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Elevated CO_2 mitigates the effects of cadmium stress on vegetable growth and antioxidant systems

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Abstract: In this study, we investigated the effects of cadmium (Cd) stress on the growth and antioxidant system of pak choi (*Brassica rapa* L.), water spinach (*Ipomoea aquatica* Forssk.), cherry radish (*Raphanus raphanistrum* subsp. *sativus* (L.) Domin) and pepper (*Capsicum annuum* L.) growing in pots under ambient CO_2 (aCO_2) or elevated CO_2 (eCO_2) conditions. In general, Cd stress reduced plant biomass and soil plant analysis development (SPAD) values under aCO_2 and eCO_2 conditions; however, the reduction was smaller under eCO_2. Cd stress significantly reduced vegetable superoxide dismutase (SOD) and catalase (CAT) activities under both aCO_2 and eCO_2 conditions; however, the decrease in cherry radish and pepper peroxidase and SOD activities and in pak choi SOD and CAT activities was significantly less under eCO_2. The Cd content of the edible parts of pak choi, water spinach and pepper was significantly lower under eCO_2 than under aCO_2. Our data suggest that eCO_2 was beneficial for the growth of the different types of vegetables, and at the same time, alleviated the degree of Cd stress by regulating the relative chlorophyll content and antioxidant capacity, and ultimately alleviated the adverse effects of Cd stress on the growth and quality of the vegetables.

Keywords: climate change; CO_2 concentration; abiotic stress; greenhouse gas; antioxidant enzymes

Prior to the industrial revolution, the concentration of CO_2, one of the main greenhouse gases, was 280 µmol/mol; today, it is over 400 µmol/mol (Sekhar et al. 2023). The continuous increase in CO_2 concentration is one of the primary challenges that need to be addressed in the global response to climate change. In addition to raising global temperatures, eCO_2 concentrations also affect other environmental factors and directly or indirectly affect plant growth, physiology and other responses in many ways, including those of vegetables. Although CO_2 is one of the most commonly used fertilisers in agricultural glasshouse facilities, the effects of eCO_2 levels on the growth of vegetables, such as tomatoes (*Solanum lycopersicum* L.) (Halpern et al. 2018), celery (*Apium graveolens* L.) (Liu et al. 2020), kale (*Brassica oleracea* L.) (Chowdhury et al. 2021), cucumbers (*Cucumis sativus* L.) (Song et al. 2020), peppers (*Capsicum annuum* L.) (Kumari et al. 2019) and aubergines (*Solanum melongena* L.) (Xu et al. 2021), vary depending on the vegetable species and other factors.

Cadmium (Cd) is a non-essential heavy metal element for plant growth and is highly mobile and readily absorbed by plants (Zulfiqar et al. 2022). At a certain level, Cd contamination can be toxic to plants, inhibiting plant growth and various physiological responses, including cellular ultrastructure (Alves et al. 2020), photosynthesis (Rafique et al. 2019) and antioxidant properties (Taie et al. 2019). However, the effects of eCO_2 and heavy metal stress conditions on plant growth and physiology are less

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well documented, and previous studies have mostly focused on crops, such as wheat (*Triticum aestivum* L.) (Khanboluki et al. 2018), ryegrass (*Lolium perenne* L.) (Shi et al. 2021) and soybean (*Glycine max* (L.) Merr.) (Blanco et al. 2022).

Although there have been many studies of the effects of eCO_2 on vegetable growth, there have been few studies of the effects of eCO_2 on the growth of vegetables growing in Cd-contaminated soil. In this study, we investigated the effects of eCO_2 on the growth and antioxidant system of four different types of vegetables: a leafy vegetable (pak choi, also known as bok choy, *Brassica rapa* L.), a stem vegetable (water spinach, *Ipomoea aquatica* Forssk.), a root vegetable (cherry radish, *Raphanus raphanistrum* subsp. *sativus* (L.) Domin) and a fruit vegetable (bell pepper, *Capsicum annuum* L.), with the aim of clarifying the physiological responses of different types of vegetables to Cd stress and eCO_2 under climate change, and to provide a theoretical basis for future green vegetable cultivation and production under climate change conditions.

