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Physicochemical soil characterisation and nutritional associations of *Laccopetalum giganteum* (Wedd) Ulbr. (Ranunculaceae) in its high- Andean habitat: a baseline for conservation

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Background: *Laccopetalum giganteum* (Wedd.) Ulbr. is an endemic species of the Peruvian Andes classified as Critically Endangered. Its conservation is constrained by limited knowledge of its soil requirements. This study aimed to characterise soil physicochemical properties in their natural habitat and evaluate their relationships with plant biometric and nutritional traits to support conservation strategies.

Methods: A total of 24 soil–plant pairs were collected from high-Andean populations near Lake Pelagatos, Ancash, Peru (4,567 m a. s. l.). Soil variables (pH, electrical conductivity, texture, macronutrients, micronutrients, and carbonates) were evaluated as independent variables, while plant variables (biometry, dry matter, and mineral composition) were considered response variables using descriptive statistics, generalised linear models (GLM), and generalised linear mixed models (GLMM).

Results: Soils were slightly alkaline (pH 7.73 ± 0.41), with moderate carbonate content ($9.22 \pm 4.76\%$), electrical conductivity of $17.8 \pm 5.4 \text{ mS}\cdot\text{m}^{-1}$, and predominantly sandy texture ($73.5 \pm 10.4\%$). Plant growth showed significant negative associations with exchangeable calcium ($\beta = -0.12$) and carbonates ($\beta = -0.06$). Positive associations were observed with zinc ($\beta = 0.10$), manganese ($\beta = 0.29$), and silt content ($\beta = 0.12$). Above-ground tissues contained $22.1 \text{ mg}\cdot\text{kg}^{-1}$ Zn and $24.2 \text{ mg}\cdot\text{kg}^{-1}$ Mn, with bioaccumulation factors of 5.8 and 43.2, respectively.

Conclusions: *L. giganteum* shows low affinity for calcareous soils and persists in marginal environments through efficient micronutrient acquisition. These findings provide a quantitative basis for substrate selection in *ex situ* propagation (pH 6.2–6.8; $\text{CaCO}_3 < 2\%$; Zn and Mn supplementation) and for identifying priority microsites for *in situ* conservation.

KEYWORDS

abiotic stress, ex-situ conservation, soil ecology, soil–plant interactions, threatened plants

1 Introduction

Feedback interactions between plants and soils play a decisive role in the dynamics of plant community assembly and composition (van der Putten et al., 2013). Soil properties such as pH, bulk density, and texture, particularly the silt and sand fractions (Guzmán et al., 2022), together with elevation and other physicochemical characteristics, exert a strong influence on the quantitative and qualitative attributes of vegetation (Shakeel, 2017). Soil variability governs key ecological processes such as speciation, dispersal, and niche selection, thereby directly influencing biodiversity patterns (Hulshof and Spasojevic, 2020).

Understanding plant–soil interactions is essential for predicting changes in the composition and productivity of plant communities (van der Putten et al., 2013). Within the Ranunculaceae family, marked ecological specificity in relation to soil conditions has been documented, representing a key consideration for the design of effective conservation programs (Gebler et al., 2022). For example, *Ranunculus sceleratus* has been reported to show positive correlations with pH, electrical conductivity (EC), organic carbon, and elements such as iron (Fe), manganese (Mn), and zinc (Zn), whereas its abundance is negatively correlated with dissolved phosphorus (P) and metals such as copper (Cu), cobalt (Co), cadmium (Cd), and lead (Pb) (Khalifa and Badr, 2021).

This edaphic specificity is particularly significant in endemic species, as less fertile environments tend to support higher levels of endemism due to specialisation within restricted habitats (de Deus et al., 2019). *Laccopetalum giganteum* represents a paradigmatic case. This tall, succulent perennial herb is the sole representative of the monotypic genus *Laccopetalum* within the Ranunculaceae family and is endemic to northern Perú (Lehnebach et al., 2007; Rodríguez et al., 2007).

Its known distribution encompasses isolated localities at elevations above 4,000 m a. s. l. in the departments of Áncash, La Libertad, and San Martín, where it grows on rocky slopes and poorly developed soils (León, 2006; Rodríguez et al., 2007). Due to its restricted distribution and the intense pressure from flower harvesting for traditional and veterinary medicine, the species has been classified as Endangered (EN) according to the International Union for Conservation of Nature criteria (León, 2006). Approximately 64% of traditional medicines prepared in northern Peru use fresh plant material, and nearly two-thirds of the medicinal plants marketed in this region are sourced from the high Andean highlands (Bussmann, 2015).

Precisely because it is a restricted and threatened endemic species, it is a priority to generate ecological knowledge to guide its

conservation. However, critical gaps remain regarding *L. giganteum*: taxonomic controversies persist (Emadzade et al., 2010; Lehnebach et al., 2007) and, more importantly, the abiotic factors that limit its establishment remain unknown. This latter aspect is particularly serious for applied conservation, as without quantitative data on its ecological requirements, it is not possible to model its potential distribution, select microsites for reintroductions or formulate substrates for *ex situ* propagation (Rodríguez et al., 2007). Among the abiotic factors influencing the establishment of *L. giganteum*, soil remains the least studied component, and its edaphic requirements have long been subject to historical uncertainty. Weberbauer (1945) assumed, without conducting soil analyses, that the species grew on calcareous soils at its type locality in Patay, La Libertad. However, subsequent collections from Conchucos recorded the species on soils derived from sandstone rather than limestone (Rodríguez et al., 2007, cited in Pera et al., 2004). León (2006) explicitly noted that this assumption required edaphological verification.

Despite this background, a critical knowledge gap remains: no study has yet characterised the physicochemical properties of the rhizosphere soils associated with *L. giganteum*, nor has any assessed how these soil properties relate to its growth and nutritional status. This lack of quantitative information on its edaphic niche leaves unresolved a fundamental question for the conservation of the species: which soil characteristics actually determine its distribution and growth?

In this context, the overall objective of this study was to characterise the physicochemical properties of soils in the natural habitats of *L. giganteum* and to assess the relationships between these soil parameters and the species' biometric traits and nutritional composition. Specifically, we tested the hypothesis that soil properties, particularly those associated with nutrient availability, act as ecological filters that explain variation in the species' vegetative performance and nutritional status. The findings provide a quantitative basis for guiding both *in situ* conservation, by identifying optimal soils to protect viable populations, and *ex situ* conservation, by designing growth substrates that replicate favourable edaphic conditions.

2 Materials and methods

2.1 Study area and sampling

The study was conducted in the natural habitats of *L. giganteum*, located in the high-Andean region on the eastern

slope of the Cordillera Blanca, in an area known as Pacracucho, near Lake Pelagatos. The site is situated at an altitude of 4,567 m a. s. l., within the district of Pampas, province of Pallasca, department of Áncash, Peru ($8^{\circ}07'49.35''$ S, $77^{\circ}45'40.64''$ W; UTM zone 18S).

This ecosystem is characterised by large rocky outcrops undergoing weathering, with stony slopes and sparse to very sparse grassland on the summits (Figure 1A). The maximum temperature ranges from 9 to 19 °C, whilst the minimum varies from −3 to 3 °C. Annual rainfall ranges from 500 to 1200 mm. The climate is rainy and cold, with dry autumn and winter (Servicio Nacional de Meteorología e Hidrología, 2021).

For sampling, 24 representative flowering adult individuals (Figure 1B) were selected during the dry season in late July 2024. The sampled plants were distributed in small, discrete clusters across the study area, reflecting the species' natural aggregation pattern. A minimum distance of approximately 10 m was maintained between individuals to minimize the risk of pseudo-replication and ensure adequate representation of spatial variability within the habitat. Each individual was collected in its entirety using destructive sampling, along with a composite rhizosphere soil sample (0–20 cm depth), thereby generating paired soil–plant samples for subsequent analysis and georeferencing.

Plant collection was conducted under a permit issued by the National Forestry and Wildlife Service (SERFOR), in accordance with the provisions of the Forestry and Wildlife Act (Ley No. 29763, 2011). A voucher specimen was deposited in the Truxillense Herbarium (HUT) at the National University of Trujillo, Perú.

