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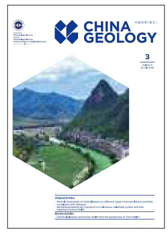

Mechanisms behind zinc transport in a calcareous soil-wheat system and their impacts on human health

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A B S T R A C T

Zinc is recognized as a vital biological element for animals and plants. Both zinc deficiency and excess will cause damage to cells, and zinc deficiency in the human body may lead to severe health problems. Zinc deficiency has been identified as a global nutritional issue. Wheat, one of the most significant food crops for humans, is primarily planted in potentially zinc-deficient, calcareous soils in China. It proves to be a major global challenge to increase the zinc concentration in wheat crops to boost crop yields and improve human health. This study investigated the growth process of wheat in calcareous soils with various zinc concentrations using outdoor pot experiments and systematically explored the characteristics and mechanism of zinc transport in the soil-wheat system. The results indicate that the zinc concentrations in various wheat organs decreased in the order of roots, stems, and leaves in the jointing stage and in the order of seeds, roots, and stems in the mature stage. Overall, the zinc enrichment in various wheat organs decreased in the order of seeds, roots, stems, and leaves. In the case of zinc deficiency in soils, wheat roots exhibited elevated zinc availability in the rhizosphere by secreting phytosiderophores. This enhances the zinc uptake capacity of wheat roots. In the case of sufficient zinc supply from soils, chelated zinc formed with citric acid as the chelating ligand occurred stably in soils, contributing to enhanced utilization and uptake rates of zinc, along with elevated transport and enrichment capacities of zinc inside the plants. The results indicate that the zinc concentration in wheat seeds can be somewhat enhanced by regulating the background value of bioavailable zinc concentration in soils. A moderate zinc concentration gradient of 1.0 mg/kg is unfavorable for zinc accumulation in wheat seeds, while a high zinc concentration gradient of 6.0 mg/kg corresponds to the highest degree of zinc enrichment in wheat seeds. This study holds critical scientific significance for enhancing the zinc supply capacity of soils, increasing the zinc concentrations in wheat seeds, and, accordingly, addressing zinc deficiency in the human body. Additionally, this study offers a mechanistic reference and basis for research on the interplay between soils, plants, and human health.

1. Introduction

Zinc, a vital biological element for animals and plants, is known as “the flower of life” and “the source of intelligence” (Yang ZF et al., 2019; Ma XD et al., 2022). It is identified as a structural cofactor that constitutes over 300 enzymes and proteins engaged in signal transduction and transcriptional regulation in organisms (Haydon MJ et al., 2007). It plays a significant role in physiological functions like body metabolism, the maintenance of biomembrane stability, and gene expression regulation (Wendy R et al., 2004). Both zinc deficiency and excess in the human body and plants will cause damage to cells. Zinc deficiency in plants will cause symptoms like littleleaf disease, leaf deformity, tree stunting, and reduced fruit production (Zhang SR et al., 2024). Zinc deficiency in the human body will result in severe health

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problems such as growth retardation and functional defects in the immune system, central nervous system, and gastrointestinal tract (Gibson SR et al., 2006; Zhu PP et al., 2021; Liu ZJ et al., 2023). Statistics indicate that over two billion people are affected by the deficiency of one or more trace elements (Gashu D et al., 2021). Notably, nearly half of the world's population suffers from zinc deficiency, with a zinc deficiency rate of up to 73% in some countries (Cakmak I et al., 2008, 2009). In China, about 80% of its population sustains zinc deficiency, primarily including adolescents, children, pregnant women, and patients (Yang XE et al., 2007). As a common global nutritional issue (Wang CY et al., 2019), zinc deficiency has developed into the fifth leading risk factor for diseases and death in developing countries (Hotz CH et al., 2004). The human body takes the required zinc nutrients directly or indirectly from plants. In most West and Central Asian countries, wheat serves as a principal food and mineral source, contributing nearly 50% of daily calorie intake, even above 70% in rural areas (Cakmak I et al., 2004). However, wheat seeds, especially those from wheat growing in zinc-deficient soils, exhibit very low zinc concentrations. As the main grain crop in northern China, wheat is primarily planted in potentially zinc-deficient, calcareous soils. Soils generally exhibit zinc concentrations ranging from 10 mg/kg to 300 mg/kg (Kaur H et al., 2024), while calcareous soils display an average total zinc concentration of 78 mg/kg, less than 100 mg/kg—the average zinc concentration in China (Liu Z, 1994). Low zinc solubility is identified as the cause of low zinc concentrations in plants, significantly reducing crop yields and the quality of seeds. Wheat, ranking as the second crop in production globally (Wang Z et al., 2023), is recognized as a vital grain product and a primary strategic food reserve (Li GX, 2020). It proves to be a major global challenge to increase the zinc concentration in wheat crops to boost crop yields and improve human health (Cakmak I et al., 2008).

Previous studies revealed that zinc in calcareous soils is predominantly bound to amorphous iron and carbonate and weakly bound to organic matter (Ma YB et al., 1997; Stephan CH et al., 2008). Since calcareous soils exhibit relatively low concentrations of bioavailable zinc, the zinc concentrations in wheat seeds produced from such soils fail to satisfy the nutritional needs of the human body for zinc (Yang XE et al., 2007; Cakmak I et al 2008; Zhang Y et al., 2010). To address zinc deficiency in the human body, the most direct measure is to improve zinc-deficient soils by increasing the concentrations of bioavailable zinc. The most effective approach to relieving the impacts of zinc deficiency on human health is to apply zinc fertilizers to staple crops. This approach is cost-effective and more easily covers all target populations at risk of zinc deficiency (Cakmak I et al., 2008). To effectively replenish zinc required by plant growth and redress zinc imbalance in plants and the human body, two methods are commonly utilized to relieve zinc deficiency of the soil-plant system: Foliar application of zinc fertilizers and applying micronutrient fertilizers to soils. Previous studies suggested that applying chelated zinc fertilizers to calcareous soils can inhibit zinc fixation in soils or replace solid zinc in soils with soluble zinc, thereby accelerating zinc diffusion by increasing the zinc diffusion concentration gradient (Prasad B et al., 1976; Metwally AI et al., 1991). This is significant for calcareous and alkaline soils. Notably, applying excessive micronutrient fertilizers beyond the absorption ability of plants constrains the enhancement of soil quality. Furthermore, it will lead to resource waste and soil-groundwater environmental challenges (Jiang WJ et al., 2023), including the heavy metal contamination of topsoils, the contamination of shallow groundwater, and the inhibition of plants' absorption of other trace elements like iron and manganese (Jalali M et al., 2008).

