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Amelioration of chromium toxicity in wheat plants through exogenous application of nano silicon

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ABSTRACT

Chromium (Cr) contamination in agricultural soils poses a risk to crop productivity and quality. Emerging nano-enabled strategies show great promise in remediating soils contaminated with heavy metals and enhancing crop production. The present study was aimed to investigate the efficacy of nano silicon (nSi) in promoting wheat growth and mitigating adverse effects of Cr-induced toxicity. Wheat seedlings exposed to Cr ($K_2Cr_2O_7$) at a concentration of 100 mg kg^{-1} showed significant reductions in plant height (29.56%), fresh weight (35.60%), and dry weight (38.92%) along with enhanced Cr accumulation in roots and shoots as compared to the control plants. However, the application of nSi at a concentration of 150 mg kg^{-1} showcased substantial mitigation of Cr toxicity, leading to a decrease in Cr accumulation by 27.30% in roots and 35.46% in shoots of wheat seedlings. Moreover, nSi exhibited the capability to scavenge oxidative stressors, such as hydrogen peroxide (H_2O_2), and malondialdehyde (MDA) and electrolyte leakage, while significantly enhancing gas exchange parameters, total chlorophyll content, and antioxidant activities (enzymatic and nonenzymatic) in plants grown in Cr-contaminated soil. This study further found that the reduced Cr uptake by nSi application was due to down-regulating the expression of HMs transporter genes (*TaHMA2* and *TaHMA3*), alongwith upregulating the expression of antioxidant-responsive genes (*TaSOD* and *TaSOD*). The findings of this investigation highlight the remarkable potential of nSi in ameliorating Cr toxicity. This enhanced efficacy could be ascribed to the distinctive size and structure of nSi, which augment its ability to counteract Cr stress. Thus, the application of nSi could serve as a viable solution for production of crops in metal contaminated soils, offering an effective alternative to time-consuming and costly remediation techniques.

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1. Introduction

The occurrence of heavy metals (HMs) in agricultural soils is a major environmental concern due to their negative impacts on living organisms and overall ecosystems (Zulfiqar and Ashraf, 2022). Human based activities, particularly industrial operations, inappropriate waste disposal, and mining cause the accumulation of several HMs like cadmium (Cd), arsenic (As), lead (Pb), nickel (Ni), mercury (Hg), and chromium (Cr) in soils (Noor et al., 2024). These hazardous HMs may persist for long stretches of time, degenerating soil fertility and quality, reducing plant growth and crop yield, and disrupting the long-term sustainability of farming operations. (Khan et al., 2022; Wei et al., 2023). Among the HMs, Cr has emerged as a significant pollutant due to its widespread utilization in many industries. Cr exists in various oxidation forms in nature, with Cr^{III} (trivalent) and Cr^{VI} (hexavalent) being the most stable (Liu et al., 2024). The elevated level of Cr in plant tissues could significantly hinder the growth and development of plants, leading to visible symptoms including necrosis, chlorosis, tissue death, wilting, and bending (Ahammed et al., 2023). In addition, it is well-established that Cr stress causes a decrease in plant chlorophyll pigment levels, disrupts photosynthesis, and impairs biomass formation (Ayyaz et al., 2021; Sun et al., 2023). Furthermore, it exacerbates oxidative stress by stimulating the overproduction of reactive oxygen species (ROS) in plant cells. The Cr-induced oxidative stress has damaging impacts on the plant tissues and cellular structures which influence the cell integrity and overall metabolic pathways (Abeed et al., 2023a, 2023b; Singh and Dhal, 2023). Consequently, research into alleviating Cr toxicity continues to be a focal point, which will facilitate the development of effective strategies to mitigate its harmful effects on plants, particularly in cereal crops (Jalil et al., 2023).

Nanotechnology is establishing itself as an exciting innovation with the potential to profoundly transform many fields, especially agriculture (Moreno et al., 2024; Singh et al., 2024). Nanoparticles (NPs) exhibit unique properties, and applications NPs has been shown to enhance plant growth, facilitate mineral absorption, and increase plant resilience to environmental stressors, such as HMs exposure, high temperatures, water scarcity, and salinity (Bhattacharjee et al., 2022; Feng et al., 2022; Gauba et al., 2023). Mukhopadhyay et al. (2022) conducted a study unveiling the potential of using NPs to mitigate HMs contamination in soils. The addition of ZnONPs enhanced rice plants to activate their antioxidant defense system and mitigate oxidative stress in the presence of Cr stress (Prakash et al., 2022). In their study, Noman et al. (2020) observed enhancements in the average growth rate and enzyme activities of wheat plants when Cu-NPs were added in treatments with Cr-induced stress. The study conducted by Kumar et al. (2023) found that TiO_2-NPs had a considerable positive impact on plant development by effectively reducing Cr accumulation in sunflower plants. Likewise, nano silicon (nSi) supplementation significantly decrease the movement of Cd from roots to shoots and ameliorated the Cd toxicity through scavenging ROS in rice and maize (Jalil et al., 2023a; Yasin et al., 2024). Furthermore, a number of experiments have shown that NPs have the ability to control plant molecular pathways by altering gene expression in response to HMs stress. Youssef et al. (2020) examined the effects of hematite nanoparticles on maize plants and found that they can enhance the activation of important genes that play a role in protecting cells against Cd toxicity. Furthermore, nSi enhances the antioxidant enzyme activity and modulates the expression of associated genes, thereby promoting plant development and improving stress tolerance of tomato plants (Wang et al., 2022). Moreover, nSi have shown their ability to improve plant development in the presence of different environmental challenges (Yuvaraj et al., 2023). Therefore, nSi have garnered significant interest in the scientific community for its potential as an effective and affordable solutions for mitigating the harmful effects of HMs on plants.

Wheat, (*Triticum aestivum* L.), is a vital cereal crop that serves as a primary food supply for almost half of the global population. It is highly valued for its abundant minerals, protein, vitamins, and carbohydrates (Bobade et al., 2024). The productivity of wheat is jeopardized by many abiotic and biotic stresses (ul Aibdin et al., 2023). Soil contamination caused by toxic HMs is a significant abiotic stress factor that leads to substantial reductions in wheat productivity (Zhang et al., 2024). Given the robust characteristics and great ameliorative ability of nSi against a variety of abiotic stressors, it is critical to investigate the underlying mechanisms by which nSi exposure alleviates Cr toxicity in wheat plants.