2.2 Soil physicochemical analysis

Soil samples were air-dried, homogenised, and sieved through a 2 mm mesh prior to analysis. Physicochemical determinations followed standardised procedures: Soil pH was measured in a

1:2.5 soil-to-water suspension, and electrical conductivity (EC) was determined in the saturation extract. Organic carbon was analyzed using the Walkley and Black method and subsequently converted to organic matter (OM). Cation exchange capacity (CIC) was determined by extraction with 1 N ammonium acetate at pH 7, and soil texture was assessed using the Bouyoucos hydrometer method. Available (AP) was extracted using the Bray and Kurtz method. Calcium carbonate (CaCO_3) content was determined by calcimetry. Exchangeable cations such as calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+), and sodium (Na^+) and available micronutrients (Fe, Cu, Zn, and Mn) were quantified by atomic absorption spectroscopy (AAS) following extraction with diethylenetriaminepentaacetic acid (DTPA).

2.3 Plant biometric and physicochemical analysis

The following biometric variables were recorded *in-situ* for each individual: total plant height to the flower (PHF), height to the tallest leaf (HTL), number of leaves (NL), stem base diameter (SBD), flower diameter (FD), floral stem diameter (FSD) (Figures 2A–C) and root diameter (RD). In the laboratory, plant samples were washed, separated into their respective organs (root, stem, leaf, and flower, as appropriate), and oven-dried at 70 °C to constant weight to determine dry matter (DM) content. The dried material was then ground and used to determine total carbohydrates (anthrone method) and mineral element concentrations. For this purpose, samples were subjected to wet acid digestion with nitric-perchloric acid ($\text{HNO}_3\text{:HClO}_4$), after which macronutrients (nitrogen, P, K^+ , Ca^{2+} , and Mg^{2+}) and micronutrients (Fe, Cu, Zn, and Mn) were quantified using inductively coupled plasma optical emission spectroscopy (ICP-OES) and atomic absorption spectroscopy (AAS). All soil and plant analyses were conducted at the Soil,

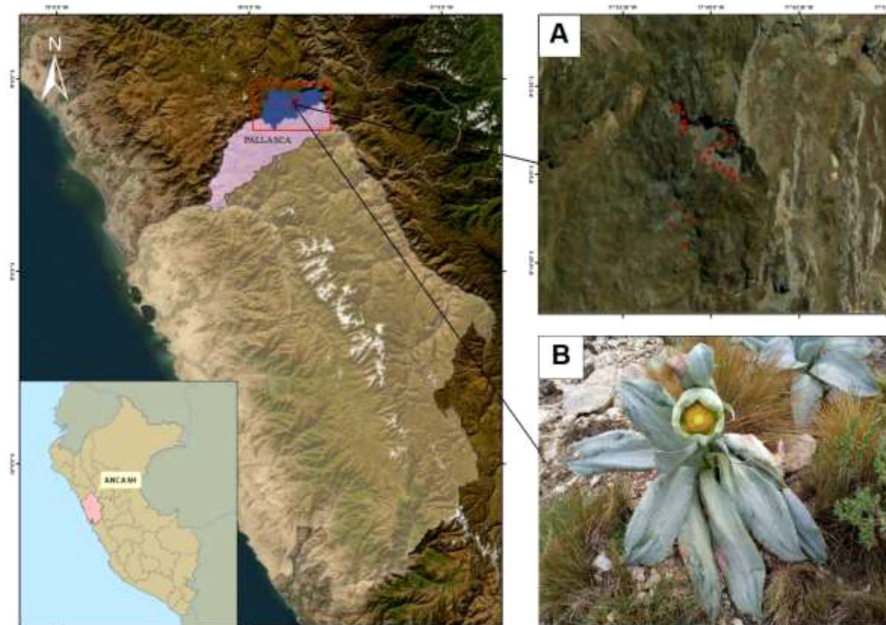


FIGURE 1
Geographic location of the study area. (A) Distribution of sampling sites and (B) *Laccopetalum giganteum* during the flowering stage.



FIGURE 2

(A) Whole plant of *Laccopetalum giganteum*. (B) Flower (locally referred to as "Botón de oro") and floral stem. (C) Natural habitat.

Water and Foliar Laboratories (LABSAF) of the National Institute of Agrarian Innovation (INIA).

2.4 Calculation of metal translocation and transfer factors

Translocation factor (TF): This index is used to evaluate the efficiency of metal transport within the plant, specifically the movement of metals from roots to above-ground tissues (Peng et al., 2020; Tripathi et al., 2021). Although sometimes referred to as accumulation, uptake, or concentration factors, these terms more appropriately describe soil-to-plant transfer indices (e.g., bioconcentration or transfer factor) rather than internal translocation (Wang et al., 2006; Chamba et al., 2017). It reflects the plant's capacity to redistribute absorbed metals to aerial parts and can be calculated using Equation 1.

$$TF = \frac{[C]_{Aerial}}{[C]_{Root}} \quad (1)$$

Where:

$[C]_{Aerial}$: It corresponds to the concentration of the element in the aerial tissues of the plant.

$[C]_{Root}$: It is the concentration of the element in the plant root.

Transfer factor (Tf): This index quantifies the efficiency of a plant's metal uptake from its surrounding substrate (soil or sediment), expressed as the ratio of the concentration in plant tissues to that in the substrate. It is calculated as shown in Equation 2 (Kacholi and Sahu, 2018; Gupta and Sinha, 2007).

$$Tf = \frac{[C]_{Plant}}{[C]_{substrate}} \quad (2)$$

Where:

$[C]_{Plant}$: Is the concentration of the metal in the whole plant.

$[C]_{substrate}$: Is the total concentration of each metal in the substrate (soil) where *Laccopetalum* grows.

2.5 Statistical analysis

A univariate descriptive analysis of soil properties was conducted, reporting the mean, coefficient of variation (CV), minimum, maximum, and 95% bootstrap confidence intervals calculated using the bias-corrected and accelerated (BCa) method. To evaluate the relationships between edaphic variables (independent) and plant response variables (dependent; biometric and compositional),

Generalised Linear Models (GLMs) and Generalised Linear Mixed Models (GLMMs) were fitted in RStudio using the glmmTMB package (Brooks et al., 2017). Prior to model fitting, explanatory variables were standardised (z-scores). Variable selection was then performed using a backwards-elimination procedure based on the Likelihood Ratio Test (LRT), implemented in the buildmer package (Voeten, 2025). To minimise multicollinearity, only variables with an adjusted variance inflation factor (VIF) < 5, estimated using the MuMIn package (Barton, 2025), were retained.

In these models, assumptions were evaluated, and the corresponding diagnostics were performed, including assessments of outliers, skewness, deviations from uniformity, and homoscedasticity, using the DHARMA package (Hartig, 2024). Table 1 summarises the selected model, the link function, the clustering factor used for random effects, and the *p*-value of the Shapiro–Wilk test for assessing the normality of the random effects. The *p*-values corresponding to the diagnostic tests are also reported. Overall, model assumptions were satisfactorily met, and diagnostic performance was adequate, except for copper, where minor deviations from homoscedasticity were observed (Table 1).

Finally, the main and interaction effects were estimated. Pairwise comparisons for interaction effects were conducted at $\alpha = 0.05$, applying false discovery rate (FDR) correction using the emmeans package (Lenth, 2025). Pairwise comparisons of the main effects were conducted based on the estimated marginal means of the modelled variable across plant organs. In contrast, comparisons of interaction

effects were performed based on the estimated strength of association between each predictor variable and the modelled variable according to plant organ. These comparisons included variables modelled using a Gamma distribution with a logarithmic link function; therefore, the estimated association, expressed as e^{β} , represents a multiplicative effect, that is, a ratio of means for the modelled variable.

3 Results

3.1 Soil physicochemical characterisation in *L. giganteum* habitats

The physicochemical properties of the soils exhibited distinct patterns across the habitat of *L. giganteum* (Table 2). Soil variability showed a pronounced spatial component, particularly for the micronutrients Cu (CV = 232.65%) and Mn (CV = 126.09%). In contrast, pH (CV = 5.35%) and sand content (CV = 14.20%) displayed comparatively low variability, indicating greater spatial stability. Chemically, the soils were characterised by slightly alkaline conditions (pH = 7.73) and low salinity (EC = 17.83 mS·m⁻¹), together with high (OM) content (11.79%) and total nitrogen (TN) concentration (10.59 mg·g⁻¹). Texturally, the soils were predominantly sandy, with sand accounting for 73.52% of the particle-size distribution, compared with 15.91% clay and 10.57% silt. The soils

TABLE 1 Model specification, assumptions, and diagnostics of the fitted models.

