
DEGRADATION, REHABILITATION,
AND CONSERVATION OF SOILS

Lanthanides in the Soil: Routes of Entry, Content, Effect on Plants, and Genotoxicity (a Review)

A. D. Kotelnikova^{a,*}, O. B. Rogova^a, and V. V. Stolbova^b

^a*Dokuchaev Soil Science Institute, Pyzhevskii per. 7, Moscow, 119017 Russia*

^b*Lomonosov Moscow State University, Moscow, 119991 Russia*

**e-mail: a.d.kotelnikova@gmail.com*

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Abstract—Lanthanides as a separate group of metals geochemically belong to rare earth elements (REEs). For a long time, they have not received proper attention of researchers, whose interest was focused on other harmful environmental pollutants. However, the importance of REEs for modern technologies along with significant gaps in the knowledge about their effects on living organisms has changed the situation. Thanks to the active interest of researchers, a fairly large body of data on REEs in various areas has been accumulated, including their chemical and physical properties, their potential in engineering and instrumentation, their content in various natural objects, effects on human health, and interaction with other living organisms at the cellular level. This review analyzes and generalizes the new information about REEs as a relevant ecological factor with a special focus on the sources of REEs, specific features in their behavior in the soil, the effects of their interaction with plants, their manifestation, and putative mechanisms at the cellular level. The economic importance of plants to humans as well as their role for the entire biosphere as primary producers and their ability to be among the first ecosystem components that respond to negative changes requires focusing on these issues. The purpose of this review is to emphasize the research aspects that need a deeper insight, in particular, the soil–plant interaction and the effect of REEs on plant cell division.

Keywords: rare earth elements, phytotoxicity, bioavailability, hormesis, mitotoxicity

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INTRODUCTION

An ever-increasing use of rare earth elements (REEs), including lanthanides, as components of new materials almost ubiquitously employed in innovative technologies, determined the need in their comprehensive studies. The REE production and processing volumes naturally increase causing, in turn, an increase in the REE concentration in the environment. Numerous research papers on various aspects of the REE behavior in natural objects have been published during the last decades.

The ability of REEs at low doses to increase the yield of crops has suggested their use as micronutrients [92]. However, the mechanisms underlying the stimulatory effects of REEs are still vague and the estimates of their eventual benefits considerably differ [61, 73]. Note here that plants are not only the components of terrestrial ecosystems that are most sensitive to pollution and the primary players in the food chain, but also have a tremendous economic value for humans. Thus, it is evidently necessary to summarize and analyze the currently available data on the behavior of REEs in the soil–plant system.

The existing Russian reviews to a greater degree consider the biochemistry of REEs and their behavior

in soil rather than their effects on plants, especially at the cellular level [5, 8]. Even recent reviews almost omit the effect of REEs on cell division [29]. Correspondingly, the goal of this review was to summarize the research information about this specific group of elements, lanthanides, as a relevant ecological factor with the special focus on the following aspects: the sources of REE entering soil, specific features of their behavior in soil, effects of REE interaction with plants, their manifestation, and putative mechanisms underlying their effects at the cellular level. Analysis of the available literature will allow us to reveal the relevant challenges for researchers and to identify the promising research directions. A special focus here is the description of cytotoxic effects, which is especially necessary since the most harmful effects of REE impact, i.e., damage of hereditary material, are primarily diagnosed at the cellular level.

LANTHANIDES AS REPRESENTATIVES OF RARE EARTH ELEMENTS

Lanthanoids, or lanthanides, occupy a special position among the chemical elements used by humans in various fields of activity. The former name means “like lanthanum”, which better reflects the

Table 1. Mean content of lanthanides in the earth's crust and soil according to published data (lower boundary of the content in the earth's crust, [127]; upper, [63]; and mean content in soil, [14])

Element	Mean content in the earth's crust, mg/kg	Mean content in soil, mg/kg
Light lanthanides		
La (lanthanum)	30–35	29.5–40
Ce (cerium)	64–66	29.5–50
Pr (praseodymium)	7.1–9.1	3–7.7
Nd (neodymium)	26–40	27.9–35
Sm (samarium)	4.5–7	4.5–6.1
Eu (europium)	0.8–2.1	1–1.9
Heavy lanthanides		
Gd (gadolinium)	3.8–6.1	3–4.7
Tb (terbium)	0.6–1.2	0.63–0.7
Dy (dysprosium)	3.5–4.5	3.8–5
Ho (holmium)	0.8–1.3	0.38–1.1
Er (erbium)	2.3–3.5	2–2.8
Tm (thulium)	0.3–0.5	0.16–0.6
Yb (ytterbium)	2.2–3.1	2.3–3.1
Lu (lutetium)	0.3–0.8	0.3–0.4

essence of the properties of these elements, rather than the latter one, meaning “following lanthanum” [18]. This family comprises 14 elements: 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 (Yb), and lutetium (Lu) [128]. Together with lanthanum (La), scandium (Sc), and yttrium (Y), they form the group of the so-called rare earth elements, REEs, or *terrae rariae*, TR [39]. Hereinafter, the terms lanthanides and RREs are used as synonyms.

As is aptly stated in one of the papers on the pharmacology and toxicology of REEs, “A Pandora's box was opened by the discovery of a black mineral specimen in Ytterby by Arrhenius in 1789” [65]. Since that time, the properties of these elements have been studied by experts in most diverse areas of research. The name rare earth elements rather refers to the fact that their pure deposits are rare as compared with other elements than to their abundance in environment [61]. Initially, the term “rare earths” denoted all poorly studied natural oxides and was assigned to lanthanides by the 18th–19th centuries, when the refractory, almost water-insoluble oxides of these metals were produced from rare minerals [88].

The lanthanides are traditionally divided into two groups according to their electron configuration that

determines their interaction with other elements, namely, light REEs, comprising the elements from La to Eu, and heavy REEs, from Gd to Lu [61]. The first group is also referred to as the cerium group and the second, as the ytterbium one. As is believed, light REEs are more soluble than heavy REEs; however, any distinct criterion for distinguishing between the elements ascribed to these groups is absent [123]. Some researchers separately consider the middle REEs, comprising the elements with medium mean atomic weights and ionic radii, for example, from Sm to Dy [54]; however, the composition of this group is rather indistinct [130].

