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Biostimulant Effects of Cerium on Seed Germination and Initial Growth of Tomato Seedlings

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Abstract: The rare earth element (REE) cerium (Ce) can act as a biostimulant in diverse crop plants. The effects of 0, 5, 10, and 15 μM Ce (supplied as $CeCl_3$ $7H_2O$) on seed germination and the initial growth of tomato (*Solanum lycopersicum* L.) cv. Vengador were evaluated. After a 12 h imbibition, the weight of the seeds treated with 15 μM Ce was 37.5% greater than that observed in the control. The germination index of the seeds treated with 5 μM Ce was greater than 100% (101.93%), though when applying 10 μM Ce this index was 17.53% lower than the control seeds. Nevertheless, Ce treatments did not significantly affect the coefficient of velocity of germination, relative seed germination, germination index, radicle length, dry biomass, or relative growth. Interestingly, shoot length increased significantly in the treatments with 5, 10, and 15 μM Ce. This tendency was also observed in the dry biomass weight and relative growth of the shoots. Hence, Ce has a stimulating effect on germination and initial growth in tomato cv. Vengador shoots. In particular, there was a priming effect of Ce on seeds, reflected in a higher weight gain in Ce-treated seeds, which indicated greater water absorption. Therefore, Ce can be an alternative to accelerate the production time of tomato seedlings in seedbeds.

Keywords: biostimulation; beneficial elements; rare earth elements; lanthanides; seed priming; hormesis

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1. Introduction

Rare earth elements (REEs) comprise 17 elements including lanthanum (La^{3+}), the lanthanides (Ln^{3+}), scandium (Sc^{3+}) and yttrium (Y^{3+}) [1]. Currently, REEs are pivotal components of modern industries and play key roles in medicine, chemistry, agriculture and livestock farming [2]. In plant biology, REEs may improve photosynthesis, biomass accumulation, and primary and secondary metabolism, as well as the activity of numerous enzymes involved in vital physiological processes such as growth, development and responses to stress [3,4].

With approximately 60 ppm, cerium (Ce) is the most abundant REE in the Earth's upper continental crust [5]. This element is demonstrated to have both positive and negative effects in plants depending on the concentrations applied, the environment and the genotypes tested, pointing to a potential hormetic effect on plant biology [3]. In tomato (*Solanum lycopersicum* L.), Ce is proven to enhance vital biochemical and physiological processes. For instance, the application of 50–250 mg/L cerium acetate, suppressed *Fusarium* wilt and improved chlorophyll content and plant growth [6]. Moreover, foliar exposure to 250 mg/L CeO_2 nanoparticles increased the fruit dry weight (67%) and lycopene content (9%), while the application of 50 mg/L cerium acetate increased the fruit lycopene content by 11% [7].

With more than 180 M metric tons produced globally in 2019, tomato is by far the most produced vegetable in the world [8]. For efficient production systems, seed germination and the development of healthy and vigorous seedlings are key factors for determining the success of the system. The timing of seed germination is one of the most crucial steps in the plant life cycle, and crop seeds such as those of tomato often start the germination process as soon as water is imbibed, completing the process usually a few days after the sowing time [9,10].

Different environmental factors such as temperature, light, and postharvest requirements represent an adaptation strategy to ensure optimal conditions for seedling development and survival in regional/local terms, whereas species displaying cosmopolitan distribution can germinate under virtually any environmental condition [11]. Furthermore, some photoreceptors may control seed germination. For instance, phytochromes are necessary for controlling seed germination and hormonal activities in plants [12,13]. In some plant species such as redroot pigweed (*Amaranthus retroflexus* L.), seed germination behavior may be affected by the time of the year in which seeds are produced, while both the environmental conditions experienced by the mother plant during seed maturation and those experienced by seeds after seed set are key factors interfering with this process [14].

To evaluate seed germination, some coefficients were developed in order to characterize the entire course of the process [15]. For instance, the coefficient of velocity of germination (CVG) analyzes the rapidity of germination. Its value rises as the number of germinated seeds increases and the time required for germination decreases. The seed germination index (GI) is a widely used test for evaluating the potential phytotoxicity of certain substances present in growth media, substrates or soils, and is estimated considering the percentage of seed germination and root elongation [16–19].

Notably, this variable can reach mean values higher than 100. Thus, GI values less than 50% indicate high phytotoxicity, values of 50 to 80% suggest moderate phytotoxicity, and values higher than 80 and less than 100% indicate that there is no phytotoxicity. If the value of GI exceeds 100%, it is considered that the substance or the treatment tested is a phytonutrient or a phytostimulant [19,20].

