

# Preliminary study of the hormetic effect of nitrate and chloride of cerium on the micropropagation of *Stevia rebaudiana* Bertoni

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## ABSTRACT

**Objective:** This study aimed to evaluate the effect of cerium nitrate and cerium chloride on morphophysiological and biochemical variables in *S. rebaudiana* grown *In vitro*.

**Design/methodology/approach:** *S. rebaudiana* explants were grown for 30 days on MS medium supplemented with cerium nitrate or chloride at 0, 10, 20, 30, 40 and 50  $\mu\text{M}$  concentrations, respectively.

**Results:** It was observed that cerium nitrate at a concentration of 10  $\mu\text{M}$  stimulated shoot proliferation ( $10.55 \pm 1.11$ ) and plant growth ( $12.12 \pm 0.51$  cm), whereas cerium chloride at the same concentration favoured plant height ( $13.25 \pm 0.53$  cm). Cerium nitrate at a concentration of 30  $\mu\text{M}$  significantly increased chlorophyll content ( $0.957 \pm 0.005$  mg  $\text{g}^{-1}$  FW). In addition, a hormetic effect was observed with both cerium salts, *i.e.*, biostimulation at low concentrations and lethal toxicity at the maximum concentration evaluated (50  $\mu\text{M}$ ), showing a greater toxic effect with the chloride counterion.

**Limitations on study/implications:** This study constitutes a preliminary *in vitro* research; although cerium has a beneficial effect during the micropropagation of *S. rebaudiana*, its effectiveness must be evaluated through additional *ex vitro* studies.

**Findings/conclusions:** Controlled and adequate doses can be used to obtain the highest biostimulant effect on *S. rebaudiana* shoot proliferation *In vitro*.

**Keywords:** Biostimulant, Stevia, Hormesis, Micropropagation, Toxicity.

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## INTRODUCTION

*S. rebaudiana* is the only species in the *Stevia* genus with non-caloric steviol glycosides up to 300 times more sweetness than sucrose (Ahmad *et al.*, 2020). Industrially, *S. rebaudiana* plants are used as raw material to extract sugar substitutes, which according to medical studies, improves health and corrects metabolic disorders such as diabetes (Patel and

Navale, 2024). In addition, it presents bioactive components with therapeutic activity in various human health conditions (Jahangir *et al.*, 2020).

Currently, a large number of propagules are required to establish commercial plantations. Conventional propagation of *S. rebaudiana* is limited by genetic variation, low seed viability and complicated rooting of vegetative cuttings, which generates a limited number of individuals (Khalil *et al.*, 2014; Ramírez-Mosqueda *et al.*, 2016; Simlat *et al.*, 2020). The growing demand for *S. rebaudiana* propagules worldwide generates the need to establish techniques for its mass propagation, as well as to improve the physiological vigour and potentiate the productivity of this crop (Angelini *et al.*, 2018; Abdelsattar *et al.*, 2023).

Plant tissue culture (PTC) is a biotechnological strategy that allows obtaining many commercial propagules in a short time and space (Negi *et al.*, 2024). This technique has been used in *In vitro* micropropagation of *S. rebaudiana* to establish commercial plantations (Sivasankarreddy *et al.*, 2021). Ramírez-Mosqueda and Iglesias-Andreu (2016) reported *In vitro* micropropagation of *S. rebaudiana* through the thin-layer method. Meanwhile, other authors established the massive micropropagation of *S. rebaudiana* through temporary immersion systems (Ramírez-Mosqueda *et al.*, 2016; Medorio-García *et al.*, 2024). Currently, natural alternatives with lower environmental impact are being sought, which can replace or minimize the use of synthetic plant growth regulators (Le *et al.*, 2020; Yang *et al.*, 2021). Sridhar and Aswath (2014) increased the number of shoots in *S. rebaudiana* using casein hydrolysates as a biostimulant. Similar results have been obtained with yeast extracts, alginates (Bayraktar *et al.*, 2016) and silver nanoparticles (Castro-González *et al.*, 2019).

