Contemporary Agriculture, Vol. 73, No. 3-4 (2024): 228-237
DOI: https://doi.org/10.2478/contagri-2024-0028
UDC: 579.64

Review Paper

ISSN 2466-4774
https://www.contagri.info/

RARE EARTH ELEMENTS, MICROORGANISMS, AND CONTROL OF PLANT DISEASES

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Submitted: 02.07.2024.
Reviewed: 26.09.2024.
Accepted: 10.10.2024.

SUMMARY

Rare earth elements (REEs) are a group of trace metals relatively abundant in the Earth's crust. REEs are widely dispersed in small concentrations throughout the environment. These elements demonstrate similar physical and chemical properties. REEs have been widely used in various areas of industry, agriculture and medicine. China was the first country to commercially apply REE products as micro-fertilizers or growth simulators in agriculture. Although REEs are not essential for living organisms, they can influence their life processes. Results of recent investigations demonstrate that hormesis commonly occurs in a variety of plants and microorganisms in response to REEs. REEs affect the growth, reproduction and metabolism of microorganisms. Microorganisms are involved in all geochemical cycles of metals. They can produce various organic acids and other substances capable of mobilizing REEs in the soil, thereby promoting their uptake by plants. Metals can be bound by microorganisms through bioadsorption, bioaccumulation, and interactions with metabolic products, which may help in reducing metal leaching and increase their availability to plants. As a result, microorganisms can be used for the revitalization of habitats polluted by metals, primarily water. It was found that REEs can directly and indirectly affect several types of plant pathogens. REEs can control some phytopathogens directly by reducing their growth and virulence in host plants, while also eliciting disease resistance response in plants. The mechanisms by which REEs act against plant diseases result from complex interactions of many biotic and abiotic factors, which indicates the multifaceted nature of this phenomenon. Current evidence confirms that REEs can control pathogens under certain conditions. However, further studies investigating the mechanisms by which REEs control pathogens and performance of individual elements are necessary for their further application.

Key words: *rare earth elements, microorganisms, bioavailability, plant pathogen control*

Abbreviations: Ce – cerium; Dy – dysprosium; Er – erbium; Eu – europium; Gd – gadolinium; Ho – holmium; La – lanthanum; Ln – lanthanide; Lu – lutetium; Nd - neodymium, Pm – promethium; Pr – praseodymium; REEs - rare earth elements; Sc – scandium; Sm – samarium; Tb – terbium; Tm – thulium; Yu - ytterbium; Y - plus yttrium

INTRODUCTION

In recent decades, rare earth elements (REEs) have drawn a lot of attention. The 17 elements that make up REEs are trace metals. Lanthanum (La), cerium (Ce), praseodymium (Pr), neodymium (Nd), promethium (Pm), samarium (Sm), europium (Eu), gadolinium (Gd), terbium (Tb), dysprosium (Dy), holmium (Ho), erbium (Er), thulium (Tm), ytterbium (Yu), lutetium (Lu), plus yttrium (Y) and scandium (Sc) are the 15 lanthanide (Ln) elements (IUPAC, 2005). Due to their comparable chemical and physical characteristics, yttrium and scandium are also regarded as REEs (Balaram, 2019). The majority of REEs found in nature have +3 valence, and their ionic radii are roughly comparable. Their interaction with other elements is determined by the Ln electron configuration. According to

Walters & Lusty (2011), there are two groups of Ln: light (LREEs) and heavy (HREEs). In comparison to compounds containing heavier ones, compounds containing LREEs are more soluble.

