

Mineral and organic fertilization influence on removal of Ni and other metals by *Berkheya coddii* grown in ultramafic soil

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ABSTRACT: Adopting management practices that enhance biomass production and metal accumulation in hyperaccumulator species is a key strategy to improve agromining efficiency. This study evaluated the effects of mineral (NPK) and organic (cattle manure) fertilization on the growth, nutritional status, and accumulation of Ni, Co, Cr, Cu, Mn, and Zn by *Berkheya coddii* cultivated in ultramafic soil. The experiment was conducted in a greenhouse using a randomized block design with three treatments: control, NPK (100:100:120 kg ha⁻¹), and cattle manure (5 Mg ha⁻¹). Both fertilization strategies improved plant nutritional status and significantly increased biomass, with mineral fertilization (NPK) exhibiting the most pronounced effect. Although shoot Ni content declined under fertilization, particularly in the NPK treatment, this was offset by a substantial biomass gain, resulting in the highest total Ni removal (35.1 g plant⁻¹), nearly double that of the control. Nickel hyperaccumulation (>1,000 mg kg⁻¹) was observed in all treatments, with the highest foliar content in unfertilized plants. The NPK also enhanced the uptake of other metals, especially Co, Cr, Mn, Zn, and Cu, confirming its broader impact on trace element accumulation. These findings underscore the key role of biomass accumulation and fertilization management in maximizing phytoextraction efficiency. Future field-based studies should explore reduced fertilization rates to balance agronomic performance, economic viability, and environmental sustainability in Ni agromining systems.

Keywords: cattle manure, hyperaccumulators, NPK, phytomining.

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INTRODUCTION

Ultramafic soils, formed from the weathering of ferromagnesian-rich rocks such as peridotites and serpentinites, are characterized by low silica content ($\text{SiO}_2 < 45\%$) (Kierczak et al., 2021). These soils typically present nutrient imbalances, with deficiencies in phosphorus (P), potassium (K), and calcium (Ca), along with elevated content of potentially toxic metals including nickel (Ni), cobalt (Co), chromium (Cr), and manganese (Mn), and a high Mg/Ca ratio (Oze et al., 2007; Echevarria, 2018; Yang et al., 2022). Such conditions impose severe constraints on the growth of most plant species (Isnard et al., 2016). However, distinct species tolerate ultramafic soils by limiting metal uptake or translocation, enabling survival under these adverse edaphic conditions (Kazakou et al., 2008). On the other hand, certain hyperaccumulator plants have evolved physiological and biochemical adaptations that allow them to tolerate and accumulate high levels of metals, such as Ni and Co, in their aerial tissues without exhibiting phytotoxic symptoms (Ghasemi et al., 2018; van der Ent et al., 2021).

Currently, approximately 750 hyperaccumulator species have been identified, with over 70 % classified as Ni hyperaccumulators, defined by leaf Ni content exceeding $1,000 \text{ mg kg}^{-1}$ (Reeves et al., 2017). Among these, *Berkheya coddii* Roessler (Asteraceae), native to South Africa, stands out for its exceptional Ni hyperaccumulation capacity, with average foliar content of $11,600 \text{ mg kg}^{-1}$ in natural habitats and records of up to $76,000 \text{ mg kg}^{-1}$ in individual leaves (Morrey et al., 1989; Mesjasz-Przybyłowicz et al., 2004). In addition to its remarkable accumulation potential, *B. coddii* produces higher biomass than most hyperaccumulator species, making it a promising candidate for agromining, a technology that involves cultivating, harvesting, and processing metal-accumulating plants to extract valuable elements from the soil (Tisserand et al., 2022). Under optimized conditions, *B. coddii* has been reported to yield up to 22 Mg ha^{-1} of dry biomass, resulting in more than 100 kg ha^{-1} of recoverable Ni in ultramafic soils (Robinson et al., 1997).

Despite the high yields obtained under experimental conditions, recent studies have reported substantial variability in biomass and metal uptake by *B. coddii*, influenced by local climate, soil properties, and management practices (Rue et al., 2020; Hipfinger et al., 2022). Among agronomic interventions, fertilization has shown relevance in improving biomass production and metal removal efficiency in various hyperaccumulator species (Bani et al., 2015; Broadhurst and Chaney, 2016; Rosenkranz et al., 2019). For instance, mineral and organic fertilization enhanced Ni yield in *Odontarrhena chalcidica* by 54 and 73 %, respectively (Bani and Echevarria, 2019). Nonetheless, the effectiveness of fertilization strategies is highly species-dependent: while manure increased biomass and Ni accumulation in *Rinorea cf. bengalensis*, it reduced plant growth in *Phyllanthus rufuschaneyi*, an effect not observed with mineral fertilization (Nkrumah et al., 2019a,b).

In Brazil, vast areas of ultramafic soils present a high potential for agromining applications. However, no native hypernickelophore species, defined as those accumulating more than $10,000 \text{ mg kg}^{-1}$ Ni in dry biomass (Jaffré et al., 2013), have been identified to date, which has limited the development and implementation of phytotechnologies for agromining or the remediation of Ni-contaminated soils (Nascimento et al., 2022). In this context, evaluating the performance of known hypernickelophore species such as *B. coddii* in Brazilian ultramafic soils can provide valuable insights into plant-metal-soil interactions under tropical conditions. These findings may serve as a foundation for future applications once native hypernickelophore species are identified and validated for use in phytotechnologies.

The Buenos Aires ultramafic intrusion in Pernambuco, Brazil, composed predominantly of serpentinized harzburgite and orthopyroxenite (Santos et al., 2020), produces soils with notably high content of bioavailable Ni, Mn, and Co (Silva et al., 2022; Lima et al., 2024a), which makes the site especially promising for Ni agromining (Nascimento et al., 2022). While *B. coddii* has achieved Ni yields of up to 168 kg ha^{-1} in temperate environments

(Robinson et al., 1997; Rue et al., 2020), its performance under fertilization in tropical soils remains underexplored (Lima et al., 2025). We hypothesized that mineral and organic fertilization can enhance biomass production and net metal removal, particularly of Ni, by *B. coddii* cultivated in ultramafic soil. Accordingly, the objectives of this study were to: (i) quantify metal content in roots and shoots of *B. coddii*; (ii) determine translocation factors; and (iii) assess biometric parameters under mineral and organic fertilization in a Brazilian ultramafic soil.