This study analyzed the biological mechanisms for boosting the nutrient uptake efficiency and quality of the soil-plant system. Using pot experiments, this study observed the entire wheat growth process in soils with different zinc concentrations and systematically explored the mechanisms behind zinc transport in the calcareous soil-wheat system. The purpose is to provide a scientific basis for research on the interplay between soils, plants, and human health.

2. Experimental materials and methods

2.1. Experimental design

This study conducted outdoor pot experiments using wheat cultivar Shixin 828, which is commonly planted in the North China Plain. Before planting, inferiors were excluded to ensure the high quality of the wheat seeds. Natural soils from a calcareous soil field in northern China were used in the experiments. Soil samples were air dried, followed by the removal of gravels and plant residues. After passing through a 10 mm nylon sieve, the soil samples were mixed thoroughly and placed equally (each 15 kg) into identical pots measuring 32 cm in diameter and 35 cm in height. As for the mineral composition, the soil samples comprised quartz (63%), plagioclase (17%), calcite (5%), dolomite (5%), mica (4%), chlorite (4%), K-feldspar (1%), and a minor amount of amphibole. Regarding general physical and chemical properties, the soil samples exhibited a pH value of 8.5, an organic matter content of 14.8 g/kg, a nitrogen concentration of 901 mg/kg, an available potassium concentration of 205 mg/kg, and a bioavailable phosphorus concentration of 16.8 mg/kg. Using the single variable method, this study prepared six groups of soils with different zinc concentration grades through exogenous application of zinc sulfate ($ZnSO_4·7H_2O$). These six groups included a control group comprising original soils (Figs. 1, 2). Each group contained six duplicate samples, totaling 36 pots of experimental soils. Experiments were conducted using the same planting method, sunlight exposure, fertilizer application rate, water consumption, temperature, and humidity, aiming to exclude the external environmental disturbances as far as possible.

The zinc concentration gradients of the experimental soils were set based on the bioavailable zinc concentrations in the original soils. The baseline value of the zinc-deficient soils was set at the lower limit of the third-grade bioavailable zinc concentration in soils specified in standard *Specification of Land Quality Geochemical Assessment* (DZ/T0295-2016) (the former Ministry of Natural Resources, 2016), thus ensuring the formation of actually zinc-deficient state of the soils (Table 1). The bioavailable zinc concentrations in experimental soils reached the second-grade bioavailable zinc concentrations in the standard. However, in alkaline soils, especially those containing calcium carbonate, the decreased zinc solubility and the increased zinc absorbed by soil colloids and carbonate lead reduced bioavailable zinc. Previous experiments indicate that the Zn^{2+} activity decreases by 100 times when the pH value increases by 1 (Sun X et al, 1988). Laboratory determination typically enables a relatively high degree of element extraction, which approximates the full adsorption capacity of active elements in soils. However, the actual element release in alkaline soils generally falls below the extracted bioavailable concentrations through laboratory determination. Therefore, given the high alkalinity of the experimental soils (pH = 8.35), the inferred bioavailable zinc concentrations were set at one-fifth of the bioavailable zinc concentrations determined through laboratory tests, thus generally falling below the critical values of the lower limits of zinc deficiency. The zinc concentration gradients of the experimental soils were determined based on DZ/T0295-2016. Specifically, the lower limit of the third-grade concentration in DZ/T0295-2016 was set as the new lowest grade. For the first-, second-, and third-grade concentrations in the standard, the averages of the former two and last two were respectively inserted between the original first and second and between the original second and third grades. Finally, the first-grade concentration was doubled. Consequently, the new five-grade bioavailable zinc concentrations were formed (Table 2). Based on the inferred bioavailable zinc concentrations, zinc sulfate solutions with different concentrations (i.e., the zinc compensation solutions), after citric acid complexation and adjustment for a neutral pH using sodium carbonate, were added to the soils, except for the control group (CK, 0 mg/kg). After the soils were mixed with the compensation solutions evenly, the soils were kept undisturbed for drying until they were not clumpy. Finally, the soils were loosened and flattened for uniform wheat sowing.

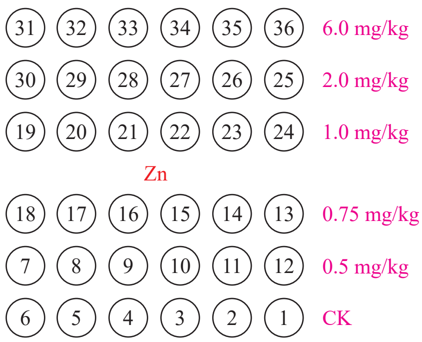

Fig. 1. Configuration of zinc concentration gradients.

2.2. Preparation of applied solutions

First, the zinc concentrations to be applied for achieving various zinc concentration gradient grades were calculated using the following equation (Equ. 1):

$$ZnCx = C_{Znx} - C_{Zn0} \quad (1)$$

where $ZnCx$ is the zinc compensation concentration to be applied for the X*th*-grade zinc concentration gradient, C_{Znx} is the standard zinc concentration in soils corresponding to the X*th*-grade zinc concentration gradient in Table 1, C_{Zn0} is the

Fig. 2. Photos showing wheat in experimental pots.

Table 1. Grades of bioavailable zinc concentrations in soils.

Index	Standard for grading	Grade 1 (rich)	Grade 2 (fairly rich)	Grade 3 (moderate)	Grade 4 (relatively deficient)	Grade 5 (deficient)
Bioavailable zinc /(mg/kg)	Specification of Land Quality Geochemical Assessment (DZ/T0295-2016)	> 3	> 1–3	> 0.5–1	> 0.3–0.5	≤ 0.3
	Grades of bioavailable zinc concentration gradients of experimental soils	6	2	1	0.75	0.5

bioavailable zinc concentration in soils (i.e., the inferred bioavailable zinc concentration in the control group), and $x\,(x=1,2,\cdots,5)$ is the grade of corresponding zinc concentration gradient.

Then, the concentrations of the zinc compensation solutions to be applied, ZnC_{sx}, were calculated using the following equation (Equ. 2):

$$Zn_M \times ZnC_{sx} = S_M \times ZnC_x \quad (2)$$

where Zn_M is the solution quantity applied to each pot per time, set at 1.5 kg; ZnC_{sx} is the concentration of the compensation solution to be applied for the X*th*-grade zinc concentration gradient, and S_M is the dry weight of the experimental soils, set at 15 kg. Accordingly, the concentrations of solutions to be applied for various grades were calculated (Table 2). The calculation results indicate that when 1.5 kg of solution for each pot and six pots for each concentration grade were adopted, the solution to be applied for each concentration grade amounted to 9 kg. Then, the quantities of raw materials (i.e., zinc sulfate) for various concentration grades were calculated while considering factors like spraying-induced loss (Table 3). To facilitate the absorption of zinc sulfate by plant roots through full complexation, the complexing concentrate of zinc sulfate was prepared using citric acid and was diluted when being applied. The specific dilution steps are as follows: (1) Raw materials were weighed for each zinc concentration grade and were then placed into a 500 ml beaker; (2) an appropriate amount of water was weighed for dissolution; (3) citric acid for complexation was added until the complete dissolution of the raw materials; (4) sodium carbonate was gradually added to adjust the pH value to 5–7; (5) after the beaker was put on a balance, water was added to the concentrate until required weight was achieved.