REEs have found wide application in various branches of industry (Kovariková et al., 2019), in agriculture as plant fertilizers, primarily in China (Kastori et al., 2023), and in medicine (Balaram, 2019). REEs affect the life processes not only in higher plants, but also in microorganisms. In addition, microorganisms can significantly affect the bioavailability of REEs and thus their uptake by plants (Jalali & Lebeau, 2021). Numerous studies have demonstrated both positive and negative effects of different doses of REEs on plant growth, yield and chemical composition, and also their ability to alleviate some ecological stress and plant infections. Even in favorable agroecological conditions for plant growth and development, plant diseases can cause significant yield losses and worsen product quality. In the conditions of intensive plant production, the application of chemical methods for pathogen control is still necessary. Bearing in mind the potential negative environmental effects of using chemical agents, increasing attention is being directed towards finding new solutions that exclude their use. In this regard, numerous tests have been conducted to explore, among other things, the interaction of REEs and microorganisms, including the potential of using REEs for controlling plant pathogens (Liu et al., 2008; Zhang et al., 2022).

Role of microorganisms in availability of rare earth elements to plants

Plants' ability to absorb REEs is indicated by their role in the development of plant diseases. REEs can be absorbed by higher plants through their roots and aerial organs. According to Hu et al. (2004), the rate of REE uptake by roots is two times lower than foliar uptake. The soil or soil solution is the primary source of REEs for plants. The amount of REEs in soil can vary greatly, from 30 to 700 mg/kg, frequently influenced by human activity (Bohn et al., 1985). The most readily available form of REEs for plants are the water-soluble and exchangeable portions. Numerous characteristics of soil affect REE bioavailability and plant absorption. The adsorption and desorption of REEs in the soil are influenced by root exudates (low-molecular-mass organic acids) (Fu et al., 2001) and the cation exchange capacity (CEC) of the soils (Kovariková et al., 2019). Adsorption and fractionation of REEs are facilitated by both inorganic and organic ligands (Duráes et al., 2014). The bioavailability of REEs improves when the soil's redox potential falls at the same pH level (Cao et al., 2002). Various other chemical and physical features of the soil also affect the bioavailability and plant uptake of REEs (Brioschi et al., 2013). On the other hand, the bioavailability of REEs and the uptake of mineral elements by plant roots are significantly influenced by the soil microflora (Jalali & Lebeau, 2021). Microorganisms participate in all geochemical cycles of heavy metals, including those involving REEs. Metabolism of microorganisms is very diverse, allowing them to interact with mineral constituents of the environment, thereby affecting the bioavailability of REEs. Heavy metals are bound by microorganisms through bioadsorption, bioaccumulation and by products of metabolism. Bioadsorption binds heavy metals to the cell surface, bioaccumulation is accumulation in the cell, while binding of metals using products of metabolism is done outside the cell of the microorganism. These processes can reduce REE leaching, thereby increasing their availability to plants. According to Andrés et al. (1991), *Mycrobacteria* perform sorption on La, Sc and Y. Andres et al. (2000) mention biosorption of Gd by several microorganisms. In bacteria *Pseudomonas aeruginosa*, europium (Eu^{3+}) binding occurs mainly extracellularly and both carboxylic and phosphate groups are seen active in binding (Texier et al., 2000). Microorganisms can take up REEs from different sources, while the intensity of uptake of individual REEs can be different. Brantley et al. (2001) reported uptake of REEs from hornblende by the soil bacterium *Arthrobacter* sp. The heavy REEs (HREEs) were markedly fractionated, the uptake increases from holmium (Ho) to lutetium (Lu).

