



Effects of Gd^{3+} and Ce^{3+} on seed germination and growth of tomato and quinoa plants

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Abstract

Several studies reported that rare earth elements (REEs) can exert both beneficial and harmful effects on plants, including improved seed germination, plant growth, and crop yield. However, these findings remain controversial and highly variable, likely due to differences in the specific REEs investigated, their concentrations, and the plant species studied. In our study we assessed the effects of increasing concentrations of gadolinium (Gd) and cerium (Ce), together with sodium citrate (used as chelating agent), on two important plant species: tomato (*Solanum lycopersicum*) and quinoa (*Chenopodium quinoa*). The aim was to establish the effects on seed germination and seedling growth, also detecting the presence of hormesis through the application of a statistical model. Seeds were placed in Petri dishes on filter paper soaked with the corresponding solution (from 10 μM to 150 μM ; deionized water used as control). After germination, shoot and root length were measured and several indexes related to germination and initial seedling growth were calculated. The results highlighted species-specific and concentration-dependent responses. In quinoa roots, Ce induced a subtle biphasic dose–response trend characterized by a growth stimulation at low concentrations (10 μM) and inhibition at higher levels. Instead, tomato shoot length increased under both REEs, while high Gd doses negatively impacted on root growth. Low concentrations of REEs could be a successful approach to stimulate plant development, particularly in initial growth stages. Nevertheless, their mechanisms and the suitable dosage remain unclear, determining the need for further studies, especially to assess the long-term effects on ecosystems.

Keywords Gadolinium · Cerium · Tomato seeds · Quinoa seeds · Hormesis

Introduction

Rare earth elements (REEs) are a group of 17 elements consisting of Yttrium (Y), Scandium (Sc) and other 15 lanthanides with an atomic number between 57 and 71. The term “rare” is improperly used and it refers to the lack of wide ore deposits: in fact, some of the lanthanides are very abundant in the Earth’s crust, especially Lanthanum (La), Cerium

(Ce) and Neodymium (Nd). The concentration of Ce in Earth's crust is about 60 mg kg^{-1} , equaling elements like copper (Cu) or overcoming others like lead (Pb— 13 mg kg^{-1}), while La and Nd concentrations are about 40 mg kg^{-1} . The data summary of the United States Geological Survey (2020) establishes that the most important reserves of REEs are located in China, Russia, Vietnam, India, Australia and Brazil (d'Aquino et al. 2009; Tao et al. 2022). REEs can also be divided into two sub-groups: light rare earth elements (LREEs) or heavy rare earth elements (HREEs). Generally, although its lightweight, Y is included in HREEs thanks to the similarity of the chemical and physical properties (Castor and Hedrick 2006; Dushyantha et al. 2020; Hughes 2014). Nowadays REEs are used in several industrial processes such as glass and ceramics production, electronic devices development, renewable energy, military equipment, medicine, farming and agriculture. Moreover, since the 1980s, many fertilizers, supplemented with REEs, have been used in China. Among the REEs, La, Ce and Nd are the most common biostimulants employed in the Chinese agriculture (d'Aquino et al. 2009; Sobarzo-Bernal et al. 2021; Tao et al. 2022). Their use led to the production of about 5.0 million tons of fertilizers and a use of 1,100 tons per year in agriculture (Ruíz-Herrera et al. 2012). The three most common fertilizers used in China contain REEs in nitrate and chloride forms, or combinations of 17 amino acids spiked with La, Ce, Praseodymium (Pr) and Nd (Pang and Peng 2002). However, their positive effects on crops have not been clearly demonstrated as well as the improvements in plant growth. In recent years, many studies have been focused on the effects of REEs on more than 100 plant species. Since several benefits have been reported, REEs fertilizers have been commercialized and employed in agriculture (Agathokleous et al. 2022; d'Aquino et al. 2009; Ben et al. 2021; Hu et al. 2002; Wang et al. 2014). According to previous studies, REEs can promote germination, increase both root growth and chlorophyll content, and even resistance/tolerance towards either against plant diseases (e.g., fungi, bacteria, insect pests, etc.), or stresses (e.g., drought, cold, heavy metals, etc.) (Agathokleous et al. 2022; Hu et al. 2002; Kaur et al. 2024). Concurrently, while low concentrations of REEs have benefits on plants, high concentrations strongly reduce plant growth. This could be explained by the "hormesis effects", a condition in which organisms have a biphasic response: low doses of usually harmful substances can have positive effects, probably inducing adaptive mechanisms in the organism, and then negative ones when a certain threshold is exceeded (Agathokleous et al. 2018; Kaur et al. 2024). Particularly, concentrations of REEs less than 0.5 mg kg^{-1} in the soil seem to have positive effects leading to yield increases up to 15% for many crops under different substrate and nutrient conditions. However, this increase is strictly related to specific growth stages (Agathokleous et al. 2018; Hu et al. 2002; Thomas et al. 2014). Despite the high number of studies, the mechanisms of actions on plants are still unknown. The main explanation involves alterations in nutrient uptake, and plant metabolism related to enzymes activity and photosynthesis, however their effects on cellular or molecular processes have not yet been well clarified (Wang et al. 2014). REEs are not essential elements and therefore there is no specific pathway of absorption in plants. According to Ben and coworkers (Ben et al. 2021), La may enter into the leaf cells of different crops through foliar spray, leading to its accumulation and as well as to other toxic elements such as lead. The root system is directly affected by REEs and as is well known, it is strictly related to water and nutrients uptake. Zhang et al. (2013), demonstrated that $\text{La}(\text{NO}_3)_3$ promotes root elongation and peroxidase activity of *Eriobotrya japonica* (Thunb.) Lindl., while $\text{Eu}(\text{NO}_3)_3$ increases root fresh weight and nitrate reductase. Xu and Chen (2011), exposed seedlings of rice to Ce^{4+} in hydroponic system, monitoring oxidant levels, suggesting that low doses may improve antioxidant defenses while high doses may have negative effects on seedling growth. Liu et al. (2022),