Variables	Distribution	Link function	AICc	Random effect		Model assumptions and diagnostics (p-values)			
				Factor	S-W	U	D	O	H
PHF	Gamma	Logarithmic	129	No	–	0.98	0.98	1.00	0.22
HTL	Lognormal	Logarithmic	109	No	–	0.80	0.61	1.00	0.24
NL	C-M-P	Logarithmic	75	No	–	0.39	0.78	1.00	0.44
SBD	Normal	Identity	123	No	–	0.93	0.79	1.00	0.35
FD	Gamma	Logarithmic	160	No	–	0.84	0.84	1.00	0.31
FSD	Normal	Identity	95	No	–	0.82	0.79	1.00	0.56
RD	Gamma	Logarithmic	44	No	–	0.95	0.73	1.00	0.48
DM	Beta	Logit	-398	Plants	0.59	0.38	0.94	0.17	0.51
TN	Gamma	Logarithmic	466	Plants	0.89	0.28	0.10	0.52	0.99
Mn	Gamma	Logarithmic	703	Plants	0.66	0.43	0.61	0.52	0.84
Zinc	Gamma	Logarithmic	791	Plants	0.09	0.38	0.08	0.17	0.44
Iron	Gamma	Logarithmic	1080	Plants	0.70	0.94	0.33	1.00	0.99
Copper	Gamma	Logarithmic	536	Plants	0.62	0.77	0.39	0.52	0.04
TC	Gamma	Logarithmic	648	Plants	0.63	0.98	0.90	0.52	0.62
Al	Gamma	Logarithmic	770	Plants	0.51	0.99	0.30	1.00	0.96
Lead	Gamma	Logarithmic	-77	Plants	0.13	0.93	0.97	0.17	0.88
Cr	Gamma	Logarithmic	-66	Plants	0.45	0.99	0.96	0.17	0.99

The table presents the distribution and link function selected to model each response variable, based on the lowest AICc value, where C-M-P denotes the Conway–Maxwell–Poisson distribution. The modelled variables included plant height to the flower (PHF), height to the tallest leaf (HTL), number of leaves (NL), stem base diameter (SBD), flower diameter (FD), floral stem diameter (FSD), root diameter (RD), dry matter (DM), total nitrogen (TN), total carbon (TC), manganese (Mn), zinc, iron, copper, aluminium (Al), lead, and chromium (Cr) in *L. giganteum*. For each modelled variable, the random-effect grouping factor is also shown, when applicable, together with the p-values from the Shapiro–Wilk normality test applied to the random-effect estimates (S-W), as well as the p-values from the diagnostic tests for uniformity (U), dispersion (D), outliers (O), and homoscedasticity (H).

TABLE 2 Descriptive statistics of soil physicochemical properties (n = 24) in *L. giganteum* habitats.

Variables	Unit	Mean	CV	Minimum	Maximum	95% CI BCa	
						Lower	Upper
TN	mg·g ⁻¹	10.59	37.09	0.97	17.28	8.89	12.11
EC	mS·m ⁻¹	17.83	30.31	10.5	29.1	15.94	20.33
pH		7.73	5.35	6.6	8.2	7.5	7.86
CaCO ₃	%	9.22	51.66	1.2	16.3	7.43	11.2
OM	%	11.79	36.08	1.3	24.1	9.9	13.44
ECEC	cmol(+)-kg ⁻¹	25.14	23.32	14.63	36.82	22.76	27.46
AP	mg·kg ⁻¹	8.53	46.34	1.1	14.3	6.89	10.11
AK	mg·kg ⁻¹	64.73	61.74	14.51	207.47	52.7	88.68
Sand	%	73.52	14.2	47	92	69.04	77.43
Silt	%	10.57	30.71	2	15	8.87	11.61
Clay	%	15.91	55.11	4	38	12.7	19.89
Calcium	cmol(+)-kg ⁻¹	21.94	26.43	10.22	33.19	19.46	24.12
Magnesium	cmol(+)-kg ⁻¹	1.17	31.54	0.71	2.01	1.05	1.35
Sodium	cmol(+)-kg ⁻¹	1.82	50.99	0.04	3.38	1.42	2.17
Potassium	cmol(+)-kg ⁻¹	0.21	45.67	0.08	0.51	0.18	0.26
Iron	mg·kg ⁻¹	25.79	39.74	13.23	48.01	22.19	30.58
Copper	mg·kg ⁻¹	0.64	232.65	0	7.09	0.28	1.79
Zinc	mg·kg ⁻¹	3.78	55.35	0.18	7.84	2.94	4.61
Manganese	mg·kg ⁻¹	0.56	126.09	0.17	3.65	0.38	1.16

The table presents a descriptive summary of soil physicochemical properties, including electrical conductivity (EC), total nitrogen (TN), calcium carbonate (CaCO₃), effective cation exchange capacity (ECEC), available phosphorus (AP), available potassium (AK), sand, silt, clay, calcium, magnesium, sodium, potassium, iron, copper, zinc, and manganese. For each variable, the mean, coefficient of variation, minimum value, and maximum value are reported. In addition, 95% confidence intervals for the mean are shown, obtained through bootstrap resampling using the bias-corrected and accelerated (BCa) method, based on 5,000 resamples and a random seed of 230,488.

also exhibited a high CEC of 25.14 cmol(+)-kg⁻¹, moderate CaCO₃ content (9.22%), and moderate levels of AP (8.53 mg·kg⁻¹) and potassium disponible (AK)(64.73 mg·kg⁻¹). Detailed values for the exchangeable cations (Ca²⁺, Mg²⁺, Na⁺, and K⁺) and micronutrients (Fe, Cu, Zn, and Mn) are presented in Table 2.

3.2 Relationships between soil properties and plant biometric traits

Soil properties exhibited distinct associations with the biometric traits of *L. giganteum*, which could be grouped into two general response patterns (Table 3). The first pattern included altitude, OM, clay content, K⁺, and Cu, all of which showed predominantly negative associations with plant traits, particularly those related to structural growth. The second pattern was represented by EC and silt content, both of which were positively associated with most of the evaluated biometric traits. Notably, silt content was the only soil variable significantly associated with root diameter (RD), exhibiting a quadratic relationship.

A third response pattern comprised Zn, Mn, and Mg²⁺, which were positively associated with most traits related to vegetative growth and floral development. However, these variables were negatively associated with the NL. In contrast, the fourth pattern included CaCO₃, Fe, P, and Ca²⁺, which showed predominantly negative associations with growth and floral development traits but were positively associated with NL.

Finally, pH and Na⁺ exhibited distinct patterns of association with the biometric traits of *L. giganteum*. Sodium was positively associated with the NL and SBD, but negatively associated FD and FSD. In contrast, pH was positively associated with plant PHF, (HTL), and FSD, while showing negative associations with NL and FD.

3.3 Relationships between soil properties and plant tissue physicochemical composition

Associations between soil properties and the physicochemical composition of *L. giganteum* tissues were identified at two levels: global associations, shared across all plant organs and summarised in Table 4, and organ-specific associations, which are illustrated in Figure 3. Moreover, marked differences in physicochemical composition were observed among roots, leaves, stems, and flowers, as presented in Figure 4. Nevertheless, these associations were not uniform across all edaphic variables or physicochemical parameters, suggesting that the effects of soil conditions on tissue composition vary according to both the soil property and the plant organ considered.

The associations shared across all plant organs revealed distinct patterns of relationships between soil variables and the physicochemical parameters of *L. giganteum* tissues. The first pattern comprised edaphic variables associated with specific tissue parameters. Within this group, altitude was positively associated with plant DM content ($e^{\beta} = 1.08$), whereas Ca²⁺ showed a positive

TABLE 3 Fixed effects of soil properties and the random effect of plant on the biometric traits of *L. giganteum*.

