



ORIGINAL ARTICLE

Growth and development of *Stevia rebaudiana* (Bertoni) through exogenous application of abscisic and jasmonic acid under cadmium stress

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ABSTRACT

Cadmium (Cd) contamination poses a critical threat to crop productivity, physiology, and human health. *Stevia rebaudiana*, a commercially important medicinal and sweetener plant, is highly vulnerable to heavy metal stress, necessitating strategies to maintain growth and quality in contaminated soils. This study investigated the capacity of abscisic acid (ABA) and jasmonic acid (JA), applied individually and combined, to mitigate cadmium-induced morphological, physiological, and biochemical impairments in *S. rebaudiana*. Plants were exposed to graded Cd levels (0, 2, 4, 6, 8, 10 mg kg⁻¹ soil) and treated with 10 μM ABA, 50 μM JA, and their combination. The results indicated that Cadmium stress significantly reduced plant height, biomass, root growth, and photosynthetic pigments while increasing oxidative stress markers (MDA and H₂O₂) accumulation. Exogenous ABA and JA substantially alleviated these adverse effects, with the combined treatment (10 μM ABA + 50 μM JA) exhibiting the most pronounced improvement across all Cd concentrations. Plants treated with 10 μM ABA + 50 μM JA displayed enhanced growth recovery, photoprotection, water balance, and oxidative damage suppression, approaching control levels at moderate Cd stress. These findings demonstrate that combined application of ABA and JA more effectively fortified stevia against Cd toxicity by modulating growth, photosynthetic pigments, osmotic adjustment, and antioxidant capacity.

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Introduction

Heavy metal pollution has been recognized as a major issue threatening the agriculture sustainability at a global scale (Vácha, 2021). Among various heavy metals, cadmium (Cd) is one of the most toxic to plants at low concentrations, and induces serious physiological and biochemical disturbances in plants even at lower concentrations (Rizwan et al., 2017). Its accumulation in plants leads to chlorosis, stunted growth, reduced biomass, and impaired photosynthesis due to its interference with the uptake of essential nutrient elements and enzyme activities (Li et al., 2023; Zulfiqar et al., 2022).

S. rebaudiana, a perennial herb belonging to the Asteraceae family, is cultivated globally for its natural non-caloric sweeteners, steviol glycosides which are about 300 times sweeter than white sugar (De Andrade et al., 2023). Today, stevia is being cultivated in Asia, including Bangladesh, and overall South America for food and pharmaceutical products (Hossain et al., 2017). However, the worldwide demand for natural sweeteners is steadily increasing because of its activity against the diabetic, obesity, bacterial, and neoplastic activities (Ceunen & Geuns, 2013). To fight against those chronic diseases and meet the market demand, we need to grow many stevia plantlets for industrial use. In Bangladesh, industrial toxic heavy metals such as cadmium have contaminated agricultural ecosystems (Pessarakli, 2019). These contaminations are crucial factors for limiting global crop

productivity and food safety. Also, threatening to human health, reducing global economic growth (Landrigan et al., 2018). Thus, elucidating the Cd tolerance mechanisms and developing strategies for increasing plant resistance to metal stress are important for sustainable stevia growth.

Phytohormones are involved in plant stress and adaptation in various crop plants are documented by various researchers (Peleg and Blumwald, 2011). ABA is a well-known stress hormone implicated in the control of stomatal aperture, osmotic adjustment and induction of stress-responsive genes (Finkelstein, 2013; Vishwakarma et al., 2017). Jasmonic acid (JA) plays a role in defense to both biotic and abiotic stresses by regulation of antioxidant systems and secondary metabolite synthesis (Wasternack and Hause, 2013; Per et al., 2018). Recently, it has been reported that exogenous application of ABA and JA can alleviate Cd toxicity in different plant species including *Lactuca sativa* (Dawuda et al., 2020), *Cosmos bipinnatus* (Yu et al., 2023), *Oryza sativa* (Li et al., 2022), *Arabidopsis thaliana* (Meng et al., 2022) and *Abelmoschus esculentus* (Wang et al., 2023). However, the influences of ABA, JA single or combined treatment on growth and development of *S. rebaudiana* under cadmium stress has not yet been well-reported. Therefore, this study was conducted to evaluate the effects of exogenous ABA and JA, applied single or in combination, on the growth, physiological traits, and biochemical responses of *S. rebaudiana* under cadmium stress.

Methodology

Plant material, experimental design and treatments

The experiment was conducted at Institute of Biotechnology and Genetic Engineering, Gazipur Agricultural University, Gazipur. *S. rebaudiana* plantlets were obtained from Bangladesh Sugarcrop Research Institute, Ishurdi, Pabna, Bangladesh. The plants were grown in plastic pots (15 cm diameter) filled with soil mixture (sandy loam: organic compost, 3:1 v/v). The greenhouse was maintained at $25\pm 2^{\circ}\text{C}$ temperature, $65\pm 5\%$ relative humidity. The experiment was conducted following factorial completely randomized design with three replicates per treatment. Each replication contain a single plant per pot.

Cadmium 0, 2, 4, 6, 8, 10 mg/kg were selected as soil treatments according to Alloway (1995), he stated that 0–1 mg/kg of cadmium in soils denotes non-pollution, 1–3 mg/kg denotes mild contamination, and 3–10 mg/kg denotes contamination. Cadmium chloride ($\text{CdCl}_2 \cdot 2\text{H}_2\text{O}$) was used as the Cd source and incorporated into the soil to achieve concentrations of 0 (control), 2, 4, 6, 8, and 10 mg Cd kg^{-1} soil. Plants were allowed to establish for two weeks before phytohormone application.

