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Research article

Effect of Cd toxicity on root morphology, ultrastructure, Cd uptake and accumulation of wheat under intercropping with Solanum nigrum L.

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ABSTRACT

In order to evaluate the effect of intercropping of the hyperaccumulator, *Solanum nigrum* L. and wheat on the absorption and accumulation of cadmium (Cd) in wheat. The experiment was conducted with three replicates, which conducted on four Cd concentrations (0, 20, 40, 60 μmol L^{-1}) in the Hoagland solution and using two planting patterns [monoculture wheat (MW), intercropping wheat and *Solanum nigrum* L. (IW，IS)]. The results showed that the addition of Cd in the solutions reduced the total root length by 19.08–55.98%, total root area by 12.35–44.48%, and total root volume by 16.01–46.00% of wheat plants. Intercropping with *Solanum nigrum* L. significantly reduced Cd contents by 28.3–47.2% and Cd accumulations by 10.08–32.43% in the roots of wheat. Transmission electron microscope (TEM) revealed that the root-tip cells of the monoculture wheat treated with Cd exhibited swollen spheres of intracellular mitochondria, disorderly arranged inner ridges of mitochondria, some damaged mitochondrial membranes, and deformed nuclear membranes. Many dense electron particles in the form of Cd were deposited in the cell gap, and the cell nucleus became smaller or even disappeared. Under the same Cd concentrations, root-tip cells of intercropped wheat showed much less density of electron particles, starch granules, and the damage to the nucleus and nuclear membrane by Cd.These results indicated that intercropping with *Solanum nigrum* L. reduced the Cd toxicity to wheat roots and decreased Cd uptake and accumulation in both the shoots and roots of the wheat.

1. Introduction

Although cadmium (Cd) is not an essential plant element, it can be readily absorbed and accumulated in plant tissues, particularly in edible parts, which may ultimately pose a risk to human health and compromise food safety [1]. Contamination of Cd in soils has become a serious environmental issue globally because of its adverse effects on plant growth [2]. Currently, according to Cd the pollution studies, the widely-disseminated Cd-contaminated vegetables and rice in southern China pose a significant public health risk [3,4] High concentration of Cd exhibited the growth and development of chlorosis, burning tips, leaf curling, and other Cd toxic

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symptoms of corn, and decreased the number and area of leaves. Besides, Metal toxicity is a complex phenomenon that affects almost every aspect of the physiology and biochemistry of plants. It needs to be solved urgently by any feasible strategy [5].

The remediation of soils contaminated with heavy metals can be conducted using chemical, physical, and biological techniques. Chemical and physical methods have the advantage of a short remediation period, but are expensive and cause secondary pollution [6]. Phytoremediation is an ecological and safe approach to remove, stabilize, render heavy metals, and has received increasing attention in recent years [7]. However, the limitation lies in the fact that the efficiency of phytoremediation is influenced by many factors, such as the slow growth of the plants and a small amount of biomass [8]. Intercropping is an ideal practice to solve this problem and the plants in the intercropping system can also effectively improve the utilization efficiency of light, water, fertilizer, and the growth space to a certain extent, as well as improve the plant production efficiency [9]. Compared with the monoculture, intercropping could improve the removal efficiency of various metals [10]. In recent years, more and more studies have utilized intercropping to improve the efficiency of phytoremediation [11]. *Solanum nigrum* L., an ideal Cd hyperaccumulator for the Cd-contaminated soil [12], which not only has superior Cd-accumulating ability, but also has strong resistance to the stress that competes for light, nutrient, and water. Wheat is one of the three major food crops in China. Among them, Ai-Kang 58 is one of the main wheat varieties planted in Henan province [13,14], which performed outstanding drought-enduring, freeze resistance, wide adaptability, and high yield behaviors [15]. Due to the complex soil properties and various environmental factors, it is difficult to distinguish the role of hyperaccumulators in competition or coordination under intercropping systems. The previous studies mainly focused on the bioavailability, migration, and transformation activities of Cd in the soil [16]. At present, there are many studies on the accumulation mechanism of heavy metals in plants [17,18], but there are few reports on the accumulation mechanism of wheat root morphology and cellular ultrastructure under intercropping pattern [19]. Observation of root cell ultrastructure acts as an important way to understand the cellular mechanism involved in Cd toxicity [20]. Besides, some studies were also conducted on root morphology but these were mainly focused on the relationship between root morphology and yield, and there is little information available on the relationships between root morphology and hyperaccumulation under intercropping pattern.