The objectives of this study were to evaluate the effects of Cr stress on plant biomass accumulation, and Cr uptake by roots and translocation from roots to shoots; assess the comparative influence of nSi on photosynthetic pigments, leaf gas exchange parameters, and the quantum yield of PSII under Cr stress; and analyze the underlying mechanisms involved in the modification of ROS homeostasis, antioxidant activity, and defense-related gene expression through foliar application of nSi concerning Cr toxicity. It was anticipated that this study could open avenues for further extensive research into the practical use of nSi to enhance crop productivity in conditions marked by a variety of abiotic stresses, particularly HMs. Moreover, assessing the impacts of NPs on wheat under Cr stress will provide new insights into the application of nanotechnology in metal contaminated soils.

2. Material and methods

2.1. Characterization of nSi

The nSi samples were purchased from Xuzhou Jiechuang, New Material Technology Co. (Guangzhou, Guangdong, China). They were kept in a sealed container at room temperature until they were used. The dimensions, structural integrity, chemical composition, and external appearance of nSi were evaluated using transmission electron microscopy (TEM; JEM-1230, JEOL, Akishima, Japan) and scanning electron microscopy (SEM; TM-1000, Hitachi, Japan). The preparation of TEM and SEM samples followed the methodology described by Ahmed et al. (2021), using an aluminum stub and a Cu grid covered with carbon. Furthermore, the SEM was combined with energy-dispersive X-ray (EDX) elemental composition analysis.

2.2. Experimental design and growth conditions

Seeds of wheat 'Yangmai-20' were collected from College of Agriculture and Biotechnology at Zhejiang University, Hangzhou, China. The seeds were subjected to surface disinfection by soaking them in a solution of 1% NaClO for 15 min and washed with deionized water for multiple times. Soil samples were collected from the research field area of the mentioned institute. It consisted of sandy clay loam and was taken at a depth of 0–15 cm. The soil was desiccated at ambient temperature and sieved through a 0.2 cm mesh. Subsequently, it was meticulously blended and characterized (Table 1). Following thorough mixing, every pot was filled with 500 g of soil and allowed to sit for 30 days to facilitate

Table 1
Properties of soil used for the pot experiment.

Physicochemical properties	
Texture	Sandy clay loam
Sand (%)	34
Silt (%)	17
Clay (%)	49
Organic matter (%)	0.29
Total Nitrogen N (%)	0.061
Available P (mg kg^{-1})	3.57
Available k (mg kg^{-1})	142
Field Capacity (%)	11.9
EC_e (dS m^{-1})	1.92
pH	8.38

metal stabilization. Initially, 10 seeds were sown per pot. After 15 days of germination, seedlings were reduced to five per pot and irrigated with a solution containing 2190 mg L^{-1} of N as $(NH_2)_2CO$, 500 mg L^{-1} of P as $(NH_4)_2HPO_4$, and 2140 mg L^{-1} of K as K_2SO_4 at 0.5 L per pot. After 21 days of growth, the seedlings were treated with potassium dichromate ($K_2Cr_2O_7$) at a concentration of 100 mg kg^{-1} and silicon oxide nanoparticles (nSi) at a concentration of 150 mg kg^{-1}, both alone and in combination (Cr + nSi), thus a total of four treatments (CK; Cr; nSi; and Cr + nSi). The pot without any treatment of Cr and nSi kept as control (CK).

The plants were watered in alternating cycles with H_2O and an improved Hoagland solution that included the following macro elements: 0.09 M of $MgSO_4$, 0.2 M of $Ca(NO_3)_2$, 0.4 M of KH_2PO_4, 0.3 of M KNO_3, 0.01 of M $FeSO_4$, 1.4 mM of $ZnSO_4$, 0.4 mM of $CuSO_4$, 10 mM of H_2MoO_4, and 0.5 mM of H_3BO_3 as needed (Ali et al., 2015). The experiment was arranged as a completely randomized design with three replications. The growth conditions included an 8-h dark period (night) followed by a 16-h light period (daytime) under a temperature of 22 °C in the dark and 25 °C under light. The relative humidity was maintained at 70%.

2.3. Chlorophyll contents, gas exchange parameters and fluorescence

To estimate chlorophyll and carotenoid contents, leaves of plants grown in different treatments were collected and rinsed for multiple times with distilled water. Afterwards, 100 mg of samples from each treatment were ground in the absence of light. The ground samples were placed into 10 mL tubes containing a buffer solution (1:1 vol ratio of ethanol and acetone). The tubes were incubated in the dark for a period of 3–5 h. Subsequently, the samples were centrifugated at a speed of 3000×*g* for 10 min. The absorbance of supernatants were measured by a spectrophotometer (SpectraMax 190) at 663 nm for chlorophyll *a*, 645 nm for chlorophyll *b*, and 470 nm for carotenoids (Armon, 1949).

The leaf greenness of plants grown in different treatments were determined using the portable SPAD meter (SPAD, Tokyo, Japan). The SPAD meter measured the difference between the transmittance of a red (650 nm) and an infrared (940 nm) light through the leaf, generating a three-digit SPAD value.

The leaf chlorophyll fluorescence (Fv/Fm) was measured using a portable fluorimeter OS-30p+ (Hudson, USA). Prior to fluorescence observations, fresh leaf samples were subjected to a 30-min darkness treatment, following the protocol outlined by Cai et al. (2019). The quantum efficacy of photosystem II, represented by the equation Fv/m = (Fm - Fo)/Fm, was determined using a solid-state light source with a wavelength of 660 nm and an intensity of 1100 μmol m^{-2} s^{-1}.

The net photosynthetic rate (*Pn*) and transpiration rate (*E*) of four individual plants in each treatment group were quantified using the LI-COR gas-exchange system (LI-6400, LI-COR Biosciences, Lincoln, NE, USA) equipped with red/blue LED light source in the leaf compartment. The measurements took place from 11:30 a.m. to 13:30 p.m. on sunny days with a bright sky.

2.4. Measurement of electrolyte leakage and proline contents

The method reported by Dionisio-Sese and Tobita (1998) was used to assess the stress-associated electrolyte leakage (EL). Recent fully expanded leaves were sliced into small pieces (about 5 mm in length) and placed in tubes containing 8 mL of deionized water. The tubes were incubated in a water bath for 2 h, and then the first electrical conductivity (EC1) was measured. The samples were autoclaved at a temperature of 121 °C for 20 min and cooled to a temperature of 25 °C prior to the measurement of the final electrical conductivity (EC2). The calculation of EL was performed using the following formula: EL = (EC1/EC2) x 100.

For the determination of proline, 100 mg fresh leaves were thoroughly mixed with 5 mL of 3% sulphosalicylic acid until fully homogenized. The mixture was subjected to centrifugation at 10,000×*g* for 15 min. Then 1 mL of the mixture was transferred into a tube containing 1 mL of acidic ninhydrin and 1 mL of glacial acetic acid. The resulting mixture was first incubated at 100 °C for 10 min, followed by cooling in an ice bath. The mixture was extracted using 4 mL of toluene. The tubes were vigorously mixed for 20 s and then cooled. Subsequently, the absorption was quantified at 520 nm using a UV–VIS spectrophotometer (Hitachi U-2910, Tokyo, Japan). The proline concentrations were determined using a standard curve and calculated on fresh weight basis as μmol g^{-1} FW (Bates et al., 1973).

