



RESEARCH ARTICLE

Exogenous glutathione enhances proline accumulation and cadmium (Cd) translocation in the leaves of *in vitro* *Celosia argentea* L.

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Abstract

Glutathione (GSH) is a tripeptide present in the nonenzymatic antioxidant system of plants. *Celosia argentea* L. is an ornamental species capable of efficiently absorbing cadmium (Cd). This study evaluated the effect of exogenous GSH on the development and Cd accumulation of *in vitro* *C. argentea* plants. The findings recorded in this study pertain to growth, biochemical and Cd accumulation parameters. Cd stress inhibited the growth of the shoots and roots of *C. argentea*. In non-stress conditions, exogenous GSH significantly enhanced root growth indices; however, Cd stress significantly alter root growth indices. At 2.5 mM GSH, the optimal concentration, root length grew by an average of 25 %, while average fresh and dry biomass increased threefold and twofold, respectively, compared to the control. Under Cd stress conditions, exogenous GSH slightly improved leaf pigmentation in *C. argentea*. Simultaneously, the proline content, which helps plants respond to stress, reached over 0.86 $\mu\text{mol/g}$ across all 3 concentrations (1, 2.5 and 5 mM), while the Cd-stressed sample without GSH had 0.44 $\mu\text{mol/g}$. Adding 2.5 mM GSH to the growing medium greatly improved the translocation factor (TF-an important measure in phytoremediation) but did not change how much Cd the plants' leaves could accumulate. The results of this study revealed that GSH has a role in the physical and chemical processes of *C. argentea* leaves when they are under stress from Cd.

Keywords: cadmium; *Celosia argentea*; exogenous glutathione; *in vitro*; stress

Introduction

Cadmium (Cd) is an element that is non-essential for the growth and development of organisms, resulting in cellular damage, disruption of homeostasis and suppression of vital enzyme activity. The presence of Cd in plant cell structures alters membrane permeability, induces water imbalance and impairs respiration and photosynthesis, thus diminishing plant life (1). Plants uptake Cd from the environment via their roots and translocate it to various organs through the xylem (2). Cadmium accumulation refers to the capacity of plants to uptake and store Cd within their tissues, exemplified in certain marine diatoms that utilise Cd as a replacement in environments lacking in zinc (3). Nonetheless, the capacity of plants to uptake Cd, particularly in edible species, raises significant concerns due to its potential detrimental effects on human health (4).

Soil washing is regarded as an inefficient and expensive technique for remediating heavy metal-contaminated soil. The treated soil exhibits alterations in its characteristics and structure (5). Phytoremediation leverages the capacity of plants to absorb and accumulate metals, rendering it a cost-effective and efficient technique for remediating soil contaminated with heavy metals (6).

Prior research has found over 450 plant species capable of absorbing and accumulating heavy metals, with several species demonstrating efficacy in simultaneously absorbing numerous types of heavy metals (7). This demonstrates the potential use of plants in remediating soil contamination. *Celosia argentea* L. is a widely favoured ornamental plant in Vietnam, owing to its compatibility with the local temperature and soil conditions (8). Numerous investigations demonstrated that this plant species can efficiently absorb Cd from the soil (9–11). Plants possess specific mechanisms to restrict the uptake of Cd because of its role as a stressor. Numerous approaches have been employed to enhance the capacity of plants to absorb these metal ions (6, 7). Glutathione (GSH) is regarded as a phytochelatin that binds to metals, facilitating the isolation of these stressors in plants (12). Furthermore, under normal settings, GSH serves as a crucial element in safeguarding plant cells from oxidative stress, which arises from several agents, including Cd as one of the contributing factors (13). Therefore, this study aims to assess the influence of GSH on the capacity of *C. argentea* to absorb Cd from culture medium, while concurrently evaluating the role of GSH in Cd-induced stress in these plants.

Materials and Methods

Celosia argentea seeds were sterilised with ethanol and NaClO grown in woody plant medium (WPM) supplemented with 30 g of sucrose and 10 g of agar, with a pH of 5.8 (8, 14). The GSH was supplied at doses of 0, 1, 2.5 and 5 mM. Simultaneously, 25 mg/L of Cd (by using CdCl₂·2.5H₂O salt) was included in the culture medium to establish Cd stress conditions following the previous studies, or it was lacking (15, 16). 30-day-old seedlings were subjected to induction for a duration of 30 days during the studies. Culture flasks were maintained at 25 °C, with a light intensity of 2000 lux, under a photo period of 16 hr of light and 8 hr of darkness.

Leaf pigments were extracted using 100 % cold ethanol and absorbance was quantified at 480, 645 and 663 nm for carotenoids and 2 types of chlorophyll, respectively. The pigment content was determined using the formula established by previous research (17, 18). The proline content was quantified by measuring the absorbance at 520 nm of the product resulting from the reaction between the plant extract and ninhydrin in an acidic condition, heated in a water bath at 100 °C (18). The plant extract in methanol:chloroform (4:1) was treated with 2 mM FeCl₂ and 5 mM ferrozine to assess chelation efficiency by measuring absorbance at 562 nm every 10 min (19). The GSH was determined by reacting to the thiol group in GSH with Ellman's reagent, which has a maximum absorbance at 412 nm (20). This research employed a Thermo Scientific Multiskan SkyHigh Spectrophotometer to assess wavelength absorption. Cadmium concentration in plant tissues was measured using inductively coupled plasma mass spectroscopy (ICP-MS) technique (21). Bioconcentration factor (BCF) was calculated as the ratio of metal concentration in plant to metal concentration in medium. Translocation factor (TF) was calculated as the ratio of metal concentration in the shoot to that in the root to evaluate the ability to transport metals from roots to the shoot of the plant (22).

