



A systematic review and meta-analysis on the root effects and toxic mechanisms of rare earth elements

Chenyi He^a, Yiping Feng^{a,*}, Yirong Deng^{a,b,**}, Longyong Lin^b, Sheng Cheng^b

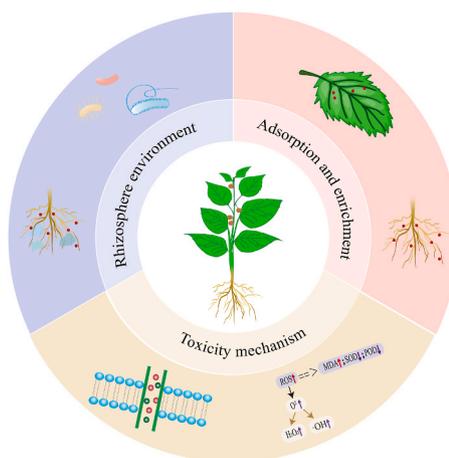
^a Guangdong Key Laboratory of Environmental Catalysis and Health Risk Control, School of Environmental Science and Engineering, Institute of Environmental Health and Pollution Control, Guangdong University of Technology, Guangzhou, 510006, China

^b Guangdong-Hong Kong-Macau, Joint Laboratory of Collaborative Innovation for Environmental Quality, Guangdong Laboratory of Soil Pollution Fate and Risk Management in Earth's Critical Zone, Guangdong Provincial Academy of Environmental Science, Guangzhou, 510045, China

HIGHLIGHTS

- REEs mainly accumulate in roots with LREEs easily moving into above-ground plants.
- Stimulated by REEs, the composition and exudation of root secretions can be altered.
- REEs affect root cell function by displacing Ca^{2+} and inducing ROS.
- Interactions between root secretions, microbes, and REEs influence plant growth.
- Meta-Analysis reveals the diverse mechanisms of REEs-induced phytotoxicity.

GRAPHICAL ABSTRACT



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ABSTRACT

Rare earth elements (REEs) have attracted much attention because of their unique physical and chemical properties. The root system is the plant organ most directly in contact with REEs, and it is critical to understand the mechanisms of interaction between the two. This paper investigates the effects of REEs on plant enrichment and fractionation, as well as on various developmental and toxicity indices of the root system. REEs are more likely to be deposited on the root surface under the influence of root secretion. The complexation between the two affects the uptake and fractionation of REEs and the altered pattern of root secretion. The toxicity mechanisms of REEs on plant root cells were lied in: (1) REEs generate reactive oxygen species after entering the plant, leading to oxidative stress and damage to plant cells; (2) REEs with higher charge-to-volume ratios compete for organic ligands with or displace Ca^{2+} , further disrupting the normal function of plant root cells. It was shown

* Corresponding author.

** Corresponding author. Guangdong Key Laboratory of Environmental Catalysis and Health Risk Control, School of Environmental Science and Engineering, Institute of Environmental Health and Pollution Control, Guangdong University of Technology, Guangzhou, 510006, China.

E-mail addresses: ypfeng@gdut.edu.cn (Y. Feng), ecoyrdeng@163.com (Y. Deng).

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that the sensitivity of inter-root microorganisms to REEs varied depending on the content and physicochemical properties of REEs. The paper also concluded with a meta-analysis of phytotoxicity induced by REEs, which showed that REEs affect plant physiological parameters. REEs, as a source of oxidative stress, triggered lipid peroxidation damage in plants and enhanced the activity of antioxidant enzymes, thus revealing the significant toxicity of REEs to plants. The phytotoxic effects of REEs increased with time and concentration. These results help to elucidate the ecotoxicology of rare earth-induced phytotoxicity.

1. Introduction

Rare earth elements (REEs) are a group of 15 lanthanides, together with yttrium and scandium. In nature, REEs exist as silicates, carbonates, phosphates, oxides, and halogen compounds (Tyler, 2004; Jaireth et al., 2014). There are approximately 270 minerals known to contain REEs (Rydel and Nowak, 2015). The unique and diverse chemical, magnetic, and luminescent properties of REEs make them important in many high-tech industries. REEs are frequently used in electronics, chemical engineering, renewable energy, medical applications, and agricultural fields (Syrvatka et al., 2022). As a non-renewable mineral resource of strategic importance, REEs have attracted widespread attention.

In the process of mining, REEs will enter the plant from the root system or foliage through soil migration, absorption, atmospheric deposition, and other ways, and will be enriched in the plant body. REEs are also used as fertilizers in agriculture to promote germination, root growth and development, chlorophyll content, and plant resistance in planted crops. It was found that the plant effects of REEs are concentration-dependent. Suitable concentrations of REEs can promote plant seed germination and root development, but high concentrations of REEs exposure would inhibit plant growth and development, and even lead to plant death (Yin et al., 2021). In general, soluble REEs compounds, including REEs chlorides, nitrates, and sulphates, are the main phytotoxic groups (Kovářiková et al., 2019).

REEs mining has significantly increased ecological pollution, especially in areas rich in REEs resources. Some of the REEs may enter into plants through root uptake or leaf deposition, posing a risk to plant growth and development, and ultimately enter into human bodies through the accumulation of the food chain, posing a potential threat to the survival and health of human beings. In this study, the effects of REEs on plant growth, physiological functions, and root effects were investigated, and the toxicity mechanism of REEs on plants was summarized to provide useful information for future in-depth studies on the effects of REEs on plants.

2. Distribution and toxicity of REEs in plants

2.1. REEs into the plant

Atmospheric REEs are enriched in the surface layer of plant leaf tissue by deposition. When the size of the nano-REEs particles is smaller than the stomatal pathways, they can penetrate plant leaves through the stomatal channels or the epidermal cuticle, and subsequently be enriched and distributed within the plant. Specifically, when the size of REE particles is less than 1.1 μm , they can effectively penetrate the surface of plant leaves through these pathways, allowing for their enrichment and distribution throughout the plant body (Birbaum et al., 2010; Zhang et al., 2011). When the particle size of REEs particles is small enough, they even penetrate the cell membrane directly into the plant without damaging the plant cells. These REEs particles enter the cell through endocytosis or other transport systems and accumulate in the tissues (Palocci et al., 2017).

Plants draw nutrients from their environment through their root systems and use them for growth. Rare earth particles are deposited in the soil, adsorbed onto the surface of the root system, and enter the root system through the active meristematic tissues at the root tip

(Gottschalk et al., 2009; Cox et al., 2016). These tissues are characterized by high cell division and high pore space, which facilitates the entry of REEs into the body (Fellows et al., 2003). REEs bioavailability is affected by plant type, with ferns accumulating much higher concentrations of REEs compared to other plant types (Tyler, 2004). The chondritic normalized REEs patterns in some plants relative to the host soil revealed obvious fractionation. For example, *Citrus reticulata* and *Brassica campestris* showed HREE depletion; *Camellia sinensis*, *Camellia oleifera*, and *Ziziphus* showed HREE enrichment; and *Gardenia jasminoides* showed positive Ce anomalies (Wang et al., 1997). Additionally, there are differences in the enrichment of REEs among different parts of the plant (Zhang et al., 2002). In the natural soil, the enrichment of REEs in the plant showed a general pattern of roots > leaves > stems > flowers > fruits > seeds (Miekeley et al., 1994). While in the mining plants, the enrichment of REEs in leaves was significantly higher, while the enrichment of REEs in roots and stems was relatively lower (Mardiyah et al., 2023).