MATERIAL AND METHODS

Soil and plant materials. The soil used in the pot experiment was yellow-brown soil collected from vegetable growing plots. The sampling depth was 0–20 cm (topsoil). Physicochemical analyses revealed that the collected soil comprised 24.0 C g/kg organic carbon, 67.58 mg/kg available nitrogen, 63.49 mg/kg available phosphorus and 169.27 mg/kg available potassium and had a total Cd content of 0.196 mg/kg (low content) and a pH of 6.53.

Four different vegetable types were used in this study: a leafy vegetable (pak choi), a stem vegetable (water spinach), a root vegetable (cherry radish), and a fruit vegetable (pepper). All the seeds were purchased from Shouguang Xian Sheng Seedling Co., Shouguang, Shandong, China.

Experimental design. An open-top gas chamber (OTC) was used to simulate eCO_2 conditions. The experimental set-up involved two CO_2 concentration levels: an ambient CO_2 level (aCO_2) and an elevated CO_2 level (eCO_2). The aCO_2 gas chamber was ventilated with natural air, which had a CO_2 concentration of 350 ± 70 μmol/mol. The eCO_2 gas chamber was ventilated with CO_2 gas to maintain the elevated CO_2 level, which had a CO_2 concentration of 700 ± 10 μmol/mol. Two Cd treatments were set up: soil that had a background Cd level but without the exogenous addition of Cd (Cd0) and soil that had a background Cd level and that was also contaminated with Cd (Cd3) by spraying with an exogenous Cd solution (3.0 mg/kg $CdCl_2$-2.5 H_2O) on 24 March 2022. The Cd-contaminated soil was allowed to air dry and then spread out, turned and mixed, accelerating its homogenisation process before setting aside at room temperature for 2 months and having a total Cd content of 3.074 mg/kg after homogenisation. Soil nutrient levels were consistent across treatments.

The experimental treatments involved three factors: vegetable cultivar, CO_2 concentration and soil Cd content (i.e., 16 treatments in total). After homogenisation, seeds of pak choi, water spinach, cherry radish or pepper were sown in separate pots (outer diameter 21 cm, height 12 cm) on 23 May 2022 in 2.0 kg of Cd0 or Cd3 soil and placed in aCO_2 or eCO_2 gas chambers, with six pots per replication and three replications per treatment. After germination, the seedlings were thinned to leave pots with five pak choi seedlings, three cherry radish seedlings, five water spinach seedlings or one pepper seedling. During the growing period (20 days after germination for pak choi, 25 days for water spinach, 35 days for cherry radish and 80 days for pepper), leaves from the same parts of the plants were selected from each pot to determine soil plant analysis development (SPAD) values, malondialdehyde (MDA) content, proline (Pro) content and antioxidant enzyme activity. During the vegetable maturity period (35 days after germination for pak choi, 40 days for water spinach, 45 days for cherry radish and 100 days for pepper), the biomass of different parts and the Cd content of edible parts were measured.

Indicator measurement

Biomass determination. For each of the 16 treatments, eight plants of the same height were selected. The roots were washed with distilled water to remove the soil before drying the plants at 105 °C until a constant weight was achieved. The dry weights were recorded.

SPAD value determination. For each treatment, three plants at the same stage of development were selected. The SPAD values of three leaves on the same part of the plant were measured using a SPAD meter (SPAD-502Plus, Tokyo, Japan).