Data are expressed as mean ± SD based on 5 replicates. Graphs are created utilising Microsoft Excel. One-way ANOVA and post-hoc Tukey variance analysis procedures with a significance level of alpha = 0.05 were done using SPSS software. Principal components analysis (PCA) and Pearson correlation were analyzed using R.

Results

Comparative analysis of exogenous GSH effects on *Celosia argentea* plants *in vitro*

Adding GSH to the culture media had no effect on *in vitro* *C. argentea* shoot growth, including shoot length and biomass (Fig. 1A, B and C), except for 2.5 mM GSH supplementation, which slightly reduced shoot height (13.76 ± 0.43 cm vs. 15.21 ± 0.36 cm of the control). Glutathione significantly affected on *C. argentea* root growth, resulting in increased length (8.21 ± 1.3 cm for the control sample and 10.29 ± 1.31 cm for the 2.5 mM GSH treatment) (Fig. 1D), fresh biomass (FW) (0.842 ± 0.190 g for the control sample and 2.738 ± 0.610 g for the 2.5 mM GSH treatment) (Fig. 1E) and dry biomass (DW) (0.091 ± 0.017 g for the control sample and 0.184 ± 0.045 g for the 2.5 mM GSH treatment) (Fig. 1F). The addition of 5 mM GSH drastically reduced root length, to 4.92 ± 0.81 cm, compared to the control treatment (8.21 ± 1.3 cm) (Fig. 1B).

Chlorophyll and carotenoid levels varied similarly between treatments. After adding exogenous GSH, leaf pigment concentration ranged from 2.1–4.1, 1.2–1.9 and 1.6–3.3 µg/g FW for chlorophyll a, chlorophyll b and carotenoid compounds, respectively (Fig. 2A, B and C). The plants grown on exogenous GSH medium showed a rapid increase in proline content at various GSH doses in root, stem and leaves (Fig. 2D, E and F). Proline content in GSH-treated leaves was consistently over 0.869 µmol/g FW compared to the control (0.370 ± 0.032 µmol/g FW). Roots with 1 mM GSH had 3.5 times more proline than the control (0.757 ± 0.042 µmol/g FW), whereas stem tissue exhibited a slight increase at 5 mM GSH (1.354 ± 0.164 µmol/g FW). The GSH in the culture medium increased endogenous GSH levels in root and shoot tissues (Fig. 2G, H and I), ensuring stability. The quantity of 1 mM GSH treatment in leaf tissue dramatically increased, reaching 1.035 ± 0.226 µmol/g FW after supplementation. *In vitro*, *C. argentea* roots exhibited no change in chelating efficacy (Fig. 2J, K and L), whereas stems showed a minor drop (22–26 % compared to 33 % in control) and leaves showed a considerable decrease (25–30 % compared to 46 % of the control) in the GSH treatments.

Evaluation of 1–5 mM exogenous GSH-mediated modulation of *Celosia argentea in vitro* under cadmium stress treatments

Exposure to Cd at 25 mg/L had a substantial effect on growth indicators. Specifically, shoot height, shoot biomass and root length were all significantly reduced (Fig. 1). The plant's growth metrics, including shoot biomass (1.401 ± 0.426 g FW and 0.114 ± 0.035 g DW), were significantly lower than the control (2.782 ± 0.428 g FW and 0.177 ± 0.021 g DW). Under conditions with and without 25 mg/L Cd (without exogenous GSH in both), shoots (12.56 ± 0.67 cm and 15.21 ± 0.36 cm) and roots (4.89 ± 0.89 cm and 8.21 ± 1.3 cm, respectively) had average lengths.

Leaf pigment, proline, endogenous GSH and chelation efficiency in *C. argentea* showed no statistically significant difference between Cd stress 25 mg/L and control (WPM only). Both studies showed approximately 3.1 µg/g FW for chlorophyll a, 1.6 µg/g FW for chlorophyll b and 2.7 µg/g FW for carotenoids in leaf pigmentation (Fig. 2A, B and C). Proline concentrations in roots and stems ranged from 0.6 to 0.8 µmol/g (Fig. 2D and E), whereas leaves contained 0.3 to 0.4 µmol/g (Fig. 2F). The GSH levels were about 0.4 and 0.17 µmol/g in roots and stems, respectively and 0.25 in leaves (Fig. 2G, H and I). Meanwhile, leaf chelate effectiveness ranged between 38.40 and 46.48 %, root 29.66–31.25 % and stem 29.53–33.89 % (Fig. 2J, K and L).

