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ORIGINAL PAPER

Distribution and Resorption Efficiency of Macroelements (N, P, K, Ca, and Mg) in Organs of *Rumex alpinus* L. in the Alps and the Giant (Krkonoše) Mountains

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Abstract
Rumex alpinus, an alpine nitrophilous species, is a troublesome weed in pastures. Nutrient uptake and distributions in the organs of *Rumex alpinus* are not well-studied. We aimed to determine the distribution of macroelements in organs of *Rumex alpinus* together with the nitrogen-phosphorus potassium ratio (NPK) and the resorption efficiency of N, P, K, calcium (Ca), and magnesium (Mg) in the Alps of Austria, Italy, and the Krkonoše (Giant) Mountains, Czech Republic. The pseudo-total and plant-available N, P, K, Ca, and Mg in soils and organs of *Rumex alpinus* (emerging, mature, and senescent leaves, petioles, stems, and rhizomes) were extracted with *aqua regia* and Mehlich-3 procedures, respectively, followed by inductively coupled plasma-optical emission spectrometry. The contents of total and available macroelements in the soils reflected high variability with localities. There was a significant effect of locality and organs on the element contents, indicating differences in nutrition. *Rumex alpinus* exhibited higher N and P contents in emerging and mature leaves than in the senescent compared to Ca and Mg. The N:P and N:K ratios in the mature leaves were within the normal range but were indicative of comparatively higher demand for P. The mean resorption efficiency for N, P, and K was 52, 50, and 22%, respectively, lower than values for most terrestrial plants (62, 65, and 70%). The relatively high availability of macroelements in soils and plant organs with low N, P, and K resorption efficiency indicates a high N, P, and especially K-demanding species of *Rumex alpinus*.

Keywords Alpine dock · Plant organs · Resorption · Weed · Nutrients

1 Introduction

The Alpine dock (*Rumex alpinus* L) of the Polygonaceae family is native to the high mountains of Western, Central, and Eastern Europe, including the Iberian and Apennine peninsula, the Alps, the Carpathians, and the Balkan Peninsula. Additionally, *R. alpinus* is native to the Caucasus (Nakhutsrishvili et al. 2017), the mountains of northern Anatolia, Armenia, and Iran.

In the Giant mountains of the Czech Republic, the introduction of *R. alpinus* was associated with German-speaking colonists from the Alps in the sixteenth century AD, used for the treatment of different diseases, such as salad and forage crop (Lokvenc 1978; Šťastná et al. 2010). For example, 2-acetyl-3-methylnaphthalene-1, 8-diol, a bioactive compound found in the leaves and roots of *R. alpinus*, possesses an antibacterial characteristic that serves as a laxative and cures jaundice, astringent, constipation, diarrhea, and eczema (Ozturk and Ozturk 2007; Grieve 2013; Mishra et al. 2018).

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Today, *R. alpinus* is considered a troublesome weedy species which infests abandoned grasslands, roads margins, and nutrient-rich sites: typically livestock resting areas, surroundings of mountain farms, and downslope of mountain chalets grasslands, with deposits of animal feces, and nutrient-rich wastewater (Bucharová 2003; Šťastná et al. 2010; Šilc and Gregori 2016). This species, however, is a perennial nitrophilous and calciphobous species, with high nitrogen (N, 66 g kg^{-1}), phosphorus (P, 7.3 g kg^{-1}), and potassium (K, 47 g kg^{-1}) contents in young leaves and an N:P ratio of about 9.1 (Bohner 2005). Another characteristic trait of this species is its ability to accumulate nitrate (NO_3^-) in young leaves (Rehder 1982; Bohner 2005; Kołodziejek 2019). *Rumex alpinus* develops on soils ranging from acid to alkaline, usually humus- and nutrient-rich, mesic-moist-wet and fine sandy, dusty, and well-ventilated throughout the year (Stachurska-Swakoń 2009; Doležal et al. 2020). As a nitrophilous plant, *R. alpinus* is well-adapted to temporal surpluses of NO_3^- and K and dis-harmonic nutrient supplies in the soil solution. Due to the absence of high-yielding, competitive fodder grasses due to unfavorable climatic conditions in mountainous regions and its competitive ability (Klimeš 1992), *R. alpinus* forms a stable but species-poor, productive permanent community dominated by a few nitrophilous herbs (Bohner 2005). Nitrophilous plants grow on nutrient-rich sites and can waste nutrients (Opačić 2022).

Indications of nutrient wasting include low nutrient-use efficiency, high nutrient contents in different organs compared to species adapted to nutrient-poor conditions, and low re-translocation of nutrients from senescent to the most photosynthetically active young leaves (Delgado et al. 2018). Except for the study by Bohner (2005), there is no scientific research on the contents and distribution of N, P, K, calcium (Ca), and magnesium (Mg) in different organs of *R. alpinus*. However, this species can be considered an excellent example of alpine nitrophilous species. So far, there are no studies on the resorption efficiency of this species and variability in its nutrition in localities with different geological substrates on a large geographical scale and at different sampling intervals.

Additionally, as a mountainous species with diverse vegetative regeneration, such as clones and seeds (Bohner 2005), knowledge of its nutrient absorption is pertinent in making inferences on *R. alpinus's* adverse implications on mountain ecosystems. Nutrient resorption is a mechanism of plant species' response to nutrient-limiting conditions, which play a pertinent role in efficient nutrient cycling—thus reducing the dependence on soil-available nutrients (Brant and Chen 2015; Thapa et al. 2020). Foliar nutrient concentrations play a vital role in nutrient resorption. However, many factors affect nutrient resorption, which directly obscures the relationships with soil nutrient availability (Yan et al. 2018; Thapa et al. 2020), e.g., variation in available content of nutrients and seasonal changes.

To fill the gap of knowledge, we determined macro element (N, P, K, Ca, and Mg) contents of both soils and organs of *R. alpinus* from four localities in the Krkonoše (Giant) Mountains (Czech Republic) and alps of Austria and Italy.

This study aimed to answer the following research questions: (i) How can the variability of soil chemical properties affect *R. alpinus* stand from different localities? (ii) How different are the contents of N, P, K, Ca, and Mg and the N:P, N:K, and P:K ratios in various organs of *R. alpinus* in different localities? (iii) How intensive is the resorption of N, P, K, Ca, and Mg from senescent to young leaves in *R. alpinus*?

2 Materials and Methods

2.1 Study Area

Rumex alpinus plants were well-studied according to their wide distribution in four localities of the Krkonoše Mountains, Czech Republic, two in Austria, and one in Italy (Fig. 1). The localities of the Krkonoše Mountains (Horní Mísečky- HM; Vítkovice v Krkonoších- VT; Libuše hut- LB; and Pec pod Sněžkou- PC; Figure S1) are characterized by podzols located on phyllite geological substrate (Němeček and Kozák 2005). In Ramsau am Dachstein (DCH) and Zilllertal (ZL), Austria, the localities are well-characterized by Calcaric Cambisol and Luvic Cambisol on limestone and Granite gneiss parent bedrock, respectively. And in Madesimo (MD), Italy, the soil is Vertic Cambisol on a sandstone geological bedrock (Jones et al. 2005). Additionally, the localities represent different altitudes and environmental conditions—precipitation, temperature, and altitudes (Table 1).

As an invasive species in the Krkonoše Mountains (Kopecký et al. 1973; Lokvenc 1978; Pyšek et al. 2012), *R. alpinus* covers approximately 70% of the area expelling indigenous plants and preventing species diversity (Náglová 2014).

2.2 Sampling and Preparation of Soils

To maximize sample collection, we adopted a judgemental approach (Frey 2018), covering the variability of soils in the locations of *R. alpinus*. In this case, we sampled the upper 10-cm soil layer with a soil probe (Purchhauer type, core diameter: 30 mm) in LB, VT, PC, HM, DCH, and MD in July 2018. In each locality, we randomly collected ten soil samples in the surroundings of *R. alpinus* stands. And these samples were mixed to form a representative sample from the localities of the Krkonoše Mountains in the Czech Republic, DCH, and MD. Soil samples were air-dried and

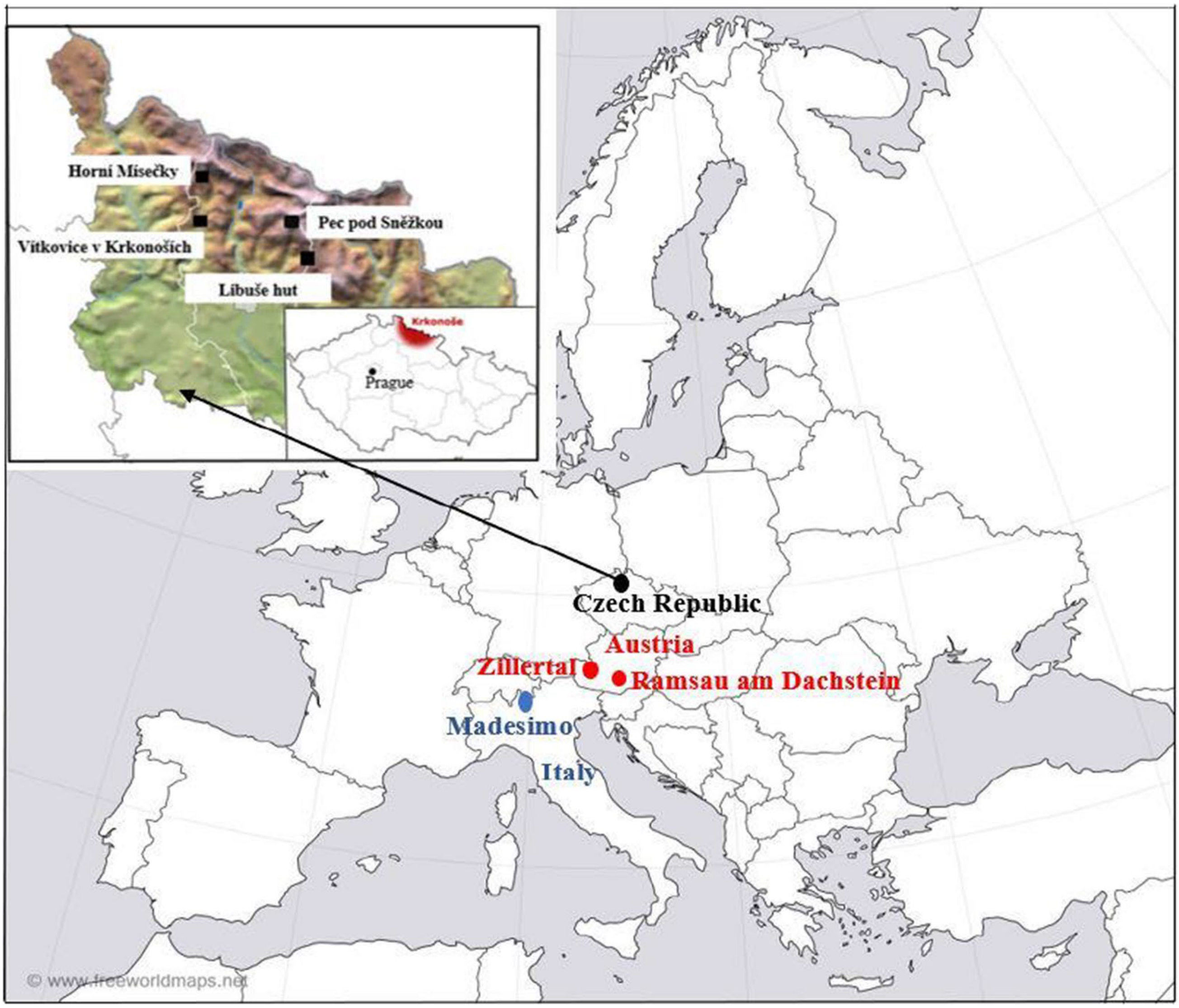

Fig. 1 Location of studied localities in the Czech Republic (Horní Mísečky—HM; Vítkovice v Krkonoších—VT; Libuše hut—LB; and Pec pod Sněžkou—PC), Ramsau am Dachstein and Zillertal in Austria, and Madesimo, Italy