Factors	PHF (cm)	HTL (cm)	NL	SBD (mm)	FD (mm)	FSD (mm)	RD (mm)
Fixed main effects							
Intercept	33.36 p < 0.001	49.711 p < 0.001	12.393 p < 0.001	44.479 p < 0.001	115.232 p < 0.001	23.086 p < 0.001	4.007 p < 0.001
Altitude (Z)	0.935 p = 0.003	0.915 p < 0.001	0.959 p = 0.004	-3.862 p < 0.001	0.944 p < 0.001	-1.4 p < 0.001	
OM (Z)	0.922 p = 0.001	0.924 p < 0.001	0.911 p < 0.001	-3.62 p < 0.001		-2.613 p < 0.001	
Clay (Z)	0.933 p = 0.03	0.938 p < 0.001	0.924 p < 0.001				
Potassium (Z)	0.952 p = 0.01	0.956 p < 0.001		-1.267 p = 0.02		-1.292 p < 0.001	
Cu (Z)		0.972 p < 0.001	0.85 p < 0.001	-1.896 p < 0.001			
EC (Z)	1.161 p < 0.001	1.079 p < 0.001		5.454 p < 0.001	1.072 p < 0.001	3.938 p < 0.001	
Silt (Z)	1.273 p < 0.001	1.129 p < 0.001		3.301 p < 0.001	1.088 p < 0.001	3.345 p < 0.001	1.124 p = 0.004
Silt (Z ²)							1.072 p = 0.002
Zn (Z)	1.104 p = 0.005	1.054 p < 0.001	0.912 p < 0.001	3.864 p < 0.001	1.053 p < 0.001	3.419 p < 0.001	
Mn (Z)	1.34 p < 0.001	1.143 p < 0.001	0.816 p < 0.001	4.439 p < 0.001	1.118 p < 0.001	4.81 p < 0.001	
Mg ²⁺ (Z)	1.171 p < 0.001	1.096 p < 0.001	0.821 p < 0.001	2.863 p < 0.001	1.061 p < 0.001	3.355 p < 0.001	
pH (Z)	1.254 p < 0.001	1.064 p < 0.001	0.838 p < 0.001		0.935 p < 0.001	2.55 p < 0.001	
CaCO ₃ (Z)	0.882 p < 0.001	0.95 p < 0.001	1.048 p = 0.04	-2.495 p = 0.001	0.932 p < 0.001	-1.642 p < 0.001	
Fe (Z)	0.906 p < 0.001	0.92 p < 0.001	1.084 p < 0.001	-2.264 p = 0.003	0.93 p < 0.001	-1.973 p < 0.001	
AP (Z)	0.854 p < 0.001	0.903 p < 0.001	1.12 p < 0.001	-4.407 p < 0.001		-3.829 p < 0.001	
Ca ²⁺ (Z)	0.881 p < 0.001	0.961 p < 0.001	1.083 p < 0.001			-0.881 p = 0.02	
Na ⁺ (Z)			1.144 p < 0.001	1.671 p = 0.02	0.922 p < 0.001	-0.851 p = 0.03	

The table presents the estimated fixed main effects, together with their corresponding p-values or significance levels, for plant height to the flower (PHF), height to the tallest leaf (HTL), number of leaves (NL), stem base diameter (SBD), flower diameter (FD), floral stem diameter (FSD), and root diameter (RD) in *L. giganteum*. In models with a logarithmic link function, fixed main effects (e^{β}) are interpreted as multiplicative effects (i.e., mean ratios) on the response variable, whereas in models with an identity link, fixed main effects (β) are interpreted as additive effects. Explanatory variables were included as standardised values (z-scores).

association with TN ($e^{\beta} = 1.10$). In contrast, Fe exhibited a weak association with total carbon (TC), with an effect size close to unity ($e^{\beta} = 0.99$). Electrical conductivity was associated with plant Mn concentration through a quadratic relationship, characterised by a positive linear component ($e^{\beta} = 1.35$) and a negative quadratic component ($e^{\beta} = 0.86$).

A second pattern was characterised by soil variables exhibiting contrasting associations with DM and TN. Specifically, OM and available AP were positively associated with DM but negatively associated with TN.

A third pattern comprised soil variables that were negatively associated with DM. This group included Mg²⁺, silt content, pH, soil Mn, and EC. Despite their negative associations with DM, these variables

were positively associated with plant Mn concentration (except for Mg²⁺) and TC content (except for pH and EC). Additionally, Mg²⁺ was positively associated with TN ($e^{\beta} = 1.07$), whereas EC showed negative associations with plant Zn ($e^{\beta} = 0.819$) and Cu ($e^{\beta} = 0.760$).

Overall differences in physicochemical traits among plant organs were assessed only for models in which no significant interaction was detected between plant organ and soil variables. This criterion was satisfied for DM, TN, and plant Mn concentration. Root tissues exhibited significantly higher DM and Mn concentrations, whereas the highest TN concentrations were observed in flowers.

Plant-organ-dependent associations were detected only for TC, Zn, Fe, and Cu concentrations in plant tissues. In these cases, the

TABLE 4 Fixed effects of soil properties and the random effect of plant on the physicochemical composition of *L. giganteum* tissues.

Factors	Plant DM (%)	Plant TN (mg·kg ⁻¹)	Plant Manganese (mg·kg ⁻¹)	Plant Zinc (mg·kg ⁻¹)	Plant Iron (mg·kg ⁻¹)	Plant Copper (mg·kg ⁻¹)	Plant TC (g·kg ⁻¹)
Fixed main effects							
Intercept	0.171 p < 0.001	14.41 p < 0.001	24.19 p < 0.001	22.11 p < 0.001	199.31 p < 0.001	2.46 p < 0.001	389.75 p < 0.001
Fe (Z)							0.991 p < 0.001
Altitude (Z)	1.082 p = 0.003						
Ca (Z)		1.10 p < 0.001					
K (Z)			1.138 p < 0.001		1.105 p = 0.01		
Cu (Z)			1.122 p < 0.001			1.323 p < 0.001	
OM (Z)	1.118 p = 0.001	0.934 p = 0.03					
AP (Z)	1.182 p < 0.001	0.920 p = 0.003			1.102 p = 0.03		0.993 p = 0.003
Mg (Z)	0.820 p < 0.001	1.079 p = 0.02					1.006 p = 0.04
Silt (Z)	0.891 p < 0.001		1.253 p < 0.001				1.007 p = 0.01
pH (Z)	0.873 p < 0.001		1.130 p < 0.001				
Mn (Z)	0.840 p < 0.001		1.136 p < 0.001				1.006 p = 0.04
EC (Z)	0.888 p < 0.001		1.074 p < 0.001	0.819 p = 0.002		0.760 p < 0.001	
EC (Z2)			1.345 p < 0.001				
EC (Z3)			0.858 p < 0.001				
Zn (Z)	0.923 p = 0.03				0.845 p = 0.002		
Clay (Z)		0.933 p = 0.003	0.845 p < 0.001			0.749 p < 0.001	0.988 p < 0.001
Random effect (σ̂)							
Plant	0.00	0.00	0.00	0.16	0.00	0.22	0.002

The table presents the estimated fixed main effects, together with their corresponding p-values or significance levels, for dry matter (DM), total nitrogen (TN), total carbon (TC), manganese, zinc, iron, and copper in *L. giganteum*. In models with a logarithmic link function, fixed main effects (e^{β}) are interpreted as multiplicative effects (i.e., mean ratios) on the response variable; in models with a logit link, they are interpreted as odds ratios. The estimated standard deviation of the random effects is also reported, with plants considered as the grouping factor. Explanatory variables were included as standardised values (z-scores).

direction and/or magnitude of the associations varied among at least one of the evaluated organs (roots, leaves, stems, or flowers). For TC (Figures 3A, B), the associations were primarily related to Ca^{2+} and K^{+} . For plant Zn concentration (Figures 3C–F), the main associations were related to silt content, Ca^{2+} , soil Mn, and OM. Plant Fe concentration (Figures 3G–J) was chiefly associated with Na^{+} , EC, Ca^{2+} , and Mg^{2+} , whereas plant Cu concentration (Figures 3K–N) exhibited distinct association patterns with soil Mn, Ca^{2+} , Na^{+} , and P. Overall, Figure 3 demonstrates that the influence of plant organ on soil–tissue relationships was not

uniform; however, leaves exhibited the most pronounced responses across several of the soil–plant associations identified.

3.4 Potentially toxic trace element concentrations and their relationship with soil properties

Associations between soil properties and the concentrations of potentially toxic trace elements (PTEs) in *L. giganteum* tissues were identified at two levels: general associations, common to all plant