2.3. Sampling

The sample data used in the experiment were primarily collected in the jointing and mature stages of wheat. In the jointing stage, five wheat seedlings and their rhizosphere soils were randomly sampled from each pot. These samples were tested for the total and bioavailable zinc concentrations in rhizosphere soils, as well as zinc concentrations in the roots, stems, and leaves of wheat seedlings. In the mature stage, all wheat plants in each pot were sampled. Given different growth characteristics, the rhizosphere soils, roots, stems, and spikes (seeds with husks) of these samples were tested. During the experiment, the relatively high outdoor temperatures in the grain-filling stage somewhat inhibited the photosynthesis of wheat leaves, affecting the synthesis and accumulation of organic matter. Besides, the relatively high temperatures at nighttime accelerated the respiration of wheat, consuming more nutrients. Both led to unsatisfactory grain-filling effects, which lowered the wheat yield. To ensure the required weights of spike samples, seeds with husks were selected in the mature stage. After sampling, plant samples, separated into different parts (i.e., roots, stems, leaves, and seeds), immediately underwent air drying and then sent to the laboratory for testing.

2.4. Sample tests

The samples were analyzed and tested at the Hebei Provincial Geological Experiment and Testing Center. Based on the wavelength dispersive X-ray fluorescence (WDXRF) spectrometry specified in the HJ780-2015 standard, total zinc concentrations in the soil samples were tested using a ZSX Primus II X-ray fluorescence spectrometer (Rigaku Corporation, Japan). The bioavailable zinc concentrations in the soil samples were determined through extraction using a diethylenetriaminepentaacetic acid (DTPA) solution and an Agilent 725 inductively coupled plasma - mass spectrometer (ICP-MS; Agilent Technologies, U.S.). Using the glass electrode method, pH values were determined with a PHS-3C pH meter (Shanghai Kangyi Instrument Co., Ltd., China). The zinc concentrations in wheat plants were examined as per the *National Food Safety Standard - Determination of Multi-Elements in Food* (GB5009.268-2016; National Health and Family Planning Commission of the People’s Republic of China, and China Food and Drug Administration; 2016), with an Agilent 7900 ICP-MS (Agilent Technologies, U.S.) being used. The complete analysis of zinc utilized national primary

Table 2. Calculated concentrations of applied solutions (1.5 kg of solution applied per time, unit: mg/kg).

Index	Measured bioavailable zinc concentration in soils	Assumed bioavailable zinc concentration in soils	Preparation of applied solution					
Bioavailable zinc concentration	1.88	0.376	Target concentration	6	2	1	0.75	0.5
			Compensated concentration	5.624	1.624	0.624	0.374	0.124
			Concentration of applied solution	56.24	16.24	6.24	3.74	1.24

Table 3. Weights of raw materials for preparing 1 kg of applied solutions (mg).

Element	Raw material			Grade 1	Grade 2	Grade 3	Grade 4	Grade 5
	Name	Molecular formula	Atomic weight/ content%	Concentration/ material weight	Concentration/ material weight	Concentration/ material weight	Concentration/ material weight	Concentration/ material weight
Bioavailable zinc	Zinc sulfate	$ZnSO_4 \cdot 7H_20$	65.39	56.24	16.24	6.24	3.74	1.24
	Molecular weight	287.56	22.74	247.32	71.42	27.44	16.45	5.45

certified reference materials for quality control, with the reported rates and the accuracy and precision compliance rates of analytical data reaching 100%.

2.5. Assessment indices

2.5.1. Enrichment coefficient

Enrichment coefficient refers to the ratio of the concentration of an element in a certain plant part to that in soils, serving as a significant indicator used to describe the accumulation trend of chemical matter in organisms (Pan YH et al., 2010; Zhang JJ, 2019). This index somewhat reflects the difficulty of transporting an element from soils to plants.

Enrichment coefficient can be calculated using the following equation (Equ. 3):

$$\text{Enrichment coefficient} = C_{plant}/C_{soil} \quad (3)$$

where C_{plant} is the concentration of an element in the roots, stems, or leaves of a plant, mg/kg, and C_{soil} is the concentration of the element in soils, mg/kg.

2.5.2. Transport coefficient

Transport coefficient refers to the ratio of the concentration of an element in the overground parts of a plant to that in its underground portion, acting as a significant indicator used to describe the transport capacity of chemical matter within organisms (Yan L et al., 2016). This index somewhat reflects the difficulty of transporting an element from the roots of a plant to its overground portion.

Transport coefficient can be calculated using the following equation (Equ 4):

$$\text{Transport coefficient} = C_{overground}/C_{underground} \quad (4)$$

where $C_{overground}$ is the total concentration of an element in the stems, leaves, and seeds of a plant, mg/kg, and $C_{underground}$ is the concentration of the element in the roots of the plant, mg/kg.

2.6. Data processing

The statistical analysis and sorting of experimental data were performed using EXCEL 2010. The statistical significance of average zinc concentrations in various wheat organs in the jointing and mature stages of wheat was tested using Tukey's test. Additionally, the correlation analysis and mapping of data were completed using SPSS 20.0 software.

3. Results and analysis

3.1. Zinc concentrations in soils and various wheat organs

In the pot experiments for wheat, exogenous zinc with concentrations of 0, 0.5 mg/kg, 0.75 mg/kg, 1.0 mg/kg, 2.0 mg/kg, and 6.0 mg/kg was respectively added to soils. Wheat plants and their rhizosphere soils were sampled in their jointing and mature stages. Then, the samples were tested for the total/bioavailable zinc concentrations in soils, as well as zinc concentrations in roots, stems, leaves, and seeds. The statistical results are shown in Table 4. According to this table, the roots, stems, and leaves of wheat exhibited average zinc concentrations of 54.2 mg/kg, 33.6 mg/kg, and 24.8 mg/kg, respectively in the jointing stage, suggesting that zinc accumulation in these organs descended in the order of roots, stems, and leaves. In the mature stage, the roots, stems, and seeds of wheat manifested average zinc concentrations of 27.2 mg/kg, 17.4 mg/kg, and 80.4 mg/kg, respectively, suggesting that zinc accumulation in these organs descended in the order of seeds, roots, and stems. Notably, the seeds showed the maximum and minimum zinc concentrations of 118 mg/kg and 58.4 mg/kg, respectively, with the minimum value exceeding the maximum zinc concentrations in roots and stems. This finding suggests that the seeds displayed more significant zinc accumulation than other wheat organs. Table 4 also reveals that the zinc concentrations in roots decreased with the continuous growth of wheat, suggesting the presence of zinc transport from roots to other organs. Additionally, the total/bioavailable zinc concentrations in soils were higher in the jointing stage than in the mature stage.