MATERIALS AND METHODS

Soil sampling and analysis

The ultramafic soil used in the experiment was collected in the municipality of Buenos Aires, Pernambuco, Brazil (07° 45' 39.4" S; 35° 24' 45.1" W), in an area with natural subcaducifolia forest vegetation. Soil was sampled at a layer of 0 to 0.20 m after litter removal. According to the Brazilian Soil Classification System (SiBCS) (Santos et al., 2018), the soil was classified as a Neossolo Litólico, equivalent to Lithic Leptosol (IUSS Working Group WRB, 2022). The soil is derived from a serpentinized harzburgite-orthopyroxenite intrusion (Santos et al., 2020). Local climate is classified as tropical rainy (As', according to Köppen classification system), with average annual rainfall of approximately 923 mm (Jacomine, 1973; APAC, 2023).

For chemical characterization, soil samples were air-dried, sieved (<2 mm), and analyzed in triplicate according to Teixeira et al. (2017). Soil pH was measured in water at a 1:2.5 (v/v) ratio. Available P, Na, and K were extracted using Mehlich-1 solution; P was determined by colorimetry, and Na and K by flame emission photometry. Exchangeable Ca, Mg, and Al were extracted with 1.0 mol L⁻¹ KCl; Ca and Mg were determined by complexometric titration with 0.0125 mol L⁻¹ EDTA, and Al by titration with 0.025 mol L⁻¹ NaOH. Potential acidity (H+Al) was extracted with 0.5 mol L⁻¹ calcium acetate and quantified by alkalimetric titration. Soil Organic Carbon (SOC) was determined by the Walkley-Black method. The bioavailability of Ni, Co, Cr, Mn, Cu and Zn was determined by extraction with DTPA (Lindsay and Norvell, 1978). To determine the total metal content, 0.5 g of soil (<100 µm) was digested with a mixture of hydrofluoric acid (HF, ~27.6 mol L⁻¹), nitric acid (HNO₃, ~15.7 mol L⁻¹), perchloric acid (HClO₄, ~11.6 mol L⁻¹), and hydrochloric acid (HCl, ~12.1 mol L⁻¹). The digestion was performed in Teflon beakers on a heating plate at 190 °C (Alvarez et al., 2001). Particle-size distribution was determined by the hydrometer method, according to Teixeira et al. (2017).

Pot experiment, biometric parameters and chemical composition of cattle manure

The experiment was carried out in a greenhouse in a randomized block design with three treatments (control, mineral fertilization, and organic fertilization) and four replications. Treatments were applied to pots containing 5 kg of ultramafic soil. Mineral fertilizer treatment consisted of 100, 100 and 125 kg ha⁻¹ of N, P and K, in the forms of NH₄NO₃ and KH₂PO₄, respectively. Organic fertilizer consisted of 5 Mg ha⁻¹ of cattle manure, incorporated into the soil 15 days before transplanting. Its elemental composition was determined by portable X-ray fluorescence (S1 TITAN 800, Bruker) (Lima et al., 2024b) and Kjeldahl method for N, following Teixeira et al. (2017), and comprised: 17,000 mg kg⁻¹ N; 25,000 mg kg⁻¹ P; 21,000 mg kg⁻¹ K; 3,000 mg kg⁻¹ Ca; 1,100 mg kg⁻¹ Mg; 2,200 mg kg⁻¹ Fe; and trace elements including 73.0 mg kg⁻¹ Mn, 40.9 mg kg⁻¹ Zn, 7.3 mg kg⁻¹ Cu, 1.5 mg kg⁻¹ Cr, 0.6 mg kg⁻¹ Ni, and 0.4 mg kg⁻¹ cobalt. Seeds were germinated in sand and vermiculite in a 1:1 volume/volume ratio. *B. coddii* seedlings were transplanted 30 days after germination and grown for 90 days. Irrigation was carried out daily with deionized water, keeping the humidity close to 80 % of the pot capacity, and monitored by weighing the pots. Plant height and number of leaves were measured at the end of the experiment.

Table 1. Chemical and physical characteristics of Brazilian ultramafic soil

Property	Unit	Value
pH(H ₂ O)		6.4
Ca ²⁺	cmol _c dm ⁻³	4.1
Mg ²⁺	cmol _c dm ⁻³	6.1
Na ⁺	cmol _c dm ⁻³	0.1
K ⁺	cmol _c dm ⁻³	0.4
H+Al	cmol _c dm ⁻³	5.5
CEC ⁽¹⁾	cmol _c dm ⁻³	10.7
P	mg kg ⁻¹	2.0
SOC ⁽²⁾	g kg ⁻¹	7.3
SOM ⁽³⁾	g kg ⁻¹	12.3
Sand	g kg ⁻¹	298
Silt	g kg ⁻¹	431
Clay	g kg ⁻¹	271
Co (Total)	mg kg ⁻¹	214.0
Cr (Total)	mg kg ⁻¹	6,600
Cu (Total)	mg kg ⁻¹	327.0
Mn (Total)	mg kg ⁻¹	2,400
Ni (Total)	mg kg ⁻¹	2,500
Zn (Total)	mg kg ⁻¹	231.0
Co (Available)	mg kg ⁻¹	15.6
Cr (Available)	mg kg ⁻¹	0.3
Cu (Available)	mg kg ⁻¹	4.3
Mn (Available)	mg kg ⁻¹	107.0
Ni (Available)	mg kg ⁻¹	29.4
Zn (Available)	mg kg ⁻¹	0.7

⁽¹⁾ Cation exchange capacity; ⁽²⁾ Soil organic carbon; ⁽³⁾ Soil organic matter.

