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Responses of ramie (*Boehmeria nivea* L.) to increasing rare earth element (REE) concentrations in a hydroponic system

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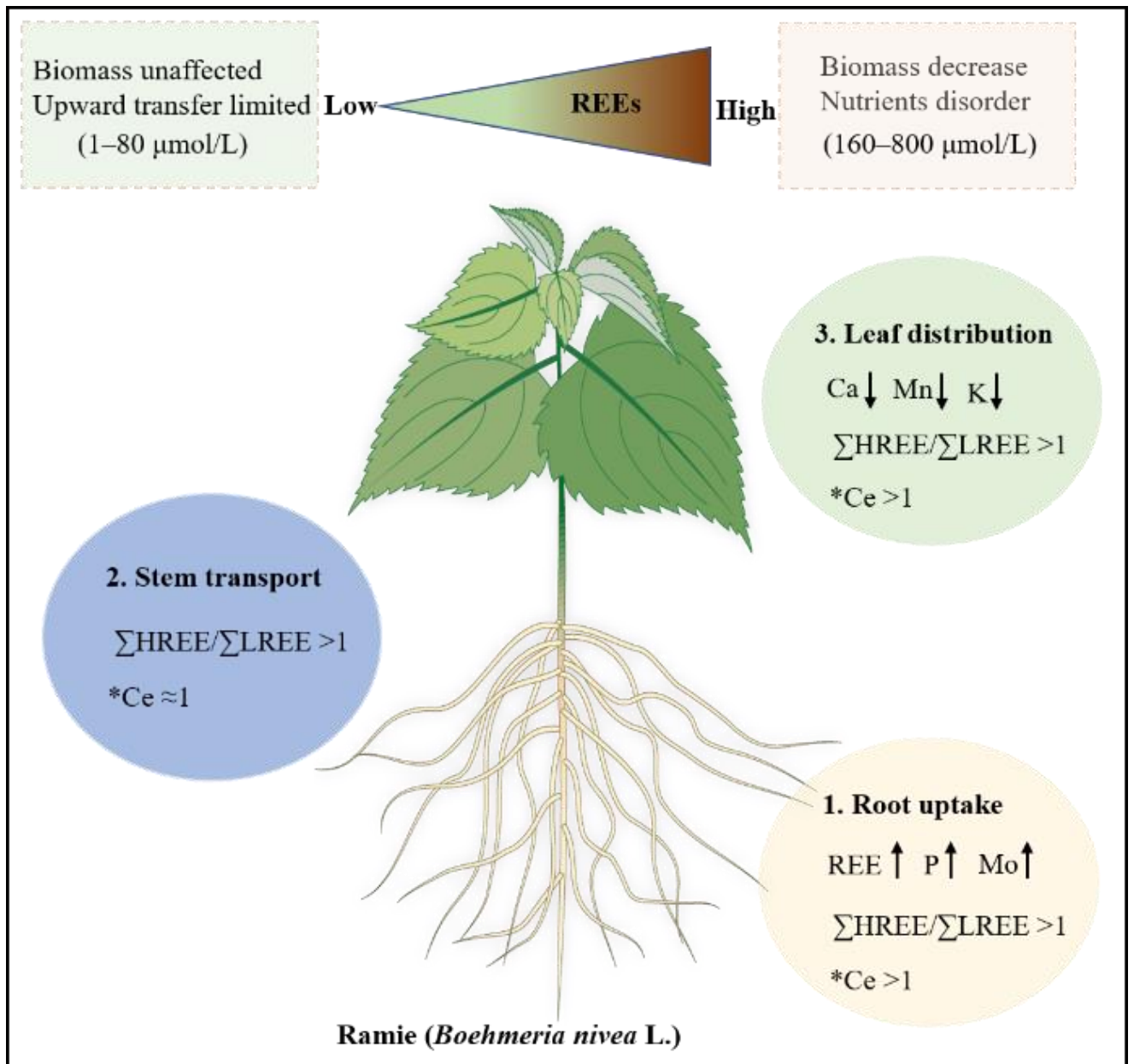
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Graphical abstract



A rare earth element (REE) tolerant fiber plant ramie (*Boehmeria nivea* L.), which retains most of the REEs in the roots.

Abstract

A number of studies have focused on the effects of rare earth elements (REEs) on crop plants, while little attention has been paid on how tolerant plant species respond to increasing mixed REE concentrations. In this study, ramie (*Boehmeria nivea* L.) was exposed to a series of REE concentrations prepared with equimolar mixtures of 16 REEs (*i.e.* 0, 1.6, 8, 16, 80, 160, 400, 800 $\mu\text{mol/L}$) in order to explore REE accumulation and fractionation characteristics in ramie and the responses of this plant to mixed REEs. Results show that ramie root and shoot biomasses are unaffected under lower REE concentrations (1.6–80 $\mu\text{mol/L}$), while the growth of ramie and the uptake of nutrients especially Ca and Mn are largely inhibited under higher REE concentrations (160–800 $\mu\text{mol/L}$). The P and Mo concentrations in the roots increase with the increasing REE concentrations in the solution, suggestive of an involvement of P and Mo in dealing with the high concentrations of REEs in this plant. The preferential uptake of Ce and heavy REEs (HREEs) and the preferential transport of HREEs within the plant lead to a positive Ce anomaly and a HREE enrichment in ramie leaves. Our study suggests that ramie could be a good candidate for the phytoremediation of heavily REE-contaminated soils (*e.g.* REE mine tailings in southern China). Our results also shed light on points to take into account in phytoremediation management strategies of REE-contaminated soils (*e.g.* P and Mo fertilization).

Keywords: phytoremediation, ramie, rare earth elements, fractionation, molybdenum, phosphorus

1. Introduction

Rare earth elements (REEs) include lanthanides (from La to Lu) plus yttrium (Y) and scandium (Sc). Lanthanides can be divided into 2 groups: light REEs (LREEs, from La to Eu) and heavy REEs (HREEs, from Gd to Lu).¹ Rare earth elements are important strategic resources for modern technologies and clean energy production.² However, the growing demand of these resources has facilitated the exploitation of ion-adsorption REE deposits in southern China, resulting in large areas of REE mine tailings.^{3,4} It was found that the concentrations of REEs in these mine tailings reached 300–1200 mg/kg, which are several times higher than those of the unmined soils nearby.⁵ These abandoned ion-adsorption REE mine tailings are subjected to runoff and erosion, leading to REE contamination of surface water and agricultural land.⁴ High concentrations of REEs may induce adverse effects on microorganisms, invertebrates, and plants,^{6–9} and pose potential threats to human health.¹⁰ Therefore, control and remediation of these REE-contaminated soils have become a serious environmental concern.

Phytoremediation is a low-cost and environmental-friendly method that employs plants to achieve remediation for metal(loid)s polluted soils.^{11,12} Among several phytoremediation strategies, phytostabilization uses plants and soil amendments to reduce the availability of metal(loid)s in the soil and limit their migration to the surface and ground waters.¹¹ The plants used for phytostabilization operations can usually survive on soils with high concentrations of certain metal(loid)s and have limited soil-to-shoot bioconcentration factors for metal(loid)s, thereby minimizing the risks of metal(loid)s entering the food chain and transferring to other environmental compartments.^{13–15} In the past decades, many efforts have been focused on phytostabilization of a series of heavy metals, *i.e.* Cd, Zn, As, Pb, *etc.* These studies found that a number of plants meet the requirements of phytostabilization, *e.g.* pioneer plant *Miscanthus sinensis*, commercial plant *Vetiveria zizanioides* or fiber plant *Boehmeria nivea* L.^{16–18} These plants improve the soil physico-chemical and biological properties and reduce the availability of heavy metals, thus alleviating the phytotoxicity.^{19,20} Those heavy metals are immobilized, or converted to less toxic forms through oxidation-reduction, complexation and precipitation within the roots or the rhizosphere of the plants.^{21,22}

Even though there is an increasing interest in the biological responses of plants to REEs, most studies focus on the effects of individual REE on crop plants *e.g.* rice, soybean and wheat.^{7,23,24} These studies found that REEs can induce a “hormesis effect”, that is, REEs can promote crop biomass production at low concentrations, but inhibit crop growth at high concentrations.²⁵ For example, La had positive effects on rice growth at 0.36–5.40 $\mu\text{mol/L}$, but negative effects on rice biomass at concentrations higher than 10.7 $\mu\text{mol/L}$ in solution.²⁶ In soybean, La promoted plant growth at 5–10 $\mu\text{mol/L}$, but reduced plant biomass, caused ultrastructural modifications

in cell walls and thylakoids at concentrations higher than 20 $\mu\text{mol/L}$ of La in solution.²⁷ Usually, REEs increase the uptake of nutrients in crop plants under low concentrations, while interfere with nutrient uptake,²⁸ destroy cell membrane structure,²⁹ damage chloroplast structure and inhibit photosynthesis under high concentrations.³⁰ Nevertheless, little attention has been paid on the response of REE-tolerant species to elevated REE concentrations.

Ramie (*Boehmeria nivea* L.) is a perennial fiber plant belonging to the Urticaceae family, which colonizes naturally at most of the tropical and subtropical regions. As ramie produces high quality of fibers for agricultural and industrial uses, it has been cultivated in south China for thousands of years (*e.g.* Jiangxi, Guangdong, Hunan, Hubei provinces). This plant produces high amount of biomass and has a dense root system, thereby acting as a choice of revegetation for reducing runoff and soil erosion.³¹ Moreover, ramie is regarded as a multi-metal tolerant plant with strong tolerance to Pb, Zn, Cd, As, and has strong adaptability to harsh conditions such as drought.³² Studies showed that ramie has very limited soil-to-shoot bioconcentration factors for heavy metals, and most heavy metals are restricted within roots.¹⁶ For instance, most Cd is bound to the cell walls, or precipitated with phosphate in the roots, while organic acids are not involved in Cd tolerance of ramie.^{33,34} However, how this species adapts to high concentrations of REEs remains unknown.

Elucidating the effects of increasing concentrations of REEs on ramie growth and nutrient uptake is key to understanding the mechanisms of tolerance within the aim of using this plant for the phytoremediation at REE-contaminated soils. In this study, a hydroponic experiment was conducted using equimolar solutions of 16 REEs to study the tolerance of ramie to REE stress. More specifically, the influence of REEs on plant biomass, nutrient accumulation, REE accumulation and fractionation, and REE-nutrient interactions in the plant tissues were determined in order to study the mechanisms of tolerance in ramie and evaluate its potential for phytoremediation at REE-contaminated soils.