reported that ramie (*Boehmeria nivea* L.), exposed to a mix of sixteen REEs when applied at low doses, accumulated them in its organs, particularly in roots; while when applied at high concentrations, a significant growth reduction was observed. The bioavailability in soil, plant species, lithological features and different properties of REEs influence their fractionation in plants. As shown by Punturo and coworkers (Punturo et al. 2018), the absorption was the highest in the vineyard leaves and grape juice, and the lowest in skins and seeds. At the same time plant cultivar affected their fractionation, showing a cultivar-specific pattern of absorption (Jiménez-Ballesta et al. 2022; Tao et al. 2022). Despite many studies on REEs effects on plants have been made the results are, in many cases, contradictory. In fact, the effects reported in these studies are positive, negative and even neutral, depending on the plant species, the type of REEs, the plant physiological conditions and the method of application (d'Aquino et al. 2009; Ruíz-Herrera et al. 2012; Sobarzo-Bernal et al. 2021). Then, their increasing concentrations in the agricultural soils and, in general, in the environment may be a serious threat for ecosystems and human health. Especially the areas where their concentration in soil is higher, the continuous environmental dispersion can lead to alarming conditions. Countries that apply fertilizers with different REEs to enhance crop yield may need monitoring operation, while the improper disposal of technology devices in landfills may result in contamination of the environment due to surface runoff (Thomas et al. 2014). As mentioned previously, Ce is the most abundant and reactive representative of LREEs and can be easily found in soil and waters. Furthermore, it is an important component of fertilizers. As a result, it easily comes into contact with crops (Tommasi et al. 2021; Tyler 2004). Gadolinium, on the other hand, has shown increasing concentration in recent years, mainly due to its use in magnetic resonance imaging as a contrast agent. Consequently, after administration, it is discharged into sewage systems and, since modern wastewater treatment plants are not capable of removing it, it ends up contaminating surface waters (Kulaksız and Bau 2011; Tepe et al. 2014; Van Der Molen and Bellin 2008). For these reasons, in the present work the effects of Ce and Gd, applied in the form of nitrates, were evaluated on seed germination and seedling growth of two very important crops. Together with Ce and Gd, sodium citrate effects were also evaluated: REEs have a high affinity to phosphate, leading to the production of a milky white precipitate in plant nutrient solutions (Evans 1990; Romero-Freire et al. 2021). Our aim was to find a sustainable chelating agent capable of solubilizing REEs in the presence of phosphate with no harmful effects on plants. Based on previous laboratory test, sodium citrate showed a high affinity towards REEs preventing their precipitation and, unlike other synthetic chelators, it has good solubility and biodegradability. Therefore, it is potentially optimal chelating agent (Anjum et al. 2015; Gracheva et al. 2024; Rauser 1999). The selected plant species were chosen thanks to their important role in food security: tomato (*Solanum lycopersicum* L.) and quinoa (*Chenopodium quinoa* Willd.). Tomato is one of the most cultivated vegetables around the world and in 2022 had an annual production of approximately 188 million tons (FAOSTAT 2023). Furthermore, its fruits are a fundamental food source for the entire Earth population (Dan et al. 2006). China (61 million tons), India (21 million tons), Turkey (13 million tons) and United States (10 million tons) are the most important producers of tomato in 2022 (FAOSTAT 2023). Conversely, quinoa is a plant species native to South America capable of growing on saline and arid soils. It is a facultative halophyte that tolerates several abiotic stresses. Moreover, it's considered healthy food due to its high seed content of essential amino acids and, therefore, highly appreciated by consumers. Last but not least, its production is increasing all around the world (Mu et al. 2023). In this context, the present study provides a comparative assessment of the effects of two REEs, Gd and Ce, on the early growth of tomato and quinoa. Gadolinium was chosen to investigate

its effects on plants, assess ecological risks, and develop strategies to mitigate potential impacts, as current studies do not fully clarify its mechanisms of interaction (Tomczuk et al. 2025). Cerium, in contrast, was selected due to the absence of a comprehensive review on how it influences plants. Understanding these interactions is essential for elucidating their ecological effects and guiding the development of targeted management strategies (Agathokleous et al. 2022). Furthermore, the influence of citrate as a chelating agent was examined to elucidate its role in modulating REEs bioavailability and plant response. Plant growth was evaluated through root and shoot length measurements, with particular attention to the identification and characterization of hormetic effects.

Materials and methods

Plant species

Tomato ('MicroTom') and quinoa ('Regalona') were selected for the experiments. Tomato 'MicroTom' is widely used as a model system in plant biology. It is a dwarf cultivar and has a relatively rapid life cycle (70–90 days), and a well-known small genome and an extensive mutant seedbank similar to the most widely used plant model system, *Arabidopsis thaliana* L. Heynh.. All the above-mentioned characteristics make MicroTom an ideal model organism to study plant growth, genetic, and physiology (Dan et al. 2006; Pepe et al. 2022). Quinoa is widely cultivated for its highly nutritious seeds and can be easily grown even in laboratory or greenhouse conditions (Ruiz et al. 2016).

Seed sterilization and experimental set

Seeds were sterilized with 70% ethanol with constant shaking for two minutes, then washed three times for one minute with distilled sterile water. Subsequently seeds were soaked in a solution of sodium hypochlorite 1.5% for fifteen minutes and finally washed again three times with distilled water. After that, 10 seeds were placed on filter paper in Petri dishes and irrigated with the corresponding solution (REEs solutions, citrate solutions or water), which represented an experimental unit. Each treatment had three replicates. Plates with seeds were incubated in a phytotron at 21° C and 60% humidity, in the darkness. Seeds were kept hydrated with the corresponding solution.

