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CERIUM AND HIGHER PLANTS

ABSTRACT: Rare earth elements (REEs) or *terrae rarae* (TR) are a group of 17 heavy metals which include 15 elements belonging to the lanthanide (Ln) group, as well as scandium and yttrium. REEs are very similar in chemical and physical properties. Lanthanides are considered as rare micro elements, which is not entirely true. Namely, the amount of cerium (Ce) in the Earth's crust is slightly higher than the amount of Cu, Pb or Zn. Except for Eu (+2 and +3) and Ce (+3 and +4), REEs usually form trivalent cations. Studies of individual REEs elements are mostly focused on the effects of Ce and La. Cerium is nowadays used in agriculture, as a microfertilizer. However, it is not essential for higher plants. The effects of Ce on life processes of plants range from stimulation to inhibition, depending on its concentration (hormesis), plant species, the stage of development, method of application and ecological factors. Lower concentrations and amounts of Ce can be beneficial for nutrient uptake, seed germination, photosynthesis, growth, dry matter accumulation and for alleviating different kinds of stress in plants. Cerium decreases oxidative stress and increases antioxidative capacity of plants. Higher concentrations of Ce reduce plant growth. Excessive amounts of Ce have cytotoxic and genotoxic effects. The available literature on the influence of lower concentrations of Ce on life processes in plants suggests positive outcomes. However, further fundamental investigations shall lead to better understanding of the physiological mechanisms of the impact of Ce on plant metabolisms.

KEYWORDS: cerium, ion uptake and interactions, photosynthesis, seed germination, growth, phytotoxicity, stress alleviating

INTRODUCTION

Cerium is one of the rare earth elements which are present in small concentrations in all parts of the biosphere (Turra, 2017). The average abundance of Ce in the Earth's crust is 66 µg/g (Tyler, 2004). In the soils worldwide, it ranges from 13 mg/kg to 273 mg/kg (Ramos et al. 2016) and in various terrestrial plants from 250 ppb to 16,000 ppb in dry matter (Bowen, 1979). Concentration of Ce

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in plant species is different. According to Kabata-Pendias (2000), the Ce concentration in plant species and organs is different. In lichens and *Briophytes* it spans from 600 to 5600, cheatgrass (*Bromus tectorum*) 300, vegetables from 2 to 50, rice straw 174, blueberry tops from 210 to 740 and in pine needles 370 ppb in dry matter. Global production of REEs has increased exponentially in the recent decades. REEs found application in numerous areas of human activity (Kovariková et al., 2019), thus Ce enters the biosphere. REEs are also used in agriculture as a mineral fertilizer or stimulator, primarily in China (Ren et al., 2016; Kastori et al., 2023). Mineral phosphorus fertilizers are characterized by a higher content of Ce (Moreira et al., 2019), as a result of which their application can lead to an increase in its concentration in arable soils. Cerium can enter plants via both root and aboveground parts. The transfer factor (soil-plant) for Ce is low (Mesa-Pérez et al., 2018). This fact, as well as the fact that Ce mainly accumulates in the roots (Liu et al., 2012), indicates that its entry into the food chain is limited, since the aerial parts of plants are most often used in nutrition. The exception are hyperaccumulator plants in which it accumulates in the above-ground organs. Cerium has synergisms and antagonisms with essential and other elements (Ramos et al., 2016). In this way, Ce influences the nutrimental status of plants. Low concentrations of Ce can in some cases act as a biostimulant in seed germination and initial growth of seedlings (Ramirez-Olvera et al., 2018) and have positive effects on photosynthesis.

Treatment with higher concentrations and doses of Ce adversely affects the life processes of plants and thus their growth, development and organic production. The phytotoxic concentration and dose of Ce decrease mitotic index, with increased mitotic aberration (Kotelnikova et al., 2019) and provoke leaf yellowing and necrotic damage and some structural alternations in leaves (Rodrigues at al., 2019). Abiotic and biotic stress conditions can cause an increase in accumulation of reactive oxygen species (ROS) in plants. Cerium is able to suppress accumulation of oxidative species and elevate the level of antioxidant enzymes (Liu et al., 2012; Li et al., 2021). Cerium may help to relieve the inhibition under some kinds of stress: potassium deficiency, cadmium toxicity, high level of UV-B radiation, drought, acid rain and salt stress.