2.5. Determination of malondialdehyde, hydrogen peroxide, and in-vitro visualization

The MDA (Malondialdehyde) values were determined using the method of Heath and Packer (1968). The samples were ground in a solution containing 0.5% TBA (thiobarbituric acid) and 20% TCA (trichloroacetic acid). After boiling it at 100 °C for 30 min. The reaction was stopped by putting the reaction solution on ice. The absorbance of was measured at 532 nm.

The hydrogen peroxide (H_2O_2) levels in recently expanded leave were quantified using the method described by Jana and Choudhuri (1982). The samples were homogenized using a phosphate buffer and then subjected to centrifugation at 13,000×*g*, as described by Jun et al. (2000). The liquid portion was combined with a solution containing (0.1% TCA (trichloroacetic acid) and 20% H_2SO_4. The absorbance was determined using a spectrophotometer at t410 nm.

In order to ascertain the localization of H_2O_2, the samples were subjected to incubation in a solution of H2DCFDA (dichlorodihydrofluorescein diacetate) at 37 °C for 30 min. Following incubation, the samples underwent three rounds of washing using phosphate buffer solution (PBS). In addition, the samples were imaged using a confocal laser scanning microscope (Olympus FV3000, Japan) at an excitation wavelength of 488 nm and an emission wavelength of 530 nm.

2.6. Determination of antioxidant defense assay

Leaf samples were pulverized using a pestle and mortar in a phosphate buffer solution (pH 7.8, 0.01M) and centrifuged at 13,000×*g* for 10 min. After centrifugation, the supernatant was examined for the presence of antioxidant enzymes using the method outlined below.

The activity of superoxide dismutase (SOD) was measured in a reaction solution containing 20 μM of riboflavin, 130 mM of methionine, 75 μM of NBT, 100 μM of EDTA-NA2, and enzyme extract. The absorbance was measured at 560 nm based on the method described by Zhang et al. (2008). The activity of peroxidase (POD) was assessed using the method described by Chance and Maehly (1955). The reaction mixture contained 25 μL enzyme extract was mixed with 1% guaiacol (v/v) and 10 mM H_2O_2 in 50 mM Tris buffer (pH 7.0) for a final volume of 750 μL. Variations in absorption associated with guaiacol oxidation (ε = 25.5 mM−1 cm−1) were measured at 470 nm.

The method given by Schaedle and Bassham (1977) was utilized to estimate glutathione reductase (GR) activity. One unit of GR activity was defined as 1 nmol of NADPH oxidized to NADP + per minute at 37 °C. The activity of ascorbate peroxidase (APX) was determined by detecting the oxidation of ascorbic acid in the presence of H_2O_2 (Nakano and Asada, 1981). A reduction in the absorbance was detected at a wavelength of 290 nm for 3 min after introducing 0.1 mM H_2O_2 to a reaction solution. The reaction solution had a final volume of 3 mL and consisted of 0.15 mL enzyme extract, 50 mM phosphate buffer with a pH of 7.0, and 0.5 mM ascorbate. To determine the contents of ascorbic acid (AsA) and reduced glutathione (GSH), the methods described by Huang et al. (2005) and Yu et al. (2003) were used, respectively.

2.7. qRT-PCR analysis of relative expression of selected genes

The root samples of wheat seedlings from each treatment were collected and frozen in liquid nitrogen, and RNA was extracted using Takara RNA extraction kit (Takara, Dalian, China). After quantifying RNA using nanodrop, and their purity was determined by gel electrophoresis with 1% agarose gel. The complementary DNA (cDNA) was generated using the Script RT reagent Kit (Takara, Dalian, China). To quantify the relative expression of genes related to Cr uptake (*TaHMA2*, and *TaHMA3*) and those encoding SOD and POD, qRT-PCR was performed using the Fast SYBR green master mix (Takara, Dalian, China) in a Light Cycler® 96 Real-Time PCR System. The primers for the mentioned genes are listed in Table 2, and *TaActin* was used as an internal control. The relative expression levels of the genes were normalized and calibrated according to the $2^{-\Delta\Delta CT}$ method (Livak and Schmittgen, 2001).

2.8. Measurement of morphological parameters

At the end of the experiment, the whole wheat plants, including both the roots and shoots, were harvested and washed with distilled water to remove soil particles. A portion of these samples were immediately preserved at a temperature of −80 °C for future investigation of molecular and physiological characteristics. The washed seedlings were briefly dried in the air and blotted on paper towels, and fresh weights were recorded. Plant lengths were measured using a calibrated scale. Both roots and shoots were subjected to oven-drying at a temperature of 70 °C for a duration of 48 h in order to ascertain their dry weight.

2.9. Determination of Cr level in plant tissues and translocation factor

Dried shoots and roots, 500 mg each, were subjected to digestion for 1 h in a solution of HNO_3 at 120 °C, followed by 6 h digestion at 140 °C in a dry thermos unit (Taitec in Tokyo, Japan). The digested samples were diluted in deionized water and measured for Cr contents using ICP-MS (inductively coupled plasma mass spectrometry) (Thermo scientific, Waltham, MA, USA). The analysis was conducted employing reference standards provided by GuoBiao Co. (Beijing, China). The translocation factor (TF) was determined by dividing the shoot Cr contents by the root Cr contents.

2.10. Statistical analysis

Data were subjected to statistical analysis by one-way ANOVA using the Statistix programme, version 8.0. (Tallahassee, FL USA). If significance occurred, mean values were separated by Fisher's Least Significant Difference (LSD) at $P < 0.05$ level. The results were presented as mean values ± standard error (n = 3).

Table 2
List of primers used for analysis of the expression of the following five genes in wheat plants.

Gene	Primer	Primer sequence
TaActin	Forward	TGCCCATTTACGAAGGATA
	Reverse	AAGACTCCATGCCGATCAT
TaHMA2	Forward	GCTTATGTGCAAAGCAAT
	Reverse	GGTCAACACCATTACTC
TaHMA3	Forward	TGGTTGGACACAAGGTTCA
	Reverse	ATTGGGTGGCTAGATTTG
TaSOD	Forward	CGAGGTCTGGAACCATCA
	Reverse	CCGAAATCCTTCTCGATC
TaPOD	Forward	TGGGCATGGGGCTTCTG
	Reverse	AGGAATGGGGGGTTGAT

3. Results

3.1. nSi – characterization

The nSi was analyzed using TEM (Fig. 1A) and SEM (Fig. 1B), which showed that the particles were generally spherical ranging from 11 to 23 nm. The dispersion of nSi particles were inadequate, and they had a tendency to form clusters. The energy-dispersive X-ray spectroscopy (EDS) examination determined the elemental composition of nSi. The analysis showed that oxygen (O) was the most abundant element, making up 59.23% of the composition. Silicon (Si) accounted for 40.70%, while phosphorus (P) made up just 0.07%, and potassium (K) and iron (Fe) were negligible (Fig. 1C).