Once seeds are successfully germinated, a rapid establishment of seedlings after planting is a prerequisite to guarantee an efficient production system. Furthermore, the relationship between the quality of the seedlings and their growth and survival after outplanting represent a critical step in horticulture [21]. Modern technologies to produce high-quality seedlings have been generated in the last few decades, though there is still a need to develop practices to be implemented in nurseries and at planting sites in order to have more productive plantations in ever-changing environments. Therefore, an in-depth, comprehensive understanding of the effect of novel inorganic biostimulants such as Ce must be developed.

In rice (*Oryza sativa* L.) seeds, doses from 2.5 to 20 μM $Ce(NO_3)_3$/mL significantly increased germination [22]. Furthermore, rice seeds treated with $CeCl_3$ $7H_2O$ (4, 8, and 12 μM) increased germination and initial growth, with respect to the control without Ce [23]. Contrarily, treating with CeO_2 nanoparticles at a concentration of 2000 mg/L did not affect germination or root length in tomato, canola (*Brassica napus* subsp. *napus*), radish (*Raphanus sativus* L.), wheat (*Triticum aestivum* L.), cucumber (*Cucumis sativus* L.), and cabbage (*Brassica oleracea* L.); lettuce (*Lactuca sativa* L.) was the only species that exhibited a slight decrease in root length upon Ce exposure [24]. Similarly, CeO_2 nanoparticles (0.1–10 mg/L) had no significant effect on the germination of tomato [25]. Furthermore, La, Y and Ce may exert limited or negative effects on the total percent of germination and the germination rate of tomato [26].

Since positive, neutral and even negative effects of Ce were reported and overall results remain controversial, further studies are needed to elucidate the regulatory mechanism of Ce underlying the potential stimulation of seed germination and plant growth. It is currently estimated that there are more than 10,000 commercial varieties of tomato worldwide, and we can expect different responses among genotypes. Therefore, this study aimed at increasing our understanding of the ability of Ce (applied as $CeCl_3$ $7H_2O$) to act as an elicitor to improve seed germination and initial seedling growth in tomato cv. Vengador, one of the most commercialized and popular varieties grown in Mexico.

2. Materials and Methods

2.1. Plant Material and Experimental Conditions

The seed company Syngenta (San Luis Potosí, SLP, Mexico) provided seeds of the tomato cv. Vengador. This cultivar exhibits high yields (350 to 450 t/ha) in mid-tech greenhouses and resistance to the main diseases caused by *Fusarium* and nematodes. Plantlet vigor is intermediate.

These seeds were pretreated by the supplier with the fungicides methyl *N*-(1H-benzimidazol-2-yl) carbamate and dimethylcarbamothioylsulfanyl *N*,*N*-dimethylcarbamod ithioate, each one at a rate of 2 g per kg of seeds. We did not apply any other sterilization/disinfection treatment before or after the experiment.

The experiment was established in a germination chamber (SMI11 Shel Lab; Cornelius, OR, USA) in the dark at 25 °C. Tomato seeds germinate after rehydration in complete darkness [27]. However, after germination, seedlings ideally receive 14 or more hours of light a day, while temperature must be kept consistently and sufficiently warm (21 to 27 °C), enabling seeds to germinate within 5 to 10 days [28]. If the seeds are exposed to light, then carbonic acid gas is decomposed, oxygen released, and carbon fixed, which hardens the seed and disrupts its integrity [13,29], thus hindering germination. Consequently, under our experimental conditions, both control seeds and seeds exposed to Ce were germinated in complete darkness.

2.2. Seed Manipulation and Treatment Application

Before treatment application, every seed was weighed separately on an analytic scale (Adventurer Ohaus Pro AV213C; Parsippany, NJ, USA). Seeds were then set to imbibition for 12 h in Ce solutions; 5, 10, and 15 µM Ce at room temperature. Control seeds were watered just with distilled water (without Ce) for imbibition. Cerium was supplied as $CeCl_3$ $7H_2O$ (Sigma-Aldrich; Saint Louis, MO, USA).

Sets of 15 imbibed seeds from each treatment were placed on filter paper in Petri dishes, which formed an experimental unit. They were kept hydrated with the corresponding Ce solution. Each treatment had four replicates (Petri dishes), which were placed in the germination chamber as described above. At 24 h intervals for 7 days, the number of germinated seeds was counted. A seed was considered germinated when its radicle attained 2 mm long.