The growing application of REEs and their individual elements in industry, agriculture and medicine will encourage further research in the field of rare earth elements. This is indicated, among other things, by a large number of published research and scientific works in recent decades, especially regarding the application of Ce and La.

Uptake, transport and distribution of cerium in plants

The concentration of Ce in plants varies widely depending on the plant species and environmental conditions. In the dry matter of the aerial part of *Brassica oleracea* var. *capitata*, the average concentration of Ce was 0.028 /µg/g (Bibak et al., 1999), in the leaves of *Agrostis capillaries* 150 /µg/g (Tyler and Olsson 2001), and in the leaves of forest species it ranged from 0.25 /µg/g to 0.55 /µg/g

(Markert and Li, 1991). The accumulation of Ce in plants largely depends on its concentration in the nutrient substrate. There is a significant positive correlation between the concentration of Ce in the shoots (leaves and stems) of barley and its total, water soluble and exchange forms in the soil (Kotelnikova et al., 2020). Cerium can enter plants via both root and aboveground parts. The uptake rate of REEs from soil solution is controlled not only by the plants themselves, but it depends of numerous ecological factors – on their concentration, exchangeable fractions and solubility in the soil, soil organic matter content, presence of other elements etc. (Brioschi et al., 2013). The mechanism of Ce uptake by plants is also insufficiently studied, therefore it is discussed here within the framework of the knowledge gained during the studies of uptake and transport of REEs. From the soil solution, the cell wall of the root cells adsorbs REEs, depending on environmental conditions, via precipitation or complexation. The transport of REEs in the root takes place in two ways: by apoplastic and symplastic pathway, where the role of REEs transporting proteins, endocytosis and ion channels is considered (Wang et al., 2019; Wang et al., 2024). Acropetal transport of mineral substances in vascular plants takes place in the xylem. The transpiration stream through the mass flow generally makes possible the acropetal transport of REEs, whereby the role of root pressure cannot be ruled out either. Acropetal transport of REEs can be influenced by numerous factors. In the xylem vessels of soybean, the majority of REEs are combined with ligands (Ding et al., 2007). In the xylem saps of hydroponically grown *Phytolacca americana,* citric acid facilates the migration of heavy RREs (HREEs) rather than light RREs (LREEs) (Yuan et al., 2017). Some REEs were immobilized during migration in xylem by chemical precipitation by phosphate particles and cell wall absorption. The transfer factor (TF) – the ratio of the element concentration in the aboveground part of plants or plants organs to its concentration in the soil – for certain REEs is typically lower than 1. The value of TF depends on numeorous factors – on the concentration of an element in the soil, the mobility of the ellement, plant species and organs. According to Kotenikova et al. (2020), in barley leaves, the Ce concentration did not exceed 1% of its concentration in soil. The TF (soil- to-plant transfer factor) in rice for Ce is 0.42 and only a small portion of taken up Ce reached the grain (Mesa-Pérez et al., 2018).

The distribution of nutrients in plants is specific for certain elements and plant species. To find out about the distribution of elements in plants is important from scientific and ecological point of view, since their presence in the edible parts of cultivated plants can allow their entrance in the food chain and thus may have, in higher concentrations, adverse health consequences. It can generally be said that distribution of REEs in organs of cultivated plants is as follows: root > leaf > stem > flower > fruit/seed (Wen et al., 2001), root > leaf > husk > grain (Mesa-Pérez et al., 2018). Cerium concentrations in rice were higher in roots than in shoots (Ramirez-Olvera et al., 2018) and it is mainly located in the cell wall of the rice roots (Liu et al., 2012). In contrast, in the plants baring capacity to hyperaccumulate RREs, their concentration in the aboveground parts is usually greater than in the roots (Wang et al., 2024). In microalga *Desmodesmus* *quadricauda*, Ce accumulates exclusively in the chloroplast compartment (Rezanka et al. 2016).