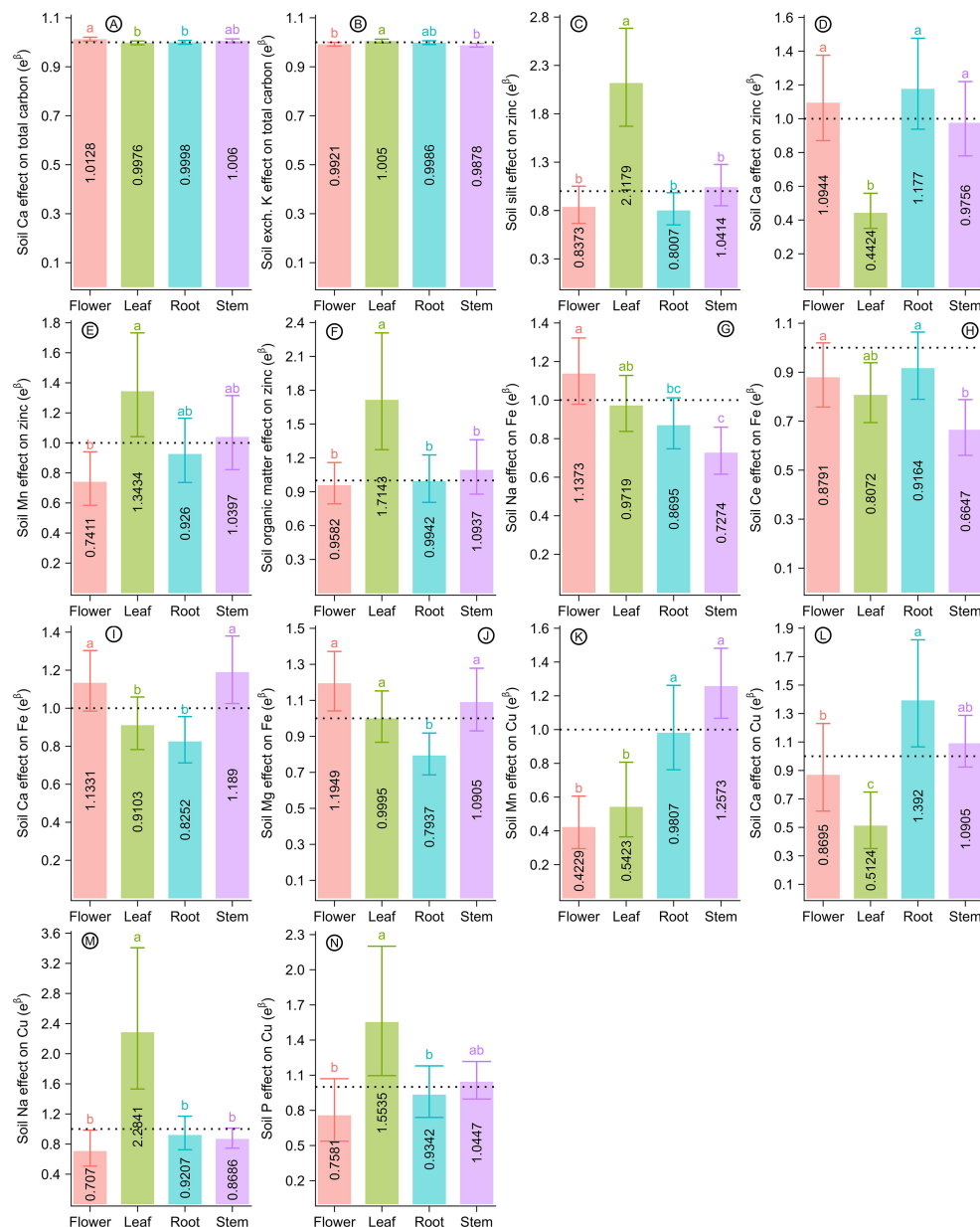


FIGURE 3

Interaction effects of soil factors on the physicochemical composition of plant organs, based on generalized linear mixed models (GLMMs). Bar plots show the estimated effects of soil physicochemical properties on carbon (A, B), zinc (C–F), iron (G–J), and copper (K–N) in different plant organs: flower, leaf, root, and stem. In each panel (A–N), the vertical axis corresponds to the magnitude of the multiplicative effect (e^{β}), whereas the horizontal axis corresponds to the plant organs, represented by bars. Each bar shows the estimated effect and its 95% confidence interval. Different lowercase letters above the upper limits of the confidence intervals indicate significant differences ($p < 0.05$, FDR-adjusted) in the magnitude of the soil–plant effect among plant organs. The dashed line indicates the reference value ($e^{\beta} = 1$). Confidence intervals located entirely above this line indicate a positive effect; those located entirely below it indicate a negative effect; and those including the reference value indicate that the effect is not statistically significant.

organs and summarised in Table 5, and organ-specific associations, shown in Figure 5. However, these associations were not consistent across all PTEs assessed.

The general associations were primarily driven by EC and altitude. Soil EC was negatively associated with Pb concentrations in *L. giganteum* tissues and exhibited a quadratic relationship with plant Al concentrations. In contrast, altitude was negatively associated with plant Cr concentrations.

Organ-specific associations were detected primarily between soil properties and the concentrations of Al, Pb, and Cr in *L.*

giganteum tissues, with the patterns of relationships varying among flowers, leaves, roots, and stems. For Al, the organ-dependent associations mainly involved altitude, pH, P, Cu, and soil textural fractions (Figures 5A–F). In the case of Pb, the associations were primarily influenced by altitude, CaCO_3 , Zn, and K^+ (Figures 5G–J). For Cr, the organ-dependent associations were primarily related to Zn and Ca^{2+} (Figures 5K, L). Overall, Figure 5 demonstrates that the modulation of soil–tissue relationships by plant organ was not uniform; however, leaves exhibited the most pronounced modulation across several of the associations observed.

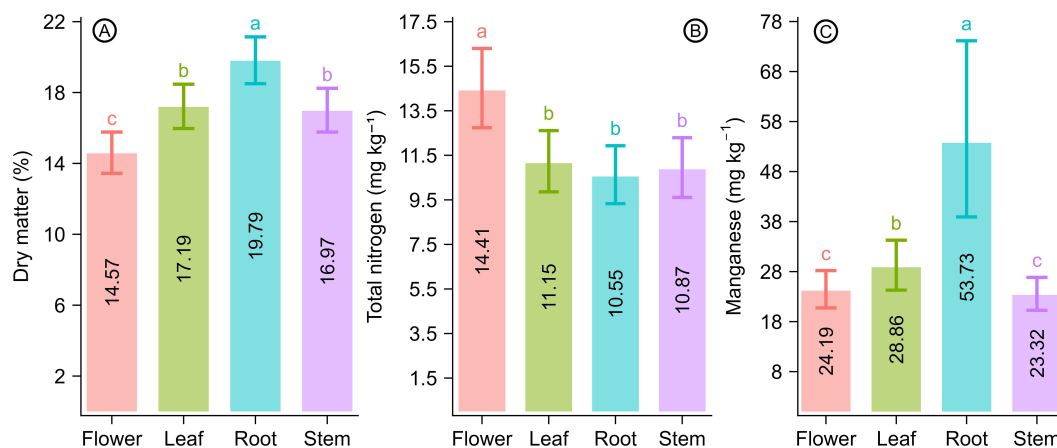


FIGURE 4

Fixed main effects of plant organs on physicochemical variables of the plant. Bar plots show the estimated effects of plant organs (flower, leaf, root, and stem) on dry matter (A), total nitrogen (B), and manganese (C). In each panel (A–C), the vertical axis corresponds to the adjusted mean, whereas the horizontal axis corresponds to the plant organs, represented by bars. Each bar contains the adjusted mean and its 95% confidence interval. Different lowercase letters above the upper limits of the confidence intervals indicate significant differences among plant organs ($p < 0.05$, FDR-adjusted).

3.5 Mobilisation and transfer of metals in *L. giganteum*

The mobilisation and transfer of metals in *L. giganteum* exhibited distinct patterns between internal translocation and soil-to-plant uptake (Figure 6). Regarding translocation from roots to aboveground tissues, Cr showed the highest translocation factor (TF), followed by Mn and Pb, indicating a greater capacity for movement of these elements to aboveground organs. Fe exhibited a mean TF value slightly above 1, although close to the reference threshold value, suggesting relatively low translocation. In contrast, Al, Cu, and Zn displayed TF values below 1, indicating limited translocation to aerial tissues and a greater tendency to be retained within the roots (Figure 6A).

Regarding soil-to-plant transfer, Cu and Zn were the only elements with transfer factor (Tf) values greater than 1, indicating preferential accumulation in *L. giganteum* tissues relative to their concentrations in the soil. In contrast, all other metals exhibited Tf values below 1, suggesting comparatively limited uptake and transfer from soil to plant tissues (Figure 6B).

4 Discussions

The findings regarding *L. giganteum* redefine its functional ecology by refuting its presumed calcicolous affinity and suggest that it should instead be recognised as a species tolerant of, or potentially restricted to, Ca^{2+} stress conditions. Its persistence in high andean niches indicates an adaptive strategy based on the active uptake of poorly available micronutrients (Zn and Mn) and the efficient phytoextraction of heavy metals (Cr, Mn, and Pb; $\text{TF} > 1$). This study represents the first attempt to elucidate the soil-plant relationships of this species and offers new perspectives for the design of more effective conservation programs, both *in situ* and *ex situ*, focused on this endemic species.