The biomass indices of *C. argentea* plants in Cd stress conditions were comparable with and without exogenous GSH supplementation. Multiple GSH contents in the Cd stress environment showed similar length parameters (7.6–10.7 cm for shoot height and 1.54–2.62 cm for root length) and were lower than *C. argentea* plants grown in the 25 mg/L Cd stress environment, reaching 12.56 ± 0.67 cm for shoot height and 4.89 ± 0.89 cm for root length (Fig. 1).

Adding GSH to *C. argentea* under Cd stress conditions increased leaf pigments at various levels. Adding 1 mM of exogenous GSH significantly increased chlorophyll a, chlorophyll b and carotenoid content compared to Cd stress treatment (5.464 ± 0.510, 2.277 ± 0.181 and 4.328 ± 0.619 µg/g FW, respectively) (Fig. 2A, B and C). The control samples and experimental plants grown

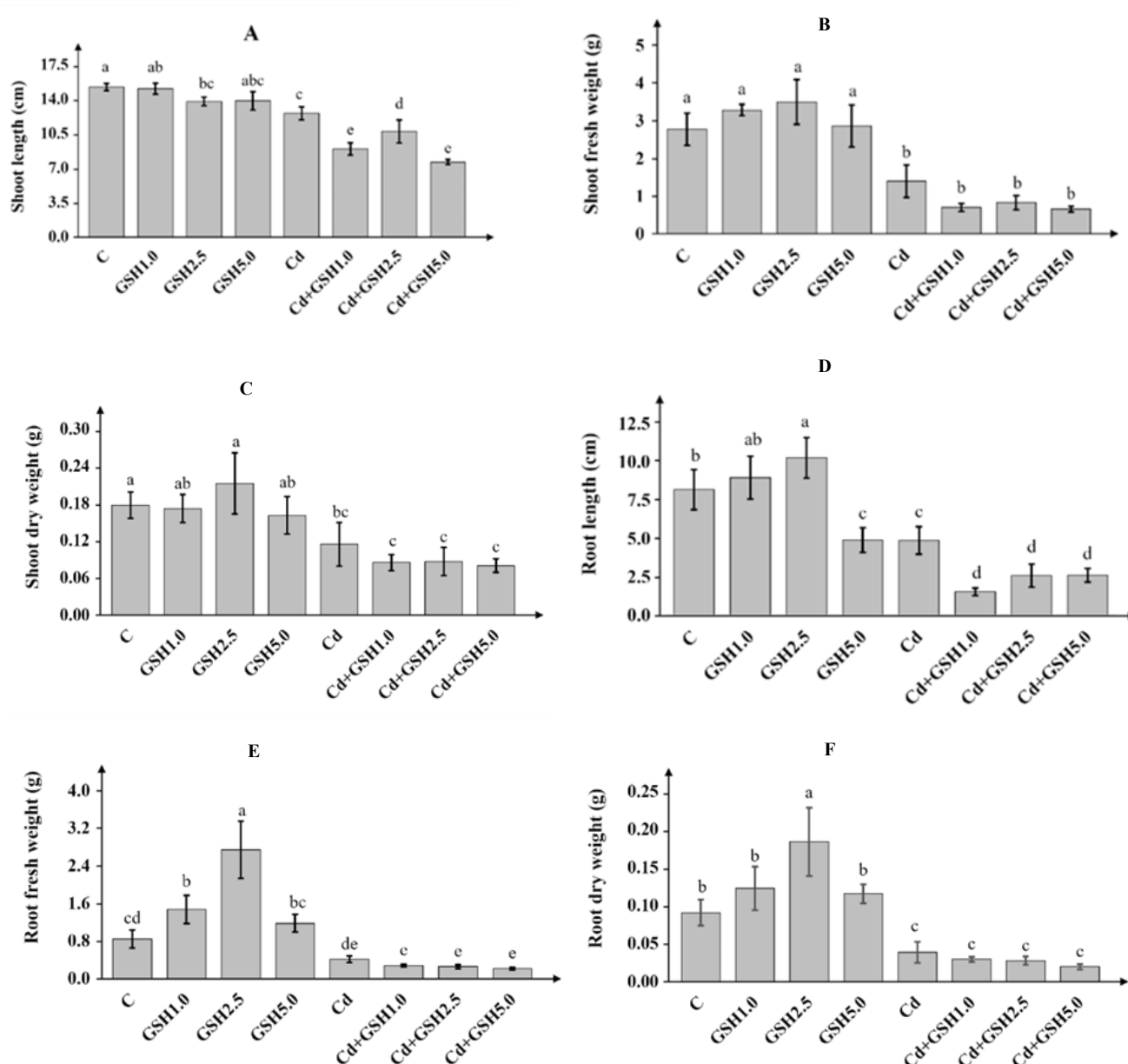


Fig. 1. Impact of different exogenous GSH concentrations on the growth parameter of *Celosia argentea* in both Cd stressed and non-stressed conditions. (A)- Shoot length, (B)- Root length, (C)- Shoot fresh weight, (D)- Root fresh weight, (E)- Shoot dry weight, (F)- Root dry weight. C: control, GSH1.0: medium with 1 mM GSH, GSH2.5: medium with 2.5 mM GSH, GSH5.0: medium with 5.0 mM GSH, Cd: medium with 25 mg/L Cd, Cd+GSH1.0: medium with 25 mg/L Cd and 1 mM GSH, Cd+GSH2.5: medium with 25 mg/L Cd and 2.5 mM GSH, Cd+GSH5.0: medium with 25 mg/L Cd and 5.0 mM GSH. The different letters show the significant differences ($p < 0.05$).