3.2. nSi promoted plant growth

The plants grown in Cr-contaminated soil showed a 29.56% reduction in plant length (height) as compared to those grown in uncontaminated soil (Fig. 2A). The addition of nSi to the Cr stressed plants resulted in a 12.31% increase in plant height, while the addition of nSi to the control plants led to an 18.07% increase in plant height. The Cr stressed plant's fresh and dry weight decreased by 35.60% and 38.92% respectively (Fig. 2B–C). However, when nSi was applied, the plant fresh and dry weights significantly increased by 21.72% and 24.91%, respectively under Cr stress, and by 40.15% and 44.19%, respectively under control conditions.

3.3. nSi enhanced photosynthetic parameters

The plants subjected to Cr-stress exhibited a substantial reduction in total chlorophyll contents and carotenoids, with decreases of 41.68% and 56.17% respectively, as compared to the control plants. The application of nSi resulted in a considerable increase in the total chlorophyll contents by 20.20% and carotenoids by 27.05% compared to control plants (Fig. 2F and I). However, the nSi supplementation substantially alleviated the adverse impacts of Cr stress, leading to a notable increase in chlorophyll and carotenoid levels by 24.38% and 15.22%, respectively, compared to respective control treatment.

In the same manner, the application of nSi greatly enhanced the photochemical efficiency (Fv/m), SPAD value, and Pn values by 9.89%, 13.63%, and 27.90% respectively, compared to the control plants. However, there was no significant change in the E value, which only revealed a 3.73% difference. Cr-stressed plants exhibited a significant decrease in Fv/m, SPAD, Pn, and E values by 25.61%, 34.37%, 37.94%, and 55.09% respectively in plants compared to the control plants (Fig. 4c and d). In contrast, nSi counteract the harmful effects of Cr on plants exposed to Cr-stress, hence improving the Fv/m, SPAD, Pn, and E values by 14.08%, 23.45%, 28.97% and 44.95% respectively (Fig. 2D, E, G, and H).

3.4. nSi reduced Cr uptake and translocation

This study revealed that the presence of nSi considerably decreased the absorption of Cr in wheat plant tissues. The plants cultivated in soil treated only with Cr had the highest levels of Cr accumulation in both root and shoot tissues compared to all other treatments (Fig. 3A and B). However, the application of nSi led to a substantial decrease in the level of Cr in both roots and shoots of the plants grown in the Cr treated soil, resulting in reductions of 27.30% and 35.46% respectively (Fig. 3A and B). The plants treated with nSi exhibited a 14.64% reduction in the translocation of Cr from the roots to the shoots when exposed to Cr stress, as compared to the respective control plants (Fig. 3C).

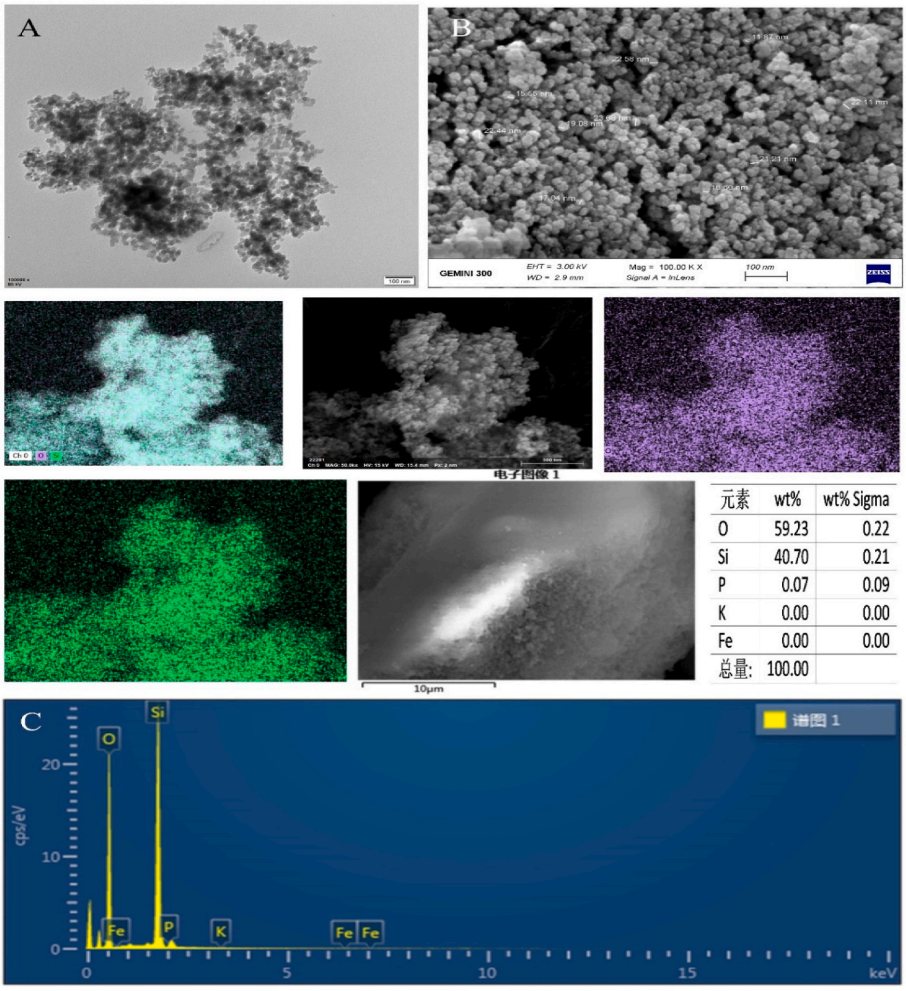

Fig. 1. Characterization of nSi by (A) TEM, (B) SEM, and (C) EDS analysis.

3.5. nSi impacted electrolyte leakage, proline contents and oxidative stress

Cr-stressed plants had a substantial rise in EL value by 55.97% and proline contents by 60.25% in comparison to the control plants. The application of nSi resulted in a considerable decrease in both EL value and proline contents, with reductions of 26.65% and 16.02% respectively, as compared to plants subjected to Cr stress. (Fig. 3D and E).