2.2. REEs enrichment and fractionation by plants

There was a tendency for mild enrichment of REEs during transfer from soil solution to the root system, and the accumulation of REEs in root tissues was positively correlated with the amount of exposure (Liu et al., 2023). In contrast, the exposure concentration of REEs in the soil had no significant effect on the amount of REEs transferred to the aboveground part (Barbera et al., 2021). The transfer of REEs from subsurface to aboveground tissues is not related to geochemistry or mining environments, but simply reflects differences in plant types (Forsyth et al., 2023). Plant type had a significant effect on the TF of total REEs and light rare earth (LREE), but not on medium rare earth (MREE) and heavy rare earth (HREE). As shown in Fig. S1, because most plants have a greater affinity for LREE and pore water chemistry limits available HREE (Brioschi et al., 2013), LREE tends to be more enriched in plant aboveground tissues than MREE and HREE (LIANG et al., 2008; Gonzalez et al., 2014). Differences in plant physiology led to variability in REEs uptake. In situ recrystallization of Si in ferns would allow substitution of MREE and HREE, whereas LREE has a larger ionic radius is more mobile and can be transported upward to reach aboveground tissues (Fu et al., 1998). Elevated MREE in plant tissues suggests that the dissolved REEs pool plays a more important role than soil mineral REEs (Forsyth et al., 2023). Significant REEs fractionation was observed in the wheat root system, characterized by relative MREE enrichment and slight M-type tetrad effect-like features (Ding et al., 2005). The degree of fractionation between LREE and HREE may reflect the amount of ligand in the xylem solution (Fu et al., 2001). Phosphorus atoms in the environment act as favorable ligands for REEs binding (Feng et al., 2024). Thus, phosphate precipitation is a crucial factor in controlling the accumulation and fractionation of REEs in the root system, potentially altering the characteristics of the normalized REEs pattern in plants (Pourret et al., 2022).

REEs speciation dominates the uptake and fractionation of REEs by plant roots. LREE are more easily enriched in plants, and the accumulation of REEs in plants is positively correlated with the concentration of REEs in the environment. As confirmed in the study, the bioaccumulation of REEs in radishes increased as the exposure concentration of REEs increased (Tagami and Uchida, 2006). REEs will also prevent their further diffusion in the plant body, e.g., through

precipitation or aggregation. For example, when CeO₂ penetrates the roots, it will precipitate or aggregate in the cell wall network, limiting its further translocation and accumulation (Ebbs et al., 2016). In addition, the enrichment degree of different REEs in different tissues of the plant body varies, as listed in Table 1.

The effects of REEs on plant growth show a dose-effect and a time-effect. It is generally recognized that REEs can promote plant growth at low concentrations, while inhibit plant growth under high concentrations exposure. REEs can regulate plant growth by affecting the content of mineral elements such as potassium, calcium, magnesium, and iron (Hu et al., 2002). At low concentrations of REEs doses, seed germination, and biomass increase. Conversely, at high concentrations, plant chlorophyll content, soluble proteins, and photosynthetic activity decrease (Liu et al., 2012). For example, low concentrations of Ce³⁺ improved the formation of PSII and increased the electron transport rate of PSII, indirectly contributing to the biosynthesis of chlorophyll. However, at high concentrations, Ce³⁺ led to the inhibition of PSII (Hong et al., 2002). REEs can also replace calcium (Ca²⁺) in intracellular enzymes, participate in enzymatic reactions, and interfere with metabolism. Appropriate concentrations of REEs improve plant resistance and reduce the toxicity of abiotic stress factors by supporting cellular defense mechanisms (Liu et al., 2013).

The duration of exposure to REEs was positively correlated with the content of REE³⁺ in plant cells. Long-term exposure to REEs may have different effects on plant growth compared to short-term exposure. For example, under La exposure at a concentration of 30 mg/kg, rice height was slightly promoted after a short-term exposure of 30 days, while exhibited an inhibitory effect when the duration was extended to 80 days (Zeng et al., 2006). The effects on plant physiological indicators and the degree of oxidative stress damage varied with the duration of exposure. Continuous exposure of maize to 25 mg/kg of CeCl₃ did not significantly affect antioxidant enzyme activities and MDA content in roots and leaves at day 28, whereas at day 90, CeCl₃ disturbed the homeostasis of the plant antioxidant system, causing significant oxidative damage in the roots and a notable increase in MDA levels (Dong et al., 2021).

With prolonged REEs exposure, the percentage of unsaturated fatty acid increases, which enhances the interaction between membrane lipid molecules, reduces the fluidity of the membrane, and ultimately destroys the function of the membrane. This also decreases the number of proteins in the plasma membrane, causing protein size reduction and deformation, which leads to abnormalities in nutrient element transport, signaling, and material metabolism (Yang et al., 2015). On the other hand, plants may develop adaptive mechanisms to counteract the negative effects of REEs in the later stages of growth. For example, maize stressed by CeO₂ NPs up-regulated the expression of Heat Shock Protein 70 to maintain membrane integrity (Zhao et al., 2012).

The physiological and toxicological effects of different REEs on some plants are summarized and listed in Table S1 and Table S2. It should be noted that the effects of REEs on plants varied considerably in different studies due to a number of factors such as the form of the REEs, the exposure concentrations, the environmental conditions in which the plants were growing and the ability of the plants themselves to adapt to the toxic effects (Zadokar et al., 2023). The effects and accumulation patterns of REEs on plants varied considerably in terms of size and chemical form. Ce³⁺ and CeO₂ NPs resulted in a significant increase in electrolyte leakage from radish root cells, whereas root leakage from bulk cerium treatment was not significantly different from that of the control group, and cumulative evapotranspiration from radish stressed with Ce³⁺ was significantly lower than that from the other treatment groups (Zhang et al., 2015). The toxicity of REEs acting on plants is primarily due to REO NPs or dissolved REE³⁺. Many studies have shown that the toxicity of REO NPs is positively correlated with the release of REE³⁺. For example, CeO₂ NPs can be converted to Ce³⁺ on the root surface of cucumber, either in soil or hydroponic environments, causing damage to the plant (Ma et al., 2015a, 2015b). The smaller the size of the

Table 1
Enrichment of REEs in different tissues of plants.

REEs	Plant	Exposure Method	Exposure results	Reference
La	Sunflower	Hydroponics	Roots: 875 µg/g; shoots: 41 µg/g when exposed to 5 µmol/L La.	Dridi et al. (2022)
	Nightshade	Foliar spraying	Exposure to 10 µmol/L and 200 µmol/L of La ³⁺ resulted in the enrichment of leaves > stems > roots > fruits in plants.	He et al. (2023)
	Lettuce	Hydroponics	Exposure to 1 µg/mL of La resulted in a 38-fold higher accumulation of La in roots than in leaf segments on day 1; the difference between roots and leaf segments was the greatest on day 2, with the highest lanthanum concentration of 0.272 µg/kg in roots and 0.0124 µg/kg in leaves.	Nazreen et al. (2017)
Ce	Sunflower	Hydroponics	Roots: 2187.5 µg/g; shoots: 31.5 µg/g when exposed to 5 µmol/L Ce.	Dridi et al. (2022)
	Spinach	Soil spray culture	The distribution pattern of REEs in spinach treated with 5 µg/mL Ce ³⁺ was leaf > root > shoot; the content of LREE was higher than that of HREE in spinach.	Hong et al. (2002)
	<i>Arabidopsis thaliana</i>	AGAR medium	There were no significant differences in root and stem Ce concentrations of CeO ₂ -NPs or CeO ₂ -bulk when exposed at concentrations lower than 500 mg/L. When exposed to 3000 mg/L, Ce concentrations in plants with CeO ₂ -NPs (Roots: 4532 mg/kg, stems: 207.7 mg/kg) were about 4.5 times higher than those in plants exposed to CeO ₂ -bulk.	Yang et al. (2017)
	Soya bean	Hydroponics	When exposed to 0.01 g/L–0.5 g/L CeO ₂ NPs, Ce content in root system increased from 389.63 mg/kg to 1302.27 mg/kg with the increase of NPs concentration. In branches, Ce content increased from 79.78 mg/kg to 404.83 mg/kg.	Li et al. (2020)
	Radish	Soil culture	The treatments of 50 mg/kg and 100 mg/kg CeO ₂ NPs significantly increased the Ce content in roots, while the increase in Ce content in leaves was not significant. CeO ₂ NPs were mainly	Gui et al. (2017)

(continued on next page)

Table 1 (continued)

