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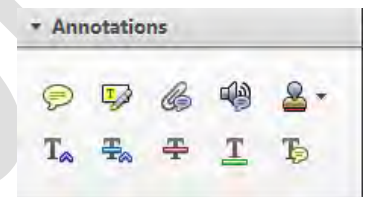


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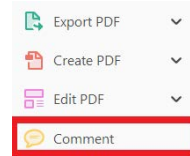
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
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4. Greater than 25% overlap at the N-termin terminus with another coding feature; ove both ends; or ORF containing a tRNA.

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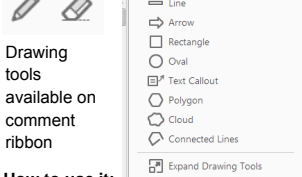
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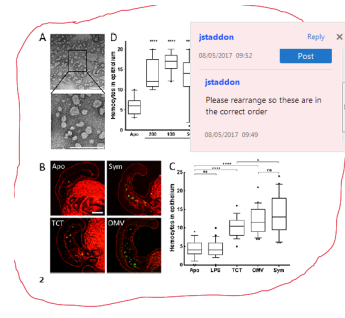


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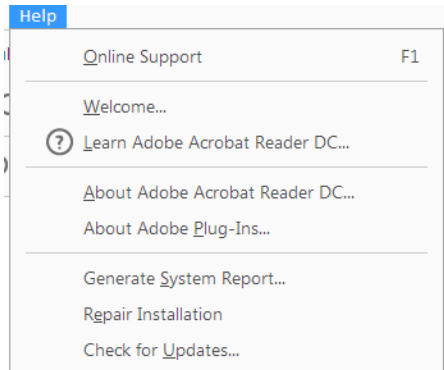
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RESEARCH ARTICLE

Differential effects of soil chemistry on the foliar resorption of nitrogen and phosphorus across altitudinal gradients

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Abstract

1. Nutrient resorption from senescing leaves prior to litterfall is a strategy for nutrient conservation in vascular plants. However, the mechanisms through which soil fertility and/or foliar nutrient status affect nutrient resorption are not yet fully known.
2. We used two 1,000-m-wide altitudinal gradients on two different bedrock types (carbonate and silicate) for analysing the interactive effects of temperature and soil chemistry on the resorption efficiency of two major nutrients, nitrogen (N) and phosphorus (P). Our objective was to assess how nutrient resorption varied across the gradients through the adaptation of individual species to changing environmental conditions rather than through changes in species composition.
3. Both N and P resorption efficiency increased across the altitudinal gradients independent of bedrock type. The main process regulating nutrient resorption was a negative feedback to nutrient availability in the soil. The negative feedback of nutrient resorption efficiency to soil nutrient status was unrelated to total soil nutrient contents but depended on concentrations of organic N forms for nitrogen resorption efficiency (NRE) and on inorganic P forms for phosphorus resorption efficiency (PRE), respectively.
4. While we hypothesized that the resorption of P, as a principally rock-derived nutrient, depended on physical–chemical processes affected by soil chemistry, our results showed that microbial P mineralization was the main source of inorganic P supply to the plants. Both NRE and PRE were effective to improve the growth potential of plants, but there was no evidence of stoichiometric adaptations of N:P RE to nutrient ratio in the soil.

KEYWORDS

altitude, bedrock, foliar chemistry, mineralization, mountain, nutrient remobilization, nutrient resorption efficiency, soil nutrient content

1 | INTRODUCTION

Remobilization of nutrients from ageing tissues is recognized as a strategy for nutrient conservation in vascular plants. In particular, nutrient resorption from senescing leaves prior to litterfall is regarded as an adaptation to nutrient deficiency (Brant & Chen, 2015). Fertilization

experiments have shown that experimentally improved soil fertility reduces the efficiency in resorbing nutrient by plants (Lü et al., 2013; Yuan & Chen, 2015). However, analyses of nutrient resorption patterns across environmental gradients at different geographic scale failed to support consistent relationships between plant nutrient resorption and soil nutrient availability. At the global scale, Yuan and Chen (2009)