In order to assess the ability of nSi to mitigate oxidative damage, we measured the levels of H_2O_2 and MDA, which are recognized as important indicators of oxidative stress (Fig. 3F and G). Plants treated with nSi showed a significant decrease in H_2O_2 and MDA contents, with reductions of 16.99% and 21.10% respectively, compared to the control plants. Furthermore, the levels of H_2O_2 and MDA contents in the plants treated with Cr increased by 57.21% and 56.30%, respectively, compared to the control plants (Fig. 3F and G). On the other hand, the addition of nSi mitigated the oxidative stress in wheat tissues by decreasing the buildup of H_2O_2 production by 24.26% and MDA contents by 21.42% in comparison to the plants grown in Cr-contaminated soil. In order to provide further evidence in reduction of oxidative stress, we examined the concentration of H_2O_2 production inside the cells through staining the leaf tissues with H2DCFDA. The cytological findings demonstrated that Cr triggered a higher buildup of H_2O_2 (Fig. 3H). However, a lower level of H_2O_2 accumulation was observed in the leaves of wheat plants treated with nSi under Cr stress as compared with respective control.

3.6. nSi strengthen antioxidant defense system

The results of our study depicted that application of nSi significantly scavenged oxidative stress through stimulating the activities of antioxidant enzymes (SOD, POD, APX, GR) as well as non-enzymatic antioxidants (AsA and GSH) when plants were grown in Cr-contaminated soil (Fig. 4). The plants cultivated under Cr stress significantly elevated the levels of SOD, POD, APX, GR, AsA, and GSH by 23.62%, 23.02%, 36.47%, 29.35%, 21.13%, and 40.41% respectively, as compared to the plants grown in uncontaminated soil. However, the nSi treatment significantly increased the SOD, POD, APX, GR, AsA, and GSH activities by 25.15%, 18.72%, 38.10%, 23.45%, 20.12%, and 38.89% respectively, as compared to the respective control plants under Cr stress conditions (Fig. 4A–F).

3.7. nSi altered the expression level of transporter and antioxidant responsive genes

The nSi application to plants grown under Cr-contaminated soil significantly enhanced the expression level of antioxidant-responsive (*TaSOD* and *TaPOD*) genes, whereas reduced the expression level of metal transporter (*TaHMA2* and *TaHMA3*) genes in wheat plants compared to respective control plants (Fig. 5). Our results showed that nSi supplementation significantly influenced the expression patterns of metal transporter genes in wheat plants when exposed to Cr, resulting in a decrease in the uptake of Cr to the plant tissues. Furthermore, nSi also governed the plant's antioxidative defense mechanism by stimulating

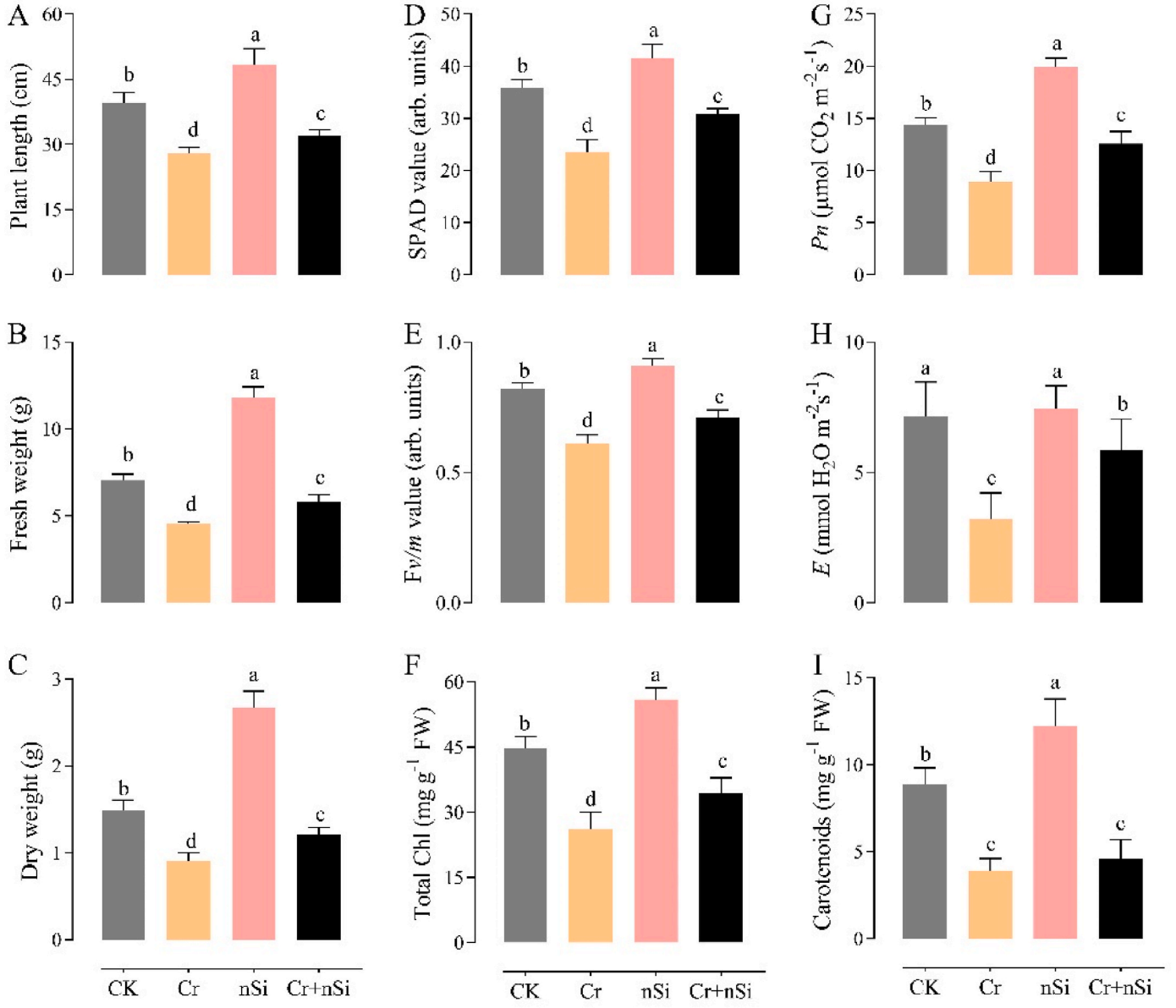

Fig. 2. Effects of nSi application on growth and photosynthetic parameters as well as chlorophyl and carotenoid contents of wheat plants grown under different treatments (CK as the control, Cr stress, nSi application, and application of both Cr and nSi). (A) Plant height, (B) fresh weight, (C) dry weight; (D) SPAD value, (E) Fv/m value, (F) total chlorophyll, (G) net photosynthetic rate, (H) transpiration rate, and (I) carotenoid contents. Each bar represents the mean of three replicates (n = 3) ± SD. Different lowercase letters on bars represent significant difference at $P \leq 0.05$ level.

antioxidant defense-responsive genes to counteract the damaging effects of Cr toxicity.