REEs	Plant	Exposure Method	Exposure results	Reference
Pr	Corn	Soil culture	absorbed by roots, and roots were more significantly affected than leaves. Roots > Stems > Leaves.	Dong et al. (2021)
	Winter wheat	Soil culture	Pr concentration in the root system was much higher than in the branches. accumulation in the root system and aboveground increased at low fertilizer concentration levels of 0 mg/kg to 10 mg/kg soil and remained constant at higher concentrations. The concentration of Pr in the root system was much higher than that in the branches. The distribution of Sm in plants is root > shoot > leaf.	Zhang and Shan (2001)
Sm	Peanut	Hydroponics	The mean root-shoot transfer factor of 364.81 mg/kg Sm ranged from 0.6% to 2.9%.	Emmanuel et al. (2010)
	Alfalfa	Soil culture	Most of the Gd accumulated in the roots, and the average uptake of Gd by the root system was 30–100 times higher than that of the stem. At any given dose, the concentration of Dy was always higher in roots than in stems. Bauhinia stems contained higher levels of Dy than roots when exposed to soil at a concentration of 1.20 mg/kg.	Hu et al. (2022)
Gd	<i>Arabidopsis thaliana</i>	Hydroponics	Er was enriched in radish and tomato to the extent of root > stem.	Liu et al. (2021c)
Dy	Radish, tomato	Soil culture	The highest concentration of REEs was found in the roots. Concentrations of REEs in field-grown maize were root >> leaf > stem > grain.	Carpenter et al. (2015)
	Chinese redbud	Soil culture	Y concentrations and transfer factors were highest in roots and lowest in leaves at concentrations of 10 ⁻³ mol/L and 10 mol/L. Under 10 ⁻³ mol/L Y exposure, the concentration of Y was 44.4 mg/kg in roots, 8.24 mg/kg in stems, and 5.5 mg/kg in the second leaves. Compared with the stems, the concentration of Y and	Carpenter et al. (2015)
Er	Radish, tomato	Soil culture		Carpenter et al. (2015)
Yb	cucumber	Hydroponics		Zhang et al. (2012)
Se	Corn	Soil culture		Xu et al. (2002)
Y	Sunflower	Hydroponics		Maksimović et al. (2012)
	Corn	Hydroponics		Maksimovic et al. (2014)

Table 1 (continued)

REEs	Plant	Exposure Method	Exposure results	Reference
REEs	cottonwood	Soil under natural strips	the rate of Y accumulation were significantly higher in roots. Y concentration and accumulation rate were significantly higher in roots compared with that in stems, indicating that Y uptake by roots was much more intense than Y transport to other parts of the plant.	Fu et al. (2001)
	citrus	Soil under natural strips	Leaf blade > Main root > Trunk > Pericarp > Pulp > Seed > Juice	Turra et al. (2013)

REO NPs the more readily they can be taken up by plants (Zhang et al., 2011), affecting the uptake of minerals and interfering with some of the ion-transporting protein through the released REE³⁺ (Dong et al., 2021).

The bioavailability of REEs to plants is a critical issue in REEs phytotoxicity evaluation. The primary factors influencing the bioavailability of REEs to plants are soil properties and plant uptake capacity. The bioavailability of REO NPs in soil is significantly lower than in aqueous environments. REO NPs tend to adsorb onto soil components with high specific surface areas and abundant charged sites, such as clay and organic matter (Ma et al., 2020). The mobility and bioavailability of REE³⁺ in soil increase at lower pH, CEC, and redox potential levels (Thomas et al., 2014). Additionally, other substances in plants can affect REEs bioavailability through mechanisms such as antagonism and/or synergism. For example, REE³⁺ and Ca²⁺ have similar chemical properties, will compete for the same binding sites, affecting plant physiology. Furthermore, REE³⁺ can form precipitates with phosphate, limiting their further translocation.

It was found that total ascorbic acid (ASC) content increased in La³⁺-treated wheat, whereas treatment with a mixture of LREE induced an increase in root ASC content only (d'Aquino et al., 2009). Current studies have focused on assessing the potential toxicological effects of single REEs rather than their mixtures. Contamination by REEs mixtures is more prevalent in natural environments, and neglecting the effects of multi-element mixture interactions and subsequent plant bioavailability can lead to an underestimation of environmental risks. Rare earth ions may compete with each other for binding to biologically active sites, making it unlikely that mixture components will have identical or independent modes of action. The toxicity of REEs mixture (additive, antagonistic, or synergistic) varies across different dosage metrics of REEs mixtures (e.g., total dissolved metal concentration and free metal activity) in hydroponic environments. For example, based on dissolved concentration, Y–La and La–Ce mixtures have additive effects, and Y–Ce mixtures have antagonistic interactions, whereas on the basis of free ionic activity, antagonistic interactions are present in all three groups and the magnitude follows a descending order: Y–Ce > Y–La > La–Ce (Gong et al., 2019). The strength of antagonism in REE mixtures may be related to the metal-ion softness index Δσ values between the two metal ions (Ownby and Newman, 2003). In more complex soil environments, the interaction pattern of mixtures varies with dose descriptors and soil type. Additionally, the toxicity and interaction of REEs mixtures are time-dependent processes, with interactions potentially shifting with increasing exposure time (Gong et al., 2021).

3. Effects of REEs on plant roots

3.1. Root absorption

It has been demonstrated that iron is closely associated with the accumulation of REEs in plants. Plants employ strategies to acquire iron, primarily categorized into strategy I (release of low molecular weight organic acids, LMWOAs) and strategy II (release of phytosiderophores), with some plants capable of employing both strategies simultaneously. Strategy I is typically associated with non-gramineous monocotyledons and dicotyledons, whereas strategy II is predominantly utilized by gramineous plants (Li et al., 2023). LMWOAs have been shown to stimulate the uptake of REEs by the root system, with an increasing effect observed over time, thereby influencing REE bioavailability (Wang et al., 2004). Additionally, LMWOAs synergized with natural organic matter to enhance soil Fe bioavailability and facilitate the release surface-adsorbed and structure-bound REEs from hydrotalcite in the soil environment (Wang et al., 2015). Strategy II involves the production and release of the organic compound phytosiderophores (PS), which serve as naturally-occurring metal chelators that selectively bind iron and form organometallic complexes (Li et al., 2023). Biosynthesis and release of plant phytosiderophores are not impaired in the presence of toxic metals, which positively affect phytosiderophores release. Plant phytosiderophores mediate the uptake of toxic metals (Gupta and Singh, 2017). For instance, phytosiderophores desferrioxamine B (DFOB) significantly increased the mobility of REEs in the soil and the uptake of REEs in *P. arundinacea* branches (Wiche et al., 2017).

The toxicity of REEs is closely related to their morphology, specific organic and inorganic ligands (Martinez et al., 2018). REEs uptake by roots will be not related to the concentration of REEs in the soil. For example, it was found that despite the high concentration of REEs at the root epidermis, the signal intensity was low in the cortical tissues and inside the endodermis, suggesting that REEs bind to the plant root surface (Saatz et al., 2016). Selective uptake of REEs ions (e.g., in the form of trivalent cations) by root cell walls, and co-precipitation of REEs ion salts, generally in the form of insoluble oxalates or phosphates, are the main mechanisms for the fixation of REEs by plant roots (Wang and Liu, 2017). In addition, it was found that the REEs could be tightly bound to the glycoproteins of the maize root system (Yuan et al., 2001). After binding to root surface proteins, the REEs slowly reached the xylem for further translocation (Tagami and Uchida, 2006).

REEs also promoted endocytosis in root cells by enhancing DNA methylation, but the enhancement was affected by time and dose (He et al., 2019). When REEs come into contact with plant roots, the REEs cations combine with free carboxyl groups such as cellulose and pectin on the cell wall, and the positive and negative charges are attracted to each other, leading to selective absorption of rare earth ions by the cell wall (Ding et al., 2005). In addition, intracellular acidity can induce the precipitation of rare earth ions and phosphates, which play a crucial role in REEs fixation in plant roots (Ding et al., 2007). The formation and transfer of ligand complexes is another key mechanism for the fractionation of REEs in plant above-ground organs (LIANG et al., 2008).