Determination of antioxidant system indexes. After thawing the leaf samples that had been frozen in liquid nitrogen, the samples were maintained at

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2 °C to 8 °C and analysed using determination kits purchased from Suzhou Kemin Biotechnology Co., Suzhou, Jiangsu, China, to determine their peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT) activities and MDA and Pro contents. To 0.1 g of each of these samples, 1.0 mL of extract was added. The samples were homogenised and then centrifuged at 8 000 rpm at 4 °C for 10 min. The supernatants were collected carefully, and antioxidant enzyme activities were measured using enzyme-linked immunosorbent assay kits. The absorbance at 470 nm for 1 min and the absorbance after 2 min were recorded to calculate POD activity. Absorbance at 450 nm was used to calculate SOD activity. CAT activity was calculated by recording the initial absorbance at 240 nm and the absorbance after 1 min. The absorbance at 532 nm and 600 nm were recorded to calculate MDA contents. About 0.1 g of each sample was homogenised in an ice bath with 1 mL of extract solution before placing in a 95 °C water bath for 10 min, centrifuging at 10 000 rpm at 25 °C for 10 min, and then measuring the Pro content in the supernatant.

Determination of Cd content. The samples were accurately weighed (0.5 g) in a boiling tube, boiled with HNO_3-$HClO_4$ (4:1), covered with a glass cap and soaked overnight, then placed on an electric hot plate at 50 °C and digested until the white smoke dissipated and the samples in the digestion solution were slightly light yellow, the heating was stopped when 1 mL of the solution remained in the beaker, then cooled, the beaker was washed several times with distilled water, filtered and fixed in a 50 mL flask, and the Cd content of each part determined using a Varian AA240 graphite furnace atomic absorption spectrometer (Palo Alto, USA).

Data analysis and statistics. Data were analysed using SPSS 22.0 (New York, USA) to perform an analysis of variance (ANOVA), Tukey's significant difference analysis and Spearman's correlation analysis. Graphs were drawn using Microsoft Office 2016 (Redmond, USA).

RESULTS

Effect of different treatments on the biomass of different types of vegetables. Under eCO_2 conditions, the biomass of pak choi, water spinach, cherry radish and pepper plants grown in Cd0 soil was significantly increased by 10.91, 32.27, 27.64 and 22.80%, respectively, compared with the biomass achieved under aCO_2 (Figure 1). Under aCO_2 conditions, the biomass of pak choi, water spinach, cherry radish and pepper plants grown in Cd3 soil