2.3. Variables Recorded

Variables measured related to germination and initial seedling growth are listed in Table 1. They included germination index (GI), relative seed germination (RSG), coefficient of velocity of germination (CVG), and relative growth of shoots (RGS) and radicles (RGR).

At day 7 after the start of imbibition, shoot and radicle lengths were measured using the freeware ImageJ (https://imagej.nih.gov/ij/ (accessed on 7 February 2021), a public domain Java image-processing program. Subsequently, seedlings were divided into shoots and radicle and dried in a forced air circulation oven (HCF-125, Riossa; Guadalajara, Jalisco, Mexico) at 70 °C for 48 h. Biomass weight was determined from dry shoot and radicle samples.

With the dry biomass weight determined in the shoots and radicles, we estimated the shoot to radicle ratio following the methodology described elsewhere [32].

Table 1. Germination parameters and relative growth of shoots and radicles, formulas, description of variables and references considered to evaluate the effect of cerium (Ce) on tomato (*Solanum lycopersicum* L.) under controlled conditions.

Parameter	Formula	Description	Reference
Germination index (GI)	$GI\ (\%) = \frac{RSG \times RGR}{100}$	RSG = relative seed germinaton RGR = relative growth of radicle	Jagadabhi et al. [18]
Relative seed germination (RSG)	$RSG = \frac{NSG_{Ce}}{NSG_{Control}} \times 100$	NSG_{Ce} = germinated seeds in the Ce treatment; $NSG_{Control}$ = germinated seeds in the control.	Tam and Tiquia [30]
Coefficient of velocity of germination (CVG)	$CVG = 100 \times \frac{\text{Total of seeds germinated}}{\sum(N_1/1+N_2/2+N_3/3...+N_7/7)}$	N_1 = seeds germinated on day 1, N_2 = seeds germinated on day 2, N_7 = seeds germinated on day 7.	Moghadam and Alaei [31]
Relative growth of shoots and radicles (RGS or RGR)	$RGS \text{ or } RGR = \frac{MLEO_{Ce}}{MLEO_{Control}} \times 100$	$MLEO_{Ce}$ = mean length of the evaluated organ in a given Ce treatment, $MLEO_{Control}$ = mean length of the evaluated organ in the control.	Tam and Tiquia [30]

2.4. Statistical Analysis

The obtained data were subjected to an analysis of variance and means were compared using the Fisher LSD test, with $\alpha = 0.05$. All statistical analyses were performed with the SAS v. 9.0 software.

3. Results

3.1. Percentage Increase in Tomato Seed Weight after 12 h Imbibition

Imbibition involves water absorption by dry seeds through the cell wall and protoplasmic macromolecules [33]. Under our experimental conditions, percent increases in seed weight after imbibition showed statistical differences among treatments. There was a positive relationship between the Ce concentration and the percent increase in seed weight. Nevertheless, only the treatment with 15 µM Ce was statistically greater than the control, outperforming it by almost 37.5% (Figure 1).

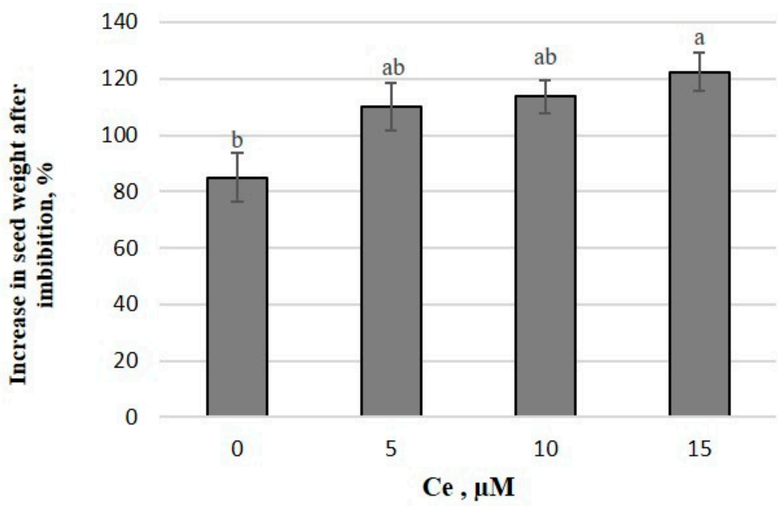

Figure 1. Percent increase in tomato (*Solanum lycopersicum* L.) cv. Vengador seed weight after 12 h imbibition in Ce solutions. Means ± SDs with different letters indicate significant statistical differences among treatments (LSD, 0.05).