REEs are distributed differently in different subcellular parts of the plant after entering the plant. For example, it was found that the content of REEs Y in the cell wall of the root system was positively correlated with the exposure concentration, but the opposite was true for the soluble fraction of the roots and branches (Zheng et al., 2018). It can be seen from the above that REEs are mainly accumulated in plant roots, where the root cell wall is the main deposition site. Plant roots can also limit the upward transport of REEs in order to maintain plant growth and protect various cell organelles.

3.2. Effects on root development

The effects of REEs on plant roots are concentration-dependent (Diatloff et al., 1995). For example, the application of four REEs (La,

Ce, Pr, and Nd) to coconut trees at different concentrations showed that low concentrations of REEs promoted the root growth of coconut trees, but at high concentrations, the uptake of nutrients P and Zn by the root system was reduced, which significantly inhibited the root growth of coconut trees (Wahid et al., 2000). For wheat exposed to La, Ce, and Y, a significant dose-effect relationship was also observed for root elongation (Gong et al., 2019). As shown in Fig. S2, appropriate amounts of REEs can promote root differentiation, improve root vigor and enhance nutrient uptake by the root system. Conversely, they can inhibit the development of the root system and negatively affect the growth and development of the plant (Ling et al., 1998).

Rare earth oxide nanoparticles (REO NPs) can also significantly affect root biomass and root morphology (López-Moreno et al., 2016). The effects on root growth varied widely among different REO NPs and plant species. Although REO NPs could not penetrate the seed coat and had little effect on seed germination, they significantly inhibited root elongation, which might be related to the size and pore space of the root surface (Ma et al., 2010).

When plants are subjected to stress, reactive oxygen radicals (ROS) act as signaling molecules to induce the production of antioxidants to control processes such as programmed cell death, abiotic stress response, pathogen defense, and systemic immunity (Mittler, 2002). It was found that mild REEs stress induced an increase in the levels of two major antioxidants, ascorbic acid (ASC) and glutathione (GSH), in the roots of wheat, while GSH was decreased in the above-ground parts, and the enzymes catalyzing the recycling reactions of ASC and GSH remained basically unchanged. Lanthanide exposure did not change the catalase (CAT) activity in the roots of the plants, but peroxidase activity in branches decreased slightly (d'Aquino et al., 2009).

Plant roots can secrete or release a variety of carbon-activated substances, and these root secretions play an important role in the networks of plant-soil environment-rhizosphere microorganisms, which helps the plant root system to obtain nutrients from the outside world. Therefore, the changes in their composition can reflect the metabolism, growth, and development of individual plants. Root secretions have a protective effect when plants are subjected to pathogen infection, developmental stages, abiotic and other stresses (Vives-Peris et al., 2020). Meanwhile, root secretions may contain some simple organic acids and amino acids that promote desorption of REEs from the soil and affect the diffusion of REEs from the soil to the root system (Chen et al., 1995).

Root secretions contain a large number of biomolecules and inorganic ions of different molecular weights, including high molecular weight organics like fatty acids and polysaccharides, as well as low molecular weight substances, such as amino acids and organic acids, with variations in their composition and content (Bais et al., 2006). Low molecular weight organic acids secreted by plant roots can form complexes with soil metal ions and affect the adsorption and desorption of soil metal ions. Under the action of low molecular weight organic acids, the adsorption of REEs in soil was inhibited, and the inhibition followed the order of citric acid > malic acid > tartaric acid > acetic acid (Shan et al., 2002). For specific carboxylates (e.g., citrate), the HREE³⁺ complex is more stable than the LREE³⁺ complex (Wiche and Pourret, 2023). Due to the presence of root secretions, REO NPs were more readily deposited or attached to the root surface (Ma et al., 2013). Plant secretions may undergo oxidation-reduction reactions on nanoparticles containing metastable shell layers (Zhang et al., 2017). Root exudate patterns may also be altered to facilitate particle transformation (Dimkpa et al., 2012).

High concentrations of low molecular organic ligands such as citrate, malate and oxalate in the inter-root solution bind to LREE, which may be one of the reasons why LREE are more readily enriched in plants (Ding et al., 2005). Plants in phosphorus deficiency release nonspecific nutrient-mobilizing root secretions (e.g., carboxylates) to mobilize insoluble phosphorus in the soil, and such root secretions also promote the mobilization of REEs in the soil through ligand complexation and H⁺ competition, exacerbating the degree of REEs enrichment in the plant

(Wiche et al., 2016; Pang et al., 2018; Monei et al., 2022). For example, inter-root secretion of acid root exudates in *Pinus americana* under phosphorus-deficient conditions, such as up-regulation of citrate and malate, is utilized in response to phosphorus deficiency (Liu et al., 2021a). REEs accumulate in the root system at the same site as the site of organic acid secretion in the root system, which contributes to the complexation and uptake of REEs in the plant root system (Singh et al., 2016). Citrate is more effective than oxalate and malate in mobilizing REEs in the soil due to its higher stability constants with REEs (Liu et al., 2023). The structure and amount of ligand released by the root or microorganism determines the stability of the complex and the number of competing ions in solution (Wiche and Pourret, 2023).

It was found that the content of REEs in the plant root system was positively correlated with Mn due to the fact that REEs may be taken up by the plant through Mn transport proteins, which is attributed to the inter-root mobilization of root exudates (Liu et al., 2021b; van der Ent et al., 2023). LREE were negatively correlated with root plant Cu, suggesting that root secretions may mobilize LREE and Cu from minerals (Liu et al., 2021a). The relative importance of root secretions and inter-root processes in hyperaccumulation varies for different elements with different plant bioavailability (Liu et al., 2021b), and REEs solubility is highly dependent on pH, so REEs accumulation may be particularly sensitive to inter-root acidification (Pollard, 2023).

3.3. Mechanisms of REEs toxicity to plant roots

The toxicity of REEs to plant root growth arises mainly from REO NPs or dissolved REE³⁺ (Ma et al., 2010). Low doses of REEs are anchored to the plasma membrane in the form of nanoscale particles, activating endocytosis as the concentration of REEs increases (Wang et al., 2014). As a signaling molecule, Ca²⁺ plays a crucial role in the signaling system of plant cells and is involved in almost all physiological and biochemical activities of organisms. A large amount of Ca²⁺ is stored in the plant cell wall as calcium pectate, and the unesterified pectinate carboxyl groups provide many binding sites for metal ions (Lai et al., 2006). Lanthanide ions (Ln³⁺) are similar in size to Ca²⁺ and the trivalent lanthanides have higher charge-to-volume ratios and therefore generally have a higher affinity for a given binding site than Ca²⁺ (Evans, 1983). Ln³⁺ therefore

readily displaces Ca²⁺ and interacts with calcium binding sites.

Ln³⁺ can enter the cell through Ca²⁺ channels in the cell membrane, regulating chlorophyll activity and photosynthetic rate, thus enhancing plant stress tolerance (Sona et al., 2000). For example, exposure of plants to a suitable concentration range of Ce³⁺ increases cell membrane protease activity, controls the entry and exit of ions, and facilitates ions transport (Yuhong et al., 2003). Exposure of CeO₂ nanoparticles to the wire fern resulted in intracellular detection of Ce³⁺, and it was found that CeO₂ nanoparticles led to the undesirable conditions of cell wall cleavage, cell membrane rupture, cytoplasmic leakage, and chloroplast damage (Garay et al., 2016). This is because the radius of Ce³⁺ is similar to that of Ca²⁺, and therefore Ce³⁺ exhibits similar effects on the stability and functionality of the membrane as Ca²⁺ and affects the ion flux into the cell in different ways (Das et al., 1988). For example, La and calmodulin (CaM) form strong interacting ligand bonds, leading to a loose and disordered molecular structure of CaM and thus inhibiting its function. However, low concentrations of La may not be able to coordinate with CaM, but rather interact with the protein through weak intermolecular forces, changing the molecular conformation of CaM (Wang et al., 2016).