Biostimulants are substances and microorganisms that induce metabolic mechanisms and responses that lead to improved plant development, nutrient uptake, stress tolerance, and vigour (Du Jardin, 2015; Trejo-Téllez and Gómez-Merino, 2023). Some light lanthanides ( $\text{La}^{3+}$ ,  $\text{Pr}^{3+}$ ,  $\text{Nd}^{3+}$ ,  $\text{Eu}^{3+}/^{2+}$ ,  $\text{Ce}^{3+}/^{4+}$ ) stand out as inorganic biostimulants because they exhibit a beneficial effect at low doses (Trejo-Téllez and Gómez-Merino, 2023). However, these compounds can induce toxic effects at high concentrations, adjusting to the response to a hormesis curve (Bello-Bello *et al.*, 2024). In plant biology, hormesis is a biphasic dose-response phenomenon in which low stressor concentrations induce beneficial effects, such as biostimulation or eustress on morphophysiological variables. In contrast, high concentrations cause inhibition or toxicity. (Godínez-Mendoza *et al.*, 2023; Erofeeva, 2022). This phenomenon has potential applications in plant biotechnology, since the statistical analysis of the hormetic curve allows for identifying the maximum stimulation dose (M) and, simultaneously, to establish the stimulation limit (LDS), which facilitates optimizing the positive response and minimizing adverse effects (Belz and Duke, 2022). Several studies detail the biostimulant effect of lanthanides on plants (Öztürk *et al.*, 2023). For example, in soybean plants, lanthanum application increased nutrient uptake and biomass production (de Oliveira *et al.*, 2015). Zhang *et al.* (2013) reported that biostimulation of medicinal plants with lanthanum, cerium, neodymium or europium can regulate secondary metabolism. Likewise, dosing with lanthanum on tobacco seedlings infected by mosaic virus decreased adverse symptoms (Yongsheng *et al.*, 2012). Cerium also has a regulatory and antagonistic effect on  $\text{Cu}^{2+}$  detoxification in *Dendrobium nobile*

(Li *et al.*, 2023) and *Spinacia oleracea* under  $Mg^{2+}$  deficiency stress (Yuguan *et al.*, 2009). However, light lanthanides present a hormetic effect; at low concentrations, they present stimulation and at high concentrations, a toxic effect, depending on the species of plant and the availability of the metal (Jiang *et al.*, 2023; Öztürk *et al.*, 2023). Cerium exhibits chemical characteristics like  $Ca^{2+}$  (Lutz *et al.*, 2012). These properties favour ionic competition (mainly with  $Ca^{2+}$  and  $Mg^{2+}$ ) for organic molecules such as chlorophylls (He *et al.*, 2020; Song *et al.*, 2021), proteins and other organic ligands (Chen *et al.*, 2000; Liu *et al.*, 2011; Dressler *et al.*, 2014; Li *et al.*, 2024). While the stimulating effect of lanthanides can modulate the expression of antioxidant proteins, photosynthetic activity and the homeostasis of micronutrients and phytohormones (Grosjean *et al.*, 2024; Li *et al.*, 2024), their toxic effect activates specific defense mechanisms, such as the synthesis of chelating compounds (phytochelatins, metallothioneins and organic acids) that facilitate the subsequent sequestration of lanthanides in the vacuole (Sharma *et al.*, 2016). Increasing interest has been in adding biostimulants to the *In vitro* culture medium to improve micropropagation efficiency and minimize production costs (Carmo *et al.*, 2021). Recently, lanthanides have emerged as a sustainable alternative, due to their biostimulant effects at concentrations in the range of 1-500  $\mu M$  (Öztürk *et al.*, 2023; Cruz-Cruz *et al.*, 2024). Studies evaluating the effect of light lanthanides in the micropropagation of plant species are limited. Therefore, this study aimed to evaluate the effect of  $Ce(NO_3)_3$  and  $CeCl_3$  on the morphology and photosynthetic pigment synthesis during *In vitro* propagation of *S. rebaudiana*.

## MATERIALS AND METHODS

### Plant material and cerium salts

*In vitro*-grown seedlings of *Stevia rebaudiana* cv. Morita II, maintained through three subcultures, were obtained from the collection of the Laboratory of Teaching and Services in Biotechnology and Plant Cryobiology at the Faculty of Chemical Sciences, Universidad Veracruzana. Cerium chloride heptahydrate ( $CeCl_3 \cdot 7H_2O$ ) and cerium nitrate hexahydrate ( $Ce(NO_3)_3 \cdot 6H_2O$ ) were procured from Merck Co. (Darmstadt, Germany).

### Treatments for the evaluation of the effect of $Ce(NO_3)_3$ and $CeCl_3$ in *In vitro* micropropagation of *S. rebaudiana*

Nodal segments measuring 3 cm in length and containing a single axillary bud were used as explants. Culture flasks were each supplemented with 30 mL of Murashige and Skoog (MS) medium (Murashige and Skoog, 1962), with three explants per flask constituting an experimental unit, and three replicates per treatment. Various concentrations (0, 10, 20, 30, 40, and 50  $\mu M$ ) of cerium chloride heptahydrate ( $CeCl_3 \cdot 7H_2O$ ) and cerium nitrate hexahydrate ( $Ce(NO_3)_3 \cdot 6H_2O$ ) were evaluated. The medium's pH was adjusted to 5.7 using 0.1 N sodium hydroxide or 0.1 N hydrochloric acid, and solidified with 3 g  $L^{-1}$  of Phytigel<sup>®</sup>. Sterilization was carried out via autoclaving at 121 °C and 115 kPa for 20 minutes. All cultures were incubated in a controlled growth chamber for 30 days at  $25 \pm 2$  °C, under an irradiance of 68  $\mu mol m^{-2} s^{-1}$  and a photoperiod of 16/8 h (light/dark).

