85.0–115.0 %), and the recovery rates of Pb in the standard soil samples were 99.17 ± 1.15 % (85.0–115.0 %).

2.4. Evaluation of Pb isotopic ratio in samples

The wheat tissue samples were ground and passed through a 200-mesh sieve. The samples were sent to the Beijing Research Institute of Uranium Geology, where trace Pb isotopic compositions were analyzed following the GB/T17672–1999 procedure, typically applied to rocks and minerals, under controlled conditions of 20 °C and 45 % humidity. Pb isotopic ratios were measured using the ISOPROBE-T thermal ionisation mass spectrometer (GV Instruments Ltd., Manchester, UK), and the samples were spotted on a rhenium ribbon with the assistance of silica gel according to the method described in the study by Zhang et al. (2022) [22]. The Pb isotopic ratios were measured in static acceptance mode. The standard material SRM981 (a commonly used Pb isotope material, National Institute of Standards and Technology, USA) was used for calibration.

2.5. The relative contribution of Pb pollution during different growth periods to straw and grain Pb

To investigate the timing of grain Pb accumulation in wheat plants, we developed a model to estimate the contributions of different wheat growth stages and wheat tissue translocation to Pb accumulation in the straw and grain.

(1) Calculation of GFR in wheat

The wheat GFR was conducive for observing the relationship between grain filling and Pb absorption, which was calculated using the following equation [6]:

$$R1 = \frac{\Delta m}{\Delta t} \tag{1}$$

where R1 represents the GFR (mg·1000 grains^{-1}·d^{-1}), m is the weight of 1000 grains for each period, Δm is the increase in grain quality per 1000 grains (mg), and Δt is the number of days between wheat sampling.

(2) Pb absorption by wheat straw was calculated as follows:

$$M\ (\mu g \cdot straw^{-1}) = C\ (\mu g \cdot g^{-1}\ DW) \times DW\ (g \cdot straw^{-1}) \tag{2}$$

where M represents the accumulation of Pb in the wheat straw of different treatments, C is the concentration of Pb in the wheat straw of different treatments, and DW is the dry weight of the wheat straw.

In this study, two methods were employed to assess the contributions of different growth stages to Pb accumulation in wheat grains:

(3) Contribution rate based on the cumulative single-stage Pb exposure addition

This method involves calculating the contribution of each growth stage by summing the Pb accumulations during that particular stage. This method helps evaluate the relative importance of each growth stage for Pb accumulation in wheat grains (Equation (3)).

$$CR_{i-1} = \frac{C_i \times B_i - C_{CK} \times B_{CK}}{\sum (C_i \times B_i - C_{CK} \times B_{CK})} \times 100 \tag{3}$$

where, C_i represents the Pb content in wheat grains under Pb exposure during different growth stages, C_{CK} represents the Pb content in a specific part of the CK, Bi represents the grain yield of wheat under Pb exposure during the different growth stages, and B_{CK} represents the grain yield of the CK wheat. The term i represents to different growth stages under Pb exposure (GS, JS, BS, FS, and MS).

(4) Contribution rate based on total-period Pb exposure comparison

This method involved comparing Pb accumulation in wheat grains under total-period exposure conditions with that of the CK. This method helps evaluate the overall impact of exposure on Pb accumulation in wheat grains throughout the entire growth period (Equation (4)).

$$CR_{i-2} = \frac{C_i \times B_i - C_{CK} \times B_{CK}}{C_{6i} \times B_{6i} - C_{CK} \times B_{CK}} \times 100 \tag{4}$$

where, C_i represents the Pb content in wheat grains under Pb exposure during different growth stages, C_{CK} represents the Pb content in a specific part of the CK, Bi represents the grain yield of wheat under Pb exposure during the different growth stages, and B_{CK} represents the grain yield of the CK wheat. The term i represents to different growth stages under Pb exposure (GS, JS, BS, FS, and MS). Here, C_{6i} and B_{6i} represent the Pb content in wheat grains and the grain yield of wheat, respectively, during each specific growth stage under Pb exposure in the T6 treatment.

(5) Isotopic contribution rate calculation

Based on the measured abundances of $^{206}Pb/^{204}Pb$, $^{207}Pb/^{204}Pb$, and $^{208}Pb/^{204}Pb$ in the samples, the contributions of Pb1 (X) and Pb2 (Y) to Pb concentration in the wheat grains of different treatments were calculated (Equation (5)) [6,16].

$$(^{206}Pb/^{207}Pb)_{Pb1} \times X + (^{206}Pb/^{207}Pb)_{Pb2} \times Y = (^{206}Pb/^{207}Pb)_{wheat}$$
$$X + Y = 1 \tag{5}$$

where X and Y represent the proportions of Pb in the Pb1 and Pb2 grains, respectively.

2.6. Statistical analysis

Statistical analyses were performed using IBM SPSS software package version 20.0. The significance of differences was evaluated using one-way analysis of variance (ANOVA) followed by a least significant difference (LSD) post-hoc test. A significance level of 5 % ($P < 0.05$) was used for all statistical analyses. Illustrations were visualised using Origin 9.0.

3. Results and discussion

3.1. Accumulation and wheat tissue distribution of Pb in different growth stages

Across treatments, Pb concentrations were elevated relative to CK and followed the order leaves > husks > roots > stems (Fig. 2). Relative to CK, MS leaves were 1.61–23.20 fold higher under T1–T6; MS husks were 3.00–34.01 fold higher; and MS stems were 2.07–10.78 fold higher (Fig. 2). These patterns indicate that foliar Pb exposure substantially increased Pb in shoots (leaves and husks), whereas roots showed only small, non-significant changes (2–9 % compared to CK across T1–T6; Fig. 2). The stronger response observed in leaves and husks aligns with foliar uptake mechanisms at the leaf surface, including penetration through the cuticle and stomata, as well as cell wall properties that enhance interception and retention of Pb [23–25]. The modest yet detectable increase in root Pb following foliar application suggests limited basipetal redistribution from shoots to roots. This may arise from senescence-driven remobilization processes analogous to those governing phosphorus redistribution, wherein phosphate is liberated from vacuoles under the regulatory control of SPX-EXS subfamily proteins, thereby elevating the soluble pool within the symplast [26,27]. In this context, Pb, likely in the form of ligand-bound complexes, could subsequently enter phloem-mediated assimilate transport streams and translocate toward active sinks, including roots [12,13,26,27].

Analysis of wheat biomass and height (Table 1) revealed that, compared with other single-stage Pb exposure treatments (T1, T3, T4, T5), T2 showed a non-significant numerical increase in plant height ($P > 0.05$) but a significant increase in biomass ($P < 0.05$). Wheat may have a low activity to Pb absorption but a high demand for water during JS, and the increased the moisture content on the straw's surface due to Pb exposure may have enhanced the water absorption and utilisation abilities of wheat, thereby resulting in increased biomass and wheat height, rather than the Pb exposure directly stimulating wheat growth [28–30]. However, Pb exposure inhibited wheat growth at other growth stages [8,31]. Based on the results presented in Supplementary Fig. S1 and Fig. 2, similar Pb concentrations were observed in wheat tissues across different treatments (T6, T1*, T2*, T3*, T4*, and T5*). Using total Pb concentration, an additional cross-set check at matched tissues/stages indicated no significant differences between T6 and T1*–T5*. These results indicate that, under continuous Pb exposure conditions (T6, T1*, T2*, T3*, T4*, and T5*), the Pb1 and Pb2 treatments did not significantly impact wheat agronomic traits or Pb concentrations in different growth stages.