3.2. Coefficient of Velocity of Germination (CVG), Relative Seed Germination (RSG), and Germination Index (GI)

The coefficient of velocity of germination (CVG) values were multiplied by 100 (values from 0 to 100). The values obtained for the CVG showed no significant difference between the seeds treated with distilled water and those with Ce (Table 2).

Table 2. Coefficient of velocity of germination, relative seed germination and index of tomato (*Solanum lycopersicum*) cv. Vengador seeds treated with cerium (Ce) under controlled conditions.

Ce, μM	Coefficient of Velocity of Germination	Relative Seed Germination (%)	Germination Index
0	48.33 ± 0.68 a	100.00 ± 1.75 a	100.00 ± 6.55 a
5	50.79 ± 3.76 a	103.51 ± 5.99 a	101.94 ± 3.60 a
10	44.31 ± 2.82 a	94.74 ± 3.50 a	82.56 ± 4.59 b
15	47.55 ± 1.52 a	100.00 ± 3.36 a	92.02 ± 3.41 ab

Means ± SDs with different letters in each column indicate significant statistical differences (LSD, 0.05).

Similarly, the relative seed germination estimated seven days after the beginning of the experiment revealed no significant differences among treatments (Table 2).

Regarding germination index, seeds treated with 5 μM Ce exhibited a mean value greater than 100% (101.93%). Though such an index was not statistically different compared to the control, it represents a biostimulant effect of Ce (Table 2). Nonetheless, seeds exposed to 10 and 15 μM Ce displayed decreased mean values in the germination index, which were nearly 18% and 8% lower than the control, respectively.

3.3. Seedling Growth and Biomass Parameters

Compared to the control, shoot length increased 63.5, 77.5, and 101% in seedlings treated with 5, 10, and 15 μM Ce, respectively (Figure 2).

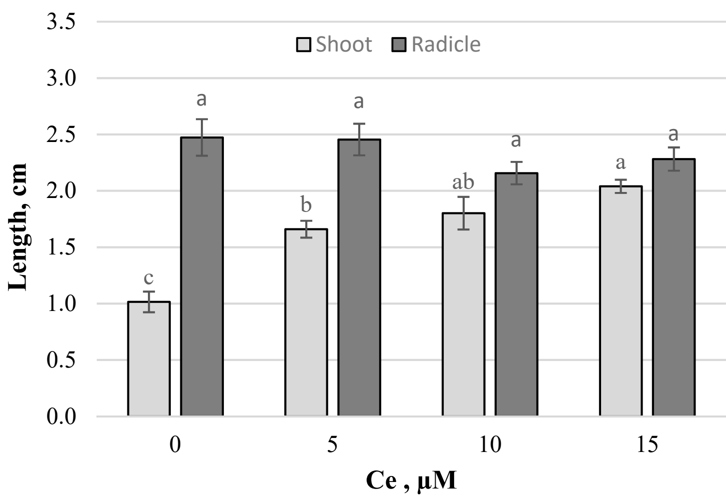

Figure 2. Shoot and radicle length of tomato (*Solanum lycopersicum* L.) cv. Vengador seedlings after seven days in germination chambers in solutions with different Ce concentrations. Means ± SDs with different letters in each parameter indicate significant statistical differences (LSD, 0.05).

However, radicle length was not affected by the Ce doses evaluated (Figure 2).

The applications of Ce increased the dry biomass of the shoots, compared to the control (Figure 3). The highest dry biomass weight of this organ was observed when applying the highest level of Ce (i.e., 15 μM Ce). Conversely, no significant differences among treatments were observed when dry biomass of the radicle was evaluated (Figure 3). Interestingly, total dry biomass weight of seedlings exposed to 15 μM Ce was the highest among all treatments evaluated (Figure 4).