Interaction of cerium with other elements

Elements with similar physical and chemical properties can compete with each other for the same binding site in cell. Cerium similarities to other important essential macronutrients such as Ca, as well as its higher charge density, render this element more available for absorption into plant tissues (Thomas et al., 2014). Trivalency gives lanthanides a much higher charge to volumes ratio and therefore they usually have much higher affinities than Ca^{2+} for the given binding sites. Ions of some lanthanides (La^{+}, Nd^{3+}, Ce^{3+}), with ion radius (Ce^{2+} 0.106 nm Ca^{2+} 0.094 nm) and coordinate number close to the Ca^{2+} ions, might partly be able to replace endogenous Ca of plants or interact positively with calcium in various physiological functions. Lanthanides (Ce^{3+}, La^{3+}) could enter the chloroplast, bind easily to chlorophyll molecule and might replace Mg^{2+} ion and coordinate the porphyrin ring in pheophytin to form lanthanide-chlorophyll (Chl)-complex, Ce-chlorophyll (Rezanka et al, 2016). The influence of Ce on concentrations of elements in plants depends on many factors, e.g. concentration, plant species, organs, features of elements etc. Appropriate concentrations of $Ce(NO_3)_3$ had a positive influence on the mineral element content of the leaves of *Cyclocarya paliurus* seedlings. The maximal increase at 0.20 mmol/L Ce treatment caused the contents of K, P and Cu increase by 105.2%, 74.5% and 133.3% respectively. The contents of Mg, Mn and Fe increased with increasing concentrations of $Ce(NO_3)_3$ from 0 to 100 mmol/L by 93.2%, 29.4% and 133.9% compared to the control (Xie et al., 2015). Cerium nitrate treatment (0 to 1.5 mM) affected differently the concentration of nutrients (K, Mg, Ca, Na, Fe, Mn, Zn, Cu and Mo) in the roots and shoots of rice. The concentration of mentioned elements changed in response to the concentration of Ce (Liu et al., 2012). Adverse effect of 0.5–25 mg/L Ce on the contents of Ca, Ng, K, Cu and Zn in wheat seedlings was reported (Hu et al., 2002). Cerium (25, 50, and 100 µM in the form of $CeCl_3$) did not affect the concentration of macro or micronutrients in rice shoots. However, in roots, the high Ce concentration decreased the concentrations of Ca, Fe, Mn, and Zn, while the Mg concentration increased (Ramirez-Olvera et al., 2018). In the rice, the application of 500 mg/kg of CeO_2 nano particles to the soil increased the concentrations of K and Ca in rice, whereas concentrations of S and Fe decreased (Rico et al., 2013a).

Effect of cerium on seed germination

Cerium can influence seed germination and initial growth of the seedlings. There are opinions that the REEs can have positive effects on seed germination by acting synergically with phytohormones that stimulate germination (Ramirez-Olvera et al., 2018). The germination rate, germination index and vigor index of naturally and artificially aged rice seeds were significantly increased with a maximum effect at 10–20 µg/mL $Ce(NO_3)_3$. It is the result of the treatments of aged seed with $Ce(NO_3)_3$ that enhanced respiratory rate and activities of superoxide dismutase, catalase and peroxidase, and decreased superoxide O^- and malondialdehyde contents (Fashui, 2002). When applying 8 µM Ce and 12 µM $CeCl_3$, germination percentage of rice seeds increased by 36.2%, while with 4 µM Ce, there were no significant differences with respect to the control. Seedlings height and root length increased significantly, by over 100%, upon addition of 4 µM, 8 µM and 12 µM Ce compared to the control (Ramirez-Olvera et al., 2018).