3.2. Correlations between zinc concentrations in soils and various wheat organs

3.2.1. Jointing stage

The analytical results of correlations between zinc concentrations in soils and various wheat organs in the

Table 4. Statistics of zinc concentrations in soils and various wheat organs (mg/kg).

Growth stage	Test item	Minimum	Maximum	Average	Standard deviation
Jointing stage	Total top in soils	72.9	108.0	80.0	7.8
	Bioavailable top in soils	1.38	14.50	3.85	3.10
	Roots	24.4	93.0	54.2	18.7
	Stems	23.9	83.5	33.6	10.2
	Leaves	19.7	29.0	24.8	2.1
Mature stage	Total top in soils	67.1	93.3	73.0	6.5
	Bioavailable top in soils	1.36	9.45	2.57	1.93
	Roots	20.0	40.4	27.2	4.8
	Stems	9.1	33.2	17.4	5.2
	Seeds	58.4	118.0	80.7	13.9

Table 5. Correlations between zinc concentrations in soils and those in various wheat organs in the jointing stage.

Zinc concentration	Total zinc in soil	Bioavailable zinc in soil	Roots	Stems	Leaves
Total zinc in soils	1	0.546**	0.344*	0.219	0.071
Bioavailable zinc in soils	0.546**	1	0.500**	0.407*	0.197
Roots	0.344*	0.500**	1	0.787**	0.609**
Stems	0.219	0.407*	0.787**	1	0.698**
Leaves	0.071	0.197	0.609**	0.698**	1

Notes: *Significant correlation (bilaterally) at a significance level of 0.05.
**Significant correlation (bilaterally) at a significance level of 0.01.

jointing stage (Table 5) indicate there existed an extremely significant correlation between total zinc and bioavailable zinc in soils, as indicated by the Spearman correlation coefficient of 0.834 ($P < 0.01$). The zinc concentrations in wheat roots and leaves exhibited extremely significant correlations with the total/available zinc concentrations in soils ($P < 0.01$), with correlation coefficients of 0.534, 0.608, 0.669, and 0.509, respectively. The zinc concentrations in wheat stems were poorly correlated with those in soils but were significantly correlated with those in leaves ($P < 0.01$), with a correlation coefficient of 0.557. The zinc concentrations in roots showed an extremely significant correlation with those in leaves ($P < 0.05$), with a correlation coefficient of 0.369. In the jointing stage—a crucial growth stage, the wheat underwent the transition from vegetative to reproductive growth. In this stage, zinc transport in the wheat primarily involved the transport of zinc absorbed by wheat roots from soils to leaves via stems. The correlations between zinc concentrations in soils, roots, and leaves imply that an increase in zinc concentration in soils can facilitate zinc transport from the roots of wheat to its overground portion.

3.2.2. Mature stage

Table 6 shows that there were significant correlations between the zinc concentrations in wheat roots and the total/bioavailable zinc concentrations in soils, as indicated by Spearman correlation coefficients. There was a significant correlation between the zinc concentrations in wheat stems and the bioavailable zinc concentration in soils. The zinc concentrations in roots exhibited a significant correlation with those in the stems exhibited, with a correlation coefficient of 0.787 ($P < 0.01$). The zinc concentrations in seeds were poorly correlated with those in soils but were significantly correlated with those in wheat roots and stems, with correlation coefficients of 0.609 and 0.698 ($P < 0.01$), respectively. The characteristics of zinc concentrations in various wheat organs in the mature stage reveal that zinc in soils was primarily transported to roots and stems in the later growth stages of wheat, with zinc in both wheat organs serving as a significant source for zinc enriched in seeds in the mature stage. Brinch-Pedersen H et al. (2003) indicated that the redistribution of zinc stored in stems and leaf sheaths to seeds in the grain-filling stage provides a crucial source of zinc in seeds. This finding aligns with the results of this study.

Table 6. Correlations between zinc concentrations in soils and those in various wheat organs in the mature stage.

Zinc concentration	Total zinc in soil	Bioavailable zinc in soil	Roots	Stems	Seeds
Total zinc in soil	1	0.546**	0.344*	0.219	0.071
Bioavailable zinc in soil	0.546**	1	0.500**	0.407*	0.197
Roots	0.344*	0.500**	1	0.787**	0.609**
Stems	0.219	0.407*	0.787**	1	0.698**
Seeds	0.071	0.197	0.609**	0.698**	1

Notes: *Significant correlation (bilaterally) at the level of 0.05. **Significant correlation (bilaterally) at the level of 0.01.

3.3. Variations in zinc concentrations in various wheat organs

Based on the pot experiments utilizing six zinc concentration gradients, this study determined the variations in zinc concentrations in different wheat organs in different growth stages (Fig. 3). In the jointing stage, the zinc concentrations in wheat roots, stems, and leaves gradually increased as the zinc concentration in soils increased, with the roots exhibiting the most pronounced increasing trend (Fig. 3a). The zinc concentrations in leaves displayed minor variations (Fig. 3c), whereas those in stems generally exhibited an increasing trend. The wheat stems from zinc-deficient soils exhibited the lowest average zinc concentration (27.9 mg/kg), while those from soils with moderate zinc concentrations manifested the highest average zinc concentration (38.7 mg/kg; Fig. 3b). The wheat leaves differed insignificantly in zinc concentration under varying zinc concentration gradients. The zinc concentrations in wheat roots under a zinc concentration gradient of 6.0 mg/kg differed significantly from those in wheat roots under other zinc concentration gradients. The zinc concentrations in wheat stems under a zinc concentration gradient of 6.0 mg/kg differed significantly from those in stems under the condition of the control group and zinc concentration gradients of 0.5 mg/kg, 0.75 mg/kg, and 1.0 mg/kg. Furthermore, the zinc concentrations in wheat stems under a zinc concentration gradient of 0.5 mg/kg differed significantly from those in wheat stems under zinc concentration gradients of 1.0 mg/kg and 2.0 mg/kg.