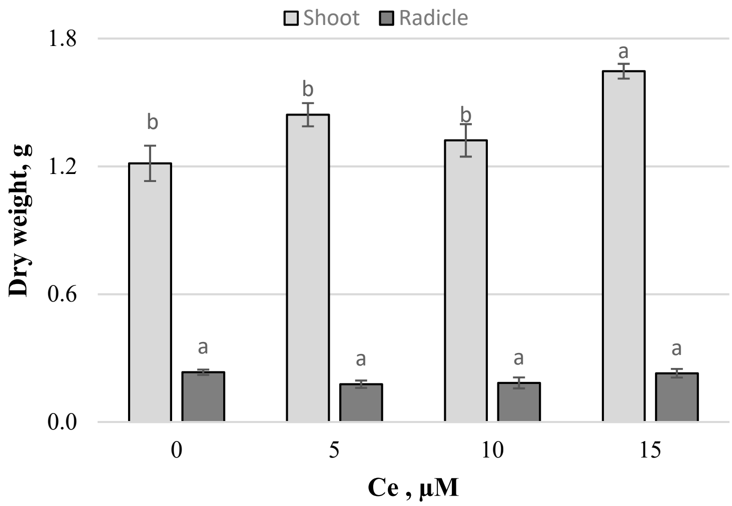

Figure 3. Shoot and radicle dry weight of tomato (*Solanum lycopersicum* L.) cv. Vengador seedlings after seven days in germination chambers in solutions with different Ce concentrations. Means ± SDs with different letters in each parameter indicate significant statistical differences (LSD, 0.05).

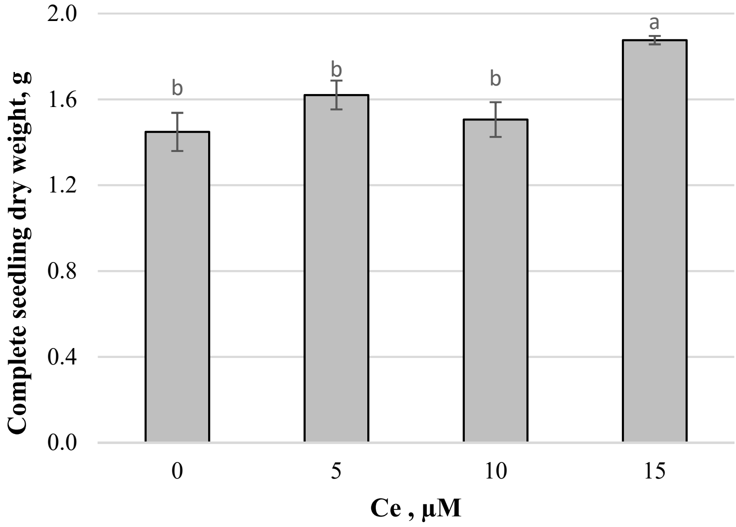

Figure 4. Complete seedling dry weight of tomato (*Solanum lycopersicum* L.) cv. Vengador seedlings after seven days in germination chambers in solutions with different Ce concentrations. Means ± SDs with different letters indicate significant statistical differences (LSD, 0.05).

3.4. Shoot to Radicle Ratio

The applications of 5 µM Ce significantly increased the shoot to radicle ratio (Figure 5). In this treatment, the mean was 59.06% higher than the control. The application of 10 or 15 µM Ce resulted in 45.5 and 41.55% increases, respectively, compared to the control, albeit these three treatments were statistically similar to one another.

3.5. Relative Growth of Shoots and Radicles

The application of Ce positively affected the relative growth of tomato seedlings in the aboveground part (Figure 6). A direct relationship between Ce doses and shoot growth was observed. In the treatment with 15 µM Ce, the relative growth was double that observed in the control.

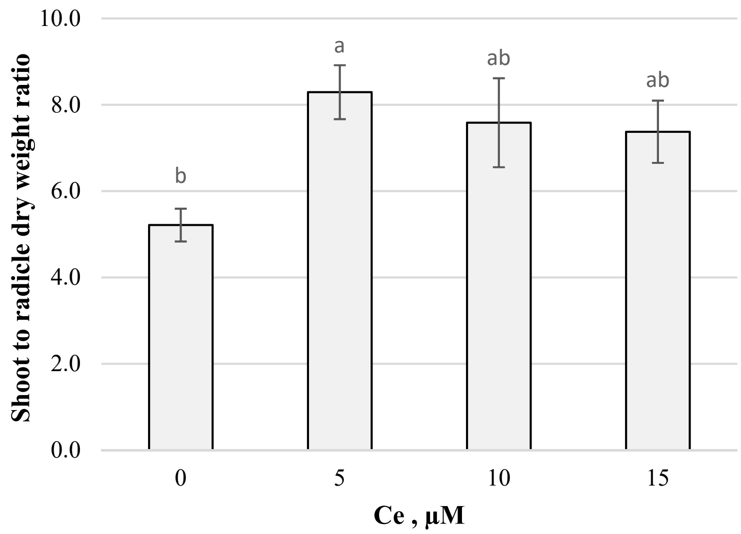

Figure 5. Shoot to radicle dry weight ratio of tomato (*Solanum lycopersicum* L.) cv. Vengador seedlings after seven days in germination chambers in solutions with different Ce concentrations. Means ± SDs with different letters indicate significant statistical differences (LSD, 0.05).