in the medium supplied with exogenous GSH but subjected to Cd stress exhibited significantly increased pigment content under this condition. Adding GSH and Cd to the growth medium did not influence proline content in roots and stems but did increase total proline in leaves (around $0.8 \mu\text{mol/g FW}$) compared to the Cd stress treatment ($0.445 \pm 0.068 \mu\text{mol/g FW}$) (Fig. 2D, E and F). Exogenous GSH supplementation enhanced intracellular GSH marginally in stems and leaves while maintaining the same trend in roots (Fig. 2G, H and I). Under Cd stress, GSH supplementation reduced chelation efficiency across all parts of plant. Specifically, roots treated with 2.5 and 5 mM GSH showed 12 % and 8 % lower chelation efficiency than the control. Compared to stress treatment of 29.53 % and 38.40 %, stems and leaves had chelation effectiveness of 17–20 % and 15–16 % via varying GSH levels in the medium (Fig. 2J, K and L).

Effects of exogenous GSH on Cd accumulation and correlation among physiological indicators in *C. argentea* *in vitro* under Cd stress

Cadmium accumulation in shoots supplemented with 2.5 mM GSH and Cd resulted in $214.216 \pm 23.681 \text{ mg/kg DW}$, while the Cd stress treatment yielded $194.191 \pm 13.847 \text{ mg/kg DW}$, with no significant difference (Fig. 3A). The other two exogenous GSH supplementation levels reduced Cd accumulation below 125 mg/kg DW in shoots. These roots showed a declining tendency below 513 mg/kg DW compared to Cd stress at $915.178 \pm 30.504 \text{ mg/kg DW}$ (Fig. 3B). The TF index revealed that adding exogenous GSH resulted in increased Cd translocation to *C. argentea* shoots at concentrations of 1 mM (0.293 ± 0.043) and 2.5 mM (0.381 ± 0.025) compared to the control (0.212 ± 0.014), whereas 5 mM concentration of exogenous GSH reduced the ability of Cd translocation to shoots of *in vitro* *C. argentea* plants (Fig. 3C). The BCF index shows similar trends as TF index (Fig. 3D).