### Evaluation of morphometric variables

After 30 days of culture, the number of shoots per explant was recorded. Plant height (cm) and root length (cm) were measured using millimeter paper. Additionally, survival rate (%) and root induction (%) were assessed. For dry weight determination, 0.5 g of plant tissue was dehydrated in Petri dishes within a drying oven at 70 °C for 48 hours. The dried samples were then weighed using an analytical balance (OHAUS PA224).

### Evaluation of photosynthetic pigment synthesis

Chlorophyll a, chlorophyll b, and total chlorophyll content were quantified following the method described by Harborne (1973). For each sample, 0.1 g of fresh leaf tissue was weighed, frozen with liquid nitrogen, and ground before being macerated in 10 mL of 80% acetone. The extracts were stored at -4 °C for 24 hours. Subsequently, the samples were filtered using Whatman No. 1 filter paper and the final volume was adjusted to 20 mL with 80% acetone. A 2 mL aliquot was transferred to quartz cuvettes and analyzed using a Genesys™ 10S UV-Vis spectrophotometer. Absorbance readings were taken at wavelengths of 645 nm and 663 nm.

### Statistical analysis

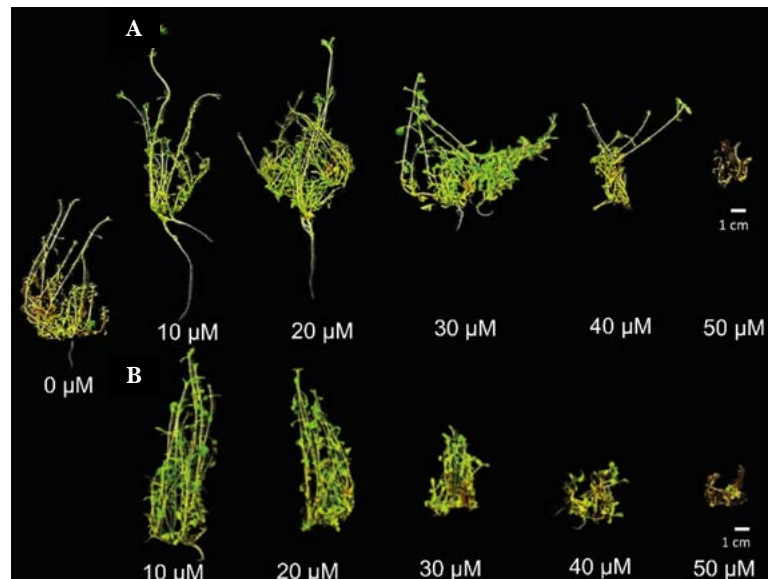
A completely randomized experimental design was employed, with all treatments replicated three times. Data were recorded and statistically analyzed using R software version 4.5.0 (<https://www.r-project.org/>). An analysis of variance (ANOVA) was performed, followed by Tukey's *post hoc* test at a significance level of  $p \leq 0.05$ . For dose-response variables exhibiting a hormetic pattern, polynomial regression models were applied (Equation 1).

$$y = \beta_0 + \beta_1x + \beta_2x^2 + \beta_3x^3 + \dots + \beta_nx^n + \varepsilon \quad (1)$$

The dataset was randomly divided into training (80%) and testing (20%) subsets for model validation. Polynomial models were fitted and evaluated based on the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and residual analysis. Predictive performance was assessed using the Root Mean Square Error (RMSE), Mean Absolute Error (MAE), and the coefficient of determination ( $R^2$ ). Additionally, the maximum stimulation dose (M) and the Limiting Dose for Stimulation (LDS) were estimated from the fitted models. Finally, a Spearman correlation analysis was conducted across all evaluated variables.

## RESULTS AND DISCUSSION

After 30 days of treatment, significant morphometric differences were observed across the evaluated response variables (Figure 1). A 100% survival rate was recorded for treatments with cerium salt concentrations ranging from 0 to 40  $\mu\text{M}$ . In contrast, the 50  $\mu\text{M}$  concentration of both  $\text{Ce}(\text{NO}_3)_3$  and  $\text{CeCl}_3$  exhibited toxic effects, resulting in 0% survival and complete inhibition of growth across all measured parameters.