4. Discussion

The global prevalence of HM pollution in agricultural soils has emerged as a significant environmental concern (Edo et al., 2024). Elevated levels of HMs have a substantial negative impact on crop productivity and agricultural output (Akbar et al., 2024). As a result, there has been ongoing effort on the development of innovative agrochemicals to minimize detrimental effects of HMs on crop plants. Nanomaterials represent one of such chemicals (Kopittke et al., 2019; Guleria et al., 2023). Nanotechnology has revolutionized precision farming by facilitating optimal utilization of resources, reducing costs, and minimizing environmental consequences (Zain et al., 2023). Nanoparticles (NPs) may indirectly or directly interact with plants, leading to increased enzymes activity, enhanced photosynthesis, and improved quality of crops (Mukarram et al., 2022). However, the ability of nSi to mitigate the detrimental impacts of Cr on plants, including the oxidative stress and structural damage caused by Cr, remain poorly understood.

The present study shows that the application of nSi significantly mitigated Cr toxicity and sustained wheat seedling growth (Fig. 2). The mitigation effects include the protection of plant photosynthesis system, reduction in Cr uptake, activation of antioxidant enzymes, and regulation of the expression of genes involved in antioxidant defense and metal uptake. Our study depicted that Cr stress had a negative impact on the total chlorophyll contents, carotenoids, and the photochemical efficiency (Fv/m) of photosystem II (PSII), leading to biomass reduction in wheat plants. Conversely, the use of nSi led to a significant increase in the total chlorophyll contents and carotenoids, SPAD value, and Fv/m value up to 55%, particularly under Cr stress (Fig. 2). These elevations enables plants to sustain photosynthesis, thus, improving plant growth. Our results agree with the findings of previous reports that nSi enhanced

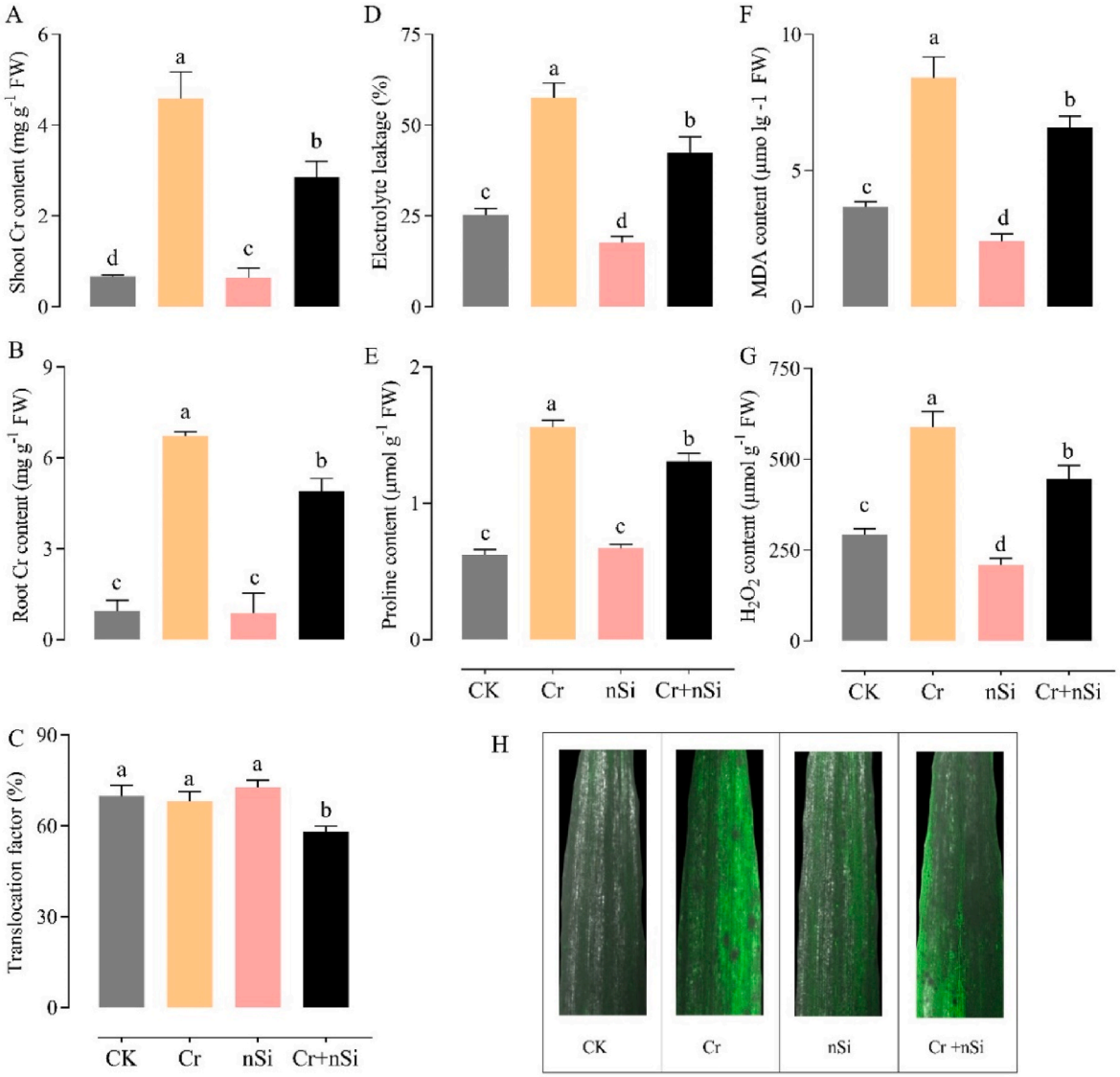

Fig. 3. Effects of nSi on Cr uptake and oxidative stress of wheat plants grown under different treatments (CK as the control, Cr stress, nSi application, and application of both Cr and nSi). (A) shoot Cr content, (B) root Cr content, (C) translocation factor, (D) electrolyte leakage, (E) proline contents, (F) MDA contents, (G) hydrogen peroxide, and (H) H2DFCA staining in wheat leaves. Each bar represents the mean of three replicates (n = 3) ± SD. Different lowercase letters on bars represent significant differences at $P \leq 0.05$ level.

photosynthesis and increase chlorophyll contents in wheat and rice plants under Cd-induced stress (Ali et al. (2019; Jalil et al., 2023b). Riaz et al. (2022) also discovered that the addition of nSi had a significant improvement in the leaf photosynthesis rate (*Pn*), transpiration rate (*Tr*), and stomatal conductance *(Gs*) of plants under combined Cu + nano Si treatment, in comparison to those plants grown under Cu treatment alone. Moreover, silicon has an active role in enhancing the light utilization efficiency of plants (Souri et al., 2021), which could contribute to the significant increase in chlorophyll contents in wheat. Thus, application of nanoparticles, such as nSi, may represent a viable approach for alleviating metal toxicity in plants and also for remediation of soils contaminated with HMs.

