Review paper

Lanthanum and cultivated plants

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Summary. Lanthanum (La), is a metallic element belonging to the group of rare earth elements (REEs). Both REEs and La are present in small concentrations in all parts of the biosphere. REEs are widely used in numerous areas of human activity. The effect of La on the life processes of plants has been studied in detail. Plants can absorb La through roots and aerial organs. Most of the absorbed La is accumulated in the root. Lanthanum affects the absorption and accumulation of other elements in plants through synergism and antagonism. Lanthanum ions might partly be able to replace calcium in plants and magnesium in chlorophyll molecules. Numerous publications point out the positive effects of La on plant growth. The stimulating and inhibitory effects of La on plant growth are associated with alternations in mineral nutrition, enzyme activity, levels of endogenous hormones, tolerance to abiotic and biotic stress, etc. Lanthanum may have a positive effect on photosynthetic rates, and is associated with differences in chloroplast development, increased light absorption, excitation energy distribution, promotion of the Hill reaction, as well as changes in the carboxylation activity of rubisco. Lanthanum might be partly able to alleviate the effect of undesirable ecological factors. In the environment, contamination and phytotoxicity of La rarely occur. The phytotoxic mechanisms of La involve necrotic damage, nutrient imbalance, destroyed cell ultrastructure, disturbance of cell proliferation, inhibition of the specific enzymes and other functional proteins, phosphate deficiency, membrane lipid peroxidation, and, as a final result, growth inhibition. Low concentrations of La favor plant growth, but the mechanisms are still not sufficiently understood. Thus, molecular-level investigations to elucidate the stimulative and toxic mechanisms of La in higher plants are desirable.

Keywords: growth, La, photosynthesis, phytotoxicity, plant, stress alleviation, uptake.

INTRODUCTION

Lanthanum (La) belongs to the group of rare earth elements (REEs). Rare earth elements are a homogeneous group of 17 transient metals. They have almost identical chemical and physical properties. With few exceptions, their valence state is +3 and their ionic radii are approximately similar. There are 15 lanthanide (Ln) elements plus yttrium (Y) and scandium (Sc) (IUPAC 2005). Scandium and yttrium are considered REEs since they have similar chemical and physi-

cal properties (Balaram 2019). The Ln group of elements is named after La. These elements are naturally present in the environment with the exception of promethium (Pm). Based on mean atomic mass, the REEs are divided into two groups: light (LREEs) (e.g. La) and heavy (HREEs) rare earth elements. REEs are present in small concentrations in all parts of the environment (Turra 2017), but not in pure metal form. Recently, REEs have found application in numerous areas of human activity. They are used in the electronic industry, chemical engineering (Kovariková et al. 2019), in agriculture

as plant fertilizers (Kastori et al. 2023b), feed additives in livestock (Tommasi et al. 2021), and in medicine (Balaram 2019). Among REEs, La is of particular importance as it is applied in agriculture to enhance crop production (Hu et al. 2004). The main sources of La are the minerals monazite and bastnaesite. Lanthanum is very easily oxidized, it exhibits two oxidation states: $+3$ and $+2$, but the $+3$ state is much more stable and therefore dominant. Lanthanum is not a rare element, it is present in small concentrations in all parts of dead and living organisms. Its effects on higher plants have often been studied in combination with other REEs. Of the individual REEs elements, research has mostly focused on the effects of La and Ce on living organisms (Ma et al. 2023). Numerous publications point out the protective effect of REEs, especially La, and Ce, against oxidative stress by increasing antioxidative capacity (Hong et al. 2017; Ciu et al. 2019). Lanthanum also influences mineral nutrition in plants. The influence of La on the concentration of nutrient elements in plants depends on many factors: its concentration, similarities to other elements, plant species, and organs (Fastovets et al. 2017). Lanthanum can also indirectly affect nutrient supply in plants, since it affects the activities of soil bacteria (Zhu et al. 2002). The impact of La on plant development depends on the growth medium. A low concentration of La leads to an increase in growth, accompanied by an increase in the concentration of photosynthesis active pigments, photosynthetic rate, and dry–matter production (Durate et al. 2018; Ciu et al. 2019). Lanthanum can improve the adverse effects of ecological factors (Zhu et al. 2018), and has a control function against pathogenic fungi (Mu et al. 2006). Because of these properties, REEs have received increasing attention as micro fertilizers in agriculture (Hu et al. 2004; Kastori et al. 2023a).