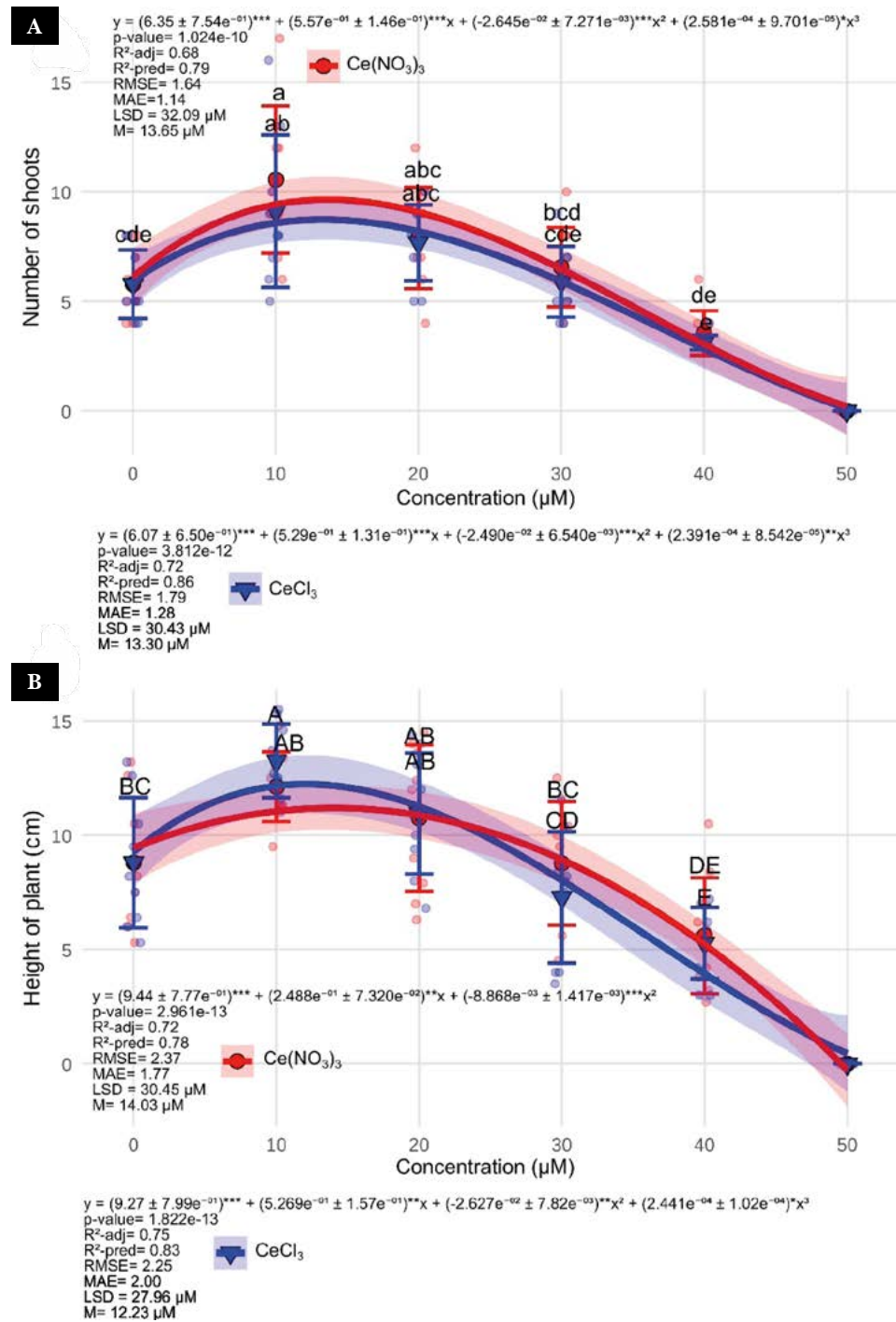
**Figure 1.** Effect of  $\text{Ce}(\text{NO}_3)_3$  and  $\text{CeCl}_3$  on *S. rebaudiana* micropropagation after 30 days. A)  $\text{CeCl}_3$  treatments; B)  $\text{Ce}(\text{NO}_3)_3$  treatments.