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1 observed decreasing nitrogen resorption efficiency (NRE) and increas-
2 ing phosphorus resorption efficiency (PRE) with increasing latitude.
3 Contrasting geographic patterns of NRE and PRE have been explained
4 considering the low soil N availability in cold high-latitude soils and the
5 low soil P availability in weathered low-latitude soils. Recent reviews
6 reported increasing values of NRE and PRE with increasing latitude,
7 paralleled by negative relationships of nutrient resorption efficiency
8 with mean annual temperature and mean annual precipitation (Vergutz,
9 Manzoni, Porporato, Novais, & Jackson, 2012; Yan, Zhu, & Yang, 2018).
10 At the regional scale, Hayes, Turner, Lambers, and Laliberté (2014)
11 observed negative correlations between total soil N and P concentra-
12 tions and NRE and PRE across a dune chronosequence in south-west-
13 ern Australia. Similarly, Achat, Pousse, Nicolas, and Augusto (2018)
14 found the remobilization rates of N, P and other major elements to be
15 regulated by soil nutrient status through negative feedback in 10 tree
16 species at forest sites in France. Conversely, no significant correlations
17 were found between both NRE and PRE and soil nutrient concentra-
18 tions in gallery forests in the Central Black Sea Region (Özbucak et
19 al., 2008). In forest sites in China, PRE is negatively related to soil P
20 content, while NRE is principally controlled by plant functional type
21 (PFT) irrespective of soil N content (Tang, Han, Chen, & Fang, 2013).
22 Nutrient concentrations in green leaves have been thought to repre-
23 sent a proxy of soil nutrient status. If so, the negative feedback of soil
24 fertility towards nutrient resorption efficiency should be mirrored by
25 negative correlations between foliar nutrient concentrations and nutri-
26 ent resorption efficiency (Liu, Liu, Guo, Wang, & Yang, 2014; Vergutz et
27 al., 2012). However, most studies failed in supporting this hypothesis
28 as nutrient resorption efficiency generally is unrelated to foliar nutrient
29 concentrations (Achat et al., 2018; Aerts, 1996; Norby, Long, Hartz-
30 Rubin, & O'Neill, 2000; Özbucak et al., 2008).

31 Patterns of nutrient resorption efficiency across altitudinal gradi-
32 ents have so far received little attention. NRE generally increases with
33 increasing altitude while PRE shows differing trends across altitudinal
34 gradients, with PRE increasing (Bilgin & Guzel, 2017), decreasing (Tang
35 et al., 2013) or varying erratically (Du, Ji, Peng, Liu, & Liu, 2017) with
36 increasing altitude. The mechanistic basis for explaining varying alti-
37 tudinal patterns of nutrient resorption efficiency still remains unre-
38 solved. Higher nutrient remobilization at high altitude can be achieved
39 by genetic adaption of individual species to cold environment (Cong
40 et al., 2018). For example, resorption efficiency of N and P of Scots
41 pine populations grown in common garden has been found to increase
42 with the latitude of seed origin suggesting potential adaptation of
43 populations from northern, colder habitats to more efficient internal
44 nutrient cycling (Oleksyn, Reich, Zytковиak, Karolewski, & Tjoelker,
45 2003). Alternatively, increasing NRE and/or PRE across altitudinal
46 gradients can be achieved by changes in species composition, with
47 species more efficient in conserving nutrients being more abundant at
48 environmentally harsher sites (Richardson, Peltzer, Allen, & McGlone,
49 2005). Higher nutrient resorption efficiency at high-altitude sites can
50 be associated with lower soil fertility because cold temperatures ham-
51 per nutrient mineralization by slowing the activity of soil microbes
52 (Sundqvist, Sanders, & Wardle, 2013). While soil N availability almost
53 totally depends on biological processes driven by soil microbes, soil

P availability is the result of complex interactions between microbial
and physical-chemical processes, the latter in turn related to the P
content of the underlying parent material (Porder & Ramachandran,
2013). The geochemical composition of parent materials, closely as-
sociated with the geological nature of bedrock (bedrock geology), is
paramount in controlling the availability of rock-derived elements,
especially potassium (K) and P (Augusto, Achat, Jonard, Vidal, &
Ringeval, 2017; Castle & Neff, 2009). Bedrock geology strongly in-
fluences the distribution and the productivity of vegetation even in
climatically homogeneous areas through indirect control on soil nutri-
ent status (Hahm, Riebe, Lukens, & Araki, 2014). Mountainous regions
are characterized by strong heterogeneity of bedrock types even at
regional and local scale. Hence, investigating patterns of nutrient re-
sorption efficiency on different bedrock types in mountains can add
to our knowledge on environmental factors affecting the ability of
mountain plants to recycle nutrients from senescing leaves.