Treatment applications

Cerium and Gd were supplied as $\text{Ce}(\text{NO}_3)_3 \cdot 6\text{H}_2\text{O}$ and $\text{Gd}(\text{NO}_3)_3 \cdot 6\text{H}_2\text{O}$ (Sigma-Aldrich; Saint Louis, MO, USA). REEs were applied in a ratio 1:3 with sodium citrate ($\text{Na}_3\text{C}_6\text{H}_5\text{O}_7 \cdot 2\text{H}_2\text{O}$ – Riedel-de Haën; Seelze, Germany) reported as citrate along the text. The seeds were exposed to increasing concentrations of each REEs: 10 μM , 30 μM , 50 μM , 70 μM , 100 μM and 150 μM (corresponding to 4.34 mg L^{-1} , 13.03 mg L^{-1} , 21.71 mg L^{-1} , 30.40 mg L^{-1} , 43.43 mg L^{-1} , and 65.14 mg L^{-1} for Ce; 4.51 mg L^{-1} , 13.54 mg L^{-1} , 22.57 mg L^{-1} , 31.60 mg L^{-1} , 45.14 mg L^{-1} , and 67.71 mg L^{-1} for Gd). To assess the effects of sodium citrate alone, the corresponding solutions were used to prepare other Petri dishes where seeds were exposed to increasing concentrations of sodium citrate. At the same time, to evaluate a possible effect of nitrates, controls with the two highest concentrations of nitrate were arranged (nitrate). Nitrates were supplied as $\text{Mg}(\text{NO}_3)_2 \cdot 6\text{H}_2\text{O}$

(Riedel-de Haën; Seelze, Germany). The Control experimental units (CNT) were watered with distilled water only.

Recorded parameters

The number of germinated seeds was counted at 24 h intervals for 7 or 10 consecutive days in the case of quinoa and tomato, respectively. A seed was considered germinated when its radicle attained 2.0 mm long. At the end of the experimentation, shoots and roots length were measured through ImageJ, a Java-based image processing software package of public domain developed at the National Institutes of Health. The data obtained allowed us to calculate several indexes such as: Germination Index (GI), Relative Seeds Germination (RSG), Relative Growth of Shoots (RGS), Relative Growth of Roots (RGR) and Coefficient of Velocity of Germination (CVG). All the parameters and the formula are listed in Table 1 (Benech Arnold et al. 1991; Jagadabhi et al. 2019; Moghadam and Alaei 2014; Sobarzo-Bernal et al. 2021; Tam and Tiquia 1994). The indexes for Ce- and Gd-treated seeds were calculated relative to the corresponding citrate-only treatment, while indices for citrate alone were calculated relative to the water control (CNT).

Statistical analysis

Data distribution was evaluated using the Shapiro–Wilk test. As normality and homogeneity of variance assumptions were violated, nonparametric statistical methods were employed. The data were analyzed using the non-parametric Kruskal–Wallis test, with a significance level set at $p < 0.05$, followed by Dunn’s test for post-hoc pairwise comparisons.. Statistical analyses were conducted in R Studio, employing the “pgirmess” and “rcompaion” packages. Additionally, data were analyzed using one-way ANOVA to evaluate differences between treatments at each concentration level. For each tested dose, treatments were grouped according to citrate alone or citrate combined with Ce or Gd. When significant differences were detected, Tukey’s Honest Significant Difference (HSD) post-hoc test was applied using the multcomp package (GLHT function) to perform pairwise comparisons among groups. Significance groups were assigned using compact letter display (CLD), and differences were considered statistically significant at $p < 0.05$. Data visualization was performed using the ggplot2 package. Dose–response relationships were

Table 1 Parameters, their formula and description calculated on seeds, shoots and roots of tomato and quinoa plants

Parameter	Formula	Description
Germination Index	$GI (\%) = \frac{RSG \times RGR}{100}$	
Relative Seeds Germination	$RSG = \frac{NSG_{treatment}}{NSG_{control}} \times 100$	NGS: number of seeds germinated
Relative Growth of Shoots	$RGS = \frac{MSL_{treatment}}{MSL_{control}} \times 100$	MSL: Mean shoots length
Relative Growth of Roots	$RGR = \frac{MRL_{treatment}}{MRL_{control}} \times 100$	MRL: Mean roots length
Coefficient of Velocity of Germination	$CVG = \frac{TGS_{treatment}}{\sum(N_s \times T)} \times 100$	TGS: Total number of germinated seeds; Ns: number of seeds per day; T: number of days from the start of the experiment

analyzed using nonlinear regression models implemented in the R package drc. To evaluate whether plant responses were consistent with a hormetic pattern, the Brain–Cousens (BC.4) model was applied, which explicitly includes a parameter describing the potential stimulatory (hormetic) effect at low doses. In addition, the log-logistic (LL.4) model was used as a standard baseline model for dose–response relationships without assuming hormesis. These models were fitted separately for each species (quinoa and tomato), organ (roots and shoots), and treatment (Ce, Gd and citrate). Model performance was evaluated based on parameter significance, convergence stability, and residual standard error. The statistical significance of the hormetic parameter (f) in the BC.4 model was used to assess evidence of biphasic (hormetic) responses, while model convergence and parameter stability were used to evaluate the reliability of each fit. Cases of model non-convergence or unstable parameter estimates were interpreted as lack of support for a defined nonlinear dose–response structure. This approach was used as an exploratory and confirmatory framework to test, rather than assume, the presence of hormesis across treatments and plants.