A significant increase in shoot number was observed at the  $10\ \mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$  treatment, with an average of  $10.5 \pm 1.11$  shoots per explant, compared to the control ( $5.7 \pm 0.52$  shoots). This was followed by the  $10\ \mu\text{M}$   $\text{CeCl}_3$  and  $20\ \mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$  treatments, which produced  $9.1 \pm 1.16$  and  $7.8 \pm 0.77$  shoots per explant, respectively (Figure 2A). Conversely, a decline in shoot formation was recorded at  $40\ \mu\text{M}$  concentrations of both  $\text{Ce}(\text{NO}_3)_3$  and  $\text{CeCl}_3$ , yielding  $3.5 \pm 0.33$  and  $3.1 \pm 0.11$  shoots per explant, respectively. At the highest tested concentration ( $50\ \mu\text{M}$ ), both cerium salts completely inhibited shoot production.

These findings are consistent with previous studies on the biostimulant activity of rare earth elements. Xu *et al.* (2016) reported a 150% increase in shoot formation compared to the control during *In vitro* micropropagation of *Anoectochilus roxburghii* treated with  $\text{La}(\text{NO}_3)_3$  and  $\text{Ce}(\text{NO}_3)_3$ . Similarly, Liu *et al.* (2021) documented enhanced shoot proliferation in *Dendrobium aphyllum* following treatment with  $100\ \mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$ . Corresponding trends were observed by Liu *et al.* (2018) in *Dianthus caryophyllus* cultured *In vitro* and exposed to lanthanum, cerium, or neodymium at concentrations ranging from  $50$  to  $150\ \mu\text{M}$ .

Significant differences in plant height were observed among the treatments (Figure 2B). The highest increase in height was recorded at  $10\ \mu\text{M}$   $\text{CeCl}_3$ , reaching  $13.2 \pm 0.53$  cm, compared to the control ( $8.8 \pm 0.95$  cm). Although the  $10\ \mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$  treatment produced an average height of  $12.1 \pm 0.51$  cm higher than the control this increase was not statistically significant. In contrast, plant growth was inhibited at  $40\ \mu\text{M}$  concentrations of both cerium salts, with  $\text{CeCl}_3$  ( $5.2 \pm 0.52$  cm) showing significant suppression relative to the control. These findings demonstrate that low concentrations of cerium promote plant elongation, whereas higher concentrations exert inhibitory effects. Furthermore, plant height and shoot number exhibited a strong positive correlation ( $\rho=0.9$ ) (Figure S1).

The marked increase in vegetative elongation at low concentrations aligns with typical responses within the hormetic dose-response framework, as reported in sugarcane



**Figure 2.** Hormetic dose-response effects of cerium salts on shoot proliferation (A) and plant height (B) in *S. rebaudiana* micropropagation after 30 days. Statistical significance is indicated as  $p < 0.05^*$ ,  $p < 0.01^{**}$ ,  $p < 0.001^{***}$ .

(Ramírez-Antonio *et al.*, 2023), rice (Ramírez-Olvera *et al.*, 2018), and other species (Rico *et al.*, 2014; Sobarzo-Bernal *et al.*, 2021), likely due to enhanced nutrient uptake and elevated metabolic activity (Yang *et al.*, 2019). Based on the shoot proliferation data, the polynomial model estimated an optimal stimulation dose (M) of 13.65  $\mu$ M for  $Ce(NO_3)_3$  and 13.30  $\mu$ M

for  $\text{CeCl}_3$ , while the Limiting Dose for Stimulation (LDS) was  $32.09 \mu\text{M}$  and  $30.43 \mu\text{M}$ , respectively. Beyond these thresholds, shoot production declined sharply. For plant height, the model estimated  $M=14.03 \mu\text{M}$  and  $\text{LDS}=30.45 \mu\text{M}$  for  $\text{Ce}(\text{NO}_3)_3$ , and  $M=12.23 \mu\text{M}$  and  $\text{LDS}=27.96 \mu\text{M}$  for  $\text{CeCl}_3$ . Both variables followed a similar pattern, with a pronounced stimulatory effect at low concentrations and marked inhibition at higher doses. Hormesis, characterized by a biphasic dose-response, occurs when low doses of a stressor (*e.g.*, biostimulants, toxic agents, UV radiation) elicit beneficial effects, while high doses result in toxicity (Erofeeva, 2023; Godínez-Mendoza *et al.*, 2023). This phenomenon has been widely documented in plants, such as *Astragalus membranaceus* treated with yeast extract (Park *et al.*, 2021), *Cucumis sativus* with chitosan (Jogaiah *et al.*, 2020), *Salvia sclarea* with zinc (Moustakas *et al.*, 2022), and *Capsicum annuum* with silicon (Trejo-Téllez *et al.*, 2020). The phytotoxicity of a compound depends on multiple factors, including its chemical nature, concentration, physicochemical properties, mechanism of action, interaction with the environment (*e.g.*, absorption and translocation), and plant-specific biological characteristics (Madanayake and Adassooriya, 2021). Recently, the phytotoxic mechanisms of lanthanum at elevated concentrations (0.1-5 mM) were elucidated in rice (Jiang *et al.*, 2023). Therefore, identifying optimal biostimulant doses within the hormetic zone is crucial and must consider plant species and environmental or chemical factors that influence lanthanide bioavailability (Erofeeva, 2022; Wiche and Pourret, 2023).