We investigated altitudinal trends of foliar resorption of N and
P, that is the nutrients most strongly involved in plant physiological
processes. Our main objective was to assess whether the efficiency
in resorbing N and P varies due to combined effects of altitude and
bedrock geology on soil chemistry. Our study was designed for in-
vestigating altitudinal patterns of nutrient resorption efficiency
resulting from adaptation of individual species to changes in soil
nutrient status across the gradient. Patterns of nutrient resorption
across environmental gradients are often determined by changes
in species composition (Achat et al., 2018; Richardson et al., 2005;
Tsujii, Onoda, & Kitayama, 2017). In order to prevent confounding
effects of compositional turnover across the altitudinal range, we
selected species that occurred with high frequency across a broad
altitudinal range on two bedrock types. We hypothesized that (1)
resorption of N, as a microbially cycled element, increases across
altitudinal gradients independent of bedrock geology because low
temperature hampers N mineralization; (2) resorption of P, as a rock-
derived element, varies differently across the altitudinal gradients
because P supply is primarily controlled by bedrock geology.

2 | MATERIALS AND METHODS

2.1 | Study areas and sampling

The study areas and the sampling design are described in Gerdol,
Marchesini, and Iacumin (2017). Shortly, the study was carried out
across two 1,000-m altitudinal gradients (c. 1,200–2,200 m above
sea level) in two areas c. 30 km apart (46°13–25'N, 11°27–43'E) in
the Dolomites (Province of Trento, northern Italy). The two areas are
climatically homogeneous with mean annual temperatures of c. 8°C
at 1,000 m and c. 3°C at 2,000 m and mean total annual precipita-
tion of c. 900 mm, mostly concentrated in the summer season that
usually does not experience aridity. The two transects were located
in environmentally similar areas, with northern aspect and mean
slope angle of c. 20° strongly differing from each other in terms of
bedrock geology. In the first area, the parent material consists of car-
bonate bedrocks (dolomite and limestone), while in the second area

the parent material consists of silicate bedrock (granitic porphyry). Six 1-ha sampling sites were set up, at c. 200-m intervals, in each of the two transects. We carried out a number of preliminary surveys directed to select species occurring with high frequency across the altitudinal gradients on both parent materials. We chose five species, each belonging to a different PFT: *Vaccinium myrtillus* (*V. myrtillus*), a deciduous shrub; *Vaccinium vitis-idaea* (*V. vitis-idaea*), an evergreen shrub; *Picea excelsa* (*P. excelsa*), a conifer tree; *Homogyne alpina* (*H. alpina*), a wintergreen forb; and *Calamagrostis villosa* (*C. villosa*), a grass.

The sites from 1,200 to 1,800 m were located in closed spruce forests. The sites at 2,000 m were located in sparse spruce forests, close to the treeline. The sites at 2,200 m were located above treeline in subalpine scrubs. In spite of such strong differences in vegetation structure and plant height, these five species accounted for at least 80% of vascular-plant cover, although the proportional cover of individual species varied among sites. The sampling was carried out in 2011 at five 5 × 5 m plots, at least 15 m apart, in each of the 12 sampling sites. In spring, we visited all sites at 2- to 3-day intervals in order to detect the start of the growing season to be used for subsequent measurements of daily leaf growth rates (Gerdol et al., 2017). Green leaves of all five species were collected during 2 days at the peak of the growing season (1–2 August). Current-year leaves were sampled for the evergreen and the wintergreen species. On the same occasion, we collected soil samples using a stainless steel cylindrical corer. At each plot, we took five subsamples that were then bulked in a composite soil sample. In October, we collected at all plots a number of senescing freshly fallen leaves of all five species for subsequent measurements of nutrient content in the litter.

2.2 | Chemical analyses

About 50 mg of oven-dried (40°C for 48 hr) leaf tissue was powdered, extracted in 3 ml of selenous H₂SO₄ at 420°C and analysed for total N concentration in green leaves (N_{leaf}) by the salicylate method and total P concentration in green leaves (P_{leaf}) by the molybdenum blue method. Total N and P concentrations in senescing leaves (N_{litter} and P_{litter}) were determined as for the green leaves. For each species, N_{leaf} and P_{leaf} were compared with N_{litter} and P_{litter} after correcting for mass loss during leaf senescence, in order to determine nutrient resorption efficiency. The mass loss correction factors (MLCF), drawn from Vergutz et al. (2012), were as follows: 0.784 for the deciduous shrub *V. myrtillus*; 0.780 for the evergreen shrub *V. vitis-idaea*; 0.745 for the conifer tree *P. excelsa*; 0.640 for the forb *H. alpina*; and 0.713 for the grass *C. villosa*. The nutrient resorption efficiencies for N and P were calculated as follows:

$$\text{NRE} = [1 - (\text{N}_{\text{litter}}/\text{N}_{\text{leaf}}) \times \text{MLCF}] \times 100.$$

$$\text{PRE} = [1 - (\text{P}_{\text{litter}}/\text{P}_{\text{leaf}}) \times \text{MLCF}] \times 100.$$