PHYSIOLOGICAL RESPONSES OF PLANTS TO LANTHANUM

Higher plants can complete their life cycle without the presence of REEs, including La. Therefore, according to current knowledge, the REEs cannot be considered essential, biogenic elements for higher plants (Kirkby 2023). The effect of REEs on the growth, organic production and yield of plants, stems from their influence on important physiological and biochemical processes of plants. A large number of scientific research and review works, regarding the influence of REEs on plants, have been published in recent decades, which clearly indicates the growing interest in this group of elements (Kastori et al. 2010, 2023a; Balarm 2019; Tommasi et al. 2021; Tao et al. 2022). Lanthanum-induced hormesis in plants has taken on renewed focus over the past years (Agathokleous 2018).

UPTAKE, DISTRIBUTION, AND ACCUMULATION OF LANTHANUM

The mechanism of La^{3+} uptake by higher plants has been insufficiently studied and is most often considered within the framework of knowledge about the uptake of REEs or light rare earth elements (LREEs) (e.g. La). The bioavailability of REEs depends largely on the physico-chemical and biological characteristics of soils. Organic acids secreted by the roots stimulate the desorption of REEs from soil particles and affect the diffusion of REEs from soil particles towards the root surface, forming complexes with REEs. Plants mainly take up REEs in the form of ions and less often as soluble complexes. REEs are mainly accumulated in the primary cell wall during the early phase of root cell growth (Brioshi et al. 2013). The cell wall components (cellulose, hemicelluloses, and pectin) have free hydroxyl and carboxyl groups that are negatively charged and can bind cations entering the apoplast. In rice seedlings, La³⁺ was mainly deposited in the cell walls of the roots (Liu et al. 2013). As much as 68% of REEs are present in the form of REEs-pectin complex in cell walls (Lai et al. 2006). After uptake, the transport of REEs in the root follows an apoplastic or symplastic pathway. For the movement of REEs towards the central cylinder of the root, the endoderm of the root (Casparian strip) represents a barrier, the same as for the other elements (Biroshi et al. 2013). The affinity of the plasma membrane affects the uptake of individual REEs elements (Hu et al. 2004). However, the role of ion channels, carriers, and pumps located in plant cell membranes in the transport of REEs through the membrane is insufficiently known. According to Liu et al. (2012b), import of $La³⁺$ ion in the root cells of rice is linked to a signal transduction pathway involving calmodulin. Endocytosis is one of the mechanisms by which matter enters the cell. Foliarly applied REEs enter leaf epidermal cells by endocytosis. Treatment of *Arabidopsis* leaves with La³⁺ triggers systemic endocytosis from leaves to roots. Systemic endocytosis impacts the accumulation of mineral elements and the development of roots and expansion of leaves (Cheng et al. 2021). When REEs directly act on the leaf or root, they activate endocytosis in the plant cell (Wang et al. 2014). It is thought to be the primary response of the plant cell to REEs. On the plasma membrane of *Arabidopsis* leaf cells, vitronectin-like protein is an anchoring site and binding target for La. This protein can act as the first line of defense against La stress, to resist entry of La into cells (Yang et al. 2016). Lanthanum first binds to the plasma membrane in the form of nanoscale particles. Endomycorrhizal fungi, especially arbuscular mycorrhizal fungi, can enable the uptake of mineral nutrients including REEs, but they can also act as a barrier to REEs. In maize and sorghum, arbuscular mycorrhizal colonization significantly reduces La contents in shoots and roots (Guo et al. 2013).

Even though lanthanum can enter plants via both roots and leaves, the uptake rate by roots is two magnitudes lower than via leaves, similarly to the other REEs (Hu et al. 2004). Uptake of La reaches peak value 48 h after spraying on leaves.