THE CONTENT OF LANTHANIDES IN THE EARTH'S CRUST, THEIR WORLD RESOURCES, AND USE

The average REE content in the earth's crust is close to 0.015% and amounts to 189 mg/g (sum of concentrations of several elements) [79, 94]. The data on the content of these elements in published sources considerably vary (Table 1) approaching the level of copper (47–55 mg/kg), lead (12.5–16 mg/kg), zinc (70–83 mg/kg), and tin (2–2.5 mg/kg) [4, 57, 126]. Even the rarest REE, thulium, is more frequently observed as compared with gold (0.004–0.0043 mg/kg), platinum (0.005 mg/kg), and iodine (0.4–0.5 mg/kg) [4, 113, 126]. The most abundant elements of this group are Ce and La, whereas Pm, which has no stable isotopes and is almost unobservable in nature, was found only in small amounts in uranium ore. Note that lanthanides follow the Oddo–Harkins rule: the elements with an even atomic number are more abundant than the adjacent elements with an odd atomic number.

These elements, frequently only several representatives of the group simultaneously, are observed in manifold accompanying minerals (phosphates, carbonates, fluorides, and silicates), prevalently in pegmatites, granites, and associated metamorphic volcanic rocks [130]. Over 250 minerals containing REEs are known; the most abundant of them are bastnaesite, monazite, xenotime, loparite, euxenite, and parisite [79]. However, only about 25% of these minerals are actually rare earths and only bastnaesite and monazite are of economic importance [25]. The so-called ion-adsorption clays are an important source for production of these metals [129].

Although REEs are rather abundant in the earth's crust, they rather do not concentrate in the commercially suitable ore fields unlike nonferrous and precious metals [67]. According to the estimate by the United States Geological Survey (USGS), the total reserve of rare earth metals in the world amounts to 88 million tons of their oxides [23]. Their largest deposits are in China and the total reserve there is estimated as 43 million tons of metal oxides, accounting for 90% of the global production during the corre-

spondingly period [73]. The clays produced only in China are the main source of several heavy REEs, such as Gd and Dy [54].

In addition to China, the bastnaesite deposits in the alkaline rock in the United States and the monazite deposits in Australia, Brazil, India, Malaysia, Republic of South Africa, Sri Lanka, and Thailand are significant for REE production. In 2008, the world production of lanthanides amounted to 124000 t [78].

According to the estimates of some experts, Russia heads the list of forecasted REE resources [21], with 16 deposits accounting for approximately 30 million tons of REE oxides [25]. The main promising deposits of the REE-containing ores as well as the refuse dumps of production fields earlier not used for extracting lanthanides are situated in the Murmansk oblast, Republic of Sakha, Irkutsk oblast, Republic of Tyva, Krasnoyarsk region, and Transbaikalia [1, 25].

Currently, the availability of REE resources and feasibility of their production and importation are the factors that in many respects determine the development of a country. In 2010, the European Commission included this group of elements in the list of raw materials critically important for new technologies in different branches of production [43]. The significance of rare earth metals places them among the other most important natural resources, such as water, oil, and iron ore [30]. REEs are irreplaceable in the economy sectors, such as clean energy, military industry, medicine, and agronomy [61, 86]. Currently, REEs are actual "vitamins of industry"; their addition considerably improves the quality of production of, for example, ceramic capacitors, used in electronic circuits as well as powerful magnets and alloys, used in aviation [15, 30, 46, 58]. Lanthanides are widely employed in the manufacture of luminescent materials; design of anticarcinogenic, antiinflammatory, and antiviral drugs, as well as nuclear radiation detectors as contrasting agents [48, 50, 80, 85, 93, 139]. The attempts are made to use lanthanides as tags for studying the migration of other elements, which is applicable to sanitary and hygienic standardization [2].

One of the hurdles associated with REE production and processing is the need in additional control of radiation safety because of frequently present admixtures of radioactive elements in REE minerals [99]. In addition, lanthanides also have radioactive isotopes [20].

An insufficient amount of this most valuable resource forces some countries to search for alternative sources of REEs and to construct plants for recycling electronic devices [99]. Additionally, phytomining, phytoextraction, and agromining techniques are developed, allowing for the extracting heavy metals from the soil of polluted areas by hyperaccumulator plant and their subsequent restoration from the biomass [94, 114].

PROPERTIES OF LANTHANIDES AS A SPECIFIC GROUP OF ELEMENTS

An important role of REEs in the development of world economy is determined by their chemical and physical properties, similar for all elements of this group [10]. Most lanthanides are trivalent metals with close ionic radii [39]. REEs are soft plastic chemically active metals. In the presence of air, their silver-white surface acquires chestnut and dark-brown color with formation of oxides [113]. All elements of the group react with water to evolve hydrogen and form insoluble oxides and hydroxides. At higher temperatures, the reactions with C, N₂, Si, P, S, halogens, and other nonmetals go rather rapidly. The density and melting temperature increase with the atomic weight except for europium and yttrium. Many REEs burn when heated to give oxides. Lanthanides are paramagnetic except for Y³⁺, La³⁺, Lu³⁺, and Ce³⁺, which are diamagnetic [113].

The REE compounds have high electric conductance and low solubility, readily precipitate, and bind to complexing ions, such as hydroxides, carbonates, fluorides, phosphates, and organic ligands [30, 143].

Individual elements of this group have their specific features although their properties are very similar. Lanthanides as the representatives of 4f elements differ only in the number of electrons at this sublevel, which is gradually filled in the series of elements and change their properties. In particular, the atomic and ionic radii gradually decrease (the so-called lanthanide contraction), which leads to an increase in the stability constants of coordination compounds and hydrolysis constants as well as to a decrease in the initial pH of precipitation of lanthanide hydroxides [84]. These regular changes in the properties most likely determine the differences in the biological effects of lanthanides [153].

In addition, Ce and Eu display variable valence in natural environment [8]. Ce, Pr, and Tb have 4+ oxidation state, while Sm, Eu, and Yb, 2+ oxidation state [84]. The periodic alteration of lanthanide properties determined by formation of coordination compounds in aqueous medium, or the so-called tetrad effect, was also observed [6]. Owing to this effect, a smooth plot of the chondrite-normalized REE content breaks into four parts [6].