Analysis of plants

At the end of the experiment, the plants were separated into leaves and roots, washed with distilled water, dried in an oven at 65 °C until constant weight, and weighed to determine biomass. The material was ground in a Willey mill, and 0.50 g was digested with 8 mL of HNO₃ (14 mol L⁻¹) and 2 mL of 30 % H₂O₂. After digestion, the extracts were filtered, and the volume was adjusted to 25 mL with ultrapure water, after which the Ni, Co, Cr, Mn, Cu, and Zn content were quantified by inductively coupled plasma optical emission spectrometry (ICP-OES, Perkin Elmer 7000 DV).

Phytoextraction potential

Phytoextraction potential of metals by *B. coddii* was evaluated using the translocation factor (TF) and bioconcentration factor (BCF), according to Silva et al. (2017). Translocation factor was calculated as the ratio of metal content (mg kg⁻¹) in leaves to that in roots, indicating the ability of the plant to translocate metals to aerial parts. The BCF was determined as the ratio of metal content (mg kg⁻¹) in leaves to that in soil, reflecting the plant accumulation capacity relative to total soil content. Additionally, net removal was calculated by multiplying the metal content (mg kg⁻¹) in leaves by the corresponding leaf dry biomass (kg), representing the total amount of metal extracted per plant.

ICP-OES determination and quality control

The content of Ni, Co, Cr, Mn, Cu, and Zn in soil and plant samples was determined by ICP-OES. Analyses were performed in duplicate, with appropriate procedural blanks. To correct for potential analytical interferences, 1 mL of a 0.5 mol L⁻¹ lutetium (Lu) solution was added to all extracts as an internal standard. Two certified reference materials from the National Institute of Standards and Technology (NIST) were used to ensure analytical quality: SRM 2711a (Montana II Soil) for soils and SRM 1570a (Trace Elements in Spinach Leaves) for plant tissues. Limits of detection (LODs) were calculated based on ten replicate measurements of procedural blanks and defined as three times the standard deviation of the blank concentrations. Metal recoveries from the certified reference materials were within acceptable ranges: Ni (95-98 %), Co (101-103 %), Cr (93-94 %), Cu (97-102 %), Mn (98-101 %), and Zn (95-96 %).

Statistical analysis

The data were assessed for normality using the Shapiro-Wilk test ($p > 0.05$). They were then submitted to analysis of variance (ANOVA), and the means were compared using the Tukey test ($p < 0.05$). The same statistical procedure was applied to biometric, nutritional, and phytoextraction variables, including TF, BCF and net removal. Graphical and statistical procedures were carried out using OriginPro (2019) and SISVAR software (version 5.8).

RESULTS AND DISCUSSION

Chemical composition of *Berkheya coddii* plants

Plants grown under the control treatment exhibited low foliar nutrient content, with 7 g kg⁻¹ of N, 0.4 g kg⁻¹ of P, and 10.8 g kg⁻¹ of K, alongside moderate Mg levels (8.5 g kg⁻¹) and high Ca content (16 g kg⁻¹) (Table 2). These values reflect the oligotrophic nature of ultramafic soils, which are typically deficient in N, P, and K. Despite these nutritional constraints, no visible deficiency symptoms were observed, suggesting the activation of adaptive physiological strategies, such as growth limitation and internal nutrient recycling, commonly reported in hyperaccumulator species (Jaffré, 1980; Isnard et al., 2016).

Mineral fertilization led to significant improvements in the nutritional status of *B. coddii*, with foliar N, P, and K content increasing by 1.8, 2.4, and 1.6 fold, respectively, compared to the control. As a result, the descending order of macronutrient content in leaves shifted to N > K > Ca > Mg > P. These gains are attributed to enhanced nutrient availability in the rhizosphere and to the plant's efficient uptake and translocation mechanisms. Fertilizers supplied N, P, and K in readily available ionic forms (NH₄⁺, NO₃⁻, H₂PO₄⁻, and K⁺), which were rapidly absorbed by the roots (Yahaya et al., 2023). Furthermore, the high mobility of these nutrients within the plant, particularly through xylem transport and phloem redistribution, facilitates their effective allocation to aboveground tissues (Wang et al., 2021).

Treatment with organic fertilizer also influenced the foliar nutrient content of *B. coddii*, although to a lesser extent than mineral fertilization. Among the macronutrients, only P exhibited a significant increase, doubling relative to the control. This response is attributed to the average P content of the applied manure (1.7 % w/w), which corresponded to an estimated application rate of 85 kg ha⁻¹ of P per pot. According to Wei et al. (2022), P content in animal manures typically ranges from 0.75 to 2.25 %, with up to 70 % in soluble forms, facilitating rapid plant uptake. Pędziwiatr et al. (2024) suggested that manure application to ultramafic soils may lead to the formation of struvite (NH₄MgPO₄·6H₂O), a phosphorus compound potentially more soluble than calcium phosphates, which could enhance P availability to plants. Conversely, foliar Mg content decreased by 26 %, possibly due to competitive interactions with other cations, such as Ca²⁺ and K⁺, released during the mineralization of organic matter (Jing et al., 2024).

Table 2. Nutrient content in *Berkheya coddii* grown in ultramafic soil under different fertilizer managements

Treatment	Ca	Mg	N	P	K
	g kg ⁻¹				
Control	16 ± 2 a	8 ± 1 a	7 ± 1 b	0.4 ± 0.1 c	10 ± 2 b
Cattle manure	13 ± 1 a	6 ± 1 b	9 ± 1 b	0.7 ± 0.2 b	13 ± 1 ab
NPK	14 ± 1 a	8 ± 1 a	20 ± 1 a	1.3 ± 0.2 a	18 ± 1 a

Equal letters in the same column indicate no significant difference according to the Tukey test ($p \leq 0.05$).