The ratio between the two nutrient resorption efficiencies was expressed as:

$$\text{N:P RE} = \text{NRE}/\text{PRE}.$$

The soil analyses were directed to determine both total nutrient concentrations and concentrations of nutrients in available forms. A 0.1-g subsample of air-dried soil was extracted and analysed for total soil N (N_{total}) as for the leaves and the litter. A 20-g subsample of air-dried soil was extracted in 200 ml of 0.5 M K₂SO₄ and analysed for NH₄ by the salicylate method and for NO₃ by the cadmium reduction method. A 1-g subsample of air-dried soil was extracted in 10% 0.5 M K₂SO₄ for determining total dissolved nitrogen (TDN). TDN was analysed by the cadmium reduction method after digestion with an oxidant reagent containing a buffer solution of boric acid (H₃BO₃), sodium hydroxide (NaOH) and potassium persulfate (K₂S₂O₈). Dissolved organic nitrogen (DON) was calculated by subtracting the sum of dissolved inorganic N fractions (NO₃ + NH₄) from TDN. Nitrate concentrations always were negligible. Hence, soil N content in available inorganic form (N_{inorg-avail}) corresponded to NH₄ concentration. Soil N content in available organic form (N_{org-avail}) corresponded to DON concentration.

A 0.1-g subsample of air-dried soil was extracted and analysed for total soil P (P_{total}) as for the leaves and the litter. A 0.5-g subsample of air-dried soil was extracted in 80 ml of 1 M KCl. A 0.5-g subsample of air-dried soil was extracted in 0.5 M NaHCO₃ adjusted to pH 8.5 with NaOH. The KCl extract contained only P_i and was therefore analysed colorimetrically at 700 nm for PO₄ (Sundqvist et al., 2014). The NaHCO₃ extract contained both inorganic and organic P fractions (P_i and P_o, respectively). The P_i fraction was determined by the molybdenum blue method while total P was determined after digesting a subsample of the extract with acidified potassium persulfate (K₂S₂O₈) in order to convert P_o into P_i. Subsequently, P_o concentration was calculated by subtracting P_i from P_{total}. Available soil P content in inorganic and organic forms (P_{inorg-avail} and P_{org-avail}, respectively) was calculated as follows:

$$\text{P}_{\text{inorg-avail}} = \text{KCl-P}_i + \text{NaHCO}_3\text{-P}_i.$$

$$\text{P}_{\text{org-avail}} = \text{NaHCO}_3\text{-P}_o.$$

All colorimetric analyses were run on a continuous flow autoanalyser (FlowSys; Systea, Anagni, Italy).

A 20-mg subsample of air-dried soil was used for analysing total soil carbon (C) concentration by a Shimadzu TOC-5000A analyser (Shimadzu Corporation, Kyoto, Japan), connected with a solid sample module (Shimadzu SSM-5000A).

Nitrogen isotopic discrimination was assessed by determining the ¹⁵N content in the soil. The measurements were carried out by an elemental analyser (EA 1110; Carlo Erba, Milan, Italy) coupled with an isotope ratio mass spectrometer (Delta Plus XP; Thermo Finnigan, Bremen, Germany). The values were expressed as δ¹⁵N:

$$\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000\text{‰},$$

where R_{sample} is the ¹⁵N:¹⁴N ratio in the sample and R_{standard} is the ¹⁵N:¹⁴N ratio in the standard (atmospheric N₂).

2.3 | Data analyses

The data of NRE, PRE and N:P RE were statistically analysed by three-way ANOVAs with species, altitude and bedrock as fixed factors. Significance of differences between the means was assessed by post hoc Fisher's LSD tests. Mean values of nutrient resorption efficiency, nutrient concentrations and their ratio in green leaves and nutrient concentrations and their ratio in the litter were calculated for each plot at all of the 12 sampling sites as the means of the corresponding variables across the five species. Leaf growth was expressed as daily growth rates (see Gerdol et al., 2017 for details). As the five species differed strongly from each other in terms of foliar traits which implied great differences in leaf growth among species, the daily growth rates were normalized for each species as follows:

$$X_{ni} = (X_{oi} : X_{max}) \times 100,$$

where X_{ni} is the normalized value of daily growth rate for the X -species at the i -site; X_{oi} is the original value of daily growth rate for the X -species at the i -site; and X_{max} is the maximum value of daily growth rate for the X -species across the 12 sites.