Therefore, the purpose of the present study was to investigate the effect of wheat intercropping with *Solanum nigrum* L. on wheat root morphology, ultrastructure, Cd uptake and accumulation, to find out the mechanism involved in the uptake of Cd by the wheat under different Cd stresses and planting patterns. The combination of changes in cell ultrastructure and differences in Cd uptake and transport can effectively reveal the stress mechanism of plants to Cd.

2. Materials and methods

2.1. Experimental design

The *Solanum nigrum* L. and wheat (*Triticum aestivum* L., Ai-Kang 58) obtained from the Farmland Irrigation Research Institute of the Chinese Academy of Agricultural Sciences (Beijing, China), which were used in our previous work [21]. The seeds with similar sizes were selected and treated with 0.5% (V/V) NaClO for 15 min, rinsed, and soaked in distilled water at 25 °C for 12 h. Then the germinated seeds were planted in a seedling growing tray with the container media. After the *Solanum nigrum* L. seedlings grew the fifth true leaf and the wheat grew a leaf, the uniform seedlings were selected and transplanted into a 500 mL black culture barrel.

The hydroponic experiment was performed in a greenhouse (25/20 °C (day/night) temperature and a 65–75% relative humidity) on August 2022. A completely randomized block design with three replicates was conducted on four Cd concentrations (0, 20, 40, 60 μmol L^{-1}) in the Hoagland solution and using two planting patterns [monoculture wheat (MW), intercropping wheat and *Solanum nigrum* L. (IW , IS)]. The seedlings were cultured in ½ strength Hoagland solution for nine days, then shifted to the full-strength Hoagland solution for another nine days. The composition of full-strength Hoagland solution was: $Ca(NO_3)_2·4H_2O$ 1.18g, KNO_3 0.51g, $MgSO_4·7H_2O$ 0.49g, KH_2PO_4 0.14g, EDTA-FeNa·$3H_2O$ 3.46 × 10^{-2} g, $MnCl_2·4H_2O$ 1.81 × 10^{-3} g, H_3BO_3 2.86 × 10^{-3} g, $ZnSO_4·7H_2O$ 2.20 × 10^{-4} g, $CuSO_4·5H_2O$ 8.00 × 10^{-5} g and $(NH_4)_6Mo_7O_{24}·4H_2O$ 1.80 × 10^{-5} g in a liter of water. Finally, seedlings were cultured in one of the solutions with four Cd concentrations (0, 20, 40, and 60 μmol L^{-1}) for another six days. The nutrient solution was replaced every three days, and the pH of the solution was adjusted to 6.5 ± 0.5 by 0.1 mol L^{-1} NaOH or 0.1 mol L^{-1} HCl. Cadmium stock solutions prepared from $CdCl_2·2.5H_2O$ and all chemicals used for this experiment were analytical grade and purchased from Beijing Haike Hongchuang Biological Technology Co., Ltd. (Beijing, China).

2.2. Samples collection and determination

After cultured 24 days, seedlings were separated into roots and shoots which were washed with tap water and deionized water. The roots were rinsed with deionized water again for three times after placed in 20 mmol L^{-1} Na_2-EDTA for 15 min. Both shoots and roots were dried at 105 °C for 30 min and then at 80 °C until constant weight. The dried samples were weighed recorded for their dry weights, then grounded with a ball mill, and passed through a 0.25 mm sieve. Plant samples were digested with $HNO_3 + HClO_4$ (4:1) [22], and the Cd contents were determined using ICP-MS (7700x, Agilent, Foster City, US). The reference material, citrus leaves [GBW10020 (GSB-11), with 0.17 ± 0.02 mg kg^{-1} Cd from the Institute of Geophysical and Geochemical Exploration, China] was used for QA/QC and the Cd concentration (within the expected standard range (0.17 ± 0.02) mg·kg^{-1}) study.

The fresh root was scanned using a scanner (EPSON PERFECTION 700, Seiko Epson Corporation , Japan), and the images were acquired by a root analysis software, WinRHIZOPro2013 (Regent Instruments Inc., Quebec, Canada). The length, surface area, and volume of roots were calculated as described by Pimentel [23].