2. Materials and methods

2.1. Plant material and growth conditions

The seeds of ramie (Zhongzhu No.1) were bought from the Institute of Bast Fiber Crops, Chinese Academy of Agricultural Sciences. Before sowing, approximately 0.5 g of seeds were sterilized in 50 mL of 5% NaClO (AR) solution for 15 min, then rinsed 5 times with deionized water. Subsequently they were sown on quartz sand with high-purity water (18.2 Ω) in a growth chamber at 25°C in the dark for 7 d. After germination, healthy and uniform seedlings with two leaves were transferred to beakers containing 1/2-strength Hoagland nutrient solution (500

$\mu\text{mol/L}$ $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, $500 \mu\text{mol/L}$ KNO_3 , $250 \mu\text{mol/L}$ $\text{MgCl}_2 \cdot 7\text{H}_2\text{O}$, $50 \mu\text{mol/L}$ KH_2PO_4 , $25 \mu\text{mol/L}$ KCl , $5 \mu\text{mol/L}$ H_3BO_3 , $0.5 \mu\text{mol/L}$ MnCl_2 , $0.1 \mu\text{mol/L}$ $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, $0.1 \mu\text{mol/L}$ $\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$, $10 \mu\text{mol/L}$ $\text{Fe}(\text{III})\text{-EDDHA}$, $1.0 \mu\text{mol/L}$ $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, AR).³⁵ The solution pH was adjusted to 5.5 ± 0.1 with 2-morpholinoethanesulphonic acid (MES)–KOH throughout the experimental period.³⁶ The nutrient solution was changed every three days. The seedlings were exposed to tungsten lamps under controlled conditions ($350 \mu\text{mol/m}^2/\text{s}$ PAR–light, 14/10 h day/night, $25/20^\circ\text{C}$ day/night and 70% relative humidity).³⁷

2.2. Plant exposure to REEs

After two weeks of nurturing, three healthy and uniform seedlings (each with six leaves) were transferred to a beaker containing 1 L of fresh nutrient solution free of P to avoid precipitation with REEs. Phosphorus was sprayed on the leaves with a KH_2PO_4 solution ($50 \mu\text{mol/L}$) once a day. A series of equimolar REE solutions were prepared by mixing chloride salts of 16 REEs (La, Ce, Pr, Nd, Sm, Eu, Gd, Tb, Dy, Ho, Er, Tm, Yb, Lu, Y and Sc, Aladdin, America). Eight REE concentrations were tested, *i.e.* 0, 1.6, 8, 16, 80, 160, 400, $800 \mu\text{mol/L}$ of REE (each REE with equal molar concentration, *i.e.* 0, 0.1, 0.5, 1, 5, 10, 25, $50 \mu\text{mol/L}$). The nutrient solution with varying REE concentrations was renewed every three days. After four weeks of REE exposure, plants were harvested and separated into leaves, stems and roots. As a result of limited plant biomass, the three ramie seedlings in each beaker were put together as one sample. Each treatment (*i.e.* each concentration of REEs) was prepared in triplicates.

Roots were washed with Milli-Q H_2O and desorbed with 0.1 M EDTA– Na_2 (Aladdin, America) solution for 30 min, and then washed 3 times with Milli-Q H_2O . Leaves and stems were washed only with Milli-Q H_2O . Plant tissues were dried at 105°C for 30 min and then at 60°C for 48 h. Dry biomass of plant tissues was weighed, then ground to fine powder ($< 0.15 \text{ mm}$). The fresh roots were scanned and the determination of root characteristics (length, surface area, volume) was conducted using WinRhizo software.

2.3. Chemical analysis

Aliquots of plant material ($100 \pm 1 \text{ mg}$) were introduced into Teflon crucibles with covers, and wetted with 1–2 drops of Milli-Q water before digestion in a mixture of concentrated HNO_3 (3 mL, GR), HCl (1 mL, GR) and HClO_4 (1 mL, GR) on a hot plate at $200 \pm 5^\circ\text{C}$ for 12 h. The mineralization solution was then evaporated at 180°C until almost complete dehydration ($< 1 \text{ mL}$). The residues were dissolved in 2 mL of concentrated HNO_3 , dried again, and re-dissolved in 15 mL of 2% HNO_3 .

Concentrations of REEs were determined using an inductively coupled plasma–mass spectrometer (ICP–MS, Agilent 7700x, USA). The internal standard used during analysis was ^{115}In at 1.5 mg L^{-1} in 2% HNO_3 , and 0.1 mL of indium solution was added to the sample solutions. Macro- and micro-nutrients were analyzed using an inductively coupled plasma optical emission spectrometer (ICP–OES, Agilent VISTA, USA). All the analyses were conducted at ALS Chemex (Guangzhou) Go., LTD. The total REE concentration (ΣREEs) was calculated as the sum of the concentrations of the 16 REEs.

2.4. REE fractionation analysis

Rare earth elements are a group of elements with similar chemical properties but they can be fractionated in soils and plants due to small but detectable variations in their behavior derived mainly from differences in ionic radii with increasing atomic number.³⁸ The ratio between LREEs and HREEs is a common index used in REE fractionation analysis. Moreover, REEs are trivalent elements, except for Ce and Eu that have variable valences (Ce^{4+} and Ce^{3+} ; Eu^{2+} and Eu^{3+}) in the environment, which can induce positive or negative anomalies in the REE distribution patterns (*i.e.* enrichment or depletion in Ce and Eu compared to REEs of close atomic number).²⁵ In hydroponic experiments, only Ce may be subjected to redox reactions, thus only Ce anomaly was considered. Rare earth element fractionation patterns and anomalies are reliable tools to trace mechanisms associated with REE accumulation and tolerance in plants under REE stress.^{39–42} For instance, a HREE enrichment in the leaves of wheat may be attributed to the facilitated transport of HREEs by small organic acids complexation.⁴¹

The ratio of LREEs to HREEs in our hydroponic solution was calculated as: $\sum(\text{LREE molar concentration in solution} \times \text{LREE molar mass}) / \sum(\text{HREE molar concentration in solution} \times \text{HREE molar mass, (mg/kg)/(mg/kg)})$, and amounted to 0.65. Therefore, $\Sigma\text{LREE}/\Sigma\text{HREE} > 0.65$ in the plant tissues means a LREE enrichment, while $\Sigma\text{LREE}/\Sigma\text{HREE} < 0.65$ means a HREE enrichment. Cerium anomaly ($^*\text{Ce}$) was calculated as $\{2\text{Ce}/[\text{La} + \text{Pr}]\}$ ((mg/kg)/(mg/kg)); $^*\text{Ce} > 1$ refers to a positive anomaly, and $^*\text{Ce} < 1$ refers to a negative anomaly. The transfer factors, which are defined as the REE concentrations in one compartment divided by the concentrations in another compartment, were also calculated through the REE transfer route (*e.g.* from solution to roots, from roots to stems, from stems to leaves and from roots to shoots).⁴³

2.5. Tolerance index analysis

Tolerance index (TI) is the ratio of the dry weight of ramie tissue for a given treatment to the dry weight of ramie tissue for the control. Tolerance index values lower than 1 indicate a decrease in biomass and suggest that plants are stressed, whereas TI values equal to 1 indicate

no effect. Tolerance index values greater than 1 indicate a net increase in biomass and suggest a growth promoting effect.⁴⁴ A value of 0.5 is considered to be the acceptable minimum of biomass production for plants growing in a metal-contaminated site.⁴⁵

2.6. Data analysis

The SPSS 20.0 statistical analysis software was used for data analysis. All results were presented as arithmetic means with standard deviation calculated on three replicates (beakers). The differences among the treatments were tested using an ANOVA followed by Duncan test at a 0.05 significance level. For one ramie organ, values with different letters refer to significant differences between the different treatments ($p < 0.05$). For some elements, the data were not normally distributed and were transformed to follow a normal distribution before being tested. Matrices of correlation were performed on the elemental concentrations (REEs and nutrients) obtained from all the treatments for ramie roots and leaves separately, using a Pearson correlation two-sided test.

3. Results

3.1. Plant growth

A significant effect of REE concentrations in solution to the growth of ramie is recorded (Figs. 1; S1). Compared to the control (0 $\mu\text{mol/L}$ REE treatment), the root biomass is higher under 1.6 $\mu\text{mol/L}$ REE treatment, while both the shoot and root biomasses show no obvious variations in the range of 8–80 $\mu\text{mol/L}$ REE treatments. However, a significant decrease in the production of both the shoot and root biomasses occurs at 160 $\mu\text{mol/L}$ and higher REE concentration treatments. The root total length, surface area and volume are the highest under the 1.6 $\mu\text{mol/L}$ REE treatment (Table S1), while no significant decrease of the total length and surface area is shown even at 800 $\mu\text{mol/L}$ REE treatment, compared with the control.

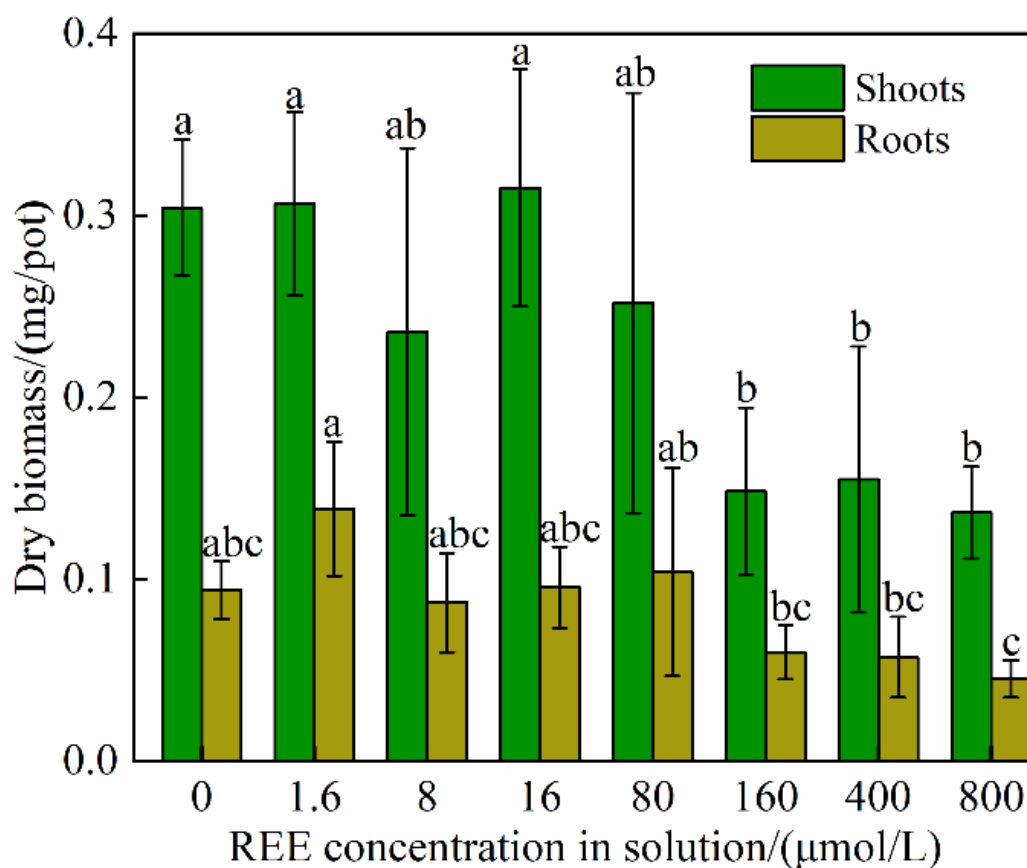


Figure 1 Variations in ramie root and shoot biomass in response to increasing REE concentrations in solution.

Under lower REE concentrations (1.6–80 $\mu\text{mol/L}$), the tolerance index (TI) of ramie varies between 0.70 and 2.45 for the roots, stems and leaves (Table S2). At higher REE concentrations (160–800 $\mu\text{mol/L}$), it decreases below 0.7 for roots and below 0.5 for leaves, and toxicity symptoms are recorded, *i.e.* yellow leaves and dead leaves with strong necrosis areas (Fig. S1). The TI of ramie stems are greater than one under all the REE treatments. Though TI of ramie leaves and roots shows no significant differences among treatments of 0–80 $\mu\text{mol/L}$ REEs, the highest TI of ramie roots and leaves is recorded at 1.6 $\mu\text{mol/L}$ REEs treatment. Hence, it can be assumed that REEs induce an hormesis effect, and toxicity occurs between 80 and 160 $\mu\text{mol/L}$ REEs in the solution.