The concentration of Absciscic acid (ABA, Sigma-Aldrich) and Jasmonic acid (JA, Sigma-Aldrich) were selected as 10 μM and 50 μM , respectively because Yu et al. (2023) reported that 10 μM ABA can alleviate Cd

toxicity in *Cosmos bipinnatus* and Chen et al. (2025) reported that 50 μM JA reduced Cd accumulation and enhanced biomass production of *Brassica chinensis*. Those phytohormones were prepared as stock solutions in ethanol and diluted to working concentrations of 10 μM for ABA and 50 μM for JA. The phytohormones were applied as foliar sprays (20 mL per plant) weekly for four weeks in the evening. Treatments are six levels of Cadmium, Cd_0 = Without Cadmium (control), Cd_2 = 2 mgkg^{-1} Cd, Cd_4 = 4 mgkg^{-1} Cd, Cd_6 = 6 mgkg^{-1} Cd, Cd_8 = 8 mgkg^{-1} Cd, Cd_{10} = 10 mgkg^{-1} Cd and four levels of phytohormone as foliar spray, T_0 = No phyto-hormone, T_1 = 10 μM ABA, T_2 = 50 μM JA, T_3 = 10 μM ABA + 50 μM JA in combination.

Morphological parameters

At 60 days after cadmium treatment initiation, growth parameters were recorded from all plants. Plant height was measured from the soil surface to the apex of the main shoot using a ruler (± 0.1 cm precision). Total leaf number per plant was counted manually. Branch number included all lateral branches arising from the main stem. Leaf size was determined by measuring the length and width of the third fully expanded leaf from the apex using a digital caliper (± 0.01 mm precision), and leaf area was calculated using the formula: Leaf area (cm^2) = Length $\times$ Width $\times 0.78$ (correction factor for *S. rebaudiana*) (Francisco et al., 2018).

For biomass determination, plants were carefully uprooted, and soil particles were gently washed from roots using distilled

water. Plants were separated into shoot and root portions. Fresh weight of shoot and root tissues was immediately recorded using an analytical balance (± 0.001 g precision). For dry weight determination, plant tissues were placed in paper bags and dried in a hot air oven at 71°C for 48 hours until a constant weight was achieved. Root parameters including root number (all visible roots ≥ 1 cm length) and root length (length of the longest root) were measured using a ruler.

Photosynthetic pigment analysis

Fresh leaf samples (0.5 g) from the third and fourth fully expanded leaves were collected from each plant and immediately processed for pigment extraction. Chlorophyll and carotenoid contents were determined following the method of Arnon (1949) with

modifications by Lichtenthaler and Wellburn (1983). Leaf tissue was homogenized in 10 mL of 80% acetone using a pre-chilled mortar and pestle under dim light conditions. The homogenate was centrifuged at 10,000 rpm for 10 minutes at 4°C . The supernatant was collected, and the extraction was repeated twice with the residue. The combined supernatants were made up to 25 mL with 80% acetone.

Absorbance of the extract was measured using a UV-Visible spectrophotometer (Model: UV-2600, Shimadzu, Japan) at wavelengths of 663 nm (chlorophyll a), 645 nm (chlorophyll b), and 470 nm (carotenoids) against 80% acetone as blank. Chlorophyll a (Chl a), Chlorophyll b (Chl b), total chlorophyll (Total Chl), and carotenoids were calculated by using the following formula:

$$\text{Chl a (mg/g FW)} = \frac{12.7 (\text{absorbance at 663 nm}) - 2.69 (\text{absorbance at 645 nm})}{1000 \times \text{Fresh weight (W)}} \times \text{Volume}$$

$$\text{Chl b (mg/g FW)} = \frac{22.9 (\text{absorbance at 645 nm}) - 4.68 (\text{absorbance at 663 nm})}{1000 \times \text{Fresh weight (W)}} \times \text{Volume}$$

$$\text{Carotenoids (mg/g FW)} = \frac{1000 (\text{absorbance at 470 nm}) - 2.270 \text{ Chl a} - 81.4 \text{ Chl b}}{229} \times \text{Vol} / (1000 \times \text{W})$$

Relative water content (RWC)

Relative water content was measured using the method Meher et al. (2017). Fresh leaf discs were weighed (FW), immersed in distilled water for 4 h, blotted dry and weighed (TW), then oven-dried at 70°C for 24 h and weighed (DW). RWC was calculated as:

Where, FW = Fresh weight of the leaf disks, DW = Dry weight of the leaf disks and TW = Turgid weight of the leaf disks.

$$\text{RWC \%} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

Malondialdehyde (MDA) content

Lipid peroxidation was estimated by measuring malondialdehyde (MDA) content using the thiobarbituric acid reactive substances (TBARS) method (Heath and Packer, 1968). Fresh leaf tissue (0.5 g) was homogenized in 5 mL of 0.1% trichloroacetic acid (TCA) and centrifuged at 12,000 rpm for 15 minutes at 4°C. One milliliter of supernatant was mixed with 4 mL of 0.5% thiobarbituric acid (TBA)

prepared in 20% TCA. The mixture was heated in a water bath at 95°C for 30 minutes, then immediately cooled in an ice bath and centrifuged at 10,000 rpm for 10 minutes. Absorbance of the supernatant was measured at 532 nm and corrected for non-specific turbidity by subtracting the absorbance at 600 nm. MDA content was calculated using an extinction coefficient of 155 mM⁻¹ cm⁻¹ and expressed as nmol g⁻¹ FW. The formula is

$$\text{MDA } \left(\frac{\text{nmol}}{\text{g}} \text{FW} \right) = \frac{(A_{532} - A_{600})}{\text{Extinction Coefficient}} \times \frac{\text{Total volume of extract (mL)}}{\text{Fresh weight of tissue (g)}} \times 1000$$