As shown in Fig. 1, REEs ions can affect plant physiological functions by replacing or interacting with Ca²⁺. In the initial stage, rare earth ions adsorb on the cell wall, compete with Ca²⁺ for organic ligands or replace Ca²⁺, and enter the cell interior through Ca channels or transporters, thus changing the chemical composition of the cell wall (Shtangeeva and Ayrault, 2007). Even other harmful substances in the environment can be transported into leaf cells through the REE³⁺-initiated CME pathway, causing more severe plasma membrane damage and exacerbating the toxicity to the plant (Cheng et al., 2022). Exposure to REEs not only induces changes in the permeability of cell membranes, but also affects the transcriptional regulation of key biosynthetic genes in plants. After entering the cytoplasm, some REEs can replace Ca²⁺ and membrane lipid macromolecules to form complex cross-linking structures or change the radius of the membrane pores and the membrane conformation, which in turn affects the proton transmembrane gradient and membrane potential.

REEs can also affect proteases and the plasma membrane redox system. The physiological activity of impact proteases is inhibited by

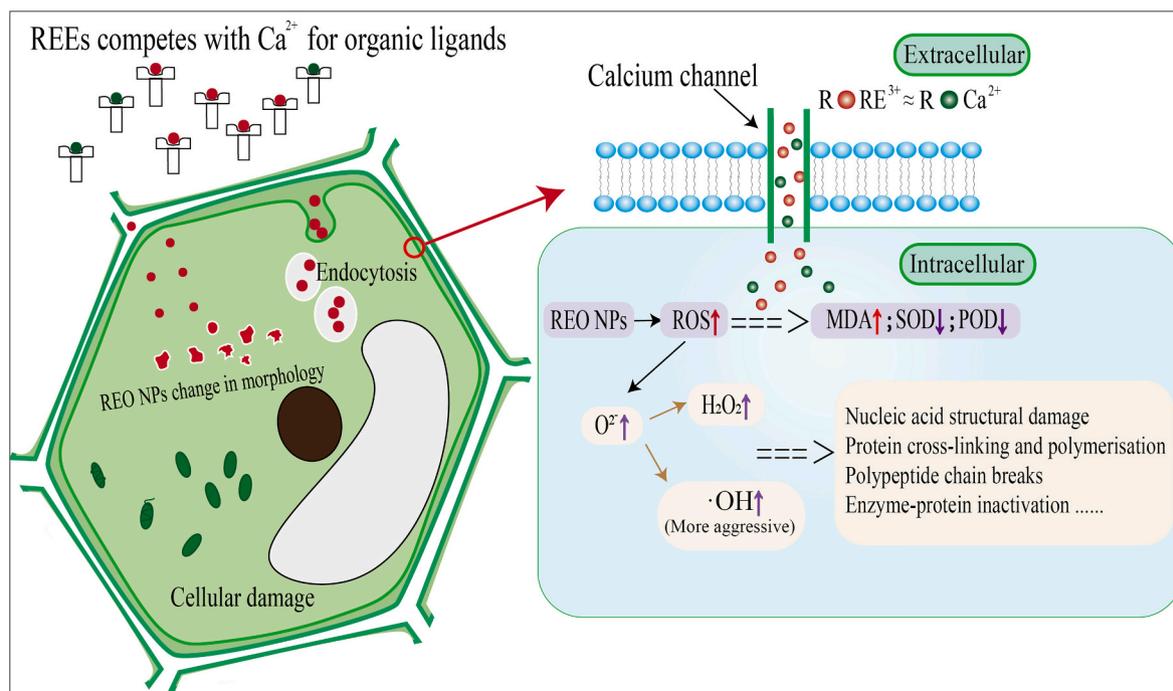


Fig. 1. Possible toxicity mechanisms of REEs to plant root cells.

high concentrations of REEs and affects the uptake of mineral elements required for plant growth (Wang et al., 2008). La^{3+} at high concentrations would complex with vimentin-like proteins (VN) to form La-VN, disrupting their expression at the plasma membrane (Wang et al., 2017). REEs also bind to plant glycoproteins. For example, Tb (III) binds to a receptor on the cytoplasmic membrane [fasiclin-like arabinogalactan protein 17 (FLA17)], which then docks to an intracellular artichoke [artichoke 2 (AP2)] to form a triplex [Tb (III)-FLA17-AP2], which ultimately initiates the intracellular CME pathway, leading to their accumulation in leaf cells (Cheng et al., 2022). In the cystoid membranes of plant chloroplasts, trivalent lanthanide cations are adsorbed on surface-exposed glutamate and aspartate residues of protein complexes within the cystoid membranes (Yuan et al., 2001).

ROs are produced as by-products in the normal metabolic pathways of organelles such as chloroplasts, mitochondria, and peroxisomes (Peralta-Videa et al., 2014). Under conditions of REEs stress, plants produce excessive amounts of ROs and cause oxidative damage to biomolecules through electron transfer (Carocho and Ferreira, 2013). This oxidative stress will lead to an imbalance of plant metabolism, impairment of photosynthesis, and limitation of plant growth and development. In other words, when plants are stressed by REEs, it will lead to excessive accumulation of ROs in the plants, resulting in lipid peroxidation, alteration of cell membrane fluidity and permeability, protein oxidation and metabolism, and ultimately leading to changes in cell structure and function (Ahlualia et al., 2021). For example, Ce (IV) is a strong oxidant with higher toxicity than Ce (III) and has the ability to induce cellular lipid peroxidation, which disrupts cellular structure and reduces membrane fluidity (Wason and Zhao, 2013). Large accumulations of ROS damage lipids and other biomolecules, which in turn disrupts mitochondria and increases mitochondrial MPTP. At the same time, ROS induce a change from Ce (III) to Ce (IV) change, which promotes the toxicity of Ce in plants. Exposure to REEs ions causes more lipid peroxidation (Feng et al., 2023). When REEs enter the mitochondria, the accumulation of large amounts of ROS destroys lipids and other biomolecules, thereby disrupting mitochondria and increasing mitochondrial MPTP. Cyt c is released into the cytoplasm via mitochondrial membrane translocation to activate Caspase-3-like, inducing PCD, and inhibiting plant growth (Wang et al., 2023). Due to the large specific surface area and small particle size of REO NPs, they can easily enter into plants and have adverse effects on them. REO NPs were able to penetrate the epidermal cell wall and plasma membrane of roots and enter the xylem ducts, which are the most important carriers for the distribution and translocation of REO NPs (Aslani et al., 2014).

Some particles may enter the pores and intercellular junctions in the cell wall, blocking the transport channels of plant nutrients and thus affecting plant growth and development (Peralta-Videa et al., 2014). In view of the high chemical activity of REO NPs, they may trigger the generation of intracellular ROS when absorbing energy in the cell or coming into contact with the electron donor of the organism (Kovacic and Somanathan, 2010). REO NPs induce ROS, lipid peroxidation, and oxidative stress in plants, which is one of the reasons for their toxic effects on plants (Rico et al., 2013).

4. Effects of REEs on plant rhizosphere microorganisms

The inter-root is a key area for nutrient exchange between plant roots and microorganisms, which has a significant impact on plant growth and development and the inter-root microbial community. Root secretion is the core source of nutrients in the inter-root, and the presence of REEs may affect the composition of plant root secretion, so we need to study the effects of REEs on plant inter-root microorganisms in depth. As an area of increased microbial activity and biomass, the inter-root zone was significantly influenced by the plant root system. Under mild exposure to REEs, plants showed an increase in root length and biomass, as well as a change in inter-root conditions, which may be one of the important factors leading to REEs partitioning. REEs added to the soil were

converted to other forms and the soluble exchange fraction decreased. At the same time, REEs form complexes with organic matter and eventually stabilize (Rogova et al., 2022).