3.2. REE accumulation in ramie organs

The total REE concentrations in different organs of ramie are shown in Fig. 2. In general, the roots have much higher REE concentrations than the stems and leaves. At lower REE concentrations in solution (1.6–8 $\mu\text{mol/L}$), the REE concentrations in ramie organs are in the order of roots > leaves > stems (Fig. 2). This order is slightly different for higher REE concentrations treatments (>8 $\mu\text{mol/L}$), namely roots > stems > leaves. Root REE

concentrations increase sharply with increasing REE concentrations in solution. At 8 $\mu\text{mol/L}$ REEs in solution, REE concentration in the roots is 3.6 times higher than at 1.6 $\mu\text{mol/L}$ REEs in solution. In stems and leaves, REE concentrations show a slight decrease with the increasing REE concentrations in solution up to 80 $\mu\text{mol/L}$, then increase markedly at higher REE concentration treatments (160–800 $\mu\text{mol/L}$). Within the tolerance range determined in this study (1.6–80 $\mu\text{mol/L}$ REEs), REE concentrations in the leaves range from 53 to 249 mg/kg. The translocation factors (REE concentrations in leaves / REE concentrations in roots) are lower for the treatments in the range of 1.6–80 $\mu\text{mol/L}$ REEs (0.01–0.09) than for those in the range of 160–800 $\mu\text{mol/L}$ REEs (0.08–0.16). The lowest translocation factor (0.01) is recorded at 80 $\mu\text{mol/L}$ REE concentration in solution (Tables S3–S5).

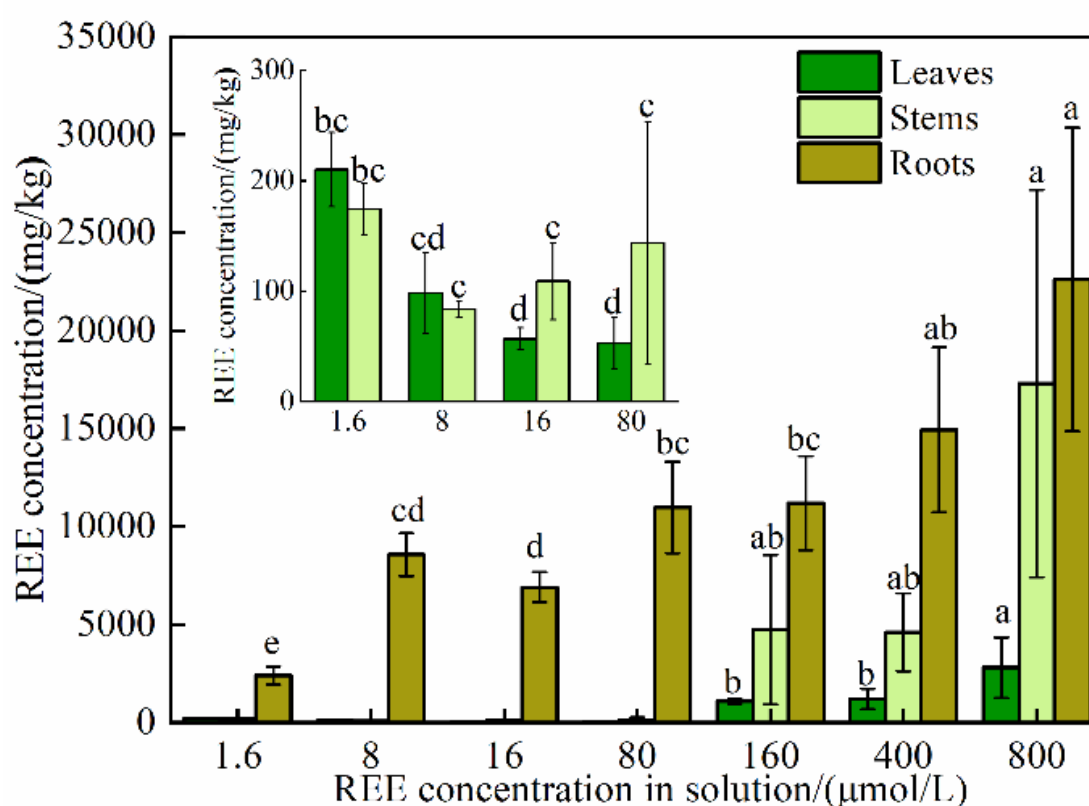


Figure 2 Rare earth element concentrations in ramie roots, stems and leaves with increasing REE concentrations in solution.

3.3. REE fractionation in ramie organs

The ratio of the sum of LREE concentrations to the sum of HREE concentrations ($\Sigma\text{LREE}/\Sigma\text{HREE}$) in the different organs ranges from 0.23 to 0.68 under all the REE treatments, except for the stems at 1.6 $\mu\text{mol/L}$ REEs ($\Sigma\text{LREE}/\Sigma\text{HREE}=1.21$) (Figs. 3a; S2). In the leaves, the $\Sigma\text{LREE}/\Sigma\text{HREE}$ ratios are lower than 0.65 (HREE enrichment) under all the treatments, and they are lower under 1.6–80 $\mu\text{mol/L}$ than under 160–800 $\mu\text{mol/L}$ REE

treatments. In the stems, the $\Sigma\text{LREE}/\Sigma\text{HREE}$ ratios are lower at 8–80 μM REE treatments (0.38–0.51) and higher at 160–800 $\mu\text{mol/L}$ REE treatments (0.58–0.61). In both the roots and the whole plant, the $\Sigma\text{LREE}/\Sigma\text{HREE}$ ratios are lower under the 1.6–16 $\mu\text{mol/L}$ REE treatments (<0.65) than the 80–800 $\mu\text{mol/L}$ REE treatments (around 0.65) (no significant fractionation). Under the same REE concentration treatment, the $\Sigma\text{LREE}/\Sigma\text{HREE}$ ratios in the leaves are lower than those in the stems.

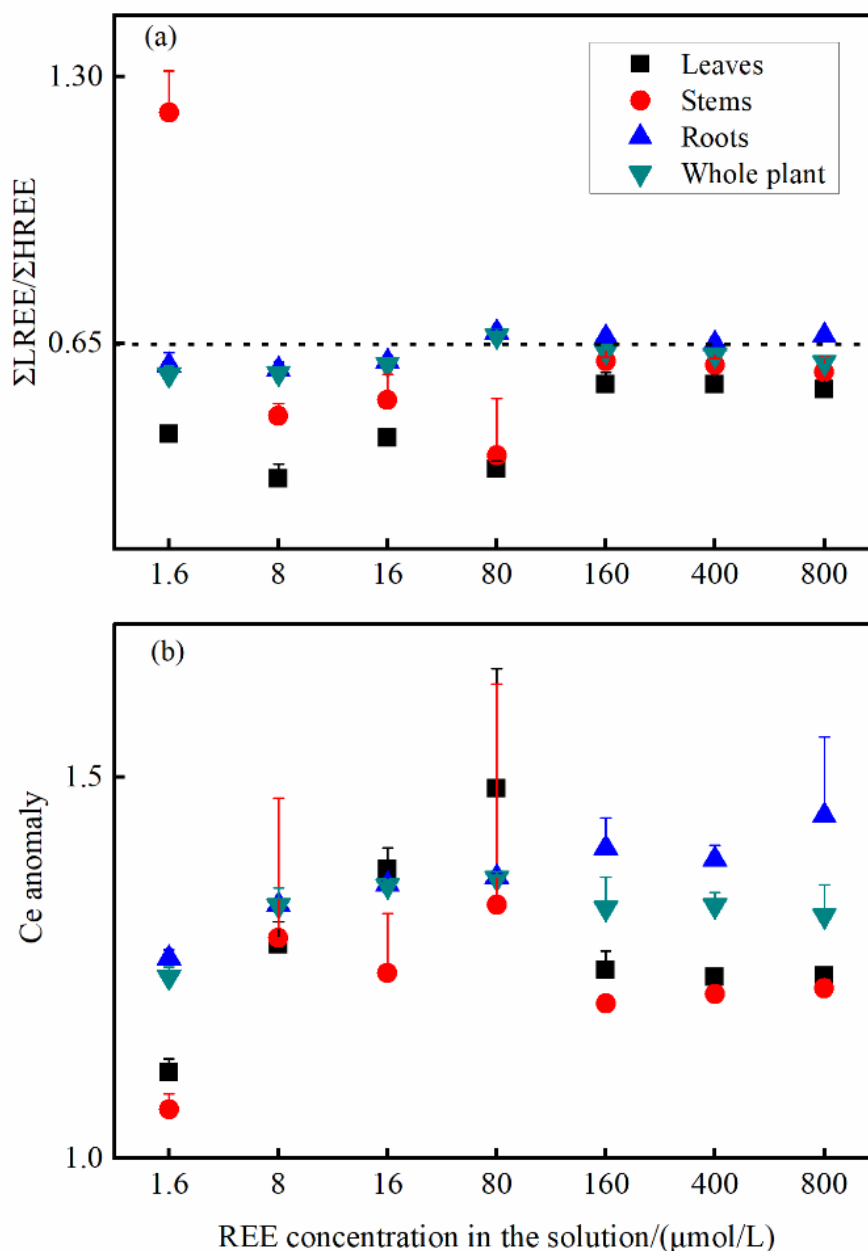


Figure 3 Rare earth element fractionation in ramie tissues with increasing REE concentrations in solution: (a) the ratio of LREEs to HREEs and (b) the Ce anomaly (b).

The $\Sigma\text{LREE}/\Sigma\text{HREE}$ ratio in the hydroponic solution is 0.65 and is indicated by the dashed line, $\Sigma\text{LREE}/\Sigma\text{HREE} > 0.65$ and < 0.65 refers to a LREE and HREE enrichment in the plant, respectively, and *Ce >1 refers to positive Ce anomaly.

Different ramie organs and the whole plant show positive Ce anomalies (1.06–1.48) under all the REE treatments (Figs. 3b, S2), that is, ramie organs accumulate more Ce than its neighbours (La and Pr). Cerium shows positive anomalies during the uptake (solution-to-plant) process, but no significant anomalies during the transport (roots-to-leaves) process (Fig. S3).

Concentrations of scandium are lower than those of the lanthanides (La to Lu) under all the REE treatments in the leaves, whereas in the roots they are higher compared to those of the lanthanides from 80 to 800 $\mu\text{mol/L}$ REE treatments. Concentrations of yttrium in ramie leaves and stems are similar to those of the lanthanides, while in the roots they are lower under all the REE treatments (Tables S3–S5).

3.4. Concentrations and relationships of nutrients in ramie organs

The addition of REEs in the solution significantly decreases the concentrations of Ca and Mn in ramie roots, stems and shoots, especially under 80–800 $\mu\text{mol/L}$ treatments (Fig. 4). The addition of REEs in the solution also decreases K, Mg, Cu and Zn concentrations in ramie roots, stems and leaves (Tables S6–S8). On the contrary, the concentrations of P in all the plant organs and Mo in the roots increase with the increasing REE concentrations in the solution. The addition of REEs in the solution has no obvious influence on the Fe concentrations in the roots, stems and leaves.