Hydrogen peroxide (H₂O₂) content

Hydrogen peroxide (H₂O₂) content was determined according to the method of Velikova *et al.* (2000). Fresh leaf tissue (0.5 g) was homogenized in 5 mL of 0.1% (w/v) TCA in an ice bath. The homogenate was centrifuged at 12,000 rpm for 15 minutes at 4°C. For the assay, 0.5 mL of supernatant was mixed with 0.5 mL of 10 mM potassium

phosphate buffer (pH 7.0) and 1 mL of 1 M potassium iodide (KI). The reaction mixture was vortexed and incubated for 1 hour in darkness at room temperature. Absorbance was measured at 390 nm against a reagent blank. H₂O₂ content was calculated using a standard curve prepared with known concentrations of H₂O₂ (0-100 µM) and expressed as µmol g⁻¹ FW using the following formula:

$$\text{H}_2\text{O}_2 \text{ (}\mu\text{mol/g FW)} = \frac{\text{Absorbance at 390 nm}}{\text{Extinction Coefficient}} \times \frac{\text{Total volume of reaction mixture (mL)}}{\text{Fresh weight of tissue (g)}}$$

Proline content

Free proline content was estimated following the ninhydrin method of Bates *et al.* (1973). Fresh leaf tissue (0.5 g) was homogenized in 10 mL of 3% sulfosalicylic acid and filtered through Whatman No. 2 filter paper. Two milliliters of filtrate were mixed with 2 mL of acid ninhydrin reagent (1.25 g ninhydrin

dissolved in 30 mL glacial acetic acid and 20 mL 6 M phosphoric acid) and 2 mL of glacial acetic acid in a test tube. The mixture was heated in a boiling water bath at 100°C for 1 hour, then the reaction was terminated by placing tubes in an ice bath. The reaction mixture was extracted with 4 mL of toluene and vortexed vigorously for 15-20 seconds. The chromophore-containing toluene layer was

aspirated, warmed to room temperature, and absorbance was measured at 520 nm against toluene blank using a spectrophotometer. Proline content was determined using a

standard curve prepared with L-proline (0-100 $\mu\text{g mL}^{-1}$) through following formula, and expressed as $\mu\text{mol g}^{-1}$ FW:

$$\text{Proline } (\mu\text{mol/g FW}) = \frac{\text{Concentration from Standard Curve } \left(\frac{\mu\text{mol}}{\text{mL}} \right) \times \text{Total volume of initial extract (mL)}}{\text{Fresh weight of tissue (g)}}$$

Total antioxidant capacity (TAC)

Total antioxidant capacity was assessed using the phosphomolybdenum method (Prieto et al., 1999). Leaf extracts were mixed with reagent solution (0.6 M sulfuric acid, 28 mM sodium phosphate, and 4 mM ammonium molybdate), incubated at 95°C for 90 min, and absorbance was measured at 695 nm. TAC was expressed as mg ascorbic acid equivalents (AAE) g^{-1} FW.

Statistical analysis

Data were subjected to two-way analysis of variance (ANOVA) using SPSS Statistics software version 26.0 (IBM Corp., USA). Treatment means were compared using Tukey's Honest Significant Difference (HSD) post hoc test at 5% significance level ($p < 0.05$). Results are presented as mean $\pm$ standard error (SE).

Results

Morphological parameters

Cadmium stress significantly affected all morphological parameters of *S. rebaudiana* in a dose-dependent manner (Table 1). Under

control conditions (Cd_0T_0), plants exhibited optimal growth with plant height of 42.5 ± 1.2 cm, 55.0 ± 2.1 leaves, 10.0 ± 0.5 branches, leaf size of 12.8 ± 0.4 cm^2 , 45.0 ± 2.3 roots, root length 16.8 ± 0.6 cm, fresh weight 18.5 ± 0.7 g, and dry weight 3.8 ± 0.2 g.

Progressive cadmium exposure (2, 4, 6, 8, and 10 mg kg^{-1} soil) resulted in substantial reductions in all growth parameters. At the highest Cd concentration (Cd_{10}T_0), untreated plants showed severe growth inhibition with plant height, leaf number, branch number, leaf size, root number, root length, fresh weight and dry weight reduced to 58.4%, 52.7%, 60%, 60.9%, 55.6%, 62.5%, 65.9% and 68.4% compared to control plants, respectively.

The exogenous application of plant growth regulator (PGR) ameliorated the adverse effects of Cd stress across all concentrations. Combined application of ABA and JA (10 μM ABA + 50 μM JA) T_3 consistently demonstrated superior performance. At Cd_{10} (10 mg kg^{-1} Cd) concentration with T_3 treatment, plant height, leaf number, branch number, leaf size, root number, root length,

Table 1. Effects of ABA and JA applied singly and in combination on growth parameters of *S. rebaudiana* under cadmium stress.