Microorganisms and plants produce a wide range of siderophores (Ahmed & Molmström, 2014). Siderophores play a significant role in the mobility of metal ions in the environment (Schalk et al., 2011). Bacteria can increase bioavailability of metals by creating siderophores, facilitating their adsorption on biomass, i.e. bioprecipitation (Diels et al., 2009). Andrés et al. (1991) reported formation of complexes of La, Y and Sc with siderophore in *Mycobacterium smegmatis*. Numerous studies point to the role of siderophores in the biological control of plant pathogens (Yu et al., 2011). Microbial extracellular polysaccharides can also increase REEs dissolution (Welch et al., 1999). According to Jalali & Lebeau (2021), plant growth-promoting Rhizobacteria are indeed able to mobilize metals and/or stimulate plant development, thereby increasing the amount of REEs extracted by the plant with a higher phytoextraction efficiency. Absorption of REEs by plants is generally higher at low pH values. Microorganisms can produce various organic acids that are capable of mobilizing REEs. *Aspergillus niger* at pH <2 predominantly produces citric acid, while at higher pH values (pH>4) it tends to produce gluconic and oxalic acids (Rasoulnia & Mousavi, 2016; Brisson et al., 2016). Rock-inhabiting fungi can mobilize REEs elements cerium and europium of a dolomite at acidic pH (Dou & Lian, 2010). Microorganisms, bacteria, fungi and plant roots are often efficient producers of oxalic acid/oxalate, a oxalate solubilizer of REE phosphates (Tyler, 2004).

After REEs enter the soil, they affect the growth, reproduction and metabolism of microorganisms. They also affect the plant resistance system (De Zelicourt et al., 2013). The influence of REEs on microorganisms can be either stimulatory or inhibitory, depending on factors such as metal concentration, duration of exposure, type of microorganism and numerous other environmental factors. In a pot experiment in the red soil-pasture system, high concentration of La was found to be harmful to bacteria, actinomycete, epiphyte and azotobacter in the soil. Bacteria, actinomycete and azotobacter showed greater sensitivity to La than epiphyte. However, the effect of La on soil microorganisms tends to diminished over time (Jiang et al., 2008). Arbuscular, endomycorrhizal fungi (AMF) can provide biotic and abiotic stress tolerance to host plants (Miransari, 2010) and improve plant growth by increasing water and nutrient uptake (Miransari, 2011). Studies have shown that mycorrhizal fungi can protect plants from pathogens by formating a compact sheath around the roots or antibiotics. AMF include fungi from the *Endogonaceae* family. Inoculation with arbuscular mycorrhizal fungi mediated the uptake of La and nutrient elements and promoted the growth of Chinese milk vetch (*Astragalus sinicus* L.), whereas a high concentration of La (20 mg/kg) significantly decreased the colonization of Chinese milk vetch roots by AMF (Chen & Zhao, 2007; 2009). When inoculated with arbuscular mycorrhizal fungi, *Glomus versiforme*, maize and sorghum exhibited significant differences in the REE (La, Ce, Pr, Nd) concentration in response to the colonization by AMF. Several studies suggest that the impact of AMF on the take-up of REEs may be related to the plant species, the AMF segregates, the specific component and the concentration of REEs within the supplement substrate. AMF can reduce the impact of REEs and devastating metal harmfulness on plants (Guo et al., 2013). Ectomycorrhizal fungi bind heavy metals in the cell wall or in the vacuole, thereby lowering their concentration in the soil solution surrounding the root system of the host plant (Kottke, 1992). This process reduces the absorption and transport of heavy metals to the above-ground organs of the plant.

Rare earth elements in the control of plant diseases

Rare earth elements are used in agricultural practices in plant production for different purposes, forms and methods (Kastori et al., 2023a). They are primarily applied as micro-nutrients to increase crop yield and quality, but they are also effective in controlling plant diseases, improving seed germination, promoting the initial growth of seedlings, and mitigating the unfavorable effects of some environmental factors (Kovariková et al., 2019; Balaram, 2019; Kotelnikova et al., 2021; Kastori et al., 2023). REEs can be applied in solid or dissolved forms, as a solution to the plant organs above ground, mixed with the soil or nutrient substrate, added to the nutrient solution, or used as a presoaking solution for seeds. Many commercial fertilizers contain rare-earth complexes containing amino acids as well as REEs in the forms of nitrate, chloride, and ammonium bicarbonate (Pang et al., 2002). In addition, there are liquid fertilizers with additional REEs and macro- and micronutrients, as well as complex NPK fertilizers (Xiong et al., 2000, Backer & Solomon, 2020). Globally, phosphate fertilizers continue to include REEs (Turra, 2018). Studies focusing on specific elemental REEs mostly examine the effects of applying La and Ce (Tommasi et al., 2020). According to Kotelnikova et al. (2020), La, Ce and Nd are among the most significant REEs for agricultural and ecologal purposes.