No significant increases in foliar N and K content were observed following organic fertilization. This outcome is likely due to the slow mineralization rate of organic matter and the temporary immobilization of nutrients within the soil microbial biomass, particularly when low manure doses are applied (Islam et al., 2021; Pruthviraj et al., 2024). While previous studies have reported that soil N content was 1.4 to 2.5 times higher with manure application rates ranging from 2.5 to 10 % (Álvarez-López et al., 2016), the dose used in the present study was below 0.5 %, which may explain the limited nutritional response observed. These findings suggest that the effectiveness of organic fertilization in systems with hyperaccumulator plants depends on the application rate. This is consistent with the results of Bani and Echevarria (2019), who reported increased N and K levels in *O. chalcidica* fertilized with chicken manure (N: 260 kg ha⁻¹; P: 390 kg ha⁻¹; K: 260 kg ha⁻¹) or pig manure (N: 260 kg ha⁻¹; P: 105 kg ha⁻¹; K: 260 kg ha⁻¹), with effects even surpassing those of mineral fertilization (N: 65 kg ha⁻¹; P: 65 kg ha⁻¹; K: 65 kg ha⁻¹).

Biometric attributes

The treatments significantly affected both plant height and leaf number in *B. coddii* ($p \leq 0.005$). Plant height varied from 15.3 cm (control) to 81.0 cm (NPK), with mean values of 26.0 ± 8.4 cm in the control, 40.2 ± 13.0 cm with cattle manure, and 68.3 ± 9.5 cm with NPK fertilization, representing increases of 1.5 and 2.6 times, respectively, compared to the control (Figure 1). Similarly, the number of leaves was significantly higher in plants receiving mineral fertilization (32 ± 4), followed by those treated with manure (21 ± 5) and the control (14 ± 1), corresponding to increases of 2.2 and 1.4 times, respectively. These growth responses are directly related to the enhanced availability of N, P, and K in readily absorbable forms, which are essential for key physiological processes underpinning plant development (Lambers, 2022). Nitrogen plays a central role in the synthesis of amino acids and structural proteins, supporting cell division and leaf formation (Ye et al., 2022). Phosphorus is involved in ATP production and the regulation of metabolic pathways linked to primary growth, while K contributes to osmotic regulation, stomatal conductance, and photosynthetic efficiency, thereby promoting carbon assimilation (Sardans and Peñuelas, 2021).

The dry mass of the aerial part was significantly affected by the treatments ($p < 0.0001$), with mean values of 2.1 ± 0.3 g plant⁻¹ in the control, 3.9 ± 0.7 g plant⁻¹ with cattle manure, and 6.6 ± 1.1 g plant⁻¹ with NPK fertilization, representing increases of 1.8 and 3.1 times, respectively, compared to the control. These gains mirrored the increases observed in plant height and leaf number, indicating a direct response to improved nutritional management. The enhanced vegetative growth promoted by fertilization stimulated stem elongation and leaf development, resulting in a larger photosynthetic surface area and, consequently, greater biomass accumulation. Similar responses have been reported in other Ni hyperaccumulator species, such as *O. chalcidica* and *R. bengalensis*, where mineral and organic fertilization stimulated increases in plant height, leaf production, and dry mass yield (Bani and Echevarria, 2019; Nkrumah et al., 2019b).

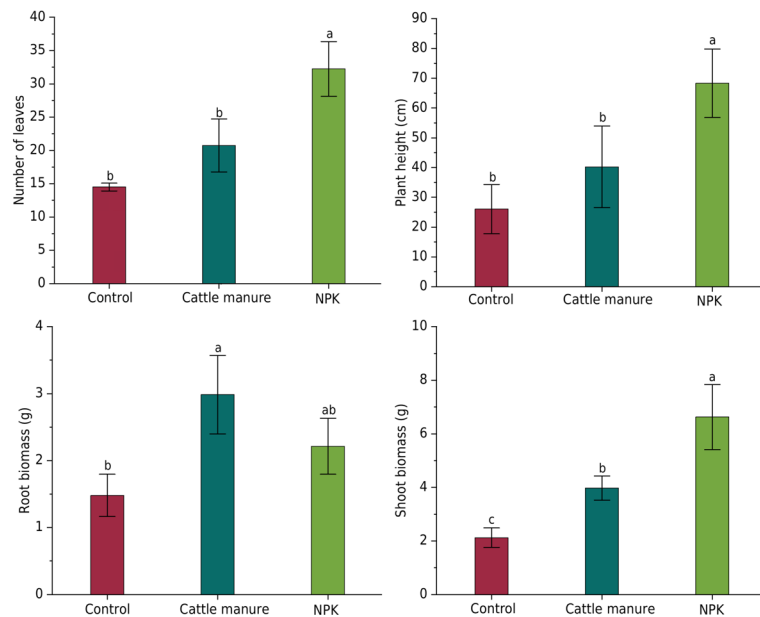


Figure 1. Effects of fertilization management on biometric parameters of *Berkheya coddii*. Means followed by the same letter do not differ significantly according to Tukey test ($p \leq 0.05$).

The high relative biomass of *B. coddii* observed in natural environments, reaching up to 300 g plant⁻¹ of dry mass in ultramafic soils of South Africa (Robinson et al., 1997), reflects adaptive mechanisms such as symbiosis with arbuscular mycorrhizal fungi (Turnau et al., 2003). Mycorrhization has been associated with increases in plant biomass and enhanced foliar content of P, K, and Ca in temperate climates (Orłowska et al., 2011). Although our study did not include treatments with mycorrhizae, the results suggest that, under tropical conditions, both organic and mineral fertilization can significantly boost biomass accumulation in *B. coddii*. While previous studies reported biomass values of 1.1-1.5 g plant⁻¹ for mycorrhized plants (Moradi et al., 2010; Orłowska et al., 2011), unfertilized plants in this study reached 2.1 g plant⁻¹, increasing to 3.9 g with organic fertilization and up to 6.6 g with mineral fertilization.