Fresh root tips were sampled and cut into 1–3 mm segments and quickly placed in a 2.5% glutaraldehyde fixator (prepared with a phosphate buffer pH = 7.2) at room temperature in the dark for 6 h. Then the sample was washed four times with phosphate buffer solution (pH = 7.2) for 0.5 h each time before transferred to 1% osmium tetroxide for fixation. The samples were dehydrated with gradient acetone (30, 50, 70, 80, 99, and 100%) at each level for 15 min and placed in epoxy resin SPURR in an oven at 70 °C for 12h. Finally, the sample was sliced using an ultra-thin microtome (EM UC6, Leica, Germany) and its morphologies was observed with a TEM (H-7500, HITACHI, Japan) [24].

2.3. Data analysis

Statistical analysis of the data was performed using SAS 9.4. All values reported were the average of three independent replicates.

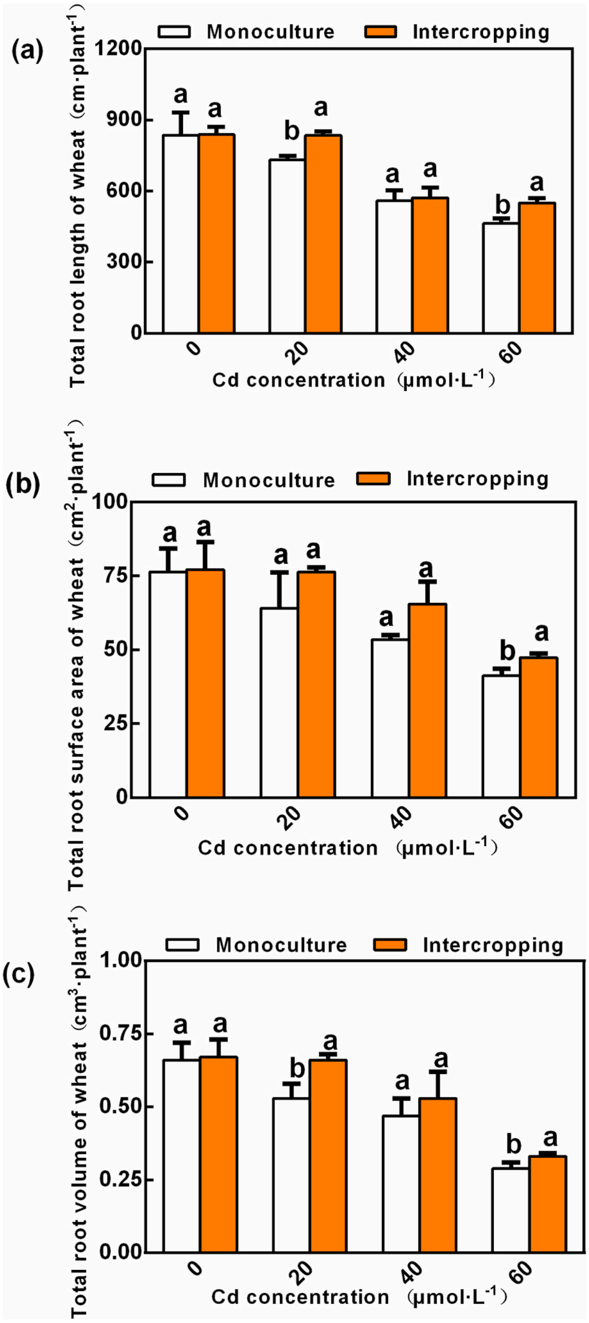

Fig. 1. The total root length (a), total root surface area (b) and total root volume of wheat (c) under different Cd stress. The bars are mean ± standard deviation (n = 3), and the different letters of the same tissue indicate that the difference at the $p < 0.05$ level is significant.

Data were tested at the significance level of $p < 0.05$ using the one-way ANOVA and Duncan's tests. Before the analysis of variance, the data were tested for homogeneity of variance. When the F value was greater than 0.05, the results were considered statistically significant.

The following formulas were used to determine the translocation factor (TF) and mass translocation factor (mTF):

TF= Cd concentration in shoots/Cd concentration in roots
mTF= Cd accumulation in shoots/Cd accumulation in roots

[Cd] is the content of Cd in a specific plant part, expressed as mg/kg^{-1}, and [mCd] is the mass of Cd in a specific plant part, expressed as μg.