Regarding root length, low concentrations of cerium did not yield statistically significant differences (Table 1). However, the highest root length ( $3.46 \pm 0.50$  cm) was observed at  $30 \mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$ . At higher concentrations (40-50  $\mu\text{M}$ ), both cerium salts significantly inhibited root development compared to the control ( $1.92 \pm 0.79$  cm). Root induction percentage improved in the 10-30  $\mu\text{M}$  range for both salts, ranging from 66% to 100%, relative to the control (55%). In contrast, treatments at 40-50  $\mu\text{M}$  resulted in a marked reduction in root induction, falling below 22%.

Luo *et al.* (2008) reported enhanced root development during the *In vitro* rooting stage of *Dendrobium densiflorum* treated with  $\text{Nd}(\text{NO}_3)_3$ . In contrast, studies in *Arabidopsis thaliana* demonstrated that lanthanum exposure inhibited primary root meristem growth due to the overproduction of reactive oxygen species (ROS), which led to increased lateral root formation and a restructured root system. These effects were associated with disrupted auxin signaling and the upregulation of genes involved in auxin biosynthesis (Liu *et al.*, 2016).

Regarding dry weight (Table 1), an increase over the control ( $0.0511 \pm 0.002$  g) was observed in treatments with  $40 \mu\text{M}$   $\text{CeCl}_3$  and  $10 \mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$ , reaching  $0.0600 \pm 0.005$  g and  $0.0565 \pm 0.006$  g, respectively; however, these differences were not statistically significant. Conversely, a significant reduction in dry weight was noted at 20, 30, and  $10 \mu\text{M}$   $\text{CeCl}_3$ , with values of  $0.0315 \pm 0.003$ ,  $0.0325 \pm 0.011$ , and  $0.0370 \pm 0.002$  g, respectively, relative to the control and the  $\text{Ce}(\text{NO}_3)_3$  treatments at 10-40  $\mu\text{M}$ . Notably, root induction ( $\rho = -0.81$ ) and root length ( $\rho = -0.58$ ) were negatively correlated with dry weight, suggesting a trade-off in resource allocation for root system development at cerium concentrations between 10 and 30  $\mu\text{M}$ . These findings also indicate a more pronounced toxic effect of cerium in its chloride form compared to its nitrate counterpart.

**Table 1.** Effect of  $\text{Ce}(\text{NO}_3)_3$  and  $\text{CeCl}_3$  on *S. rebaudiana* micropropagation after 30 days of treatments on morphometric and biochemical variables.

Cerium salt	Concentration ( $\mu\text{M}$ )	Root length (cm)	Root induction (%)	Dry weight (g)	Chlorophyll a ( $\text{mg g}^{-1}$ FW)	Chlorophyll b ( $\text{mg g}^{-1}$ FW)	Total chlorophyll ( $\text{mg g}^{-1}$ FW)
Control	0	1.92 $\pm$ 0.79cde	55.5	0.0511 $\pm$ 0.002a	0.404 $\pm$ 0.019b	0.194 $\pm$ 0.001b	0.599 $\pm$ 0.018b
$\text{Ce}(\text{NO}_3)_3$	10	2.28 $\pm$ 0.69a	66.6	0.0565 $\pm$ 0.006a	0.207 $\pm$ 0.015d	0.107 $\pm$ 0.010de	0.315 $\pm$ 0.025d
	20	1.61 $\pm$ 0.50abc	66.6	0.0521 $\pm$ 0.003a	0.364 $\pm$ 0.010bc	0.169 $\pm$ 0.005bc	0.533 $\pm$ 0.016bc
	30	3.46 $\pm$ 0.50bcd	100	0.0510 $\pm$ 0.001a	0.630 $\pm$ 0.000a	0.327 $\pm$ 0.005a	0.957 $\pm$ 0.005a
	40	0.58 $\pm$ 0.39de	22.2	0.0560 $\pm$ 0.007a	0.209 $\pm$ 0.009d	0.104 $\pm$ 0.018de	0.314 $\pm$ 0.008d
$\text{CeCl}_3$	10	1.94 $\pm$ 0.55ab	77.7	0.0370 $\pm$ 0.002b	0.218 $\pm$ 0.017d	0.107 $\pm$ 0.008de	0.326 $\pm$ 0.026d
	20	1.98 $\pm$ 0.50abc	88.8	0.0315 $\pm$ 0.003b	0.331 $\pm$ 0.013c	0.146 $\pm$ 0.003cd	0.477 $\pm$ 0.017c
	30	2.80 $\pm$ 0.44cde	100	0.0325 $\pm$ 0.011b	0.181 $\pm$ 0.021d	0.088 $\pm$ 0.013e	0.270 $\pm$ 0.034d
	40	0.16 $\pm$ 0.16e	11.1	0.060 $\pm$ 0.005a	0.186 $\pm$ 0.001d	0.118 $\pm$ 0.009de	0.305 $\pm$ 0.008d