Undoubtedly, the current active use of REEs increases their concentration in the environment. This problem has been noted by several researchers, who explain the manifestation of toxic effects on biota and humans with lanthanide pollution [41, 86]. However, it is difficult to definitely state whether the REE concentration actually increases in the areas not associated with their production and application since the data on the REE content in the soils there in earlier period are sparse. In particular, analysis of the lichens from herbaria in Italy harvested starting from the 1980s failed to find any significant changes in the concentrations of lanthanides [101].

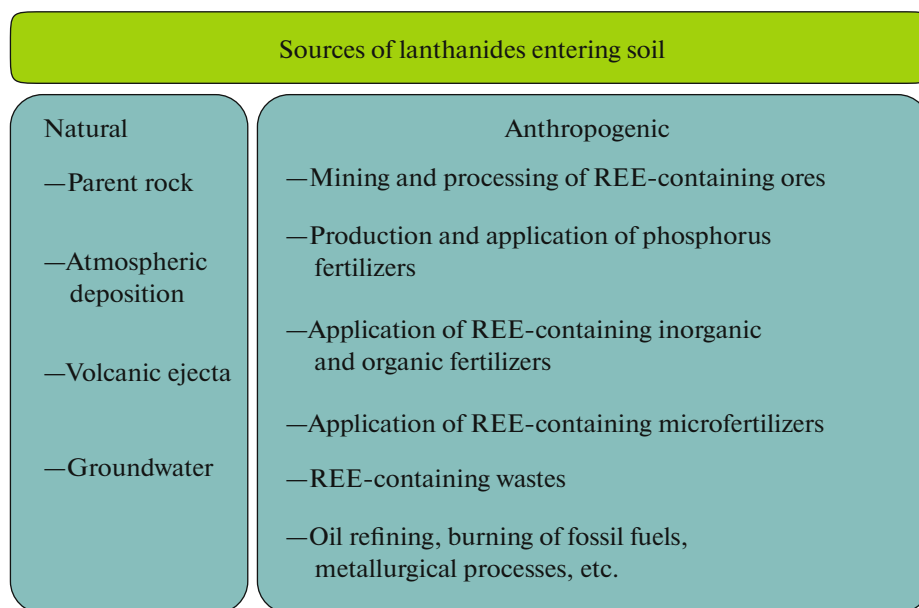


Fig. 1. Main sources of the lanthanides entering soil.

Presumably, lanthanides are not as toxic as other heavy metals and metalloids, such as Cd or As, but may be chronically toxic to humans and cause long-term adverse effects. In particular, a long exposure to high REE doses correlates with a decrease in the IQ in children, disturbances of blood circulation and immune systems, decrease in the human nerve conduction velocity, and increase in atherosclerosis prevalence [140, 151, 156, 157]. This suggests the need in development of standards for REE content in environment and foodstuff. The corresponding standards are currently absent although several researchers attempt to provide the relevant scientific criteria and solutions [70, 82, 123].

The similarity of chemical properties of lanthanides was regarded as the sufficient reason to forecast the toxicity of the entire REE series; however, several studies demonstrate a decrease in toxicity with an increase in the atomic number, which is explainable by higher stability constants of heavy lanthanides [61]. In the absence of complexing ligands, the toxicity of lanthanides increases with the atomic weight. A higher toxicity of Ce to plants as compared with La is shown, which is explainable with a higher Ce charge density, allowing for its easier adsorption [59]. Note that the toxicity to the amphipods *Hyalella azteca* decreases from La to Er but grows from Tm to Lu [36]. Thus, the differences in toxicity of individual REEs require a deeper insight into their individual properties and specific features of the interaction with plants of each lanthanide.

ROUTES OF ENTRY AND CONTENT OF LANTHANIDES IN SOILS

Bedrocks are the main source of REEs in soils; the REE content in the bedrock decreases in the following

order: granite > Quaternary deposits > basalt > purple sandstone > red sandstone (figure) [76, 98]. Note that the content of light lanthanides in the soil-forming rocks is always higher as compared with heavy lanthanides. The ratio of light to heavy lanthanides is specific of different rocks and is mainly inherited by the soil [77]. According to Bohn et al. [34], the REE content in soil varies from 30 to 700 mg/kg. The content of REEs in the upper soil layer, where they can be assimilated by plants and can actively interact with the other biota, considerably varies and reaches 100–200 mg/kg [92, 105].

This content can increase to 1000 mg/kg as a result of human activities [91]. In particular, the mean REE content in China soils is 177 mg/kg and reaches 243 mg/kg in agricultural soils. Owing to their high mobility, these metals are readily dispersed from the tailing dumps of REE production by air and water flows. As a result, the total REE concentration in neighboring soils reaches 870–1100 mg/kg [94]. The La and Ce concentrations in the soil near a Baotou tailing reservoir (China) leap to 11000 and 23600 mg/kg, respectively, which is several hundredfold higher as compared with the mean concentrations for this region (Inner Mongolia) [64].

The most important anthropogenic source of REEs entering the soil is associated with the manufacture and use of organic and mineral (especially phosphate) fertilizers [9, 35, 74, 104, 116, 133]. The concentration of lanthanides in apatites considerably varies reaching over 1600 mg/kg [111]. Up to 50–60% of the lanthanides contained in the raw material passes into superphosphate during its production; high concentrations of Ce, La, and Nd are observed in the final product. In addition, limestone contains REEs as

impurities. Correspondingly, a long-term use of phosphate fertilizers can pretty well elevate the concentration of lanthanides in soil and plants [27, 62].

During the last decades, some Asian countries commenced applying lanthanides as microfertilizers, thereby creating a new route of entry of these elements to soil and adjacent media [92]. In China, the REE-fertilized area has reached 4 million hectares, resulting in annual entry of 50 to 100 million tons (calculated for oxides) of REEs to agroecosystems [92]. The use of REE-fertilizers spread to Korea, Japan, Australia, Switzerland, and Philippines [45]. The Research Center for Agriculture Application of Rare Earth Elements in China recommends a dose of 0.7 to 3.6 kg/ha of REE fertilizers. However, a wide use of REEs as a fertilizer concurrently with the traditional melioration techniques may have negative ecological consequences. For example, the concurrent use of REE fertilizers and urea causes an increase in the N_2O emission from the soil [138].