The mean values of NRE, PRE and N:P RE were regressed on altitude in order to assess the altitudinal patterns of the three variables on the two bedrock types. Relationships of the nutrient resorption efficiencies and their ratios with the variables related to foliar chemistry and litter chemistry were assessed by Pearson's product-moment correlation coefficients. Relationships of the nutrient resorption efficiencies and their ratio with the variables related to soil chemistry were assessed by stepwise multiple linear regressions based on stepwise forward selection of the explanatory variables. In particular:

NRE was regressed on N_{total} , $N_{inorg-avail}$, $N_{org-avail}$, soil $\delta^{15}N$, soil C:N and soil pH;

PRE was regressed on P_{total} , $P_{inorg-avail}$, $P_{org-avail}$, soil C:P and soil pH;

N:P RE was regressed on soil C:N, soil C:P and soil pH.

All statistical computations were carried out using the package Statistica 6.0 (StatSoft©; Version 6; StatSoft Inc., Tulsa, OK, USA).

3 | RESULTS

3.1 | Nutrient resorption efficiency, foliar chemistry and litter chemistry

Species identity was the far largest source of variance for nutrient resorption efficiencies and their ratio (Table 1). NRE, PRE and N:P RE were influenced to a similar extent by altitude, while bedrock exerted a much stronger effect on PRE than on NRE and N:P RE (Table 1). The strength of altitude \times bedrock interactions was about double for PRE and N:P RE than for NRE. The five species presented consistent altitudinal patterns of nutrient resorption efficiencies and their ratio on the two bedrock types, as demonstrated by similarly low species \times altitude, species \times bedrock and

TABLE 1 Percentage of variance associated with the F values of three-way ANOVAs for nutrient resorption efficiencies and their ratio. Abbreviations and df : Species (Sp; 4,234); Altitude (A; 5,234); Bedrock (B; 1,234); Sp \times A (20,234); Sp \times B (4,234); A \times B (5,234); Sp \times A \times B (20,234)

	Nitrogen resorption efficiency	Phosphorus resorption efficiency	N:P RE
Species (Sp)	79.08	70.30	76.71
Altitude (A)	11.53	9.19	6.60
Bedrock (B)	0.72	8.04	2.56
Sp \times A	2.66	3.18	3.82
Sp \times B	0.59	1.14	0.82
A \times B	3.02	6.22	6.24
Sp \times A \times B	2.39	1.92	3.25

species \times altitude \times bedrock interactions for NRE, PRE and N:P RE (Table 1). The overall mean NRE was 57%, with the five species being ranked as follows: *C. villosa* (80%) > *H. alpina* (58%) > *P. excelsa* (48%) = *V. myrtillus* (47%) = *V. vitis-idaea* (47%). The overall mean PRE (67%) was higher than NRE, and the species ranking was rather similar to, but not overlapping with, that for NRE, that is *C. villosa* (78%) > *H. alpina* (69%) = *P. excelsa* (69%) > *V. vitis-idaea* (63%) > *V. myrtillus* (54%). The NRE and PRE increased linearly across the altitudinal gradients both on carbonate bedrock and on silicate bedrock, but the slopes of the regression lines were steeper on silicate bedrock (Figure 1a,b). The overall mean N:P RE was 0.84. The N:P RE was <1 in four out of the five species which suggests that P was generally resorbed to a greater extent than N. The species ranking was as follows: *C. villosa* (1.03) > *V. myrtillus* (0.88) = *H. alpina* (0.84) > *V. vitis-idaea* (0.74) = *P. excelsa* (0.71). The N:P RE increased linearly with increasing altitude on carbonate bedrock but was stable across the altitudinal gradient on silicate bedrock (Figure 1c).