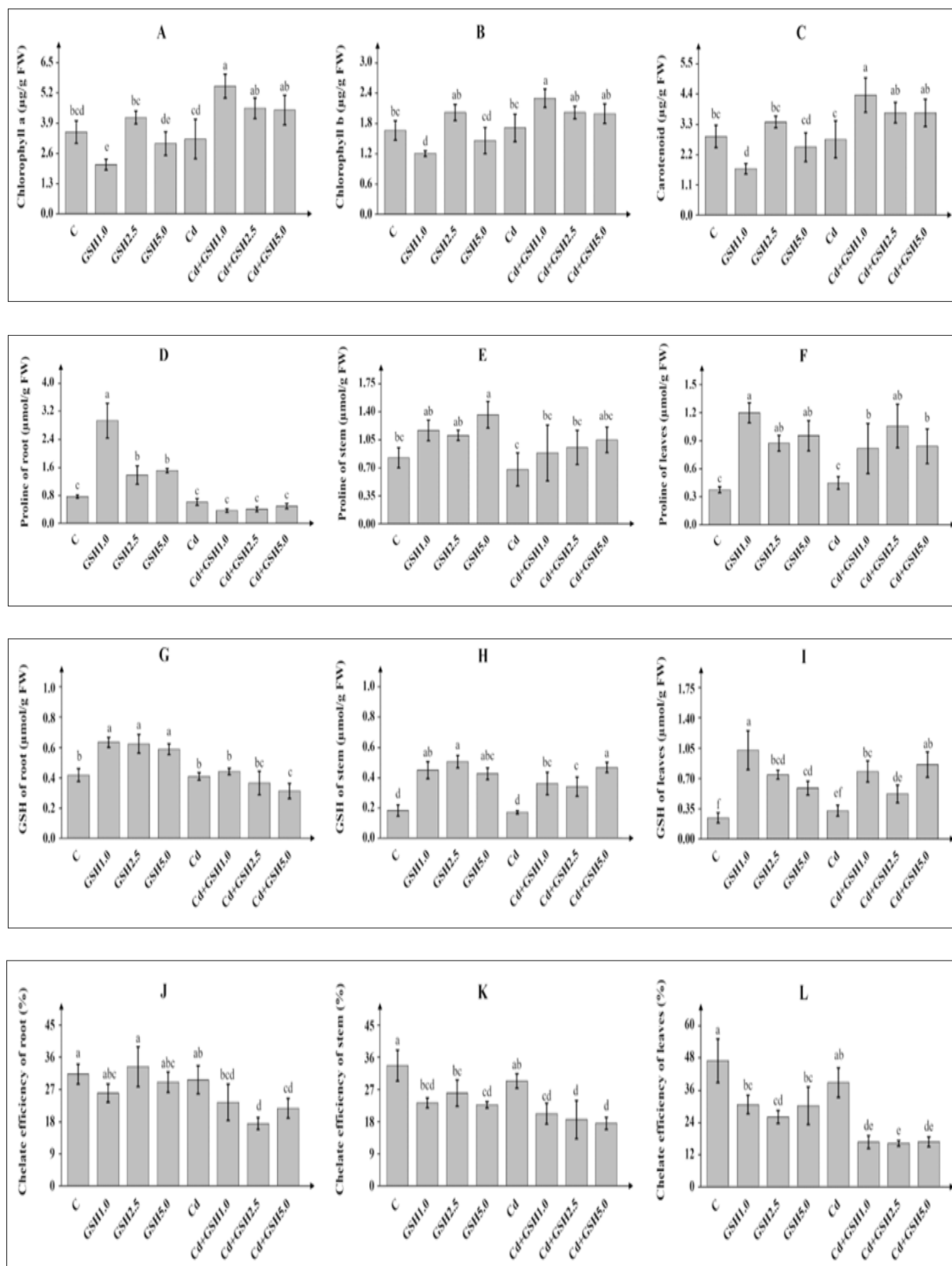


Fig. 2. Impact of different exogenous GSH concentrations on the biochemical parameters of *Celosia argentea* in both Cd stressed and non-stressed conditions. (A)- Chlorophyll a, (B)- Chlorophyll b, (C)- Carotenoid, (D)- Root proline content, (E)- Stem proline content, (F)- Leaves proline content, (G)- Root GSH content, (H)- Stem GSH content, (I)- Leaves GSH content, (J)- Root chelating efficiency, (K)- Stem chelating efficiency, (L)- Leaves chelating efficiency. C: control, GSH1.0: medium with 1 mM GSH, GSH2.5: medium with 2.5 mM GSH, GSH5.0: medium with 5.0 mM GSH, Cd: medium with 25 mg/L Cd, Cd+GSH1.0: medium with 25 mg/L Cd and 1 mM GSH, Cd+GSH2.5: medium with 25 mg/L Cd and 2.5 mM GSH, Cd+GSH5.0: medium with 25 mg/L Cd and 5.0 mM GSH. The different letters show the significant differences ($p < 0.05$).