The control of plant diseases primarily relies on application of fungicides, special agrotechnical measures and cultivation of disease-tolerant genotypes. Difficulties in creating genotypes tolerant to plant diseases, as well as the need to reduce pesticide residues in agricultural products and the environment have led to explorations of alternative disease control methods. It was established that REEs and individual elements of REEs not only favorably influence physiological processes that promote plant growth and development but also mitigate the adverse effects of stress factors (Tao et al., 2022). Numerous research results have demonstrated that applying REEs in optimal amounts reduces the severity of plant diseases and enhances plant resistance (Mu et al., 2004). The disease resistance can not result from one mechanism only but from the interaction of many mechanisms. REEs can control some phytopathogens directly and reduce their virulence to host plants, while also stimulating host plants to elicit disease responses and resistance. REEs can indirectly affect the resistance of plants by influencing metabolic processes that are important for their tolerance to diseases. As early as 1980, Chinese researchers documented the effectiveness of REEs in controlling diseases of rice blight and cabbage soft decay (Challaraj & Maruthamuthu, 2013). Bai & Deng (1995) reported that cotton blight was controlled by soaking of seeds in the solution of REEs. This treatment reduced disease by 20- 40%, improved cotton production and enhanced the resistance to blight by inducing plant resistance mechanisms. Since the middle of the last century, extensive research has been conducted demonstrating the role of REEs in controling various plant diseases.

Five-year field trials revealed that application of a complex containing rare-earth elements (La, Ce, Nd, Pr) and 17 amino-acids not only stimulated wheat growth and increased yield but also effectively controled stripe rust of wheat and improved the quality of crops (Li et al., 1991). Wang & Liu (1993) found that REEs had controlling effect on *Ophiobolus graminis* disease of wheat similar to that of fungicide triadimefon. Furthermore, it was recorded that

REEs had immediate inhibitory effects on pathogenic bacteria such as *Clavibacter michigenensis*, *Pseudomonas solanacearum*, *Ewinia chrysanthemi* and *Xanthomonas oryzae* (Zhang et al., 1997).

It was demonstrated that soaking seeds in soil solution rich in REEs significantly mitigates crown rot disease caused by *Aspergillus niger* in groundnut plants. Therefore, REEs can be used to effectively control the crown rot disease in groundnut. The application of REEs activities reduced the activities of pectinase and cellulase of the fungi, while simultaneously increasing plant biomass, total chlorophyll content, number of root nodules and stress-resistant product (phenols) (Challaraj & Maruthmuthu, 2013). According to the same authors, La, Ce, and Nd significantly lowered *Aspergillus niger* enzymatic activity and reduced the amount of fungal mat forming on plant roots at the apex. Furthermore, it was found that REEs influenced plant metabolism, disrupted *Aspergillus niger* pathogenicity and infection process, and encouraged plant growth. The average concentration of REEs in the soil is significantly higher in the REEs mining areas than in the general soil. Wang (2011) reported that microbial biomass was hindered in regions with significant REE buildup and that the bacterial diversity was higher in non-REE mining areas than in the mining areas. He et al. (2007) demonstrated that REEs had strong inhibitory effects on *Candida albicans*, *Staphylococcus aureus* and *Escherichia coli*. Wang et al. (2017a) observed that fluctuations in soil REE concentration, alongside with soil characteristics, significantly impact the variety and abundance of bacteria present in the soil. Additionally, it was noted that REE neodymium (Nd) influences the development, pectinase activity, and mycelium permeability of the fungal pathogen known as *Fusarium oxysporum*.