oven-dried at 60 °C for 48 h (Francová et al. 2017). For the homogenous fraction under 2 mm, we analyzed for macroelement contents. The representative soil samples were divided to obtain three replicates (sub-samples) per locality and sent to the laboratory for chemical analysis.

2.3 Sampling and Preparation of Plant Organs

Organs of *R. alpinus* (Fig. 2) were collected in a mono-dominant stand covering 100 m^2 in all localities. At each locality, we randomly collected ten emerging semi-developed leaf blades (E), ten fully developed mature leaf blades (M), ten senescent yellow, red, or brown semi-dry leaf blades (S), ten petioles from mature leaves (Pe), ten stems without seeds (St), and three rhizomes developed in the last two years (Fig. 3). All collected samples were put into paper bags and transported to the laboratory.

Laboratory protocol: Plant organs were cleaned from soil and other residues using distilled H_2O and then dried at 70 °C for 48 h. Each organ sample immediately was mixed to obtain one representative sample per locality. Next, we ground the representative organ samples per locality with an IKA® A11. The representative organ sample of each locality was homogenized and divided into three replicates for further elemental analysis.

The samples from the Krkonoše Mountains were collected twice in 2018, in July (Summer—S) and October (Autumn—A). Samples from the Alps were collected only in July 2018 (summer), approximately at the same time as in the Krkonoše Mountains.

Table 1 Description of studied localities in the Giant (Krkonoše) Mountains, Czech Republic, and in the Alps of Austria and Italy

Locality	Geographical location	Altitude [m a.s.l.]	Mean annual precipitation [mm]	Mean annual temperature [ºC]	Soil type	Geological substrate
Czech Republic						
Libuše hut, Velká Úpa (LB)	50°41′19″N 15°46′43″E	700	850	6.5	Podzol	Phyllite
Vítkovice v Krkonoších (VT)	50°41′56″N, 15°31′41″E	650	900	5.5	Podzol	Phyllite
Pec pod Sněžkou (PCS)	50°41′46″N, 15°44′8″E	815	850	5.5	Podzol	Phyllite
Horní Mísečky (HM)	50°44′2″N, 15°34′5″E	1050	1000	4.5	Podzol	Phyllite
Austria						
Ramsau am Dachstein (DCH)	47°27′1″N, 13°37′1″E	1650	1100	3.8	Calcaric Cambisols	Limestone
Zillertal (ZL)	47°14′21″N 12°7′39″E	1650	933	3.9	Luvic Cambisol	Granite gneiss
Italy						
Madesimo MD)	46°26′13″N, 9°21′27″E	1600	2000	2.0	Vertic Cambisols	Sandstone

2.4 Chemical Analyses and Analytical Methods

The total content of P, K, Ca, and Mg in plant organ and soil samples were extracted with USEPA 3052 (International Organization for Standardization, USEPA 1996) procedure using a mixture of nitric (HNO_3), hydrochloric (HCl), and hydrofluoric (HF) acids.

Procedure: A mass of 0.25 g of homogenized *R. alpinus* individual organs was mineralized in a mixture of 9 mL of HNO_3, 3 mL of HCl, and 1 mL of HF and heated in a sealed 60-mL VWR® PTFE Jar on a hot plate at 150 °C for 24 h. After 24 h, 1 mL of hydrogen peroxide (H_2O_2) was added to each sample and evaporated on a hot plate at 50 °C for 24 h. Evaporated samples were diluted in 20 mL of 2% HNO_3 for 2 h and filtered. The content of the total element of each plant organ sample was determined with inductively coupled plasma-optical emission spectrometry (ICP-OES; 720 Series, Agilent Technologies, USA). We used the same procedures and analytical device to obtain the total content of macroelement for all the soil samples. The total content of N in plant organ and soil samples was determined by the Dumas method with the DUMATHERM® Nitrogen determination system (http://www.gerhardt.de).

The plant-available fractions of P, K, Ca, and Mg in soil samples were extracted by Mehlich-3 reagent (Mehlich 1984) and determined with ICP-OES (Varian VistaPro, Mulgrave, Australia). The plant-available content of the studied elements was determined in an accredited laboratory EKO-Eko-Lab Zamberk (www.ekolab.zamberk.cz). Soil pH $_{[H2O]}$ was measured in all soil samples in three replicates at a ratio of 1:2 (soil: water) with a Voltcraft PH-100 ATC pH meter manufactured by I & CS spol s r.o. (Czech Republic).

2.5 Statistical Analyses

Data was tested by the Shapiro–Wilk W-test for normality and met assumptions for parametric tests. Factorial analysis of variance (ANOVA) was used to evaluate the effect of locality, organ, and their interaction on the content of different elements in biomass samples. One-way ANOVA was used to evaluate the effect of locality on the elemental composition of soils and organs and terms on the element contents of biomass samples. Additionally, we applied the ANOVA model to evaluate the effect of locality and season on the N:P, N:-K, and K:P ratios and on *NuR*. In the case of significant ANOVA, a post hoc comparison using the Tukey higher significance difference (HSD) test was applied. Moreover, we used a correlation analysis to evaluate the relationship between the total and plant-available content of elements in the soil and content elements in the soil and mature leaves. All statistical analyses were performed using the STATISTICA 13.3 program (www.statsoft.com).

2.6 Estimation of N, P, K Ratio and Nutrient Resorption (Nur)

To characterize the nutritional status of the plants, we estimated the N:P, N:K, and K:P ratios in mature and senescent leaves (aboveground biomass) after the critical values for vascular plants (Olde Venterink 2003), with the following values and interpretations.

i. N-limited N:P < 14.5 and N:K < 2.1
ii. P-limited or P + N-limited N:P > 14.5 and K:P > 3.4
iii. K-limited or K + N-limited, N:K > 2.1 and K:P < 3.4

NuR for N, P, K, Ca, and Mg were calculated after Vergutz et al. (2012) as

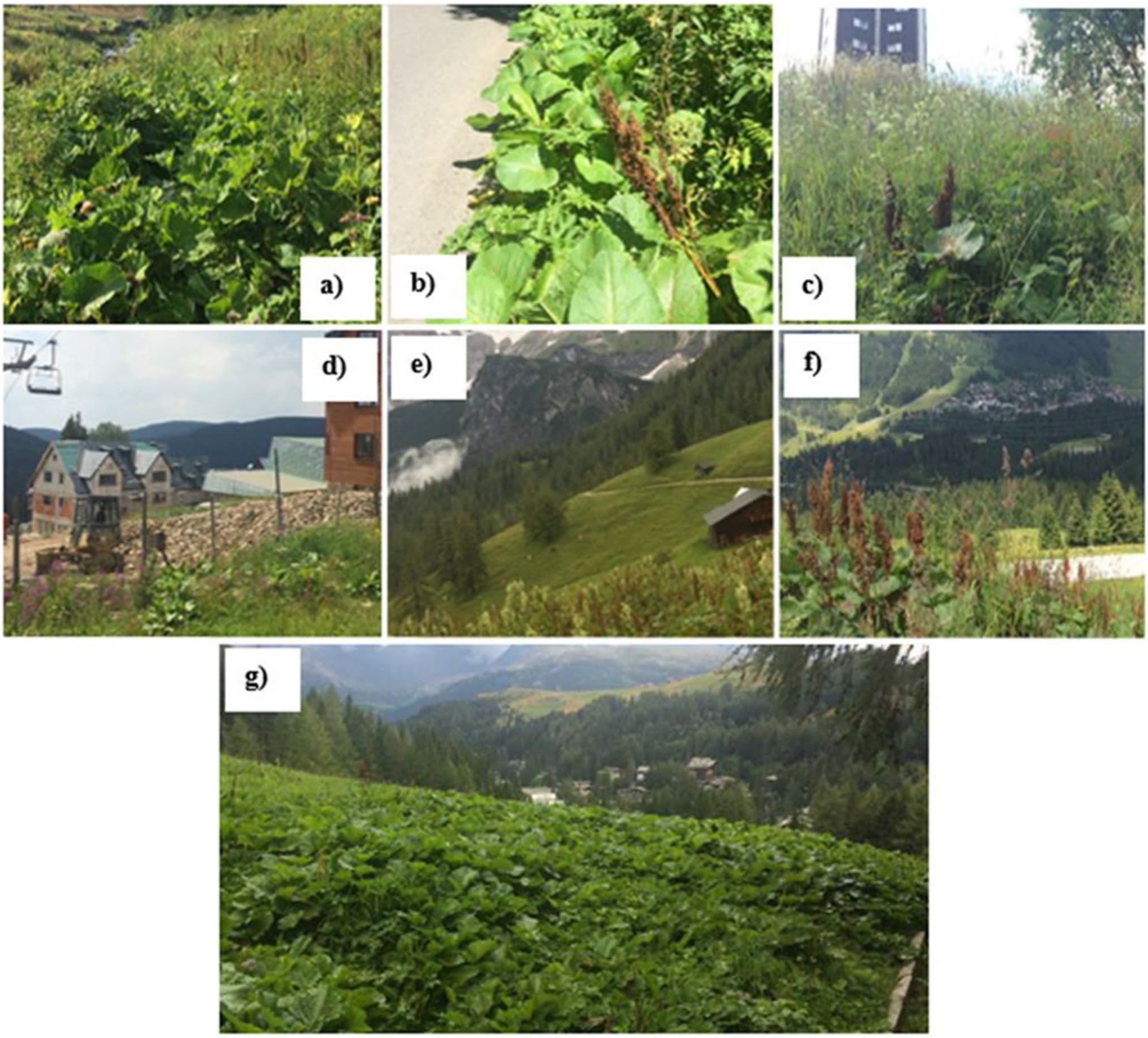

Fig. 2 *Rumex alpinus* stands in (**a**) Libuše hut, (**b**) Vítkovice v Krkonoších, (**c**) Pec pod Sněžkou, (**d**) Horní Mísečky, (**e**) Ramsau am Dachstein (DCH), (**f**) Zillertal (ZL), and (**g**) Madesimo (MD)

$$NuR = 1 - \left(\frac{content\ of\ elements\ in\ senescent\ leaves}{contents\ of\ elements\ in\ mature\ leaves}\right) \times 100$$