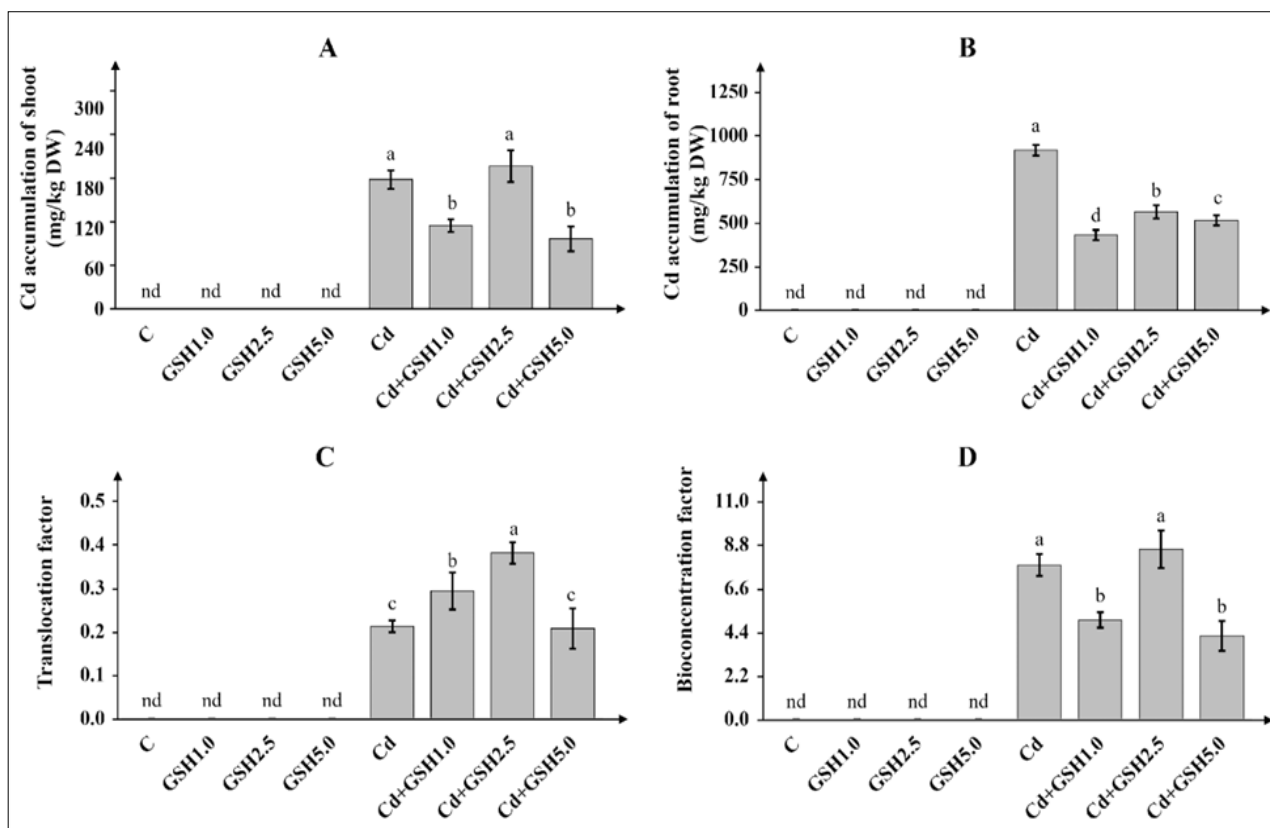


Fig. 3. Impact of different exogenous GSH concentrations on the Cd accumulation of *Celosia argentea*. (A)- Shoot Cd accumulation, (B)- Root Cd accumulation, (C)- Translocation factor, (D)- Bioconcentration factor. nd: data were below the detection limit or not calculated. C: control, GSH1.0: medium with 1 mM GSH, GSH2.5: medium with 2.5 mM GSH, GSH5.0: medium with 5.0 mM GSH, Cd: medium with 25 mg/L Cd, Cd+GSH1.0: medium with 25 mg/L Cd and 1 mM GSH, Cd+GSH2.5: medium with 25 mg/L Cd and 2.5 mM GSH, Cd+GSH5.0: medium with 25 mg/L Cd and 5.0 mM GSH. The different letters show the significant differences ($p < 0.05$).

The growth and biochemical characteristics of the *C. argentea* plant exhibited substantial changes when it was given GSH and grown in culture media with different concentrations from 0 mM to 5 mM, both with and without Cd stress. The findings of PCA revealed that PCA1 (dim1) and PCA2 (dim2) explained 71.2 % of the data. The culture media studies without GSH supplementation, GSH and Cd supplementation and GSH supplementation only conditions, all showed evident clustering (Fig. 4). The correlation between growth and biochemical parameters was evaluated and it was shown to be increasing (Fig. 5). Specifically, we observed some noticeable differences when we supplemented the culture medium with GSH and Cd compared to the condition without Cd stress. The indicators of leaf pigmentation and GSH levels were negatively correlated with shoot and root growth, as revealed by Pearson correlation analysis. The accumulation of Cd in tissues was negatively associated with shoot and root growth characteristics. Proline content was positively linked with GSH content.

Discussion

Plant roots can uptake nitrogen from many sources, including organic and inorganic compounds. For the organic nitrogen uptake pathways, proteases, either bound to the cell wall/membrane or free and of plant origin, are present in the roots and are released to hydrolyze proteins into peptides or oligopeptides for active cellular absorption (23). Exogenous GSH is a tripeptide and thus an oligopeptide; therefore, its exogenous application may facilitate easier absorption by plant roots through similar uptake

mechanisms for small peptides. Exogenous GSH has minimal effect on shoot growth in *C. argentea*, although it enhances growth indices in the roots. The root growth-promoting role of GSH has been evidenced in research involving various species, including the enhancement of lateral root development and the stimulation of adventitious root formation (24, 25). Glutathione exerts a concentration-dependent influence on plant physiology and growth; exogenous GSH maximally stimulated shoot height of wheat at a concentration of 2 mM, whereas shoot fresh biomass peaked at 0.5 mM (26). In our investigation, a concentration of 2.5 mM demonstrated optimal root development. Auxin is critically vital in regulating root growth and development. Previous studies indicate that GSH depletion in mutant plants diminishes auxin sensitivity (27), suggesting that GSH is likely involved in the regulation of root architecture under stress circumstances. The incorporation of GSH into the culture media in this study indicated that enhanced root growth parameters may be associated with heightened auxin sensitivity in *C. argentea* roots, particularly with the inclusion of 2.5 mM GSH in the medium. Glutathione has had limited impact on shoot growth; nevertheless, exogenous GSH has significantly reduced oxidative stress in plants, particularly in shoots (28, 29).

Glutathione's role in plant defense under specific stressors was demonstrated by numerous prior studies (26, 30, 31). Chlorophyll is an essential compound for providing energy sources for plants. In our results, GSH enhanced chlorophyll content under Cd stress conditions. This outcome aligns with previous research on heat and drought stress (26). Proline functions as a metal chelator and a defender of cellular components against the detrimental