In the mature stage, the zinc concentrations in wheat roots and stems exhibited roughly the same variation trends as those in soils. Specifically, the former generally increased with the latter, with the amplitude, however, proving small (Fig. 3d, e). Under various zinc concentration gradients of soils, roots and stems exhibited significantly lower zinc concentrations in the mature stage than in the jointing stage (Fig. 4). The respective average zinc concentrations in roots and stems decreased to 24.8–33.9 mg/kg and 14.2–23.3 mg/kg in the mature stage from 39.7–81.0 mg/kg and 27.9–38.7 mg/kg in the jointing stage. The zinc concentrations in roots under a zinc concentration gradient of 6.0 mg/kg differed significantly from those in roots under other zinc concentration gradients. Moreover, the zinc concentrations in stems under a zinc concentration gradient of 6.0 mg/kg differed greatly from those in stems under the conditions of the control group and zinc concentration gradients of 0.5, 0.75, and 1.0 mg/kg. Besides, seeds exhibited pronounced zinc enrichment. The wheat seeds exhibited the lowest average zinc concentration of 68.6 mg/kg in soils with moderate zinc (zinc concentration gradient: 1 mg/kg) and the highest average zinc concentration of 88.9 mg/kg in soils with abundant zinc (zinc concentration gradient: 6.0 mg/kg). The seeds displayed significantly different zinc concentrations under zinc concentration gradients of 1.0 mg/kg and 6.0 mg/kg. However, zinc concentrations in seeds under both zinc concentration

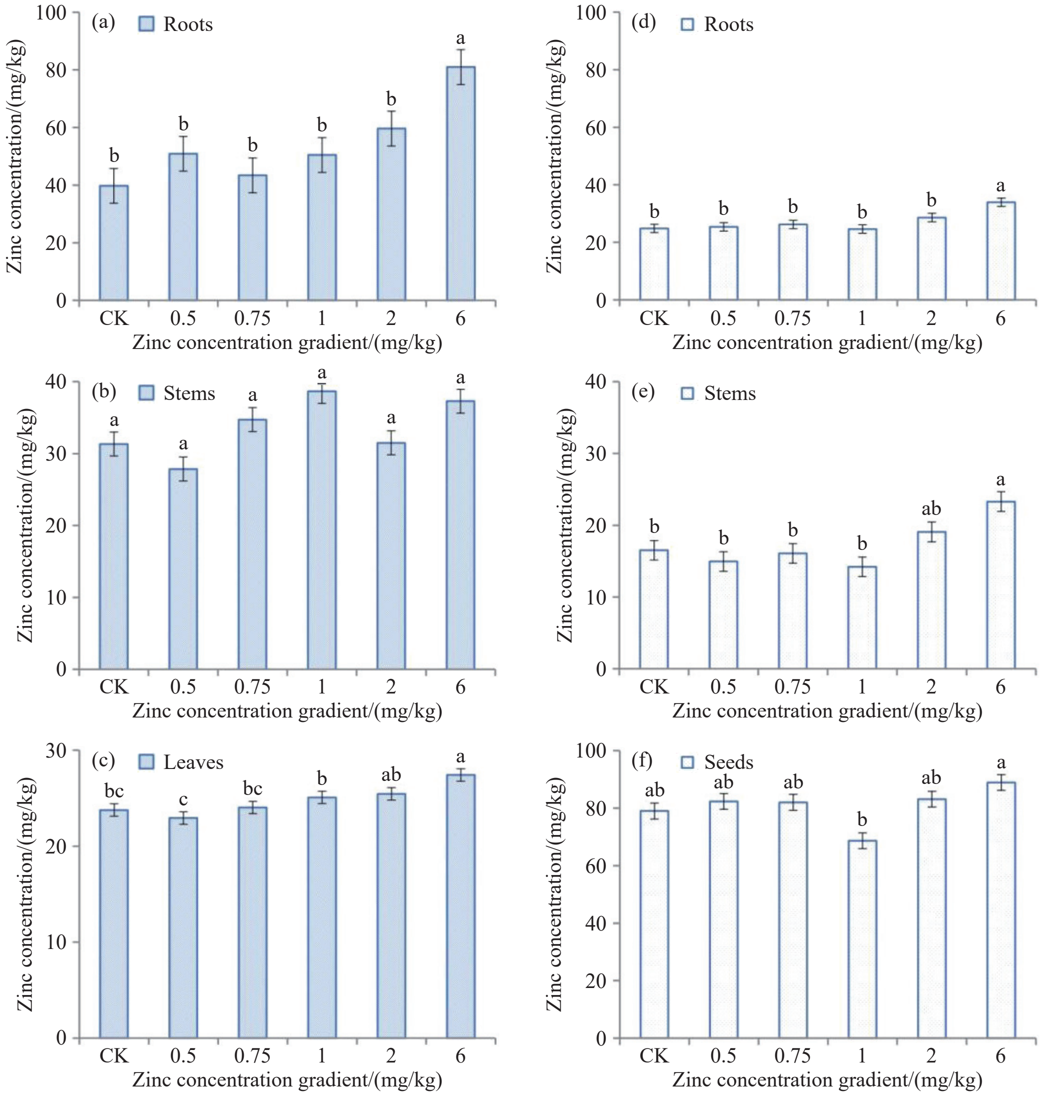

Fig. 3. Average zinc concentrations in the roots, stems, leaves, and seeds of wheat in the jointing and mature stages and their statistical significances determined using Tukey's test (left column: jointing stage; right column: mature stage). a–roots in the jointing stage; b–stems in the jointing stage; c–leaves in the jointing stage; d–roots in the mature stage; e–stems in the mature stage; f–seeds in the mature stage (lowercase letters a, b, and c denoting significance ($P < 0.05$)).

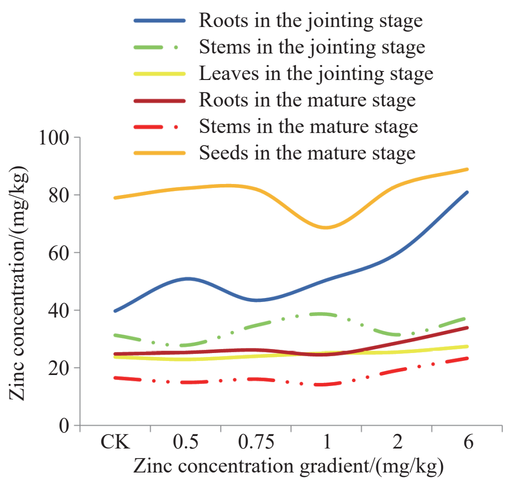

Fig. 4. Variations in zinc concentrations in various wheat organs in different growth stages.

gradients differed insignificantly from those in seeds under other zinc concentration gradients.