3. Results

3.1. Effect of intercropping with *Solanum nigrum* L. on root growth of wheat treated with different Cd concentrations

Fig. 1 shows the effect of Cd concentration on total length, surface area, and volume of wheat roots. It was observed that the decreased of all these characteristic root parameters decreased with the increase of the Cd concentrations in hydroponic solution. There was no significant difference of root growth indexes between MW and IW under the control condition (no Cd added) while all these root measurements for IW had higher root growth attributes than MW under Cd stress (Fig. 1). The total root length, total root surface area, and total root volume of IW with the treatment of 20 μmol L^{-1} Cd were 1.14, 1.01, 1.23 times higher than these of monoculture wheat, respectively. Under 60 μmol L^{-1} Cd treatment, the total root length, total root surface area, and total root volume of IW were 1.19, 1.15, and 1.14 ($p < 0.05$) times higher than MW, respectively. Although the results showed that all the parameters of wheat root growth were affected by the Cd stress. But with the increase of the Cd stress, a larger decreasing slope for all parameters were shown on MW than IW, indicating that the intercropping with *Solanum nigrum* L. alleviated the effect of Cd on wheat root growth.

3.2. Effect of intercropping with *Solanum nigrum* L. on wheat biomass under different Cd stresses

There was no difference in biomass between MW and IW for non-Cd treatments (Table 1). Under the same Cd stress, the shoots and roots biomass of IW were higher than these of MW. The roots biomass of IW treated with 40 μmol L^{-1} Cd was 10.87 and 20.00% higher than these of MW, respectively. The biomass of shoots and roots of IW treated with 60 μmol L^{-1} Cd was 23.08 and 33.33% higher than these of MW. The Cd stress inhibited the growth of shoots and roots of wheat for both MW and IW since the shoot and roots biomass decreased with the increase of Cd concentration. The results demonstrated that under different Cd concentrations, intercropping with *Solanum nigrum* L. promoted the growth of wheat roots and shoots for almost all the tested Cd concentrations. At a high Cd concentration (60 μmol L^{-1}), the shoots and roots biomasses of IW was increased 23% and 25%, which significantly increased in comparison with that of MW.

3.3. Effect of intercropping with *Solanum nigrum* L. on Cd absorption of wheat under different Cd stresses

In the control samples (non-Cd), both MW and IW had no significant difference in Cd contents in shoots and roots of wheat. However, the Cd content of wheat roots was significantly higher than shoots. The Cd contents in wheat shoots and roots were increased significantly with the increase of Cd concentrations in solution, but the increase of Cd contents in roots of MW was greater than these of IW. Compared with MW, the Cd contents in IW treated with 20, 40 and 60 μmol L^{-1} Cd decreased by 17.53, 16.00 and 26.80% for shoots and 28.30, 43.94, 47.20% for roots, respectively (Fig. 2a and b). The results showed that the Cd contents of IW was decreased significantly, and intercropping with *Solanum nigrum* L. minimized the Cd absorption in wheat.

3.4. Effect of intercropping with *Solanum nigrum* L. on Cd accumulation of wheat under different Cd stresses

Under non-Cd stress, there was no significant difference in Cd accumulation in shoots and roots of MW and IW. Cadmium accumulation in shoots and roots of IW were lower than these in MW (Table 2). The accumulation of Cd were 14.60–16.74 g.plant^{-1} and

Table 1
Differences in biomass of monoculture and intercropping wheat under different Cd stress.

Cd concentration (μmol·L^{-1})	Shoots (g·plant^{-1})		Roots (g·plant^{-1})	
	MW	IW	MW	IW
0	0.22 ± 0.02a	0.21 ± 0.02a	0.08 ± 0.01a	0.10 ± 0.01a
20	0.18 ± 0.02a	0.19 ± 0.01a	0.06 ± 0.00a	0.08 ± 0.01a
40	0.15 ± 0.01a	0.17 ± 0.01a	0.05 ± 0.01a	0.06 ± 0.01a
60	0.13 ± 0.03b	0.16 ± 0.01a	0.04 ± 0.00b	0.05 ± 0.00a

Note: The data in the table are mean ± standard deviation (n = 3), and the different letters of the same tissue indicate that the difference at the $p <$ 0.05 level is significant. MW, Monoculture Wheat; IW, Intercropping Wheat.