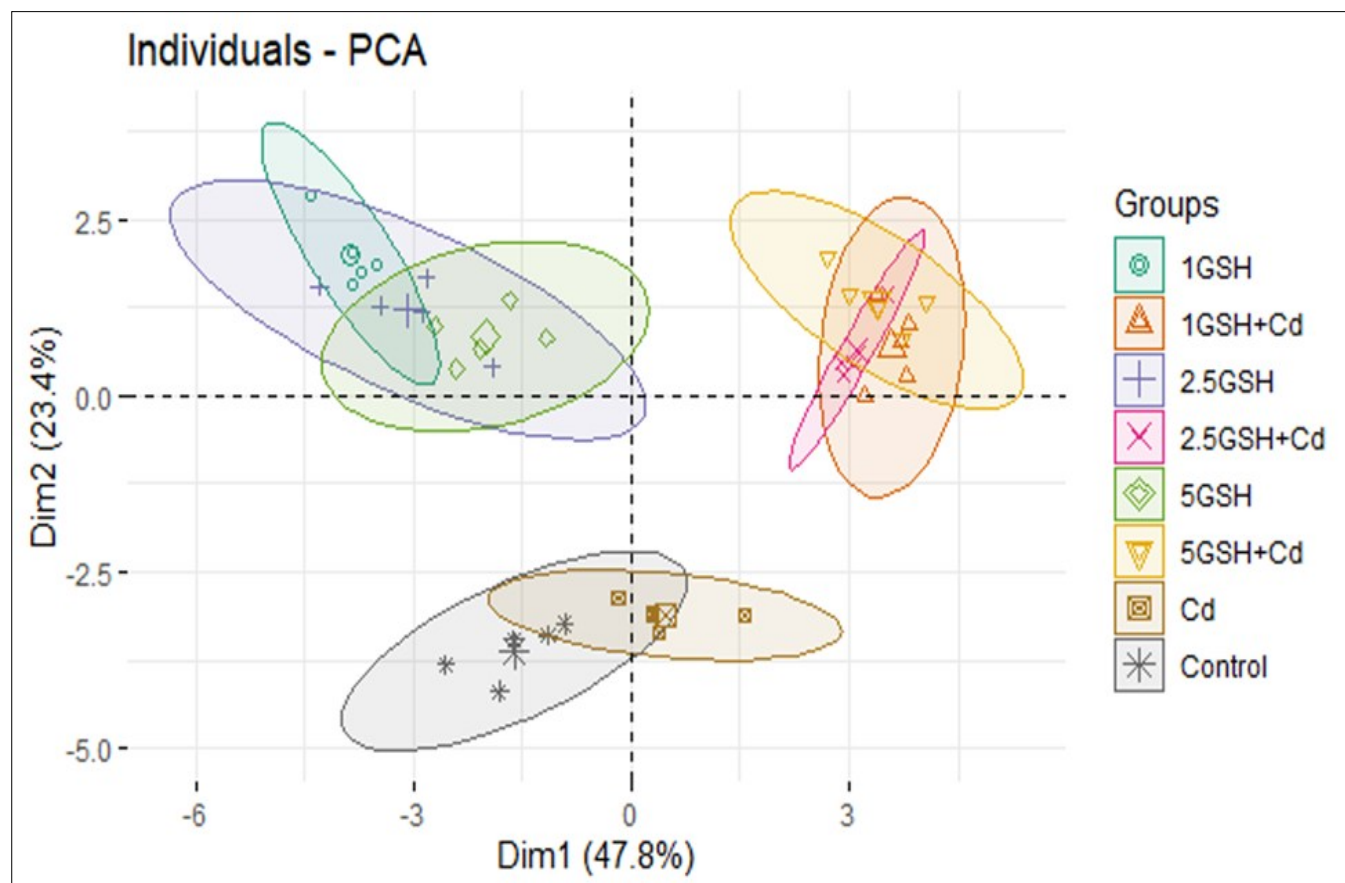


Fig. 4. Principal component analysis plot showing clustering based on treatment. 1GSH: medium with 1 mM GSH, 2.5GSH: medium with 2.5 mM GSH, 5GSH: medium with 5.0 mM GSH, Cd: medium with 25 mg/L Cd, 1GSH+Cd: medium with 25 mg/L Cd and 1 mM GSH, 2.5GSH+Cd: medium with 25 mg/L Cd and 2.5 mM GSH, 5GSH+Cd: medium with 25 mg/L Cd and 5.0 mM GSH, control: WPM only.