The N_{leaf} presented no distinct altitudinal patterns on either bedrock types (Table 2). The P_{leaf} was lowest at 1,200–1,400 m on carbonate bedrock but was lowest at 2,000–2,200 m on silicate bedrock. Consequently, the $N:P_{leaf}$ presented contrasting patterns on the two bedrock types, with highest values at low altitudes on carbonate bedrock and highest values at high altitudes on silicate bedrock (Table 2). The altitudinal pattern of $\delta^{15}N_{(leaf-soil)}$ was much similar on the two bedrock types with slightly negative values at 1,200–1,800 m and strongly negative values at 2,000–2,200 m (Table 2). The N_{litter} moderately decreased across the altitudinal gradients on both bedrock types. The P_{litter} on carbonate bedrock increased moderately from 1,200 to 2,000 m and declined again at 2,200 m. Conversely, the P_{litter} on silicate bedrock strongly decreased across the whole altitudinal gradient. The $N:P_{litter}$ decreased across the altitudinal gradient on carbonate bedrock and increased across the altitudinal gradient on silicate bedrock, thus mirroring the altitudinal trends of the $N:P_{leaf}$ (Table 2). The leaf growth rate fluctuated irregularly across the altitudinal gradient on carbonate bedrock but definitely increased with increasing altitude on silicate bedrock (Table 2).

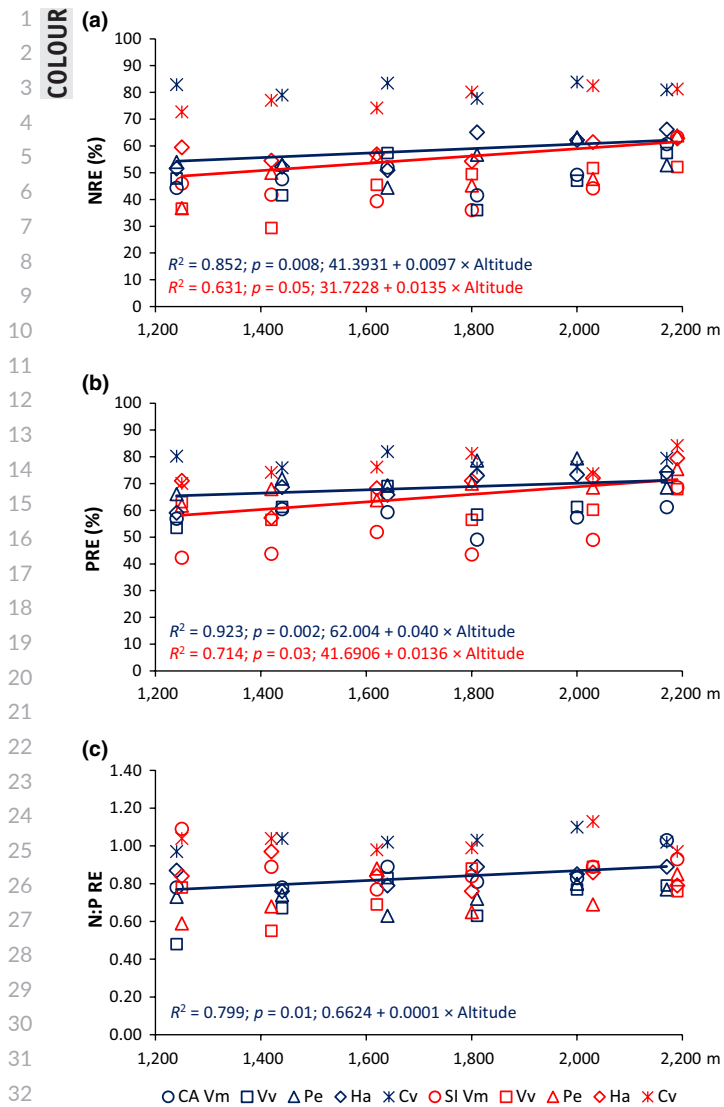


FIGURE 1 Nitrogen resorption efficiency (NRE), phosphorus resorption efficiency (PRE) and N:P RE values in leaves of five species across altitudinal gradients on carbonate bedrock (blue symbols) and silicate bedrock (red symbols). Significant ($p < 0.05$) linear regression lines for the overall means are shown separately across the two gradients [blue lines: carbonate bedrock (CA); red lines: silicate bedrock (SI)]

3.2 | Soil chemistry

N_{total} and $N_{\text{inorg-avail}}$ generally were similar or presented erratic fluctuations across the altitudinal gradients on both bedrock types (Table 3) while $N_{\text{org-avail}}$ decreased more or less regularly across the altitudinal gradients. The altitudinal trend of $N_{\text{org-avail}}$ mirrored that of soil $\delta^{15}\text{N}$ that increased, that is became less negative, with increasing altitude on both bedrock types (Table 3). P_{total} presented a clear increasing trend with increasing altitude on carbonate bedrock and decreased irregularly across the altitudinal gradient on silicate bedrock. $P_{\text{inorg-avail}}$ decreased with increasing altitude on both bedrock types. $P_{\text{org-avail}}$ did not show any clear altitudinal trend on either bedrock types (Table 3). C_{total} generally decreased across the

altitudinal gradients although such pattern was sharper on carbonate bedrock (Table 3). The soil N:P definitely declined across the altitudinal gradient on carbonate bedrock and tended to increase across the altitudinal gradient on silicate bedrock (Table 3). The soil C:N decreased with increasing altitude on carbonate bedrock and fluctuated across the altitudinal gradient on silicate bedrock. The soil C:P presented contrasting patterns in relation to bedrock type, that is, a decreasing trend on carbonate bedrock and an increasing trend on silicate bedrock. The soil pH was overall stable across the gradients, with slightly higher values on carbonate bedrock (Table 3).