Cd Concentration (mgkg ⁻¹)	Treatment	Plant Height (cm)	Leaf Number	Branch Number	Leaf Size (cm ²)	Root Number	Root Length (cm)	Fresh Weight (g)	Dry Weight (g)
Cd ₀	T ₀	42.5±1.2a	55.0±2.1a	10.0±0.5a	12.8±0.4a	45.0±2.3a	16.8±0.6a	18.5±0.7a	3.8±0.2a
	T ₀	38.2±1.1b	49.0±1.8b	8.7±0.4b	11.2±0.3b	39.0±2.0b	14.5±0.5b	15.8±0.6b	3.2±0.1b
Cd ₂	T ₁	40.5±1.0a	52.3±1.9ab	9.5±0.4a	12.0±0.4ab	42.0±2.1a	15.8±0.5a	17.2±0.6a	3.5±0.2ab
	T ₂	39.8±1.1ab	51.0±2.0ab	9.2±0.4ab	11.7±0.4ab	41.0±2.0ab	15.3±0.5ab	16.8±0.6ab	3.4±0.2ab
	T ₃	41.2±1.0a	53.5±2.0a	9.7±0.5a	12.3±0.4a	43.5±2.2a	16.2±0.6a	17.8±0.7a	3.6±0.2a
Cd ₄	T ₀	33.8±1.0c	42.0±1.6c	7.3±0.3c	9.5±0.3c	33.0±1.7c	12.2±0.4c	12.5±0.5c	2.5±0.1c
	T ₁	37.5±1.1b	47.0±1.8b	8.5±0.4b	10.8±0.3b	38.0±1.9b	14.0±0.5b	15.2±0.6b	3.0±0.2b
	T ₂	36.2±1.0b	45.5±1.7b	8.2±0.4b	10.4±0.3b	36.5±1.8b	13.5±0.5b	14.5±0.6b	2.9±0.1b
	T ₃	39.0±1.1ab	49.5±1.9ab	9.0±0.4ab	11.5±0.4ab	40.0±2.0ab	14.8±0.5ab	16.5±0.6ab	3.3±0.2ab
Cd ₆	T ₀	28.5±0.9d	35.0±1.4d	6.0±0.3d	7.8±0.3d	27.0±1.5d	9.8±0.4d	9.2±0.4d	1.8±0.1d
	T ₁	33.2±1.0c	41.0±1.6c	7.5±0.4c	9.2±0.3c	33.5±1.7c	12.0±0.5c	12.8±0.5c	2.5±0.1c
	T ₂	31.8±0.9cd	39.0±1.5cd	7.0±0.3cd	8.8±0.3cd	31.5±1.6cd	11.2±0.4cd	11.8±0.5cd	2.3±0.1cd
	T ₃	35.8±1.1bc	44.5±1.7bc	8.2±0.4bc	10.0±0.3bc	36.0±1.8bc	13.2±0.5bc	14.5±0.6bc	2.8±0.2bc
Cd ₈	T ₀	23.2±0.8e	30.0±1.2e	5.0±0.2e	6.5±0.2e	23.0±1.3e	8.2±0.3e	7.5±0.3e	1.5±0.1e
	T ₁	28.8±0.9d	36.5±1.4d	6.5±0.3d	8.0±0.3d	29.0±1.5d	10.5±0.4d	10.5±0.4d	2.1±0.1d
	T ₂	27.0±0.9de	34.0±1.3de	6.0±0.3de	7.5±0.3de	27.0±1.4de	9.8±0.4de	9.5±0.4de	1.9±0.1de
	T ₃	31.5±1.0cd	40.0±1.5cd	7.3±0.3cd	9.0±0.3cd	32.5±1.6cd	11.8±0.5cd	12.2±0.5cd	2.4±0.1cd
Cd ₁₀	T ₀	17.7±0.7f	26.0±1.0f	4.0±0.2f	5.0±0.2f	20.0±1.1f	6.3±0.3f	6.3±0.3f	1.2±0.1f
	T ₁	26.2±0.8de	33.5±1.3de	5.8±0.3de	7.2±0.3de	26.5±1.4de	9.2±0.4de	9.8±0.4de	1.9±0.1de
	T ₂	25.2±0.8e	31.5±1.2e	5.5±0.3e	6.8±0.3e	24.5±1.3e	8.5±0.3e	9.0±0.4e	1.7±0.1e
	T ₃	31.2±0.9cd	37.0±1.4cd	6.8±0.3cd	8.5±0.3cd	30.0±1.5cd	10.8±0.4cd	11.5±0.5cd	2.2±0.1cd

Data expressed as mean ± Standard error. Means followed by the same letter (s) within a column do not differ significantly at $P \leq 0.05$ by Tukey's HSD test.

[Cd₀ = Without Cadmium (control), Cd₂ = 2 mgkg⁻¹ Cd, Cd₄ = 4 mgkg⁻¹ Cd, Cd₆ = 6 mgkg⁻¹ Cd, Cd₈ = 8 mgkg⁻¹ Cd, Cd₁₀ = 10 mgkg⁻¹ Cd, T₀ = No phyto-hormone, T₁ = 10 µM ABA, T₂ = 50 µM JA, T₃ = 10 µM ABA + 50 µM JA]

fresh weight, dry weight reached 76.3%, 42.3%, 70%, 70%, 50%, 71.4%, 82.5%, 83.3% respectively, improvement than untreated plants. Individual hormone applications T₁ (10 µM ABA) and T₂ (50 µM) also showed significant improvements, though generally less pronounced than the combined treatment.

Photosynthetic pigments and relative water content

Photosynthetic pigment concentrations and relative water content (RWC) exhibited marked declines under Cd stress (Table 2). Control plants (Cd₀T₀) maintained chlorophyll a at (2.85±0.08) mg g⁻¹ FW, chlorophyll b at

$1.48 \pm 0.05 \text{ mg g}^{-1} \text{ FW}$, carotenoids at $0.88 \pm 0.03 \text{ mg g}^{-1} \text{ FW}$, total chlorophyll at $4.33 \pm 0.09 \text{ mg g}^{-1} \text{ FW}$, and RWC at $85.7 \pm 1.2 \%$.