Fig. 4 shows variations in zinc concentrations in various wheat organs under six zinc concentration grades of soils. In the jointing stage, zinc absorbed by roots mostly accumulated in roots, with part of it being transported to stems and leaves. In the mature stage, seeds manifested far higher zinc concentrations than other wheat organs, suggesting that zinc accumulated in roots and stems was largely transported to seeds.

3.4. Zinc enrichment and transport coefficients of various wheat organs

The zinc enrichment and transport coefficients of various wheat organs in the experiments are shown in Tables 7 and 8. According to both tables, seeds exhibited the highest zinc enrichment coefficient over the life cycle of wheat. Seeds under all zinc concentration gradients except for 1.0 mg/kg exhibited zinc enrichment coefficients exceeding 1, with an average of 1.11. In contrast, other wheat organs all displayed

Table 7. Zinc enrichment and transport coefficients of wheat in the jointing stage.

Zircon concentration gradient	Enrichment coefficient of roots	Enrichment coefficient of stems	Enrichment coefficient of leaves	Transport coefficient
CK	0.53	0.42	0.32	1.43
0.5 mg/kg	0.67	0.37	0.30	1.03
0.75 mg/kg	0.57	0.46	0.32	1.45
1.0 mg/kg	0.65	0.50	0.33	1.39
2.0 mg/kg	0.74	0.39	0.31	0.97
6.0 mg/kg	0.87	0.40	0.29	0.82
Average	0.67	0.42	0.31	1.18

Table 8. Zinc enrichment and transport coefficients of wheat in the mature stage.

Zircon concentration gradient	Enrichment coefficient of roots	Enrichment coefficient of stems	Enrichment coefficient of seeds	Transport coefficient
CK	0.36	0.24	1.14	3.88
0.5 mg/kg	0.36	0.21	1.18	3.86
0.75 mg/kg	0.38	0.23	1.18	3.73
1.0 mg/kg	0.35	0.20	0.98	3.36
2.0 mg/kg	0.39	0.26	1.12	3.57
6.0 mg/kg	0.41	0.28	1.07	3.35
Average	0.37	0.24	1.11	3.63

zinc enrichment coefficients of less than 1. In the jointing stage, the enrichment coefficients of various wheat organs descended in the order of roots, stems, and leaves, all exhibiting a gradually increasing trend with zinc concentration in soils. In the mature stage, the zinc enrichment coefficients of various wheat organs decreased in the order of seeds, roots, and stems. Overall, the zinc enrichment in various wheat organs decreased in the order of seeds, roots, stems, and leaves.

In the jointing stage, the zinc transport coefficients, reflecting the zinc transport capacity from the underground parts of wheat to its overground portions, all exceeded 1 under conditions of soils with deficient (CK and a zinc concentration gradient of 0.5 mg/kg), relatively deficient (zinc concentration gradient: 0.75 mg/kg), and moderate (zinc concentration gradient: 1.0 mg/kg) zinc. In soils with abundant and relatively abundant zinc, more zinc accumulated in roots in the jointing stage, with transport coefficients below 1. In the mature stage, the transport coefficients all exceeded 3 under various zinc concentration gradients. Notably, the zinc transport coefficients exceeded 3.7 in soils with deficient (CK and a zinc concentration gradient of 0.5 mg/kg) and relatively deficient (zinc concentration gradient: 0.75 mg/kg) zinc. The zinc transport coefficients generally decreased with an increase in the zinc concentration in soils, being lowest (3.35; average: 3.63) under a zinc concentration gradient of 6.0 mg/kg. These characteristics of the zinc enrichment and transport coefficients suggest that the zinc concentrations in wheat seeds can be effectively enhanced by regulating the background value of zinc in soils.

4. Discussion

4.1. Zinc migration mechanisms in soils and wheat plants

The aforementioned experimental results indicate that the total/bioavailable zinc concentrations in soils were higher in the jointing stage than in the mature stage during the wheat growth. The zinc concentrations in roots and leaves exhibited extremely significant correlations with the total/bioavailable zinc concentrations in soils. Furthermore, the zinc concentrations in roots and stems gradually decreased with the wheat growth. All these fully indicate the occurrence of zinc migration between soils and wheat plants. Previous studies demonstrated that zinc migration in soils is predominantly driven by diffusion. Oliveria MME et al. (2010) found that 99% of zinc in soils reaches the surface of plant roots through diffusion, with zinc diffusion rate in soils identified as the primary factor influencing zinc uptake in plants (Modaihsh AS, 1990; Metwally AI et al., 1991). In soil solutions, zinc occurs as Zn^{2+} and complex ions like $Zn(OH)^+$, $ZnCl^+$, and $ZnNO^{3+}$, which are prone to be absorbed by clay minerals, carbonate, and organic matter. Notably, in alkaline or calcareous soils, zinc ions are prone to form insoluble compounds such as $Zn(OH)_2$/$ZnCO_3$ precipitates, leading to reduced zinc diffused concentration and, accordingly, a decreased zinc diffusion rate (Clarke AL et al, 1968; Melton JR et al, 1973). This hinders zinc uptake in plants. With an 18-electron configuration, zinc ions exhibit high electrostatic field strength, prone to form complex ions (Liu YJ, 1984). In the pot experiments in this study, citric acid was used as the chelating ligand. When citric acid is combined with zinc ions, chelates with a ring structure will be formed by the carboxyl (COOH) and hydroxyl (OH) ligands, the carbon chains of citric acid, and zinc ions. The Zn^{2+} in chelated zinc is encapsulated in the chelating ligands (Fan JY, 2024), leaving a small contact area between Zn^{2+} and soil colloids. This prevents zinc from being fixed in soils. Alternatively, solid zinc in soils is replaced and transformed into soluble zinc, increasing the zinc diffusion rate (Karak T et al., 2005). Since chelated zinc can exist stably in soils, zinc elements are less likely to combine with other substances to reduce solubility, thereby enhancing zinc utilization and uptake.

Zinc uptake and transport in plants is a complex process. The Zn^{2+} or chelated zinc absorbed by roots from soils experiences long-distance transport in plants, while the zinc enrichment in soils leads to zinc accumulation in plants. In the vegetative growth stage of wheat, the zinc concentrations in the roots, stems, and leaves of wheat, specifically in roots, gradually increase with the zinc concentration in soils. After zinc in soils enters the xylem of roots, it is transported to overground organs like leaves by the transpirational pull. Besides, it can be transported to other organs after being laterally transported to phloem (Hart JJ et al., 2006). The uptake of zinc from soils around the roots decreases the zinc concentration in the soils. As a result, a zinc concentration gradient is formed, ensuring continuous zinc diffusion.