Table 1
Traits and dry weight of wheat plants.

Treatment	Dates (2022)	Exposure duration(d)	Plant height (cm)	Dry weight (g/plant)
CK	\	0	69.25 ± 1.03a	4.85 ± 0.08b
T1	14 Feb - 07 Mar	21	67.94 ± 1.47a	4.78 ± 0.09b
T2	08 Mar - 05 Apr	29	69.38 ± 0.92a	5.10 ± 0.08a
T3	06 Apr - 20 Apr	15	68.23 ± 1.18a	4.83 ± 0.12b
T4	21 Apr −15 May	25	68.25 ± 0.77a	4.88 ± 0.11b
T5	16 May - 25 May	10	68.67 ± 1.85a	4.79 ± 0.10b
T6	14 Feb - 25 May	100	66.74 ± 0.32b	4.81 ± 0.03b

Notes: Different letters (a, b) within a column denote significant differences at $P < 0.05$; Sowing date was Oct 25, 2021. Exposure duration correspond to growth stages: T1 (GS), T2 (JS), T3 (BS), T4 (FS), T5 (MS), T6 (continuous from GS to MS).

3.2. Effects of FS on wheat yield, GFR, and Pb accumulation dynamics

To gain insight into the responses of wheat straw and grains to Pb exposure, the GFR and yield of wheat grains were analyzed. As grain filling progressed, wheat yield gradually increased. However, under different exposure treatments (T1–T6), Pb exposure was found to affect wheat yield during the grain filling process (FS1–FS3, MS). Compared

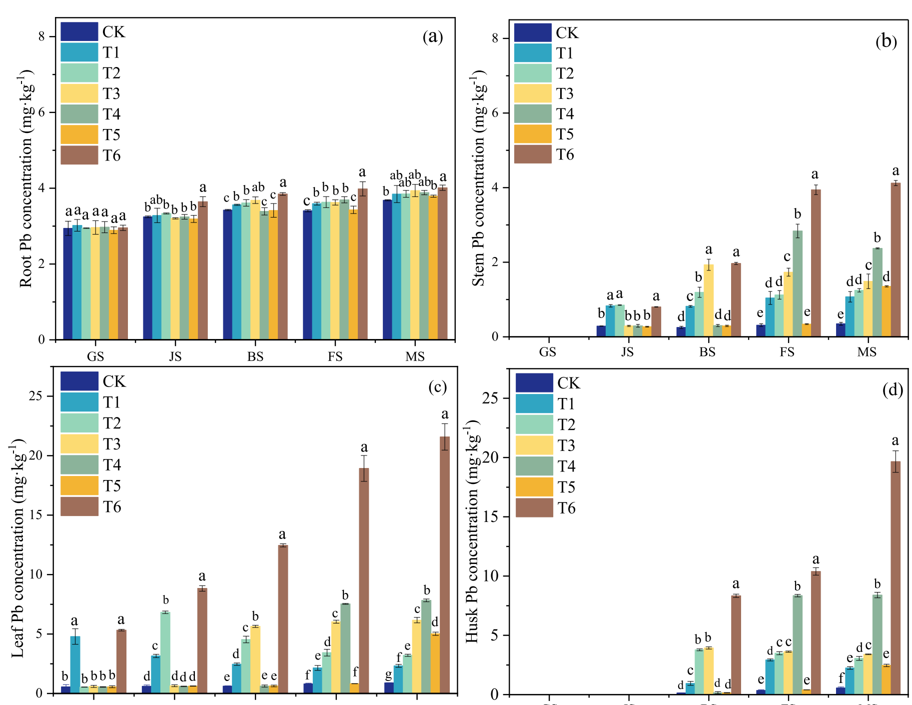

Fig. 2. Distribution of Pb concentration in root (a), stem (b), leaf (c), husk (d) at different growth stages (mg·kg^{-1}).
Note: Different letters (a–g) in figures indicate significant differences within the same stage ($P < 0.05$).

with the CK, the wheat yield T1–T6 treatments decreased by 2.53 %, 2.75 %, 0.40 %, 4.06 %, 1.18 %, and 6.35 %, respectively (Fig. 3a). Changes in wheat grain filling under different growth stages were evaluated to further understand the effects of Pb exposure on wheat yield. The GFR typically increased steadily before gradually decreasing, reaching its peak during the FS2 (Fig. 3b). Notably, the GFR trends in CK and T3 overlapped significantly, indicating that Pb exposure during the BS did not reduce the GFR. In contrast, the most significant inhibition of the GFR was observed in T4 and T6. Among the treatments, the maximum GFR was lowest in T6 and T4, both of which reached their peak on the sixteenth day, followed by a rapid decline towards the end of the FS (Fig. 3b). Pb exposure during the FS contributed to a yield reduction of 4.06 % (Fig. 3a and b), potentially due to Pb interference with the uptake and transport of essential nutrients, such as nitrogen, phosphorus, and potassium [32,33]. Additionally, Pb exposure may negatively affect stomatal conductance and gas exchange in wheat, causing excessive stomatal closure, reducing carbon dioxide ingress, and ultimately limiting photosynthesis [34–36].

To further understand Pb accumulation in grains at different stages and the interconnection between GFR, continuous monitoring of Pb accumulation was conducted throughout the wheat life cycle. During the FS1, grain Pb concentrations in CK-T6 were 0.07, 0.27, 0.57, 0.41, 0.43, 0.08, and 0.82 mg kg^{-1}, respectively (Fig. 3c), indicating early divergence among treatments. Notably, T2 showed greater straw biomass than other single-stage exposures (Table 1; $P < 0.05$) and, correspondingly, higher grain Pb at FS1 ($P < 0.05$), consistent with enhanced vascular transfer together with filling substrates such as sugars and amino acids [23,37,38]. As filling progressed, between treatment differences widened; by MS, grain Pb under T4 and T6 reached 2.20 and 3.81 mg kg^{-1}, exceeding CK (0.08 mg kg^{-1}) and the other single-stage treatments, T1 (0.31), T2 (0.77), T3 (0.73), T5 (0.13) (mg·kg^{-1}, $P < 0.05$; Fig. 3c). Consistent with limited physiological activity at MS [39–41], T5 produced low grain Pb accumulation per 1000 grains (6.41 μg·1000 grains^{-1}), which did not differ from CK (4.24 μg·1000 grains^{-1}; $P > 0.05$) (Fig. 3d).