Higher dry weights were recorded in *In vitro* seedlings treated with 10-40  $\mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$ . This increase may be attributed to cerium accumulation in cell walls, chelating molecules, and calcium-binding sites, which, in turn, may promote nutrient uptake through induced systemic endocytosis (Lai *et al.*, 2006; Cheng *et al.*, 2012; Kovařiková *et al.*, 2019). On the other hand, seedlings exposed to 10-40  $\mu\text{M}$   $\text{CeCl}_3$  exhibited reduced dry weight, possibly due to the counterion effect. While chloride acts as a micronutrient involved in osmoregulation, elongation growth, and nitrate/water efficiency (Geilfus, 2018a; Hu *et al.*, 2023), elevated chloride levels may disrupt nitrate assimilation (Geilfus, 2018b). Significant differences in photosynthetic pigment content were also observed among treatments (Table 1), with strong positive correlations ( $\rho \geq 0.85$ ) among pigment variables (Figure S1). The highest chlorophyll a content (0.630 $\pm$ 0.000  $\text{mg g}^{-1}$  FW) was obtained at 30  $\mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$ , significantly higher than the control (0.404 $\pm$ 0.019  $\text{mg g}^{-1}$  FW). In contrast, significantly reduced chlorophyll a levels were observed in the 30  $\mu\text{M}$   $\text{CeCl}_3$ , 40  $\mu\text{M}$   $\text{CeCl}_3$ , 40  $\mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$ , and 10  $\mu\text{M}$   $\text{CeCl}_3$  treatments, with values of 0.181 $\pm$ 0.021, 0.186 $\pm$ 0.001, 0.209 $\pm$ 0.009, and 0.218 $\pm$ 0.017  $\text{mg g}^{-1}$  FW, respectively.

For chlorophyll b, the 30  $\mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$  treatment also showed a significant increase (0.327 $\pm$ 0.005  $\text{mg g}^{-1}$  FW) over the control (0.194 $\pm$ 0.001  $\text{mg g}^{-1}$  FW), whereas the greatest decrease was observed at 40  $\mu\text{M}$   $\text{CeCl}_3$  (0.088 $\pm$ 0.013  $\text{mg g}^{-1}$  FW). Regarding total chlorophyll, the highest content was recorded in the 30  $\mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$  treatment (0.957 $\pm$ 0.005  $\text{mg g}^{-1}$  FW), which was significantly greater than the control (0.599 $\pm$ 0.018  $\text{mg g}^{-1}$  FW). In contrast, treatments with 30  $\mu\text{M}$   $\text{CeCl}_3$ , 40  $\mu\text{M}$   $\text{CeCl}_3$ , and 40  $\mu\text{M}$   $\text{Ce}(\text{NO}_3)_3$  showed significant reductions, with values of 0.270 $\pm$ 0.034, 0.305 $\pm$ 0.008, and 0.314 $\pm$ 0.008  $\text{mg g}^{-1}$  FW, respectively. These results indicate that cerium nitrate enhances photosynthetic pigment synthesis, whereas cerium chloride either has no effect or exerts a negative impact.

Several studies have reported the biostimulatory effects of light lanthanides on pigment biosynthesis through the upregulation of photosynthesis-related enzymes (Yuguan *et al.*,

2009; Sobarzo-Bernal *et al.*, 2021). Additionally, nitrate ions (the counterion in  $\text{Ce}(\text{NO}_3)_3$  serve as a direct nitrogen source, reduced to nitrite ( $\text{NO}_2^-$ ) and subsequently to ammonium ( $\text{NH}_4^+$ ) via nitrate and nitrite reductase enzymes, thus promoting chlorophyll and amino acid synthesis (Wang *et al.*, 2012). In contrast,  $\text{CeCl}_3$  reduced pigment levels, likely due to chloride's antagonistic effect on nitrate uptake (Geilfus, 2018b). Related toxic effects of lanthanides have also been observed in rice (*Oryza sativa*), where lanthanum exposure increased foliar Cu, Mn, and Zn levels, while decreasing Mg content and photosynthetic pigment concentrations. Photosystem activity was impaired due to reduced electron transport and increased energy dissipation, attributed to structural damage in proteins, chloroplasts, and thylakoid membranes (Jiang *et al.*, 2023).