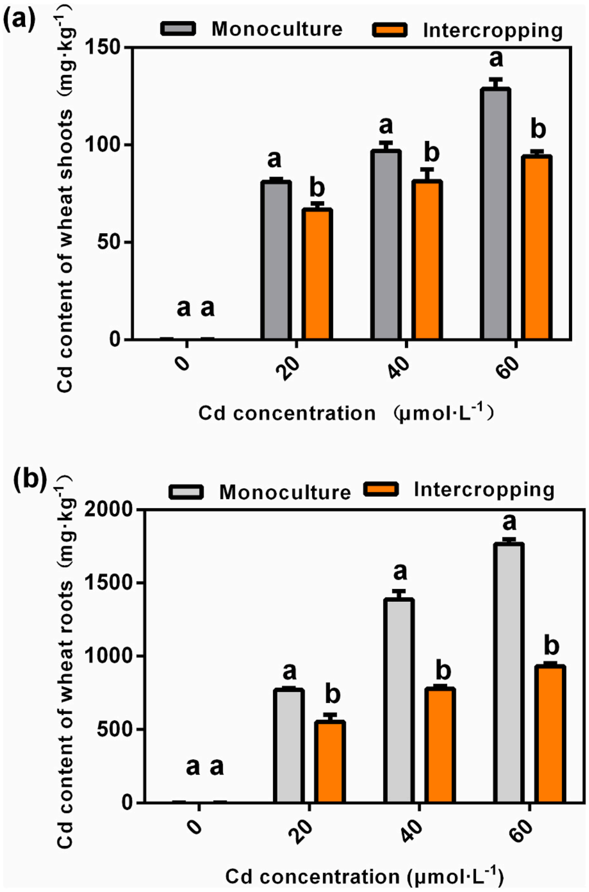

Fig. 2. Cd content of wheat shoots (a) and roots of wheat (b) under monoculture and intercropping. The bars are mean ± standard deviation (n = 3), and the different letters of the same tissue indicate that the difference at the $p < 0.05$ level is significant.

12.70–15.08g.plant^{-1} in the shoots of IW and MW, respectively. The shoos and roots Cd accumulation of IW under Cd stress were decreased compared with MW, the roots Cd accumulation of IW treated with40, and 60 μmol L^{-1} were significantly decreased by32.43, 29.51%, respectively. The results showed that with the increase of Cd stress intensity, the Cd accumulation of wheat was increased, and intercropping with *Solanum nigrum* L. inhibited the Cd accumulation of shoots and roots in wheat.

3.5. Effect of intercropping Solanum nigrum L. on translocation factor (TF) and mass translocation factor (mTF) of wheat under different Cd stress

Under different Cd stress, the TF of IW was greater than that of MW (Fig. 3 (a)). The TF of MW was 0.07–0.11, and IW was 0.08–0.12. Compared with MW treated with 20, 40 and 60 μmol L^{-1}, the TF of IW increased by 15.78, 49.64 and 38.67%, respectively. Under 20 μmol L^{-1} Cd treatment, there was no significant difference in mTF between IW and MW. The mTF of IW increased significantly by 36.92 and 28.47% compared with these of MW under 40 and 60 μmol L^{-1} Cd treatments (Fig. 3b). The results showed that

Table 2
Accumulations of Cd in shoots and roots of monoculture and intercropping wheat under different Cd stress.

Cd concentration(μmol·L^{-1})	Cd accumulation of shoots (μg·plant^{-1})		Cd accumulation of roots (μg·plant^{-1})	
	MW	IW	MW	IW
0	0.03 ± 0.00a	0.02 ± 0.00a	0.13 ± 0.03a	0.14 ± 0.00a
20	14.60 ± 1.39a	12.70 ± 0.68a	48.75 ± 2.91a	43.84 ± 1.66a
40	14.91 ± 1.81a	13.77 ± 0.61a	68.92 ± 8.54a	46.57 ± 5.68b
60	16.74 ± 1.20a	15.08 ± 0.94a	70.61 ± 1.28a	49.77 ± 5.24b

Note: The data in the table are mean ± standard deviation (n = 3), and the different letters of the same tissue indicate that the difference at the $p < 0.05$ level is significant. MW, Monoculture Wheat; IW, Intercropping Wheat.

intercropping with *Solanum nigrum* L. promoted the transfer of Cd from the wheat roots to shoots, and the Cd mTF of IW treated with 40 and 60 μmol L^{-1} Cd was increased significantly.