Overall, the impact of Pb exposure on Pb accumulation in grains was much greater than its effect on grain yield. The trends in GFR and Pb accumulation rate in wheat grains were similar (Fig. 3b–e). However, Pb accumulation exhibited a lag effect, with the maximum accumulation rate in CK, T1, T2, T3, and T5 occurring around the 16th day, while in T4

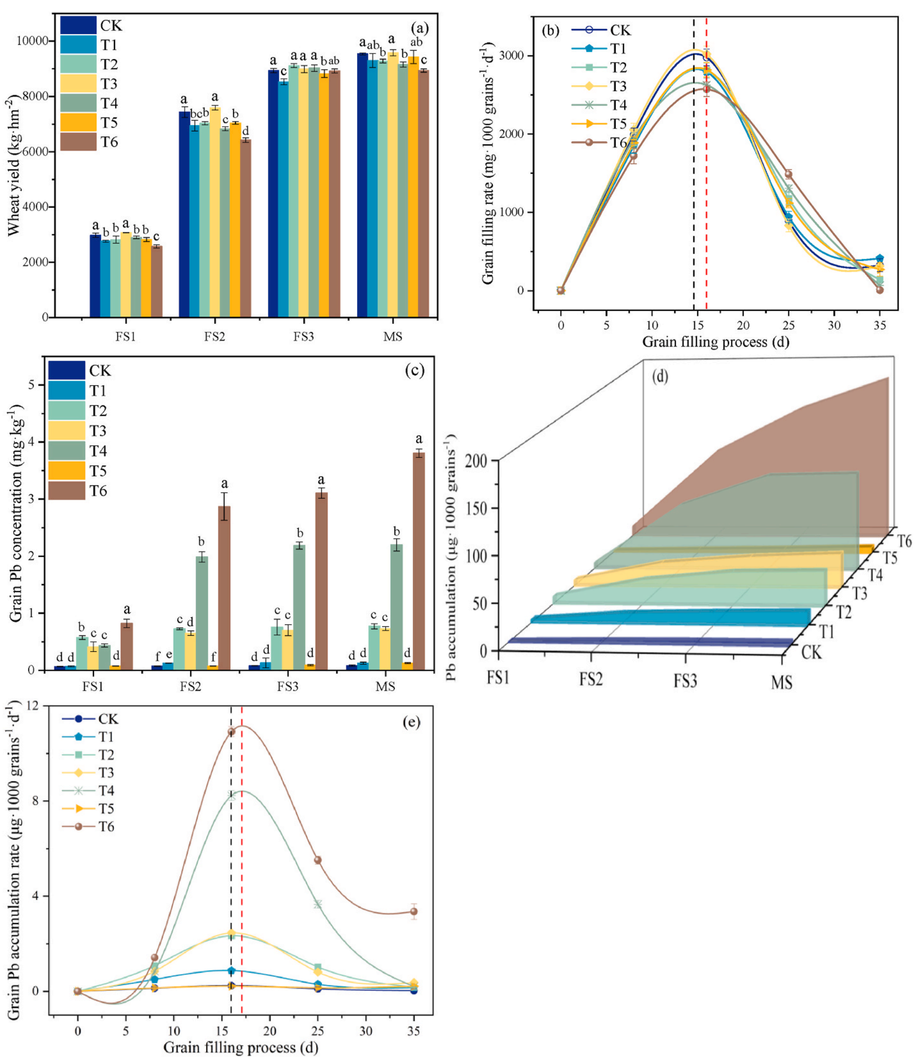

Fig. 3. (a) Wheat yield (kg·hm^{-2}), (b) Grain filling rate in wheat grains at different filling processes (mg·1000 grains^{-1}); (c) Pb concentration in wheat grains in different filling stages (mg·kg^{-1}); (d) Pb accumulation in per 1000 grains of wheat (μg·1000 grains^{-1}) and (e) Accumulation rate of Pb in per 1000 grains of wheat (μg·1000 grains^{-1} ·d^{-1}).
Note: FS1 (DAS = 185; April 28, 2022), FS2 (DAS = 193; May 6, 2022), and FS3 (DAS = 202; May 15, 2022) represent the early, middle, and late stages of the grain filling period, respectively, while MS is the maturity stage. Different letters (a, b, c, d, e, f) in the figure indicate significant differences within the same stage ($P < 0.05$).

and T6, it peaked around the 17th day. This lag might be attributed to the initial physiological mechanisms of wheat resistance to Pb toxicity. As the duration of Pb exposure increases, these defense mechanisms may weaken, leading to an increased rate of Pb accumulation in the grains. Additionally, the delay in reaching the maximum Pb accumulation rate compared to the peak GFR may be linked to the mechanism of Pb transport to the grains along with filling materials. Pb transport rate might have reached its peak only once these materials have accumulated to a sufficient level. These adaptive responses include the chelation, transport, and storage of Pb ions, as well as the activation of reactive oxygen species scavenging systems [42,43]. In wheat under Pb stress, these defenses encompass antioxidant systems (e.g., SOD, CAT, APX for ROS scavenging), chelation/sequestration via phytochelatins and metallothioneins for vacuolar compartmentalization, ionomic redistribution through transporters like NRAMP and ZIP, and osmotic adjustment with proline accumulation, initially prioritizing cellular protection and Pb retention in vegetative tissues to delay grain translocation until prolonged exposure saturates them (e.g., depleted antioxidants) [44–46], as evidenced by the observed lag effect. These mechanisms allow wheat to efficiently manage and transport Pb, thereby significantly increasing Pb accumulation in the grains [9,47,48].

3.3. The key period of Pb absorption in wheat straw

To reveal the sensitivity and adaptive changes in wheat straw to Pb exposure at different growth stages, we monitored straw Pb across the life cycle and applied exposure within single stages. When Pb was applied within a single stage, straw Pb rose rapidly during that stage. The highest increase was observed during the FS (T4), reaching up to 21.65 μg·straw^{-1}, indicating that wheat plants exhibited strong growth activity and absorption capacity during this stage, thus leading to relatively high Pb accumulation. In contrast, the Pb accumulation during the individual stages (Pb exposure) of the GS (T1), JS (T2), BS (T3), and MS (T5) increased by 5.85, 9.60, 10.80, and 4.97 μg·straw^{-1}, respectively (Fig. 4). Pb exposure had a relatively small impact on Pb accumulation in wheat plants during GS and MS. This is because the temperature was low during GS, the growth vigour of wheat was weakened, the accumulation ability was reduced, and the accumulation of Pb was relatively low [49]. However, the MS marks the end of the wheat life cycle, during which various plant tissues, including leaves, stems, and roots, begin to senesce and deteriorate. The nutrient requirements of wheat gradually decreased, resulting in the lowest Pb accumulation at this stage [6].

Two mathematical models were used to quantitatively assess the contribution of each stage to Pb accumulation in wheat straw. The contribution rate under single stage exposure relative to the CK (CR_{i-1}) was 12.45 %, 15.47 %, 18.85 %, 41.87 %, and 11.36 % for GS, JS, BS, FS, and MS, respectively. The share of total accumulation under full-period Pb exposure (CR_{i-2}) was 12.24 %, 15.20 %, 18.82 %, 41.14 %, and 11.16 % for the same stages (Fig. 5). The contribution rate during the grain FS was significantly higher than that during the other stages, attaining 41.87 % (CR_{i-1}) and 41.14 % (CR_{i-2}). The second highest was BS, which attained 18.85 % (CR_{i-1}) and 18.52 % (CR_{i-2}). In terms of different growth stages, wheat plants mainly undergo reproductive growth during the GS, with minimal biomass changes. During the FS, wheat undergoes vegetative growth and requires a significant amount of external nutrients. Pb is absorbed by wheat plants through pathways typically used for nutrient uptake, allowing it to mimic essential ions and accumulate in plant tissues at a relatively high rate [7,50–52]. This indicates that the grain FS was the most sensitive and susceptible stage for Pb accumulation in wheat plants throughout the experimental period.