Throughout the growth process of wheat, the zinc concentrations in roots, stems, and leaves of wheat peak in the early stage and then decrease in the mature stage, aligning with the findings of Dang HK et al. (2010).

4.2. Mechanisms behind zinc accumulation in various wheat organs

This study reveals that the zinc concentrations in various wheat organs did not exhibit simple linear correlations with the zinc concentration gradients of soils (Zhang SR et al., 2024). In the early growth stages of wheat, the zinc concentrations in various wheat organs gradually increased as the zinc concentrations in soils increased from deficient to relatively deficient, moderate, and relatively abundant, to abundant levels sequentially. However, zinc concentrations in roots under zinc-deficient conditions (zinc concentration gradient: 0.5 mg/kg) of soils exceeded those under the conditions of relatively deficient (zinc concentration gradient: 0.75 mg/kg) and moderate (zinc concentration gradient: 1.0 mg/kg) zinc. Under relatively abundant and abundant zinc conditions of soils, the zinc concentrations in roots increased with the zinc concentrations in soils. In contrast, the zinc concentrations in leaves changed slightly with the zinc concentrations in soils. The wheat stems exhibited the lowest zinc concentration under the zinc-deficient condition of soils and the highest zinc concentration in the case of moderate zinc in soils. These findings suggest that wheat roots have a strong ability to absorb zinc in a low-zinc soil environment. The uptake, accumulation, transport, and distribution of zinc in plants are influenced by factors like the Zn^{2+} concentration in the rhizosphere, the growth conditions of roots, and the rhizosphere environment (Cakmak I et al., 2008; Li GX, 2020). Previous studies indicated that plant roots can activate potential nutrients in them by secreting organic matter with low molecular weight, which influences their zinc uptake (Marschner H, 1995). Under the zinc-deficient conditions of soils, the wheat roots secret phytosiderophores of the mugineic acid (MA) family under zinc deficiency stress (Rengel Z et al., 1998). The phytosiderophores can activate zinc in soils, thus enhancing zinc mobility in rhizosphere soils, contributing to significant zinc accumulation in soils around roots, and facilitating zinc uptake in plants (Walter A et al., 1994). The wheat roots exhibited lower zinc concentrations in the control group compared to similar zinc-deficient conditions with a zinc concentration gradient of 0.5 mg/kg. This occurred because no organic acid was added to the control group. In contrast, in the experimental group, the complex formed by zinc and organic acid can promote zinc migration to the root surfaces, enhancing the zinc uptake in roots (Hu XY et al., 2002). Previous studies revealed that adding 2×10^{-3} mol/L of citric acid to soils could increase the mobility of Zn^{2+} by nearly 100-fold (Xu WH, 2005; Hodgson JF et al., 1967). This induces the conversion of solid zinc to soluble zinc complexes under the action of organic acid. The increased zinc concentration in soil solutions increases the zinc concentration gradient at the root-liquid interface, thus promoting zinc transport to roots.

In the later growth stages of wheat, the zinc redistribution within wheat leads to significantly decreased zinc concentrations in roots and stems and zinc accumulation in seeds under different zinc concentrations in soils. The zinc redistribution is closely associated with the zinc supply capacity of soils. Under zinc-deficient conditions, zinc preferentially accumulates in stem tips, juvenile leaves, and roots, with zinc absorbed by roots largely transported to leaves (Dang HK et al., 2010). In the mature stage, almost all zinc in leaves is transported to seeds (Palmgren MG et al., 2008; Fig. 5). Under a high zinc supply capacity (zinc concentration gradient: 6.0 mg/kg), the zinc concentrations in roots and stems increased, while the wheat seeds exhibited insignificant zinc accumulation. This suggests that the extra zinc in wheat was transported to roots and stems rather than seeds. As revealed by the mechanisms underlying zinc transport in various wheat organs throughout the growth process of wheat, the most significant factor restricting zinc concentrations in seeds is the roots' uptake and utilization efficiency of zinc in soils. The experimental results in this study indicate that under moderate zinc conditions (zinc concentration gradient: 1.0 mg/kg) in soils, the zinc concentration in wheat seeds was the lowest. This occurred because in an environment with low zinc concentrations, wheat roots secrete phytosiderophores of the MA family to enhance the availability of zinc in the rhizosphere. As a result, the zinc uptake capacity of roots is enhanced, and zinc is transported to seeds for storage via roots, stems, and leaves. In the case of sufficient zinc supply in soils, chelated zinc, which occurs stably in soils, helps enhance zinc utilization and uptake rates while maintaining zinc solubility. In this case, the zinc transport and accumulation capacities of wheat are also enhanced.

4.3. Zinc transport and accumulation patterns in wheat

The wheat exhibited average zinc transport coefficients of 1.18 and 3.63, respectively in the jointing and mature stages. Both transport coefficients exceeded 1, suggesting that wheat organs have high transport capacities for zinc in soils and that the transport capacities gradually increase with the growth of the wheat. The wheat exhibited the highest transport coefficient (exceeding 3.73) in zinc-deficient soils in the mature stage of wheat. In this stage, the enrichment coefficients of seeds all exceeded 1 under various zinc concentration gradients, except for 1.0 mg/kg, where the enrichment coefficient of seeds was 0.98. The results of zinc concentrations in wheat seeds under different zinc concentration gradients of soils reveal that the zinc concentrations in seeds decrease by 13.12% under moderate zinc conditions (zinc concentration gradient: 1.0 mg/kg) compared to the control group. In contrast, the zinc concentrations in seeds increase by 4.18%, 3.84%, 5.19%, and 12.55%, respectively, under soils with deficient, relatively