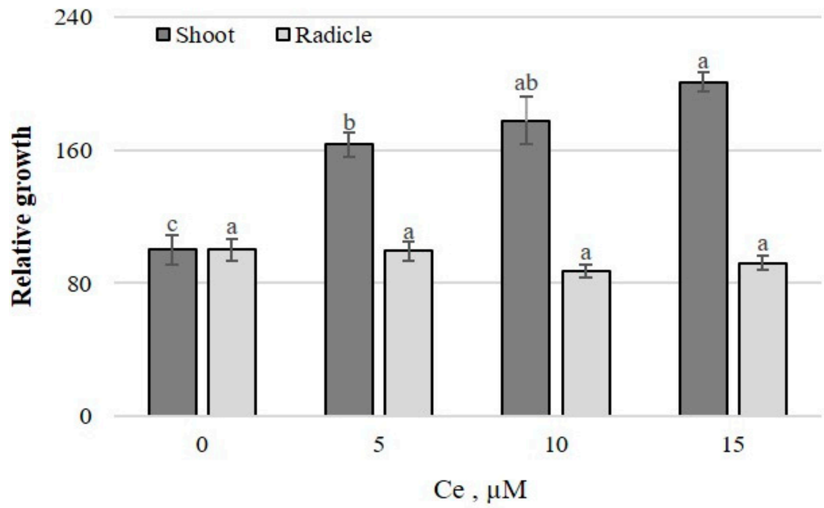

Figure 6. Relative growth of shoots and radicles of tomato (*Solanum lycopersicum* L.) cv. Vengador seedlings after seven days in germination chambers, treated with solutions with different Ce concentrations. Means ± SDs with different letters in each parameter indicate significant statistical differences (LSD, 0.05).

The relative growth response described in shoots was not evident in radicles, and there were no statistical differences among treatments.

4. Discussion

Rare earth elements (REEs) comprise a series of 17 chemical elements, including the lanthanide series from lanthanum (La) to lutetium (Lu), scandium (Sc) and yttrium (Y) in the periodic table [34]. The technical term REE has much more to do with the difficulty of separating out each of the individual elements from relatively rare minerals than with the scarcity of any of them. In fact, REEs can be more abundant on Earth than other commonly used metals. For instance, Ce is the 26th most abundant element in the Earth's crust and is more abundant than copper (Cu) [35,36].

When applied at appropriate concentrations, REEs such as Ce can enhance seed germination [37,38]. Seed vigor, water absorption, and the permeability of the cytoplasmic membrane of seed cells during imbibition and germination may all be improved by REEs [39,40]. In our experiment, Ce treatments increased seed weight after imbibition (Figure 1). Furthermore, the coefficient of velocity of germination, relative seed germination and the germination index were nearly 2–3% higher in Ce-treated seeds as compared to the control, though such differences were just numerical and not statistically significant (Table 2).

Tomato seeds do no need light to start the germination process, which is controlled by diverse factors including the phytochrome system [13,41]. Phytochrome A (phyA) plays an important role during the well-studied transition of seedlings from dark to light growth. The role of phytochromes during skotomorphogenesis (dark development) prior to reaching light suggests that these molecules must play a role even in the dark. Indeed, phyA participates in the regulation of carbon flux through major primary metabolic pathways, such as glycolysis, beta-oxidation, and the tricarboxylic acid cycle. Additionally, phyA is involved in the attenuation of root growth soon after reaching light, possibly via the control of sucrose allocation even before the seedling reaches the light. Presumably, by participating in the control of major metabolic pathways, phyA sets the stage for photomorphogenesis for the dark grown seedling in anticipation of light [42,43].

Under our experimental conditions, germination occurred due to the nutrient reserves in the endosperm or cotyledons of the seeds, while the early developmental stages of the seedlings did not require photosynthetic activity to succeed. Once the seed germinates and the shoot is formed, this organ grows under the soil until it reaches the surface. Once the shoot reaches the soil surface and is in contact with light, the chloroplast differentiation takes place and thus photosynthesis starts.

Considering a germinated seed whose radicle was at least 2 mm long, the greatest percentage of germination occurred from day 4–6 after sowing. Thus, seedling growth covered a period of 1 to 3 days, during which we observed shoot elongation promoted by the reserves still provided by the seed itself and not by the photosynthetic activity of the growing seedling [44,45]. Notably, such elongation was distinguishable among treatments and consequently attributed to the application of Ce. Thus, the evaluation of the shoot/root ratio is justified given such arguments.