Results

Quinoa seedling growth assessment

In Fig. 1 the results of shoot growth of quinoa seedlings under different treatments are reported. Control seedlings (CNT), irrigated only with deionized water, showed shoot mean length of about 2.5 cm, while the seedlings treated with nitrates ($\text{Mg}(\text{NO}_3)_2 \cdot 6\text{H}_2\text{O}$ solution; nitrate) reached a length of about 2.8 cm, suggesting that nitrate treatment had only a minor effect on shoot growth compared to the control (Fig. S1a). Citrate alone did not produce noticeable effects on shoot development, with mean values comparable to the CNT across all tested concentrations. Compared to the CNT, statistically

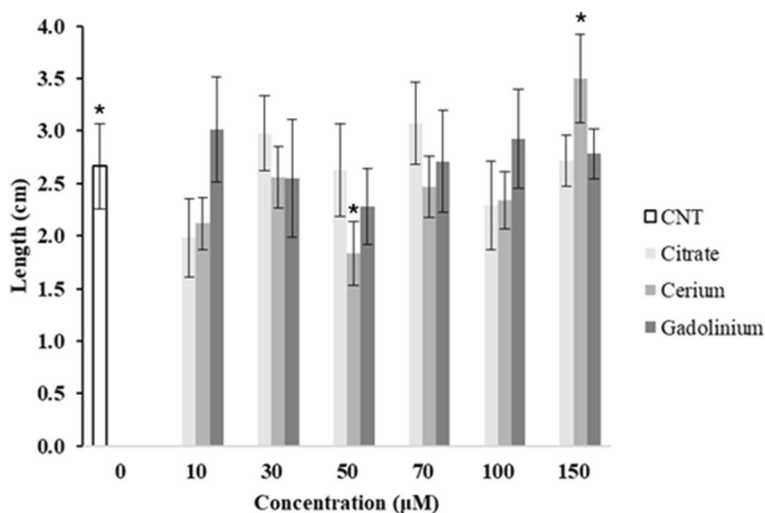


Fig. 1 Means $\pm$ standard deviation of shoots length of quinoa seedlings exposed to Ce, Gd or sodium citrate; * statistically significant differences by means of the Kruskal–Wallis test with $p=0.05$

significant differences can be detected only for shoot of seedlings exposed at Ce 50 μM and Ce 150 μM . In particular, Ce 50 μM induced a significant inhibition of shoot elongation while the highest Ce concentration promoted shoot development. While, Gd at all concentrations did not produce noticeable effects on quinoa shoots with mean values similar to the control seedlings. Similarly, all comparisons with citrate alone resulted in non-significant differences ($p > 0.05$), indicating that the addition of Ce or Gd with citrate does not modify shoot growth under the tested conditions. This suggests the absence of both synergistic or antagonistic interactions, with citrate remaining the main factor influencing the response.

The results regarding quinoa root growth are reported in Fig. 2. Controls irrigated with deionized water showed a mean root length of about 1.0 cm, while nitrate treatment reached a maximum average of 1.4 cm (Fig. S1b). Citrate positively influenced seedling development, confirming its role as a chelating agent that promotes root elongation. The effect was more evident at low and medium concentrations, with a peak around 50 μM (approximately 5.0 cm), whereas at higher concentrations (100 and 150 μM) the response tended to plateau. When REEs were applied in combination with citrate, a further modulation of root growth was observed. The addition of Ce with citrate significantly enhanced root length compared to citrate alone (Table 2), but only at the lowest concentration (10 μM), indicating a synergistic interaction under these conditions. At higher concentrations, no significant differences were detected, suggesting that citrate plays a dominant role and that the contribution of Ce becomes negligible. Similarly, the citrate–Gd combination showed a stronger effect than citrate alone at intermediate concentrations (10, 50, and 70 μM), where significant increases in root length were recorded. At higher concentrations (100 and 150 μM), the effect was not significantly different from citrate alone, supporting a dose-dependent response and a synergistic interaction limited to specific concentration ranges.

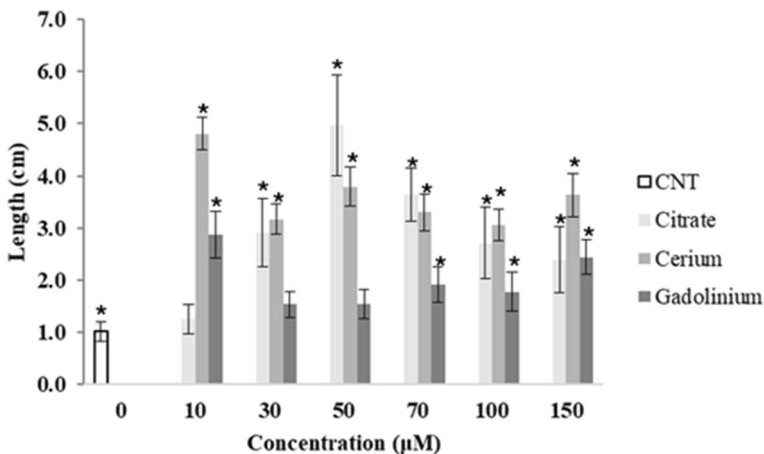


Fig. 2 Means $\pm$ standard deviation of roots length of quinoa seedlings exposed to Ce, Gd or sodium citrate; * statistically significant differences by means of the Kruskal–Wallis test with $p = 0.05$

Table 2 Comparison of Ce and Gd treatments with the corresponding citrate concentrations at each dose

Species	Organ	Treatment	Dose (μM)	Effect vs citrate	Statistical significance	Interaction
Quinoa	Shoot	Ce	All	No Effect	n.s	None
Quinoa	Root	Ce	10	Increase	*	Synergistic
Quinoa	Root	Ce	50, 70, 100, 150	No Effect	n.s	None
Quinoa	Shoot	Gd	All	No Effect	n.s	None
Quinoa	Root	Gd	10, 50, 70	Increase	*	Synergistic
Quinoa	Root	Gd	100, 150	No Effect	n.s	None
Tomato	Shoot	Ce	30–100	Decrease	*	Antagonistic
Tomato	Root	Ce	30–100	Increase	*	Synergistic
Tomato	Shoot	Gd	30, 70, 150	Increase	*	Synergistic
Tomato	Root	Gd	30–70	Decrease	*	Antagonistic

Effects are expressed as changes in growth relative to citrate alone (“vs citrate”) and classified as increase, decrease, or no change based on one-way ANOVA followed by Tukey’s HSD test. “n.s.” indicates non-significant differences ($p > 0.05$). Interaction types (synergistic or antagonistic) were inferred from the direction of significant effects relative to citrate.