3 Results

3.1 Soil Chemical Properties

There was a significant effect of locality on soil reactions ($pH_{[H2O]}$) and the total and plant-available contents of all analyzed elements (Tables 2 and 3). Except for the slightly acidic reaction in DCH, soils in all other localities were moderately acidic. The pH ranged from 5.2 to 6.1 in LB and DCH, respectively (Table 2). The content of total N was from 1.33 in DCH to 9.02 g kg^{-1} in HM. The content of total P ranged from 0.42 to 1.01 g kg^{-1} in DCH and HM, respectively. The total K ranged from 11.8 in LB to 22.5 g kg^{-1} in MD, while Ca ranged from 1.04 in HM to 42.25 g kg^{-1} in DCH. Moreover, the total Mg content was from 1.11 in LB to 9.46 g kg^{-1} in DCH.

Available P content was from 20 to 51 mg kg^{-1} in MD and DCH, respectively (Table 3). Meanwhile, available K content ranged from 33 in VT to 129 mg kg^{-1} in MD, with Ca ranging from 547 in VT to 5133 mg kg^{-1} in DCH. The plant-available Mg content ranged from 116 in LB and

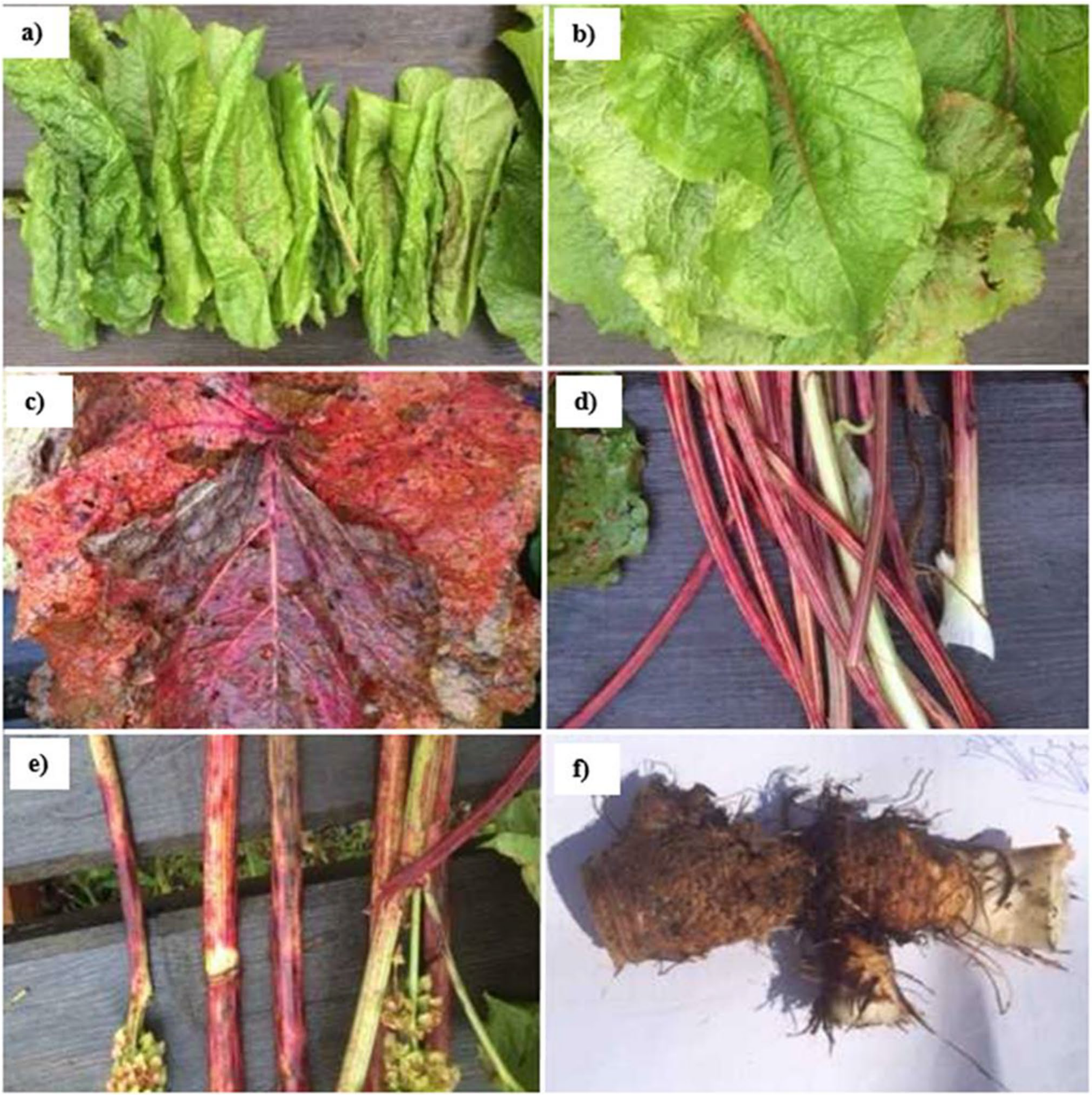

Fig. 3 Sampled organs of *Rumex alpinus*: (**a**) emerging, (**b**) mature, (**c**) senescent leaf blades, (**d**) petioles from mature leaves, and (**e**) stems from flowering plants, and (**f**) 2-year-old rhizome

VT to 207 mg kg^{-1} in MD. There was no significant correlation between total and plant-available P, K, Ca, and Mg in the soils (Table 4a).

3.2 Elemental Content of Plant Organs

There was no significant correlation between total N, P, K, Ca, and Mg in the soils and the same elements in the mature leaves (Table 4b). Meanwhile, this was similar in the case of plant-available P, K, and Mg except for Ca ($r = 0.91$, $p = 0.01$; Table 4c). The total content of macroelements in all organs' overall localities and terms (autumn and summer) are in Figs. 4 and 5.

We recorded a significant effect on the content of elements in organs in each locality. The overall mean contents of N, P, K, Ca, and Mg in organs across all the localities were significantly different (Table S1). Total N ranged from 3 in stems from HM_A to 67 g kg^{-1} in emerging

Table 2 The pH and total content (mean ± SE) of elements in the upper 10-cm soil layer from six localities. The *p* value was obtained by one-way ANOVA. Using the Tukey post hoc test, the mean values of each element with the same letter among localities were not significantly different. * $p < 0.01$ ** $p < 0.001$

Locality		LB	VT	PC	HM	DCH	MD
pH (H_2O)*		5.2 ± 0.3c	5.7 ± 0.03abc	5.9 ± 0.1ac	5.6 ± 0.1abc	6.1 ± 0.4a	5.3 ± 0.2c
N **	(g kg^{-1})	2.92 ± 0.03e	3.0 ± 0.04d	2.98 ± 0.02e	9.02 ± 0.02c	1.33 ± 0.02b	2.36 ± 0.03a
P **	(g kg^{-1})	0.77 ± 0.06ab	0.76 ± 0.10ab	0.75 ± 0.02ab	1.01 ± 0.27a	0.42 ± 0.01b	0.63 ± 0.06ab
K *	(g kg^{-1})	11.8 ± 0.4c	17.3 ± 2.1a	14.4 ± 0.7ab	10.9 ± 0.9c	16.0 ± 0.1ab	22.5 ± 1.7c
Ca *	(g kg^{-1})	2.51 ± 0.49ab	3.47 ± 1.5ab	5.69 ± 1.04b	1.04 ± 0.16c	42.25 ± 0.68a	1.17 ± 0.14c
Mg *	(g kg^{-1})	1.11 ± 0.29b	3.76 ± 2.34b	1.62 ± 0.43b	1.54 ± 0.61b	9.46 ± 0.23a	2.10 ± 0.09b

Abbreviations of localities: *LB* Libuše hut, *VT* Vítkovice v Krkonoších, *PC* Pec pod Sněžkou, *HM* Horní Mísečky, *DCH* Ramsau am Dachstein, *ZL* Zillertal, *MD* Madesimo

Table 3 Mean content (± SE) of plant-available (Mehlich-III) P, K, Ca, and Mg in the upper 10-cm soil layer from six studied localities. The *p* value was obtained by one-way ANOVA. Using the Tukey post hoc test, the mean values of each element with the same letter among localities were not significantly different

Locality	LB	VT	PC	HM	DCH	MD	*p*-value
P (mg kg^{-1})	38 ± 2.2b	37 ± 3.7b	41 ± 3.1ab	49 ± 6.3a	51 ± .7a	20 ± 1.7c	< 0.001
K (mg kg^{-1})	121 ± 5.1b	33 ± 2.8c	128 ± 5.7a	127 ± 3.3a	124 ± 3b	129 ± 4.6a	< 0.001
Ca (mg kg^{-1})	1689 ± 24.2c	547 ± 11.6e	4454 ± 20.4b	1130 ± 17.9d	5133 ± 16.8a	1465 ± 23c	< 0.001
Mg (mg kg^{-1})	116 ± 2.9d	116 ± 5.8d	395 ± 6.7a	120 ± 5.6d	153 ± 7c	207 ± 4.1b	< 0.001

Abbreviations of localities: *LB* Libuše hut, *VT* Vítkovice v Krkonoších, *PC* Pec pod Sněžkou, *HM* Horní Mísečky, *DCH* Ramsau am Dachstein, *ZL* Zillertal, *MD* Madesimo

Table 4 The relationship between the content of (a) Total and plant-available elements in soil, (b) total elements in soil and mature leaves, and (c) plant-available in soil and total elements in mature leaves

(a) Total and plant-available in soil					
Parameter	P	K	Ca	Mg	
Regression equation	y = 0.04 + 0.003*x	y = 0.13 − 0.002*x	y = 1.57 + 0.09*x	y = 0.21 − 0.01*x	
Correlation coefficient (r)	r = 0.10	r = −0.17	r = 0.75	r = −0.20	
p value	p = 0.68	p = 0.74	p = 0.08	p = 0.71	
(b) Total in soil and mature leaves					
Parameter	N	P	K	Ca	Mg
Regression equation	y = 47.31 + 0.76*x	y = 3.76 − 0.39*x	y = 16.32 + 0.28*x	y = 1.78 + 0.02*x	y = 2.11 − 0.003*x
Correlation coefficient (r)	r = 0.29	r = −0.11	r = 0.63	r = 0.64	r = −0.06
p value	p = 0.58	p = 0.83	p = 0.18	p = 0.17	p = 0.90
(c) Plant-available in soil and total content in mature leaves					
Parameter	P	K	Ca	Mg	
Regression equation	y = 3.37 + 2.80*x	y = 23.48 − 25.88*x	y = 1.45 + 0.20*x	y = 2.15 − 0.24*x	
Correlation coefficient (r)	r = 0.05	r = −0.54	r = 0.91	r = −0.20	
p value	p = 0.93	p = 0.27	p = 0.01	p = 0.71	

leaves from VT_S (Fig. 4a). The total N content in ascending order in organs' overall localities and terms was St < R < Pe < S < M < E (Table S1).