3.3 | Relationships between nutrient resorption efficiency and the nutrient status of leaves, litter and soil

Both NRE and PRE presented strong negative correlations with N_{litter} and P_{litter} , respectively (Table 4). The resorption efficiency of the two nutrients was unrelated to nutrient concentrations in green leaves (Table 4). Furthermore, NRE was negatively correlated with $\delta^{15}\text{N}_{(\text{leaf-soil})}$ (Table 4). The N:P RE was unrelated to $N:P_{\text{leaf}}$ and $N:P_{\text{litter}}$ (Table 4). Both NRE and, especially, PRE presented positive correlations with leaf growth while the N:P RE was unrelated to leaf growth (Table 4).

Nitrogen resorption efficiency, PRE and N:P RE all presented significant correlations with at least one of the soil chemistry variables (Table 5). $N_{\text{org-avail}}$ and soil $\delta^{15}\text{N}$ were the best predictors of NRE, the former with negative correlation and the latter with positive correlation, while N_{total} was marginally positively related to NRE (Table 5). $P_{\text{inorg-avail}}$, with negative correlation, and C:P and P_{total} , both with positive correlations, were the best predictors of PRE. Soil C:P, with negative correlation, was the best predictor of N:P RE (Table 5).

4 | DISCUSSION

In spite of strong differences among species in terms of nutrient resorption efficiency, the low species \times bedrock and species \times altitude \times bedrock interactions indicate that the overall patterns of nutrient resorption efficiency reflected similar behaviour of the five species across the gradient. Altitude significantly affected nutrient resorption although much less than species identity. Altitudinal gradients represent complex gradients across which several environmental factors vary more or less linearly with altitude (Körner, 2007). Four of these factors can affect nutrient resorption in plants either directly (temperature and length of the growing season) or indirectly (soil moisture and soil nutrient content). The results of our study exclude the hypothesis of direct effects of environmental factors on nutrient resorption. Warm temperature may enhance nutrient resorption through delayed leaf senescence in autumn, that is by increased duration of the growing season (Estiarte & Peñuelas, 2015; Fu et al., 2018). Should temperature-mediated slower speed of leaf senescence be responsible for increased levels of nutrient resorption, this would

TABLE 2 Mean (± 1 SE) values of total N concentration in green leaves (N_{leaf}), total P concentration in green leaves (P_{leaf}), N:P ratio in green leaves ($N:P_{\text{leaf}}$), difference between $\delta^{15}\text{N}$ of green leaves and $\delta^{15}\text{N}$ of soil ($\delta^{15}\text{N}_{(\text{leaf-soil})}$), total N concentration in senescing leaves (N_{litter}), total P concentration in senescing leaves (P_{litter}), N:P in senescing leaves ($N:P_{\text{litter}}$) and normalized daily growth rate across altitudinal gradients on two bedrock types ($N = 5$)