The intensity of absorption and thus accumulation of La in plants depends first on the concentration of accessible La in the nutrient medium. When the concentrations of La in the medium increases, its accumulation in shoots and in roots increases. At higher uptake rates, La induces oxidative stress that negatively affects plant growth (Liu et al. 2012a). Šmuc et al. (2012) have found that the transfer factor (TF) for La in rice plants on paddy soil was 0.53. A similar result (TF (plant/soil) = 0.5) for rice was reported by Mesa-Pérez et al. (2018). The TF depends on plant species. In REEs hyperaccumulators plants with an above-ground REEs concentration >1000 µg/g the TF is >1 (Wang et al. 20024). In hyperaccumulator *Dicranopteris linearis*, the TF of total and individual REEs were >1 (Liu et al. 2021). Organic ligand EDTA increased the uptake of REEs because it promoted their desorption from the soil. According to Wu et al. (2013) amino acids, as chelators, may have a positive effect on the uptake of La and yttrium (Y). Organic acids also promote the uptake of La (Han et al. 2005), and acid rain increases the bioavailability of La (Zhang et al. 2017). Acropetal transport in plants takes place in xylem vessels. Organic ligands contribute to the long upward transfer of REEs in the xylem. However, some REEs may be immobilized in/ on the roots and during transport in the xylem caused by phosphate precipitation and absorption to cell walls (Ding et al. 2006). Complexation of REEs with ligands can reduce the cell wall adsorption and phosphate precipitation so that the concentration of soluble REEs increases. The distribution of La is organ-specific. According to Mesa-Peréz et al. (2018), the accumulation of La in different parts of rice follows the order: root>leaf>husk>grain, which indicates that the uptake of La and its accumulation in roots is much higher than the translocation rate from root to shoot. The roots of maize plants can accumulate approximately 60% of total La uptake (Duarte et al. 2018). A similar distribution in plants was also found for other REE elements (Maksimović et al. 2012). According to Brioschi et al. (2013), the concentration of REEs in aerial tree organs are about 10 to 100 times lower than in roots. As observed by Wang et al. (2014), La in horseradish can be transported from the treated leaves to roots and finally to soil. In soybeans, the translocation rate of La from treated leaves to grains was not linear. Only 3.2% of the total applied amount was translocated from leaves to grains (Rodrigues et al. 2020). Studies of Redling (2006) confirmed very low concentrations of REEs in cereal grains and products made out of grains after the application of REEs as micro-fertilizers. The transfer factors of REEs in rice were

very low, confirming weak accumulation of La in rice grain (Mesa-Pérez et al. 2018). From an ecological point of view, the small amount of translocation of REEs into the edible part of numerous cultivated species is a significant finding, since it indicates a limited possibility of their entry into the food chain.

EFFECTS OF LANTHANUM ON MINERAL NUTRITION

Various antagonistic or synergistic mechanisms enable the interaction of La^{3+} during the uptake of mineral elements by plants. Based on research results to date, it can be concluded that the influence of La on the uptake, accumulation, and transport of elements in plants depends primarily on the applied concentration of La and on the plant species. In addition, it is specific for certain elements and organs of the plant. By changing the concentration of certain elements, especially biogenic ones, La can directly and indirectly affect the flow of particular physiological and biochemical processes and thus the growth and development of plants, as well as the biological value of the products of cultivated species.

The relationship between La^{3+} and Ca^{2+} was studied in detail. Lanthanides have similar physicochemical properties and atomic structures to those of Ca (Henderson 2013). Some lanthanide ions (La³⁺, Nd³⁺, Ce³⁺), with an effective ion radius and coordinate number close to $Ca²⁺$ ions, might partially be able to replace cell Ca or interact positively with Ca in various physiological functions. La^{3+} ions have a higher affinity to Ca-binding sites than Ca^{2+} itself and therefore can reactivate Ca2+ to interact with Ca-binding sites (Kovariková et al. 2019). Lanthanum is referred to as super Ca (Yin et al. 2021). La³⁺ binds to the binding sites of $Ca²⁺$ on the plasma membrane, which is reflected in the stability of the membrane and the uptake and transport of Ca. La^{3+} is considered an inhibitor of the Ca²⁺ channel (Kotelnikova et al. 2021). Lanthanum has also been used as a blocker to test the importance of Ca channels in plants. In citrus leaves, Ca concentration was significantly negatively correlated with La concentration. (Yin et al. 2021). Lanthanides (La³⁺, Ce³⁺) could enter chloroplasts, bind easily to chlorophyll molecules, and might even replace Mg^{2+} ion and convert the porphyrin ring in pheophytin to form lanthanide-chlorophyll (Chl)-complex (Chl-a-La-pheophytin)²⁺, Ce-chlorophyll (Rezanka et al. 2016).