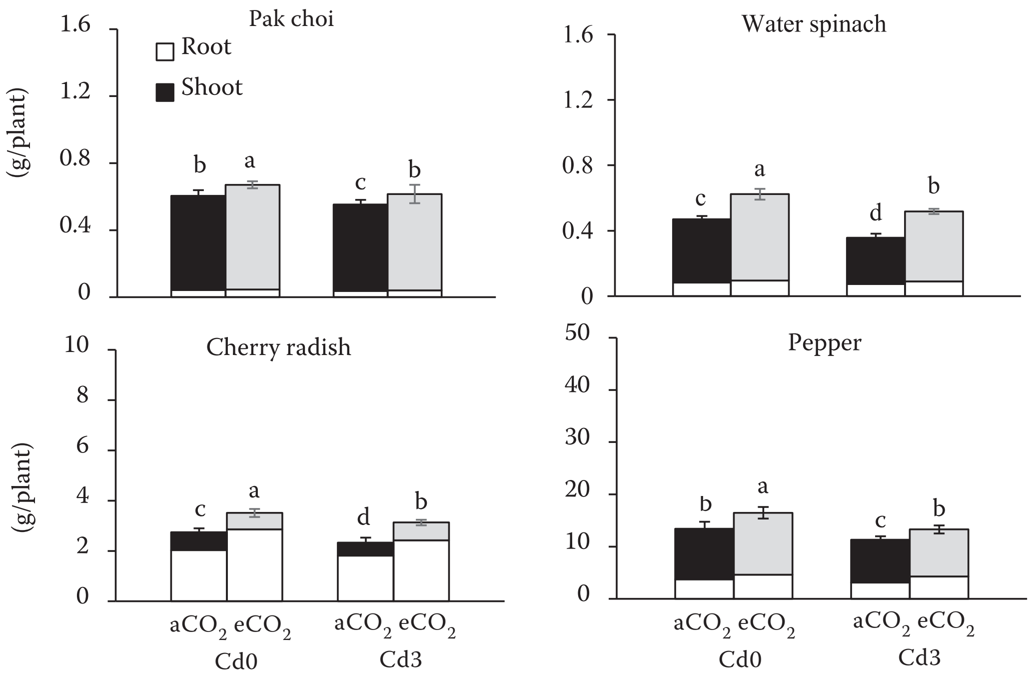

Figure 1. Biomass of four different types of vegetable grown under ambient (aCO_2, 350 ± 70 µmol/mol) or elevated CO_2 (eCO_2, 700 ± 10 µmol/mol) concentrations in soil with a background Cd level (Cd0, no exogenous addition) or in Cd-contaminated soil (Cd3, addition of 3.0 mg/kg). Data points represent means ± standard deviation; $n = 5$. Data points with different lowercase letters are significantly different ($P < 0.05$) according to Tukey's test

https://doi.org/10.17221/125/2023-PSE

was significantly reduced by 8.43, 23.99, 15.27 and 15.50%, respectively, compared with the biomass of plants grown in Cd0 soil.

Effect of different treatments on the SPAD values of different types of vegetables. Under eCO_2 conditions, the SPAD values of pak choi and water spinach grown in Cd0 soil significantly increased by 16.50% and 20.48%, respectively, and significantly increased by 20.69% and 23.13%, respectively, when grown in Cd3 soil compared with those achieved under aCO_2 (Figure 2). The SPAD values of pak choi and water spinach grown in Cd3 soil were significantly lower (12.12% and 12.76%, respectively) than those of plants grown in Cd0 soil under aCO_2, and significantly lower (8.96% and 10.84%, respectively) than those of plants grown in Cd0 soil under eCO_2 conditions. The SPAD values of cherry radish plants grown in Cd3 or Cd0 were not significantly different under eCO_2. The SPAD value of pepper leaves grown in Cd3 soil was significantly lower (15.62%) than those of Cd0 pepper plants under aCO_2 (15.62%) and eCO_2 (11.29%) conditions.

Effect of different treatments on the antioxidant system of different types of vegetables. POD, SOD and CAT activities of pak choi grown under eCO_2 conditions were significantly higher than those of plants grown under aCO_2 conditions, whereas the MDA content was significantly lower (Table 1). However, the SOD and CAT enzyme activities of pak choi grown under Cd stress were significantly lower than those of plants grown in Cd0 soil, and the MDA content was significantly higher. POD and SOD activities of cherry radish grown under eCO_2 conditions were significantly higher than those of plants grown under aCO_2 conditions, whereas MDA and Pro contents were significantly lower. However, POD, SOD and CAT enzyme activities of cherry radish plants grown under Cd stress were significantly lower than those of plants grown in Cd0 soil, and the Pro content was significantly higher. POD, SOD and CAT enzyme activities of water spinach and pepper plants grown under Cd stress were significantly lower than those of plants grown in Cd0 soil,