In the literature, there are also many papers in which the favorable effect of Ce application on seed germination has not been confirmed. Cerium treatments did not significantly affect the rate of germination, relative seed germination and germination index (Sobarzo-Bernal et al., 2021). Nevertheless, Ce can also reduce seed germination and seedling growth. At a low soil pH (i.e. pH=4), Ce decreases the germination of radish and tomato seeds, which is associated with higher mobility and availability of Ce in the soil (Thomas et al., 2014). Pre-soaking of *Triticum durum* seeds for 2 h and 4 h with low concentrations (0.01 and 0.1 mM) of light REEs (La, Ce, Pr, Nd and Gd) had no effect on seed germination. Higher concentrations (1 mM and 10 mM) induced significant decrease in germination compared to controls (d'Aquino et al., 2009). Treatments by CeO_2 nanoparticles, in the concentration of 2000 mg/L, did not influence germination of seeds or root length in tomato, canola, radish, and cabbage, whereas lettuce was the only species that exhibited a slight decrease in root length upon Ce exposure (Ma et al., 2010). According to Wang et al. (2012), CeO_2 nanoparticles (0.1–10 mg/L) had no significant effect on seed germination of tomato.

Cerium effects on photosynthesis

The effects of Ce on phytosynthesis were studied in detail. There are publications pointing out that positive effects on photosynthesis are associated to several physiological and biochemical indices, including synthesis and content of photosynthetic pigments, chloroplast development and structure, light absorption, transport and conversion, as well as carboxylation activity of Rubisco. The photosynthetic pigments content is one of the important factors that effect plant growth and development through photosynthesis. Not only the total content of photosynthetic pigments is significant, but also their mutual relationship, the ratio of chlorophyll a/b and a+b/carotenoids (Manios et al., 2003). Literature data indicate that application of the lower concentrations of Ce have positive effects, while higher have negative effects on chlorophyll content and photosynthesis. According to Liu et al. (2012) in rice seedlings, content of chlorophyll a, b, and a + b was increased at 0.05 mM and 0.1 mM $Ce(NO_3)_3$, but decreased at 0.5 mM, 1.0 mM and 1.5 mM Ce. In green alga *Desmodesmus quadricauda*, treatment with 10 µM $CeCl_3$ caused increase of total chlorophyll content and decrease of the ratio of chlorophyll a/b from 2.45 in control plants to 1.21 in Ce-treated plants. The untreated algae contained 14.52 mg of chlorophylls/g of DW, while those treated with Ce contained 19.86 mg/g of DW (Rezanka et al., 2016). According to Chu et al. (1996), $CeCl_3$ could accelerate the synthesis of chlorophyll a in *Spirulina platensis*. In barley, no noticeable changes were found in the content of chlorophyll a and b pigments and their ratio under application of up to 200 mg Ce/kg air-dry soil (Kotelnikova et al., 2020). In spinach grown in pot culture experiments, Ce stimulated chlorophyll formation (Hong et al., 2002). The favorable influence of some REEs elements on the content of chlorophyll is explained by the replacement of Mg in the center of the chlorophyll molecule with the REEs element during its formation (Rezanka et al., 2016) and due to that fact more Mg is available for the formation of new chlorophyll molecules. Chlorophyll and lutein in the chloroplasts are able to form chlorophyll a-Ce, chlorophyll a-Pr and other chlorophyll-REEs complexes. In the fern *Dicpetris dichotoma*, the content of Ce-chlorophyll was 19.40% (Wei et al., 2005). Ramirez-Olvera et al. (2018) reported that the application of 100 μM Ce decreased the photosynthetic pigments chlorophyll a and b content by over 60% in rice. Zicari et al. (2018) also reported a decrease in the content of chlorophylls and carotenoids when higher concentrations of Ce (0.5 and 1 mM) were used to treat in *Lemna minor*. Intracellular localizations of lanthanides (Ne, Ce Gd, La) in *Desmodesmus quadricauda* were different: Nd and Ce were localized in the chloroplasts, while La and Gd were in the cytoplasm (Rezanka et al., 2016). Ren et al. (2007) also reported accumulation of Ce in chloroplast. According to Liu et al. (2012) in the rice leaves, exposition to 1.0 mM Ce resulted in disorderly arranged thylacoids and the chloroplast has gained more rounded instead of ellipsoidal shape.

Cerium solution sprayed onto the leaves at a concentration of 400 mg/L can partially alleviate the photoinhibition and during the midday depression it increases the photochemical efficiency (Fv/Fm) and photosynthetic performance index (PIABS) of *Pseudostellaria heterophylla* (Ma et al., 2022). The optimum concentration of $CeCl_3$ in nutrient solution that enhance photosynthesis in wheat seedlings was 0.2 to 0.5 mg/L, for cucumber from 1 to 5 mg/L, and for sunflower 15 m/L (Chu et al., 1996). Liu et al. (2012) found that higher concentrations of Ce have negative, while lower may have positive effects on photosynthesis in rice seedlings.