Tomato seedling growth assessment

The results of the effects of Ce, Gd and citrate applications, at different concentrations, on tomato shoots are shown in Fig. 3. The mean length of shoots treated only with deionized water (CNT) is about 2.5 cm, as well as the nitrate (Fig. S1c). Citrate alone did not exhibit any significant effect on shoot development, as mean values remained comparable to the control across all tested concentrations. Compared to CNT, statistically significant differences can be detected after Ce treatment from 30 μM onwards, highlighting an increase

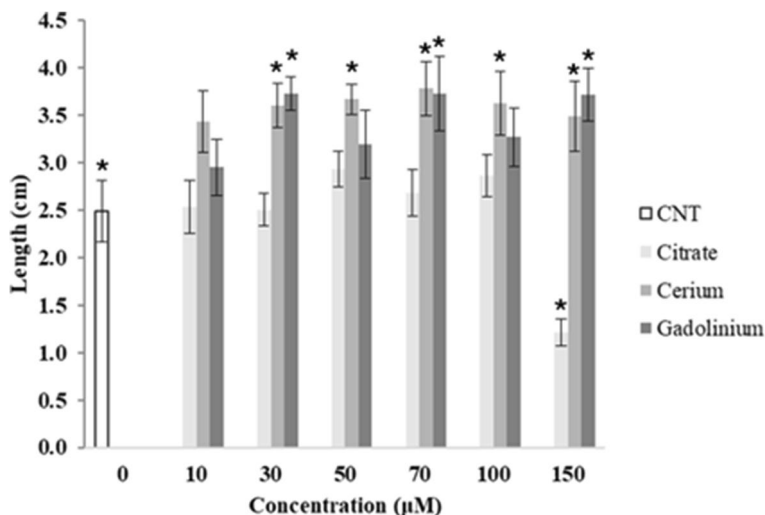


Fig. 3 Means $\pm$ standard deviation of shoots length of tomato seedlings exposed to Ce, Gd or sodium citrate; * statistically significant differences by means of the Kruskal–Wallis test with $p = 0.05$

on shoot growth with a mean length from 3.5 cm to 4.0 cm. Shoot length did not follow a linear pattern after the exposure to increasing doses of Gd; statistically significant differences were detected at 30 μM , 70 μM and 150 μM Gd when compared to CNT and even to the corresponding dose of citrate alone. When each Ce treatment was compared to the corresponding dose of citrate alone, the effects on tomato shoots were particularly evident and a drastic inhibition of shoot growth was displayed (Table 2). In fact, shoots of tomato seedlings treated with the highest concentration of citrate reached a mean length of only 1.0 cm. Despite this, even at the lowest citrate concentrations (30–100 μM), a reduction in shoot length was observed.

Figure 4 reports the effects of the different treatments on tomato roots. Controls reached a mean root length of about 8.3 cm. Nitrate showed similar results, with a mean root length around 8 cm (Fig. S1d). Only citrate increased tomato root length with a maximum of about 11.0 cm at 100 μM . Compared to CNT, the exposure of tomato roots to different REEs concentrations negatively affected the growth. In particular, a negative effect on tomato roots can be detected at Ce 10 μM and 100 μM , while the lowest mean length of about 3 cm was observed at the highest Gd concentration (150 μM). When Ce and Gd treatments were compared with the corresponding doses of citrate alone, contrasting effects emerged, suggesting different interaction patterns. In the case of Ce, concentrations of 30, 50, 70, and 100 μM significantly increased root length relative to citrate, indicating a synergistic effect. Conversely, Gd treatments at 30, 50, and 70 μM resulted in a reduction of root length compared to citrate alone, pointing to an antagonistic interaction (Table 2).

Quinoa germination parameters

The results of growth indexes (GI, RGR, RGS and CVG) of quinoa seedlings exposed to Ce, Gd and citrate are reported in Table 3. The parameters for CNT (irrigated with only deionized water) were always 100%, except for CVG which was 52.4. Ce treatment positively affected quinoa growth at the lowest concentration (10 μM) reporting an enhancement for GI, RGR and CVG. In particular, GI and RGR showed an increase of 189% and

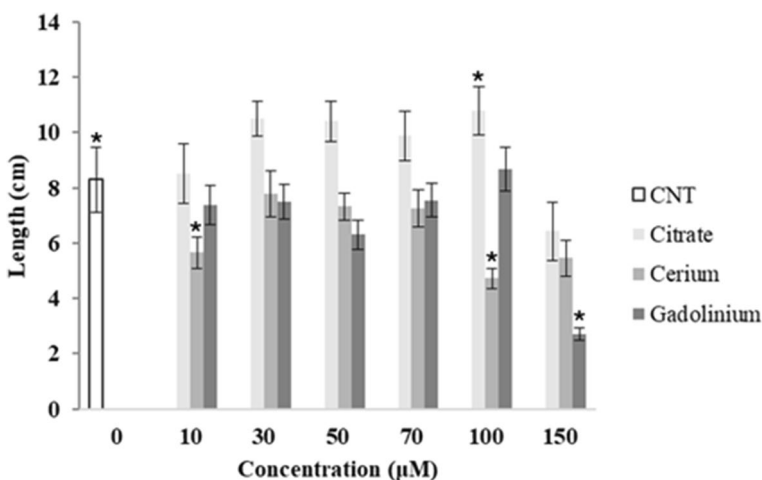


Fig. 4 Means $\pm$ standard deviation of roots length of tomato seedlings exposed to Ce, Gd or sodium citrate; * statistically significant differences by means of the Kruskal–Wallis test with $p=0.05$