REE additives are also used in livestock breeding. This may also lead to the REE entry to soil with manure, used as an organic fertilizer [113]. The other anthropogenic sources comprise aerial pollution of soils during REE mining and metal production [76, 84, 91].

Remediation of the REE-polluted aquatic and soil ecosystems currently is a serious ecological challenge in several regions. Since the 1990s, REEs are regarded as one of the major pollutants in China [94]. After several decades of wide use of REE fertilizers, they are prohibited in China [60].

Several publications report the data that can form the basis for the standards of lanthanide content, which are now extremely necessary. In particular, a concentration of 30 mg/kg soil is permissible for lanthanum according to Kozhevnikova [17].

The data on the content of lanthanides in soils of Russia are sparse and mainly refer to the areas with high lanthanide concentrations, technogenic and natural anomalies [7, 84]. The recent advent of inductively coupled plasma atomic emission spectrometry, allowing for sufficiently easy determination of REE concentrations with a high accuracy, induced the studies on their content and distribution in soils of different types [3, 16, 17, 24, 84] (Table 2). However, accumulation of these data and their generalization are still relevant.

BEHAVIOR OF LANTHANIDES IN SOIL

Numerous factors influence the concentration and mobility of REEs in soil, such as soil genesis and weathering, adsorption/desorption processes, soil physical and chemical properties including pH, and the content of organic matter and clay minerals [76, 116, 130, 142, 150].

Most likely, the lanthanides redistribute between the soil components owing to complexing, adsorption,

and ion exchange processes. Note that the main soil sorbents (iron and manganese oxides or hydroxides and clay minerals) take up lanthanides in different manners depending on the specific chemical features of elements as well as the content and composition of soil organic matter [53, 84]. Recent studies suggest a high degree of REE binding in soil by metal–organic complexes [53]. This may determine a high bioavailability of lanthanides to plants via decomposition of humate and fulvate compounds by rhizospheric microorganisms.

A larger part of the REEs entering the soil with fertilizers appears to be bound to ferromanganic oxides, organic matter, and sulfides. Note that part of them still remains water-soluble, exchangeable, and carbonate-bound, regarded as available to plants. The chemical species formed in situ by exogenous REEs that entered soil depend also on the physicochemical soil characteristics [141].

In general, the lanthanides that entered the soil via anthropogenic activity (exogenous lanthanides) are usually represented by more soluble and reactive compounds as compared with the metals of a natural origin, and, correspondingly, are more bioavailable. Their entry may interfere with the balance of REE biogeochemical cycles in environment and have a negative effect on the integrity of soil system [113].

Various areas differ in the REE content in the soil; the REE content in plant products is usually rather low but display specific features characteristic of individual areas. Several currently proposed methods are able to trace the origin of different food products, for example, wine, pumpkin seed oil, and tea, according to their REE fingerprints [28, 77, 154].

Initially, the methods designed to assess the toxicity of the aquatic media and soils containing heavy metals took into account only the total concentration of elements in the assayed medium. However, the activity of free metal ions is regarded as a more reliable predictor of toxicity as compared with the total concentration of a metal since the physicochemical characteristics, such as the presence of organic and inorganic ligands, influence the deportment and behavior of metals in aquatic medium and soil [40].

One of the state-of-the-art tools for assessing the effects of mobile and bioavailable metal compounds on their toxicity is the biotic ligand model (BLM) theory [60]. The BLM takes into account two aspects, namely, chemical speciation of metals and competition of cations. The concept that the degree of toxicity of a metal in a studied medium is determined by the share of the metal ions bound to biologically active centers, or biotic ligands, forms the background for this model. As is assumed, the toxic cations competing with the ions of other metals appear to be bound to biological ligands, which weakens their toxicity in the studied medium. Several studies have demonstrated that this theory is applicable to bivalent metals [60].

Table 2. Concentration of lanthanides in the upper layer of some soils in Russia

Region	Soil	Source	Concentration of element in the upper layer (0–20 cm), mg/kg													
			La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu
Moscow oblast (Prioksko-Terrasnyi Nature Biosphere Reserve)	Iron-illuvial podzolized soddy podbur	[24]	4.1	9.9	0.9	19.6	4.1	0.30	3.4	0.09	2.1	0.10	0.92	0.05	1.5	0.06
Moscow oblast (Prioksko-Terrasnyi Nature Biosphere Reserve)	Mucky-humus gley soil	[24]	12.5	28.5	2.6	55.4	11.5	0.74	9.4	0.22	5.4	0.25	2.25	0.10	3.3	0.11
Vologda oblast	Soddy calcareous leached soil	[84]	22.86	44.38	5.23	20.05	3.74	0.66	3.13	0.42	2.24	0.44	1.24	0.19	1.15	0.22
Kirov oblast	Soddy podzolic loamy soil	[11]	9.4	24.2	2.3	9.0	1.6	0.37	2.6	0.21	1.4	0.23	0.88	0.17	1.1	0.16
Amur oblast	Raw-humus burozem	[3]	25.43	51.83	5.22	19.89	3.72	0.89	3.90	0.45	2.41	0.42	1.29	0.17	1.12	0.16
Perm krai	Humus alluvial h soil	[53]	25	55	6.2	23	4.8	1.1	4.2	0.6	3.5	0.7	2.0	0.28	1.9	0.29
Perm krai	Soddy podzolic soil	[53]	9.4	20	2.4	8.9	1.7	0.39	1.6	0.23	1.3	0.26	0.80	0.11	0.70	0.10

However, the data favoring the applicability of BLM to trivalent metals (and REEs are mainly trivalent) are yet insufficient and the corresponding studies are in progress.

Thus, the chemical forms of exogenous lanthanides in soil are still a relevant problem as well as the soil ligands as factors of their sorption/desorption. The distribution of all REEs according to the types of compounds they form in soil matrix will quantitatively determine their bioavailability and biological activity towards higher plants.