The pattern of P recorded by *R. alpinus* was variable depending on the locality and terms (Fig. 4b). The content of P ranged from 0.2 g kg^{-1} in stems at MD to 6.2 g kg^{-1} in emerging leaves at VT_S. The P content in ascending order in organs' overall localities and terms was St < R < S < Pe < M < E (Table S1). The K content ranged from 7 in the rhizome at MD_S to 44 g kg^{-1} in the petiole at VT_S (Fig. 4c). The K content in ascending order in organs' overall localities and collection terms was R < St < S < M < E < Pe (Table S1). The content of Ca ranged from 0.8 in emerging leaves at MD_S to 11.7 g kg^{-1} in senescent leaves at VT_A. The Ca content in ascending order in organs' overall localities and

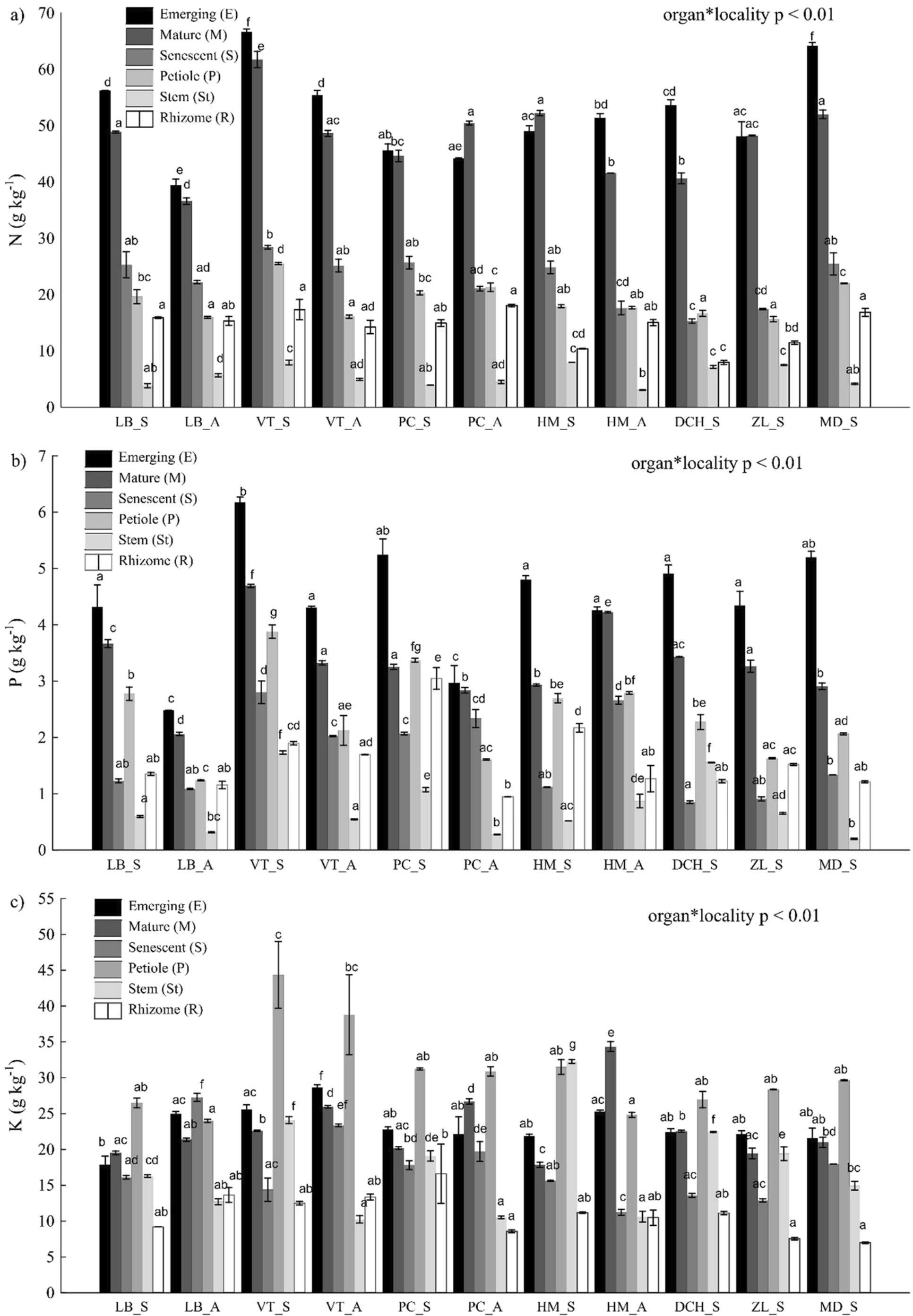

Fig. 4 Effect of locality on the content (mean ± SE) of (**a**) N, (**b**) P, and (**c**) K in different organs of *R. alpinus*. The *p* value for organ, locality, and organ*locality was obtained by factorial ANOVA. The content of elements in individual organs ' overall localities was evaluated by one-way ANOVA. Using the Tukey post hoc test, overall mean values with the same letter were not significantly different. Abbreviations of localities: LB_S (Libuše hut_Summer), LB_A (Libuše hut_Autumn), VT_S (Vítkovice v Krkonoších_Summer), VT_A (Vítkovice v Krkonoších_ Autumn), PC_S (Pec pod Sněžkou_Summer), PC_A (Pec pod Sněžkou_ Autumn), HM_S (Horní Mísečky_Summer), HM_A (Horní Mísečky_ Autumn), DCH_S (Ramsau am Dachstein_Summer), ZL_S (Zillertal_Summer), and MD_S (Madesimo_Summer)

terms were E < M < St < Pe < R < S (Table S1). There was the highest Mg content in senescent leaves and the lowest in stems for all the localities (Fig. 5b). There was a similar pattern of Mg and Ca in organs' overall localities and terms (Figs. 5a, b). The content of Mg ranged from 0.3 in stems at LB_A to 5 g kg^{-1} in senescent leaves at VT_S. Again, Mg content in ascending order in organs' overall localities and terms was St < R < Pe < E < M < S (Table S1).

In the Krkonoše Mountains, there was a significant effect among different organs and terms for the elements in all localities (Fig. 6). The content of N was slightly higher in summer than in autumn (Fig. 6a). Except for senescent leaves, the content of P was significantly higher in summer than in autumn Fig. 6b). In all three categories of leaves, the K content was higher in autumn, while in stems, in summer (Fig. 6c). The Ca content was significantly lower in emerging and mature leaves and stems in summer than in autumn

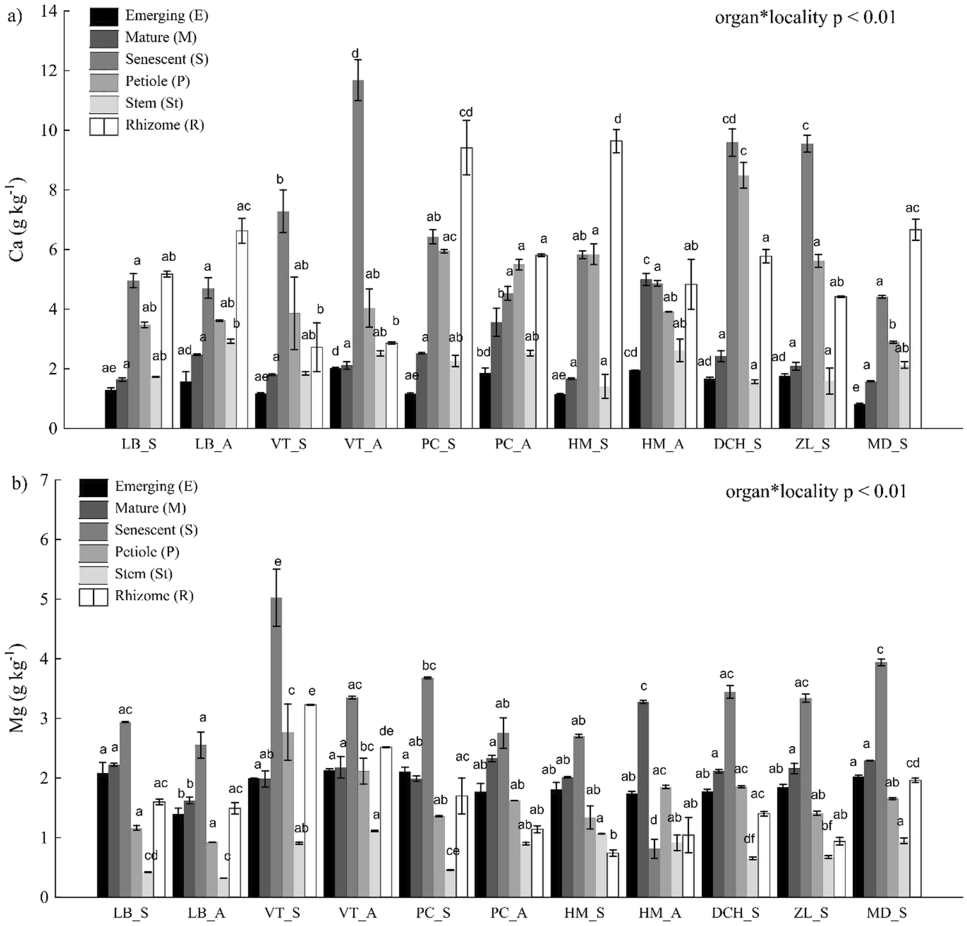

Fig. 5 Effect of locality on the content (mean ± SE) of (**a**) Ca and (**b**) Mg in different organs of *R. alpinus*. The *p* value for organ, locality, and organ*locality was obtained by factorial ANOVA. The content of elements in individual organs ' overall localities was evaluated by one-way ANOVA. Using the Tukey post hoc test, overall mean values of organs with the same letter were not significantly different. Abbreviations of localities: LB_S (Libuše hut_Summer), LB_A (Libuše hut_Autumn), VT_S (Vítkovice v Krkonoších_Summer), VT_A (Vítkovice v Krkonoších_ Autumn), PC_S (Pec pod Sněžkou_Summer), PC_A (Pec pod Sněžkou_Autumn), HM_S (Horní Mísečky_Summer), HM_A (Horní Mísečky_Summer), DCH_S (Ramsau am Dachstein_Summer), ZL_S (Zillertal_Summer), and MD_S (Madesimo_Summer)

(Fig. 6d). The content of Mg was significantly higher in summer than in autumn only in senescent leaves (Fig. 6e).