Table 3 Results of growth parameters for quinoa plants exposed to Ce, Gd or citrate

Treatment (μM)	GI	RGR	RGS	CVG
Ce10	289.3 $\pm$ 4.6*	385.7 $\pm$ 4.6*	106.8 $\pm$ 4.3	80.0 $\pm$ 2.6*
Ce30	94.3 $\pm$ 4.3	108.8 $\pm$ 2.9	86.0 $\pm$ 2.2	56.5 $\pm$ 3.7
Ce50	76.5 $\pm$ 6.2	76.5 $\pm$ 3.6	69.9 $\pm$ 5.1*	56.5 $\pm$ 4.0
Ce70	77.5 $\pm$ 9.9	90.4 $\pm$ 0.8	80.3 $\pm$ 1.5	63.2 $\pm$ 6.1
Ce100	113.0 $\pm$ 8.5	113.0 $\pm$ 2.3	102.4 $\pm$ 2.4	66.7 $\pm$ 2.4
Ce150	104.8 $\pm$ 10.4	151.4 $\pm$ 0.3	128.8 $\pm$ 5.7	90.0 $\pm$ 5.3*
Gd10	158.7 $\pm$ 10.1*	230.9 $\pm$ 3.9*	152.1 $\pm$ 2.2*	73.3 $\pm$ 2.8
Gd30	42.2 $\pm$ 5.5*	52.7 $\pm$ 4.2*	85.6 $\pm$ 3.5	75.0 $\pm$ 3.4
Gd50	31.0 $\pm$ 1.7*	31.0 $\pm$ 3.1*	86.9 $\pm$ 4.5	86.7 $\pm$ 3.4*
Gd70	48.8 $\pm$ 3.5*	52.5 $\pm$ 2.7*	88.2 $\pm$ 8.8	72.2 $\pm$ 3.9
Gd100	56.3 $\pm$ 2.6*	65.7 $\pm$ 6.6*	128.0 $\pm$ 2.1	63.2 $\pm$ 5.1
Gd150	117.4 $\pm$ 2.3	101.7 $\pm$ 4.8	102.4 $\pm$ 6.7	68.2 $\pm$ 6.0
Citrate10	179.4 $\pm$ 6.2*	123.4 $\pm$ 1.0	74.4 $\pm$ 9.5	36.4 $\pm$ 2.3
Citrate30	392.4 $\pm$ 5.4*	287.8 $\pm$ 2.0*	111.9 $\pm$ 8.4	33.3 $\pm$ 3.1*
Citrate50	580.6 $\pm$ 4.4*	491.3 $\pm$ 7.5*	98.7 $\pm$ 3.2	41.9 $\pm$ 4.1
Citrate70	459.3 $\pm$ 10.0*	360.9 $\pm$ 6.3*	115.4 $\pm$ 1.1	53.8 $\pm$ 8.1
Citrate100	340.8 $\pm$ 5.1*	267.7 $\pm$ 2.2*	85.9 $\pm$ 4.3	63.6 $\pm$ 6.5
Citrate150	280.8 $\pm$ 6.0*	237.6 $\pm$ 2.3*	102.1 $\pm$ 6.6	76.5 $\pm$ 6.9

Values are expressed as mean percentage $\pm$ standard deviation. Asterisks indicate statistically significant differences compared to the CNT (100%) based on the Kruskal–Wallis test followed by multiple comparisons ($p < 0.05$).

285%, respectively. Instead, the CVG was almost doubled with respect to the CNT. The values obtained for the CVG showed no significant difference between the CNT quinoa seeds and those exposed to all Ce doses, with only a consisting increase of CVG at 150 μM Ce. Gadolinium exposure followed a different pattern: although the lowest concentration (10 μM) positively affected quinoa growth, the intermediate concentrations (from 30 μM to 100 μM) negatively affected the indexes, showing statistically significant differences in comparison to CNT. The negative effect was particularly evident on roots, resulting in low values of RGR and GI. Citrate positively affected quinoa growth, particularly at the root level, as shown by the high values of GI and RGR. The maximum values of GI and RGR indexes were reached at the middle concentration (50 μM ; 580 and 491, respectively).

Tomato germination parameters

The growth indexes calculated for tomato seedlings are reported in Table 4. The CVG of tomato plants irrigated with only deionized water was 2.8%, while all the treatments at all concentrations positively affected the velocity of germination reaching the maximum values with Gd 150 μM and Ce 10 μM exposures (22.8 and 22.5%, respectively). Citrate 150 μM was the only exception; although the CVG increased, the index reached only 9.8%, indicating a slower growth velocity of seedlings. The exposure of tomato seedlings to Ce highlighted a different effect on roots and shoots. In fact, almost all concentrations (particularly 150 μM) induced positive effects on RGS index, while GI and RGR were always lower or comparable to the CNT. Particularly, Ce 100 μM negatively affected GI and

Table 4 Results of growth parameters for tomato plants exposed to Ce, Gd or citrate