In REE-treated seeds, the oxygen evolution rate is stimulated, which triggers greater metabolic activity and generates more energy for growth [39]. REEs have a synergistic effect with a burdock fructo-oligosaccharide, which constitutes an important energy source during germination [46]. Similarly, chlorophyll content, antioxidant enzyme activity, and secondary metabolites can be enhanced in response to REEs, including Ce [4]. These responses may explain, at least in part, the results observed in our study.

The coefficient of velocity of germination (CVG) value rises as the number of germinated seeds increases and the time required to germinate decreases. The values of this coefficient range from 0 to 100, with high values approaching 100 indicating a quick germination, while values near 0 indicate that germination is very slow or even inhibited [47]. This coefficient is used as a measure of the rate and time-spread of germination [10]. In our study, the CVG fluctuated between 44.3 and 50.78%, and there were no statistical differences among the treatments. Nonetheless, the mean CVG in seeds treated with 5 µM Ce was 5.1% higher than the control. Coincidently, in cabbage, carrot (*Daucus carota* L.), corn (*Zea mays* L.), cucumber, lettuce, oat (*Avena sativa* L.), onion (*Allium cepa* L.), soybean (*Glycine max* (L.) Merr.), and tomato, the application of 250 to 1000 mg/L Ce nanoparticles did not affect seed germination [48].

In our study, relative seed germination was estimated by taking into consideration the number of seeds germinated in the treatments adding Ce, and the number of seeds germinated in the control multiplied by 100. Significant effects of Ce were not found in this parameter either. However, the mean RPTG in seeds treated with 5 µM Ce was 3.5% higher than in the control. In rice, significant increases in seed germination were found when seeds were treated with 2.5 to 20 µg/mL $Ce(NO_3)_3$ [49]. Likewise, the application of 4, 8, and 12 µM $CeCl_3\ 7H_2O$ to rice seeds significantly increased germination [23].

When estimating the germination index (GI), both the percentage of germination and its velocity are considered [10]. This index may indicate negative, neutral or positive effects of treatments (i.e., metals or other chemical elements) tested if mean values are below, near or above 100% [50]. When testing the effects of metals in plant biology, the GI is often used as an indicator of the degree of inhibition or stimulation such elements may cause in plants [20]. For instance, biostimulant effects of ionic ($FeCl_3$), micro- and nano-sized zerovalent iron (nZVI) were detected in common cress (*Lepidium sativum* L.), white mustard (*Sinapis alba* L.), and sweet sorghum (*Sorghum bicolor* var. *saccharatum*) after the estimation of GI [50]. Coincidently, in pepper (*Capsicum annuum* L.) cv. jalapeño and serrano, the application of 50 m V increased the GI by approximately 20% compared to the untreated control [51], thus pointing to a biostimulant role of V in this crop species.

Seedlings treated with 5, 10, and 15 µM Ce increased shoot length by 63.5, 77.5, and 101%, respectively, compared to the untreated control (Figure 2). In rice, the application of 4, 8 or 12 µM Ce enhanced initial growth and number of tillers in seedlings during the vegetative stage [23]. Similarly, in cowpea (*Vigna unguiculata* L.), the application of up to 17.841 µM Ce stimulated shoot growth [52]. In *Arabidopsis thaliana*, the treatment with 0.5 µM $Ce(NO_3)_3$ increased plant height by 60.8% [53].

Radicle length was not affected by the Ce doses evaluated (Figure 2). In cowpea, the application of 0.713, 3.568, and 17.841 µM Ce increased root growth by 20.5, 39.7, and 67.1%, respectively, compared to the control, while 89.2 and 446.0 µM Ce inhibited radicle growth by 38.4 and 49.3%, respectively, compared to the control [52]. In general, high Ce concentrations adversely affect roots more than shoots, and the negative effects of Ce on root growth may be attributed to a decrease in the cell division rate [54].

Under our experimental conditions, Ce increased dry biomass of the shoots, with the highest dry biomass weight in seedlings treated with 15 µM Ce (Figure 3). Conversely, dry biomass of the radicles was statistically similar among treatments (Figure 3). Interestingly, the highest total dry biomass weight was observed in seedlings exposed to 15 µM Ce (Figure 4). In rice seedlings, fresh and dry biomass weight of shoots and roots more than doubled with the application of Ce, with respect to the control [23]. In rice as well, the addition of 5 to 15 mg/mL $Ce(NO_3)_3$ increased the dry weight of the seedling by more than 50% [49]. Likewise, in 30-day-old coriander (*Coriandrum sativum* L.), the application of 125 mg/kg CeO_2 nanoparticles significantly increased biomass production, and seedlings exhibited longer shoots than the control [55]. Lettuce plants treated with 5 to 25 mg/L cerium ammonium nitrate $[(NH_4)_2Ce(NO_3)_6]$ increased dry biomass weight [56]. Such stimulatory effects of Ce on biomass production can be attributed, at least in part, to the enhanced photosynthetic activity promoted by Ce [57].