These findings highlight the potential of nutrient management strategies to enhance growth performance under tropical conditions, although further studies are needed to directly compare the effects of fertilization and mycorrhization in this context. The dry mass of roots also varied significantly among treatments ($p < 0.05$), with mean values of 1.4 ± 0.3 g in the control, 2.9 ± 0.6 g with organic fertilization, and 2.2 ± 0.5 g with NPK, corresponding to increases of 2.0 and 1.5 times, respectively. Nutrient composition of the manure supplied approximately 85 kg ha⁻¹ of nitrogen, 125 kg ha⁻¹ of phosphorus, and 105 kg ha⁻¹ of potassium. In addition to supplying nutrients, organic fertilization exerts indirect beneficial effects, including improvements in soil physical, chemical, and biological properties, which are likely to have contributed to the observed increase in root biomass (Bani et al., 2024).

Metal content in roots and leaves of *Berkheya coddii*

Metal content in the roots of *B. coddii* varied significantly among treatments (Figure 2). In the control treatment, the following decreasing order was observed: Ni (323 mg kg⁻¹) > Cr (115 mg kg⁻¹) > Cu (77 mg kg⁻¹) > Zn (65 mg kg⁻¹) > Mn (64 mg kg⁻¹) > Co (5 mg kg⁻¹). This distribution contrasts markedly with the order of metal availability estimated by DTPA extraction in the soil (Mn > Ni > Co > Cu > Zn > Cr), revealing a substantial mismatch between extractable content and actual root uptake. This discrepancy underscores the limitations of DTPA in ultramafic soils, where a significant portion of nickel is associated with residual or poorly soluble mineral fractions, rendering it inaccessible to conventional

extractants (van der Ent et al., 2019; Nascimento et al., 2022, 2024). In this study, the Ni content in roots was over 30 times higher than the DTPA-extractable value, demonstrating the remarkable capacity of *B. coddii* to mobilize and absorb this metal. In contrast, elements such as Mn and Co, which appeared highly soluble according to DTPA, exhibited relatively low content in the roots, reinforcing the species' physiological selectivity in metal uptake (Keeling et al., 2003; Rue et al., 2020).

Mineral fertilization (NPK) led to significant increases in root content of Ni ($579 \pm 34 \text{ mg kg}^{-1}$), Mn ($141 \pm 25 \text{ mg kg}^{-1}$), Cu ($127 \pm 10 \text{ mg kg}^{-1}$), Zn ($112 \pm 28 \text{ mg kg}^{-1}$), and Co ($13 \pm 3 \text{ mg kg}^{-1}$), corresponding to increases of 1.8, 2.2, 1.6, 1.7 and 2.7 times respectively, compared to the control. These increases reflect not only potential changes in the chemical availability of metals in the soil but, more importantly, a physiological response of the plant driven by improved nutritional status. The supply of N, P, and K stimulated vegetative growth and biomass accumulation, which in turn enhanced transpiration rates and the flow of water and solutes toward the roots (Tappero et al., 2007). This increased transpiration stream can elevate the concentration of metal ions, such as Ni^{2+} , in the soil solution near the rhizosphere, thereby facilitating their uptake even under conditions of limited solubility (Moradi et al., 2010). These findings suggest that fertilization not only supports plant nutrition but also enhances the physiological mechanisms underlying metal absorption, reinforcing the potential of *B. coddii* for agromining applications and highlighting its efficiency in acquiring both nutrients and trace elements in nutrient-poor environments.

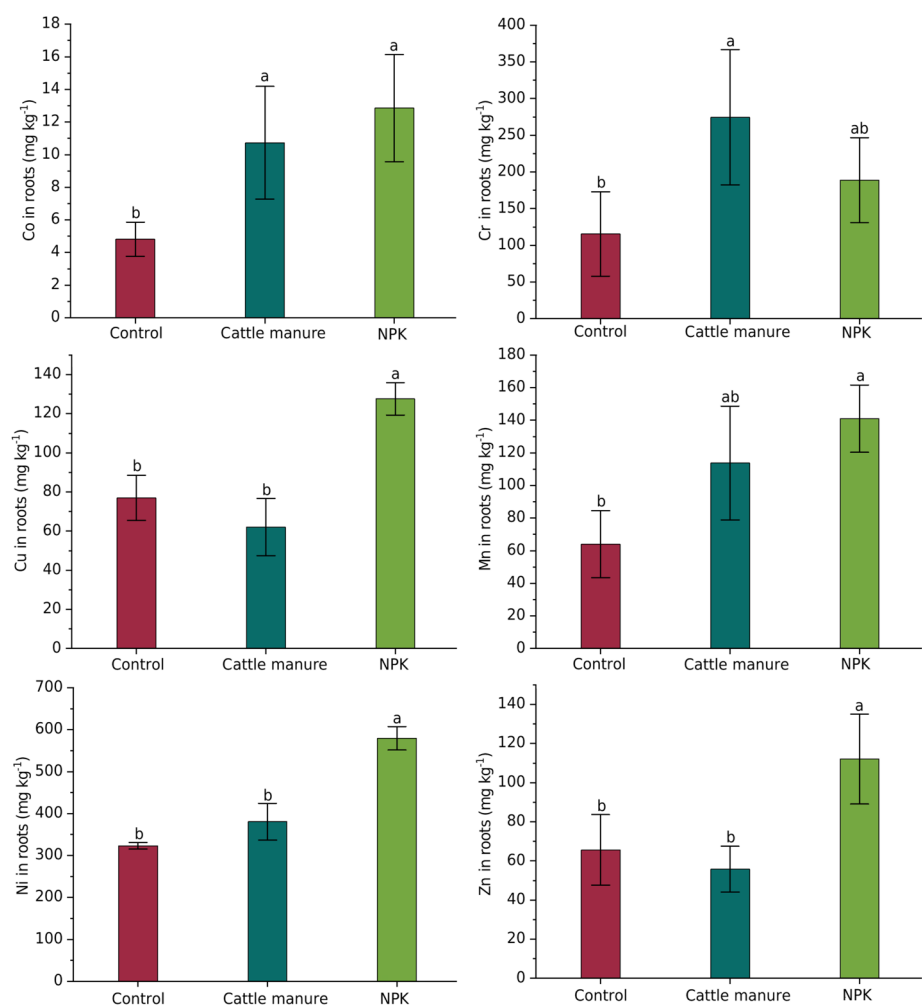


Figure 2. Mean ($\pm$ standard deviation) content of Co, Cr, Cu, Mn, Ni, and Zn in roots of *Berkheya coddii* grown in Brazilian ultramafic soil. Means followed by the same letter do not differ significantly according to Tukey test ($p \leq 0.05$).