The application of nSi resulted in a considerable reduction in Cr uptake and translocation from the roots to the shoots. The exact mechanism underlying the reduction of Cr uptake is unclear at this time. One possibility could be the nSi induced downregulation of metal transporter-related genes as discussed below. Another possibility could be due to the binding or adsorption of Cr to nSi. Cr^{VI} can be adsorbed by Si through hydrogen bond, hydrophobic interaction, electrostatic interaction, and ligand and ion exchange (Jain et al., 2018; Liu et al., 2019). Mehmood et al. (2022) reported that green synthesized nSi effectively adsorbed Cr^{VI} through different functional groups, such as (-COOH and -OH) and significantly removed Cr from aqueous solutions. The adsorption of Cr to Si would decrease the bioavailability of Cr in soil, thus reducing plant uptake and translocation of Cr. Nanoparticles in reduction of plant uptake of HMs have also been reported by others. Mohammadi et al. (2020) found that FeONPs significantly reduced the accumulation of Cr and its translocation from roots to shoots in sunflower plants. Noman et al. (2020) observed a reduction in accumulation of Cu within wheat plants when exposed to CuNPs.

The current investigation also showed that nSi application scavenged oxidative stress. Wheat seedlings grown under Cr stress increased the production of MDA and H_2O_2 (Fig. 3). It is known that HMs can cause lipid peroxidation, leading to an increase in MDA content and oxidative damage, which, in turn, causes an upsurge of oxidative stress (ROS including O^{-2}, H_2O_2, and OH^- radicals) (Singh and Dhal, 2023). Subsequently, ROS could damage organelles and cell structures and functions (Mansoor et al., 2023). In this study, exogenous application of nSi

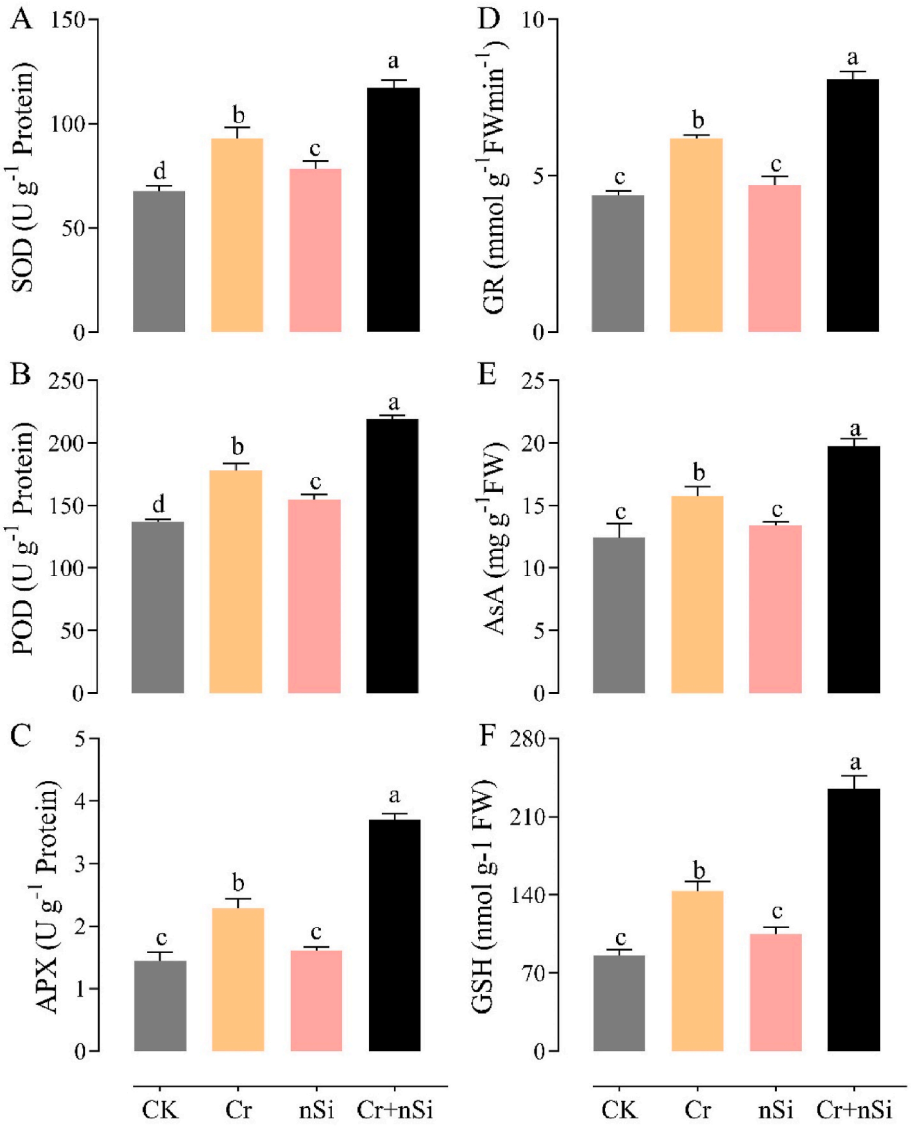

Fig. 4. Effects of nSi application on the activities or levels of enzymatic and nonenzymatic antioxidants in wheat plants grown under different treatments (CK as the control, Cr stress, nSi application, and application of both Cr and nSi). (A) SOD, (B) POD, (C) APX, (D) GR, (E) AsA, and (F) GSH. Each bar represents the mean of three replicates (n = 3) ± SD. Different lowercase letters on bars represent significant differences at $P \leq 0.05$ level.

increased the activities of SOD, POD, and APX as well as the content of GR, AsA, and GSH, which could significantly scavenge oxidative damage to wheat plants (Fig. 4). These results agree with the report of Alam et al. (2022), nSi reduced the toxic effects of metals by diminishing lipid peroxidation, as demonstrated by a reduction in MDA contents (Fig. 3F). Similarly, nSi enhanced the performance of antioxidative enzymes, leading to a decrease in lipid peroxidation and alleviating the harmful impacts of HMs toxicity, such as Cd (Hussain et al., 2019). The application of nSi to wheat plants under Cu-induced stress resulted in enhanced activity of antioxidants and protein synthesis (Riaz et al., 2022). Tripathi et al. (2016) discovered a substantial increase in the activities of several antioxidant enzymes, including SOD, APX, and GR, in maize tissues treated with nSi when exposed to arsenic-induced stress. Consistent with our research, Adrees et al. (2022) proposed that the utilization of nSi enhanced the development of plants and reduced oxidative stress in wheat by controlling the antioxidative defense mechanism and limiting the Cr uptake.