Lanthanum also affects nitrogen metabolism. A low concentration of La^{3+} (0.08 mM) affects the assimilation of nitrogen in the roots of soybean seedlings by activating key enzymes (NR, NiR, GDH, GS, and GOGAT) in the assimilation of NO_3^- and NH_4^+ . The application of higher concentrations of La³⁺, such as 1.20 or 0.40 mM, had an unfavorable effect on the above mentioned processes (Zhang et al. 2017).

After a 0.08 mmol/L La treatment of soybean, the relative contents of intracellular nutrient elements (N, P, K, Ca, Mg, Fe) did not change significantly. When La concentration was increased to 0.40 and 1.20 mmol/L, the relative contents of the intracellular nutrient elements decreased significantly. A combined treatment of 0.08 mmol/L La and pH 4.5 acid rain downregulated the NR transcriptional level and caused deformation in membrane structures (Xia et al. 2017). High doses of La in rice lead to damage of the outer membrane of the chloroplast and to a decrease in the concentration of essential elements in the chloroplast, especially P, Mg, K, Ca, Mn, Fe, Ni, Cu, Zn, and Mo. As a result, the biosynthesis of chlorophyll is limited, which leads to a significant reduction in photosynthesis and thus to reduced growth and organic production in plants (Hu et al. 2016b). Increased concentrations of La in barley leaves significantly decreased concentrations of P, K, Mg, Cu, and Fe in leaves and increased concentrations of Ca in leaves and Si in stems (Fastovets et al. 2017). The concentration of Mg, Ca, Fe, Mn, Cu, and Mo in horseradish treated with 20 μ mol/L La³⁺ increased, with concomitant changes in the concentration of glucosinolates (Yang et al. 2019). According to Lian et al. (2019), treatment with LaNO_3 improves phosphorus-use efficiency under Pdeficiency and alleviates the negative effects of P-deficiency on chlorophyll content and photosynthesis in *Vigna angularis* seedlings. Ramírez-Martínez et al. (2012) studied the effects of different La concentrations (5 to 40 μ M) and sources $(La(NO)$ ₃ and $LaCl₃$) on K, Ca, and La accumulation in the leaves of tulips grown in hydroponics, under greenhouse conditions. Significant differences were observed, with the highest accumulation of the above mentioned elements in plants treated with $LaCl₃$.

EFFECT OF LANTHANUM ON PHOTOSYNTHESIS

The influence of REEs on the growth and organic production of plants is primarily based on their effect on photosynthesis (Kovariková et al. 2019; Ma et al. 2022). Among the REEs, the effect of La on photosynthesis has been studied in the most detail. The influence of La on photosynthesis primarily depends on the applied concentration of La and the method of its application. According to Cui et al. (2019), maize seeds pre-treated by soaking in a solution of 800μ mol/L LaCl₃ developed larger green leaf areas, aboveground dry biomass, chlorophyll and carotenoid contents and leaf area duration, which prolonged the functional periods of leaves and increased photosynthetic capacity. The application of 25 µM and 50 µM La in the nutrient solution led to a slight increase in maize growth, accompanied by an enhanced photosynthetic rate, as well as chlorophyll index (Duarte et al. 2018). Oliveira et al. (2015) also reported an increase in photosynthetic rate and chlorophyll content by

application of 5 µM and 10 µM La in soybean. According to Hu et al. (2016b), a low level of La^{3+} (0.08 mM) in rice did not change the chloroplast ultrastructure, but it increased the levels of chloroplast mineral elements, transcription of ATPase subunits and Mg^{2+} -ATPase activity, promoting plant photosynthesis and growth. Wen et al. (2011) concluded that treatment with low concentrations of La^{3+} (0.08 mmol/L) and the resulting increase in net photosynthesis in soybean seedlings are due to improvements in the photosynthetic process, including absorption of light energy, electron transport, and conversion of light energy by the photosynthetic apparatus. Foliar spraying with $LaCl₃$ solution at concentrations between 20 mg/L and 240 mg/L, in field experiments, increased photosynthetic rates, stomatal conductance, intercellular CO₂ concentrations, chlorophyll fluorescence parameters, and levels of photosynthetic pigments in a cultivated medicinal plant, *Amorphophallus sinensis* (Li et al. 2020).