The application of higher Nd concentrations decreases dry weight of mycelium and pectinase activity while increasing permeability of the mycelium cell membrane. Conversely, when Nd concentration was in the lower range, between 2 mg/L and 180 mg/L, *Fusarium oxysporum* growth was enhanced in a solid medium (Zhang et al., 2007). Wahid et al. (1998) examined foliar levels of RREs, including La, Ce, Pr, Sm, Gd, and Th, in coconut palms in relation to root wilt-disease. The results of their research revealed no significant differences between diseases and healthy palm trees, except for Gd level, which was lower in diseased trees.

The mining of REE minerals reduces bacterial diversity and stimulates growth of dominant bacteria, such as *Bradyrhizobium*, *Acinetobacter*, *Buttiauxella*, *Bacillus*, and *Bukholderia*. They can degrade the pollutants formed by mining of minerals containing REEs. Furthermore, REEs affect the bacterial community structures in the rhizosphere and phyllosphere of rice, fully provide the growth-promoting function of endophytes, and promote rice growth (Zhang et al., 2022).

La is one of the most important REEs, extensively studied for its role in preventing plant diseases. According to some research findings, low quantities of La may stimulate the growth of certain harmful bacteria and fungi. Higher La concentrations, on the other hand, have substantial harmful or even inhibitory effects on bacteria and pathogenic fungi. This is most likely due to changes in key enzymatic activities, which have an impact on metabolism. The reaction of pathogens to La depends on the concentration of La, which leads to inhibition. The pathogen-suppression potential of lanthanum is comparable to that of certain conventional and organic fungicides. According to Mu et al. (2006a), REEs and the fungicide triadimefon both exhibited a comparable inhibitory impact on *Ophiobolus graminis* disease in wheat. In solid culture media, lanthanum significantly inhibits the growth of *Rhizoctonia solani* fungus mycelia, with EC50 and EC95 (indicating 50% and 95% inhibition of mycelial growth or pathogen spore germination) of La being 171.9 and 667.7 mg La/L, respectively. Pectinase, protease, and cellulase are disease-related enzymes that are activated by lanthanum. At La203 concentrations above 50 mg/L, fungal mycelial growth is considerably inhibited, resulting in reduced quantity and activity of these disease-related enzymes, while the pathogen's pathogenicity also declines (Hu et al., 2005). Additionally, Mu et al. (2006a) observed that La affects pathogenic fungi. With EC50 between 130 and 320 mg La/L, La exhibits significant toxicity to the pathogenic fungi in the following (descending) order: *Scelerotinia sclerotiorum* < *Fusarium solani* < *Fusarium oxyspoxum* < *Rhizoctonia solani* < *Pythium sp*. Pathogenic fungi were discovered to have severely restricted mycelial development and aberrant morphological features, such as increased ramifications, malformation, partial swelling, etc, probably caused by the changes in the enzyme activity and overall metabolism. Liu et al. (2008) found that applying La in the range from 20 to 320 mg/L through leaf spraying was effective in controlling *Rhizoctonia solani* in rice. The EC50 of La was measured on rice plants one and seven days post-spraying, with values of 128.7 and 128.1 mg/L observed in vivo. Treating *Isatis indigoatic* by soaking its seeds in solutions containing varying amounts of La (40 to 320 mg/L), followed by planting in soil infected with a combination of *Rhizoctonia solani* and *Fusarium solani*, showed notable control over diseases such as seed rot, bud rot, and root rot. The treatment enhanced both the germination rate and growth of *Isatis indigotica* seedlings. Zhang et al. (2000) found that a concentration range of 30 to 450 mg La_2O_3/L hindered the development of the rot-inducing fungus *Sclerotinia sclerotiorum*, with stronger inhibitory effects observed at higher concentrations. The pectinase activity in the specified fungi in a liquid medium also rose when the La_2O_3 concentration was increased.