Naturally occurring rhizosphere bacteria *Arthrobacter oxydans* and *Kocuria rosea* release a variety of deferroxamine-like, bacillibactin-like, and surfactant-like chemical compounds, which mobilized REEs and enhanced their bioavailability (Schwabe et al., 2021). REEs affected the bacterial α -diversity in the soil following order of inter-root bacteria > root bacteria > foliar bacteria > leaf bacteria (Jin et al., 2023). High concentrations of La harmed the inter-root bacterial community, and the similarity of OTU clustering of the fungal community decreased with increasing concentrations of La (Hao et al., 2021). The inter-root microorganisms showed sensitivity to differences in REEs content and physicochemical properties, and most of the inter-root OTU counts and Shannon indices of rice cultivated in the mining area were lower than those in the non-mining area (Zhang et al., 2022). Under iron-deficient conditions, a mixture of deferroxamine and bacilli produced by the iron oxidizing bacterium *B. ferrooxidans* ATW2 affects the solubility of REEs in the soil (Schwabe et al., 2021). The effects of REEs on inter-root microorganisms are also limited by environmental factors such as Available phosphorous (AP), Ammonia nitrogen, Available Potassium (AK), pH, C/N, and so on. For example, the effects on two common phosphorus fertilizers, SSP and CMP, were different. SSP was weakly acidic, leading to a decrease in soil pH, which promoted the solubilization of REEs, thus reducing the abundance and diversity of soil inter-root bacteria, while significantly affecting the structure of the bacterial community. At the gate level, the relative abundance of Acidobacteria increased significantly. On the contrary, the addition of CMP increased the soil pH and significantly decreased the concentration of REEs in the soil solution. Although the addition of CMP had little effect on the abundance of the bacterial community, it significantly increased the diversity of the bacterial community (Jin et al., 2019). Inter-root microorganisms play an important role in the protection of plants under rare earth stress. In the case of complex pollution by REEs and ammonia nitrogen due to mineral resource extraction, the diversity of inter-root bacteria was reduced, affecting root secretion fractions and inter-root microbial communities. However, under the influence of environmental factors, inter-root microorganisms may form beneficial flora for mitigating the combined contamination, such as *Rhizobium retardum* and *Candida controllata*, which function as nitrogen-fixing and anti-REEs-stressing bacteria, thus promoting plant growth (Zhang et al., 2022).

5. Meta-analysis of REEs induced plant toxicity

5.1. Data collection and collation

Online databases were investigated through PubMed and Web of Science. The search covered the entire period of available publications, with the last update taking place on February 18, 2024. Use the subject words: rare earth, toxicity, toxic effects, plants, phytotoxicity, and the free words of each subject word in PubMed for combined queries. The search modes of the two search databases are shown in Table S3 and Table S4. The references of this article are also taken as one of the sources of literature acquisition. To be included in this meta-study, articles must be published in peer-reviewed journals and papers. After excluding duplications, 125 articles were examined in detail for inclusion eligibility. At this stage, articles and observations are excluded if one or more of the following conditions are met: (1) Review articles; (2) non-toxicity test articles; (3) The research object is microorganism; (4) Non-research concerns; (5) Other factors combined with rare earth stress; (6) Response variable data is missing; (7) The content of the literature is not comprehensive, and the available information does not allow to estimate it. This filtering resulted in 45 articles that were selected for the database created (Text S1). The working flow chart of the research retrieval process and results is shown in Fig. S3.

The experimental duration and REEs concentration in the literature

were converted into days and mg/L, respectively. When standard errors (SE) are presented in the paper, they are converted to Standard Deviation $SD = SE \times \sqrt{n}$. By using WebPlotDigitizer rendering software to extract the graph data (Burda et al., 2017) (<https://automeris.io/WebPlotDigitizer/>). After extraction, a total of 45 articles (a total of 1015 observations) were identified.

The plant physiological parameters involved in this study include: plant biomass; Plant photosynthesis; Macronutrients; Oxidative stress. The above parameters are classified into the following categories (Table S5): (1) plant dry weight biomass (DW), plant fresh weight biomass (FW); (2) Chlorophyll, Fv/Fm; (3) macronutrients (P, K); (4) Catalase (CAT), Hydrogen peroxide (H_2O_2), Malondialdehyde (MDA), Peroxidase (POD), Superoxide dismutase (SOD), Peroxidase Stain (POX), Glutathione (GSH), Glutathione S-transferase (GST). In addition, the factors affecting plant growth were also collected. According to REEs, REEs were divided into two subgroups: (1) LREE (La, Ce, Pr, Nd, Pm, Sm, Eu); (2) HREE (Gd, Tb, Dy, Ho, Er, Tm, Yb, Lu, Y). According to the duration of action, they were divided into 3 subgroups: (1) ≤ 7 days; (2) (7,60] days; (3) >60 days. Plants are divided into: (1) Roots (2) Stems (3) Leaves. In some literatures, stems and leaves are grouped together into above-ground parts. According to REEs concentration, it could be divided into 4 subgroups: (1) ≤ 10 mg/L; (2) (10,100] mg/L; (3) (100,1000] mg/L; (4) >1000 mg/L.

The 1015 data results collected were sorted and classified (Table S6), and Review Manager 5.4 was used for meta-analysis. In this study, random-effects models were used along with standardized mean difference (SMD) to assess plant responses to REEs, resulting in more credible meta-analysis results. The model was diagnosed by funnel diagram. The more symmetrical the funnel shape, the higher the reliability of the conclusion.

5.2. REEs effects on plants in general

The extracted data were summarized and sorted into four categories of indicators, and the overall influence of REEs on various indicators of plants was analyzed (Fig. 2). In terms of plant growth, REEs application had significant effect on plant dry weight biomass (SMD = -0.28 ; 95% CI: 0.54, -0.03) had significant inhibitory effect on fresh weight biomass (SMD = -0.17 ; 95% CI: -0.5 , 0.16) had no significant effect.

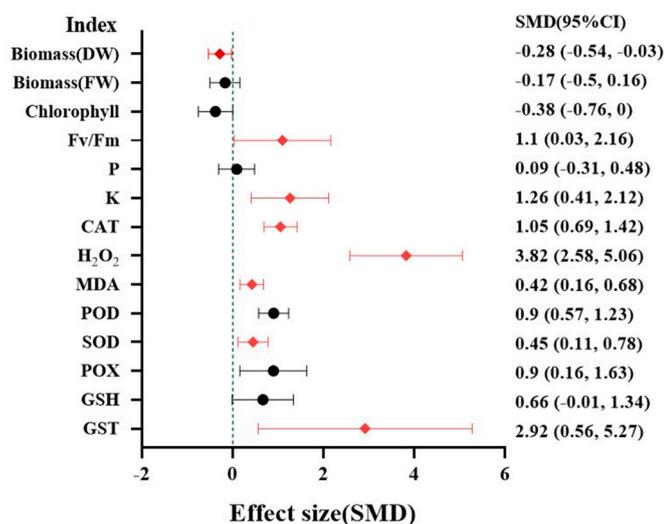


Fig. 2. Average changes of physiological indexes of plants after REEs application. The center point of the line segment represents the average effect, the horizontal bar represents the 95% confidence interval (CI), and the red diamond block line segment represents the significant influence variable. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The changes of plant dry matter accumulation were affected by stress variables (Gonzalez et al., 2019). Under REEs stress, plant dry weight biomass decreased, indicating that RE had a negative effect on plant uptake and accumulation of dry matter. In terms of the effect of REEs on photosynthesis, the effects of REEs on plant chlorophyll (SMD = -0.38 ; 95% CI: -0.76 , 0) had no statistically significant effect. The chlorophyll fluorescence parameter Fv/Fm reflects the photosynthetic performance and is used to characterize the stress effect on plants (Madriaza et al., 2019). Under the effect of REEs, the Fv/Fm (SMD = 1.1; 95% CI: 0.03, 2.16) had a significant promoting effect. For REEs application, the absorption of macronutrients (P, K) by plants was increased, among which the absorption of K(SMD = 1.26; 95% CI: 0.41, 2.12) had significant absorption.