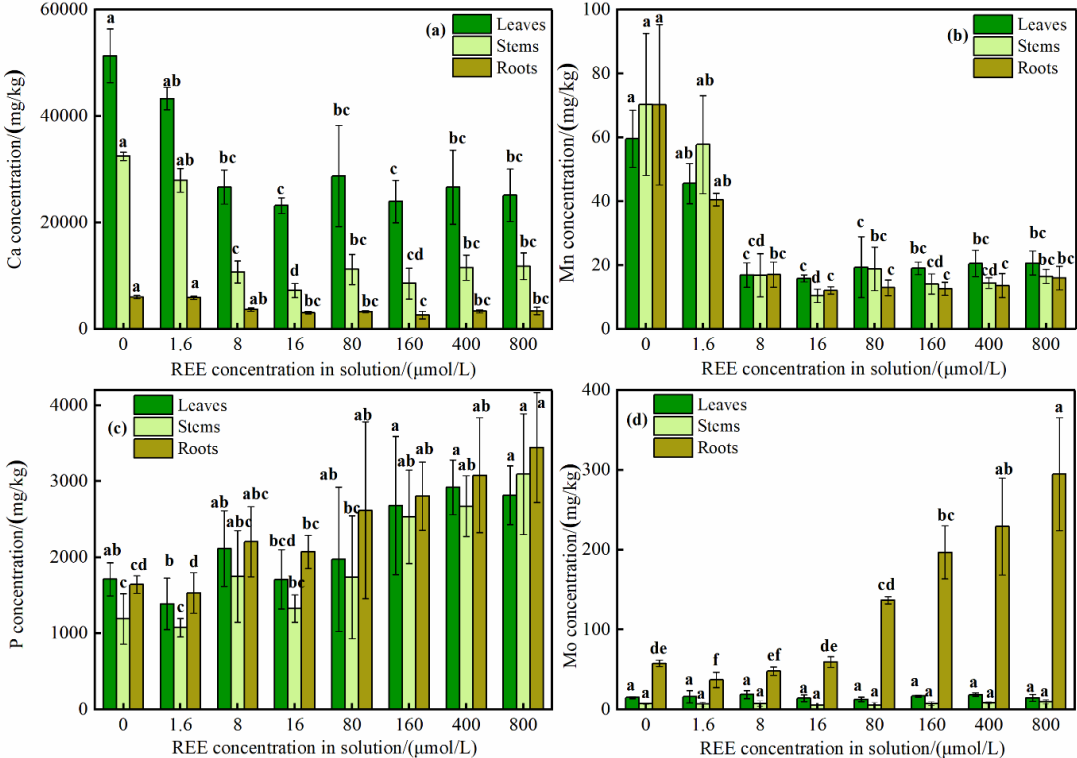


Figure 4 Concentrations of nutrients in ramie leaves, stems and roots with increasing REE concentration in solution: (a) Ca concentrations, (b) Mn concentrations, (c) P concentrations and (d) Mo concentrations.

The correlation matrices among nutrient and REE concentrations in ramie roots and leaves are shown in Fig. 5. In the roots, REE concentrations are positively correlated with P and Mo concentrations ($R=0.85$ and 0.91 respectively, $p < 0.05$), and negatively correlated with K, Mn and Zn concentrations ($R=-0.46$, -0.45 and -0.49 respectively, $p < 0.05$). In the leaves, only P concentrations show an obvious positive relationship with REE concentrations ($R=0.51$, $p < 0.05$). In both the roots and leaves, P is positively correlated with Mo concentrations ($R=0.85$ and 0.39 respectively, $p < 0.05$).

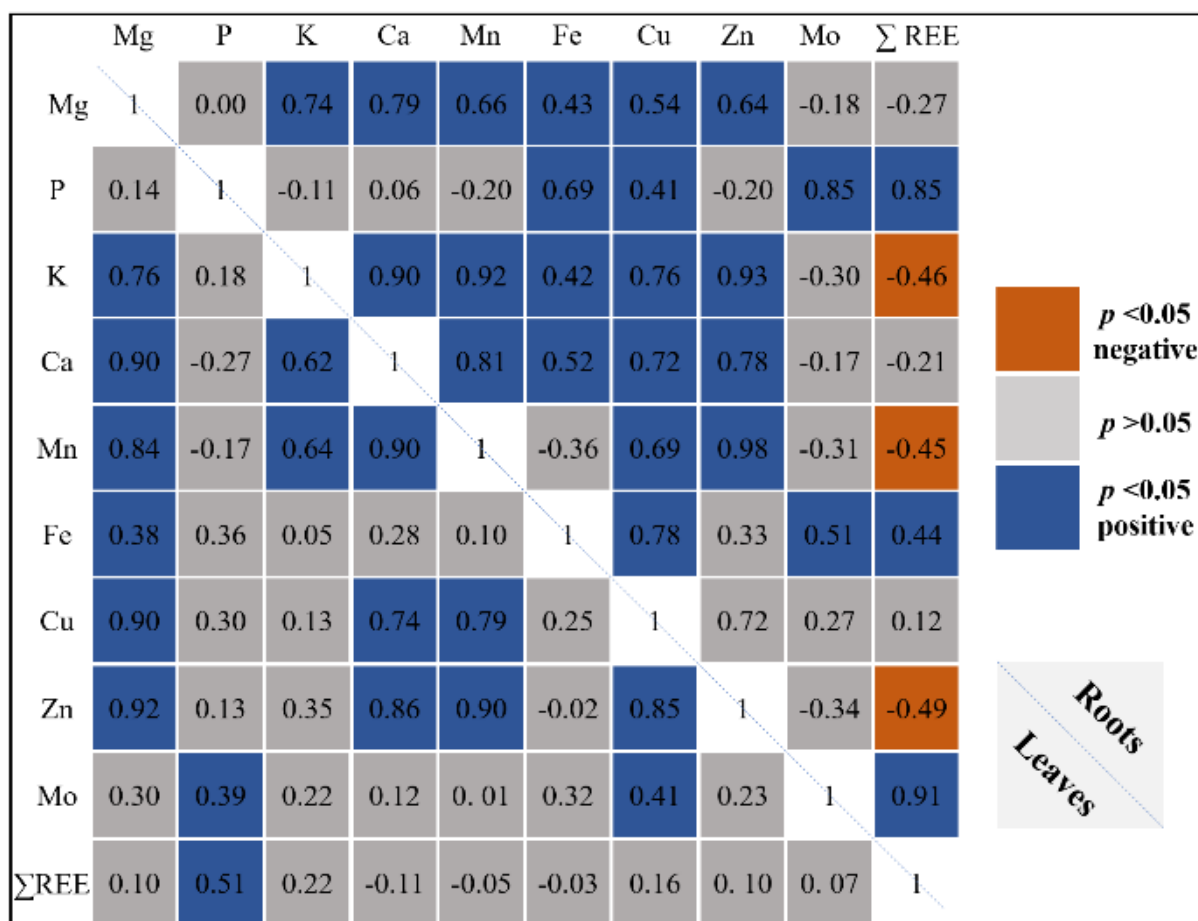


Figure 5 Correlation matrices performed on elemental concentrations obtained under 0–800 $\mu\text{mol/L}$ REE treatments in ramie roots (upper triangular matrix) and in leaves (lower triangular matrix).

The values in the matrix are the Pearson correlation coefficient (R) between element concentrations. The higher the R^2 value is, the higher degree of correlation (positive or negative) between the two element concentrations is. The color of the box refers to the significance level of the correlation (p -value).

4. Discussion

4.1. Response of ramie to increasing REE concentrations

Investigations on plant tolerance to REEs have been often conducted on crop plants. These studies showed that crop plants always have relatively low tolerance to REEs.²⁴ However, in the REE hyperaccumulator plant *Phytolacca americana*, a decrease of plant biomass was recorded at mixed REE concentrations up to 50–100 $\mu\text{mol/L}$ in the hydroponic solution (similar pH and nutrient composition with this study).³⁷ In this study, increasing REE concentrations in solution have no adverse effect on ramie growth from 1.6 to 80 $\mu\text{mol/L}$, suggesting that ramie has a tolerance capacity similar to the REE hyperaccumulator plant *P. americana*, and much stronger than common crop plants.

The Ca, Mn and K concentrations in ramie roots and shoots are significantly decreased by the addition of REEs in the solution. It has been proposed that REEs might be taken up through K^+ , Ca^{2+} ion channels, hence the addition of REEs might reduce the uptake of K and Ca.^{36,37} Studies also found that Mn and REEs were co-localized in the REE hyperaccumulator *Dicranopteris linearis*,⁴⁶ and the addition of LaCl_3 could inhibit the uptake of Mn by *P. americana*,⁴⁷ indicative of a competitive uptake of REEs and Mn in plants. The decrease of the nutrients (*e.g.* K, Ca, Mn, Mg, Zn) in ramie organs may be also ascribed to the damage of cells (*e.g.* cell members and chloroplast) under high REE concentrations.

Some studies highlighted that the most significant toxic symptom of REEs is the inhibition of P uptake.⁴⁸ However, an increase of P concentration with the addition of REEs is found in both ramie roots and shoots. Based on previous studies on wheat, REE fractionation (*e.g.* $\Sigma\text{LREE}/\Sigma\text{HREE}$) between roots and solution was mainly controlled by cell wall absorption and phosphate precipitation.⁴¹ Moreover, electron microscopy and X-ray microanalysis have also shown deposits containing REEs and P in the extracellular space of root tissue of *Cucumis sativus*.⁴⁹ The positive correlation between REEs and P is coherent with the assumption that phosphate precipitation might contribute to the detoxification and accumulation of REEs in both ramie roots and shoots. The positive relationship between Mo and REE concentrations in the roots is suggestive of Mo involving in dealing with REE stress in ramie, *e.g.* the potential formation of REE molybdate complexes. A similar increase of Mo concentration was also observed in the roots of maize under 10 $\mu\text{mol/L}$ Y treatment.⁴⁸ Moreover, Mo was considered to have a synergistic effect with P,⁵⁰ which might enhance the precipitation of REEs with P and/or Mo in plants. Molybdenum was also found to increase the expression level of genes related to heavy metal (Cd) uptake, transport and sequestration.^{51,52} Though Mo concentrations in ramie shoots are not influenced by REE addition in the hydroponic experiment, high

concentrations of REE exposure may lead to Mo and P deficiency within plants in the field.⁵³ Nevertheless, the potential role of P and Mo in the uptake and accumulation of REEs in ramie remains to be proved.

4.2. REE accumulation and fractionation in ramie with increasing REE concentrations

Most studies focused on the effects of REEs individually on plants, however, the soils always contain varying concentrations of the 16 mixed REEs.^{42,54} In ramie, the whole plant and roots show HREE enrichments under 1.6–16 $\mu\text{mol/L}$ treatments or no significant fractionation under 80–800 $\mu\text{mol/L}$ treatments, suggestive of a preferential uptake of HREEs, or an unselective uptake of REEs by ramie roots depending on the range of REE concentrations in solution. Lower $\sum\text{LREE}/\sum\text{HREE}$ ratios are recorded in the leaves than the stems. This preferential accumulation of HREE in ramie leaves under 1.6–80 $\mu\text{mol/L}$ treatments could be ascribed to the preferential root-to-leaf transport of HREEs compared with LREEs. Previous studies have demonstrated that small organic acids in the xylem sap may play a key role in the HREE enrichment of wheat leaves.⁴¹ In the xylem saps of the REE hyperaccumulator plant *P. americana*, citric acid facilitated the transport of HREEs rather than LREEs, leading to a HREE enrichment in the leaves.³⁷ Therefore, the significant HREE enrichment in ramie leaves could indicate that selective complexation by organic chelators contributes to the long distance transfer of HREEs in xylem. The decrease of the HREE enrichment pattern in the leaves under higher REE concentrations (160–800 $\mu\text{mol/L}$) could be a result of toxicity. The lower root-to-shoot translocation factor of Sc compared to those of the lanthanides suggests that Sc tends to be restricted within the roots. Alternatively, Y behaves rather similarly with the lanthanides during the uptake and transport processes.