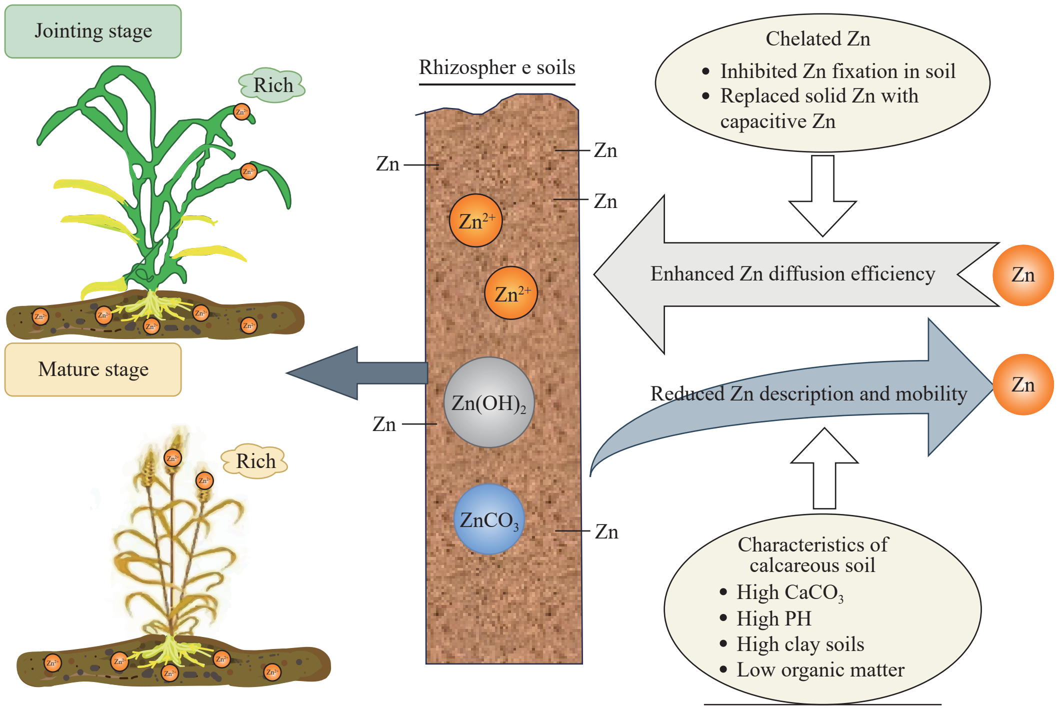

Fig. 5. Schematic diagram showing the mechanisms behind zinc transport in the calcareous soil-wheat system.

deficient, relatively abundant, and abundant zinc compared to the control group. These findings indicate that exogenous chelated zinc can somewhat improve zinc quality in wheat seeds. The experiments in this study provide a valuable reference for the application of chelated zinc fertilizers to plant roots. Given that the experiments utilized potentially zinc-deficient, calcareous soils in northern China—a type of strongly alkaline soils, it is necessary to determine the concentrations of zinc compensation solutions by investigating the zinc migration patterns in different types of soils.

Major wheat producing areas of China are primarily distributed in calcareous soil areas in northern China. However, calcareous soils, characterized by high pH, high calcium carbonate content, and low organic matter content, significantly reduce the number of bioavailable zinc in soils and impair the bioavailable zinc's capacity to migrate to wheat roots, ultimately restricting zinc uptake in wheat (Zhao AQ, 2015). Previous studies indicated that wheat seeds in China exhibit zinc concentrations ranging from 13.2 mg/kg to 84.9 mg/kg, with an average of 31.4 mg/kg. The wheat seeds from the Huanghuai wheat growing region display an average zinc concentrations of 30.6 mg/kg. In this region, the wheat seeds from Shandong and Henan provinces show average e zinc concentrations of 28.2 mg/kg and 33.8 mg/kg, respectively, while those from Hebei Province exhibit the lowest average e zinc concentration of 13.2 mg/kg (Chu HX et al., 2022). Some researchers found that in areas where soils exhibit high bioavailable zinc concentrations, wheat seeds also show high zinc concentrations, suggesting the zinc concentrations in seeds increase with the bioavailable zinc concentrations in soils (Murphy KM et al., 2008; Karami M et al., 2009). Furthermore, it has also been discovered that in areas where wheat seeds display high zinc concentrations, soils also manifest high bioavailable zinc concentrations (Oury FX et al., 2006; Karami M et al., 2009). Wheat, a major food and mineral source for Chinese residents, contributes 21.7% of their daily demand for zinc (Ma GS et al., 2008). Besides, the zinc concentration in wheat seeds is four times that in wheat flour (Liu DY et al., 2017). The World Health Organization (WHO) recommends a daily zinc intake of 12 mg to 16 mg for adults, while the U.S. Food and Nutrition Board recommends a zinc intake of 15 mg for adults (Ma YP et al, 2020). As published by the Chinese Nutrition Society in 2017, the appropriate daily zinc intake for male and female adults in China averages 10 mg (Chu HX et al., 2022). Insufficient zinc in wheat seeds is the main cause of hidden hunger for the partial population. Applying zinc fertilizers serves as a quick and effective approach to increase zinc concentrations in wheat seeds in the short term. Notably, the type and application method of zinc fertilizers influence plants' utilization efficiency of zinc. By observing the transport, conversion, uptake, and utilization of zinc fertilizers entering calcareous soils, this study explored the zinc diffusion patterns in zinc-deficient, calcareous soils. Accordingly, this study revealed the zinc supply capacity of soils and the mechanisms to enhance fertilizer efficiency in the major wheat producing areas in northern China. The results of this study hold critical scientific significance for enhancing the zinc supply capacity of soils, increasing the zinc concentrations in wheat seeds, and, accordingly, addressing zinc deficiency in the human body.

5. Conclusions

(i) In the jointing stage, the zinc absorbed by wheat roots from soils is transported to leaves via stems, with zinc concentrations in various wheat organs decreasing in the order of roots, stems, and leaves. In the mature stage, the zinc absorbed by roots and stems is largely transported to seeds, with zinc concentrations in various wheat organs decreasing in the order of seeds, roots, and stems. Overall, the zinc enrichment in various wheat organs decreases in the order of seeds, roots, stems, and leaves.

(ii) The analysis of the experimental results reveals the mechanisms behind zinc transport in wheat under different zinc concentrations of soils. Under the zinc-deficient conditions of soils, zinc deficiency stress and the action of organic acid jointly enhance the availability of zinc in the rhizosphere and the zinc uptake capacity of roots. In the case of sufficient zinc supply in soils, chelated zinc formed with citric acid as the chelating ligand occurs stably in soils, contributing to enhanced zinc utilization and uptake rates. In this case, the zinc transport and accumulation capacities of wheat are also enhanced.

(iii) The zinc concentration in wheat seeds can be somewhat enhanced by regulating the background value of bioavailable zinc concentration in soils. The experimental results of this study indicate that a moderate zinc concentration gradient (1.0 mg/kg) is unfavorable for zinc accumulation in wheat seeds, while a high zinc concentration gradient (6.0 mg/kg) corresponds to the highest degree of zinc enrichment in wheat seeds. The results of this study hold critical scientific significance for improving the zinc supply capacity of calcareous soils, increasing the zinc concentration in wheat seeds, and, accordingly, addressing zinc deficiency in the human body.

CRediT authorship contribution statement

Su-rong Zhang, Jun-quan Yang and Da-ming Wang conceived of the presented idea and developed the theory. Ji-hong Liu, Xue-sheng Gao and Jing Zhang carried out the experiment. Xiao-long Duan, Jian-hua Wang and Ling-zhi Yang verified the analytical methods. All authors discussed the results and contributed to the final manuscript.

Declaration of competing interest

The authors declare no conflicts of interest.

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