Finally, the oxidative stress damage of plants was measured by CAT, H_2O_2 , MDA, POD, SOD, POX, GSH and GST. According to the data results, REEs application had no significant effects on POD activity, POX activity and GSH content in plants. The contents of H_2O_2 and MDA in plants increased significantly, and the activities of CAT, SOD and GST increased significantly. H_2O_2 is an important ROS entity that plays an important role in a variety of physiological processes in plants. When H_2O_2 is produced in excess, it can damage cells and affect plant growth (Kumar et al., 2023). The increase of MDA content indicated that plants experienced oxidative stress damage under REEs stress. Superoxide dismutase (SOD) and catalase (CAT) inhibit mitochondrial permeability and are the first line of defense against superoxide and hydrogen peroxide (Ambrosone et al., 2005). The antioxidant GST is activated to remove excess ROS. In summary, REEs application had an effect on various physiological indexes of plants.

5.3. Effects of REEs on different parts of plant indexes

Plants are categorized into root and shoot, where some of the literature studies determined the plant leaf parts. Fig. S4 shows the effect on the growth of plant parts under different REEs applications. Fig. S4a and Fig. S4b show that there was inhibition of plant root biomass and shoot biomass by application of REEs irrespective of fresh weight versus dry weight. The inhibitory effect on shoot biomass was more pronounced than root biomass. Interestingly, plant P content (Root SMD = -0.55 ; 95% CI: -1.2 , 0.1) (Shoots SMD = -0.55 ; 95% CI: -1.2 , 0.1) was lower than that of K in both below-ground and above-ground parts. This is due to the fact that REE^{3+} can bind with phosphate to form $REPO_4$ precipitates, which limit plant phosphorus uptake and utilization (Ding et al., 2005). The application of REEs increased the values of all oxidative stress indicators in the plants and some oxidative stress damage occurred in all parts. SOD activity was significantly higher in plant roots (SMD = 0.23; 95% CI: -0.22 , 0.68) compared to plant shoots (SMD = -0.18 ; 95% CI: -0.78 , 0.41). Moreover, MDA content (SMD = 0.51; 95% CI: 0.3, 0.72) was significantly increased in roots. Plant roots are important organs for absorbed nutrients, and most RE applications act on plant roots, REEs can enter into plant roots through root endocytosis, which can easily cause damage to plant roots and affect normal plant growth (Li et al., 1998).

Leaf chlorophyll content was reduced (Fig. S4C), but there was no statistically significant effect, which could be the result of a combination of many other factors. The Fv/Fm value, which is an indicator of the efficiency of primary or potential light energy conversion in photosystem II (PS II), was significantly increased by REEs (SMD = 1.1; 95% CI: 0.03, 2.16). Rare earth ions increase the number of electrons transferred by the electron transport chain by displacing Ca^{2+} in the chloroplast matrix and increase the photosynthetic rate of plants (Xiaoqing et al., 2007).

5.4. Effects of different REEs types on different parts of plant indexes

REEs were grouped into two categories, LREE and HREE, to explore the effects of different types of REEs on plants (Fig. S5). Comparison of

Fig. S5a and Fig. S5c revealed that compared to LREE, HREE roots dry weight biomass (SMD = -0.58; 95% CI: -1.67, 0.5), fresh weight biomass (Shoots SMD = -1.25; 95% CI: -3.82, 1.32) (Roots SMD = -0.96; 95% CI: -1.83, -0.09), Fv/Fm (SMD = -0.11; 95% CI: -0.82, 0.6), root P content (SMD = -38.22; 95% CI: -62.14, -14.31), root K content (Roots SMD = -0.76; 95% CI: -1.72, 0.21), Shoot K content (Shoots SMD = -0.57; 95% CI: -3.14, 2) were suppressed. Comparison of Fig. S5b and Fig. S5d revealed that both showed an increasing effect on most of the oxidative damage indicators. Among them, the MAD content (Roots SMD = 9.10; 95% CI: 3.79, 14.42) (Leaves SMD = 9.14; 95% CI: 4.31, 13.97) and leaf SOD activity (SMD = 2.28; 95% CI: 1.37,3.18) were significantly increased in HREE compared to LREE. It has been reported that the toxicity of REEs increases with their atomic mass at the same concentration (Manusadzianas et al., 2020). The toxic effects of REEs are controlled by their morphology in solution and their partitioning between specific ligands and active solids (Martinez et al., 2018). The ionic radius of HREE is smaller than that of LREE, and most

ligands bind stronger to HREE than to LREE (Tang and Johannesson, 2010). These suggest that HREE is more likely than LREE to inhibit plant growth.

5.5. Effects of REEs on different parts of plants with different action times for each indicator

The duration of exposure to REEs is a critical factor influencing their phytotoxicity. Extended exposure leads to greater inhibition of plant growth (Fig. 3). When REEs were applied for ≤ 7 days, the P content in plant leaves (SMD = 3.23; 95% CI: 1.82, 4.65) and K content in roots (SMD = 3.58; 95% CI: 0.42, 6.74) were promoted, whereas root P was significantly reduced (SMD = -38.22; 95% CI: -62.14, -14.31). REE³⁺ strongly interacts with phosphate to form REEs phosphate precipitates, effectively immobilizing REEs and limiting their uptake by plant roots (Jin et al., 2020). The oxidative damage effects became more pronounced in plant leaves exposed to REEs for more than 7 days, with