Brioschi et al.⁵⁵ speculated that the positive Ce anomaly in plant xylem sap could be associated to the formation of REE-oxyhydroxide particles during the transport process. However, no significant Ce anomaly is found during the transport process in our study. This means that the Ce positive anomalies in both the ramie roots and leaves are owing to the uptake processes. One possible reason is that Ce (III) may be oxidized to CeO₂ (IV) particles on the roots surface under aeration condition. These particles may be solubilized by organic acids secreted by ramie roots, or probably activate endocytosis of the root cells membrane,²⁹ thus promoting the preferential adsorption and uptake of Ce. Though a large part of Ce exists as CeO₂ in the soils and is thus less available than other REEs, the higher concentration of Ce and the preferential absorption of Ce on the roots may result in a positive Ce anomaly in the leaves of a series of plant species.⁵⁶ Under acid soil condition, Thomas et al.⁵⁷ found that Ce was the most toxic REE for the local plant species. Under hydroponic condition, Rodrigues et al.⁵⁸ also found that foliar application of Ce was more harmful than that of La.

4.3. Implications for phytoremediation

A suitable plant species for phytostabilization should exhibit high tolerance to pollutants, high biomass production and retain the pollutants in roots or in the rhizosphere. The REE concentrations in the soil solution (simulated by 0.001 mol/L CaCl₂ extraction) of ion-adsorption REE mine tailings in southern China ranged from 1.41 to 66 µmol/L,⁵⁹ which are generally within the REE tolerance range of ramie. Therefore, ramie might be a good candidate for the phytomanagement on these REE-rich mine soils. Rare earth elements easily form precipitates with P in the soil and soil solution. However, phosphate might also play an indispensable role in REE tolerance and detoxification within both ramie roots and shoots. Similarly, Mo may also involve in dealing with the high concentration of REEs within plants. The addition of P and Mo fertilizers could be a good management strategy for the phytostabilization on REE-contaminated soils using ramie. Cerium is thought to be less soluble in the soils in many former studies. However, future phytoremediation practices should pay more attention to Ce, as the plants could take up more this REE than its neighbours. Ramie has the advantage of producing high amounts of biomass and fibers and developing an extensive root system. As a consequence, promoting the use of ramie in mine tailings may fulfill a dual purpose of stabilizing the soils and contaminants and providing a potential economic value. Field experiments are underway to confirm to use of ramie for phytostabilization of ion-adsorption REE mine tailings.

5. Conclusions

The current hydroponic experiment revealed that ramie could adapt to REE concentrations up to 80 µmol/L, which is comparable to the REE hyperaccumulator plant *P. americana*. Moreover, REEs in ramie are mainly retained within the roots and the upward transfer is limited. Under high REE concentrations (160–800 µmol/L), the uptake of nutrients especially Ca and Mn by ramie is largely inhibited. On the contrary, P and Mo concentrations in ramie roots increase with the increase of REE concentration in the solution. Precipitation of P and Mo with REEs could be involved in the mechanisms developed by the plant to deal with the high concentrations of REE within ramie roots and shoots. Moreover, significant REE fractionations are recorded in ramie tissues during the uptake, transport and accumulation processes. The preferential adsorption and uptake of Ce by the roots and the preferential transport of HREEs by the stems could explain the positive Ce anomaly and HREE enrichment in ramie leaves, respectively. Our study supports the idea that ramie could be a good candidate for phytoremediation at REE-contaminated soils, *e.g.* ion-adsorption REE mine tailings with high concentrations of REEs in southern China.

Author contributions

Chang Liu and Ye-Tao Tang conceived the study; Chang Liu, Mei-Na Guo and Yi-Ming Yang performed the experiments; Chang Liu, Yi-Ming Yang and Wen-Shen Liu analyzed the data, prepared tables and figures; Chang Liu, Wen-Shen Liu, Hermine Huot, Jean Louis Morel and Ye-Tao Tang wrote and reviewed the manuscript; Rong-Liang Qiu, Jean Louis Morel and Ye-Tao funded and supervised all aspects of the project.

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Supplementary material

Responses of ramie (*Boehmeria nivea* L.) to increasing rare earth element (REE) concentrations in a hydroponic system

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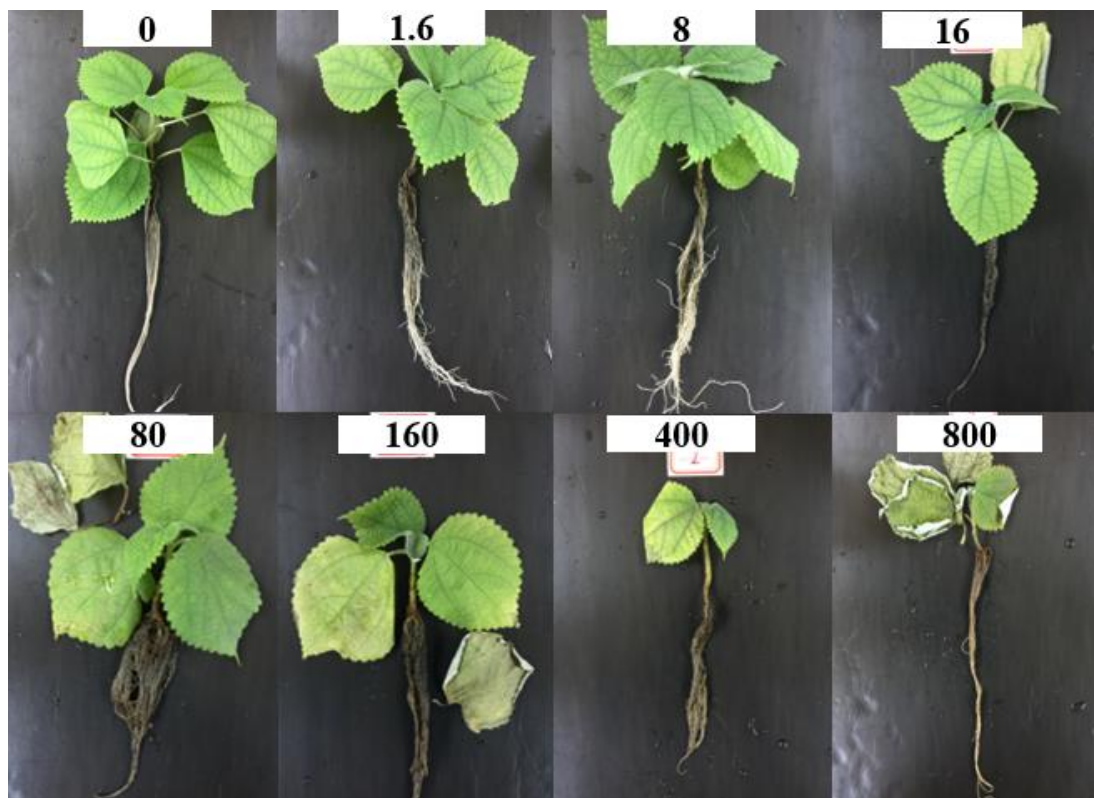


Fig. S1 Ramie growth in response to increasing REE concentrations in solution after 4 weeks treatment. The solution contains 0, 1.6, 8, 16, 80, 160, 400, 800 $\mu\text{mol/L}$ REEs (each REE with equal molar concentration, *i.e.* 0, 0.1, 0.5, 1, 5, 10, 25, 50 $\mu\text{mol/L}$).

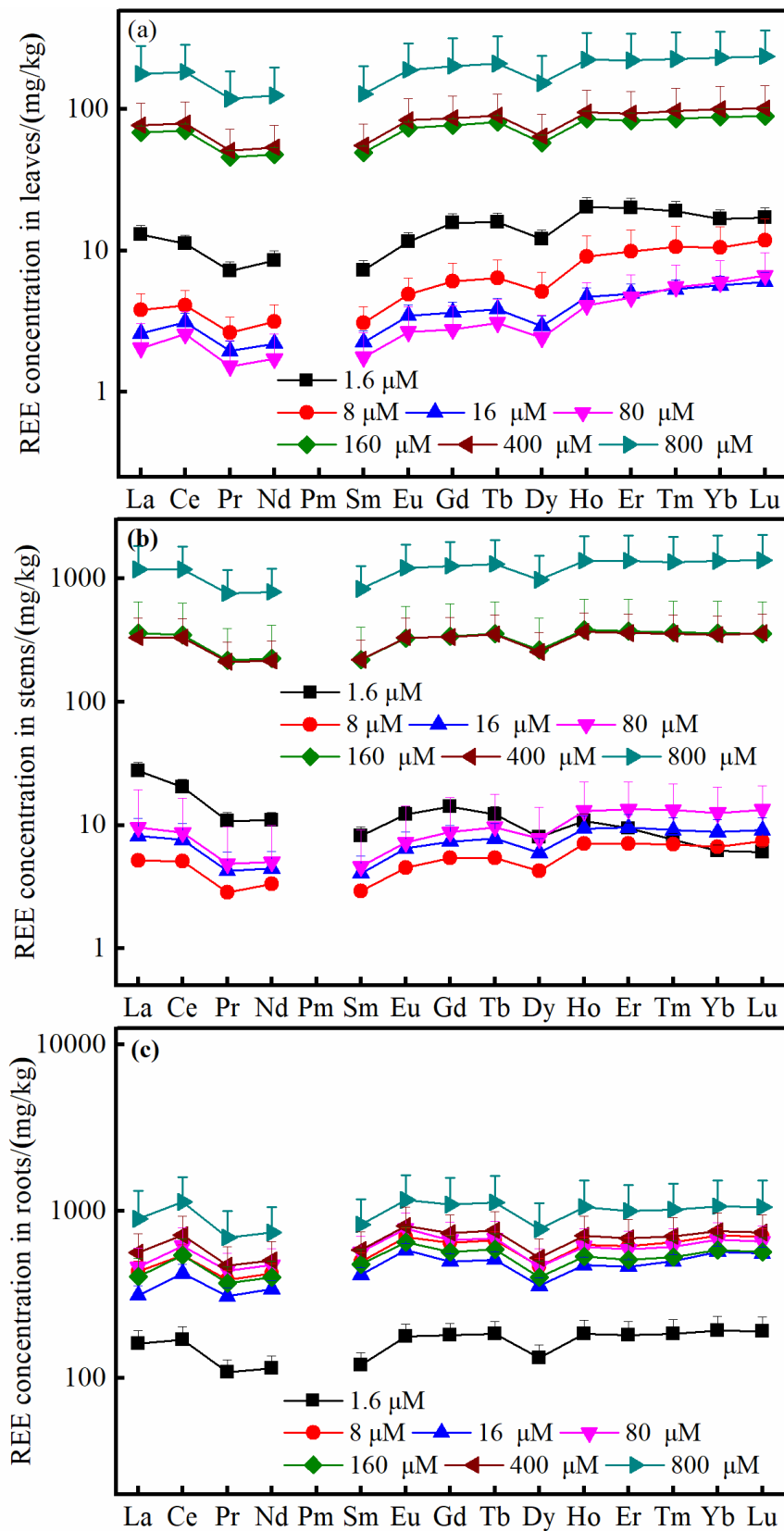


Fig. S2 Rare earth element concentrations (REE distribution patterns) in (a) leaves, (b) stems and (c) roots with increasing REE concentrations in solution.