Treatment (μM)	GI	RGR	RGS	CVG
Ce10	53.1 $\pm$ 1.2*	66.4 $\pm$ 9.7*	135.6 $\pm$ 4.4	22.5 $\pm$ 2.1*
Ce30	70.2 $\pm$ 3.5*	74.1 $\pm$ 5.2	143.9 $\pm$ 5.2*	20.7 $\pm$ 1.8*
Ce50	74.3 $\pm$ 4.2	70.3 $\pm$ 3.4*	125.2 $\pm$ 2.3	21.8 $\pm$ 1.0*
Ce70	73.5 $\pm$ 2.5	73.5 $\pm$ 3.3	141.0 $\pm$ 3.0	20.0 $\pm$ 2.3*
Ce100	41.3 $\pm$ 7.8*	43.8 $\pm$ 7.6*	126.4 $\pm$ 4.5	21.3 $\pm$ 2.7*
Ce150	100.8 $\pm$ 2.0	84.8 $\pm$ 4.2	288.3 $\pm$ 10.1*	17.8 $\pm$ 2.6*
Gd10	86.7 $\pm$ 3.5	86.7 $\pm$ 4.1	116.5 $\pm$ 2.1	20.0 $\pm$ 3.1*
Gd30	75.1 $\pm$ 1.1*	71.3 $\pm$ 6.5	149.0 $\pm$ 3.3*	21.3 $\pm$ 1.5*
Gd50	64.0 $\pm$ 2.4*	60.6 $\pm$ 6.3*	109.0 $\pm$ 1.1	20.4 $\pm$ 2.1*
Gd70	72.5 $\pm$ 1.9	76.3 $\pm$ 3.4	138.8 $\pm$ 2.2	22.4 $\pm$ 1.4*
Gd100	89.6 $\pm$ 5.2	80.6 $\pm$ 2.5	114.1 $\pm$ 1.7	21.7 $\pm$ 3.0*
Gd150	47.3 $\pm$ 4.8*	42.0 $\pm$ 5.9*	307.3 $\pm$ 9.8*	22.8 $\pm$ 2.7*
Citrate10	206.8 $\pm$ 9.8*	103.4 $\pm$ 1.8	103.3 $\pm$ 2.5	19.8 $\pm$ 2.4*
Citrate30	242.5 $\pm$ 7.9*	127.6 $\pm$ 2.4	102.1 $\pm$ 1.8	18.1 $\pm$ 1.7*
Citrate50	227.7 $\pm$ 6.3*	126.5 $\pm$ 4.3	119.6 $\pm$ 6.4	21.4 $\pm$ 2.0*
Citrate70	240.0 $\pm$ 5.7*	120.0 $\pm$ 3.6	109.5 $\pm$ 5.3	19.0 $\pm$ 3.4*
Citrate100	235.8 $\pm$ 6.6*	131.0 $\pm$ 3.5	116.9 $\pm$ 2.4	21.7 $\pm$ 2.4*
Citrate150	125.0 $\pm$ 5.8	78.2 $\pm$ 7.4	49.4 $\pm$ 8.7*	9.8 $\pm$ 2.6

Values are expressed as mean percentage $\pm$ standard deviation. Asterisks indicate statistically significant differences compared to the CNT (100%) based on the Kruskal–Wallis test followed by multiple comparisons ($p < 0.05$).

RGR with a reduced value of 41% and 43%, respectively. Gadolinium exposure similarly affected the indexes, with lower values for GI and RGR and higher values for RGS. Gadolinium 50 μM and 150 μM affected roots and shoots. Citrate exerted a high toxicity on tomato shoots at 150 μM , resulting in RGS of only 49%. The exposures at other doses did not affect both RGR and RGS in comparison to CNT, while GI was positively influenced by 10 μM to 100 μM citrate.

Hormesis effect

A dose–response analysis was performed using two nonlinear models, Brain–Cousens hormesis and log-logistic models, for roots and shoots of quinoa and tomato treated with Ce, Gd and citrate. Across both quinoa and tomato, nonlinear dose–response modelling consistently failed to provide robust evidence of hormesis. However, differences in model behavior between the two species highlight distinct levels of response stability. In quinoa, Ce and Gd treatments showed mixed model performance depending on organ (Table 5). Shoot responses generally allowed model convergence but without a statistically significant hormetic component, while root responses were often unstable or not identifiable, particularly for Ce. Gd root also showed severe parameter instability, and Gd shoot failed to converge entirely. Citrate treatments in quinoa similarly did not show significant hormetic terms, although root responses showed a weak, non-confirmed tendency toward biphasic behaviour. In tomato, model instability was even more pronounced (Table 5). Ce root responses showed complete lack of reliable parameter estimation, while Ce shoots

Table 5 Summary of the hormesis parameter (f and p value) estimated from the Brain–Cousens model across species (quinoa and tomato), organs (roots and shoots), and treatments (Ce, Gd and citrate); ns is not statistically significant ($p > 0.05$)

Species	Organ	Treatment	f	p value	
Quinoa	Root	Ce	Not estimable	-	Model unstable
	Shoot	Ce	0.0449	0.50	ns
	Root	Gd	0.0012	0.77	ns
	Shoot	Gd	-	-	Model failed to converge
	Root	Citrate	-0.0270	0.089	Weak, not significant trend
	Shoot	Citrate	-0.0030	0.49	Ns
Tomato	Root	Ce	Not estimable	-	Model unstable
	Shoot	Ce	-0.0036	0.47	Ns
	Root	Gd	-0.2162	0.26	Ns
	Shoot	Gd	-0.00665	0.46	Ns
	Root	Citrate	-0.1752	0.32	Ns
	Shoot	Citrate	-0.0814	0.27	Ns

converged but without evidence of hormesis. Gd treatments in roots showing strong parameter instability and shoot models failing to converge. Citrate-treated tomato plants again showed dose-dependent responses but no significant hormetic component in either organ. Overall, while both species exhibited dose-dependent variability in response to Ce, Gd, and citrate, quinoa showed slightly more model stability in shoot systems. In both species and across all treatments and organs, the results indicate that the observed biological responses are not consistent with hormesis but are better explained by dose-dependent physiological and chemical interactions that differ in intensity and stability between species.