3.6. Effect of intercropping Solanum nigrum L. on ultrastructure of wheat root-tip cells under different Cd stress

Fig. 4 shows the ultrastructure of root-tip cells of MW treated with 20 μmol L^{-1} and 60 μmol·L-1 Cd .At 20 μmol L^{-1} Cd (Fig. 4 a, b), the mitochondria in the cells were swollen spheres, some mitochondrial membranes were damaged, and the nuclear membranes were all deformed. Compared with the root-tip cells of MW, the starch grains in IW cytoplasm were significantly reduced. The starch granules in the cytoplasm of IW were significantly reduced, and only scattered sporadically between the nuclear membrane and the cell membrane. The wheat root-tip cells of the two planting patterns were severely distorted and the cell wall was deformed at a 60 μmol L^{-1} Cd concentration (Fig. 4c and d). The nucleus membrane were damaged to a large extent and a large amount of dense electron particles in the form of Cd were deposited in the cell gap. The nucleus of the cell became smaller or even disappears. Compared with the root-tip cells of IW treated with 60 μmol L^{-1} Cd, the root-tip cells of MW were more deformed, the number of starch granules in the cells increased significantly, the cell walls and the nuclear membrane were more recessed, and the formation of Cd was dense. Electronic particles are not only collected in cell membranes and vacuoles, but also widely distributed in the cytoplasm. The results showed that under the same Cd concentration stress, intercropping with *Solanum nigrum* L. inhibited the absorption of Cd^{2+} in the solution by the wheat root, reduced the dense electronic particles in the cell, and inhibited the synthesis of starch granules in the wheat root cell.

4. Discussion

4.1. The effect on wheat root morphological parameters

Elevated Cd concentrations adversely affected the root morphological characters such as surface area, volume, and diameter. Since roots are in direct contact with a nutrient medium, their morphology influences the uptake of water, minerals, and metals. Therefore, it is important to study root morphological alteration under Cd-induced stressl [25]. In the current study, the roots growth parameters such as length, surface area, and volume of wheat have been influenced by the planting patterns and Cd stress. When wheat seedlings were cultured in nutrient solutions with 20, 40 , and 60 μmol L^{-1} Cd for six consecutive days, the growth of roots was inhibited and all

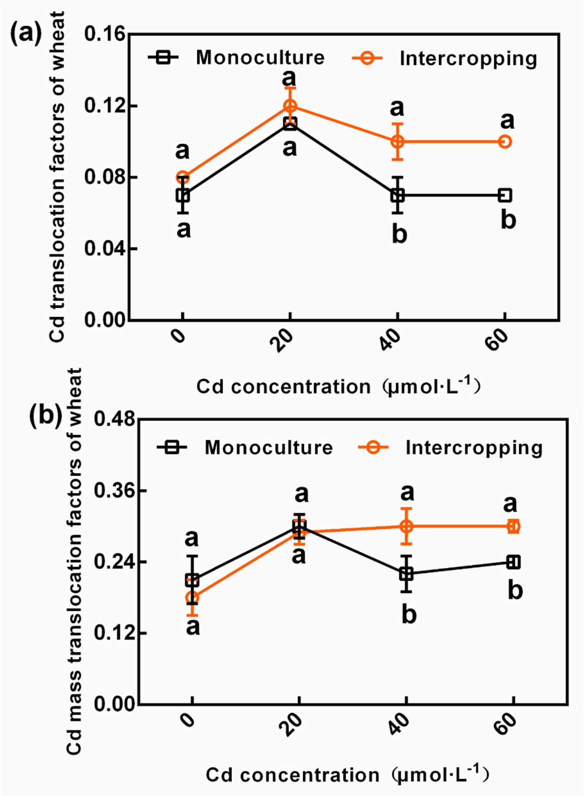

Fig. 3. TF of wheat (a) and mTF of wheat (b) under different Cd concentration stresses. The bars are mean ± standard deviation (n = 4), and the different letters of the same tissue indicate that the difference at the $p < 0.05$ level is significant.