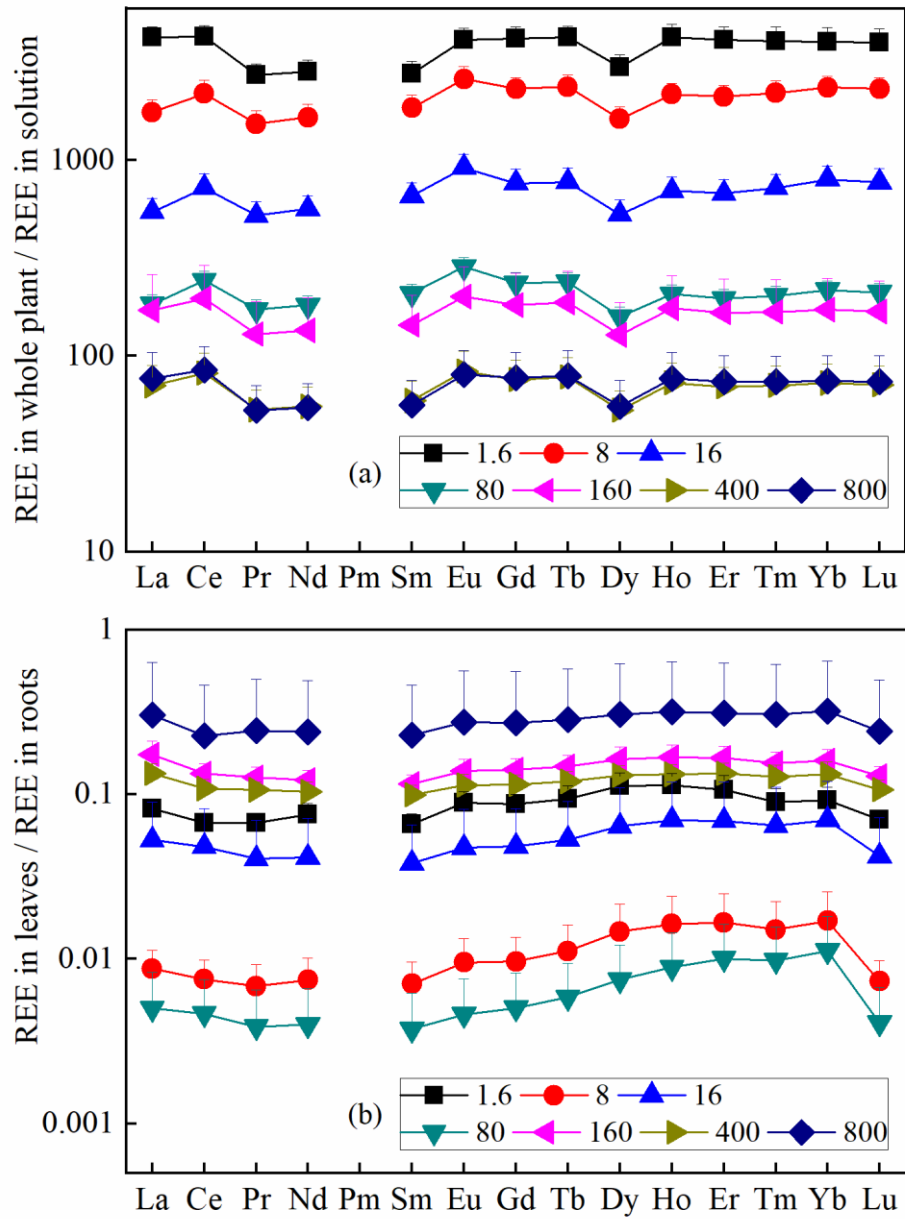


Fig. S3 Rare earth element fractionation patterns during the uptake (a) and transport (b) processes.

Table S1. Root characteristic parameters of ramie in response to increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | Total Root Length (cm) | Root Surface Area (cm^2) | Root Volume (cm^3) |
|---|------------------------------|--|----------------------------------|
| 0 | 1170 \pm 350 ^b | 212 \pm 31.2 ^c | 3.15 \pm 0.05 ^b |
| 1.6 | 1610 \pm 174 ^a | 284 \pm 9.37 ^a | 4.00 \pm 0.17 ^a |
| 8 | 1610 \pm 123 ^a | 249 \pm 5.76 ^b | 3.08 \pm 0.09 ^{bc} |
| 16 | 1290 \pm 33.9 ^b | 252 \pm 3.36 ^b | 3.94 \pm 0.21 ^a |
| 80 | 1100 \pm 71.4 ^b | 199 \pm 19.3 ^c | 2.85 \pm 0.37 ^{bcd} |
| 160 | 1050 \pm 34.3 ^b | 193 \pm 4.72 ^c | 2.82 \pm 0.05 ^{bcd} |
| 400 | 1270 \pm 14.2 ^b | 202 \pm 16.1 ^c | 2.57 \pm 0.38 ^{cd} |
| 800 | 1190 \pm 58.7 ^b | 201 \pm 11.1 ^c | 2.71 \pm 0.17 ^d |

Table S2. Ramie tolerance index (TI) with increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | Leaves | Stems | Roots |
|---|-------------------------------|-------------------------------|--------------------------------|
| 0 | 1.00 ^a | 1.00 ^b | 1.00 ^{abc} |
| 1.6 | 1.02 \pm 0.28 ^a | 1.13 \pm 0.31 ^b | 1.50 \pm 0.49 ^a |
| 8 | 0.70 \pm 0.31 ^{ab} | 1.76 \pm 1.00 ^{ab} | 1.00 \pm 0.39 ^{abc} |
| 16 | 0.91 \pm 0.18 ^a | 2.45 \pm 0.86 ^a | 1.02 \pm 0.16 ^{abc} |
| 80 | 0.71 \pm 0.26 ^{ab} | 1.97 \pm 0.89 ^{ab} | 1.08 \pm 0.54 ^{ab} |
| 160 | 0.39 \pm 0.15 ^b | 1.63 \pm 0.48 ^{ab} | 0.65 \pm 0.19 ^b |
| 400 | 0.44 \pm 0.17 ^b | 1.16 \pm 0.17 ^b | 0.62 \pm 0.29 ^b |
| 800 | 0.38 \pm 0.05 ^b | 1.27 \pm 0.63 ^{ab} | 0.49 \pm 0.12 ^c |

Table S3. Rare earth element concentrations in ramie leaves (mg/kg) with increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | 1.6 | 8 | 16 | 80 | 160 | 400 | 800 |
|---|-------------------------------|-------------------------------|-------------------------------|-------------------------------|------------------------------|-------------------------------|------------------------------|
| La | 13.0 \pm 2.00 ^{bc} | 3.80 \pm 1.16 ^{cd} | 2.58 \pm 0.46 ^{de} | 2.04 \pm 1.00 ^e | 68.2 \pm 7.70 ^b | 77.2 \pm 33.4 ^b | 178 \pm 103 ^a |
| Ce | 11.2 \pm 1.59 ^{bc} | 4.08 \pm 1.15 ^{cd} | 3.11 \pm 0.48 ^d | 2.56 \pm 1.14 ^d | 71.0 \pm 7.97 ^b | 79.3 \pm 33.7 ^b | 183 \pm 105 ^a |
| Pr | 7.16 \pm 1.18 ^{bc} | 2.61 \pm 0.78 ^{cd} | 1.95 \pm 0.34 ^{de} | 1.52 \pm 0.78 ^e | 45.7 \pm 5.18 ^b | 51.0 \pm 21.3 ^b | 118 \pm 68.0 ^a |
| Nd | 8.50 \pm 1.48 ^{bc} | 3.13 \pm 0.99 ^{cd} | 2.19 \pm 0.38 ^{de} | 1.71 \pm 0.86 ^e | 47.9 \pm 5.56 ^b | 53.6 \pm 22.9 ^b | 125 \pm 71.5 ^a |
| Sm | 7.26 \pm 1.20 ^{bc} | 3.08 \pm 0.93 ^{cd} | 2.24 \pm 0.46 ^{de} | 1.75 \pm 0.86 ^e | 49.2 \pm 5.77 ^b | 55.2 \pm 23.2 ^b | 128 \pm 73.8 ^a |
| Eu | 11.6 \pm 1.79 ^{bc} | 4.89 \pm 1.50 ^{cd} | 3.45 \pm 0.67 ^{de} | 2.66 \pm 1.35 ^e | 73.9 \pm 7.41 ^b | 83.3 \pm 35.5 ^b | 190 \pm 105 ^a |
| Gd | 15.8 \pm 2.44 ^{bc} | 6.07 \pm 2.11 ^{cd} | 3.65 \pm 0.64 ^{de} | 2.75 \pm 1.28 ^e | 77.2 \pm 8.22 ^b | 86.5 \pm 37.7 ^b | 203 \pm 117 ^a |
| Tb | 15.8 \pm 2.53 ^{bc} | 6.36 \pm 2.24 ^{cd} | 3.84 \pm 0.73 ^{de} | 3.08 \pm 1.43 ^e | 81.5 \pm 8.79 ^b | 90.2 \pm 38.1 ^b | 209 \pm 119 ^a |
| Dy | 12.1 \pm 1.81 ^{bc} | 5.12 \pm 1.90 ^{cd} | 2.92 \pm 0.54 ^{de} | 2.42 \pm 1.07 ^e | 58.0 \pm 7.36 ^b | 64.3 \pm 27.9 ^b | 152 \pm 86.5 ^a |
| Ho | 20.3 \pm 3.43 ^{bc} | 9.06 \pm 3.64 ^{cd} | 4.67 \pm 0.79 ^d | 4.08 \pm 1.85 ^d | 85.3 \pm 11.4 ^b | 95.4 \pm 41.5 ^b | 224 \pm 124 ^a |
| Er | 20.0 \pm 3.44 ^{bc} | 9.87 \pm 4.05 ^{cd} | 4.97 \pm 0.85 ^d | 4.65 \pm 2.06 ^d | 83.1 \pm 11.1 ^b | 93.0 \pm 40.8 ^b | 222 \pm 123 ^a |
| Tm | 19.0 \pm 3.19 ^{bc} | 10.6 \pm 4.33 ^{cd} | 5.31 \pm 0.87 ^d | 5.50 \pm 2.35 ^d | 85.9 \pm 10.6 ^b | 97.4 \pm 42.7 ^b | 226 \pm 124 ^a |
| Yb | 16.7 \pm 2.63 ^{bc} | 10.5 \pm 4.25 ^{cd} | 5.65 \pm 0.96 ^d | 5.93 \pm 2.57 ^d | 88.2 \pm 12.2 ^b | 100 \pm 44.3 ^b | 232 \pm 124 ^a |
| Lu | 17.1 \pm 2.88 ^{bc} | 11.8 \pm 5.03 ^{cd} | 5.99 \pm 1.04 ^d | 6.64 \pm 2.99 ^d | 89.1 \pm 12.9 ^b | 101 \pm 45.1 ^{ab} | 237 \pm 127 ^a |
| Sc | 0.72 \pm 0.39 ^f | 1.43 \pm 0.11 ^e | 1.99 \pm 0.78 ^{de} | 3.36 \pm 1.25 ^{cd} | 28.5 \pm 7.18 ^b | 19.9 \pm 7.01 ^{bc} | 56.3 \pm 17.4 ^a |
| Y | 13.9 \pm 2.17 ^{bc} | 5.69 \pm 2.38 ^c | 2.39 \pm 0.39 ^d | 2.28 \pm 0.93 ^d | 44.6 \pm 5.24 ^b | 47.5 \pm 22.1 ^b | 110 \pm 58.5 ^a |
| Σ REEs | 210 \pm 33.5 ^{bc} | 98.0 \pm 36.3 ^{cd} | 56.9 \pm 10.0 ^d | 52.9 \pm 23.3 ^d | 1080 \pm 126 ^b | 1200 \pm 516 ^b | 2790 \pm 1550 ^a |