Cd exposure induced progressive degradation of photosynthetic pigments. At the highest concentration (Cd_{10}To), chlorophyll a decreased to $1.05 \pm 0.03 \text{ mg g}^{-1} \text{ FW}$, chlorophyll b to $0.60 \pm 0.02 \text{ mg g}^{-1} \text{ FW}$, carotenoids to $0.38 \pm 0.01 \text{ mg g}^{-1} \text{ FW}$, total chlorophyll to $1.65 \pm 0.04 \text{ mg g}^{-1} \text{ FW}$ which was 63.2%, 59.5%, 56.8%, and 61.9% respectively, reduction than control plants. RWC similarly declined to $58.3 \pm 0.8 \%$, resulting a 32% reduction compare to control plants.

The PGR treatments significantly mitigated pigment degradation. The T_3 ($10 \mu\text{M ABA} + 50 \mu\text{M JA}$) treatment demonstrated optimal protection across all Cd concentrations. At Cd_{10}T_3 , chlorophyll a recovered to $2.03 \pm 0.06 \text{ mg g}^{-1} \text{ FW}$ which was a 93.3% improvement over untreated, chlorophyll b to $1.08 \pm 0.04 \text{ mg g}^{-1} \text{ FW}$ (80% improvement), carotenoids to $0.68 \pm 0.02 \text{ mg g}^{-1} \text{ FW}$ (78.9% improvement), and total chlorophyll to $3.11 \pm 0.07 \text{ mg g}^{-1} \text{ FW}$ (88.5% improvement). RWC increased to $73.5 \pm 1.0 \%$ (26.1% improvement).

At lower Cd concentrations Cd_2 ($2 \text{ mg kg}^{-1} \text{ Cd}$) and Cd_4 ($4 \text{ mg kg}^{-1} \text{ Cd}$), plants treated with $10 \mu\text{M ABA} + 50 \mu\text{M JA}$ maintained pigment levels comparable to control conditions.

Biochemical parameters of S. rebaudiana

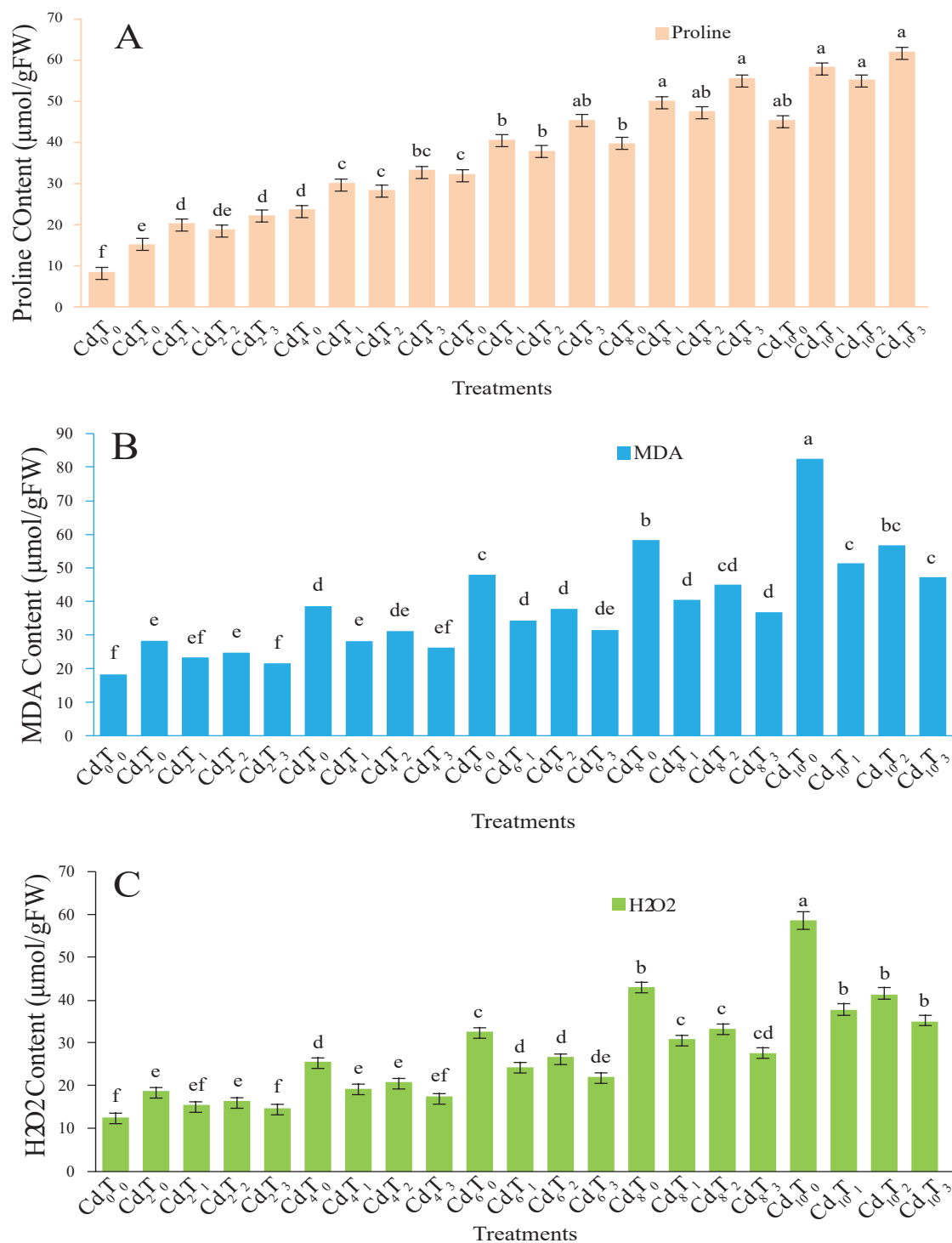
Cd stress induced substantial alterations in biochemical stress markers (Figure 1). Proline content, MDA content, and H_2O_2

concentration increased progressively with Cd exposure, while total antioxidant capacity (TAC) showed variable responses depending on stress severity.