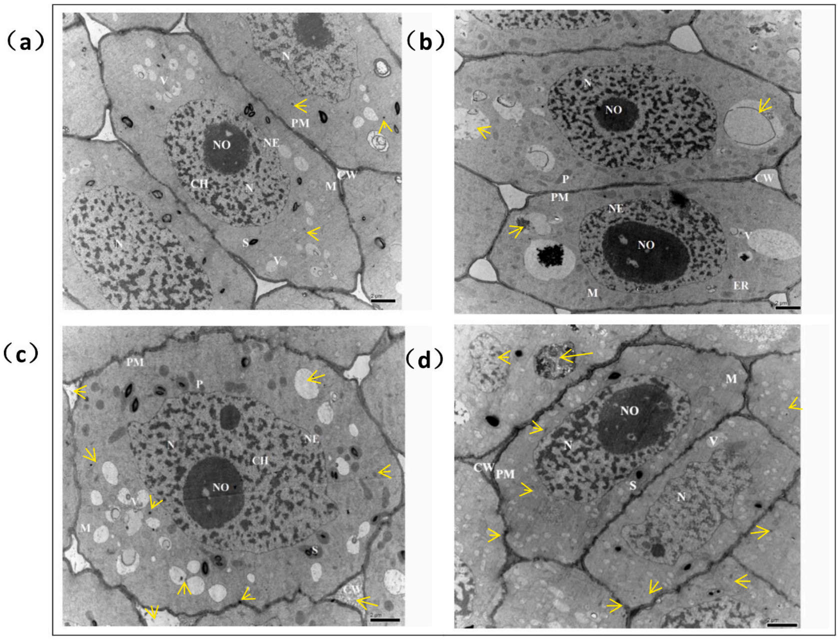

Fig. 4. The ultrastructure of root tip cells of MW (a) and IW (b) treated with 20 μmol L^{-1} Cd and root tip cells of MW (c) and IW (d) treated with 60 μmol L^{-1} Cd. Note：The different structures of wheat root cells are represented by these white letters in the picture: N (nucleus), NO (nucleolus), CH (chromatin), NE (nuclear envelope), V (vacuole), M (mitochondria), P (plastid), S (starch granule), PM (plasma membrane), CW (cell wall) and ER (endoplasmic reticulum), Cd deposition (→) in the form of electronic dense particles deposited or attached. Monocropping wheat and intercropping wheat treated with 20 μmol L^{-1} Cd (Panels a and b); Monocropping wheat and intercropping wheat treated with 60 μmol L^{-1} Cd (Panels c and d). MW, Monoculture Wheat; IW, Intercropping Wheat.

these parameters of roots were reduced obviously, indicating that Cd stress inhibited plant growth. This is because excessive Cd enters the plant cells which results in a series of physiological toxicity processes [26]. It was reported that excessive Cd stress disrupted the system balance between the generation and removal of active oxygen in plants and caused lipid peroxidation damage [27]. In the present research, we found that intercropping with *Solanum nigrum* L. promoted wheat root growth in comparison with MW, which was consistent with the research results that the root length and root surface area of broad bean intercropped with accumulators were significantly higher than that of monoculture broad bean [28].

4.2. The effect on wheat biomass of roots and shoots

In the present research, there was an overall reduction in plant growth attributes under Cd stress. And the reduction in wheat shoots biomass was similar to the reduction in its roots that as the concentration of Cd increases, the biomass decreases in the nutrient media. When the concentration of Cd in the solution exceeds the tolerance capacity of plants, Cd toxicity indirectly influenced the physiological metabolism and various aspects of plant growth. Cd toxicity of wheat was expressed in the growth form, with the main symptoms of wheat chlorosis and root tip browning, leading to the decrease of biomass [29]. The biomass of wheat shoots and roots were decreased under Cd stress. This is supported by the work of other researchers, who found that biomass was reduced in the two cotton genotypes when plants exposed to Cd, indicating that Cd stress inhibited plant growth [20]. However, this finding was in consistent with our previous result that the biomass of wheat shoots under intercropping was higher than that of monoculture under same Cd stress [21], which indicated that intercropping with *Solanum nigrum* L. reduced the toxic effect of Cd on wheat.