4.1 A marginal habitat: stress due to alkalinity, salinity, and low water retention

Alpine soils remain largely understudied due to their inaccessibility, and their pronounced heterogeneity complicates comparisons across studies (Donhauser and Frey, 2018). In this context, the soils in which *L. giganteum* thrives exhibit characteristics typical of environments subjected to multiple abiotic stressors, including a slightly alkaline pH (7.73), moderate carbonate content (9.22%), and a predominantly sandy texture (73.5% sand). This edaphic profile is consistent with descriptions of rocky habitats composed of sandstone and limited pedogenic development reported for the species (Rodríguez et al., 2007). Similarly, *Ranunculus macropetalus* (Ranunculaceae) in the high Andean region of Ancash has been documented growing on rocky and stony slopes and on the summits of large rock outcrops, surrounded by sparse grasslands (Cano et al., 2011; Trinidad et al., 2013). The combination of a slightly alkaline pH and low water-retention capacity associated with sandy texture suggests that the plant may be subject to persistent physiological drought, even in high-mountain ecosystems. In contrast, related species such as *Krapfia macropetala* (Ranunculaceae) have been reported to grow in soils with a pH below 7 and a loamy-sandy texture (Bravo et al., 2025). Notably, sandy soils are typically associated with relatively low CEC; however, the high OM content observed in soils inhabited by *Laccopetalum* appears to be driving a CEC of $25.14 \text{ cmol}(+)\cdot\text{kg}^{-1}$. Furthermore, strongly calcareous soils can reach CEC values as high as $67.85 \text{ cmol}(+)\cdot\text{kg}^{-1}$ (Kulkarni et al., 2020), with CaCO_3 showing a strong positive relationship with CEC (Razzaghi et al., 2021). In addition, sandy soils generally exhibit low water retention capacity and provide limited buffering against environmental stressors (Donhauser and Frey, 2018), particularly in surface horizons (Praeg et al., 2019) and on steep, rocky slopes characteristic of the Peruvian Andes, where the Ranunculaceae family are commonly found (Roca et al., 2014). Within this context, our results revealed high spatial variability ($\text{CV} > 100\%$ for Cu and Mn), indicating a

TABLE 5 Fixed effects of soil properties and the random effect of plant on trace element concentrations in *L. giganteum* tissues.

Factors	Aluminium (mg·kg ⁻¹)	Lead (mg·kg ⁻¹)	Chromium (mg·kg ⁻¹)
Fixed main effects			
Intercept	21.65 p < 0.001	0.73 p < 0.001	0.62 p < 0.001
Electrical conductivity (Z)	0.770 p < 0.001	0.937 p < 0.001	
Electrical conductivity (Z2)	1.182 p = 0.002		
Altitude (Z)			0.936 p = 0.007
Random effect ($\hat{\sigma}$)			
Plant	0.09	0.00	0.00

The table presents the estimated fixed main effects, together with their corresponding p-values or significance levels, for aluminium, lead, and chromium in *L. giganteum*. In these models, fixed main effects (e^{β}) are interpreted as multiplicative effects (i.e., mean ratios) on the response variable. The estimated standard deviation of the random effects is also reported, with plants considered as the grouping factor. Explanatory variables were included as standardised values (z-scores).

patchy or microsite-driven distribution, a common ecological strategy in extreme environments that allows plants to exploit localised heterogeneity in resource availability (Gallardo et al., 2010). This pattern likely explains the naturally fragmented populations of *Laccopetalum* (León, 2006). A comparable distribution has been reported for *Krapfia weberbaueri* (Ranunculaceae) in the Cordillera Blanca (Ancash), where it occurs in discrete patches between 4,200 and 4,800 m a. s. l (Roca et al., 2014).

4.2 Response to calcium and carbonates: evidence of tolerance rather than preference

The soils in the sampled areas, located between 4,000 and 5,000 m a. s. l., exhibit characteristics typical of Rendzinas within the paramosolic region (Zamora, 1972); that is, locally distributed, weakly developed soils formed from calcareous parent material on sloping terrain. Within this context, a key finding of the present study is the consistent negative association between *L. giganteum* growth and soil levels of Ca²⁺ and CaCO₃. This result provides the first quantitative evidence supporting León (2006) observation that questions Weberbauer (1945) hypothesis of a calcicolous affinity. To date, the species has only been documented on sandstone substrates in Conchucos (Ancash), as reported by Pera et al. (2004) and cited in Rodríguez et al. (2007).

Our results indicate that *L. giganteum* tolerates, but does not thrive under, high Ca conditions. Previous studies have shown that at pH > 5.5, Ca²⁺ can contribute between 59% and 83% to the effective cation exchange capacity (ECEC) of soils (Solly et al., 2020). In this context, the suppressive effects observed in our models ($e^{\beta} < 1$) may be explained by several interacting mechanisms. First, elevated bicarbonate concentrations may induce iron chlorosis. Although the measured DTPA-extractable Fe (25.79 mg·kg⁻¹) suggests marginally adequate levels, its effective availability is reduced at pH 7.73 due

to decreased solubility and slower reduction kinetics (Barton and Abadía, 2006). Furthermore, increases in soil organic carbon, together with elevated Ca and pH, may inhibit the crystallisation of disordered iron forms, further limiting Fe availability (Rowley et al., 2020). This condition is directly associated with reduced photosynthetic capacity (Lucena, 2000). Second, ionic competition may reduce the availability of other essential cations, such as K⁺ and Mg²⁺. It should be noted that disproportionate cation concentrations can lead to imbalances in the soil. Similarly, deviations from the typical cation dominance sequence (Ca²⁺ > Mg²⁺ > K⁺ > Na⁺) may result in ionic imbalances in plants (Seifu et al., 2023). In high-mountain environments, especially on steep slopes with coarse-textured soils, CEC and exchangeable Mg²⁺ and K⁺ levels are often low due to the abrupt changes characteristic of high-mountain terrain (Khuvsugul et al., 2022). Additionally, calcareous soils are frequently associated with shallow soil profiles and reduced water retention capacity. These constraints are exacerbated in steep, coarse-textured soils, where infiltration is limited, and the risks of nutrient loss and erosion are high, often accompanied by a shallow, truncated A horizon (Alene and Haftu, 2024). In contrast, soils under native Andean forests tend to exhibit greater infiltration capacity (Chávez-Collantes et al., 2025). Taken together, these findings highlight that the distinction between tolerance and preference is critical for conservation. Substrates designed for *ex situ* propagation should therefore aim to optimise growth conditions by adjusting pH and reducing carbonate content, rather than replicating the original edaphic environment.

4.3 A micronutrient-specialist strategy: efficient acquisition of Zn and Mn

The strongest positive associations between soil properties and plant growth were observed for the micronutrients Zn and Mn. In alkaline soils, the availability of these elements is markedly reduced due to precipitation and immobilisation processes (Alloway, 2008). In particular, low Zn availability is commonly associated with high CaCO₃ content (>15%) in neutral to alkaline-soils (Seifu et al., 2023), whereas reduced Mn availability is primarily related to increasing soil pH (Hailegnaw et al., 2020). The strong predictive role of these micronutrients suggests that *L. giganteum* may have developed efficient acquisition mechanisms under limiting conditions, potentially involving the exudation of phytosiderophores or rhizosphere acidification (Marschner, 2011).

In this context, the growth and productivity of aromatic and medicinal plants are closely related to abiotic stressors, such as drought, temperature extremes, and heavy metal exposure, which can constrain plant development (Kadioğlu, 2025). These stressors are known to alter metabolic processes and, consequently, may increase the synthesis of bioactive compounds, thereby enhancing their potential benefits for human health. Within this framework, *L. giganteum* is regarded as a medicinal species highly valued by traditional healers in the region. According to local knowledge, it is used to treat conditions such as bronchitis, asthma, and rheumatism (Bussmann, 2015). Additionally, it has been attributed antiparasitic properties and is believed to stimulate fertility in animals (Rodríguez et al., 2007). Despite its widespread traditional