In control plants (Cd_0To), proline, MDA, H_2O_2 , and total antioxidant capacity (TAC) were recorded at $8.5 \pm 0.4 \mu\text{mol g}^{-1} \text{ FW}$, $18.3 \pm 0.7 \text{ nmol g}^{-1} \text{ FW}$, $12.5 \pm 0.5 \mu\text{mol g}^{-1} \text{ FW}$, and $38.5 \pm 1.5 \text{ mg AAE g}^{-1} \text{ FW}$, respectively. Under the highest Cd treatment (Cd_{10}To), these parameters increased markedly: proline rose to $45.8 \pm 1.5 \mu\text{mol g}^{-1} \text{ FW}$ (a 438.8% increase), MDA to $82.5 \pm 2.5 \text{ nmol g}^{-1} \text{ FW}$ (350.8% increase), and H_2O_2 to $58.7 \pm 1.9 \mu\text{mol g}^{-1} \text{ FW}$ (369.6% increase). In contrast, TAC showed only a modest increase to $42.3 \pm 1.6 \text{ mg AAE g}^{-1} \text{ FW}$.

The PGR application modulated these stress responses where T_3 ($10 \mu\text{M ABA} + 50 \mu\text{M JA}$) treatment induced the highest proline accumulation ($62.3 \pm 2.0 \mu\text{mol/g FW}$ at Cd_{10}T_3), while simultaneously reducing oxidative damage markers (MDA: $47.2 \pm 1.6 \text{ nmol/g FW}$, 42.8% reduction; H_2O_2 : $35.2 \pm 1.2 \mu\text{mol/g FW}$, 40% reduction compared to Cd_{10}To). Most notably, T_3 treatment enhanced TAC to $68.7 \pm 2.4 \text{ mg AAE/g FW}$ (62.4% increase over untreated Cd_{10} plants).

This pattern persisted across all Cd concentrations, with T_3 consistently promoting higher proline accumulation, greater TAC, and reduced lipid peroxidation and oxidative stress. The enhanced proline synthesis combined with elevated antioxidant capacity under T_3 treatment indicated more effective protective mechanisms.



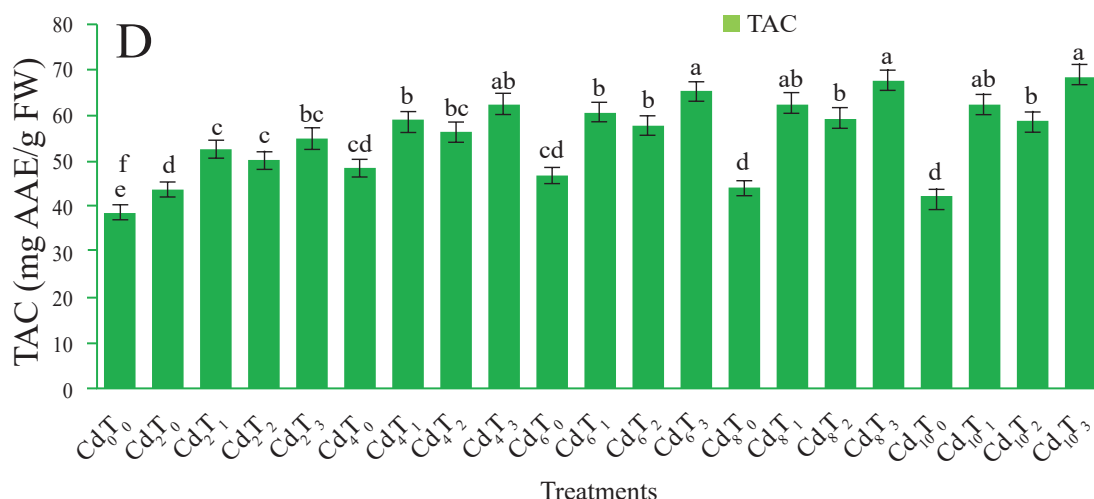


Fig. 1. Effects of Cd stress and phytohormone application on (A) proline content, (B) MDA content, (C) H_2O_2 content and (D) Total anti-oxidant content (TAC) in *S. rebaudiana*. Error bars indicate standard error. Different alphabetical letters on the bars show significant differences among the treatments ($p < 0.05$).

[Cd₀ = Without Cadmium (control), Cd₂ = 2 mg kg⁻¹ Cd, Cd₄ = 4 mg kg⁻¹ Cd, Cd₆ = 6 mg kg⁻¹ Cd, Cd₈ = 8 mg kg⁻¹ Cd, Cd₁₀ = 10 mg kg⁻¹ Cd, T₀ = No phyto-hormone, T₁ = 10 μ M ABA, T₂ = 50 μ M JA, T₃ = 10 μ M ABA + 50 μ M JA]

Discussion

Morphological responses to Cd stress and mitigation by PGR

The study demonstrates that Cd stress severely impairs morphological development of *S. rebaudiana*, with progressive reductions in growth parameters at increasing metal concentrations. This growth inhibition aligns with previous findings in various plant species, where Cd interferes with cell division, cell elongation, and nutrient uptake (Li et al., 2023; Zulfiqar et al., 2022). At 10 mg kg⁻¹ Cd, the 58-68% declines in growth parameters reflect severe phytotoxicity because Cd is

nonessential heavy metal and causes disruption of several physiological phenomena.