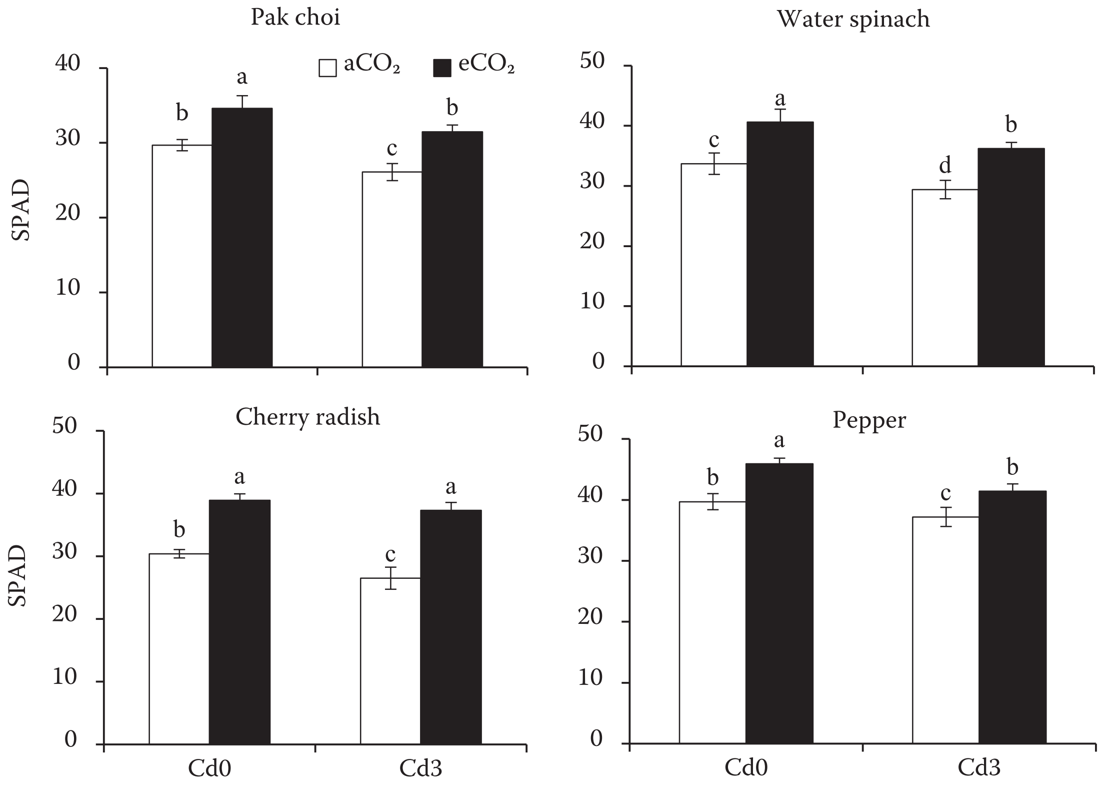

Figure 2. Soil plant analysis development (SPAD) values of different vegetables grown under ambient (aCO_2, 350 ± 70 µmol/mol) or elevated CO_2 (eCO_2, 700 ± 10 µmol/mol) concentrations in soil with a background Cd level (Cd0, no exogenous addition) or in Cd-contaminated soil (Cd3, addition of 3.0 mg/kg). Data points represent means ± standard deviation; *n* = 5. Data points with different lowercase letters are significantly different ($P < 0.05$) according to Tukey's test

https://doi.org/10.17221/125/2023-PSE

Table 1. Effect of different treatments on the antioxidant system of different types of vegetables