On the other hand, fertilization with cattle manure resulted in a greater accumulation of Cr in the roots ($274 \pm 96 \text{ mg kg}^{-1}$), representing a 2.4-fold increase compared to the control, along with elevated Co levels ($11 \pm 4 \text{ mg kg}^{-1}$, +120 %). These effects are not attributed to the presence of these metals in the manure itself, but rather to the chemical and biological transformations induced by organic matter in the soil. During decomposition, manure releases low-molecular-weight organic acids that can complex and solubilize poorly labile forms of Cr and Co that were previously unavailable to plants (Miao et al., 2013; Nascimento et al., 2024). Additionally, the stimulation of microbial activity and increased root exudation contribute to rhizosphere acidification, enhancing the dissolution of metal-bearing oxides, silicates, and possibly spinel-type minerals, thereby increasing the bioavailability of these elements (van der Ent et al., 2019; Pedziwiatr et al., 2024). Despite the increases in root content of Cr, Cu, and Zn, their foliar content did not differ significantly among treatments (Figure 3). Chromium levels in the aerial part ranged from 2.6 to 6.9 mg kg^{-1} , with mean values of 4.0 mg kg^{-1} in the cattle manure treatment and 5.6 mg kg^{-1} in the control. For Cu, values ranged from 4.4 to 12.4 mg kg^{-1} , with averages of $6.7 \pm 1.7 \text{ mg kg}^{-1}$ under cattle manure and $8.7 \pm 2.1 \text{ mg kg}^{-1}$ in the control. Zinc content varied from $32 \pm 4 \text{ mg kg}^{-1}$ (cattle manure) to $53 \pm 12 \text{ mg kg}^{-1}$ (control). These results suggest that *B. coddii* possesses physiological mechanisms that restrict the translocation of certain trace elements to the aerial parts, even when root uptake is enhanced by fertilization. Such mechanisms likely involve compartmentalization in root vacuoles or selective transport at the root-shoot interface, strategies commonly reported in metal-tolerant and hyperaccumulator species (Kaur and Garg, 2021).

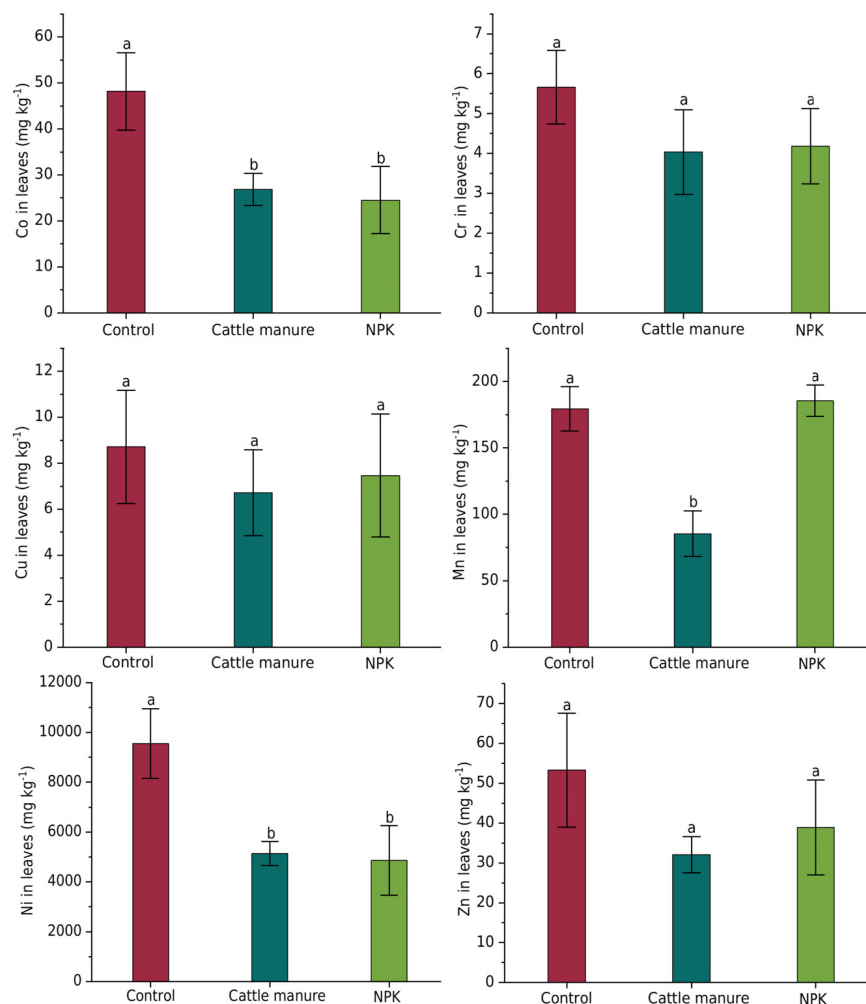


Figure 3. Mean ($\pm$ standard deviation) content of Co, Cr, Cu, Mn, Ni, and Zn in leaves of *Berkheya coddii* grown in Brazilian ultramafic soil. Means followed by the same letter do not differ significantly according to Tukey test ($p \leq 0.05$).