The application of nSi induced the expression of genes related to Cr uptake and antioxidant enzymes. The ability of nSi to influence gene expression has been reported by Prajapati et al. (2023). The results of our study also depicted that nSi supplementation to plants grown under Cr-contaminated soil significantly enhanced the expression level of antioxidant-responsive genes (*TaSOD* and *TaPOD*), whereas reduced the expression level of metal transporter genes (*TaHMA2* and *TaHMA3*) in wheat plants compared to respective control plants (Fig. 5). The reduced expression of *TaHMA2* and *TaHMA3* coincides with the reduced uptake of Cr in plants (Fig. 3), and the increased expression of *TaSOD* and *TaPOD* concurs with the increased activities of antioxidant enzymes (Fig. 4), thus contributing to the mitigation of Cr toxicity in wheat plants. Other reports also showed that nSi could enhance the development of soybeans by effectively reducing absorption of mercury and stimulating the activity of antioxidant enzymes and transcription factors, including *MYC, ZIP* and *WRKY* genes (Li et al., 2020; Nie et al., 2021). Nevertheless, this study demonstrated how nSi mitigates metal stress by activating antioxidant enzymes and limiting Cr uptake and translocation, thus minimizing detrimental effects on photosynthesis. However, there are still important gaps remaining, such as how nSi affects these processes at molecular levels, and how to manipulate plants for better adaptation to metal stresses using appropriate nanoparticles. Additionally, field trials are required to examine the extended

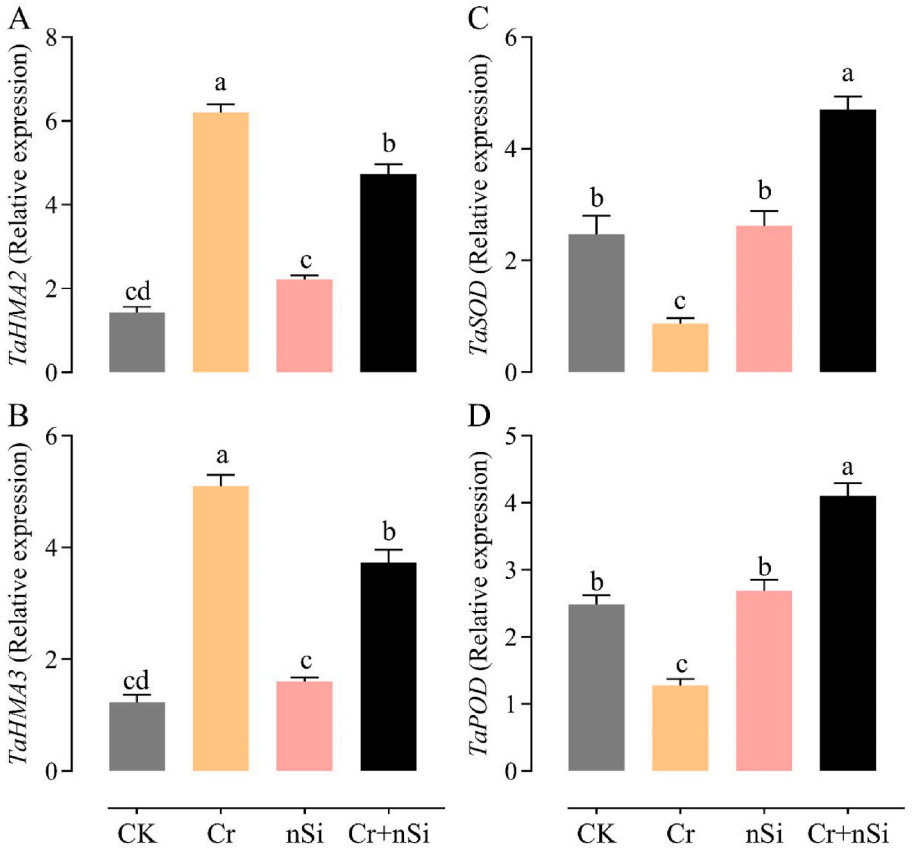

Fig. 5. The relative expression of (A) *TaHMA2*, (B) *TaHMA3*, (C) *TaSOD*, and (D) *TaPOD* genes in wheat plants grown under different treatments (CK as the control, Cr stress, nSi application, and application of both Cr and nSi). Each bar represents the mean of three replicates (n = 3) ± SD. Different lowercase letters on the bars represent significant differences at $P \leq 0.05$ level.

effectiveness and ecological durability of NPs amendments in HMs contaminated soils.

5. Conclusion

This study investigated the effects of nSi on mitigating Cr toxic effects in wheat plants at seedling stage when grown in Cr-contaminated soil. Results showed that wheat plants exposed to Cr toxicity reduced plant height and biomass, chlorophyll content, gas exchange attributes, carotenoids, and increased reactive oxygen species. The exogenous application of nSi significantly decreased Cr uptake and translocation during plant growth by reduced expression of Cr transporter genes (*TaHMA2* and *TaHMA3*) in wheat seedlings. Meanwhile, genes encoding to SOD and POD (*TaSOD* and *TaPOD*) were upregulated, and antioxidant enzyme activities (SOD, POD and APX) increased, suggesting the roles of nSi in mitigation of Cr-induced oxidative stress in wheat plants. These findings underscore the potential utility of nSi as an effective strategy for alleviating HM stress and enhancing crop growth and productivity. Ongoing research in this area promises a more comprehensive investigation of the role of nSi in reduction of Cr toxicity in plants, which will increase our understanding of the role of nSi and the use of nSi for improving plant tolerance to HMs.

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CRediT authorship contribution statement

Sanaullah Jalil: Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Faisal Zulfiqar:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Anam Moosa:** Writing – review & editing, Conceptualization. **Jianjun Chen:** Writing – review & editing. **Raheela Jabeen:** Writing – review & editing. **Hayssam M. Ali:** Writing – review & editing. **Waleed A.A. Alsakkaf:** Writing – review & editing. **Hafiza Ayesha Masood:** Writing – review & editing. **Iman Mirmazloum:** Writing – review & editing. **Abdullah Makhzoum:** Writing – review & editing. **Jiansheng Chen:** Writing – review & editing. **Amany H.A. Abeed:** Writing – review & editing. **Heba S. Essawy:** Writing – review & editing.

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.

Data availability

Data will be made available on request.

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