Vegetable	Treatment		POD activity	SOD activity	CAT activity	MDA content	Pro content
			(U/g)			(µmol/g)	(mg/g)
Pak choi	aCO_2	Cd0	187.54 ± 17.54^b	23.26 ± 1.73^b	3.14 ± 0.21^b	4.04 ± 0.13^b	0.16 ± 0.05^a
		Cd3	155.33 ± 13.43^c	19.82 ± 2.01^c	2.06 ± 0.14^c	4.75 ± 0.09^a	0.12 ± 0.03^b
	eCO_2	Cd0	207.10 ± 11.65^a	28.51 ± 1.85^a	4.28 ± 0.17^a	3.55 ± 0.18^c	0.11 ± 0.01^b
		Cd3	194.35 ± 19.01^{ab}	24.73 ± 0.96^b	3.33 ± 0.22^b	3.87 ± 0.21^b	0.13 ± 0.02^b
Water spinach	aCO_2	Cd0	234.21 ± 9.64^b	57.84 ± 2.57^b	5.77 ± 0.24^b	5.33 ± 0.14^b	0.45 ± 0.01^b
		Cd3	208.14 ± 14.57^c	42.67 ± 3.60^c	4.86 ± 0.26^c	5.75 ± 0.17^a	0.57 ± 0.05^a
	eCO_2	Cd0	261.03 ± 21.13^a	61.15 ± 3.51^a	6.31 ± 0.18^a	4.61 ± 0.08^c	0.33 ± 0.03^c
		Cd3	229.46 ± 8.46^b	59.84 ± 2.49^b	5.47 ± 0.31^b	5.14 ± 0.13^b	0.43 ± 0.04^b
Cherry radish	aCO_2	Cd0	163.66 ± 14.38^c	21.58 ± 1.81^c	3.44 ± 0.20^c	3.66 ± 0.21^a	0.28 ± 0.02^b
		Cd3	138.25 ± 9.27^d	17.39 ± 1.53^d	3.82 ± 0.16^{ab}	3.82 ± 0.20^a	0.35 ± 0.04^a
	eCO_2	Cd0	189.81 ± 10.03^a	29.49 ± 1.04^a	4.10 ± 0.11^a	2.53 ± 0.15^c	0.24 ± 0.02^c
		Cd3	175.02 ± 8.48^b	24.43 ± 2.07^b	3.73 ± 0.25^b	2.91 ± 0.11^b	0.28 ± 0.03^b
Pepper	aCO_2	Cd0	473.44 ± 36.70^b	87.60 ± 3.88^b	6.16 ± 0.33^b	5.57 ± 0.24^b	0.70 ± 0.05^b
		Cd3	401.20 ± 29.62^c	71.22 ± 4.75^c	5.22 ± 0.15^d	6.01 ± 0.22^a	0.83 ± 0.06^a
	eCO_2	Cd0	518.62 ± 31.48^a	93.57 ± 3.61^a	6.76 ± 0.20^a	4.83 ± 0.18^d	0.55 ± 0.04^c
		Cd3	486.30 ± 21.09^b	86.30 ± 5.09^b	5.73 ± 0.22^c	5.16 ± 0.22^c	0.67 ± 0.06^b

aCO_2 – ambient CO_2 (350 ± 70 µmol/mol); eCO_2 – elevated CO_2 (eCO_2, 700 ± 10 µmol/mol); Cd0 – soil with background Cd level (no exogenous addition); Cd3 – Cd-contaminated soil (addition of 3.0 mg/kg); POD – peroxidase; SOD – superoxide dismutase; CAT – catalase; MDA – malondialdehyde; Pro – proline. Different lowercase letters for the same vegetables in the same column indicate significant differences between treatments ($P < 0.05$)

whereas MDA and Pro contents were significantly higher under both aCO_2 and eCO_2 concentrations.

Effect of different treatments on the cadmium content of edible parts of different types of vegetables. Under Cd stress, the Cd content of the edible part of pak choi, water spinach, cherry radish and pepper was significantly higher under aCO_2 and under eCO_2 conditions than that of plants grown in Cd0 soil (Figure 3). However, under eCO_2, the Cd content of the edible part of pak choi, water spinach, and pepper plants grown in Cd0 soil was significantly lower (29.71, 34.97 and 26.40%, respectively) than that of plants grown under aCO_2. Furthermore, the Cd content of the edible part of pak choi, water spinach, cherry radish, and pepper plants grown in Cd-contaminated soil was significantly lower than that of plants grown in Cd0 soil under eCO_2.

Analysis of variance of different factors affecting the growth and antioxidant index of different types of vegetables. CO_2 concentration and Cd treatment significantly affected the growth, antioxidant indexes and Cd content of the edible parts of the four types of vegetable (Table 2), except for the Pro activity of pak choi, which was not significantly affected by Cd treatment. The interaction of CO_2 concentration and Cd treatment significantly affected the POD activity of pak choi, the SOD activity of water spinach and the CAT activity of cherry radish, as well as the Cd content of the edible parts of pak choi, water spinach and cherry radish.