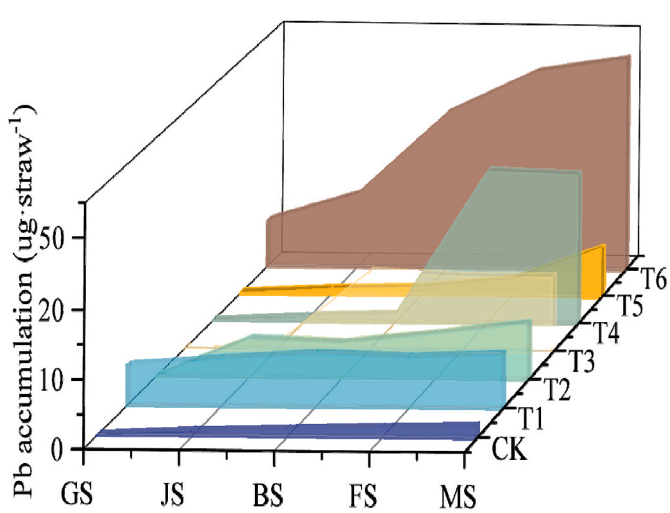

Fig. 4. Accumulation of Pb in wheat straw in different treatment groups at different stages (μg·straw^{-1}).

3.4. The key period of Pb accumulation in wheat grains

To further investigate the contribution of different growth stages to Pb accumulation in wheat grains, we evaluated the contribution rates using the CR_{i-1} and CR_{i-2} calculation models. In CR_{i-1}, the contributions of GS, JS, BS, FS, and MS were 5.98 %, 18.56 %, 18.07 %, 56.21 %, and 1.18 %, respectively; in CR_{i-2}, they were 6.19 %, 23.78 %, 18.70 %, 58.16 %, and 1.22 % (Fig. 6). Thus, FS is the primary stage, accounting for about 56.21 %–58.16 % of grain Pb, while JS provides a secondary contribution (about 18.56 %–23.78 %), with BS comparable but lower. By contrast, GS and MS contribute little to grain Pb. The lower shares of GS and BS are consistent with reduced physiological activity early in development and the shorter duration of BS [49]. The BS accounted for only a small portion of the wheat growth period (15 days). This may have resulted in a relatively small amount of Pb being absorbed and accumulated in the grains, thereby reducing the contribution rate during the FS.

To elucidate the sources of Pb in wheat grains, we compared Pb accumulation under single-stage foliar exposures with that under continuous exposure across all growth stages. In treatments involving

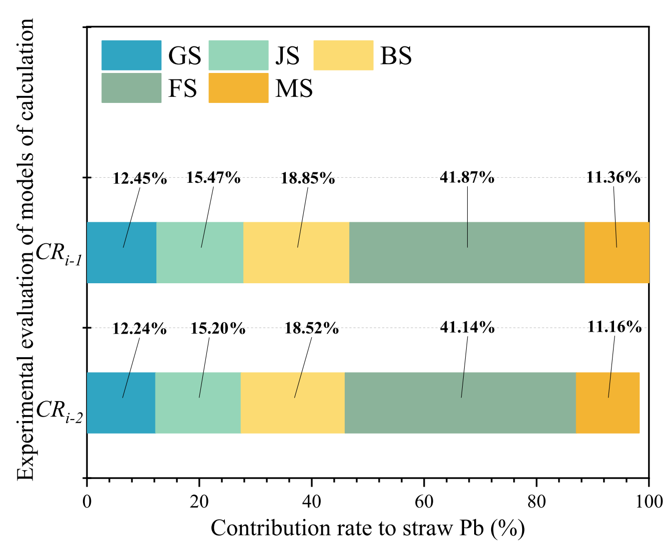

Fig. 5. The relative contribution rate of different growth stages to Pb accumulation in straw under different calculation evaluation models.
Note: CR_{i-1}: Calculates the contribution of each growth stage by summing Pb accumulation, evaluating the relative importance of each stage in wheat straw Pb accumulation (single-stage cumulative contribution rate); CR_{i-2}: Compares Pb accumulation under total-period stress to the CK, assessing the overall impact of stress throughout the growth period (full-period exposure contribution rate).

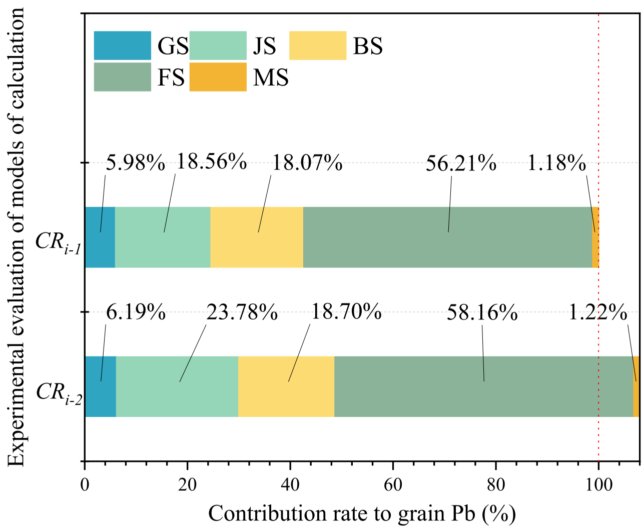

Fig. 6. The relative contribution rate of different growth stages to Pb accumulation in grain under different calculation evaluation models.
Note: CR_{i-1}: Calculates the contribution of each growth stage by summing Pb accumulation, evaluating the relative importance of each stage in wheat grain Pb accumulation (single-stage cumulative contribution rate); CR_{i-2}: Compares Pb accumulation under total-period stress to the CK, assessing the overall impact of stress throughout the growth period (full-period exposure contribution rate).

exposure during the GS, JS, and BS (T1–T3), grain Pb primarily originated from the redistribution of Pb previously sequestered in vegetative tissues. This remobilization occurs concomitantly with the translocation of photosynthates during FS to sustain grain development [50–53]. Conversely, exposures during the FS or MS (T4–T5) resulted in grain Pb derived from both remobilization and direct deposition during filling. Quantitative apportionment via modeling estimated the contribution of redistribution at 42.61–48.67 %, with direct input accounting for 57.39–59.38 % during the FS–MS period (Fig. 6). As previously noted, Pb frequently complexes with organic ligands such as phytochelatins, enabling its integration into phloem-mediated assimilate transport toward developing grains [12,13]. Accordingly, leaf-to-grain translocation follows an analogous two-step mechanism: initial remobilization akin to phosphorus dynamics during senescence, succeeded by long-distance phloem-mediated delivery to the grain sink. This process is substantiated by studies in other cereals, notably rice, where heavy metals are remobilized from vegetative compartments to grains during late reproductive phases, aligning with the pronounced FS contribution documented herein [9,54,55]. These findings highlight the FS as a pivotal phase in wheat ontogeny for direct Pb transfer to grains, exhibiting elevated contribution rates in both empirical and modeled assessments. Analogous to essential micronutrients, non-essential toxicants like Pb exploit these nutrient conduits, culminating in grain accumulation [50–52].

As mentioned above, the influence of different growth stages on Pb accumulation in wheat straw and grains follows the order: FS > JS, BS > GS > MS. This finding underscores the FS as the critical period for Pb accumulation in both straw and grains. The observed coupling between Pb uptake in straw and subsequent accumulation in grains highlights the complex, interconnected dynamics of Pb translocation within the plant. Pb absorbed at various growth stages undergoes dynamic redistribution between straw and grains, emphasizing the necessity of addressing Pb accumulation in straws.