The relationship between each of the studied elements among the overall dataset of biomass samples (above- and below-ground biomass) is given in Figures S2 and S3. Except for the strong positive relationship between N and P ($r = 0.85$, $p < 0.001$; Figure S2a), all the other elements recorded weak correlations ($r = 0.12 - 0.43$), while Ca content was negatively correlated with N, P, and K ($r = -0.17$—0.39; Figures S2d, S2e, and S2f).

3.3 N:P, N:K, and K:P Ratios

The N:P, N:K, and K:P ratios for mature and senescent leaves in each locality are in Table 5. The N:P ratio in mature leaves ranged from 9.8 to 17.9 in HM_A and MD_S. The N:P ratio in senescent leaves ranged from 6.6 to 22.2 in HM_S and autumn, respectively. The mean N:P ratio overall localities were 15 for mature and senescent leaves.

The N: K ratio in mature leaves ranged from 1.2 at HM_A to 2.9 at HM_S. The N: K ratio in senescent leaves ranged from 0.82 to 2.0 in LB_A and VT_S. The mean N:K ratios were 2.2 and 1.4 in mature and senescent leaves, respectively. The K:P ratio in mature leaves ranged from 4.8 to 10.4 in VT_S and LB_A, respectively. The K:P ratio in senescent leaves ranged from 4.2 to 25 in HM_A and LB_A. The mean K:P ratios were 7.1 and 12 in mature and senescent leaves, respectively.

3.4 Resorption of N, P, K, Ca, and Mg

There were varied effects of localities on the resorption of N, P, K, Ca, and Mg (Table 6). The *Nur* of N ranged from 39 to 64%, and the mean N resorption overall localities were 52%. The *Nur* of P ranged from 18 to 75%, with the mean overall localities of 50%, while K was from 10 to 67%. However, we recorded *Nur* of – 28%, indicating more K in senescent than mature leaves. The mean resorption overall localities were 22%.

The *Nur* of Ca and Mg were negative. The only exception was the positive resorption of Ca (2%) and Mg (75%) at HM_A. The negative values for Ca *Nur* ranged from – 22 to – 457%, with mean overall localities of – 211%. The negative values of Mg *Nur* ranged from – 18 to – 153%, with mean overall localities of – 50%.

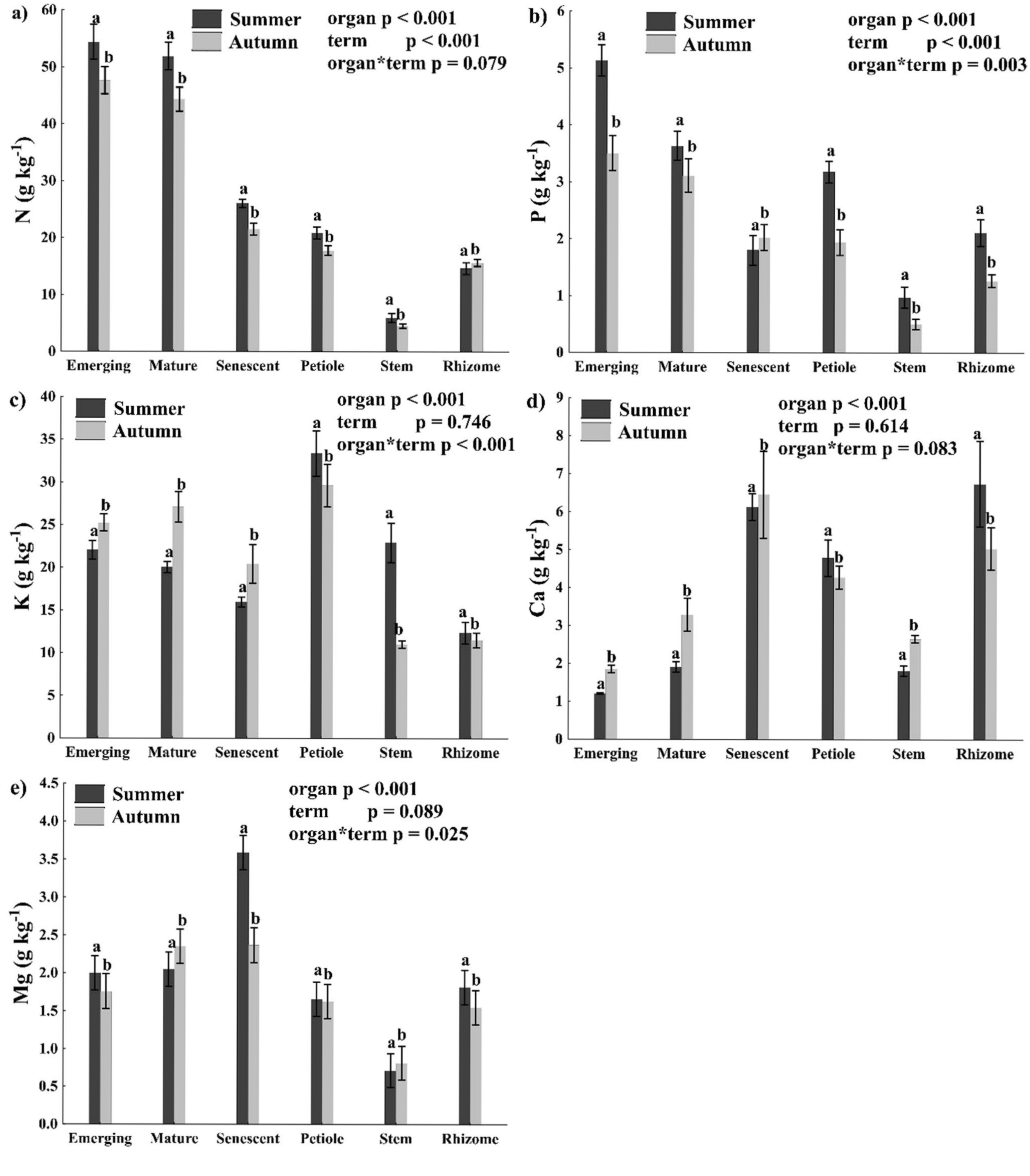

Fig. 6 Effect of terms (summer and autumn) on the content (mean ± SE) of (**a**) N, (**b**) P, (**c**) K, (**d**) Ca, and (**e**) Mg in different organs of *R alpinus* collected from the Giant (Krkonoše) Mountains. The *p* value for organ, locality, and organ*locality was obtained by factorial ANOVA. The *p* value of terms in individual organs was evaluated by one-way ANOVA

4 Discusssion

Different organs of *R. alpinus* reflected varied contents of macroelements. The variability in the contents of N, P, K, Ca, and Mg in the organs directly relates to their contents in the soils. The variation in elemental contents resulted from soil-forming processes, site-specific environmental conditions, and anthropogenic activities per locality

Table 5 The ratio (mean ± SE) between elements N:P, N: K, and K:P in mature and senescent leaves of *R. alpinus*. Differences between localities were obtained by one-way ANOVA—asterisk indicates results significant at $p < 0.001$. Using the Tukey (HSD) post hoc test, mean values with the same letter among localities were not significantly different

Variable	Locality											
	LB_S	LB_A	VT_S	VT_A	PC_S	PC_A	HM_S	HM_A	DCH_S	ZL_S	MD_S	Mean
N:P Mature*	13.3 ± 0.2ab	17.8 ± 0.5a	13.2 ± 0.4ab	14.6 ± 0.3b	13.7 ± 0.1ab	17.8 ± 0.2a	17.8 ± 0.02a	9.8 ± 0.04c	11.9 ± 0.3b	14.8 ± 0.5b	17.9 ± 0.6a	15 ± 0.6
N:P Senescent*	20.5 ± 1.3a	20.5 ± 0.4a	10.2 ± 0.6bc	12.4 ± 0.6b	12.4 ± 0.4b	9.0 ± 0.4bc	22.2 ± 0.9a	6.6 ± 0.6c	18 ± 0.001a	19.2 ± 0.9a	19.1 ± 1.5a	15 ± 1.1
N:K Mature*	2.50 ± 0.03b	1.7 ± 0.04c	2.7 ± 0.1ac	1.8 ± 0.03c	2.2 ± 0.03d	1.9 ± 0.01b	2.9 ± 0.08a	1.2 ± 0.02e	1.8 ± 0.06c	2.48 ± 0.1ad	2.48 ± 0.1ad	2.2 ± 0.1
N:K Senescent*	1.57 ± 0.12ac	0.82 ± 0.03c	2.0 ± 0.20a	1.08 ± 0.06ab	1.44 ± 0.01ac	1.07 ± 0.05ab	1.59 ± 0.08ac	1.57 ± 0.17ac	1.13 ± 0.01ab	1.36 ± 0.03ab	1.42 ± 0.11b	1.4 ± 0.1
K:P Mature*	5.3 ± 0.03ah	10.4 ± 0.04a	4.8 ± 0.05gf	7.8 ± 0.04 cd	6.2 ± 0.03e	9.4 ± 0.04b	6.1 ± 0.16e	8.1 ± 0.13c	6.6 ± 0.03ef	5.96 ± 0.03dh	7.2 ± 0.39 g	7.1 ± 0.4
K:P Senescent*	13 ± 0.15b	25 ± 0.34b	5.1 ± 0.21e	11.5 ± 0.04c	8.6 ± 0.19d	8.4 ± 0.001d	14 ± 0.12b	4.2 ± 0.04e	16 ± 0.08a	14 ± 0.35b	13 ± 0.03b	12 ± 1.2