ROUTES OF ENTRY, ACCUMULATION, AND CONTENT OF LANTHANIDES IN PLANTS

Plants can sorb REEs through the surface of their leaves when sprayed; however, the main route of their entry is through roots [125]. Lanthanides are absorbed to the xylem through thin cell walls of the root hairs and are then transported to other parts of the plant [114]. The ability of plants to assimilate lanthanides from solutions and soil has been studied in several species. The review by Brown et al. [37] suggests that soil chelates and applied fertilizers influence the sorption of REEs; in this process, potassium and nitrogen fertilizers increase the sorption and phosphate fertilizers decrease it. In the soil–root system, low molecular weight organic acids, being important components of root exudates (for example, citric and malic acids), can increase desorption of light lanthanides as well as their uptake by plants from the soil [118]. This is associated with chelating and/or complexing properties of acids, which can influence the solubility of metal compounds in soil.

The Casparian strips on roots, which limit the uptake of lanthanides to the other part of the organism, are among the main factors associated with morphology. This mechanism that minimizes the entry of metals to the upper plant parts, housing important growth and development processes, such as photosynthesis, is regarded as a tool decreasing the toxic impact [114]. Thus, the content of lanthanides is typically increased in the roots and decreases in the row roots > leaves > stems > seeds/fruits [38, 141, 145]. Note that distribution pattern of lanthanides may depend on particular plant species. In particular, the distribution in corn (*Zea mays* L.) is more contrasting as compared with rice (*Oryza sativa* L.) [89]. The plant seeds have a semipermeable layer differing in its location depending on the plant species. This layer limits the entry of some substances to the embryo, as is demonstrated for lanthanum in the switchgrass (*Panicum virgatum* L.) seeds [68]. The researchers explain the absence of the effect of lanthanum on seed germination by the presence of this layer, which prevents its negative impact on the embryo.

A comparison of the accumulation factors in the soil–plant (ferns) system shows that the REEs in a water-soluble form are easier transported to the upper soil horizon to the roots and from the leaf stalk to blade than from the stem to the stalk [155]. Presumably, the mechanisms underlying the lanthanide assimilation in ferns differ from those in other species. In particular, the REE concentration in fern tissues decrease in the row leaves > stems > roots.

The content of individual lanthanides (except for cerium) in the plant roots is similar to the content of the REE soluble species in the upper horizon of the soils where these plants grow. The lanthanides in soil are typically in a trivalent state except for Eu and Ce. The latter, being in a tetravalent state, is more likely to precipitate via hydrolytic reactions, which interferes with its accumulation in plants [94].

Most studies of the REE accumulation by plants involved the objects simultaneously containing several elements, i.e., artificial mixtures with certain concentrations of lanthanides, or soil samples containing the elements at natural concentrations and ratios. The studies of this kind do not allow the individual specific features of REE accumulation by plants to be revealed [61]. Thus, comprehensive model experiments are necessary to study the sorption of individual lanthanides and their mixtures by plants aiming to clarify their putative competition as well as predictable accumulation mechanisms and patterns if possible.

Noteworthy is the ability of REEs to accumulate although in small amounts in the edible plant parts after applying REE fertilizers. This requires additional studies aiming to reveal the putative toxic effects [141]. In general, the studies of REE toxicity and chronic biological effects demonstrate that the acceptable daily intake for humans is 0.1–1.2 mg/kg (oxides). According to the assessment of REE consumption with foodstuff in China, the daily intake with cereals, vegetables, and other products may reach 1.75–2.25 mg, which does not exceed the level recommended for this country [125].

The REE content in plants considerably varies, which may be in part determined by their specific features [141]. In particular, the range of La concentration in plants reaching five orders of magnitude is observed in Japan [81], which the authors explain not only by different concentrations in soils, but also by particular differences between plant species. Some ferns growing in the sites with a high REE content accumulate to 3000 mg/kg lanthanum and may be regarded as accumulators of this element, whereas the concentration in spruce needles is as low as 10 ng/g [136, 144]. The wheat *Triticum durum* Desf. displays the highest accumulation ability among crops and the hickory *Carya tomentosa* Lam., among trees [13].

Different plant species growing in the same site take in different REEs at unstable ratios [49, 137]. In addition to species specificity, individual accumula-

tion specificity is observed since individuals of the same species display the corresponding differences [146]. The differences in REE accumulation between species and individuals are in part explainable with the pH in the rhizosphere, which depends on the plant species and growth stage and determines the availability of the metals contained in soil [114].

THE EFFECT OF LANTHANIDES ON PLANTS

The most important property of REEs, especially of light lanthanides, that determine the effect on the biota is their ionic radii, which are close to that of calcium. The ionic radius of calcium is 9.9×10^{-2} nm, and varies from 8.5×10^{-2} to 1.15×10^{-1} nm for the trivalent lanthanide ions [37]. This allows REE ions to competitively react and actually replace calcium in many biochemical processes taking place in living organisms, which, in turn, leads to inhibition of enzymes, destabilization of the cell membrane, and so on [37, 71].

Note that a strong binding of trivalent ions with the negatively charged ligands of the plant cell wall interferes with an experimental study of their intercellular transport and the routes they use to enter metabolism; correspondingly, the relevant literature fails to give the precise answer on which mechanism allows REEs to enter the cell [118].

Presumably, the capability of penetration strongly depends on environmental conditions, which can change the speciation of elements and influence their mobility [37]. In particular, trivalent La within weakly dissociating compounds in a colloidal solution fails to penetrate the plant cell membrane, whereas La^{3+} ion passes through it [55].

Lanthanides are detectable in different parts of the intracellular space putatively simulating the behavior of chemical analogs. Entering the root cells through the membrane and intracellular calcium channels, La^{3+} can be involved in the signal transduction networks via calmodulin, a calcium-binding protein [95]. In the cells of the root meristem, lanthanum starts to interact with the components of the nucleus [115, 132]. The ability to penetrate through calcium channels is characteristic not only of lanthanum. Gadolinium is detectable in the cells of the roots exposed to this metal [8]. Deposits of light lanthanides taken up from soil are observable in the cell wall, intercellular space, plasmalemma, vesicles, and vacuoles of the root epidermal cells of the fern, a hyperaccumulator of lanthanides; however, they were undetectable in the Casparian strips on the adventitious roots [118]. As for cerium, it appeared not only to penetrate into the cell, but also to accumulate in the nucleus [73].