Wang et al. (2022) demonstrated that La^{3+} significantly enhances laccase activity in *Shiraia bambussicola*, without impeding fungal growth at the ideal concentration. Following adjustments in both the concentration of La^{3+} and the duration of exposure, the laccase activity increased by approximately ten times in comparison to the control. This parasitic fungus, found on branches of various bamboo species, is utilized for both medicinal and industrial purposes. Reactive oxygen species (ROS) and nitric oxide (NO) not only regulate laccase activity but also enhance membrane permeability in hyphal cells to facilitate laccase secretion. In addition, La inhibits soil-borne pathogenic fungi such as *Rhizoctonia solani*, *Fusarium solani*, and *Pythium* species. Concentration above 200 mg La_2O_3/L inhibits *Pythium* sp. and *Rhizoctonia solani* mycelium growth by over 50%, while concentrations above 300 La_2O_3 mg/L have similar effects on *Fusarium solani* (Mu et al., 2006). Increasing La concentrations elevates activity of pectinase, proteinase, and cellulose enzymes per gram of mycelia in pathogenic fungi. The increase in La concentration led to a significant inhibition of mycelium growth, resulting in a decrease in total enzyme activity. Pathogens' metabolites are crucial pathogenic factors causing harm to plant tissues. In the mentioned study, the impact of La on toxins produced by harmful fungi was examined through seed germination.

Pathogenic toxins (fusaric acid, aryl organic acid) solution in which La is not added inhibit germination of *Isatis indigotica* and *Lolium perenne* seeds. However, addition of La to the pathogenic solution remarkably improves seed germination.

REEs can stimulate the biosynthesis of secondary metabolites in higher plants and microorganisms, often by prompting particular enzymes that regulate their biosynthesis. Applying various amounts of cerium nitrate to *Cyclocarya paliurus* leaves led to higher levels of secondary compounds such as triterpenoids, quercetin and kaemferol (Xie et al., 2015). In another study, Inacka & Ochi (2011) showed that the presence of scandium simulated the synthesis of bacilysin and amylase by *Bacillus subtilis*. Kawai et al. (2007) found that adding scandium chloride at concentrations of 10-100 µmol/L could boost the production of actinomycin, actinorhodin, and streptomycin by 2-25 times in *Streptomyces antibioticus*, *Streptomyces coelicolor* A3, and *Streptomyces griseus*, respectively. The impact of lanthanum on enzymes, such as pectinase, cellulase, and proteinase, may play a crucial role in managing rare earth elements for combating plant diseases.

Possible indirect effects of REEs on pathogenic infection

The majority of pathogens enter host plants passively through natural openings (stoma, hydathodes, lenticels and nectar glands) or wounds – fungi, bacteria and viruses. Some pathogens penetrate plants actively using a special mechanism, by creating enzymes that break down the barrier cuticular layers and cell walls. Pathogen entry into host plants through cell wall degradation is more important in facultative parasites compared to obligate parasites (Mu et al., 2006). As the primary cell wall consists of cellulose, pectin and glycoproteins, enzymes such as cellulase, pectinase and proteinase have a significant role in cell wall degradation, and can be considered as important pathogenic enzymes. Lanthanum affects the activity of these enzymes in fungi and can thus impact their pathogenicity (Zhang et al., 2000; Mu et al., 2006).

Plant pathological processes are influenced by three key factors: the pathogen, the host and environmental conditions. Unfavorable conditions for life processes can impair the growth and development of plants, weakening their vitality and reducing their resistance to some pathogens. REEs affect the physiological and metabolic processes in plants (Kovariková et al., 2019; Kastori et al., 2023), influencing plant vitality. The research findings suggest that the impact of REEs on life processes and plant growth can range from ineffective to stimulating or inhibitory, depending on the type of element, concentration, plant species, application method, and environmental conditions. Agathokleous et al. (2019) emphasize the link between rare earth elements (REEs) and hormesis, where low concentrations have the stimulating impact, while high concentrations have inhibitory (toxic) effects on plant life processes.