In the case of Cr, this pattern aligns with known retention mechanisms in the roots, such as adsorption to cell wall components, particularly at cation-exchange sites in the xylem parenchyma, and sequestration in root cell vacuoles (Kumar and Maiti, 2013). Root compartmentalization, together with the formation of apoplastic barriers, represents an effective defense strategy that restricts the systemic mobility of Cr and protects photosynthetic tissues from toxicity (Mangabeira et al., 2006; Chao and Chao, 2025). For Cu and Zn, their inherently low mobility in the xylem and high affinity for intracellular ligands lead to tightly regulated transport pathways that limit their redistribution to aerial tissues even under conditions of increased availability (Sasaki et al., 2016). Although both Cu and Zn are micronutrients, they can become phytotoxic when accumulated beyond physiological thresholds, as observed in *Hordeum vulgare* L. and *Vigna unguiculata* (L.) Walp., where their accumulation triggered oxidative stress responses, including elevated peroxidase and superoxide dismutase activity and catalase inhibition (Ogunkunle et al., 2018; Li et al., 2022).

Manganese exhibited significant variation among treatments ($p \leq 0.05$). The highest foliar content was observed under NPK fertilization ($185 \pm 10 \text{ mg kg}^{-1}$), followed by the control ($179 \pm 15 \text{ mg kg}^{-1}$), while cattle manure significantly reduced Mn levels in the leaves to $85 \pm 15 \text{ mg kg}^{-1}$, representing a 52 % decrease relative to the control. Since root Mn content remained relatively stable across treatments, the decline in foliar Mn suggests a limitation in metal translocation. This restriction may be attributed to the complexation of Mn^{2+} by low-mobility organic compounds derived from manure (Wajid et al., 2020), to the negative regulation of xylem transporters induced by organic acids, or to competition with Co^{2+} and Cr^{3+} for common transport pathways, given the increased accumulation of these elements in the roots. Similar findings were reported by Najeeb et al. (2009), who showed that the application of organic acids in *Juncus effusus* enhanced Mn retention in the roots and reduced its translocation to the shoots, supporting the hypothesis that organic compounds can modulate the systemic mobility of manganese.

In our study, the highest foliar Co content was recorded in the control treatment ($48 \pm 9 \text{ mg kg}^{-1}$), while Ni averaged $9,500 \pm 1,300 \text{ mg kg}^{-1}$, ranging from 7,400 to $10,900 \text{ mg kg}^{-1}$. These results indicate a marked predominance of Ni accumulation in the aerial tissues, which may have limited the phytoextraction of cobalt. This pattern is consistent with previous reports that describe antagonistic interactions between Ni and Co uptake (Rue et al., 2020; Pędziwiatr et al., 2024; Lima et al., 2025). Thus, the high Ni:Co ratio (11:1) in the ultramafic soil used in this study likely exerted competitive pressure at the root uptake sites, favoring preferential absorption of Ni and limiting Co translocation. Fertilization with cattle manure and NPK significantly reduced Ni content in the shoots by 46 and 49 %, respectively, resulting in mean values of $5,100 \pm 500$ and $4,800 \pm 1,100 \text{ mg kg}^{-1}$, with no significant difference between the two treatments. A similar trend was observed for Co, with content decreasing to $27 \pm 3 \text{ mg kg}^{-1}$ under manure and $24 \pm 7 \text{ mg kg}^{-1}$ under NPK, representing reductions of 44 and 49 %, respectively. This reduction pattern is consistent with previous findings showing that the application of soil amendments such as MgCO_3 , CaCO_3 , or both natural and synthetic chelating agents can reduce Ni accumulation in the aerial parts of *B. coddii* (Robinson et al., 1997, 1999; Pędziwiatr et al., 2018; Lima et al., 2025).

These reductions may be associated with ionic competition at root transport sites, particularly under mineral fertilization, when significant increases in root divalent cation content were observed (Keeling et al., 2003; Rue et al., 2020). Another plausible explanation is the dilution effect, in which the significant biomass increase promoted by fertilization reduces the relative content of Ni and Co in leaf tissues (Hipfinger et al., 2022). However, although the dilution hypothesis is consistent with the observed trends, it does not fully account for the results. Orłowska et al. (2011) demonstrated that mycorrhizal inoculation can simultaneously enhance both biomass and Ni content, suggesting that dilution alone cannot explain the decline in metal accumulation. A complementary explanation is the

restriction of Ni translocation from roots to shoots, potentially driven by the precipitation of metal phosphates in the rhizosphere due to elevated P availability from fertilization (Robinson et al., 2003). This mechanism was further supported by Orłowska et al. (2013), who observed the co-localization of Ni and P in rhizosphere tissues, indicating the physicochemical sequestration of Ni at the root level.

Translocation, bioconcentration and removal of metals

Translocation factors (TFs) varied substantially among elements and treatments, reflecting differences in metal mobility from roots to shoots. In the control treatment, *B. coddii* exhibited high translocation capacity for nickel (TF = 27) and cobalt (TF = 9), while other elements presented considerably lower values: Zn (0.7), Mn (0.3), Cu (0.2), and Cr (0.05) (Table 3). Under mineral fertilization (NPK), there was a general decline in TFs, except for Mn, which increased to 1.3. The TF for Ni dropped to 8.5 and for Co to 2.2, suggesting increased root retention, possibly due to the formation of insoluble complexes or enhanced root biomass. Similarly, Cu (0.1), Zn (0.4), and Cr (0.03) exhibited reduced translocation under NPK. In the cattle manure treatment, TFs for Ni (12.7) and Co (3.5) were higher than those observed with mineral fertilization, although still lower than in the control, indicating an intermediate effect of organic fertilization on metal mobility. Manganese (0.9) and Zn (0.5) also showed slightly higher values compared to NPK. The lowest TFs across all treatments remained those of Cr (0.02) and Cu (0.1), confirming the restricted systemic transport of these elements. This variability in translocation factors highlights the physiological selectivity of *B. coddii* in metal transport, with a pronounced preference for Ni and Co, elements tightly associated with its hyperaccumulating phenotype.