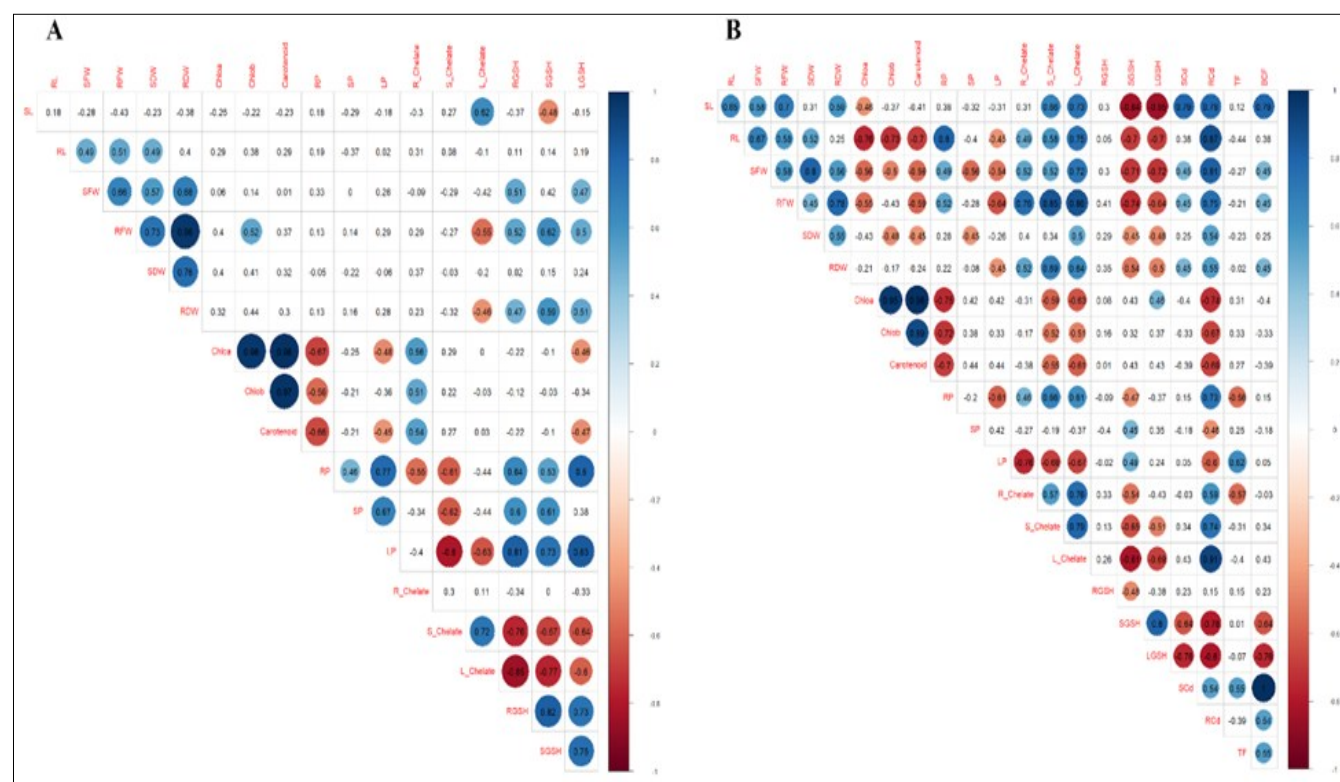


Fig. 5. Pearson correlation analysis among treatments. (A)- Under control conditions; (B)- Cd stress with GSH applied at concentrations of 0–5 mM. SL: Shoot height, RL: Root length, SFW: Shoot fresh weight, RFW: Root fresh weight, SDW: Shoot dry weight, RDW: Root dry weight. Chloa: Chlorophyll a, Chlob: Chlorophyll b, RP: Root proline content, SP: Stem proline content, LP: Leaves proline content, RGSH: Root GSH content, SGSH: Stem GSH content, LGSH: Leaves GSH content, R_chelate: Root chelating efficiency, S_chelate: Stem chelating efficiency, L_chelate: Leaves chelating efficiency. SCd: Shoot Cd accumulation, RCd: Root Cd accumulation, TF: Translocation factor, BCF: Bioconcentration factor. The color scale indicates the correlation coefficient: blue represents positive correlations, red represents negative correlations and the intensity of color as well as circle size correspond to the strength of the correlation.

effects of various stressors (32). Under Cd stress circumstances, GSH and proline exhibited a positive correlation with one another (33, 34). The introduction of exogenous GSH elevated proline levels in *Celosia* leaf tissue under both culture conditions (with and without Cd stress), as documented in our work. This suggests that the detrimental effects of Cd stress on *C. argentea*, influenced by exogenous GSH, are attributable to the elevation of proline levels. In plants, GSH is often formed in leaves (35); however, several studies indicate that GSH can also be produced in roots or tissues triggered by oxidants (36, 37). These observations indicate that exogenous GSH can also be efficiently absorbed and translocated within the plant body. Exogenous GSH from our study may be assimilated by roots and transported to shoots via xylem (38). The notion is corroborated by the findings of elevated GSH levels in the stems and leaves of *C. argentea* in this study. Under specific conditions, GSH may be hydrolysed in the roots by enzymes such as γ -glutamyl transpeptidase, yielding precursors like cysteine, which may explain the absence of a rise in GSH concentration in the roots in our study (38).

A plant species is classified as a hyperaccumulator of cadmium (Cd) when it can accumulate 100 mg/kg DW (13). Our analysis indicates that *C. argentea* is a hyperaccumulator, but its Cd-extraction capacity is low due to its TF being under 1. An indicator frequently assessed for the heavy metal-extraction efficiency of hyperaccumulator species, based on recent studies, is that the TF must exceed 1 (39). The introduction of 2.5 mM exogenous GSH resulted in a notable improvement of the TF index in *C. argentea*. This outcome suggests a compelling technique to augment the extraction capacity of prospective species in phytoremediation.

Conclusion

Under cadmium stress conditions, exogenous GSH supplementation significantly increased the levels of photosynthetic pigments, glutathione and proline in *Celosia argentea*. Additionally, the TF value increased by 1.8 times with 2.5 mM GSH added demonstrating that the optimal concentration of GSH was critical for enhancing cadmium translocation from the roots to the shoots in *C. argentea*.

Authors' contributions

DPT, TTH and BVL conceived the research project. DPT designed and performed the experiments, analysed the data and wrote the manuscript. DPT, TTH and BVL edited the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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