During photosynthesis, chlorophylls and carotenoids play a key role; therefore, their content in the green organs of plants is extremely important. Soaking the seeds of *Festuca arundinacea* in the appropriate concentration of La (La_2O_3) solution increases chlorophyll content, promotes photosynthesis, and improves growth and development. The peak value was reached at 400 mg $\text{La}_2\text{O}_3/\text{L}$ (Liu et al. 2008). A low concentration of La (0.1 mM) in the nutrient solution increases the concentrations of photosynthetic pigments, whereas higher concentrations significantly suppress them in rice seedlings (Liu et al. 2012a). According to Gracia-Jiménez et al. (2017), under hydroponic greenhouse conditions, addition of 10 μ M La to the nutrient solution stimulated the biosynthesis of chlorophylls in sweet pepper varieties. A positive effect of La on chlorophyll content is probably due to increased levels of essential macronutrients involved in chlorophyll biosynthesis (He et al. 2020). No noticeable changes were found in the content of chlorophyll a and b in the green mass of barley plants grown on soil to which was added 10 mg/kg to 200 mg/kg of lanthanides (La, Ce, and Nd) (Kotlenikova et al. 2020). Different concentrations of La3+ (10 mg/L to 100 mg/L) were used to soak seeds of *Salvia miltiorrhiza*. As lanthanum concentration increases to 30 mg/L, the chlorophyll content and chlorophyll a/b level reached a turning point, increasing by 43.43%, and 4.61%, respectively, in comparison with the control (Su et al. 2018).

High concentrations of La reduce the concentration of photosynthetic pigments and thus photosynthesis. In leaves of citrus plants, 4 mM/L La significantly reduced chlorophyll a, b, and carotenoid content, which is consistent with the symptoms of toxicity, yellow leaves (50% to 70%), and burst veins due to dehydration (Yin et al. 2021). According to Liu et al. (2018), 5 mg/L La_2O_3 nanoparticles in nutrient solution were phytotoxic to maize. In addition, >10 mg/L

 La_2O_3 nanoparticles had adverse effects on the chlorophyll content. In a pot experiment, where the soil (sod-podzolic soil) was sprayed with different concentrations of LaCl_{3} , the concentrations of chlorophyll a, b, and carotenoids in barley leaves decreased significantly at 100 mg/kg La (Fastovets et al. 2017). The presence of La in the culture medium can lead to oxidative stress which leads to a disturbance of the chloroplast structure and a decrease in photosynthetic pigment content that finally damages photosynthesis (Hu et al. 2016a).

EFFECTS OF LANTHANUM ON PLANT GROWTH

Numerous results from both theoretical and practical research published in recent decades, primarily from Chinese research teams, indicate that small concentrations of REEs, including La, have been used in agriculture to improve crop productivity for decades (Kastori et al. 2023b). The stimulating and inhibiting effects of La on plant growth are associated with alternations in mineral nutrition, photosynthetic rate, tolerance to abiotic and biotic stresses, the activity of enzymes that are related to ROS generation, and levels of endogenous hormones (Cui et al. 2019). Under hydroponic growth conditions, La at 5 µM and 10 µM increased root and shoot biomass in soybeans. Growth reduction was reported at a concentration >10 μ M (Oliveira et al. 2015). When La(NO₃)₃ at concentrations of 1.0 μ M – 3.0 μ M was added to the rooting medium of *Eriobotrya japonica* in vitro, it significantly increased the rooting rate and root fresh weight, promoting root elongation (Zhang et al. 2013). A positive effect on root growth is most often associated with the intensity of cell division in the root tips (Kotelnikova et al. 2019). Microtubules are very important components of the cytoskeleton of higher plants. Liu and Hasenstein (2005) report that La can contribute to changes in microtubule organization in maize root protoplasts. At high concentrations, La leads to stagnation of root growth, while at low concentrations the cytoskeleton is stabilized. Under hydroponic culture, heavy REE (Y) and light REE (La, and Ce) caused significant adverse effects on root elongation of wheat (Gong et al. 2019). Soaking of *Salvia miltiorrhiza* seeds in a solution containing low concentrations of La can promote the accumulation of dry matter in seedlings, but high concentrations are not conducive to dry matter production (Su et al. 2018). In field experiments, 100 mg/L LaCl₃ solution was applied (sprayed) daily to Chinese cabbage leaves for eight days. This treatment promoted growth and resulted in increased fresh and dry weight of the cabbage, whereas the fresh and dry weight of the stems and leaves increased (Ma et al. 2014). Diatloff et al. (2008) reported, under hydroponic conditions, that the addition of La did not increase the growth of corn and mungbean. The growth of citrus was stimulated at La <0.5 mmol/L