Tissue mineral nutrient concentrations affect plant disease resistance in various ways (Weinmann et al., 2023). In addition, the plant microbiome, which can also be affected by REEs, significantly influences resistance of plants to pathogens (Rabelo de Faria et al., 2021).

The impact of nitrogen (N) on plants' vulnerability to pathogens is intricate, depending on factors such as N level, infection patterns of different pathogens, and the form of N supplied. Ammonium and nitrate ions often have contrasting effects on disease severity (Huber & Graham, 1999). According to Weinmann et al. (2023), providing appropriate amount of nitrogen can exacerbate diseases caused by obligate biotrophic pathogens while reducing diseases caused by facultative ones. REEs can impact nitrogen availability for plants by influencing the behavior of soil bacteria responsible for nitrogen transformation. Nitrification rates in red soil rose by 20% at 0.15 mg La/g dry soil but declined at higher La concentrations. In well-drained soils, the intensity of ammonification decreased at La levels of 0.06 to 1.2 mg La/g salt, while in paddy soil, it increased by 25 times at 0.9 mg La/g soil (Zhu et al., 2002).

An amount of 500 µg/L of lanthanum enhanced N and P uptake in spinach (Hong et al., 2002). REEs can also impact nitrogen metabolism in plants.

Application of lanthanum nitrate and europium nitrate increased nitrate reductase activity, a key enzyme in nitrate and calcium assimilation in *Eriobotrya japonica* (Zhang et al., 2013). Spraying La and Ce in field plot experiments raised vitamin C and nitrate levels in spring Chinese cabbage, but lowered them in autumn Chinese cabbage (Ma et al., 2014). The use of mixed rare earth fertilizer in Chinese cabbage and rape plants in field settings boosted soluble sugar, titratable acid, sugar/acid ratio, and vitamin C content in spring. It also reduced nitrate levels (Ren et al., 2016).

The Ca concentration in plants can influence plant diseases in many ways. Calcium has an important role in recognizing pathogenic invasion at the plasma membrane. Pathogenic invaders change the membrane potential and increase the rapid influx of Ca ions in the cytosol, increasing cytosol Ca concentration, which acts as a secondary messenger in early plant immune responses (Hilleary et al., 2020). Calcium is important for biomembrane stability, modifying cell wall metabolism and enhancing the activity of pectin methylesterase, which contributes to the cell wall structure (Langer et al., 2019). Certain pathogenic fungi and bacteria release pectolytic enzymes, such as polygalacturonases. The decomposition of pectates in the cell wall and middle lamella is mediated by polygalacturonase, which is inhibited strongly by Ca concentrations (Sasanuma & Suzuki, 2016). Calcium-polygalacturonases are required in the middle lamella for cell wall stability. Some REEs (La^{3+}, Nd^{3+}), which have an effective ion radius similar to Ca ions, may be partially able to replace endogenous Ca of plants, acting as substitutes or antagonists for calcium ions (Tyler, 2004). REEs can alter membrane stability, inhibit catalytic activities of Ca-dependent enzymes, decrease H^+ secretion and Na^+ transport and regulate stomata movements through the effects on cytosol-free Ca. It is believed that most of the biological effects of REEs in plants result from their influence on cytosol-free Ca concentrations. Calcium, as a secondary messenger, is used by almost all eukaryotic cells in a large number of cellular reactions. Research on the effect of La on the cytosol-free Ca content in plants has yielded mixed results. For example, Lu et al. (2019) reported no significant increase in cytosol-free Ca concentration when La was applied in doses from 0.2 g/L to 5.0 g/L. Conversely, Zhang et al. (2016) found that a lower concentration of 20 mg La/L increased free Ca levels, while higher dosages of 200 mg/L and 300 mg/L decreased them. Liu et al. (2012a) reported slight decreases in free Ca level by 0.2 mmol La/L. For increased Ca concentration in the cytosol to affect the signal transduction, certain proteins in the cytosol selectively and specifically bind Ca. The most studied is calmodulin (CaM), a low molecular weight protein that reversibly binds Ca with high affinity and selectivity. Amann et al. (1992) reported that europium (III) ions can replace Ca ions in CaM (II) and still retain their ability to activate NAD kinase in plants. Lanthanum has been used to block Ca channels involved in signal transduction in plants (Levis & Spalding, 1998). According to Wei & Zhou (2000), neodymium seems to be able to partially replace Ca in cell membranes of oilseed rape during Ca starvation. Magnesium is an essential component of the chlorophyll molecule and plays a crucial role in photosynthesis. Lanthanides (La^{3+} Ce^{3+}) can enter the chloroplast, bind easily to chlorophyll, and substitute Mg^{2+} ion in the chlorophyll molecule, as well as coordinate the porphyrin ring in pheophytin to form lanthanide–chlorophyll (Chl)-complex $(\text{Chlorophyill-a-La -pheophytin})^{2+}$ (Rezanka et al., 2016). Low concentrations of La have a stimulatory effect on the concentrations of photosynthetic pigments, whereas higher concentrations significantly inhibit them in rice seedlings (Liu et al., 2012). A positive effect of La on chlorophyll content is probably a result of the increased essential macroelements involved in chlorophyll biosynthesis (He et al., 2020). According to Gerendás & Führs (2013), from the perspective of plant resistance to pathogens, the ratio of Mg content to some other nutrients (Ca, K) is more significant than its status.