The shoot to root to ratio (S:R) is defined as the dry weight of the shoot biomass divided by the dry weight of the root (i.e., radicle) biomass. This parameter depends upon the partitioning of photosynthates, which may be affected by environmental stimuli such as temperature, luminosity, humidity and nutrient availability. This ratio represents one of the key factors enabling plants to survive and succeed in challenging environments, and a faster development of shoots provides species with the advantage of a larger canopy to compete for light and space [32]. Under our experimental conditions, Ce increased the S:R ratio (Figure 5), and thus contributed to our plants being better able to cope with challenging environments imposed by global warming and climate change.

The observed enhanced relative growth of the shoots demonstrates the biostimulant effect of Ce in tomato (Figure 6). A direct relationship between the Ce doses and shoot growth was evident. Interestingly, the application of 15 µM Ce produced a relative growth twice that observed in the control. The reference value, from which the relative growth of shoots and roots was estimated, corresponds to that obtained in the control. Data of shoot and root growth observed in the control were assigned the value of 100%. This percentage value of the control (100%) is placed as the denominator in the corresponding formula. Hence, in the case of the control, when the value of 100 is substituted both in the numerator and the denominator in the formula, the result is equal to 1, which is multiplied by 100, equaling to 100 again. As observed in Figure 6, values greater than 100 in the relative growth of the shoots indicate a higher growth of shoots in the treatments using Ce compared to the control. Conversely, values less than 100 recorded in the roots indicate lower root growth in some treatments where Ce was applied, compared to the control.

Lanthanum (La), a member of the REEs, can induce hormetic dose responses in plants [58–61]. Hormesis is a natural dose response phenomenon characterized by a low-dose stimulation causing positive effects, and a high dose inhibition triggering toxic effects [62,63]. This phenomenon refers to adaptive responses of biological systems to moderate environmental challenges through which the system improves its functionality to face more severe challenges [64,65]. In our current study, we can observe biostimulant effects of Ce in tomato, especially in the aboveground portion of the seedlings. Though Ce did not significantly affect all parameters determined during the germination process, we can also observe numerical increases regarding the coefficient of velocity of germination (CVG), relative seed germination (RSG), and germination index (GI) in seeds treated with 5 µM Ce. We are currently performing more in-depth statistical analyses to define the hormetic curves triggered by Ce in tomato seeds and seedlings during the early developmental stages. Coincidently, in cowpea, the application of 0.713 to 17.841 µM Ce (supplied as $Ce[NO_3]_3\,_6H_2O$) promoted the accumulation of dry matter, while doses above 17.841 µM Ce caused negative effects on this variable [52]. Similar responses were observed in two cosmopolitan weed species exposed to leaf aqueous extracts from artichoke thistle (*Cynara cardunculus* L.) [66].

Though positive effects of Ce were also reported in root tissues, including enhanced formation of adventitious roots, cell differentiation, and root morphogenesis [23,40], no stimulatory effects of Ce were observed in radicles under our experimental conditions.

Summarizing, we can claim that Ce can act as a potent inorganic biostimulant to enhance germination and initial shoot growth in tomato. In particular, a priming effect of Ce was observed on seeds, reflected in higher weight gain in seeds treated with this element, indicating greater water absorption. Furthermore, Ce stimulated shoot growth and biomass production, albeit no significant effects were observed on radicle growth.

5. Conclusions

The REE cerium stimulated a significant increase in seed weight after imbibition and enhanced shoot length and biomass production. Moreover, relative shoot growth and the shoot to radicle (S:R) ratio were also significantly increased. Therefore, Ce can be used as a powerful inorganic biostimulant to promote seed germination and shoot growth, resulting in a more efficient production of tomato seedlings capable of overcoming challenging environments. Significant progress in novel sequencing technologies and advances in omics sciences are allowing a deeper understanding of the uptake and transport of Ce and other REEs in plants. Such tremendous strides are enabling a more precise classification of plants according to their ability to absorb, transport and accumulate Ce, which in turn is helping us to determine whether they are Ce competent or not, in order to establish efficient Ce application programs under sustainable agricultural approaches.

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