and inhibited at concentrations >1 mmol/L (Yin et al. 2021). In water culture conditions, under osmotic stress, the height of the lavender seedlings treated with 0.04 mmol/L, 0.08 mmol/L, and 0.12 mmol/L LaCl₃ increased by 21.3%, 33.4% and 22.5%, respectively (Zhu et al. 2018).

Germination can be considered to be the initial stage of growth in seed-propagated plants. According to Su et al. (2018), La application has a significant biphasic effect on germination and seedling growth: stimulation (Ramírez-Olvera et al. 2018) as well as inhibition of seed germination, especially following application of higher concentrations of REEs (Aquino et al. 2009).

PHYTOTOXICITY OF LANTHANUM

Anthropogenic activity involving use of REEs has led to increased levels of REEs in the environment, which can have negative consequences (Balaram 2019). In the environment, contamination and phytotoxicity caused by a single REE are rarely present, whereas contamination with mixtures of REEs is far more prevalent. REEs are not strongly toxic for living organisms (Laveuf and Cornu 2009). Only low concentrations of La are phytotoxic. The toxic mechanisms of La involve inhibition of some enzymes and other functional proteins, phosphate deficiency, membrane lipid peroxidation, etc. According to Xia et al. (2017), with the application of higher concentrations of La, the balance between the production and scavenging of reactive oxygen species (ROS) was broken, membrane lipid peroxidation occurred, malondialdehyde (MDA) accumulated, and membrane permeability increased in soybean seedlings. Rodrigues et al. (2020) demonstrated that following foliar treatment of soybean plants with 200 mg/L and 2000 mg/L solution of $La(NO₃)₃$, the plants exhibited yellowing and necrotic damage on the leaves and the epidermal wax expressed obvious changes. In faba bean seedlings, La caused disturbances in cell proliferation cycles. In addition, it was shown that the damage to seedlings induced by La was due to impairment of DNA structure (Wang et al. 2011). Nutrient imbalance, DNA lesions, and DNA-protein crosslinks contributed to growth retardation of *Vicia faba* seedlings exposed to concentrations of 1-8 mg/L of La^{3+} in the nutrient solution (Wang et al. 2012). At higher accumulations, La induces oxidative stress that negatively affects chlorophyll and increases malondialdehyde and $\rm{H}_{2}\rm{O}_{2}$ concentrations in plant tissues (Liu et al. 2012a). A reduction in soybean growth was recorded at concentrations above 10 µmol La/L (Rodrigues et al. 2020). According to Hu et al. (2016a) high levels of La^{3+} destroyed the chloroplast ultrastructure and decreased the contents of chloroplast mineral elements and chlorophyll, the transcription of ATPase subunits and $\rm Mg^{2+}$ ATPase activity, inhibiting photosynthesis and growth in rice.

LANTHANUM AND PLANT STRESS

During the growing season, plants can be exposed to the adverse effects of abiotic factors which induce the synthesis of specific molecules, including ROS. This may lead to damage to cellular components and peroxidation of membrane lipids. In this context, the influence of La on alleviating the effects of stressors, such as heavy metals, was the subject of research. Heavy metals represent a group of detrimental pollutants, which are toxic at high concentrations, especially Cd, Pb, Hg, and Cu (Babula et al. 2008). Cadmium toxicity causes oxidative damage due to overproduction of O^2 , H_2O_2 and MDA (Wu et al. 2014). REEs and among them, La, can mitigate the adverse effects of toxic concentrations of heavy metals. According to Ren et al. (2016), after mixed REEs treatments, heavy metal (Cd, Pb Ni, Cu Zn) content in Chinese cabbage and rape leaves and stems decreased.