3.5. Validation of the key period of Pb accumulation in grains under Pb exposure based on isotopic technique

To validate our findings, we performed stable Pb isotope-labeling experiments. Isotope analysis technology provides accurate results and helps us precisely assess the sources and accumulation processes of Pb in wheat grains [56]. According to the results shown in Figs. S1 and S2, under Pb exposure throughout the wheat growth stages, no significant differences in Pb concentrations were observed in wheat tissues and grains among the T1*–T5* treatments. Additionally, the application of different types of Pb (Pb1 and Pb2) did not result in significant differences in Pb concentrations in the wheat leaves, husks, and grains. Throughout the exposure period, there was no significant increase in Pb concentration in the wheat roots. Root uptake of Pb occurs through the absorption of Pb ions from the rhizosphere soil. However, foliar application of Pb solutions primarily affects the leaves, and the uptake of Pb in the roots may be limited by the concentration and solubility of Pb in the rhizosphere soil [35,57,58]. This may restrict the uptake and transport of Pb in the roots, thus resulting in no significant increase in root Pb concentration [23,59–61].

Measured isotope ratios in MS grain spanned $^{208}Pb/^{206}Pb$ = 2.1193–2.1453 and $^{206}Pb/^{207}Pb$ = 1.1221–1.1579 (Fig. 7a), which fall between the signatures of Pb1 and Pb2, as expected for mixtures. A simple two endmember mixing analysis showed a strong alignment of grain isotope ratios with the Pb1–Pb2 axis ($R^2 = 0.93$), indicating that the grain pool reflects a mixture of these sources with limited fractionation during transfer [6,16]. Using equation (5), source apportionment yielded Pb1 shares of 92.62 %, 83.75 %, 70.30 %, 48.94 %, and 91.19 % for T1* through T5*, respectively, with complementary Pb2 shares of 7.38 %, 16.25 %, 20.70 %, 51.06 %, and 0.81 % (Fig. 7b). The T4* therefore contributed about 51 % of grain Pb directly from the FS, whereas the contributions from GS and MS were small (about 7 % and about 1 %, respectively). These values agree closely with the model based estimates from CR_{i-1} and CR_{i-2}, which assigned about 6 % to GS and about 1 % to MS (Fig. 6). In the T1*–T3* treatment, Pb2 was only subjected to one-stage exposure, and the rest of the period was Pb1 exposed; the contribution from Pb2 in the grain was considered to be the redistribution of Pb accumulated in the wheat shoots before FS. During this critical phase, Pb is actively redistributed from the straw to the grains via the vascular system [42,62], contributing 40.62 %–42.61 % (GS, JS, BS) of the total Pb accumulation (Fig. 6). Isotopic analysis further confirmed that 44.33 % of the Pb in grains originated from redistribution of Pb stored in the shoots before FS, while 51.87 % came from newly absorbed Pb during the FS to MS stages (Fig. 7b). Notably, 51.06 % of the Pb in grains was absorbed during the FS, which represents only 13.89 % of the total growth period (over the 25-day FS). In summary, the grain FS is an extremely important period for Pb absorption in wheat grains. To enhance pollution control during the FS, the integration of effective management strategies, such as the application of foliar barrier agents, should be prioritized in wheat cultivation. Silicate-based sprays (e.g., potassium silicate, sodium silicate, or calcium silicate) can form a protective layer on leaf surfaces, thereby reducing heavy metal penetration and translocation to grains [63,64]. Therefore, the development of novel foliar barrier agents specifically designed for application during FS represents a critical direction for future research aimed at mitigating Pb absorption in wheat.

4. Conclusions

This study systematically evaluated the contributions of different growth stages to Pb accumulation in wheat straw and grains using two mathematical models, which were then accurately quantified using stable isotope techniques. The effects of different stages on straw and grain Pb accumulation in wheat were in the following the order of FS > JS, BS > GS > MS. The grain FS of wheat is the key period for Pb accumulation in straws and grains. Additionally, 41.14–41.87 % of the

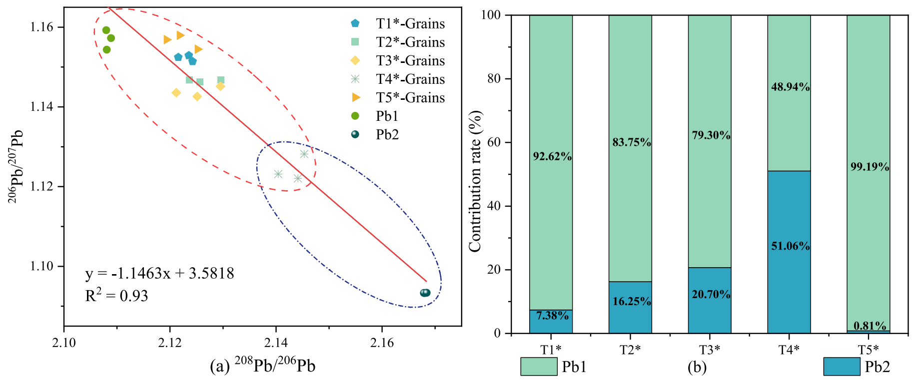

Fig. 7. (a) $^{206}Pb/^{207}Pb$-$^{208}Pb/^{206}Pb$ scatter plot of wheat tissue, Pb1 and Pb2, (b) Contribution ratio of (Pb1, Pb2) to Pb in wheat grain under Pb stress.
Note: Pb1 is an untreated lead solution ($PbNO_3$, Fu Chen (Tianjin) Chemical Reagent Co., Ltd), and Pb2 is an isotopically adjusted lead solution (SRM 981, NIST, Gaithersburg, MD, USA).

total Pb accumulation in wheat straws and 51.06–58.16 % of the Pb accumulation in wheat grains occurred at the grain FS. Moreover, a significant portion (57.39–59.38 %) of Pb in grains was derived from direct uptake at the grain FS rather than redistribution of Pb from wheat shoots. Therefore, to effectively reduce or eliminate the risk of Pb in wheat grains, measures should be implemented to minimize atmospheric deposition during the grain filling period and prevent direct contact between wheat shoots and airborne Pb. These actions would not only improve crop safety but also support cleaner production practices by reducing Pb contamination in agricultural systems.

CRediT authorship contribution statement

Fuyong Liu: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Chuang Ma:** Supervision, Investigation, Funding acquisition, Formal analysis, Data curation. **Jun Yang:** Supervision, Investigation, Data curation. **Mario Berrettoni:** Writing – review & editing, Supervision, Conceptualization. **Silvia Zamponi:** Supervision, Investigation, Formal analysis. **Aihua Gao:** Supervision, Investigation, Formal analysis. **Nan Liu:** Supervision, Conceptualization. **Ke Zhang:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jafr.2025.102430.

Data availability

Data will be made available on request.