Table S4. Rare earth element concentrations in ramie stems (mg/kg) with increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | 1.6 | 8 | 16 | 80 | 160 | 400 | 800 |
|---|-------------------------------|-------------------------------|-------------------------------|--------------------------------|-------------------------------|-------------------------------|-------------------------------|
| La | 27.6 \pm 4.62 ^{bc} | 5.13 \pm 0.59 ^d | 8.14 \pm 3.23 ^{cd} | 9.59 \pm 9.81 ^d | 362 \pm 286 ^{ab} | 332 \pm 144 ^{ab} | 1180 \pm 658 ^a |
| Ce | 20.4 \pm 3.07 ^{bc} | 5.08 \pm 0.24 ^{cd} | 7.58 \pm 2.72 ^{cd} | 8.64 \pm 8.02 ^d | 349 \pm 279 ^{bc} | 330 \pm 141 ^{ab} | 1180 \pm 640 ^a |
| Pr | 10.8 \pm 1.88 ^{bc} | 2.82 \pm 0.16 ^c | 4.26 \pm 1.77 ^c | 4.84 \pm 4.88 ^c | 218 \pm 176 ^{ab} | 211 \pm 91.4 ^{ab} | 758 \pm 406 ^a |
| Nd | 11.0 \pm 1.69 ^{bc} | 3.31 \pm 0.27 ^c | 4.44 \pm 1.65 ^c | 5.00 \pm 4.95 ^c | 226 \pm 190 ^{ab} | 215 \pm 96.0 ^{ab} | 778 \pm 419 ^a |
| Sm | 8.11 \pm 1.62 ^{bc} | 2.90 \pm 0.20 ^c | 4.04 \pm 1.58 ^c | 4.61 \pm 4.49 ^c | 219 \pm 182 ^{ab} | 219 \pm 97.6 ^{ab} | 819 \pm 441 ^a |
| Eu | 12.3 \pm 1.97 ^{bc} | 4.49 \pm 0.17 ^c | 6.44 \pm 2.28 ^c | 7.22 \pm 7.16 ^c | 329 \pm 267 ^{ab} | 333 \pm 143 ^{ab} | 1220 \pm 654 ^a |
| Gd | 14.1 \pm 2.11 ^{bc} | 5.43 \pm 0.15 ^c | 7.35 \pm 2.55 ^c | 8.82 \pm 7.91 ^c | 341 \pm 283 ^{ab} | 335 \pm 150 ^{ab} | 1260 \pm 703 ^a |
| Tb | 12.3 \pm 1.97 ^{bc} | 5.43 \pm 0.15 ^c | 7.75 \pm 2.61 ^c | 9.66 \pm 8.16 ^c | 356 \pm 288 ^{ab} | 353 \pm 152 ^{ab} | 1310 \pm 743 ^a |
| Dy | 7.96 \pm 0.95 ^{bc} | 4.22 \pm 0.23 ^c | 5.93 \pm 1.85 ^c | 7.75 \pm 6.28 ^c | 262 \pm 214 ^{ab} | 252 \pm 112 ^{ab} | 969 \pm 558 ^a |
| Ho | 10.8 \pm 1.51 ^{bc} | 7.09 \pm 0.40 ^c | 9.35 \pm 2.65 ^c | 13.1 \pm 9.26 ^c | 381 \pm 300 ^{ab} | 367 \pm 158 ^{ab} | 1390 \pm 813 ^a |
| Er | 9.41 \pm 1.09 ^b | 7.09 \pm 0.40 ^b | 9.49 \pm 2.77 ^b | 13.4 \pm 9.12 ^b | 376 \pm 301 ^a | 360 \pm 155 ^a | 1390 \pm 838 ^a |
| Tm | 7.62 \pm 0.97 ^c | 6.93 \pm 0.24 ^c | 9.04 \pm 2.46 ^c | 13.3 \pm 8.27 ^{bc} | 365 \pm 291 ^{ab} | 355 \pm 151 ^{ab} | 1360 \pm 824 ^a |
| Yb | 6.17 \pm 0.73 ^d | 6.63 \pm 0.58 ^{cd} | 8.73 \pm 2.44 ^{cd} | 12.6 \pm 7.88 ^{bc} | 359 \pm 291 ^{ab} | 349 \pm 147 ^{ab} | 1380 \pm 836 ^a |
| Lu | 6.00 \pm 0.67 ^d | 7.39 \pm 0.69 ^{cd} | 9.06 \pm 2.41 ^c | 13.3 \pm 7.62 ^{bc} | 357 \pm 284 ^b | 362 \pm 153 ^b | 1400 \pm 856 ^a |
| Sc | 1.32 \pm 1.51 ^d | 4.21 \pm 5.62 ^{cd} | 1.49 \pm 0.95 ^d | 2.34 \pm 0.71 ^{bcd} | 14.8 \pm 9.99 ^{bc} | 24.2 \pm 17.3 ^{ab} | 1500 \pm 64.4 ^a |
| Y | 8.50 \pm 1.39 ^{bc} | 5.32 \pm 0.30 ^d | 5.99 \pm 1.40 ^{cd} | 9.23 \pm 5.90 ^{cd} | 219 \pm 178 ^{ab} | 202 \pm 88.0 ^{ab} | 7660 \pm 454 ^a |
| Σ REEs | 174 \pm 23.6 ^{bc} | 83.5 \pm 6.95 ^c | 109 \pm 34.8 ^c | 143 \pm 110 ^c | 4730 \pm 3820 ^{ab} | 4600 \pm 1990 ^{ab} | 17300 \pm 9880 ^a |

Table S5. Rare earth element concentrations in ramie roots (mg/kg) with increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | 1.6 | 8 | 16 | 80 | 160 | 400 | 800 |
|---|------------------------------|-------------------------------|------------------------------|--------------------------------|--------------------------------|--------------------------------|-------------------------------|
| La | 160 \pm 31.7 ^d | 434 \pm 67.4 ^{abc} | 313 \pm 45.6 ^{cd} | 463 \pm 141 ^{abc} | 407 \pm 116 ^{bc} | 562 \pm 173 ^{ab} | 899 \pm 429 ^a |
| Ce | 169 \pm 32.8 ^d | 546 \pm 83.0 ^{bc} | 422 \pm 57.1 ^{cd} | 618 \pm 174 ^{ab} | 544 \pm 135 ^{bc} | 719 \pm 217 ^{ab} | 1130 \pm 468 ^a |
| Pr | 108 \pm 20.2 ^c | 386 \pm 55.5 ^{ab} | 308 \pm 39.4 ^{bc} | 441 \pm 117 ^{ab} | 370 \pm 94.1 ^{ab} | 471 \pm 143 ^{ab} | 696 \pm 302 ^a |
| Nd | 114 \pm 21.6 ^c | 425 \pm 60.6 ^{ab} | 341 \pm 42.3 ^{bc} | 475 \pm 121 ^{ab} | 402 \pm 103 ^{ab} | 507 \pm 149 ^{ab} | 743 \pm 316 ^a |
| Sm | 119 \pm 22.6 ^c | 496 \pm 66.8 ^{ab} | 416 \pm 42.8 ^{bc} | 568 \pm 137 ^{ab} | 480 \pm 112 ^{ab} | 585 \pm 169 ^{ab} | 833 \pm 345 ^a |
| Eu | 177 \pm 33.2 ^c | 702 \pm 92.5 ^{ab} | 583 \pm 59.3 ^{bc} | 786 \pm 189 ^{ab} | 653 \pm 147 ^{ab} | 819 \pm 235 ^{ab} | 1160 \pm 486 ^a |
| Gd | 180 \pm 33.2 ^c | 644 \pm 72.3 ^{ab} | 499 \pm 56.0 ^{bc} | 672 \pm 185 ^{ab} | 571 \pm 141 ^{ab} | 739 \pm 211 ^{ab} | 1090 \pm 494 ^a |
| Tb | 185 \pm 34.3 ^c | 668 \pm 80.9 ^{ab} | 513 \pm 56.8 ^{bc} | 685 \pm 185 ^{ab} | 592 \pm 142 ^{ab} | 767 \pm 223 ^{ab} | 1130 \pm 500 ^a |
| Dy | 131 \pm 26.4 ^c | 466 \pm 56.4 ^{ab} | 356 \pm 43.6 ^{bc} | 465 \pm 131 ^{ab} | 402 \pm 99.0 ^{ab} | 525 \pm 154 ^{ab} | 777 \pm 344 ^a |
| Ho | 184 \pm 38.5 ^c | 626 \pm 73.9 ^{ab} | 475 \pm 54.7 ^{bc} | 613 \pm 174 ^{ab} | 537 \pm 137 ^b | 713 \pm 216 ^{ab} | 1060 \pm 469 ^a |
| Er | 181 \pm 38.1 ^c | 616 \pm 79.5 ^{ab} | 465 \pm 47.3 ^{bc} | 588 \pm 171 ^{ab} | 511 \pm 131 ^{ab} | 687 \pm 205 ^{ab} | 1000 \pm 434 ^a |
| Tm | 183 \pm 40.4 ^c | 649 \pm 83.2 ^{ab} | 502 \pm 46.9 ^{bc} | 612 \pm 173 ^{ab} | 532 \pm 129 ^{abc} | 707 \pm 209 ^{ab} | 1020 \pm 436 ^a |
| Yb | 192 \pm 42.4 ^b | 712 \pm 83.2 ^a | 570 \pm 49.8 ^{ab} | 674 \pm 179 ^a | 582 \pm 136 ^{ab} | 762 \pm 216 ^a | 1070 \pm 459 ^a |
| Lu | 191 \pm 41.6 ^b | 706 \pm 78.6 ^a | 557 \pm 51.9 ^{ab} | 655 \pm 162 ^a | 569 \pm 128 ^{ab} | 745 \pm 206 ^a | 1060 \pm 463 ^a |
| Sc | 36.5 \pm 7.38 ^f | 249 \pm 30.8 ^e | 409 \pm 43.6 ^{de} | 2420 \pm 156 ^{cd} | 3820 \pm 725 ^{bc} | 5330 \pm 1400 ^b | 8430 \pm 2280 ^a |
| Y | 81.9 \pm 17.5 ^d | 244 \pm 40.5 ^{abc} | 176 \pm 29.7 ^{cd} | 240 \pm 70.4 ^{abc} | 219 \pm 59.9 ^{bc} | 297 \pm 90.1 ^{ab} | 496 \pm 235 ^a |
| Σ REEs | 2390 \pm 474 ^e | 8570 \pm 1090 ^{cd} | 6900 \pm 760 ^d | 11000 \pm 2340 ^{bc} | 11200 \pm 2400 ^{bc} | 15000 \pm 4210 ^{ab} | 22600 \pm 7750 ^a |