Phytochelatins (PCs) play an important role in detoxification by transporting Cd^{2+} to the vacuole (Cobbett and Goldsbrough 2002). Cd tolerance in *Lactuca sativa* was enhanced when synchronously treated with La. The latter enhances the accumulation of mRNA corresponding to the phytochelatin synthetase gene, and phytochelatin content both in the leaf and root (He et al. 2005).

Lanthanum can improve the adaptability of lavender plants to osmotic (water) stress. The presence of La could enhance the content of essential oils in flowers and leaves by approximately 18% to 19%, and the content of soluble sugars under water stress. The mechanism by which La could alleviate injuries to lavender induced by water stress relies on increasing the content of soluble sugars (Zhu et al. 2018). Osmosis caused by PEG made wheat seedlings' leaves produce more ROS; and consequently, wheat seedling leaves were oxidatively damaged. Treatment with $0.1 \text{ mM } L\text{a}_3$ resulted in an increase in the activities of antioxidant enzymes. Lanthanum seems to enhance the capacity of the oxygen species scavenging system, alleviating the oxidative damage induced by osmotic stress (Zhang et al. 2006).

Water stress caused by drought is often the cause of reduced growth and development of plants and thus loss of yield of cultivated species. Closure of stomata under conditions of water stress reduces transpiration and carbon dioxide assimilation. Due to the decrease in the availability of carbon dioxide, reducing equivalents are directed to oxygen, which becomes a source of ROS. Consequently, disturbances between prooxidative processes and antioxidative enzyme systems in plants take place. According to Cui et al. (2019), LaCl₃ increases the activities of antioxidant enzymes in maize. Lanthanum delays the senescence of *Lolium longiflorum* cut flowers by improving their antioxidant defense system and water-retaining capacity (Shan and Zhao 2015).

Acid rains can be a significant environmental problem.

They can directly adversely affect plants, but also indirectly, by changing the chemical properties and availability of soil nutrients to plants. Low concentrations of La³⁺, 0.08 mmol/L, could alleviate the toxic effects of acid rain of pH ranging between 3.5 and 4.5 (Wen et al. 2011). According to Li et al. (2003), La^{3+} reduces the relative permeability of cell membranes and thus protects membranes under acid rain stress by inhibiting the leakage of electrolytes.

The potentially harmful effects of increased UV-B intensity on biological systems have attracted global attention (Kataria 2017). The results of Wang et al. (2009) indicated that La³⁺ alleviated the oxidative damage induced by UV-B radiation in soybean plants by either reacting with ROS directly, or by improving the plant's defense systems.

In numerous tests, it was established that REEs can mitigate not only the adverse effects of environmental factors, but they can also significantly control the occurrence of plant diseases. The mechanism by which REEs act against plant diseases is very complex. REEs may reduce the virulence of a pathogen to a host plant, but they also may induce the expression of plant disease resistance genes (Mu et al. 2004). According to Fastovets et al. (2017), La increases plant biomass and possibly improves plant resistance to pathogens due to increased Si accumulation in plants.

CONCLUSION

Lanthanum belongs to the group of rare earth elements. They are characterized by similar physical and chemical properties and are widely distributed in low concentrations in the biosphere. In recent decades, REEs elements have received considerable attention, as they have found wide applications in various fields of industry, agriculture, and medicine. Out of the individual REEs elements, research has been mostly focused on studying the effects of La and Ce on living organisms. According to current knowledge, REEs cannot be considered essential, biogenic elements for higher plants. During lanthanum-induced hormesis in plants, low concentrations stimulate and high inhibit life processes. The effects of La on the growth, development, and yield of plants, stem from their influence on significant physiological and biochemical processes in plants. Lanthanum influences the mineral nutrition of plants during various antagonistic or synergistic mechanisms during the uptake of mineral elements. The influence of La on the growth and organic production of plants is primarily based on their effect on photosynthesis. La stimulated synthesis of photosynthetic pigments, chloroplast development, increased light absorption, promoting the Hill rection, as well as carboxylation activity of rubisco. Lanthanum can also increased the activity of enzymes related to ROS generation, and levels of endogenous hormones. Lanthanum can alleviate the effects of different stressors, such as heavy metals, UV-B radiation, acid rain, osmotic and drought stress, and increase the activities of antioxidant enzymes. Contamination and phytotoxicity of La rarely occur.

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