The effect of cerium on plant growth

In Chinese agriculture, REEs have been used to improve the nutrition status of cultivated plants for more than three decades (Hu et al., 2004) and have been extended to other countries (Wang et al., 2008). The treatment with Ce ($nCeO_2$, Ce(III) and Ce (IV)) has hormotic effect on growth and depends on many factors – plant species and vegetative stage, the applied dose and means of application, management conditions etc. In rice seedlings, in water culture, the total nodal root length (at 0.05 and 0.1 mM Ce) and shoot height (at 0.1 mM Ce) increased significantly compared with the control whereas at 0.5 mM, 1.0 mM and 1.5 mM Ce they decreased (Liu et al., 2012). Fashui et al. (2002a) found that Ce increases chlorophyll content and photosynthetic rate and stimulates the growth of spinach. Root length and height of rice seedling increased by over 100% upon application of 4,8 µM and 12 µM $CeCl_3$ (Ramirez-Olvera et al., 2018). In *Lemna minor* 0.1 mM Ce increased growth, but 1 mM Ce caused oxidative stress (Zicari et al., 2018). In *Arabidopsis thaliana,* Ce promotes floral initiation and reproductive growth in concentrations of about 0.5 to 10 µmol/L (He and Loh, 2000). Low concentrations of Ce increased the growth of cowpeas, with the maximum enhancement (23.91% for shoot and 67.53% for root length) observed at 17.84 µM Ce (Shyam and Acry, 2012). Cerium nitrate at 1–15 mg/L promoted callus growth and formation of adventitious roots on the stem of *Dioscorea zingiberensis* (Wang et al., 2010).

Cerium can also reduce plant growth. According to Hu et al. (2002) application of Ce can reduce roots length and dry matter mass both of the roots and shoots in wheat (Hu et al., 2002). According to Rodrigues et al. (2019) foliar treatments of soybean with Ce did not affect plant height, number of leaves and pods. Salgado et al. (2020) also did not observe a significant effect on the growth of common bean when applying increasing doses of $Ce(NO_3)_2$.

Higher concentrations of REEs can be phytotoxic. Toxicity effects of REEs include a number of endpoints, such as cytogenetic effects, growth inhibition and organ-specific toxicity (Pagano et al., 2015). The phytotoxicological database of individual REEs is mostly confined to Ce and La. Kotelnikova et al. (2019) found that Ce toxicity on onion evinced in reduced root growth and mitotic index, with increased mitotic aberrations at Ce concentration 200 mg/kg soil. Liman et al. (2019) reported that CeO_2 nanoparticles and microparticles (12.5–100 ppm) had cytotoxic and genotoxic effects in onions for 4 h. The Ce^{3+} caused deleterious effects and cell death when sweet potatoes were exposed to 20–80 mg Ce/L, in nutrient solution (Jiang et al., 2017). In hydroponic culture, Ce exerted significant adverse effects on wheat root elongation (Gong et al., 2019). In greenhouse conditions, foliar application of 200 mg/L and 2,000 mg/L Ce on the leaves of the soybean provoked yellowing and necrotic damage, presented collapsed cells and caused structural alteration to the epidermal cells (Rodrigues et al., 2019). Foliar treatment with 80–300 µM Ce reduced the yield of horseradish (Wang et al., 2017). Certain plant species show different sensitivity to the presence of higher concentrations of Ce. Sunflower and radish are highly sensitive to Ce (Moreira et al., 2019) and maize is less sensitive than mungbean (Diatloff et al., 1995).