Abbreviations of localities: *LB* Libuše hut, *VT* Vítkovice v Krkonoších, *PC* Pec pod Sněžkou, *HM* Horní Mísečky, *DCH* Ramsau am Dachstein, *ZL* Zillertal, *MD* Madesimo. *S* summer, *A* autumn, *LB_S* Libuše hut summer)

Table 6 Resorption of elements (*1 − (senescent ÷ mature) × 100)*. Differences between localities (mean ± SE) were evaluated by one-way ANOVA. The asterisk indicates results significant at $p < 0.001$. Using the Tukey post hoc test, the mean values of each element with the same letter among localities were not significantly

Variable	LB_S	LB_A	VT_S	VT_A	PC_S	PC_A	HM_S	HM_A	DCH_S	ZL_S	MD_S	Mean
						%						
N*	48 ± 4.9bc	39 ± 1.7bc	54 ± 1.6acd	48 ± 1.7bc	42 ± 3.8bd	58 ± 0.6ab	52 ± 2.5ac	58 ± 2.9ab	62 ± 0.1ab	64 ± 0.3a	51 ± 3ac	52 ± 8
P*	66 ± 1.5ac	47 ± 1.2bd	40 ± 3.9b	39 ± 0.5b	36 ± 1.7b	18 ± 4.2e	62 ± 0.4af	37 ± 1.9b	75 ± 0.7b	72 ± 2.1ac	54 ± 0.8^{df}	50 ± 4
K*	17 ± 3.4acd	− 28 ± 5.8b	36 ± 10de	10 ± 0.1f	12 ± 5.6f	26 ± 7ad	13 ± 3.2a	67 ± 2.7a	40 ± 2.3e	34 ± 5.2 cd	14 ± 4.1ac	22 ± 5
Ca*	− 204 ± 26abd	− 90 ± 12 cd	− 304 ± 45abf	− 457 ± 65f	− 154 ± 7bcd	− 29 ± 11de	− 249 ± 13abc	2 ± 6a	− 299 ± 49abf	− 359 ± 42af	− 179 ± 0.2ab	− 211 ± 30
Mg*	− 32 ± 2ab	− 57 ± 8abc	− 153 ± 7d	− 55 ± 14abc	− 85 ± 5c	− 18 ± 8b	− 34 ± 2ab	75 ± 5a	− 63 ± 7ac	− 55 ± 9abc	− 72 ± 3ac	− 50 ± 11

The nutrient resorption was done after Vergutz et al. (2012)

Abbreviations of localities: *LB* Libuše hut, *VT* Vítkovice v Krkonoších, *PC* Pec pod Sněžkou, *HM* Horní Mísečky, *DCH* Ramsau am Dachstein, *ZL* Zillertal, *MD* Madesimo. *S* summer, *A* autumn

(Jungová et al. 2022). For example, localities with reduced soil acidity recorded high Ca and Mg contents. The pH range partly supports the dissolution of the elements and subsequent bioaccessibility. In DCH, the comparative low acidity predominantly remained influenced by the Limestone parent rock. Notwithstanding, *R. alpinus* demonstrates tolerance for many soils with diverse chemical properties (Krahulec and Bureš 2019).

The total N content in Krkonoše Mountains localities was similar to other studied sites and corresponds to the long-term fertilizer grassland experiment by Hejcman et al. (2014), except for locality HM, which was 3 times higher. Meanwhile, this resulted from the steep topography of the locality, which accumulated N in the topsoil (Gros et al. 2004; Burt and Rice 2009). Conversely, the low N content in DCH resulted from the inclined position on the North Slope of the Alp, where N losses incur due to leaching and denitrification from low temperatures (Aerts and Chapin 2000; Brant and Chen 2015). Meanwhile, *R. alpinus*, as a nitrophilous plant species, requires a high N supply and adequately high P (Müllerová et al. 2014; Šilc and Gregori 2016; Kołodziejek 2019).

The mean content of N in all the leaves was higher (22.6–52.2 g kg^{-1}) than herbages from different plant communities, e.g., *Utica dioica* (23.2 g kg^{-1}) and many other grassland species—7 to 17 g kg^{-1} (Müllerová et al. 2014; Hejcman et al. 2014; Vondráčková et al. 2014). Consequently, *R. alpinus* utilize large amounts of N in the aboveground biomass (Klimeš et al.1993; Klimešová and Klimeš 1996; Bohner 2005), supported by higher N content in emerging leaves (high metabolic part) than senescent in all the localities (Brant and Chen 2015). The high N content in the emerging leaves is utilized mainly at the cellular level, primarily for enzymatic activities (e.g., increase nitrate reductase activities) and to enable photosynthesis (Bohner 2005; Evans and Clarke 2019) while playing a vital role in the mobility and storage of other nutrients (Canton et al. 2005). Also similar to other alpine plants with high nutrients in the above-ground organs, e.g., *Gentiana rigescens* (Zhang et al. 2020). The relatively similar content of N in the senescent leaves in all the localities is associated with the moderately acidic condition of the soils, which contributes to the dissolution of elements for further bioavailability. The content of N was lowest in the stem and rhizome. The stem serves as a transport conduit from roots to photosynthetic tissues, with lower nutrient contents compared to, e.g., the leaf (Müllerová et al. 2014; Brant and Chen 2015). Nitrogen contents in the rhizomes were lower compared to Bohner (2005). In this study, the rhizomes of *R. alpinus* are comparatively N-rich in the contents of mountain grassroots (Hejcman et al. 2014).

Although the total P content was comparatively lower than most recorded values in the mountain soil ecosystem (1.11 – 1.88 g kg^{-1}; Hejcman et al. 2014; Zhou et al. 2022), the plant-available portion was relatively higher than many other mountain soils, e.g., soils in the community of *Polygono-Trisetion* (Hejcman et al. 2007; Pavlů et al. 2011, 2013). However, the total P content (0.8 g kg^{-1}) in mountain grassland recorded by Semelová et al. (2008) was similar to this study, indicating wide variability of P content in mountain soils. The high P content in emerging and mature leaves supports their high metabolic activities (Vance et al. 2003; Vondráčková et al. 2014; Gao et al. 2019). In the petiole (transport conduit), the relatively high P content in all localities relates to the formation of chelates, with cellular compartments. The contents of individual N and P nutrients in mature and senescent leaves differed at different localities, indicating competitive interactions between species. Localities affected by human activities often result in higher N and P, which may increase competitor organisms for *R. alpinus* seedlings (Zaller 2004; Šilc and Gregori 2016). Additionally, *R. alpinus* can acquire N and P from the soil profile highly facilitated by mycorrhizae (Aerts and Chapin 2000; Bohner 2005). Our results confirm that high leaf N and P contents as a trait for leaf longevity, high photosynthetic, and growth rates are central to *R. alpinus* communities (Vance et al. 2003; Grime et al. 2007; Vergutz et al. 2012; Brant and Chen 2015).

The strategy of plants with nutrient-rich foliage is fast growth and dominance in nutrient-rich ecosystems, which increases eutrophication. Thus, *R. alpinus* is a problematic weed (Stachurska-Swakoń 2009; Delimat and Kiełtyk 2019) and invasive species in the Krkonoše Mountains (Šťastná et al. 2010; Pyšek et al. 2012).

The N:P and N: K ratios in mature leaves of *R. alpinus* are within the range in plant tissues and indicate a comparatively high P demand. The mean resorption of N (52%) and P (50%) was smaller compared to the average percentage of many other vascular plants (62.1 N to 64.9% P) (Vergutz et al. 2012; Brant and Chen 2015; Kong et al. 2020). Compared to senescent leaves, mature leaves have rapid biomass production and thus higher N and P demands, which could be possible drivers of higher N and P resorption efficiency in this study (Minden and Venterink 2019). The significant difference in the resorption of N and P between seasons in the Krkonoše localities indicates that the mature leaves are metabolically active during the summer. The N and P resorption efficiencies in leaves of *R. alpinus* had similar patterns in all the studied localities. The highly effective N and P resorption in *R. alpinus* leave indicate better internal cycling of these elements and the ability of this species to cope with low soil N and P availability (Hejcman et al. 2014). Compared to *Deschampsia caespitosa* (Hejcman et al. 2014), which commonly grows in the *Rumicetum alpini* community, the resorption intensity of P by *R. alpinus* was similar. Thus, the ratio between N and P indicates whether N or P limits plant growth, not the absolute N and P content in plant tissues. Plants with element restrictions in nutrient-rich habitats, despite adequate N content, often have low N:P ratios (Thompson et al. 1997; Ding et al. 2022). The growth of boreal and temperate plants tends to be more N-limited because of N losses due to leaching and denitrification at lower temperatures (Aerts and Chapin 2000; Brant and Chen 2015). This pattern suggests that plant growth might be limited mainly by P availability, particularly in pastures.

The range of total K content in all localities probably was connected with the parent rock (Prášková and Němec 2016). The plant-available K content was relatively similar in all the studied localities except for the VT locality. In VT, the lowest available K resulted from partly taken K via environmental losses, e.g., graminoids, conifers, and forbs that grow in the vicinity (Vergutz et al. 2012). Soils with high organic matter and low clay resist the release of K by weathering clay minerals to compensate for K removal, which is affected by the management regime in the vicinity (Pavlů et al. 2013).

Our study indicated the highest K content in the petiole. Notably, K is a highly mobile element and is re-translocated from an organ to other organs via phloem transport, especially in summer (Chen et al. 2016; de las Heras et al. 2017). Additionally, the high content of H_2O in the petiole is responsible for K enrichment (Tůma et al. 2004; Bohner 2005).

The resorption content of K was 22% compared to the 70% recorded by Vergutz et al. (2012), probably because most of K was in the petiole. Thus, there is K wastage. Plants tend to allocate higher quantities of nutrients to leaves, except for senescent leaves, to facilitate faster growth for competitive advantage during shorter growing seasons (Brant and Chen 2015). Hence, *R. alpinus* recorded high content of K in juvenile and mature leaves. Thus, K deficiency in soil is perhaps more limiting for *R. alpinus* than N and P deficiency (Pavlů, unpublished data). Eventually, this corresponds to the findings of Šťastná et al. (2010) that *R. alpinus* is a plant species with a high absorption capacity for K and is a bioindicator of soils rich in K.