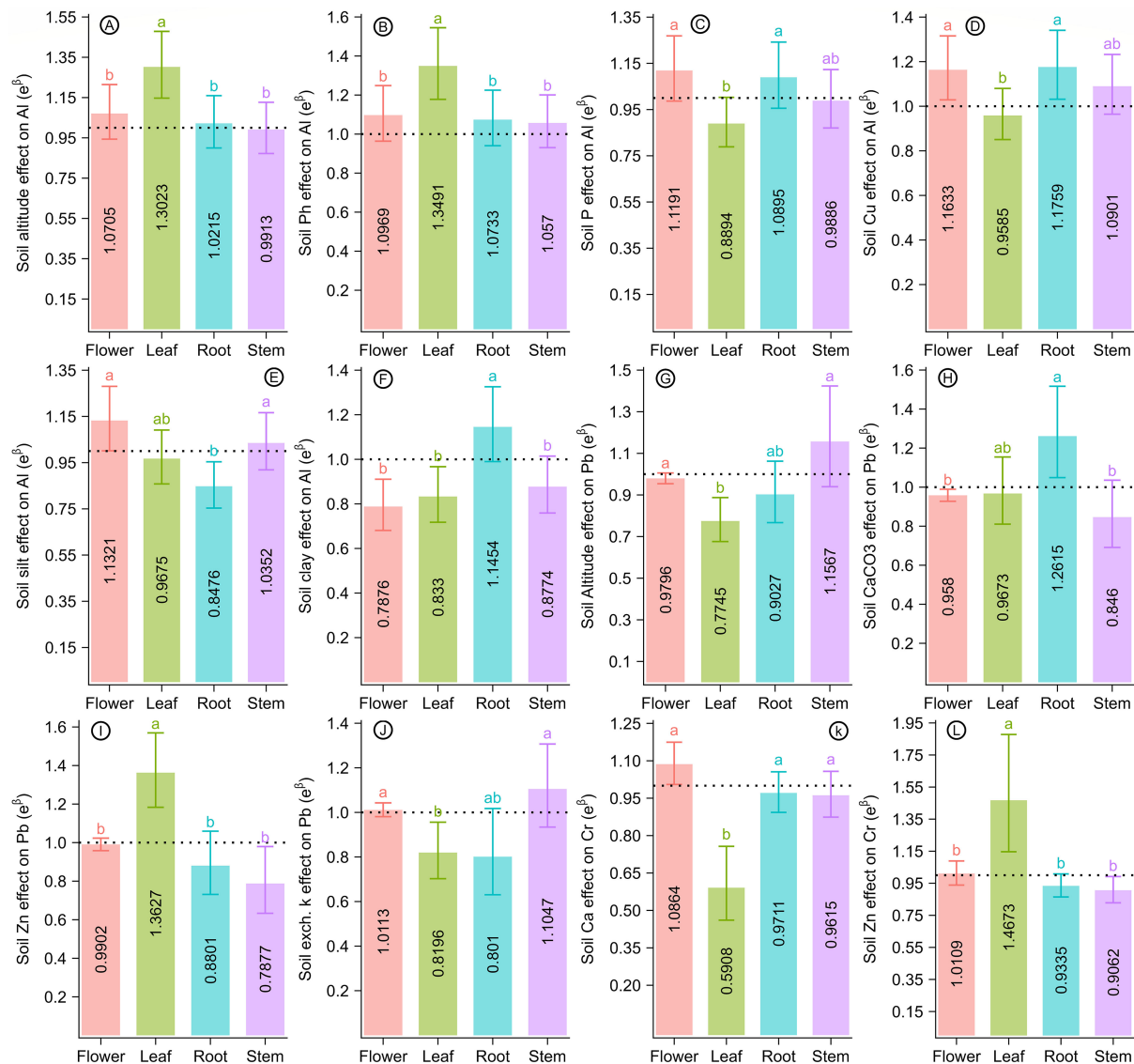


FIGURE 5

Estimated interaction effects of soil factors on potentially toxic trace elements in plant organs, based on generalized linear mixed models (GLMMs). Bar plots show the estimated effects of soil physicochemical properties and altitude on aluminum (A–F), lead (G–J), and chromium (K–L) in different plant organs: flower, leaf, root, and stem. In each panel (A–L), the vertical axis corresponds to the magnitude of the multiplicative effect (e^β), whereas the horizontal axis corresponds to the plant organs, represented by bars. Each bar shows the estimated effect and its 95% confidence interval. Different lowercase letters above the upper limits of the confidence intervals indicate significant differences among plant organs ($p < 0.05$, FDR-adjusted) in the magnitude of the soil–plant effect. The dashed line indicates the reference value ($e^\beta = 1$). Confidence intervals located entirely above this line indicate a positive effect; those located entirely below it indicate a negative effect; and those including the reference value indicate that the effect is not statistically significant.

use, there remains a lack of scientific evidence to substantiate and elucidate these medicinal properties.

4.4 Nutritional homeostasis and exclusion of toxic elements

Models of tissue composition revealed complex relationships in which the internal concentrations of several elements (e.g., P and Zn) did not show linear correlations with their availability in the soil, suggesting the operation of possible active homeostatic mechanisms. The plant appears to regulate its internal elemental composition within an optimal range despite external fluctuations, a trait commonly observed in species adapted to nutrient-poor soils

(Chapin, 1980). Adaptive mechanisms within the Ranunculaceae have been widely documented across species, indicating that responses are shaped not only by specific environmental pressures but also by a high degree of evolutionary plasticity, enabling persistence across contrasting habitats. For example, *Ranunculus acris* has been reported to tolerate a wide range of environments, including marginal conditions, although its development is constrained by soil moisture. At wetter sites, these plants were 26% smaller than those in semi-arid conditions (Kołodziejek and Michlewska, 2015), demonstrating adaptive plasticity. Similarly, in *Ranunculus gunnianus*, where soil water availability is a limiting factor, the species responds by developing wider xylem vessels and increased leaf area (Stoddard et al., 2017). These findings suggest that both

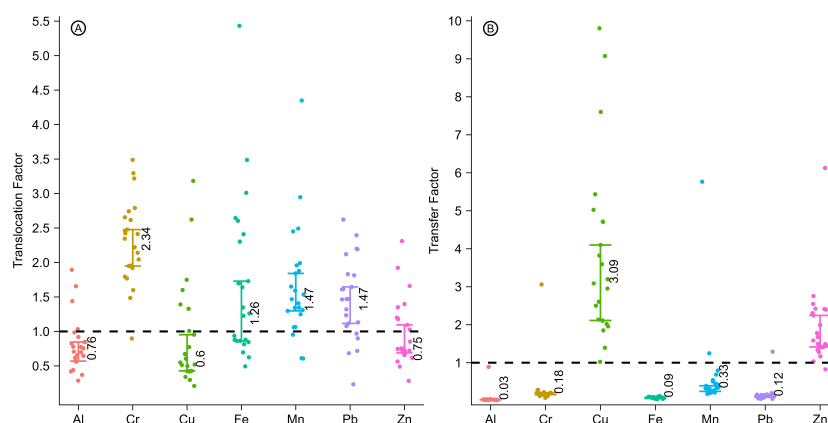


FIGURE 6

Metal mobilisation and transfer in *L. giganteum*. (A) shows the translocation factor (TF), whereas (B) shows the transfer factor (Tf), calculated based on the total concentration of each element in the soil. Values represent the median, and error bars correspond to the 95% bootstrap confidence intervals of the median, estimated using the bias-corrected and accelerated (BCa) method with 5,000 resamples and a random seed of 23,0488.

species have developed morphological adjustment mechanisms that facilitate persistence under contrasting environmental conditions, reinforcing phenotypic plasticity as a key strategy for survival in heterogeneous habitats.

At the same time, the low concentrations of Al, Pb, and Cr, together with parsimonious uptake models, suggest the likely presence of an efficient exclusion strategy. This capacity to restrict the uptake of potentially toxic elements, particularly Al, whose mobility increases under acidic soil conditions, represents a critical adaptation for survival in marginal and potentially contaminated soils (Kochian et al., 2015). Similarly, *Ranunculus acris* has been reported to shift towards a more ruderal strategy in response to soil conditions, which appears to represent a balanced adaptive response (Wala et al., 2023).

4.5 Mobilisation and transfer of metals in *L. giganteum*

The Ancash region of Peru is characterised by numerous environmental liabilities that contribute to elevated metal levels and acid mine drainage, which leach into soils and freshwater sources, thereby posing a persistent risk to both human and environmental health (Kee et al., 2018). In this context, bioremediation processes, particularly those involving the bioaccumulation of metals by plants and microorganisms, have received increasing attention in recent years. Accordingly, it is essential to further investigate the potential of such organisms through comprehensive studies to maximise their capacity to mitigate heavy metal pollution (Darlington et al., 2023). Within this framework, our results indicate that *L. giganteum* exhibits a significant efficiency in translocating Cr, Mn, and Pb (TF > 1), suggesting a potential role in phytoremediation. One of the few available studies on *Ranunculus ternatus* (Ranunculaceae) reports the presence of similar elements, although it identifies K⁺, Ca²⁺, Fe, Mg²⁺, Mn, and Zn as the most abundant (Dai et al., 2024). Notably, the prominence of Mn and Fe is consistent with the patterns observed in our findings.