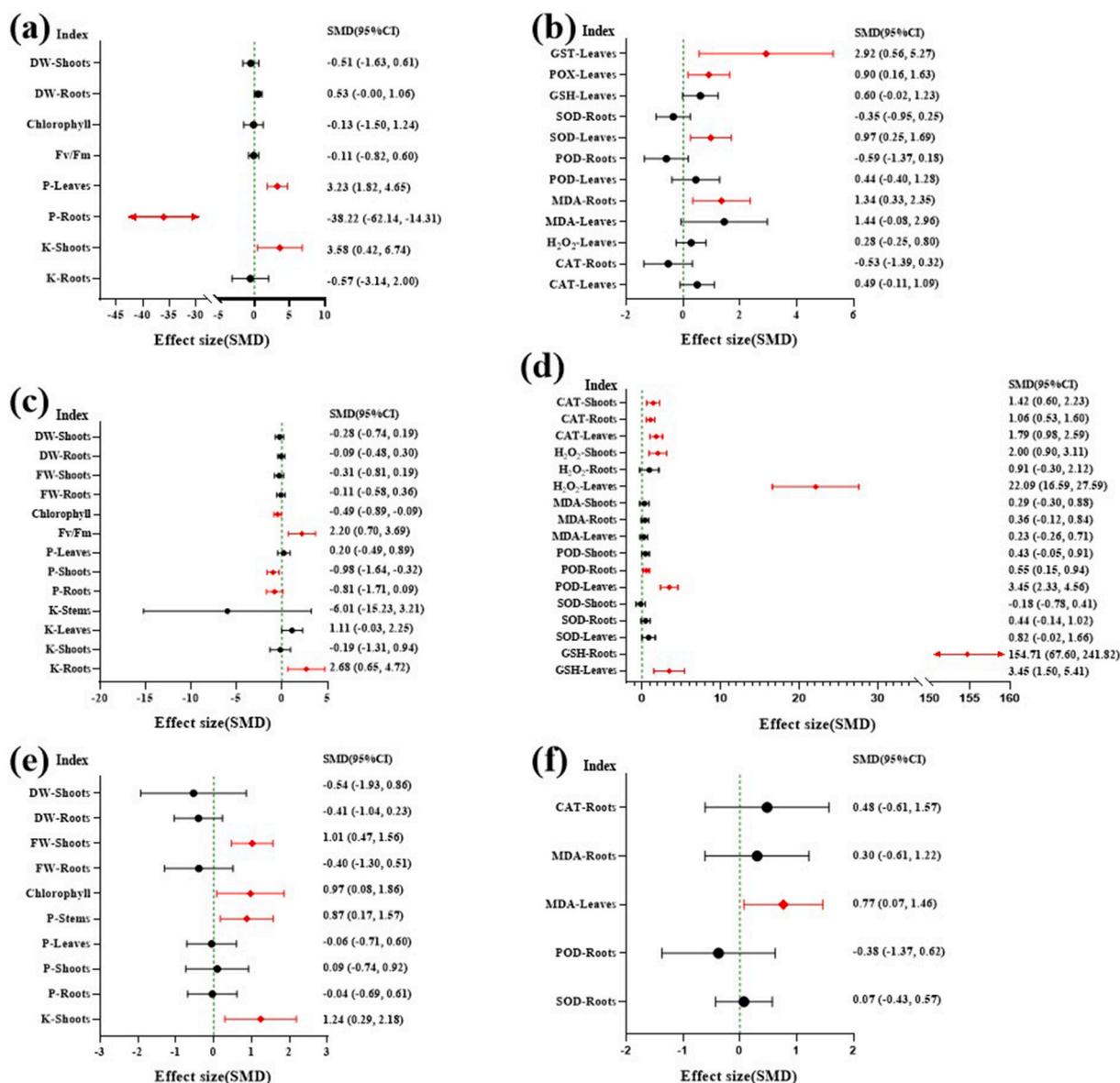


Fig. 3. The effects of REEs on plant indexes were as follows: (a) Growth state indexes with REEs ≤ 7 days; (b) The oxidative stress index with the duration ≤ 7 days; (c) Growth status indicators for time of action (7,60) days; (d) Oxidative stress indices for time of action (7,60) days; (e) Indicators of growth status with duration of action >60 days; (f) Oxidative stress index with duration >60 days. The center point of the line segment represents the average effect, the horizontal bar represents the 95% confidence interval (CI), and the red diamond block line segment represents the significant influence variable. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

significant enhancement of GST (SMD = 2.92; 95% CI: 0.56, 5.27), POX (SMD = 0.90; 95% CI: 0.16, 1.63), and SOD (SMD = 0.97; 95% CI: 0.25, 1.69) activities in plant leaves, along with a significant rise in MDA (SMD = 1.34; 95% CI: 0.33, 2.35) content in roots.

As the duration of REEs exposure increased (7 days–60 days), plant chlorophyll content (SMD = -0.49; 95% CI: -0.89, -0.09) and nutrient P content (Shoots SMD = -0.98; 95% CI: -1.64, -0.32) (Roots SMD = -0.81; 95% CI: 1.71, 0.09) were significantly suppressed. Concurrently, the degree of oxidative stress damage in plants intensified, with increases in GSH content in leaves and roots, H₂O₂ content in leaves and shoots, as well as some enzyme activities (POD in leaves and roots, and CAT in all parts of the plant) significantly elevated. Interestingly, prolonged stress exposure (>60 days) led to significant increase in aboveground fresh weight (SMD = 1.01; 95% CI: 0.47, 1.56), and chlorophyll content (SMD = 0.97; 95% CI: 0.08, 1.86), indicating enhanced photosynthetic potential. Moreover, uptake of P nutrients in stem tissues (SMD = 0.87; 95% CI: 0.17, 1.57) and K nutrients in aboveground tissues (SMD = 1.24; 95% CI: 0.29, 2.18) also increased significantly. This increase in nutrient element concentrations in aboveground tissues may be attributed to enhanced root translocation capacity (Dang et al., 2024) or biotransformation-induced damage to root cell membranes, leading to membrane lipid peroxidation and altering the fluidity and permeability of the cell membranes, thereby affecting the uptake of a large number of nutrients (Dwivedi et al., 2018; Wu et al., 2023). These findings suggest that plants exhibit tolerance to REEs, but prolonged exposure can disrupt the plant's natural defense system with potentially harmful consequences.

Overall, the dry weight biomass of plant roots decreased while oxidative stress damage increased with prolonged REEs exposure. Plants responded by activating reactive oxygen species scavenging systems and antioxidants, leading to enhanced enzyme activities. For example, leaf GSH content, leaf H₂O₂ content, and some tissue enzyme activities (root SOD, leaf POD, root POD, root CAT, leaf CAT) were increased. Conversely, with longer exposure durations, leaf SOD, root MDA, and leaf MDA contents decreased compared to short-term exposure levels, possibly indicating the acquisition of adaptive mechanisms by plants to mitigate the negative effects of REEs during later growth stages. In summary, the toxic effects of REEs were correlated with exposure duration, with prolonged exposure impairing plant growth and exacerbating oxidative stress damage (Wang et al., 2016).

5.6. Effects of concentrations of REEs on different parts of plant indexes

The toxicity of REEs to plants is also influenced by the concentration of REEs. When plants are exposed to suitable concentrations of REEs, they can significantly reduce abiotic stresses in plants and support their antioxidant potential (He et al., 2005). By comparing the effects of different concentrations of REEs on plant indicators (Fig. S6), it was found that positive effects on plant indicators (fresh weight biomass, chlorophyll, Fv/Fm, P, and K) were observed when the REEs concentration was ≤10 mg/L. Except for the K content indicator, the indicators showed inhibitory effects when the REEs concentration was at (10 mg/L, 100 mg/L), (100 mg/L, 1000 mg/L), and >1000 mg/L. This inhibitory effect was strengthened with increasing concentration. Plants with high concentrations of REEs showed a decrease in biomass, a decrease in chlorophyll content, and an increase in the degree of oxidative stress, all of which can lead to plant death (Gwenzi et al., 2018).

5.7. Publication bias

In this study, article publication bias was analyzed through a funnel plot. The better the symmetry of the shape of the funnel plot, with the studies evenly distributed on both sides, the lower the degree of bias and the higher the credibility of the conclusions. When the sample size is larger, the error is smaller, the standard error is smaller, and the distribution is closer to the top; when the sample size is smaller, the error is

larger, the standard error is larger, and the distribution is closer to the bottom. Fig. S7 funnel plots are better symmetrically distributed on the left and right sides, concentrated above the 95% confidence interval.

6. Conclusions

REEs are attached to plant surfaces by adsorption and deposition and affect plant growth and development due to their unique physical and chemical properties. LREE is more easily enriched in plants than HREE. Different application methods affect the distribution of REEs in plants. Generally speaking, REEs have a dose-dependent effect on plants, with certain concentration and time effects. Different plants showed different physiological responses to different REEs, and further research is needed in this area. REEs affect root elongation and development when they are directly applied to plant roots. The composition and exudation pattern of root secretions may change under the stimulation of REEs. The toxicity of REEs to plants is mainly manifested by the excessive production of ROSs in plants, which leads to lipid peroxidation and plant damage. In addition, REEs compete with Ca²⁺ for organic ligands or displace Ca²⁺, altering the chemical composition of the cell wall. The presence of nanoparticles may block the normal physiological functions of plants and affect the normal growth of plants. Meta-analysis of the phytotoxic responses induced by REEs revealed that the experimental results of most of the studies indicated that REEs exposure was significantly toxic to plants. In the presence of REEs, the material accumulation capacity of plants was reduced and the increase in MDA content indicated that plants experienced oxidative stress. To eliminate excessive ROS, ROS scavenging systems (e.g., SOD, POD, and CAT) and antioxidants (e.g., GST, GSH) were activated and enzyme activities were enhanced in plants. HREE produced stronger phytotoxicity than LREE. Plant damage increased as the duration of REEs action increased. These results help us to make a more accurate prediction of the phytotoxicity of REEs. At present, the research on the effects of REEs on plants as well as the underlying mechanisms still needs to be improved. By comparing more experimental data, the optimal concentration of REEs for plant growth and development can be analyzed. The interaction between root secretion, inter-root microorganisms, and REEs has not been fully explained and understood. Therefore, more direct experimental data are needed to support research in this field.

CRedit authorship contribution statement

Chenyi He: Writing – original draft, Investigation, Data curation, Conceptualization. **Yiping Feng:** Writing – review & editing, Supervision, Resources, Project administration, Conceptualization. **Yirong Deng:** Supervision, Resources, Project administration. **Longyong Lin:** Software, Investigation, Formal analysis, Data curation. **Sheng Cheng:** Writing – review & editing, Visualization, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.chemosphere.2024.142951>.

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