DISCUSSION

Elevated CO_2 concentration can regulate photosynthesis by affecting the content and activity of Rubisco and RCA (Rubisco activase), key enzymes of photosynthesis, as well as gene expression, and affect the photosynthetic rate (Wang et al. 2020). The growth and biomass of different types of vegetables in different soils were promoted under eCO_2, and that CO_2 concentration had a significant effect on the biomass of the four vegetables used in the study. This is likely to be because CO_2 is a raw material for photosynthesis in plants, and its concentration increases the substrate for photosynthetic reactions, improves photosynthetic efficiency and promotes plant growth, and ultimately affects the apparent growth index and biomass accumulation of plants. Our findings support those of Yuan et al. (2017), who

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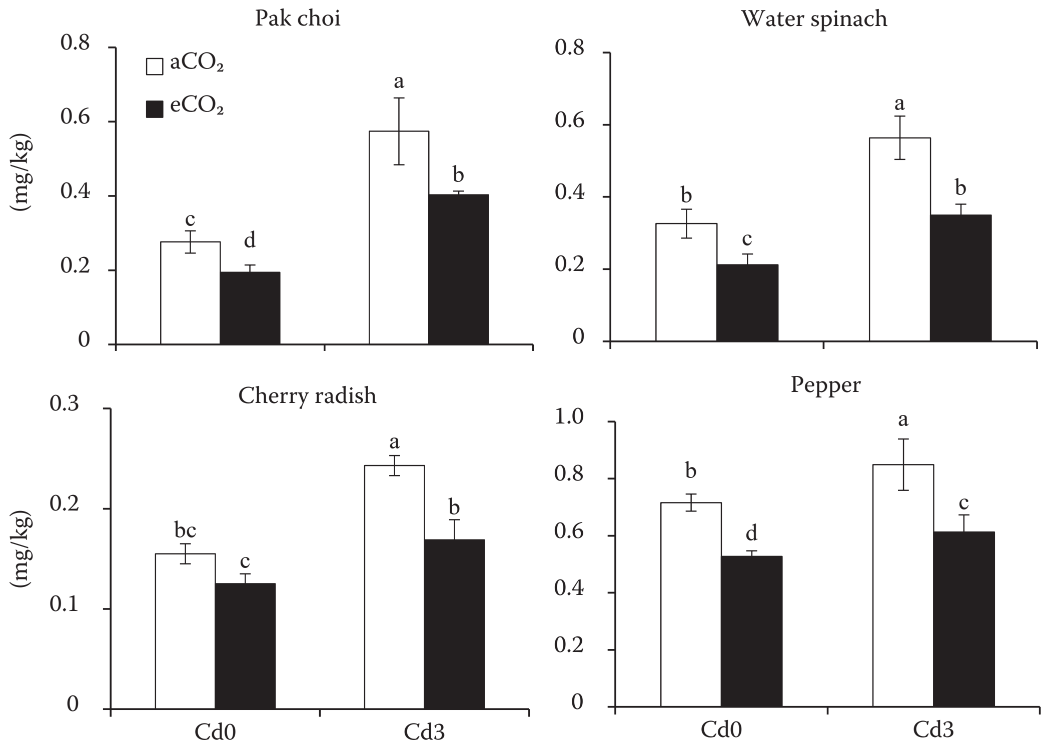

Figure 3. The cadmium (Cd) content of edible parts of different types of vegetables grown under ambient (aCO_2, 350 ± 70 μmol/mol) or elevated CO_2 (eCO_2, 700 ± 10 μmol/mol) concentrations in soil with a background Cd level (Cd0, no exogenous addition) or in Cd-contaminated soil (Cd3, addition of 3.0 mg/kg). Data points represent means ± standard deviation; *n* = 5. Data points with different lowercase letters are significantly different (*P* < 0.05) according to Tukey's test

Table 2. Analysis of variance of CO_2 concentration, cadmium (Cd) stress and interactions affecting the growth and antioxidant indexes of different types of vegetables