Our study indicates that Cr exhibits the highest mobility from roots to above-ground tissues, suggesting that *L. giganteum* may possess a highly specialised long-distance transport mechanism for this element. In contrast, for Al and Cu, the species appear to adopt a root exclusion or sequestration strategy, whereby roots function as a physiological barrier, limiting toxicity in photosynthetic tissues. Consistent with this pattern, studies on *Ranunculus sceleratus* (Ranunculaceae) have reported high accumulation of trace metals, particularly in the order Cu > Mn > Pb, with greater concentrations in roots than in stems (Farahat and Galal, 2017). This species has been characterised as a metal excluder with potential for phytostabilisation, especially for Mn. In the case of Fe and Zn, our results suggest an amphigonic distribution between roots and above-ground tissues, likely reflecting a strict homeostatic regulation. This mechanism may ensure adequate metabolic supply while preventing excessive metal accumulation and associated phytotoxicity in aerial tissues.

The results suggest that *L. giganteum* may have developed specialised mechanisms for micronutrient acquisition, particularly for Zn. This element is essential for the plant due to its key physiological and metabolic roles; however, at concentrations exceeding 10,000 mg.kg⁻¹, Zn becomes toxic and may lead to plant mortality (Bhat et al., 2025). In contrast, both Cu and Zn exhibited TF > 1, indicating active and selective bioaccumulation from the soil. Based on these findings, *L. giganteum* may be considered an accumulator of essential micronutrients, representing a key adaptive trait for survival in high-Andean environments. Similar patterns have been reported in *Ranunculus sceleratus* L. (Ranunculaceae), where bioaccumulation factors greater than 1 were observed in shoots for Ni, Cu, and Pb, and in roots for Cd, Ni, Cu, Pb, Zn, and Fe. However, translocation factors (TF) for heavy metals were generally below 1 (Khalifa and Badr, 2021), which indicates that this species is a suitable candidate for phytostabilisation and/or phytoextraction of the most-studied metals. Further evidence within the family indicates that even when Ca²⁺, Fe, and K⁺ concentrations in sediments and water exceed permissible limits, species such as *Ranunculus sphaerospermus* can maintain these concentrations within acceptable ranges (Karahana, 2022), reflecting effective regulatory mechanisms for the

accumulation of these elements. Likewise, *Ranunculus circinatus* Sibth. (Ranunculaceae) has been reported to accumulate significant amounts of heavy metals (Удэ et al., 2022).

It can be hypothesised that *L. giganteum* has potential for metal phytoextraction, given its similarities to other species within the group. This argument is supported by the shared evolutionary origin of alpine buttercups from a common lowland ancestor (Paun et al., 2005) and by the phylogenetic clustering of North American species within a single clade (Hörandl and Emadzade, 2011). Based on our findings, *L. giganteum* can be characterised as a species with notable biotechnological potential for the phytoextraction of micronutrients (Cu and Zn) and heavy metals (Cr, Mn, Pb) in high-Andean soils, making it a promising candidate for phytoremediation applications. In this context, it is important to note that conventional physical and chemical remediation methods are often expensive and may pose environmental risks (Kumar et al., 2022). In contrast, phytoremediation is widely recognised as a safe, environmentally sustainable, and cost-effective biological method, capable of mitigating metal contamination without causing adverse impacts on ecosystems (Taylor et al., 2011).

4.6 Study limitations and future research perspectives

It is important to recognise that, although the associations identified are statistically robust, they do not establish direct causal relationships. The observational nature of the study precludes ruling out the influence of unmeasured factors, such as rooting depth, water table dynamics, or rhizosphere microbial communities, which may collectively modulate nutrient availability and plant growth (Bardgett and Putten, 2014). Additionally, climate change has been associated with the upward migration of plant species, accompanied by the development of adaptive mechanisms that enable them to maintain stable growth under increasing environmental stress.

The high spatial variability observed suggests that future research should adopt a nested sampling design to unravel effects at different spatial scales. Historical and current soil data at each study site are incomplete and, in many cases, subjective. Therefore, there is a need to develop standardised methodological approaches to harmonise data across sites; this represents a critical adaptation measure in the context of climate change, particularly in data-deficient regions such as the tropical Andes (Cuesta et al., 2012). In this regard, it is essential, especially for species known from a single locality, to implement systematic exploration and collection programmes, ideally within a collaborative research framework (León et al., 2006). To validate the proposed causal mechanisms (e.g., the toxic effects of CaCO₃ or the efficiency of Zn uptake), controlled dose–response experiments under *ex-situ* conditions are required. Furthermore, studies of phenotypic plasticity using reciprocal transplant experiments could help elucidate the genetic basis of these adaptations. Complementarily, *in-situ* sampling combined with genome sequencing represents a crucial first step towards identifying the mechanisms underlying tolerance to calcareous environments (Bontpart et al., 2024). Finally, the plant's homeostatic capacity could be further investigated through soil analyses for potentially toxic elements and through controlled experiments to assess *Laccopetalum* phytoremediation capacity.

This study represents the first effort to address the existing knowledge gap regarding *L. giganteum*, particularly concerning soil nutrient content and its influence on the species. It is likely that this species has undergone rapid adaptive diversification in response to different ecological niches in mountainous regions (Hörandl et al., 2005). In the current context, climate change and anthropogenic pressures are accelerating processes such as species migration, morphological shifts, and, in extreme cases, local extinction (Zevallos and Lavado-casimiro, 2022). This situation is further exacerbated by the harvesting of wild medicinal plants from high-mountain ecosystems, which are predominantly herbaceous and are often collected with their roots, leading to overexploitation and, in many cases, the loss of endemic species (Gonzales De La Cruz et al., 2014). Given these challenges, it is imperative to prioritise research as a fundamental tool for designing effective biodiversity conservation strategies, particularly for species such as *L. giganteum*.

5 Conclusions

The soils in which *L. giganteum* grows are characterised by multiple abiotic stressors, including an alkaline pH (7.73), moderate CaCO₃ content (9.22%), and a predominantly sandy texture. These conditions create an environment with severe constraints on water and nutrient availability and high spatial heterogeneity in micro-nutrient distribution.

Statistical models revealed consistent negative associations between plant growth and soil levels of Ca²⁺ and carbonates, thereby refuting the long-standing hypothesis of calcicolous affinity and demonstrating that *L. giganteum* tolerates, but does not benefit from, Ca rich soils, which likely act as a limiting factor.

The growth and development of *L. giganteum* showed the strongest positive associations with micronutrient availability, particularly Zn and Mn, which are typically limited in alkaline soils. This pattern suggests that the species has developed efficient physiological mechanisms to acquire these scarce nutrients, representing a key adaptation for survival in this marginal ecological niche.

The species exhibits a strong capacity for nutrient homeostasis, regulating internal concentrations independently of soil availability, and functions as an efficient excluder of potentially toxic elements such as Al. This reinforces its adaptation to edaphically hostile environments. These traits, together with its capacity to phytoextract micronutrients (Cu and Zn) and heavy metals (Cr, Mn, Pb) in high-Andean soils, position *L. giganteum* as a species with considerable biotechnological potential and a promising candidate for phytoremediation applications.

Biological richness alone does not guarantee its preservation without an integrated cycle of taxonomic characterisation, scientific research, and use valorisation. Without such support, endemic species such as *L. giganteum* face imminent risks of genetic erosion and cultural loss, thereby restricting their biotechnological potential, particularly for phytoremediation applications. This study seeks to address critical knowledge gaps by analysing the soil–plant relationships of this species and proposes dual conservation strategies within the current context of climate change:

- i. *In situ* conservation: the delineation of optimal ecological microsites, a critical aspect given that approximately 16% of key occurrence sites are believed to overlap with current concessions.
- ii. *Ex situ* conservation: the establishment of technical criteria for laboratory propagation programs aimed at the protection of endemic species.

For *ex-situ* propagation and the establishment of pilot cultivation systems, the use of substrates with a loamy-sandy texture (sand < 70%), pH adjusted to 6.2–6.8, total carbonates < 2%, and organic matter > 5% with a C/N ratio < 15 is recommended. Additionally, targeted supplementation of micronutrients in plant-available forms is advised, specifically Zn (2–4 mg·kg⁻¹) and Mn (5–10 mg·kg⁻¹), as determined by DTPA extraction. These recommendations, derived from edaphic associations quantified in the species' natural habitat, move beyond historical assumptions and provide concrete technical criteria to reduce the risk of failure in *ex-situ* conservation initiatives.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

RQ: Writing – original draft, Conceptualization, Data curation, Investigation, Methodology, Validation, Visualization. UA: Data curation, Formal analysis, Methodology, Software, Writing – original draft. HR: Validation, Writing – review & editing. TY: Methodology, Writing – review & editing. RS: Conceptualization, Formal analysis, Funding acquisition, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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