Several studies oppositely estimate the penetrating ability of REEs. In particular, it is demonstrated that lanthanum, similar to neodymium, is unable to enter the cytoplasm and can accumulate only on the outer

membrane surface [73]. Several studies report an increase in the resistance of cell membranes along with the inability of lanthanides to penetrate into the cell [12]. Presumably, the REE capability of penetration considerably depends on the plant species-specific features.

Having entered the cell, REEs can bind to macromolecules (nucleic acids, proteins, and polysaccharides) to form complexes with biotic ligands [136].

For a long time, REEs were regarded as elements neither necessary for plant growth and development, nor toxic in any way. Starting from the second half of the last century, part of the studies on the effect of these metals on plants suggested that they can be used as fertilizers. Note that the REE-fertilizers are recommended for seed or foliar application since the lanthanides applied to soil become poorly available to plants and fail to give the required effect, while an increase in their dose has a negative result [8].

The effects of small REE doses, which are regarded as positive have been repeatedly demonstrated, including a rapid La-induced growth of oat (*Avena sativa* L.) coleoptiles, favorable effects of La and Ce on the growth and development of wheat (*T. durum* Desf.), and an increase in the length of *Arabidopsis thaliana* roots after addition of these elements to nutrient medium [66, 69, 100]. Other positive effects have been also observed, in particular, stabilization of the membrane, a decrease in the water loss by plants, an increase in the efficacy of hormones and nitrogen fixation, and a decrease in accumulation of toxic elements, such as cadmium [141, 149]. The ability of lanthanides to decrease the injuries caused by ultraviolet radiation and to increase the contents of sugars and vitamin C has been also observed [45]. An increase in the length of rice (*O. sativa* L.) roots caused by low doses of lanthanum is also demonstrated [96].

The experience of applying REE microfertilizers demonstrates an up to 10% increase in the crop yield [72]. However, the biochemical mechanism of the increase in crop productivity as well as the long-term consequences of this impact on the components of environment and human health after consuming such products is still vague. Another still disputable issue is whether the effects, such as an increased root and shoot growth, can be regarded as positive. The plant responses of this kind may indicate a stress and impairment of biochemical reactions in the organism, for example, of hormonal regulation. Summing up of the available data suggests that the low concentrations of lanthanides induce a hormetic effect. In particular, this is demonstrated when exposing the common sunflower (*Helianthus annuus* L.) and bok choy cabbage (*Brassica chinensis* L.) to lanthanum and neodymium: a hormetic effect on the root and shoot masses appeared at low doses of these elements, whereas both elements were toxic at high doses [114].

Many researchers also report opposite results suggesting a negative effect of REEs, namely, a decrease in the plant growth, development, and yield, via interfering with some physiological, biochemical, and molecular processes [121]. In particular, a decrease in the growth rate of maize (*Z. mays* L.), mung bean (*Vigna radiata* L.), barley (*Hordeum vulgare* L.), and wheat roots has been observed [47, 75, 106, 132]. La, Nd, and Pr inhibit the growth of oat (*A. sativa* L.) coleoptiles [107]. A negative effect on the growth characteristics and a decrease in the parameters of photosynthesis of tomato (*Solanum lycopersicum* L.) seedlings are explained by the ability of lanthanum to boost the formation of reactive oxygen species (ROS), thereby stimulating lipid peroxidation [121].

REEs can influence the physiological activity of plants. In particular, the chlorophyll with lanthanum and cerium instead of magnesium was observed in ferns; this chlorophyll variant is able to partially or completely replace normal chlorophyll in the correspondingly reactions. As is assumed, this has a favorable effect on the activity of photosynthesis [94]. It is shown that the corresponding REE concentrations can increase the rate of photosynthesis in the peanut (*Arachis hypogaea* L.) plants [51]. The REE-assisted increase in plant photosynthetic activity is explainable with an increase in the enzyme activity, development of chloroplasts, and growth in the chlorophyll concentration in plants.

Different mechanisms underlying the interaction of lanthanides with plants determine the changes in the plant elemental composition. REEs can regulate plant growth by altering the uptake of mineral nutrients [73]. Close solubility values of iron and lanthanum phosphates determine the competition of ions and the effect of lanthanum on the content of iron and phosphorus in plant tissues [37, 131]. The replacement of calcium with a REE, which is determined by close ionic radii, may lead to the deficiency in this necessary element [76]. The stimulation of K, Ca, and Mn uptake induced with small doses of La (6.9 and 13.9 mg/kg) was observed for rice (*O. sativa* L.). However, an increase in the La dose to 69.4 and 138.9 mg/kg reduced the accumulation of these nutrients [96]. A decrease in the Fe and Cu contents in the roots and shoots of the soybean (*Glycine max* (L.) Merrill) and Zn content in its shoots, associated with a decrease in photosynthetic activity and biomass, was observed starting from the La concentration in solution of 2.8 mg/L [45]. The authors also report an increase in the concentrations of Mg and P in plants, which presumably explains the preservation of the chlorophyll content with an increase in the dose of La since Mg is a structural component of the photosynthetic pigment and P is necessary for production of ATP (adenosine triphosphate), the source of energy for the metabolic processes, including biosynthesis of chlorophyll. REEs increase the rate of nitrogen transition from an inorganic to organic form, which has a positive effect

on the protein synthesis and regulation of nutrient balance [104].

Numerous studies assess the effect of lanthanides on different plant species. The main object of these studies is a solution–plant system, when plants are grown using solutions of REE salts or nutrient media. The studies utilizing artificial mixtures or directly soils are considerably fewer. In the experiments with La- and Nd-containing nutrient media, the 50% inhibitory concentration (IC50) for the roots of the bok choy cabbage (*B. chinensis* L.) and sunflower (*H. annuus* L.) roots was assessed as 139 and 188 mg/kg for La and 222 and 258 mg/kg for Nd, respectively [114]. The authors compare these data to the REE concentrations in the soils of Australia, Germany, and Japan, amounting to 105, 305, and 98 mg/kg, respectively. Thus, the concentrations in soil are comparable to the observed range of inhibitory concentrations for the tested species. However, the metals in soil solution can be in other chemical forms, which will alter the response of the test objects.