The exogenous PGR treatment, especially the combined ABA and JA application 10 μ M ABA + 50 μ M JA being most notable, suggest that altered physiology could be ameliorated. It has been reported that ABA triggers stomatal closure and osmotic adjustment during stress, while JA induces defense gene expression as well as secondary metabolism (Zhang et al., 2006; Wasternack and Hause, 2013). Kim et al. (2021) also observed similar synergistic effects of ABA and JA in attenuating heavy metal stress by associating the enhanced growth with

Table 2. Effects of ABA and JA applied singly and in combination on photosynthetic pigment and relative water content of *S. rebaudiana* under cadmium stress.

Cd Concentration (mgkg ⁻¹)	Treatment	Chlorophyll a (mg g ⁻¹ FW)	Chlorophyll b (mg g ⁻¹ FW)	Carotenoids (mg g ⁻¹ FW)	Total Chlorophyll (mg g ⁻¹ FW)	RWC (%)
Cd ₀	T ₀	2.85±0.08a	1.48±0.05a	0.88±0.03a	4.33±0.09 a	85.7±1.2a
	T ₀	2.52±0.07b	1.32±0.04b	0.78±0.03b	3.84±0.08 def	79.5±1.1b
Cd ₂	T ₁	2.70±0.08ab	1.42±0.05ab	0.84±0.03a	4.12±0.09 abc	83.2±1.2a
	T ₂	2.65±0.07ab	1.38±0.05ab	0.82±0.03ab	4.03±0.09 bcd	82.5±1.1ab
	T ₃	2.75±0.08a	1.45±0.05a	0.86±0.03a	4.20±0.09 ab	84.5±1.2a
Cd ₄	T ₀	2.18±0.06c	1.15±0.04c	0.68±0.02c	3.33±0.07 ij	73.8±1.0c
	T ₁	2.48±0.07b	1.30±0.04b	0.78±0.03b	3.78±0.08 efg	79.0±1.1b
	T ₂	2.40±0.07b	1.25±0.04b	0.75±0.03b	3.65±0.08 fg	77.5±1.1b
	T ₃	2.58±0.07ab	1.36±0.05ab	0.82±0.03ab	3.94±0.09 cde	81.2±1.1ab
Cd ₆	T ₀	1.82±0.05d	0.95±0.03d	0.58±0.02d	2.77±0.06 m	68.2±0.9d
	T ₁	2.22±0.06c	1.18±0.04c	0.72±0.03c	3.40±0.07 hi	75.5±1.0c
	T ₂	2.10±0.06cd	1.12±0.04cd	0.68±0.02cd	3.22±0.07 ijk	73.8±1.0cd
	T ₃	2.35±0.07bc	1.25±0.04bc	0.78±0.03bc	3.60±0.08 gh	78.0±1.1bc
Cd ₈	T ₀	1.48±0.04e	0.78±0.03e	0.48±0.02e	2.26±0.05 o	63.5±0.9e
	T ₁	1.95±0.05d	1.05±0.04d	0.65±0.02d	3.00±0.06 kl	71.2±1.0d
	T ₂	1.85±0.05d	1.00±0.03d	0.62±0.02d	2.85±0.06 lm	69.5±0.9d
	T ₃	2.10±0.06cd	1.12±0.04cd	0.72±0.03cd	3.22±0.07 ijk	74.8±1.0cd
Cd ₁₀	T ₀	1.05±0.03f	0.60±0.02f	0.38±0.01f	1.65±0.04 p	58.3±0.8f
	T ₁	1.75±0.05d	0.95±0.03d	0.58±0.02d	2.70±0.06 mn	68.0±0.9d
	T ₂	1.62±0.05de	0.88±0.03de	0.54±0.02de	2.50±0.06 n	66.2±0.9de
	T ₃	2.03±0.06cd	1.08±0.04cd	0.68±0.02cd	3.11±0.07 jk	73.5±1.0cd

Data expressed as mean ± Standard error. Means followed by the same letter (s) within a column do not differ significantly at $P \leq 0.05$ by Tukey's HSD test.

[Cd₀ = Without Cadmium (control), Cd₂ = 2 mgkg⁻¹ Cd, Cd₄ = 4 mgkg⁻¹ Cd, Cd₆ = 6 mgkg⁻¹ Cd, Cd₈ = 8 mgkg⁻¹ Cd, Cd₁₀ = 10 mgkg⁻¹ Cd, T₀ = No phyto-hormone, T₁ = 10 µM ABA, T₂ = 50 µM JA, T₃ = 10 µM ABA + 50 µM JA].

increased activities of antioxidant enzymes along with reduced oxidative damage.

The enhanced efficacy of 10 μM ABA + 50 μM JA (T_3) treatment on the restoration plant height, leaf attributes and root traits indicates that combined PGR treatments could provide superior overall stress protection than individual ones. This may be due to contribution of ABA (improve water relation and osmotic adjustment) and complement the JA-induced activation of defense pathways (Per et al., 2018).

Photosynthetic pigment protection under Cd stress

The marked reduction in chlorophyll a and b, and carotenoids caused by Cd stress confirm the documented mechanisms of heavy metal phytotoxicity. Cd replaces magnesium from chlorophyll molecules, suppresses the enzymes involved in chlorophyll biosynthesis, and enhances the activity of chlorophyllase (Parmar et al., 2013; Küpper et al., 2007). The 60-63% photosynthetic pigment reduction observed at 10 mg kg^{-1} Cd in this study corresponds well to what has been reported for stress sensitive species.

The pigment retention induced by PGR application, would be the important protective way for stress. The T_3 (10 μM ABA + 50 μM JA) was able to maintain the Chl level 88-93% higher than unstressed untreated plants indicates that urges up a number of protective activities. ABA is reported to mediate stomatal conductance and decrease the level of photooxidative stress by preventing over-

accumulation of light energy (Munemasa et al., 2015), whereas JA induces production of photoprotective compounds and increases chloroplast antioxidant defenses (Huang et al., 2019).