Bioconcentration factors (BCFs) were low for most of the analyzed elements, reflecting the limited ability of *B. coddii* to accumulate these metals from the soil, except for nickel. In the control treatment, the BCF for Ni was 3.7, indicating a strong affinity for this element, one of the defining characteristics of hyperaccumulator species. In contrast, the BCFs for Co, Cr, Cu, Mn, and Zn remained below 0.2 across all treatments, indicating low relative uptake of these metals. Both mineral and organic fertilization slightly reduced the BCF for Ni, to 1.9 and 2.0, respectively. This reduction may be attributed to a dilution effect associated with increased biomass or to decreased metal bioavailability resulting from interactions with other nutrients. Overall, these findings reinforce the selective absorption of Ni by *B. coddii*, even under contrasting fertilization regimes.

Table 3. Bioconcentration and translocation factors and removal of metals (mg plant⁻¹) by *Berkheya coddii* grown in Brazilian ultramafic soil under different fertilization managements

Treatment	Co	Cr	Cu	Mn	Ni	Zn
Translocation factor (TF)						
Control	9.0 ± 1.03 a	0.05 ± 0.025 a	0.2 ± 0.035 a	3.0 ± 0.91 a	26.8 ± 3.64 a	0.7 ± 0.13 a
Cattle manure	3.5 ± 0.53 b	0.02 ± 0.012 a	0.1 ± 0.022 b	0.9 ± 0.14 c	12.7 ± 2.05 b	0.5 ± 0.07 b
NPK	2.2 ± 0.79 b	0.03 ± 0.003 a	0.1 ± 0.038 b	1.3 ± 0.18 b	8.5 ± 2.42 b	0.4 ± 0.07 b
Bioconcentration factor (BCF)						
Control	0.2 ± 0.034 a	0.001 ± 0.00 a	0.03 ± 0.007 a	0.07 ± 0.006 a	3.7 ± 0.50 a	0.2 ± 0.05 a
Cattle manure	0.1 ± 0.030 b	0.001 ± 0.00 a	0.02 ± 0.007 a	0.03 ± 0.004 b	2.0 ± 0.47 b	0.1 ± 0.045 b
NPK	0.1 ± 0.014 b	0.001 ± 0.00 a	0.02 ± 0.005 a	0.07 ± 0.006 a	1.9 ± 0.163 b	0.2 ± 0.017 a
Metal removal						
Control	0.09 ± 0.02 b	0.01 ± 0.004 b	0.02 ± 0.008 b	0.38 ± 0.08 b	19.9 ± 4.62 b	0.11 ± 0.01 b
Cattle manure	0.10 ± 0.01 b	0.01 ± 0.004 b	0.03 ± 0.008 a	0.33 ± 0.07 b	20.8 ± 2.62 b	0.12 ± 0.02 b
NPK	0.18 ± 0.03 a	0.03 ± 0.012 a	0.05 ± 0.010 a	1.25 ± 0.2 a	35.1 ± 4.03 a	0.25 ± 0.08 a

Equal letters in the same column indicate no significant difference according to the Tukey test (p≤0.05).

Metal removal by *B. coddii* grown in ultramafic soil was significantly influenced by the fertilization regimes. Nickel exhibited the most pronounced response, with statistically significant differences among treatments ($p = 0.0034$). The NPK treatment resulted in the highest Ni removal, averaging $35.1 \text{ mg plant}^{-1}$ (ranging from 32.5 to $41.1 \text{ mg plant}^{-1}$), representing a 76 % increase compared to the control ($19.9 \text{ mg plant}^{-1}$). The cattle manure treatment showed an intermediate value, averaging $20.8 \text{ mg plant}^{-1}$ (range: 16.7 to $23.2 \text{ mg plant}^{-1}$), which did not differ significantly from the control. In contrast, the NPK treatment significantly outperformed cattle manure, resulting in approximately 68 % greater Ni removal.

Analysis of variance revealed significant differences among treatments in the removal of Co, Cr, Cu, Mn, and Zn ($p \leq 0.05$). In general, the removal pattern followed the same trend observed for Ni, with the sequence $\text{NPK} > \text{cattle manure} \approx \text{control}$, except for Cu, whose removal followed the pattern $\text{NPK} = \text{cattle manure} > \text{control}$. In the NPK treatment, the average removals of Co, Cr, Cu, Mn, and Zn were 0.18, 0.03, 0.04, 1.25, and $0.25 \text{ mg plant}^{-1}$, respectively. These values represented increases of 50, 60, 62, 69, and 57 % compared to the control, which consistently showed the lowest removal rates. The cattle manure treatment yielded intermediate values for all elements, with no significant differences relative to the control, except for Cu, for which removal was statistically equivalent to the NPK treatment.

CONCLUSIONS

Mineral fertilization with NPK ($100:100:120 \text{ kg ha}^{-1}$) proved to be the most effective strategy for enhancing biomass and Ni removal by *B. coddii* in Brazilian ultramafic soil. Although foliar Ni content decreased under fertilization, the substantial increase in biomass offset this reduction, resulting in approximately twice the total Ni removal compared to the control. This reinforces the central role of biomass accumulation in maximizing phytoextraction efficiency. In addition to Ni, NPK fertilization significantly increased the uptake and removal of other metals, including Co, Cr, Cu, Mn, and Zn, confirming its broader effect on trace element mobilization and absorption. Copper was the only element for which cattle manure promoted removal rates similar to those with NPK, whereas for the other metals, organic fertilization resulted in intermediate or non-significant increases.

Our findings highlight the physiological selectivity of *B. coddii* for Ni and Co, and the influence of fertilization regimes on both metal uptake and translocation patterns. While the results underscore the potential of NPK fertilization to optimize metal phytoextraction in tropical ultramafic soils, further field trials and long-term assessments are needed to validate these outcomes under real-world conditions. Future research should also explore reduced fertilization rates to balance agronomic performance with economic viability and environmental sustainability in Ni agromining systems.

DATA AVAILABILITY

The data will be provided upon reasonable request.

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