The mature leaves of *R. alpinus* were moderately K co-limited because the N:K ratio was above 2.1 (Olde Venterink et al. 2003; Minden and Olde Ventering 2019), especially during summer in all localities, as they undergo higher N metabolic activities (López-Lefebre et al. 2001). Meanwhile, K metabolic activity is much higher in the petiole. Strong N-limitation in all localities was in senescent leaves. Additionally, sufficient K and P-limitations occurred by a K:P ratio above 3.4 in the mature and senescent leaves (Olde Venterink et al. 2003).

The high availability of Ca and Mg in locality PC is partly from the different compositions of an organic substrate as the locality is on a building plot (Müllerová et al. 2011). The total contents of elements in the soils were higher than plant-available, indicating different patterns of element distributions (Hejcman et al. 2009; Müllerová et al. 2014). The total content of elements is of less value in diagnosing plants' nutrient deficiencies (Cole et al. 2016) as they are relatively insoluble.

Comparatively low contents of Ca and Mg were in the stems as a conduit with low metabolic activity but high mobility of elements, which leads to translocation into plant apices (Anton and Mathe-Gaspar 2005; Gaweda 2009; Vondráčková et al. 2014). The mean contents of Ca and Mg in emergent and mature leaves were low, especially Ca *Rumex alpinus* does not require an increased supply of essential nutrients, e.g., Ca and Mg, during the growing season. Meanwhile, the highest contents of Ca and Mg were recorded in senescent leaves as *R. alpinus* is an "oxalate plant" that regulates excessive Ca in tissues by precipitation of Ca-oxalate (White and Broadley 2003; Vondráčková et al. 2014).

Calciophobic plant species, such as *R. alpinus*, are characterized by a relatively low Ca:Mg and high K:Ca ratio in their leaves (Bohner 2005). The translocation of Ca from senescent leaves and rhizomes to mature and emerging leaves is strongly restricted. The least resorption of Ca and Mg were stored in the mature leaves, as their contents tend to decrease with age (Jones 2012). Thus, negative values show an indication of restricted resorption in senescent leaves. *Rumex alpinus* discriminates Ca and Mg uptake, characterized by relatively low contents (Bohner 2005). Bohner (2005) reported that *R. alpinus* discriminates Ca for nutrient uptake (stored in rhizome) due to the high content of H_2O-soluble oxalate together with a comparatively low content of H_2O-soluble malate in the mature leaves. And this is confirmed by the negative mean resorption of Ca and Mg (−211% and −50%, respectively). Thus, *R. alpinus* discriminates Ca and Mg uptake (van Heerwaarden et al. 2003). Additionally, Ca content cannot be mobilized from older tissues and redistributed through the phloem to other parts of plants and is conserved in the leaves as a structural element (White and Broadley 2003; Kazakou et al. 2007).

Although the resorption of Mg is generally low in all the localities, there was high resorption of Mg (75) during the autumn in HM. Further studies on the resorption efficiency of Mg, considering the effects of many environmental parameters, are required.

5 Conclusions

The comparative study revealed high variability in the distribution and accumulation of phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) in different organs of *R. alpinus* in all the localities. Although variation in the content of macroelements in organs indicates their functionality and peculiar characteristic of *R. alpinus*, their availability is associated with environmental conditions, geological substrates, element content in the soil, pH, and seasons. Notwithstanding, there was a clear pattern of high accumulation of nitrogen (N) and P, especially in the emerging and mature leaves, and Ca in the senescent leaves in all localities.

These relatively low resorptions for Ca and Mg indicate low nutrient use efficiency and re-translocation of these nutrients from senescent to young leaves. As a consequence, *R. alpinus* is considered oxalate, according to the high Ca and Mg in their senescent leaves. The resorption content of N and P was higher compared to the average percentage of other terrestrial plants. *Rumex alpinus* exhibit less resorption of K, an indication of nutrient waste, and simultaneously a high K demand.

Rumex alpinus have N:P and N:K ratios within the normal range in plant tissues but show a comparatively high demand for P. Due to the high nutrient demands of *R. alpinus*, it inhabits only nutrient-rich localities, which encourages significant degradation of various vegetation.

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Declarations

Conflict of interest The authors declare no competing interests.

References

Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Anton A, Mathe-Gaspar G (2005) Factors affecting heavy metal uptake in plant selection for phytoremediation. Z Naturforsch C 60:244–246

Bohner A (2005) *Rumicetum alpini* Beger 1922—species composition, soil-chemical properties, and mineral element content. Wulfenia 12:113–126

Brant AN, Chen HYH (2015) Patterns and mechanisms of nutrient resorption in plants. Critical Reviews in Plant Sci 34:471–486. https://doi.org/10.1080/07352689.2015.1078611

Bucharová A (2003) *Rumex alpinus* v Krkonoších – rozšíření a management. Rumex alpinus in the Giant Mountains - distribution and management. Master's Thesis, Charlse University in Prague, Czech Republic

Burt JW, Rice KJ (2009) Not all ski slopes are created equal: disturbance intensity affects ecosystem properties. Ecol Appl 19:2242–2253. https://doi.org/10.1890/08-0719.1

Canton FR, Suarez MF, Canovas FM (2005) Molecular aspects of nitrogen mobilization and recycling in trees. Photosyn Res 83:265–278. https://doi.org/10.1007/s11120-004-9366-9

Chen Q, Mu X, Chen F, Yuan L, Mi G (2016) Dynamic change of mineral nutrient content in different plant organs during the grain filling stage in maize grown under contrasting nitrogen supply. Eur J Agron 80:137–153. https://doi.org/10.1016/j.eja.2016.08.002

Cole JC, Smith MW, Penn CJ, Cheary BS, Conaghan KJ (2016) Nitrogen, phosphorus, calcium, and magnesium applied individually or as a slow-release or controlled-release fertilizer increase growth and yield and affect macronutrient and micronutrient concentration and content of field-grown tomato plants. Sci Hortic 211:420–430. https://doi.org/10.1016/j.scienta.2016.09.028

de las Heras J, Hernández-Tecles EJ, Moya D (2017) Seasonal nutrient retranslocation in reforested *Pinus halepensis* Mill. stands in Southeast Spain. New Forests 48:397. https://doi.org/10.1007/s11056-016-9564-2

Delgado M, Valle S, Reyes-Díaz M, Barra PJ, Zúñiga-Feest A (2018) Nutrient use efficiency of Southern South America Proteaceae Species. Are there general patterns in the Proteaceae family? Front Plant Sci. 9:883. https://doi.org/10.3389/fpls.2018.00883

Delimat A, Kiełtyk P (2019) Impact of troublesome expansive weed *Rumex alpinus* on species diversity of mountain pastures in Tatra National Park, Poland. Biologia 74:15–24. https://doi.org/10.2478/s11756-018-0148-9

Ding D, Arif M, Liu M, Li J, Hu X, Geng Q, Yin F, Li C (2022) Plant-soil interactions and C: N: P stoichiometric homeostasis of plant organs in riparian plantation. Front Plant Sci 13:979023. https://doi.org/10.3389/fpls.2022.979023

Doležal J, Kurnotová M, Šťastná P, Klimešová J (2020) Alpine plant growth and reproduction dynamics in a warmer world. Phytol 228:1295–1305. https://doi.org/10.1111/nph.16790

Evans JR, Clarke C (2019) The nitrogen cost of photosynthesis. J Exp Bot 70:7–15. https://doi.org/10.1093/jxb/ery366

Francová A, Šillerová H, Chrastný V, Kocourková J, Komárek M (2017) Suitability of selected bioindicators of atmospheric pollution in the industrialized region of Ostrava, Upper Silesia, Czech Republic. Environ Monit Assess 189:478. https://doi.org/10.1007/s10661-017-6199-5

Frey BB (2018) The SAGE encyclopedia of educational research, measurement, and evaluation, 4th edn. SAGE Publications, Inc. https://doi.org/10.4135/9781506326139

Gao J, Song Z, Liu Y (2019) Response mechanisms of leaf nutrients of endangered plant (*Acer catalpifolium*) to environmental factors varied at different growth stages. Glob Ecol Conserv 17:e00521. https://doi.org/10.1016/j.gecco.2019.e00521

Gaweda M (2009) Heavy metal content in common sorrel plants (*Rumex acetosa* L.) obtained from natural sites in Malopolska province. Pol J Environ Stud 18:213–218

Grieve M (2013) Botanical. com: a modern herbal. https: //www.botanical.com/botanical/mgmh/r/rhubar14.html. Accessed 19 Feb 2022

Grime JP, Hodgson JG, Hunt R (2007) Comparative plant ecology: a functional approach to common British species, 2nd edn. Castlepoint Press, Colvend, UK

Gros R, Monrozier LJ, Bartoli F, Chotte JL, Faivre P (2004) Relationships between soil physico-chemical properties and microbial activity along a restoration chronosequence of alpine grasslands following ski run construction. Appl Soil Ecol 27:7–22. https://doi.org/10.1016/j.apsoil.2004.03.004

Hejcman M, Klaudisová M, Štursa J, Pavlů V, Hakl J, Schellberg J, Hejcmanová P, Rauch O, Vacek S (2007) Revisiting a 37years abandoned fertilizer experiment on *Nardus* grassland in the Czech Republic. Agric Ecosyst Environ 118:231–236. https://doi.org/10.1016/j.agee.2006.05.027

Hejcman M, Száková J, Schellberg J, Tlustoš P (2009) The Rengen Grassland Experiment: soil contamination by trace elements after 65 years of Ca, N, P, and K fertilizer application. Nutr Cycl Agroecosyst 83:39–50. https://doi.org/10.1007/s10705-008-9197-8

Hejcman M, Jouany C, Cruz P, Morel C, Stroia C, Theau JP (2014) Subsoil P status could explain the absence of resilience in plant species composition of subalpine grassland 63 years after the last fertilizer application. Sci Agric Bohem 45(2):75–84. https://doi.org/10.7160/sab.2014.450201

Jones JB (2012) Plant nutrition and soil fertility manual, 2nd edn. CRC Press, Boca Raton, pp 78–80

Jones RJA, Houšková B, Bullock P, Montanarella L (2005) Soil resources of Europe, 2nd edn. European Soil Bureau Research Report No.9, Office for Official Publications of the European Communities, Luxembourg pp 47–200

Jungová M, Asare MO, Jurasová V, Hejcman M (2022) Distribution of micro- (Fe, Zn, Cu, and Mn) and risk (Al, As, Cr, Ni, Pb, and Cd) elements in the organs of *Rumex alpinus L.* in the Alps and Krkonoše Mountains. Plant Soil 477:553–575. https://doi.org/10.1007/s11104-022-05440-2