The effect of PGR treatment on carotenoids content deserves to be particularly stressed. Carotenoids have two functions, as accessory pigments in light harvesting and also as important antioxidants that can scavenge reactive oxygen species and prevent photoinhibition of photosystem II (Jahns and Holzwarth, 2012). The 79% increment of carotenoid content in T_3 (10 μM ABA + 50 μM JA)-treated plants at Cd_{10} (10 mg kg^{-1} Cd) indicates a higher potential for photoprotection. A parallel observation was reported by Sirhindi et al. (2016) in *Glycine max* under nickel stress, it was found that JA treatment enhanced carotenoid biosynthesis via up-regulation of phytoene synthase genes.

The preservation of RWC under phytohormone treatment also indicates the protective function of the hormones. The 26 % increase in RWC at $\text{Cd}_{10}T_3$ (10 mg kg^{-1} Cd + 10 μM ABA + 50 μM JA) as compared to control plants suggests better cellular water relations that are important for maintenance of turgor pressure and metabolism. The well-known role of ABA in stomatal regulation and aquaporin gene expression would probably contribute to this enhancement (Aroca et al., 2012).

The positive correlation between pigment retention rate and plant growth parameters

indicates that photosynthetic capacity maintaining may be one of the primary mechanisms for morphological enhancements which is associated with the treatment of PGR. This relation highlights integration of stress responses and balance between the protection of photosynthetic machinery and overall performance in plants grown under metal-induced stress.

Biochemical adaptations and antioxidant responses

The remarkable change of proline, MDA, H_2O_2 in plant in response to cadmium are typical stress responses. Proline is an adaptive osmoprotectant, which stabilizes proteins and membranes as well as acting as IS ROS scavenger (Hayat et al., 2012). At $Cd_{10}T_0$ ($10 \text{ mgkg}^{-1} \text{ Cd}$) 439% excess in proline content is reflected, suggesting strong stress-dependent accumulation. However, the greater increase under T_3 ($10 \text{ }\mu\text{M ABA} + 50 \text{ }\mu\text{M JA}$) treatment ($62.3 \text{ }\mu\text{molg}^{-1} \text{ FW}$) together with lower contents of oxidative damage markers indicates that plants have switched from inducible to systemic protective accumulation.

The MDA, a lipid peroxidation product, is an accurate index of oxidative damage to the membranes of cells. The equivalent of at least 351% MDA increase on $Cd_{10}T_0$ ($10 \text{ mgkg}^{-1} \text{ Cd}$) indicates a severe membrane injury. The T_3 ($10 \text{ }\mu\text{M ABA} + 50 \text{ }\mu\text{M JA}$) induced 43% reduction reflects a protective effect against oxidative stress. Likewise, the 40% decrease

of H_2O_2 content in response to T_3 ($10 \text{ }\mu\text{M ABA} + 50 \text{ }\mu\text{M JA}$) treatment following high Cd exposure indicated stimulated activity of antioxidant enzymes. These results are also consistent with the study of Kim et al. (2021) in which superoxide dismutase, catalase, and ascorbate peroxidase activities were found to be increased by ABA and JA co-application in heavy metal stressed plants.

The most important result is that the total antioxidant capacity increased by 62% upon T_3 treatment at Cd_{10} . Increased TAC is probably mediated through the activation of enzymatic and non-enzymatic antioxidants. JA is characterized to activate the transcription factors involved in the regulation of antioxidant gene expression and ABA promotes biosynthesis of antioxidants metabolites like flavonoid and phenolics (Farooq et al., 2016). Combined treatment enhanced stress mitigation through increased TAC production, indicating that the complementary activation of various antioxidant pathways takes place.

The combined effect of the increased proline accumulation, TAC and decreased levels of markers related to oxidative damage when plants are subjected to $10 \text{ }\mu\text{M ABA} + 50 \text{ }\mu\text{M JA}$ (T_3) suggests that a well-arranged stress defense strategy is in place. This phenomenon indicates that PGR treatment transforms from passive defense under stress to active coping with the stress, which is in line with a concept of stress priming presented by Martinez-Medina et al. (2016).

Conclusion

Cadmium contamination severely impaired the growth, physiology, and biochemical homeostasis of *Stevia rebaudiana*, confirming its sensitivity to heavy metal stress. However, exogenous application of ABA and JA particularly their combined application significantly mitigated Cd-induced toxicity by enhancing photosynthetic efficiency, maintaining cellular water balance, reducing lipid peroxidation, and strengthening antioxidant defenses. In this study, *Stevia* plants treated with the combined application of ABA and JA (10 μ M ABA + 50 μ M JA) produced better phenotypic responses and accumulated higher photosynthetic pigments, relative water, and proline content as compared to Cd stress plants only. Overall, the study establishes ABA + JA co-application as an efficient, low-cost, and environmentally compatible approach for improving *Stevia* performance in Cd-polluted soils. This strategy offers strong potential for sustainable *Stevia* cultivation in industrially contaminated regions and warrants further evaluation under field conditions.

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Conflict of Interest

The authors affirm that no financial or commercial relationships that might be

construed as a potential conflict of interest existed during the course of the research.

Author Contributions

Supervision, conceptualization, funding acquisition: Md. Ashraful Haque and Shah Mohammad Naimul Islam; Investigation, initial draft, data analysis, writing: Md. Abul Kalam Azad; Methodology: Haider Iqbal Khan; Data curation, visualization, review and editing: Md. Ali-ahad and Samia Jahan Purnota.

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