When testing soils, most of the positive effects are observed at the applied REE doses in available forms below 10 mg/kg [49]. However, REEs in these studies are used as nitrates, which interfere with assessing the particular effect of lanthanides since nitrates also have a positive effect on the plant growth [61].

Thus, the data on the REE effects on plants contain many contradictions. Some contradictions are mainly determined by the difference in the REE concentrations used for testing as well as by individual responses of test objects and differences in the effects manifested at different developmental stages. It is clear that the revealing of the threshold between the potential positive effects of REE low doses, their hormesis effect, and negative impact of increased concentrations remains a relevant challenge. Note that it is necessary to control the changes taking place in the organisms at the cellular and biochemical levels since the reactions at macrolevel can be delayed as compared with the changes at microlevel, or can result from the negative effects unnoticeable without application of the corresponding methods.

THE EFFECT OF LANTHANIDES ON PLANT CELL DIVISION

A few studies on the REE activity towards plant cell division and the existing contradictions in the corresponding data prevent from any unambiguous inferences on the effects of lanthanides on these processes. The first attempts to estimate the effects of various metals on cell division using an *Allium* test demonstrated the ability of La and Ce to decrease the cell proliferation and cause aberrations [42, 87]. Wang et al. [134, 135] described the lanthanum-induced DNA lesions in *Vicia faba* L. seedlings, which together with the unbalance of nutrient elements in plants were

likely reasons of the root growth retardation. A study of the effect of praseodymium and neodymium on bean seedlings demonstrates a clastogenic effect (formation of chromosome breaks), leading to serious disturbances of the cell cycle, including induction of micronuclei [76]. A considerable increase in the number of micronuclei was later observed in the maize roots exposed to REE nitrates [75]. A statistically significant mitotoxic effect (a decrease in the cell division activity) was observed in three plant species physiologically distinct from one another: wheat (*T. durum* Desf.), garlic (*Allium sativum* L.), and pea (*Pisum sativum* L.) [12, 44, 148]. In addition, the inhibition of cell growth resulting from spindle misorientation after exposure to REEs was observed in experiments with animals [37].

Note that a stimulatory effect of REEs is observable in a narrow range of low concentrations. The stimulatory effect of low lanthanide concentrations on the root growth, presumably associated with cell division activity, was repeatedly described [52, 90, 124, 134, 147]. This may be determined by a hormetic effect, observed at low concentrations of lanthanides [102]. In particular, addition of low lanthanum concentrations (2.8–22.2 mg/L) to nutrient solutions activates the proliferation of soybean (*G. max* L.) root tip cells, which is most likely a hormetic effect [45]. Concurrently, the authors report an increase in the proportion of the cells with mitotic abnormalities. An increase in the number of dividing cells was observed in *V. faba* at a holmium concentration in solution of <4 mg/L; however, an increase in the concentration induced cytotoxic and genotoxic effects (an increase in the number of cells with chromosome aberrations) [109]. The further increase in REE concentration in solution decreased the rate of cell division. Note here that a growth in plant weight shown in several studies is explainable with formation of polyploid cells [112].

Acting as a Ca^{2+} channel blocker, La controls the ROS level in plant cells. Note that part of researchers explain a negative effect of lanthanides on the cell by their ability to increase ROS generation. The excess ROS production caused by an abiotic stress induces lipid peroxidation and damage of macromolecules (for example, DNA) leading even to cell death [32]. This is confirmed by Siddiqui et al. [121], who report an overproduction of ROS as well as an increase in the malondialdehyde accumulation and the activity of an H_2O_2 -producing enzyme, glucose oxidase (GOx), in the cells of tomato (*S. lycopersicum* L.) seedlings effected by lanthanum. Since malondialdehyde is the final product of plasma peroxidation, it is regarded as a marker of the lipid peroxidation induced by the stress impact of heavy metals [148]. Note that the excess of generated ROS is able to directly influence the chromosome structure and the function of cell mitotic apparatus, testable by an increase in the rate of mitotic abnormalities and chromosome aberrations. This correlation has been proved for the factors of a radiation

nature when analyzing the mechanism of indirect effect of radiation and the specific features in the effect of low ionizing radiation on cells [19].

The manifestation of cytotoxic effects during mitosis is explained by the changes at the early stages of the cell cycle, taking place in the interphase before the beginning of mitosis. For example, this can be associated with the inhibition of DNA synthesis in S phase of cell cycle or its disturbance in G2 phase [119]. La^{3+} was shown to arrest the cell cycle progression at G1/S and S/G2 of interphase (cell cycle checkpoints), which can be a mechanism underlying the inhibition of root growth [134, 135].

Entering the cell, lanthanum can alter the structure of microtubules [97]. At a high concentration, this can arrest the growth of root cells and, on the contrary, can stabilize cytoskeleton at low concentrations.

Numerous studies report a dose-dependent decrease in the plant root growth caused by various stress factors; however, the mechanism of this phenomenon remains vague. It is well established that a steady growth of roots is regulated by a combination of the cell division activity in the meristematic zone and subsequent cell elongation in the growth zone [120]. The available research data suggest that the toxicity of lanthanides for plant roots is mainly determined by the disturbed cell proliferation since the root growth activity usually decreases in parallel with the mitotic activity in apical meristem. As a rule, the decrease in mitotic index correlates with an increase in the number of cells carrying various mitotic abnormalities, i.e., the cell cycle abnormalities particularly lead to a decrease in proliferative activity [44, 108]. An analogous correlation was observed when studying the effect of cerium solution on the root tip cells of garlic (*A. sativum* L.) [148]. The researchers who have shown the ability of lanthanum to enter the root meristematic cells and interact with the nuclear components also explain the arrest of root growth with the inhibition of cell division rather than of cell extension [132]. A similar correlation between the macro and micro characteristics of toxicity (changes in the root growth activity, mitotic activity, and the number of cells with mitotic abnormalities) is usually observable in the soils polluted with heavy metals [116]. Note that such regular correlations between the root growth and mitotic activity may be characteristic only of a short exposure time. In particular, the absence of correlation between the mitotic activity of the apical meristem of *V. faba* L. seedlings exposed to La^{3+} for 15 days and the root length was demonstrated [134].