Cerium role in alleviating stresses in plants

During vegetation season, plants can be exposed to unfavorable abiotic factors, which adversely affect same physiological and biochemical processes and in this way their growth and development. A number of abiotic, ecological factors can cause oxidative stress in plants, i.e. disturbance in the balance that exists between pro-oxidative processes and the antioxidant system of plants. Abiotic stress factors can lead to the creation of reactive oxygen species (ROS), increase permeability of plasma membrane and decrease activities of antioxidant enzymes (Liu et al., 2009). Pathogenic infection can also cause an increase in the formation of ROS as a part of the plant's defense system (Li et al., 2021). Reactive oxygen species are produced by reduction or activation of O_2 and they are very reactive and cytotoxic in all organisms. Reactive oxygen species like hydrogen peroxide (H_2O_2), single oxygen ($^1O_2$), hydroxyl radical ($^{\cdot}OH$) and superoxide anion ($O_2^{\cdot}$–) cause disturbances in the growth and development of plants, lead to damage of cellular components and peroxidation of membrane lipids (Siddiqui et al. 2019). Numerous authors have shown the protective effect of REEs, especially Ce and La, against oxidative stress by increasing antioxidative capacity (Hong et al. 2017, Cui et al., 2019). In addition, Ce^{3+} elevated the activities of superoxide dismutase (SOD), catalase (CAT), ascorbic acid peroxidase (APx), guaiacol peroxidase (POD) and glutathione reductase (GR) (Hong et al., 2017). Cerium nanoparticles at 62.5 mg $nCeO_2$/L reduce the generation of H_2O_2 in rice roots by 75%. At 125 mg $nCeO_2$/L, the roots showed enhanced lipid peroxidation and electrolyte leakage, while at 500 mg/L the $nCeO_2$ increased H_2O_2 generation in roots (Rico et al., 2013). Positive effects of Ce^{3+} on alleviating stresses are attributed to its capacity to enhance the antioxidant potential of plants. Cerium solutions (400 mg/L) sprayed onto the leaves increase the activities of SOD, POD, and CAT by 22.71%, 31.49% and 69,79% respectively, in the leaves of perennial herb *Pseudostellaria heterophylla* (Ma et al., 2022). According to Salgado et al. (2020), this mechanism is believed to be the conversion of $O_2^{\cdot}$– to (H_2O_2) by Ce^{3+} and further oxidation of Ce^{3+} to Ce^{4+}. Next, Ce^{4+} could oxidate $O_2^{\cdot -}$ to O_2, while it itself is reduced to Ce^{3+}.

Calcium (Ca^{2+}) is an essential element for plant and is involved in many living processes. Chemical properties of Ce^{3+} are similar to Ca^{2+}, therefore Ce^{2+} could occupy a Ca^{2+} position and bind to different components in plants as "supercalcium" (Ni, 2002). Cerium added to Ca-deficient media in the spinach plants could substitute for Ca and improve spinach growth. Fresh weight, dry weight and chlorophyll content of spinach were increased by 39.9%, 45% and 64% compared to those of plants cultivated in Ca-deficient media (Liu et al., 2008). Cerium improves the absorption and transfer of light and converses efficiency of light energy in spinach chloroplasts under Ca deficiency (Huang et al., 2008; Huang et al., 2008a). In Ca-deficiency media, Ce decreased the permeability of plasma membrane, malondialdehyde and ROS (superoxide radicals, hydrogen peroxide) and increased the antioxidative enzymes such as SOD, CAT, APX, GPX and glutathione content (Liu et al., 2009). Cerium could relieve the inhibition of Ca deprivation on nitrogen metabolism in spinach (Liu et al., 2008).

Treatment of maize shoots with 15 µM $CeCl_3$ relieved inhibition of photosynthesis and growth as well as PSI and PSII injury caused by exposure to potassium (K^+) deficiency, salt stress (80 mM NaCl) and combination of K^+ deficiency and salt stress. Chemical differences between K^+ and Ce^{3+} are large, therefore Ce^+ might not improve photosynthesis by substituting K^+, but might improve photosynthesis by preventing oxidative stress or by activating enzymes under K^+ deficiency (Qu et al., 2013).