Lignification and silicon (Si) deposition enhance mechanical stability in epidermal tissues and can provide resistance against penetration of fungal pathogens directly through the cuticule and epidermal cell wall. This mechanism significantly contributes to increased resistance to fungal disease (Wang et al., 2017). Moreover, higher concentration of La increased Si concentration in barley stems (Fastovets et al., 2017).

Fungal pathogens may also penetrate host tissues through stomata (Pryce-Jones et al., 1999). REEs can influence the stomatal apparatus. In young maize plants, the presence of yttrium reduces stomatal length and width while increasing stomatal density (Maksimović et al., 2014).

Different adverse factors can cause oxidative stress in plants, i.e. imbalance between pro-oxidative processes and the antioxidant system of plants (Kastori et al., 2023). Pathogenic infections can cause increased formation of reactive oxygen species (ROS) as part of the plant's defense system (Li et al., 2021). ROS primarily damage the plasma membrane by oxidizing phospholipids and increasing membrane permeability, which can lead to cell death. Numerous authors have determined the protective effect of REEs, especially La and Ce, against oxidative stress by increasing antioxidative capacity (Hong et al., 2017; Cui et al., 2019).

CONCLUSION

REEs are a series of 17 elements with nearly identical chemical and physical properties. They are widely distributed in low concentrations in all parts of the biosphere. Recently, REEs have found applications in numerous areas of human activity, including industry, medicine, and agriculture, where they are used as plant fertilizers (mostly in China) and feed additives in livestock production. Although REEs are not essential for living organisms, they can influence their life processes. Low doses of REEs can stimulate the metabolic processes of living organisms, whereas high doses inhibit them. Recent studies have demonstrated that hormesis commonly occurs in a variety of plants and microorganisms in response to REEs. Microorganisms have a very significant and complex role in the biosphere. REEs can affect the activity and growth of soil microflora, while microorganisms with their metabolites, can affect the bioavailability of REEs and their uptake by plants. It was found that REEs had a significant effect on many plant diseases, both directly and indirectly. Direct effects can manifest in reducing phytopathogen virulence, but also inducing disease resistance in the host plants. Indirect effects of REEs on plant disease control stem from their ability to influence physiological activities of plants, fostering their growth and development, as well as resistance to unfavorable environmental factors.

***Acknowledgements*:** This manuscript was funded by the Ministry of Science, Technological Development and Innovation of the Republic of Serbia (Grant Number 451-03-65/2024-03/200117).

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Conflict of interest: The authors declare that they have no conflict of interest.

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