References

[1] S. Li, J. Wu, L. Ma, Economic, energy and environmental consequences of shifting from maize-wheat to forage rotation in the North China Plain, J. Clean. Prod. 328 (2021) 129670, https://doi.org/10.1016/J.JCLEPRO.2021.129670.
[2] Y. Zhang, H. Wang, Q. Lei, J. Luo, S. Lindsey, J. Zhang, L. Zhai, S. Wu, J. Zhang, X. Liu, T. Ren, H. Liu, Optimizing the nitrogen application rate for maize and wheat based on yield and environment on the Northern China Plain, Sci. Total Environ. 618 (2018) 1173–1183, https://doi.org/10.1016/J.SCITOTENV.2017.09.183.
[3] X. Wu, Q. Cai, Q. Xu, Z. Zhou, J. Shi, Wheat (Triticum aestivum L.) grains uptake of lead (Pb), transfer factors and prediction models for various types of soils from China, Ecotoxicol. Environ. Saf. 206 (2020) 111387, https://doi.org/10.1016/J.ECOENV.2020.111387.
[4] M. Boskabady, N. Marefati, T. Farkhondeh, F. Shakeri, A. Farshbaf, M. H. Boskabady, The effect of environmental lead exposure on human health and the contribution of inflammatory mechanisms, a review, Environ. Int. 120 (2018) 404–420, https://doi.org/10.1016/J.ENVINT.2018.08.013.
[5] C. Liu, Y. Xu, L. Wang, Q. Huang, X. Yan, Y. Sun, X. Qin, X. Liang, Variations in cadmium and lead bioaccessibility in wheat cultivars and their correlations with nutrient components, J. Agric. Food Chem. 72 (2024) 1768–1778, https://doi.org/10.1021/ACS.JAFC.3C08234.
[6] C. Ma, F. Liu, P. Xie, K. Zhang, J. Yang, J. Zhao, H. Zhang, Mechanism of Pb absorption in wheat grains, J. Hazard. Mater. 415 (2021) 125618, https://doi.org/10.1016/J.JHAZMAT.2021.125618.
[7] C. Ma, P. Xie, J. Yang, F. Liu, H. Hu, J. Du, K. Zhang, L. Lin, H. Zhang, Relative contribution of environmental medium and internal organs to lead accumulation of wheat grain, Sci. Total Environ. 818 (2022) 151832, https://doi.org/10.1016/J.SCITOTENV.2021.151832.
[8] C. Wang, H. Jin, C. Zhong, J. Wang, M. Sun, M. Xie, Estimating the contribution of atmosphere on heavy metals accumulation in the aboveground wheat tissues induced by anthropogenic forcing, Environ. Res. 189 (2020) 109955, https://doi.org/10.1016/J.ENVRES.2020.109955.
[9] U. Ashraf, A.S. Kanu, Q. Deng, Z. Mo, S. Pan, H. Tian, X. Tang, Lead (Pb) toxicity; physio-biochemical mechanisms, grain yield, quality, and Pb distribution proportions in scented rice, Front. Plant Sci. 8 (2017) 234771, https://doi.org/10.3389/FPLS.2017.00259/BIBTEX.
[10] H. Liu, J. Zhou, M. Li, R. Xia, X. Wang, J. Zhou, Dynamic behaviors of newly deposited atmospheric heavy metals in the Soil-Pak choi system, Environ. Sci. Technol. 56 (2022) 12734–12744, https://doi.org/10.1021/acs.est.2c04062.
[11] A.M. Carey, G.J. Norton, C. Deacon, K.G. Scheckel, E. Lombi, T. Punshon, M. Lou Guerinot, A. Lanzirotti, M. Newville, Y. Choi, A.H. Price, A.A. Meharg, Phloem transport of arsenic species from flag leaf to grain during grain filling, New Phytol. 192 (2011) 87–98, https://doi.org/10.1111/J.1469-8137.2011.03789.X.
[12] B.Y. Huang, F.J. Zhao, P. Wang, The relative contributions of root uptake and remobilization to the loading of Cd and as into rice grains: implications in simultaneously controlling grain Cd and as accumulation using a segmented water management strategy, Environ. Pollut. 293 (2022) 118497, https://doi.org/10.1016/J.ENVPOL.2021.118497.
[13] Y. Wang, Y. Xu, X. Liang, L. Wang, Y. Sun, Q. Huang, X. Qin, L. Zhao, Soil application of manganese sulfate could reduce wheat Cd accumulation in Cd contaminated soil by the modulation of the key tissues and ionomic of wheat, Sci. Total Environ. 770 (2021) 145328, https://doi.org/10.1016/J.SCITOTENV.2021.145328.
[14] J. Zhou, The effect of water flooding at grain-filling stage on the uptake of heavy metal(loid)s by rice in slightly alkaline paddy soil, Environ. Sci. Pollut. Res. 29 (2022) 31363–31373, https://doi.org/10.1007/S11356-021-18328-Y/METRICS.
[15] C. Ma, F. Liu, J. Yang, N. Liu, K. Zhang, M. Berrettoni, H. Zhang, The newly absorbed atmospheric lead by wheat spike during filling stage is the primary reason for grain lead pollution, Sci. Total Environ. 870 (2023) 161965, https://doi.org/10.1016/J.SCITOTENV.2023.161965.
[16] Q. Lin, W. Dai, J.Q. Chen, Y. Jin, Y. Yang, Y.Y. Wang, B.F. Zhang, J.M. Fan, L. P. Lou, Z.G. Shen, C.F. Shen, J.D. Mao, Airborne lead: a vital factor influencing rice