Anyhow, the mechanism underlying the effect of lanthanides on cell structures and mitotic cycle remains vague. In particular, along with a negative effect of REEs on mitotic activity and the share of cells with various abnormalities, lanthanum at a low concentration (1.4 mg/L) displays the ability to prevent

the salt stress–induced programmed cell death in the rice root tips [90].

The inconsistency of the available data on the effect of REEs on the mitotic apparatus of cell is also explainable with a species-specific response of test objects. The effects of this kind have been earlier observed using other tested substances, for example, wastes of aluminum industry, when a plant species (*Allium cepa* L.) responds to the impact by an increased cell division activity, whereas an opposite response is observed for another species (*Lactuca sativa* L.) [122]. This demonstrates the need to employ different test systems so that their wide range would be able to the fullest extent reflect the effect of tested substance on organisms.

A study conducted in the Orenburg oblast (Russia) demonstrates a direct correlation between the frequencies of chromosome aberrations assessed using an *Allium* test and the REE load factor for water bodies and water flows [26]. However, these results fail to prove that the REE content is the particular factor that determines the mutagenicity of the tested bottom sediments since they could well be contaminated with other toxicants omitted in that study.

The earlier mentioned manifestations of the oxidative stress caused by the impact of lanthanides on cells (including an increase in the ROS content, lipid peroxidation, and decrease or increase in catalase, superoxide dismutase, and other enzyme activities) can be involved in the processes leading to cytogenetic effects [102]. Xu et al. [148] believe that Ce^{4+} at a high concentration damages the spindle and thus causes chromosome sticking, fragmentation, bridges, and lagging in the *A. sativum* root tips, observed when testing cerium solutions [148]. The chromosome sticking in mitosis is usually explained by the effect on histones (nuclear proteins) and tangling of chromatin fibers [31, 83]. This can further lead to other chromosome abnormalities, such as irregular chromosome segregation, chromosome bridges, fragmentation, star-like chromosome structures, and eventual cell death. An abnormal (disintegrated) metaphase usually results from the negative alterations of the spindle apparatus [110].

An increase in the number of cells with a C-metaphase in the soybean roots was observed after testing the La solution with a low concentration (2.8 mg/L) [45]. During the so-called C-mitosis, the cell division is arrested in metaphase as a result of spindle inactivation (presumably, because of tubulin acetylation), which is characteristic of the effect of colchicine or an analogous mitotic poison. C-mitosis is accompanied by disassembly of microtubules of the mitotic apparatus, delayed kinetochore segregation, and overcontracted chromosomes [83]. Depending on the degree of the damage to the mitotic apparatus in C-mitosis, the following events are observable: chromosome scattering, sticking, ball-like metaphase, and metaphase with two groups of chromosomes (pseudo-anaphase).

During the C-metaphase, chromosomes become shorter and more condensed as compared with a normal mitosis. The impaired spindle formation delays the cell division in metaphase (to 4–5 days) [33]. The outcome of a C-mitosis differs depending on the degree of damage of the cellular structures, namely, cell death, formation of a single polyploid nucleus (i.e., chromosomes are divided into daughter chromatids but remain in the same nucleus), or several micronuclei with different numbers of chromosomes; however, restoration of the mitotic apparatus and a normal outcome are also possible.

CONCLUSIONS

During the last decades, lanthanides have gained great importance in human economic activity. An increase in their concentration in environment is inevitable and, thus, requires the effects of REEs on ecosystems and their components to be assessed and their permissible concentrations in soil and agricultural products and the doses of consumption to be determined. Presumably, the main challenge is to find the boundary between the low REE concentrations, which potentially have positive hormetic effects (or which are at least safe), and the higher concentrations, potentially causing negative toxic effects. Note that the threshold concentration of the effect positive in terms of agricultural plants must not have any genotoxic effect at the cellular level.

All studies of the REE genotoxicity considered in the last section of the review used solutions containing lanthanides at different concentrations. However, it is necessary to take into account that soils have a buffer capacity and are able to alter the toxicity of applied substances [56]. The practice of standardization of the heavy metals and several other pollutants in soil demonstrates that their total content cannot be the only characteristic allowing their behavior and effect on living organisms to be estimated. The bioavailability of pollution components must be taken into account as well as their dynamics in soil [103]. Some researchers assert that the direct toxicity of soils, which can influence the substances that entered there, can be higher or lower than the toxicity of the corresponding soil extracts. Frequently, these extracts fail to reflect the actual degree of soil toxicity under natural conditions [22]. The dependence of bioavailability on chemical and physical soil properties has been demonstrated for many elements, lanthanides included [92, 152]. Thus, further studies must include testing of several soil types differing in the consequences of REE application. The chemical forms of lanthanides in soils and types of their binding by the soil components sorbing/desorbing REEs are insufficiently studied and require closer attention. It has been shown that the composition and properties of the host medium considerably influence the mobility, bioavailability, and toxicity of lanthanides. Note that the REEs signifi-

cantly differ in the dependence of their toxicity on their chemical characteristics as well as the presence or absence of ligands. The translocation and distribution of REEs in individual parts of the plant organism require separate attention; this issue is important not only for characterization the putative mechanisms of their biological effect, but also for assessing the quality of the corresponding plant products. The data on the coefficients of REE biological accumulation are almost absent in the literature. A comparative analysis of the information about the heavy metal compounds and mobility in soil is a useful tool for this purpose. In addition, lanthanides have radioactive isotopes, some of them being fission products. A considerable dataset obtained by radioecological studies of the soil compounds containing fission products and the quantitative characteristics of their transition to the aboveground plant parts may be used for analysis and prediction of the behavior of stable lanthanide isotopes.

Standardized biotesting procedures are a convenient tool allowing the results of different studies on the forms of REE toxicity to be compared. An important advantage of such methods is the possibility of testing in the soil–plant system. The sensitivity of biotesting makes it possible to detect genotoxicity of the soils with a low REE content, whereas the traditional pollution indicators, such as the concentration of heavy metals, in this case may fail to show any ecological risk [80].

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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