4.3. The effect on Cd accumulation in wheat roots and shoots

The study of plant mechanisms for accumulating metals and countering their toxicity stress helps to improve our comprehension of the processes of metal element and detoxification. In whole plants, roots are the primary sites to which heavy metals gain access. In most cases, heavy metals are readily taken up by the plant through the root and transported to the aerial parts by xylem vessel. However, much amount of them is stored in roots compared to shoots [30], this finding was consistent with our result. The reason for it could be attributable to the roots have many transition metal transport proteins that improve the ability of Cd^{2+} extraction, but the process of Cd transport to the shoot was affected by factors such as Cd concentration in the culture medium, and the Cd transport to the shoot was much lower than the absorption amount of root [31], Previously study has shown that intercropping between heavy metal hyperaccumulators and cash crops may reduce the concentration of Cd in food crops [32]. This finding was consistent with our result, which intercropping with *Solanum nigrum* L. inhibited the absorption of Cd by the roots of wheat and reduced the Cd contents of wheat shoots and roots. This might be due to *Solanum nigrum* L. has a strong ability to compete for Cd absorption. It was found that intercropping increased the accumulation of As in the centipede grass and reduced the concentration of As in the leaves of the mulberry tree [33]. This finding was in agreement with our result that intercropping with *Solanum nigrum* L. inhibited the absorption and accumulation of Cd by wheat. Some researchers believe that different planting patterns show the different species diversity, and plant diversity can reduce the adverse effects of polymetallic pollution on plant growth [34]. In conclusion, the present study demonstrated that intercropping with *Solanum nigrum* L. alleviated the Cd toxicity of wheat.

4.4. *The effect on wheat root-tip cells ultrastructure*

The roots are directly exposed to the soil and affected by Cd-contamination. Therefore, this organ must tolerate the Cd stress to keep the whole plant alive and the root tip is also suggested to function as a sensor. Thus, the investigation on Cd-induced ultrastructural changes in roots is important. Due to the complementary relation between the structure and function of plants, the effect of Cd on the cellular organization is important for understanding the physiological alterations. Electron microscopy helps to assess damage at the tissue and ultrastructural levels providing a basis for macroscopic examination [25]. Compared with those of MW, the density of electron particles and starch granules decreased in the root cells of IW, and the degree of Cd damage in the nucleus and nuclear membrane of root cells of IW was alleviated, Which may be due to the decreased antioxidant capacity induced by Cd, the activity of catalase in the roots was reduced and Cd toxicity could destroy plant root cell structure [35]. Higher Cd stress led to severe damage in the cell structure [36]. Khan et al. [37]found that the cell structure of cucumber root tips exposed to 100 μmol L^{-1} Cd stress showed obvious disorder. The observed mitochondrial swelling was possibly related to the change of stress-energy state. The deposits in it came from the storage form of the Cd complex. Intercropping with *Solanum nigrum* L. reduced the damage of wheat root cells under Cd stress and promoted the growth of the wheat root system compare to MW. The main reason is that intercropping with *Solanum nigrum* L. inhibited the absorption of Cd in the solution by wheat, and the toxic effects of free Cd in wheat root cells on the roots were reduced. Moreover, other cations inhibited the linear and saturation absorption by competing with Cd^{2+} in the roots [38].

5. Conclusion

In the present research, with the increase of Cd concentration, the total root length, the total root surface area, and the total root volume of wheat showed a downward trend. In the intercropping system, *Solanum nigrum* L. has a strong ability to compete for Cd absorption, which inhibited the absorption and accumulation of Cd by wheat. Compared with MW, the Cd concentration dropped significantly in shoots and roots of IW. With the increase of Cd concentration stress, the deformation of wheat root tip cells became more serious, and the nuclear membrane was sunken to a greater degree, which resulted in the strengthening of the toxic effect of Cd on wheat root tip cells. Under the same Cd concentration, less dense electron particles formed by Cd in wheat root tip cells intercropped with *Solanum nigrum* L., which alleviated the toxic effect of Cd to wheat roots.

Author contribution statement

Li Wang: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.
Rong Zou: Analyzed and interpreted the data.
Jinghang Cai: Contributed reagents, materials, analysis tools or data.
Guihua Liu: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data.
Song Qin: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data.
Ya Jiang: Analyzed and interpreted the data.
Guanqun Chai: Analyzed and interpreted the data.
Chengwu Fan: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

Data availability statement

Data will be made available on request.

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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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