lead accumulation in China, J. Hazard. Mater. 427 (2022) 128169, https://doi.org/10.1016/J.JHAZMAT.2021.128169.
[17] P. Gao, P. Xue, J. Dong, X. Zhang, H. Sun, L. Geng, S. Luo, J. Zhao, W. Liu, Contribution of PM2. 5-Pb in atmospheric fallout to Pb accumulation in Chinese cabbage leaves via stomata, J. Hazard. Mater. 407 (2021) 124356, https://doi.org/10.1016/j.jhazmat.2020.124356.
[18] S. Navabpour, A. Yamchi, S. Bagherikia, H. Kafi, Lead-induced oxidative stress and role of antioxidant defense in wheat (Triticum aestivum L.), Physiol. Mol. Biol. Plants 26 (2020) 793–802, https://doi.org/10.1007/S12298-020-00777-3/METRICS.
[19] E. Farajzadeh Memari-Tabrizi, A. Yousefpour-Dokhanieh, M. Babashpour-Asl, Foliar-applied silicon nanoparticles mitigate cadmium stress through physio-chemical changes to improve growth, antioxidant capacity, and essential oil profile of summer savory (Satureja hortensis L.), Plant Physiol. Biochem. 165 (2021) 71–79, https://doi.org/10.1016/J.PLAPHY.2021.04.040.
[20] J. Lian, L. Cheng, X. Zhai, R. Wu, W. Liu, J. Pan, M.J.I. Shohag, X. Xin, Z. He, X. Yang, Foliar spray of combined metal-oxide nanoparticles alters the accumulation, translocation and health risk of Cd in wheat (Triticum aestivum L.), J. Hazard. Mater. 440 (2022) 129857, https://doi.org/10.1016/J.JHAZMAT.2022.129857.
[21] S. Sen Raychaudhuri, P. Pramanick, P. Talukder, A. Basak, Polyamines, metallothioneins, and phytochelatins—Natural defense of plants to mitigate heavy metals, Stud. Nat. Prod. Chem. 69 (2021) 227–261, https://doi.org/10.1016/B978-0-12-819487-4.00006-9.
[22] M. Zhang, L. Tang, H. Ji, Elements and Pb isotopic composition as evidence for contaminant-metal dispersal in surficial soil and sediment of drinking water source in Beijing, China, Sci. Total Environ. 837 (2022) 155682, https://doi.org/10.1016/J.SCITOTENV.2022.155682.
[23] X. Ouyang, J. Ma, Y. Liu, P. Li, R. Wei, Q. Chen, L. Weng, Y. Chen, Y. Li, Foliar cadmium uptake, transfer, and redistribution in Chili: a comparison of foliar and root uptake, metabolomic, and contribution, J. Hazard. Mater. 453 (2023) 131421, https://doi.org/10.1016/J.JHAZMAT.2023.131421.
[24] M. Yadav, N. George, V. Dwibedi, Emergence of toxic trace elements in plant environment: insights into potential of silica nanoparticles for mitigation of metal toxicity in plants, Environ. Pollut. 333 (2023) 122112, https://doi.org/10.1016/J.ENVPOL.2023.122112.
[25] U. Zulfiqar, M. Farooq, S. Hussain, M. Maqsood, M. Hussain, M. Ishfaq, M. Ahmad, M.Z. Anjum, Lead toxicity in plants: impacts and remediation, J. Environ. Manag. 250 (2019) 109557, https://doi.org/10.1016/J.JENVMAN.2019.109557.
[26] Y. Wang, F. Wang, H. Lu, Y. Liu, C. Mao, Phosphate uptake and transport in plants: an elaborate regulatory system, Plant Cell Physiol. 62 (2021) 564–572, https://doi.org/10.1093/PCP/PCAB011.
[27] W. Jiang, D. Liu, Pb-induced cellular defense system in the root meristematic cells of Allium sativum L, BMC Plant Biol. 10 (2010) 1–8, https://doi.org/10.1186/1471-2229-10-40/FIGURES/3.
[28] Z. Ahmad, E.A. Waraich, S. Akhtar, S. Anjum, T. Ahmad, W. Mahboob, O.B. A. Hafeez, T. Tapera, M. Labuschagne, M. Rizwan, Physiological responses of wheat to drought stress and its mitigation approaches, Acta Physiol. Plant. 40 (2018) 1–13, https://doi.org/10.1007/S11738-018-2651-6/METRICS.
[29] M. Khataar, M.H. Mohhamadi, F. Shabani, Soil salinity and matric potential interaction on water use, water use efficiency and yield response factor of bean and wheat, Sci. Rep. 81 (8) (2018) 1–13, https://doi.org/10.1038/s41598-018-20968-z, 2018.
[30] G.C. Sigua, J.M. Novak, D.W. Watts, M.G. Johnson, K. Spokas, Efficacies of designer biochars in improving biomass and nutrient uptake of winter wheat grown in a hard setting subsoil layer, Chemosphere 142 (2016) 176–183, https://doi.org/10.1016/J.CHEMOSPHERE.2015.06.015.
[31] R. Bian, S. Joseph, L. Cui, G. Pan, L. Li, X. Liu, A. Zhang, H. Rutlidge, S. Wong, C. Chia, C. Marjo, B. Gong, P. Munroe, S. Donne, A three-year experiment confirms continuous immobilization of cadmium and lead in contaminated paddy field with biochar amendment, J. Hazard. Mater. 272 (2014) 121–128, https://doi.org/10.1016/J.JHAZMAT.2014.03.017.
[32] M. Imtiaz, M.S. Rizwan, M.A. Mushtaq, M. Ashraf, S.M. Shahzad, B. Yousaf, D. A. Saeed, M. Rizwan, M.A. Nawaz, S. Mehmood, S. Tu, Silicon occurrence, uptake, transport and mechanisms of heavy metals, minerals and salinity enhanced tolerance in plants with future prospects: a review, J. Environ. Manag. 183 (2016) 521–529, https://doi.org/10.1016/J.JENVMAN.2016.09.009.
[33] M. Lamhamdi, O. El Galiou, A. Bakrim, J.C. Nóvoa-Muñoz, M. Arias-Estévez, A. Aarab, R. Lafont, Effect of lead stress on mineral content and growth of wheat (Triticum aestivum) and spinach (Spinacia oleracea) seedlings, Saudi J. Biol. Sci. 20 (2013) 29–36, https://doi.org/10.1016/J.SJBS.2012.09.001.
[34] A. Avellan, J. Yun, B.P. Morais, E.T. Clement, S.M. Rodrigues, G.V. Lowry, Critical review: role of inorganic nanoparticle properties on their foliar uptake and in planta translocation, Environ. Sci. Technol. 55 (2021) 13417–13431, https://doi.org/10.1021/ACS.EST.1C00178.
[35] M. Shahid, C. Dumat, S. Khalid, E. Schreck, T. Xiong, N.K. Niazi, Foliar heavy metal uptake, toxicity and detoxification in plants: a comparison of foliar and root metal uptake, J. Hazard. Mater. 325 (2017) 36–58, https://doi.org/10.1016/J.JHAZMAT.2016.11.063.
[36] J. Yang, Y. Yu, C. Ma, H. Zhang, Direct absorption of atmospheric lead by rapeseed siliques is the leading cause of seed lead pollution, J. Hazard. Mater. 443 (2023) 130284, https://doi.org/10.1016/J.JHAZMAT.2022.130284.
[37] X. Hou, H. Han, L. Cai, A. Liu, X. Ma, C. Zhou, G. Wang, F. Meng, Pb stress effects on leaf chlorophyll fluorescence, antioxidative enzyme activities, and organic acid contents of Pogonatherum crinitum seedlings, Flora 240 (2018) 82–88, https://doi.org/10.1016/J.FLORA.2018.01.006.
[38] A. Kumar, M.N.V. Prasad, Plant-lead interactions: transport, toxicity, tolerance, and detoxification mechanisms, Ecotoxicol. Environ. Saf. 166 (2018) 401–418, https://doi.org/10.1016/J.ECOENV.2018.09.113.
[39] H. Huang, M. Rizwan, M. Li, F. Song, S. Zhou, X. He, R. Ding, Z. Dai, Y. Yuan, M. Cao, S. Xiong, S. Tu, Comparative efficacy of organic and inorganic silicon fertilizers on antioxidant response, Cd/Pb accumulation and health risk assessment in wheat (Triticum aestivum L.), Environ. Pollut. 255 (2019) 113146, https://doi.org/10.1016/J.ENVPOL.2019.113146.
[40] K. Jiang, B. Wu, C. Wang, Q. Ran, Ecotoxicological effects of metals with different concentrations and types on the morphological and physiological performance of wheat, Ecotoxicol. Environ. Saf. 167 (2019) 345–353, https://doi.org/10.1016/J.ECOENV.2018.10.048.
[41] C. Wei, Q. Jiao, E. Agathokleous, H. Liu, G. Li, J. Zhang, S. Fahad, Y. Jiang, Hormetic effects of zinc on growth and antioxidant defense system of wheat plants, Sci. Total Environ. 807 (2022) 150992, https://doi.org/10.1016/J.SCITOTENV.2021.150992.
[42] S.A. Ghuge, G.C. Nikalje, U.S. Kadam, P. Suprasanna, J.C. Hong, Comprehensive mechanisms of heavy metal toxicity in plants, detoxification, and remediation, J. Hazard. Mater. 450 (2023) 131039, https://doi.org/10.1016/J.JHAZMAT.2023.131039.
[43] W.G. Shi, W. Liu, W. Yu, Y. Zhang, S. Ding, H. Li, T. Mrak, H. Kraigher, Z. Bin Luo, Abscisic acid enhances lead translocation from the roots to the leaves and alleviates its toxicity in Populus × canescens, J. Hazard. Mater. 362 (2019) 275–285, https://doi.org/10.1016/J.JHAZMAT.2018.09.024.
[44] M. Anas, M.S. Bashir, K. Saleem, A. Noor, U.M. Quraishi, Adaptive mechanisms of wheat cultivars to lead toxicity through enhanced oxidative defense, ionomic redistribution, and anatomical modifications, J. Plant Physiol. 303 (2024) 154370, https://doi.org/10.1016/J.JPLPH.2024.154370.
[45] M. Aslam, A. Aslam, M. Sheraz, B. Ali, Z. Ulhassan, U. Najeeb, W. Zhou, R.A. Gill, Lead toxicity in cereals: mechanistic insight into toxicity, mode of action, and management, Front. Plant Sci. 11 (2021) 587785, https://doi.org/10.3389/FPLS.2020.587785/XML.
[46] M. Gupta, V. Dwivedi, S. Kumar, A. Patel, P. Niazi, V.K. Yadav, Lead toxicity in plants: mechanistic insights into toxicity, physiological responses of plants and mitigation strategies, Plant Signal. Behav. 19 (2024), https://doi.org/10.1080/15592324.2024.2365576.
[47] I. Gul, M. Manzoor, N. Hashim, G.M. Shah, S.P.T. Waani, M. Shahid, V. Antoniadis, J. Rinklebe, M. Arshad, Challenges in microbially and chelate-assisted phytoextraction of cadmium and lead – a review, Environ. Pollut. 287 (2021) 117667, https://doi.org/10.1016/J.ENVPOL.2021.117667.
[48] M. Malik, S. Mahmood, S. Noreen, R. Abid, S. Ghaffar, S. Zahra, T. Shah, A. Ahmad, Lead contamination affects the primary productivity traits, biosynthesis of macromolecules and distribution of metal in durum wheat (Triticumdurum L.), Saudi J. Biol. Sci. 28 (2021) 4946–4956, https://doi.org/10.1016/J.SJBS.2021.06.093.
[49] M.U. Hassan, M.U. Chattha, I. Khan, M.B. Chattha, L. Barbanti, M. Aamer, M. M. Iqbal, M. Nawaz, A. Mahmood, A. Ali, M.T. Aslam, Heat Stress in Cultivated Plants: Nature, Impact, Mechanisms, and Mitigation strategies—a Review, vol. 155, 2020, pp. 211–234, https://doi.org/10.1080/11263504.2020.1727987.
[50] S.C. Kunene, K.S. Lin, N.V. Mdlovu, Y.S. Lin, N.B. Mdlovu, Speciation and fate of toxic cadmium in contaminated paddy soils and rice using XANES/EXAFS spectroscopy, J. Hazard. Mater. 383 (2020) 121167, https://doi.org/10.1016/J.JHAZMAT.2019.121167.
[51] C. Larue, H. Castillo-Michel, S. Sobanska, N. Trcera, S. Sorieul, L. Cécillon, L. Ouerdane, S. Legros, G. Sarret, Fate of pristine TiO2 nanoparticles and aged paint-containing TiO2 nanoparticles in lettuce crop after foliar exposure, J. Hazard. Mater. 273 (2014) 17–26, https://doi.org/10.1016/J.JHAZMAT.2014.03.014.
[52] J. Zhou, B. Du, H. Liu, H. Cui, W. Zhang, X. Fan, J. Cui, J. Zhou, The bioavailability and contribution of the newly deposited heavy metals (copper and lead) from atmosphere to rice (Oryza sativa L.), J. Hazard. Mater. 384 (2020) 121285, https://doi.org/10.1016/J.JHAZMAT.2019.121285.
[53] N. Sarwar, Saifullah, S.S. Malhi, M.H. Zia, A. Naeem, S. Bibia, G. Farida, Role of mineral nutrition in minimizing cadmium accumulation by plants, J. Sci. Food Agric. 90 (2010) 925–937, https://doi.org/10.1002/JSFA.3916.
[54] M. Faizan, P. Alam, A. Hussain, F. Karabulut, S.H. Tonny, S.H. Cheng, M. Yusuf, M. F. Adil, S. Sehar, S.O. Alomrani, T. Albalawi, S. Hayat, Phytochelatins: key regulator against heavy metal toxicity in plants, Plant Stress 11 (2024) 100355, https://doi.org/10.1016/J.STRESS.2024.100355.
[55] T. Gu, Z. Qi, Y. Wang, S. Chen, J. Yan, H. Qiu, Y. Yu, Z. Fang, J. Wang, J. Gong, An endophytic fungus interacts with the defensin-like protein OsCAL1 to regulate cadmium allocation in rice, Mol. Plant 17 (2024) 312–324, https://doi.org/10.1016/J.MOLP.2023.12.022.
[56] Z. Tao, Q. Guo, C. Liu, R. Wei, X. Han, Y. Lang, Z. Guo, J. Hu, X. Dong, Lord Famiyeh, Slight transition in Chinese atmospheric Pb isotopic fingerprinting due to increasing foreign Pb, Environ. Pollut. 323 (2023) 121296, https://doi.org/10.1016/J.ENVPOL.2023.121296.
[57] S. Dong, X. Jing, S. Lin, K. Lu, W. Li, J. Lu, M. Li, S. Gao, S. Lu, D. Zhou, C. Chen, B. Xing, L. Mao, Root hair apex is the key site for symplastic delivery of graphene into plants, Environ. Sci. Technol. 56 (2022) 12179–12189, https://doi.org/10.1021/ACS.EST.2C01926/SUPPL_FILE/ES2C01926_SI_005.MP4.
[58] H.W. Tan, Y.L. Pang, S. Lim, W.C. Chong, A state-of-the-art of phytoremediation approach for sustainable management of heavy metals recovery, Environ. Technol. Innov. 30 (2023) 103043, https://doi.org/10.1016/J.ETI.2023.103043.
[59] A. Emamverdian, Y. Ding, F. Mokhberdoran, Y. Xie, Heavy metal stress and some mechanisms of plant defense response, Sci. World J. 2015 (2015), https://doi.org/10.1155/2015/756120.