In this study, a significant increase in the number of shoots per explant was observed in *In vitro* plants exposed to low concentrations of cerium salts. In contrast, high concentrations of lanthanides suppressed shoot formation, likely due to the disruption of membrane proteins and the activation of metabolic reprogramming to mitigate stress induced by elevated cerium ion levels (Erofeeva, 2023; Jiang *et al.*, 2023). Thus, precise and controlled dosing is essential to maximize the biostimulant potential of cerium for promoting shoot proliferation in *S. rebaudiana* under *In vitro* conditions.

## CONCLUSION

The biostimulant effects of  $\text{Ce}(\text{NO}_3)_3$  and  $\text{CeCl}_3$  were clearly demonstrated during the *In vitro* micropropagation of *S. rebaudiana*, with significant enhancements in shoot proliferation and plant height. Notably,  $\text{Ce}(\text{NO}_3)_3$  at concentrations of 10-20  $\mu\text{M}$  produced the greatest increases in shoot number and dry weight. A hormetic response was identified, wherein low concentrations of lanthanide salts stimulated plant growth, while higher concentrations (40-50  $\mu\text{M}$ ) exerted phytotoxic effects. These findings underscore the critical importance of optimizing biostimulant dosages to maximize physiological benefits within the hormetic range.

Further research is warranted at additional evaluation levels such as in temporary immersion bioreactors and *ex vitro* conditions to validate and fine-tune the effective concentrations for large-scale applications. Moreover, the integration of omics approaches could provide valuable insights into the molecular mechanisms underpinning the biostimulant activity of cerium-based compounds.

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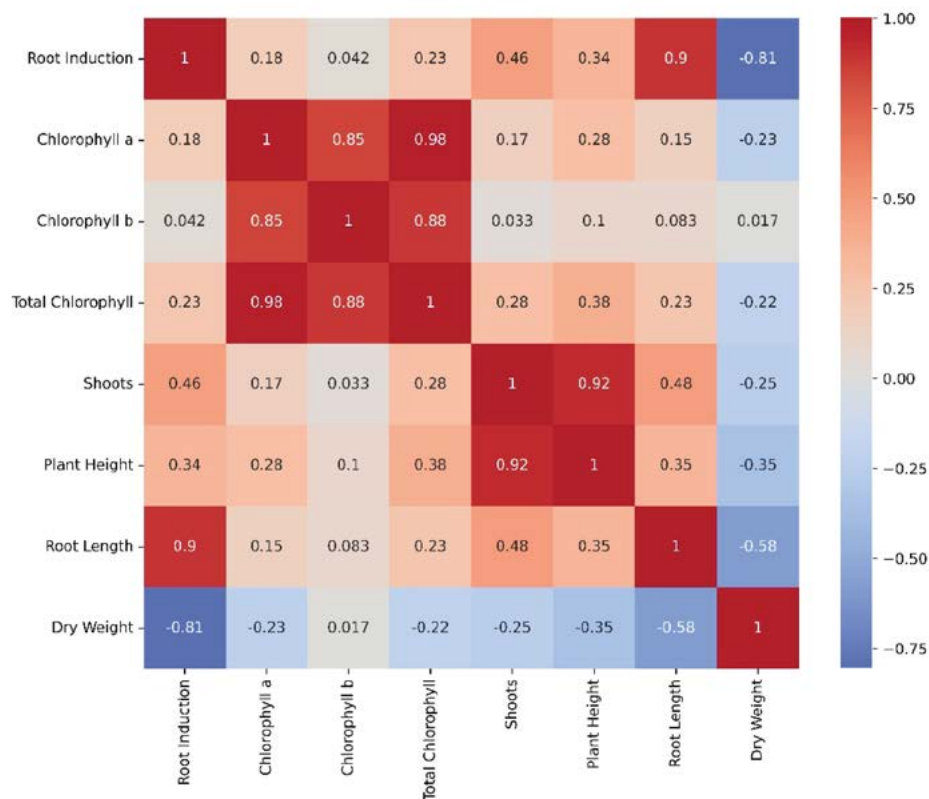
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### Supplementary material



**Figure S1.** Spearman correlation matrix of morphophysiological and biochemical variables in *S. rebaudiana* micropropagation after 30 days of  $\text{Ce}(\text{NO}_3)_3$  and  $\text{CeCl}_3$  treatments.