Discussion

Anthropogenic activities have led to the dispersion of REEs into the environment causing an increase in their concentration in air, soil and water. China is the main user of REEs as fertilizers and their positive effects on crop yield, such as an increase of seed germination, root growth, chlorophyll content and a general capability of plants to tolerate stress, have been reported. Otherwise, the effects of REEs on plants are still poorly understood and therefore further studies are needed to clarify their mechanisms (Kaur et al. 2024). In this framework, our study aimed to assess the effects of two REEs (Ce and Gd) and citrate on two plant species, quinoa and tomato.

Effects of REEs on shoot and root growth of seedlings

Several studies present in scientific Chinese literature highlight the positive effects of La at low concentrations leading to growth promotion and encouraging their use as fertilizers. However, recent studies have not achieved the same results raising doubts about the effects of REEs. However, more recent work has questioned these beneficial effects, highlighting species-dependent and sometimes inhibitory responses. For example, Thomas

et al. (2014) showed that La and Ce can reduce plant biomass in a species-specific manner. Similarly, Liu et al. (2021) reported that Gd promotes growth at low concentrations but inhibits development at higher levels in *Arabidopsis thaliana*. Our results are consistent with this concentration-dependent dual behavior. In quinoa, low doses of Ce (10 μM) and Gd (10 μM) promoted growth responses, whereas higher concentrations generally reduced performance. In contrast, tomato seedlings were more sensitive overall, showing predominantly negative responses, particularly in roots. Shoot responses in tomato were more variable, with some stimulation observed at intermediate concentrations, while root growth was more strongly inhibited at higher doses. The dose-specific analysis allowed us to separate REEs effects from those of citrate, a common and biodegradable chelating agent that enhances metal mobility and uptake in plants due to its ability to complex trivalent ions (Hoyt and Gewanter 1992; Ibrahim 2023). This approach suggests that citrate–REEs interactions can be synergistic or antagonistic depending on species, organ, and concentration, although these interpretations remain statistically inferred.

Effects of REEs on germination

The GI in the CNT was 100%, and similar values were observed under most REEs treatments, indicating no major effects on seed germination or root elongation. GI values below 80% were considered phytotoxic, while values above 120% indicated stimulation. In quinoa, low REEs doses showed clear positive effects, with Ce 10 μM increasing GI up to ~189% and Gd 10 μM showing moderate stimulation (~58%). In contrast, tomato seedlings were generally unaffected or negatively impacted, particularly at high Gd concentrations, confirming previous findings. The CVG, which reflects germination speed, was 52.4% in quinoa controls and remained largely unchanged across treatments, except for increases at specific doses (e.g., 150 μM Ce, 10 μM Ce, and 50 μM Gd). Tomato showed a much lower baseline CVG (~2.8%), but all REEs treatments enhanced germination speed, unlike previous studies reporting no effect. Citrate had no impact on quinoa CVG, while in tomato it increased germination speed at most concentrations, except at the highest dose (150 μM), where values were comparable to the control.

REEs and hormesis

Numerous studies have reported hormetic responses in plants, where low doses of potentially toxic substances, including REEs, can stimulate growth while higher concentrations become inhibitory. Although these biphasic responses are widely described, the underlying physiological and molecular mechanisms remain poorly understood and are often attributed to the modulation of phytohormones and stress-related pathways (Cedergreen et al. 2007; Eze et al. 2021). In particular, elements such as La and Ce have been frequently associated with hormetic effects, with low concentrations enhancing plant performance and higher doses inducing toxicity, possibly through oxidative stress mechanisms (Agathokleous et al. 2022; Agathokleous et al. 2018; Kaur et al. 2024). In contrast with this general framework, our dose–response analysis did not provide robust evidence of hormesis in either quinoa or tomato. Although some dose-dependent variations were observed, nonlinear modelling using both Brain–Cousens and log-logistic approaches did not detect statistically significant hormetic components. In quinoa, model convergence was achieved more consistently in shoots than in roots, but without confirming biphasic responses. Root data, particularly under Ce and Gd treatments,

showed instability and poor parameter identifiability, preventing reliable interpretation. Similarly, citrate treatments showed only weak and non-significant tendencies toward biphasic patterns. In tomato, the lack of hormesis was even more evident, with frequent model instability and failure to converge, especially for Gd treatments and root responses. While some increases in growth at specific concentrations were observed, these did not follow a consistent biphasic trend and therefore cannot be interpreted as true hormetic responses. Instead, the observed variability is more likely attributable to dose-dependent physiological effects and species-specific sensitivity to REEs and their interaction with citrate. Although previous studies have suggested that Gd may induce biphasic responses in plants (*e.g.*, Caiyun Zhang et al. 2019)), our results do not support a clear hormetic pattern. For instance, quinoa roots showed increased growth at low Gd concentrations followed by inhibition at higher doses, but this trend was not consistent across organs nor statistically supported by the models. Overall, our findings suggest that, under the tested conditions, plant responses to Ce, Gd, and citrate are better explained by complex, dose-dependent interactions rather than true hormesis. This highlights the importance of combining statistical modelling with cautious biological interpretation, as apparent stimulatory effects at low doses do not necessarily reflect a genuine hormetic mechanism.

Conclusions

Nowadays REEs are widely used in many anthropogenic fields, leading to increasing concentrations in the environment. Our study shows that Ce and Gd can induce dose-dependent effects on plant growth exhibiting a subtle biphasic dose–response trend in root growth, with a slight stimulation observed at low Ce concentrations (10 μM), whereas higher concentrations did not result in clear inhibition. These findings suggest that low concentrations of REEs could be a successful method for enhancing plant growth, in particular during the early stages of crop development. However, our knowledge is still too far from understanding the application dosage, the bioavailability and the effects on most plant species. More studies are needed to better understand the mechanisms of REEs and to assess the long-term effects on the environment.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflicts of interest The authors declare no competing interests.

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