[60] P. Fan, L. Wu, Q. Wang, Y. Wang, H. Luo, J. Song, M. Yang, H. Yao, S. Chen, Physiological and molecular mechanisms of medicinal plants in response to cadmium stress: current status and future perspective, J. Hazard. Mater. 450 (2023) 131008, https://doi.org/10.1016/J.JHAZMAT.2023.131008.

[61] C. Zhou, M. Huang, H. Ren, J. Yu, J. Wu, X. Ma, Bioaccumulation and detoxification mechanisms for lead uptake identified in Rhus chinensis Mill. seedlings, Ecotoxicol. Environ. Saf. 142 (2017) 59–68, https://doi.org/10.1016/J.ECOENV.2017.03.052.

[62] F.J. Zhao, P. Wang, Arsenic and cadmium accumulation in rice and mitigation strategies, Plant Soil 446 (2019) 1–21, https://doi.org/10.1007/S11104-019-04374-6, 2019 4461.

[63] H. Lu, S. Qin, J. Zhao, P. Pan, F. Wang, S. Tang, L. Chen, K. Akhtar, B. He, Silicon inhibits the upward transport of Cd in the first internode of different rice varieties in a Cd stressed farm land, J. Hazard. Mater. 458 (2023) 131860, https://doi.org/10.1016/J.JHAZMAT.2023.131860.

[64] M. Wang, C. Mu, X. Lin, W. Ma, H. Wu, D. Si, C. Ge, C. Cheng, L. Zhao, H. Li, D. Zhou, Foliar application of nanoparticles reduced cadmium content in wheat (Triticum aestivum L.) grains via long-distance "Leaf-Root-Microorganism" regulation, Environ. Sci. Technol. 58 (2024) 6900–6912, https://doi.org/10.1021/ACS.EST.3C10506.