Table S6. Nutrient concentrations in ramie leaves (mg/kg) with increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | 0 | 1.6 | 8 | 16 | 80 | 160 | 400 | 800 |
|---|--------------------------------|--------------------------------|--------------------------------|-------------------------------|--------------------------------|-------------------------------|--------------------------------|--------------------------------|
| Na | 266 \pm 48.8 ^{bc} | 162 \pm 68.4 ^d | 167 \pm 23.5 ^d | 248 \pm 26.4 ^c | 650 \pm 69.5 ^a | 332 \pm 126 ^{bc} | 254 \pm 16.3 ^c | 449 \pm 202 ^{ab} |
| Mg | 8320 \pm 1050 ^a | 8550 \pm 246 ^a | 6630 \pm 855 ^{ab} | 5190 \pm 261 ^b | 6330 \pm 2250 ^{ab} | 6240 \pm 151 ^{ab} | 6850 \pm 1380 ^{ab} | 6420 \pm 972 ^{ab} |
| P | 1710 \pm 217 ^{ab} | 1390 \pm 340 ^b | 2110 \pm 499 ^{ab} | 1710 \pm 389 ^{ab} | 1970 \pm 949 ^{ab} | 2680 \pm 908 ^a | 2920 \pm 358 ^a | 2820 \pm 386 ^a |
| S | 3281 \pm 421 ^{abc} | 2610 \pm 599 ^{bcd} | 3480 \pm 686 ^{abc} | 1900 \pm 474 ^d | 2540 \pm 566 ^{cd} | 3780 \pm 238 ^{ab} | 3880 \pm 360 ^a | 3780 \pm 794 ^{ab} |
| K | 26000 \pm 1570 ^{ab} | 31400 \pm 5680 ^a | 30100 \pm 2430 ^{ab} | 18800 \pm 354 ^c | 23800 \pm 4060 ^b | 24600 \pm 1100 ^b | 25000 \pm 3200 ^b | 28300 \pm 4100 ^{ab} |
| Ca | 51300 \pm 5060 ^a | 43300 \pm 2100 ^{ab} | 26700 \pm 3200 ^{bc} | 23200 \pm 1460 ^c | 28700 \pm 9490 ^{bc} | 24000 \pm 3970 ^c | 26600 \pm 6930 ^{bc} | 25100 \pm 4950 ^{bc} |
| Mn | 59.6 \pm 8.99 ^a | 45.6 \pm 6.30 ^{ab} | 16.9 \pm 3.77 ^c | 15.9 \pm 1.04 ^c | 19.4 \pm 9.46 ^c | 19.0 \pm 1.99 ^{bc} | 20.6 \pm 4.14 ^{bc} | 20.6 \pm 3.76 ^{bc} |
| Fe | 160 \pm 8.91 ^a | 137 \pm 12.7 ^a | 151 \pm 23.3 ^a | 160 \pm 20.7 ^a | 260 \pm 229 ^a | 179 \pm 9.99 ^a | 171 \pm 26.9 ^a | 171 \pm 15.8 ^a |
| Cu | 15.9 \pm 2.00 ^a | 9.28 \pm 0.31 ^{ab} | 6.63 \pm 1.64 ^{bc} | 5.12 \pm 1.01 ^c | 6.00 \pm 2.56 ^c | 6.25 \pm 1.22 ^{bc} | 7.09 \pm 1.56 ^{bc} | 7.05 \pm 1.74 ^{bc} |
| Zn | 124 \pm 8.41 ^a | 93.5 \pm 21.0 ^{ab} | 54.4 \pm 11.6 ^{bc} | 46.7 \pm 2.59 ^c | 54.8 \pm 30.0 ^c | 57.0 \pm 5.56 ^{bc} | 64.9 \pm 19.1 ^{bc} | 61.3 \pm 10.0 ^{bc} |
| Mo | 14.7 \pm 1.37 ^a | 15.9 \pm 7.61 ^a | 18.6 \pm 5.15 ^a | 14.2 \pm 4.29 ^a | 12.4 \pm 2.83 ^a | 16.8 \pm 1.19 ^a | 18.3 \pm 2.12 ^a | 14.6 \pm 4.33 ^a |

Table S7. Nutrient concentrations in ramie stems (mg/kg) with increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | 0 | 1.6 | 8 | 16 | 80 | 160 | 400 | 800 |
|---|-------------------------------|--------------------------------|--------------------------------|-------------------------------|--------------------------------|--------------------------------|---------------------------------|--------------------------------|
| Na | 1000 \pm 443 ^a | 738 \pm 599 ^{ab} | 1210 \pm 323 ^a | 198 \pm 76.4 ^b | 388 \pm 68.9 ^{ab} | 414 \pm 195 ^{ab} | 500 \pm 71.9 ^{ab} | 975 \pm 547 ^a |
| Mg | 4580 \pm 1330 ^a | 4070 \pm 241 ^{ab} | 2430 \pm 626 ^{cd} | 1800 \pm 132 ^d | 2990 \pm 727 ^{abc} | 1850 \pm 174 ^d | 2530 \pm 563 ^{bcd} | 2490 \pm 616 ^{cd} |
| P | 1190 \pm 331 ^c | 1080 \pm 121 ^c | 1750 \pm 602 ^{abc} | 1330 \pm 179 ^{bc} | 1740 \pm 808 ^{bc} | 2530 \pm 615 ^{ab} | 2670 \pm 399 ^{ab} | 3090 \pm 793 ^a |
| S | 1170 \pm 758 ^c | 1300 \pm 82.0 ^{bc} | 990 \pm 104 ^c | 1440 \pm 286 ^{abc} | 2370 \pm 349 ^a | 2000 \pm 452 ^{ab} | 1630 \pm 530 ^{abc} | 2180 \pm 1020 ^{ab} |
| K | 51500 \pm 7960 ^a | 44700 \pm 8060 ^{ab} | 22500 \pm 6120 ^{cd} | 13100 \pm 575 ^e | 17700 \pm 3580 ^{de} | 16700 \pm 7270 ^{de} | 20600 \pm 3630 ^{cde} | 32800 \pm 4800 ^{bc} |
| Ca | 32500 \pm 790 ^a | 28000 \pm 2230 ^{ab} | 10700 \pm 2090 ^c | 7280 \pm 1320 ^d | 11200 \pm 2820 ^{bc} | 8560 \pm 2920 ^{cd} | 11500 \pm 2370 ^{bc} | 11800 \pm 2530 ^{bc} |
| Mn | 70.4 \pm 22.2 ^a | 57.8 \pm 15.3 ^{ab} | 16.8 \pm 6.76 ^{cd} | 10.5 \pm 2.08 ^d | 18.9 \pm 6.81 ^{bc} | 14.1 \pm 3.16 ^{cd} | 14.4 \pm 1.69 ^{cd} | 16.5 \pm 2.23 ^{bc} |
| Fe | 204 \pm 27.1 ^a | 195 \pm 81.5 ^{ab} | 168 \pm 156 ^{ab} | 111 \pm 8.27 ^{ab} | 140 \pm 96.9 ^{ab} | 127 \pm 29.6 ^{ab} | 240 \pm 84.0 ^a | 89.1 \pm 52.9 ^b |
| Cu | 13.8 \pm 2.08 ^a | 7.00 \pm 1.96 ^{ab} | 5.18 \pm 1.76 ^{bc} | 4.09 \pm 0.15 ^c | 5.79 \pm 2.06 ^{bc} | 7.28 \pm 1.34 ^{ab} | 7.76 \pm 2.16 ^{ab} | 14.9 \pm 8.38 ^a |
| Zn | 253 \pm 10.9 ^a | 245 \pm 65.0 ^a | 87.4 \pm 26.8 ^b | 50.7 \pm 5.46 ^c | 75.5 \pm 28.3 ^{bc} | 91.3 \pm 31.1 ^b | 90.9 \pm 10.3 ^b | 208 \pm 144 ^a |
| Mo | 7.05 \pm 0.88 ^a | 6.68 \pm 2.35 ^a | 7.30 \pm 3.27 ^a | 5.25 \pm 0.43 ^a | 5.21 \pm 3.68 ^a | 7.44 \pm 2.31 ^a | 8.44 \pm 1.21 ^a | 9.52 \pm 2.75 ^a |

Table S8. Nutrient concentrations in ramie roots (mg/kg) with increasing REE concentrations in solution

| Treatment ($\mu\text{mol/L}$ of REEs) | 0 | 1.6 | 8 | 16 | 80 | 160 | 400 | 800 |
|---|-------------------------------|--------------------------------|--------------------------------|-------------------------------|--------------------------------|--------------------------------|-------------------------------|-------------------------------|
| Na | 318 \pm 17.8 ^{ab} | 353 \pm 134 ^a | 229 \pm 3.52 ^{abcd} | 158 \pm 14.1 ^{cd} | 149 \pm 61.4 ^d | 204 \pm 29.0 ^{bcd} | 261 \pm 75.9 ^{abc} | 330 \pm 130 ^{ab} |
| Mg | 1940 \pm 517 ^{ab} | 2020 \pm 471 ^a | 1270 \pm 288 ^c | 1220 \pm 67.4 ^c | 1400 \pm 64.3 ^{abc} | 1280 \pm 301 ^{bc} | 1180 \pm 172 ^c | 1120 \pm 185 ^c |
| P | 1640 \pm 117 ^{cd} | 1530 \pm 267 ^d | 2200 \pm 462 ^{abc} | 2070 \pm 219 ^{bc} | 2620 \pm 1160 ^{ab} | 2800 \pm 449 ^{ab} | 3080 \pm 757 ^{ab} | 3440 \pm 724 ^a |
| S | 3360 \pm 322 ^a | 1910 \pm 335 ^b | 1780 \pm 276 ^b | 1970 \pm 93.9 ^b | 1990 \pm 144 ^b | 2100 \pm 224 ^{ab} | 1920 \pm 167 ^b | 1870 \pm 237 ^b |
| K | 36500 \pm 2340 ^a | 25800 \pm 2870 ^{ab} | 14500 \pm 1110 ^{bc} | 13100 \pm 950 ^{cd} | 11800 \pm 2090 ^{cd} | 13400 \pm 1380 ^{cd} | 13000 \pm 460 ^{cd} | 11500 \pm 2900 ^d |
| Ca | 6030 \pm 337 ^a | 5900 \pm 302 ^a | 3690 \pm 320 ^{ab} | 3070 \pm 248 ^{bc} | 3310 \pm 155 ^{bc} | 2650 \pm 735 ^c | 3350 \pm 266 ^{bc} | 3420 \pm 721 ^{bc} |
| Mn | 70.2 \pm 25.1 ^a | 40.5 \pm 1.97 ^{ab} | 17.1 \pm 3.98 ^{bc} | 12.1 \pm 1.16 ^c | 12.9 \pm 2.42 ^c | 12.7 \pm 2.05 ^c | 13.6 \pm 3.75 ^c | 16.0 \pm 3.73 ^{bc} |
| Fe | 1540 \pm 158 ^a | 1110 \pm 265 ^{ab} | 1370 \pm 157 ^{ab} | 467 \pm 615 ^b | 1320 \pm 242 ^{ab} | 1430 \pm 251 ^a | 1300 \pm 234 ^{ab} | 1490 \pm 315 ^a |
| Cu | 26.7 \pm 1.00 ^a | 12.7 \pm 1.13 ^{cd} | 13.3 \pm 1.32 ^{bcd} | 5.20 \pm 6.78 ^d | 13.0 \pm 2.03 ^{cd} | 14.1 \pm 1.20 ^{bc} | 14.9 \pm 2.69 ^{bc} | 17.8 \pm 2.67 ^{ab} |
| Zn | 512 \pm 140 ^a | 246 \pm 24.8 ^{ab} | 97.1 \pm 24.4 ^{bc} | 81.0 \pm 17.3 ^{bc} | 70.0 \pm 30.5 ^c | 78.3 \pm 13.1 ^c | 70.6 \pm 7.97 ^c | 74.9 \pm 14.5 ^c |
| Mo | 57.7 \pm 3.93 ^{de} | 36.8 \pm 9.50 ^f | 47.9 \pm 5.10 ^{ef} | 59.4 \pm 6.62 ^{de} | 137 \pm 4.55 ^{cd} | 197 \pm 33.2 ^{bc} | 229 \pm 60.5 ^{ab} | 295 \pm 70.9 ^a |