Kazakou E, Garnier E, Navas ML, Roumet C, Collin C, Laurent G (2007) Components of nutrient residence time and the leaf economics spectrum in species from Mediterranean old-fields differing in successional status. Funct Ecol 21:235–245. https://doi.org/10.1111/j.1365-2435.2006.01242.x

Klimeš L (1992) The clone architecture of *Rumex alpinus* (*Polygonaceae*). Oikos 63:402–409

Klimeš L, Klimešová J, Osbornová J (1993) Regeneration capacity and carbohydrate reserves in a clonal plant *Rumex alpinus*: effect of burial. Veget 109:153–160

Klimešová J, Klimeš L (1996) Effects of rhizome age and nutrient availability on carbohydrate reserves in *Rumex alpinus* rhizomes. Biológia 51:457–461

Kołodziejek J (2019) Growth and competitive interaction between seedlings of an invasive *Rumex confertus* and co-occurring two native *Rumex* species in relation to nutrient availability. Sci Rep 9:3298. https://doi.org/10.1038/s41598-019-39947-z

Kong M, Kang J, Han C-L, Gu Y-J, Siddique KHM, Li F-M (2020) Nitrogen, phosphorus, and potassium resorption responses of alfalfa to increasing soil water and P availability in a semi-arid environment. Agronomy 10:310. https://doi.org/10.3390/agronomy10020310

Kopecký K (1973) Je šťovík alpinský (*Rumex alpinus* L.) v Orlických horách původní? Is the Alpine sorrel (*Rumex alpinus*) native to the Eagle Mountains? Preslia, Praha 45:132–139

Krahulec F, Bureš L (2019) Alpine and subalpine habitats. In: Jongepierová I, Pešout P, Prach K (eds) Ecological restoration in the Czech Republic II. Nature Conservation Agency of the Czech Republic UNIPRESS spol. s r.o. p 49

Lokvenc T (1978) Toulky krkonošskou minulostí. Wandering through the Krkonoše past. Available via https://www.databazeknih.cz/knihy/toulky-krkonosskou-minulosti-265524. Accessed 2 July 2022

López-Lefebre LR, Rivero RM, Garcia PC, Sanches E, Ruiz JM, Romero L (2001) Effect of calcium on mineral nutrient uptake and growth of tobacco. J Sci Food Agric 81:1334–71338. https://doi.org/10.1002/jsfa.948

Mehlich A (1984) Mehlich-3 soil test extractant—a modification of Mehlich-2 extractant. Commun Soil Sci Plant Anal 15:1409–1416

Minden V, Olde Ventering H (2019) Plant traits and species interactions along gradients of N, P and K availabilities. Funct Ecol 33:1611–1626. https://doi.org/10.1111/1365-2435.13387

Mishra A, Mehdi S-R, Ali Shariati M, Yahia M, Salim Al-S, Abdur R, Bahare S, Milan Ž, Majid S-R, Poonam G, Javad S-R, Hafiz S, Marcello I (2018) Bioactive compounds and health benefits of edible *Rumex* species—a review. Cell Mol Biol 64:27–34. https://doi.org/10.14715/cmb/2018.64.8.5

Müllerová J, Vítková M, Vítek O (2011) The impacts of road and walking trails upon adjacent vegetation: Effects of road building materials on species composition in a nutrient poor environment. Sci Total Environ 409:3839–3849.https://doi.org/10.1016/j.scitotenv.2011.06.056

Müllerová V, Hejcman M, Hejcmanová P, Pavlů V (2014) Effect of fertilizer application on *Urtica dioica* and its element concentrations in a cut grassland. Acta Oecol 59:1–6. https://doi.org/10.1016/j.actao.2014.05.004

Náglová S (2014) Invasion of *Rumex alpinus* L. in Krkonoše Mountains. Master's Thesis, Charles University of Prague, Czech Republic

Nakhutsrishvili G, Batsatsashvili K, Rudmann-Maurer K, Korner C, Spehn E (2017) New indicator values for Central Caucasus flora. Nakhutsrishvili G et al. (eds.), Plant diversity in the central great Caucasus: a quantitative assessment, Geobotany Studies, Pp 145–159. https://doi.org/10.1007/978-3-319-55777-9_6

Němeček J, Kozák J (2005) Status of soil surveys, inventory, and soil monitoring in The Czech Republic. In: Jones RJA, Houšková B, Bullock P, Montanarella L (eds). Soil resources of Europe, 2nd edn. European Soil Bureau Research Report No.9, Office for Official Publications of the European Communities, Luxembourg, pp. 103–109

Olde Venterink H, Wassen MJ, Verkroost AWM, de Ruiter PC (2003) Species richness-productivity patterns differ between N-, P-and K-limited wetlands. Ecology 84:2191–2199. https://doi.org/10.1023/A:1017922715903

Opačić N, Radman S, Uher SF, Benko B, Voća S, Žlabur JŠ (2022) Nettle cultivation practices from open field to modern hydroponics: a case study of specialized metabolites. Plant 11:483. https://doi.org/10.3390/plants11040483

Ozturk S, Ozturk A (2007) Antibacterial activity of aqueous and methanol extracts of *Rumex alpinus.* and *Rumex caucasicus*. Pharm Biol 45:83–87

Pavlů L, Pavlů V, Gaisler J, Hejcman M, Mikulka J (2011) Effect of long-term cutting versus abandonment on the vegetation of a mountain hay meadow (*Polygono-Trisetion*) in Central Europe. Flora 206:1020–1029. https://doi.org/10.1016/j.flora.201107.008

Pavlů L, Pavlů V, Gaisler J, Hejcman M (2013) Relationship between soil and biomass chemical properties, herbage yield, and sward height in cut and un-managed mountain hay meadow (*Polygono-Trisetion*). Flora 208:599–608. https://doi.org/10.1016/j.flora.2013.09.003

Prášková L, Němec P (2016) Bazální monitoring zemědělských půd – pH a obsah živin 1995 – 2013. ÚKZÚZ Brno. [Basal monitoring of agricultural soils—pH and nutrient content 1995 – 2013]. http://eagri.cz/public/web/file/458807/BMP_ZIVINY_text_opr.pdf. Accessed 11 Jan 2020

Pyšek P, Danihelka J, Sádlo J, Chrtek J Jr, Chytrý M, Jarošík V, Kaplan Z, Krahulec F, Moravcová L, Pergl J, Štajerová K, Tichý L (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity, and invasion patterns. – Preslia 84: 155–255

Rehder H (1982) Nitrogen relations of ruderal communities (*Rumicion alpini*) in the Northern Calcareous Alps. Oecologia 55:120–129

Semelová V, Hejcman M, Pavlů V, Vacek S, Podrázský V (2008) The grass garden in the giant mts. (Czech Republic): residual effect of long-term fertilization after 62 years. Agric Ecosyst Environ 123:337–342. https://doi.org/10.1016/j.agee.2007.07.005

Šilc U, Gregori M (2016) Control of alpine dock (*Rumex alpinus*) by non-chemical methods. Acta Biol Slov, Ljubljana 59(1):23–32

Stachurska-Swakoń A (2009) Syntaxonomical revision of the communities with *Rumex alpinus* L. in the Carpathians. Phytocoenologia 39(2):217–234. https://doi.org/10.1127/0340-269X/2009/0039-0217

Šťastná P, Klimeš L, Klimešová J (2010) Biological flora of Central Europe: *Rumex alpinus* Dipl Thesis, Charles University of Prague L. Perspect Plant Ecol Syst 12:67–79. https://doi.org/10.1016/j.ppees.2009.06.003

Thapa N, Barik SK, Upadhaya K (2020) Local edaphic factors influence leaf nutrient resorption efficiency of evergreen and deciduous

trees: a case study from montane subtropical old-growth and regenerating forests of Meghalaya. Trop Ecol 61:21–31. https://doi.org/10.1007/s42965-020-00063-z
Thompson K, Parkinson JA, Band SR, Spencer RE (1997) A comparative study of leaf nutrient concentrations in a regional herbaceous flora. New Phytol 136:679–689. https://doi.org/10.1046/j.1469-8137.1997.00787.x
Tůma J, Skalický M, Tůmová L, Bláhová P, Rosůlková M (2004) Potassium, magnesium and calcium content in individual parts of *Phaseolus vulgaris* L. plant as related to potassium and magnesium nutrition. Plant Soil Environ 50(1):18–26. https://doi.org/10.17221/3637-PSE
USEPA Method *3052* (1996) Microwave assisted acid digestion of siliceous and organically based matrices. https://www.epa.gov/sites/production/files/2015-12/documents/3052.pdf. Accessed 7 Feb 2019
Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol 157:423–447. https://doi.org/10.1046/j.1469-8137.2003.00695.x
van Heerwaarden LM, Toet S, Aerts R (2003) Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. Oikos 101:664–669. https://doi.org/10.1034/j.1600-0706.2003.12351.x
Vergutz L, Manzoni S, Porporato A, Ferreira Novais R, Jackson RB (2012) Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol Monogr 82:205–220. https://doi.org/10.1890/11-0416.1
Vondráčková S, Hejcman M, Száková J, Müllerová V, Tlustoš P (2014) Soil chemical properties affect the concentration of elements (N, P, K, Ca, Mg, As, Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn) and their distribution between organs of *Rumex obtusifolius*. Plant Soil 379:231–245. https://doi.org/10.1007/s11104-014-2058-0
White PJ, Broadley MR (2003) Calcium in plants. Ann Bot 92:487–511. https://doi.org/10.1093/aob/mcg164
Yan T, Jiaojun Z, Kai Y (2018) Leaf nitrogen and phosphorus resorption of woody species in response to climatic conditions and soil nutrients: a meta-analysis. J For Res 29:905–913. https://doi.org/10.1007/s11676-017-0519-z
Zaller JG (2004) Competitive ability of *Rumex obtusifolius* against native grassland species: above- and below-ground allocation of biomass and nutrients. J Plant Dis Protect 19:345–351
Zhang J, Wang Y, Cai C (2020) Multi elemental stoichiometry in plant organs: a case study with the Alpine herb *Gentiana rigescens* across Southwest China. Front Plant Sci 11:441. https://doi.org/10.3389/fpls.2020.00441
Zhou H, Ma A, Zhou X, Chen X, Zhang J, Gen P, Liu G, Wang S, Zhuang G (2022) Soil phosphorus accumulation in mountainous alpine grassland contributes to positive climate change feedback via nitrifier and denitrifier community. Sci Total Environ 804:150032. https://doi.org/10.1016/j.scitotenv.2021.150032

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