Vegetable	Effect	Biomass	SPAD	POD	SOD	CAT	MDA	Pro	Cd
Pak choi	CO_2	***	***	***	***	***	**	**	**
	Cd	***	**	***	**	***	*	ns	***
	CO_2 × Cd	ns	ns	*	ns	ns	ns	**	*
Water spinach	CO_2	**	**	**	***	***	***	**	***
	Cd	***	***	*	**	**	*	*	***
	CO_2 × Cd	ns	ns	ns	*	ns	ns	ns	ns
Cherry radish	CO_2	**	**	**	*	*	**	*	**
	Cd	**	*	**	***	***	*	*	***
	CO_2 × Cd	ns	ns	ns	ns	*	ns	ns	*
Pepper	CO_2	***	**	***	***	**	**	**	***
	Cd	**	***	*	**	***	**	*	***
	CO_2 × Cd	ns	ns	ns	ns	ns	ns	ns	ns

Values represent the means ± standard error; *n* = 5. **P* < 0.05; ***P* < 0.01; ****P* < 0.001; ns – not significant. ANOVA factors: CO_2 level – ambient level (aCO_2, 350 ± 70 μmol/mol) and elevated CO_2 level (eCO_2, 700 ± 10 μmol/mol); Cd level – soil with a background Cd level (Cd0, no exogenous addition) and Cd-contaminated soil (Cd3, addition of 3.0 mg/kg). SPAD – soil plant analysis development; POD – peroxidase; SOD – superoxide dismutase; CAT – catalase; MDA – malondialdehyde; Pro – proline

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used a CO_2 automatic control system and an OTC to simulate the effect of eCO_2 on the photosynthetic physiological characteristics of pepper. They showed that eCO_2 promoted pepper growth and increased total plant biomass.

POD, SOD and CAT are important plant antioxidant enzymes, and MDA and Pro are important osmoregulatory substances. The main damage caused to plants by heavy metals is peroxidative stress, which generates a large number of reactive oxygen radicals. This, in turn, causes metabolic dysregulation in plants, causing peroxidation of biomolecules and membrane lipids, injuring the cell membrane system and, thus, affecting plant growth (Molaei et al. 2012). After peroxidative stress caused by a short period or a low level of heavy metal stress, plants eliminate excessive reactive oxygen radicals by increasing the activity of antioxidant enzymes to resist the stress (Thatoi et al. 2014). The POD, SOD and CAT activities of the four different types of vegetables decreased, and MDA and Pro content levels increased under Cd stress conditions, indicating that the vegetables resisted stress through antioxidant regulation and osmoregulation. However, owing to the degree of Cd stress that plants were subjected to in this study, the antioxidant regulation capacity of the different vegetables was unable to resist membrane lipid peroxidation, and the antioxidant enzyme activity decreased. Similar findings were reported by Jia et al. (2018). Under eCO_2, significantly higher Cd concentrations were found in the grain of three rice cultivars than under aCO_2 but lower levels in the grain of the other three cultivars. In this study, the POD, SOD and CAT activities of water spinach and pepper plants grown under eCO_2 were significantly increased, and the MDA and Pro contents were significantly decreased under both soil treatments. Our findings suggest that the plant response to heavy metals when grown under eCO_2 conditions may vary depending on the plant species.

An eCO_2 concentration affects the accumulation of heavy metals by plants (Huang et al. 2017). A study by Kim and Kang (2011) showed that eCO_2 significantly increased the total biomass and accumulation of Pb in roots and shoots of pine (*Pinus*) seedlings. Shi et al. (2021) found that the growth rate of *Lolium perenne* increased by 30% to 75% when subjected to Cd stress and eCO_2 levels and that the Cd accumulation rate decreased by 36% to 42%, leading to a decrease in the Cd content of roots and shoots. However, Huang et al. (2017) concluded that atmospheric CO_2 concentrations could have positive effects on soil fertility and the rhizosphere microenvironment under heavy metals. In this study, the Cd content in the edible parts of pak choi, water spinach and pepper were significantly reduced when grown under eCO_2 in the different soil treatments. The reason for this finding may be that an increase in CO_2 concentration promotes photosynthesis and carbon and nitrogen metabolism in different vegetables; therefore, more energy substances are synthesised, increasing the content and activity of various antioxidant enzymes, which helps plants to resist heavy metal stress (Wang et al. 2022).

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