Some results suggest that Ce could partly substitute Mg. Soaking of spinach seeds in 15 µM $CeCl_3$ and further plant growth under Mg^{2+} deficiency lead to decreased MDA and ROS and increased activities of the antioxidative defense system – the activity of SOD, CAT, APX, GPX, GR, antioxidants (e.g. carotenoids and glutathione), and improved overall spinach growth (Ze et al., 2009). It was found that $CeCl_3$ promotes chlorophyll synthesis, activities of two key enzymes in CO_2 assimilation (Rubisco carboxylase and Rubisco activase) and expression of *rbcL, rbcS* and *rca*, thus leading to the enhancement of spinach growth under Mg-deficient conditions (Ze et al., 2009a). Under Mg deficiency, 20 µM Ce in culture solution in maize can prevent inhibition of synthesis of photosynthetic pigments, improve light energy absorption and conversion, oxygen evolution and the activity of photo-phosphorylation and its coupling factor Ca^{2+}-ATPase (Zhou et al., 2011). Treatment with 15 µmol/L $CeCl_3$ in spinach grown in Mg deficiency significantly promoted the activity of the key enzymes of nitrogen metabolism (NR, NiR, GDA, GS, urease, GPT, and GOT) (Yin et al., 2009).

Manganese (Mn) is an essential plant micronutrient which has important functions in many metabolic processes. Addition of 20 µM Ce in nutrient solution promoted maize growth through the enhancement of chlorophyll synthesis, the activity of Rubisco and Rubisco activase, and the expression of *rbcL*, *rbcS*, and *rca* under Mn^{2+} deficiency (Gong et al., 2011). Manganese deprivation in maize may disturb photochemical reaction of chloroplasts strongly, which could be improved by addition of 15 µM $CeCl_3$. However, it is not clear whether Ce affected the photochemical reaction of Mn-deprived maize seedlings (Qu et al., 2012).

In the last decades, there have been a vast number of reports on the presence and phytotoxicity of heavy metals, such as lead, cadmium, mercury and chromium. Lead (Pb) stress could significantly inhibit photosynthesis (Kastori et al., 1998). The treatment by 15 µmol/L $CeCl_3$ could alleviate harmful effect of exposition of spinach to 100 µmol $PbCl_2$/L. It was found to improve light absorption and distribution of excitation energy in both photosystems FSI and FSII and increase activity of photochemical reaction and oxygen evolution in spinach chloroplasts (Zhou et al., 2009). Cadmium (Cd) stress inhibits the plant growth, chlorophyll contents, photosynthesis parameters, chloroplast development and leads to significant alteration in antioxidant defense in rice seedlings. In a hydroponic experiment, the growth of rice seedlings was markedly inhibited by 100 µM Cd and the inhibition was significantly alleviated by 10 µM Ce. Rice seedlings treated with Ce exhibited higher SOD, POD and CAT activities compared with the Cd-stressed plants, indicating a better O^- and H_2O_2 scavenging ability. The mechanism of Ce action in those rice seedlings is partly related to improved light use efficiency, increased antioxidant activity and decreased oxidative stress (Wu et al., 2010).

Enhanced ultraviolet-B radiation (UV-B) affects some physiological processes in plants (Wu et al., 2010). Exposition of hydroponically grown *Brassica* *juncea* seedlings to two levels of UV-B radiation (0.15 W/m^2 and 0.35 W/m^2) decreased chlorophyll content, net photosynthesis rate, transpiration rate, stomatal conductance and water use efficiency, but concomitantly increased membrane permeability and activities of antioxidant enzymes (SOD, CAT, POD). The protective effect of Ce on seedling exposed to UV-B radiation was demonstrated and it was superior at 0.15 W/m^2 UV-B (Liang et al., 2006). Cerium alleviated the inhibition of the photosynthesis in hydroponically grown soybean seedlings to a certain extent. The changes of photosynthetic rate were mainly influenced by the effect of Ce on the reaction of Hill and apparent quantum yield (AQY) at low level of UV-B radiation (0.15 W/m^2) (Liang et al., 2006a). It has been reported that Ce protected photosynthetic apparatus from UV-B radiation by stimulating the accumulation of UV-B absorbing compounds, such as flavonoids and carotenoids and by eliminating reactive oxygen species.

Global climate change is a present condition and a concern for the future. Drought is a part of the global climate changes. Both the intensity and duration of droughts are expected to increase (Grillakis, 2019). Cerium was shown to alleviate water stress in common bean, increasing its survival rate and growth. Cerium application increases photosynthesis rate, chlorophyll content and water use efficiency under water stress (Salgado et al., 2020). Cerium (20 mg $CeCl_3$/L) could alleviate water stress induced by UV-B radiation (0.15 and 0.45 W/m^2) by regulating the osmotic and metabolic absorption of water, photosynthesis and growth of soybean seedlings (Mao et al., 2012). Cerium also effects chilling resistance of cucumber seedlings (Li, 2010).

Acid rain is not a new phenomenon; it is created by the dissolution of acidic oxides, especially sulfur dioxide, sulfur trioxide and nitrogen oxides. They are the result of atmospheric pollution. In extreme cases, the pH value of acid rain sediments can be 3.0. Acid rains increase the permeability of plant cell membranes, reduce pollen germination, plant resistance to drought and diseases, etc. Cerium can alleviate the inhibitory effects of acid rain on seed germination and growth of barley due to the elimination of excessive free radicals induced by acid rain and improvement of the synthesis of chlorophyll and growth of roots (Huang et al., 2000).

Soil salinity influences plant production in many areas of the world. Salt stress causes adverse effect on photosynthesis, energy production, lipid metabolism and other life processes in plants (Kasim et al., 2016). Exposure to NaCl (150 mM) markedly inhibited the growth on Jerusalem artichoke, declined in the chlorophyll content and increased oxidative stress; this inhibition was significantly alleviated by application of 0.1 mM $CeCl_3$. Authors speculate that reduced water stress and photosynthesis, due to applied Ce, might be associated with its effect on growth in the present stress condition (Li et al., 2017).

CONCLUSION

Cerium is one of the rare earth elements belonging to lanthanides. Out of the rare earth elements, the effects of Ce and La on the living world have been studied in most detail. Cerium is widely distributed in living and dead nature. Thanks to its influence on the physiological and biochemical processes of plants, it has application in agriculture. Cerium is not an essential, biogenic element for higher plants, but at lower concentrations it can stimulate some life processes in them: uptake of ions, seed germination, photosynthesis, growth and development, accumulation of organic matter, chemical composition and tolerance to some unfavorable abiotic stress conditions (higher concentrations of toxic heavy metals, drought, deficiency of some essential elements, UV-B radiation, acid rain, etc.). Higher concentrations of Ce are phytotoxic. Further studies are needed to better understand the mechanisms of action of Ce on plant metabolism in order to understand the stimulating effect of lower and phytotoxic effects of higher concentrations of Ce.

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ЦЕРИЈУМ И ВИШЕ БИЉКЕ

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РЕЗИМЕ: Церијум припада групи елемената ретких земаља (ЕРЗ). Њих чине 17 елемената, 15 из лантаноид серије и скандијум и итријум. Елементи ретких земаља у малим концентрацијама широко су распрострањени у природи. Одликују се сличним хемијским и физичким особинама. Они су нашли примену у бројним областима човекове активности, као и у биљној производњи у виду микрођубрива. Од ЕРЗ у биолошким исраживањима најдетаљније је проучено дејство церијума и лантана на животне процесе виших биљака. Церијум није биогени, неопходни елеменат за нормално растење и развиће биљака. Биљке церијум усвајају преко корена и надземних органа, а у највећој мери се накупља у корену. У бројним истраживањима је утврђено да ниже концентрације церијума могу повољно утицати на одређене физиолошке процесе (усвајање појединих јона, синтезу фотосинтетички активних пигмената, фотосинтезу, клијање семена, толерантност према неповољним еколошким чиниоцима, растење и накупљање органске материје). Веће концентрације церијума делују фитотоксично, изазивају цитолошке и морфолошке промене. Поред бројних резултата истраживања о утицају церијума на животне процесе виших биљака потребна су даља сазнања да би се његово повољно дејство на физиолошке и биохемијске процесе биљака боље разумело и ефекасније искористило.

КЉУЧНЕ РЕЧИ: усвајање и интеракција јона, клијање семена, фотосинтеза, раст, фитотоксичност, ублажавање стреса