Altitude (m)	N_{leaf} (mg/g)		P_{leaf} (mg/g)		$N:P_{\text{leaf}}$		$\delta^{15}\text{N}_{(\text{leaf-soil})}$	
	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate
1,200	16.5 \pm 1.19 B	17.5 \pm 0.98 c	0.94 \pm 0.02 C	1.79 \pm 0.07 a	17.4 \pm 1.1 A	10.0 \pm 0.6 d	-2.77 \pm 0.29 A	-4.11 \pm 0.50 b
1,400	15.7 \pm 1.14 B	18.5 \pm 1.08 bc	1.07 \pm 0.03 C	1.71 \pm 0.08 ab	14.8 \pm 1.0 B	10.9 \pm 0.6 cd	-3.47 \pm 0.33 A	-2.21 \pm 0.22 a
1,600	20.3 \pm 1.22 A	21.2 \pm 0.94 a	1.43 \pm 0.05 B	1.61 \pm 0.04 b	14.1 \pm 0.5 B	13.2 \pm 0.5 b	-3.72 \pm 0.40 A	-2.38 \pm 0.40 a
1,800	19.9 \pm 1.44 A	20.5 \pm 1.14 ab	1.44 \pm 0.05 B	1.61 \pm 0.05 b	13.7 \pm 0.7 B	12.7 \pm 0.6 bc	-3.06 \pm 0.32 A	-3.12 \pm 0.32 ab
2,000	20.8 \pm 1.19 A	18.9 \pm 0.95 abc	1.65 \pm 0.06 A	1.22 \pm 0.04 c	12.8 \pm 0.6 B	16.0 \pm 1.0 a	-6.02 \pm 0.25 B	-6.20 \pm 0.39 c
2,200	18.7 \pm 0.99 AB	20.2 \pm 0.70 ab	1.46 \pm 0.08 B	1.29 \pm 0.07 c	13.5 \pm 0.8 B	16.8 \pm 1.1 a	-7.25 \pm 0.52 C	-5.78 \pm 0.45 c
N_{litter} (mg/g)	P_{litter} (mg/g)		$N:P_{\text{litter}}$		Leaf growth rate (%)			
	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate
1,200	10.5 \pm 0.9 AB	10.8 \pm 0.8 abc	0.42 \pm 0.04 C	0.90 \pm 0.05 a	25.3 \pm 1.1 A	12.3 \pm 0.7 c	56.9 \pm 2.5 B	46.9 \pm 2.9 bc
1,400	9.0 \pm 0.6 B	12.8 \pm 0.9 a	0.46 \pm 0.02 C	1.00 \pm 0.05 a	19.5 \pm 1.1 B	13.1 \pm 0.7 c	69.5 \pm 3.0 A	39.6 \pm 2.8 c
1,600	10.7 \pm 0.7 AB	13.1 \pm 1.0 a	0.58 \pm 0.03 B	0.75 \pm 0.03 b	18.5 \pm 0.9 BC	17.2 \pm 0.9 b	49.4 \pm 2.0 C	44.2 \pm 2.5 c
1,800	11.0 \pm 0.9 A	12.5 \pm 1.0 ab	0.60 \pm 0.04 B	0.75 \pm 0.05 b	18.1 \pm 0.6 BC	16.6 \pm 0.6 b	48.4 \pm 3.2 C	54.7 \pm 3.1 b
2,000	10.2 \pm 1.0 AB	10.1 \pm 0.7 bc	0.67 \pm 0.07 A	0.56 \pm 0.03 c	15.1 \pm 0.8 D	18.2 \pm 1.1 b	53.0 \pm 2.4 BC	66.8 \pm 2.9 a
2,200	8.8 \pm 0.5 B	9.4 \pm 0.5 c	0.56 \pm 0.04 BC	0.42 \pm 0.04 d	16.4 \pm 0.7 CD	23.5 \pm 1.2 a	59.9 \pm 4.0 B	72.6 \pm 3.6 a

Note. The values are the overall means for five species. In each column, the means followed by different letters (capital letters for carbonate bedrock and small letters for silicate bedrock) differ significantly ($p < 0.05$) from each other based on Fisher's LSD post hoc tests.

TABLE 3 Mean (± 1 SE) values of total soil N concentration (N_{total}), soil N content in available inorganic form ($N_{\text{inorg-avail}}$), soil N content in available organic form ($N_{\text{org-avail}}$), soil $\delta^{15}\text{N}$, total soil P concentration (P_{total}), soil P content in available inorganic form ($P_{\text{inorg-avail}}$), soil P content in available organic form ($P_{\text{org-avail}}$), total soil C concentration (C_{total}), soil N:P, soil C:N, soil C:P and soil pH across altitudinal gradients on two bedrock types ($N = 5$)

Altitude (m)	N_{total} (mg/g)		$N_{\text{inorg-avail}}$ ($\mu\text{g/g}$)		$N_{\text{org-avail}}$ ($\mu\text{g/g}$)	
	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate
1,200	14.5 \pm 1.1 A	12.0 \pm 1.4 bc	62 \pm 8 A	54 \pm 8 bc	223 \pm 26 A	293 \pm 55 ab
1,400	13.9 \pm 0.4 A	11.1 \pm 2.9 bc	57 \pm 12 A	58 \pm 8 bc	264 \pm 21 A	263 \pm 53 ab
1,600	14.7 \pm 2.0 A	13.7 \pm 3.7 ab	47 \pm 14 A	85 \pm 17 ab	209 \pm 31 AB	248 \pm 76 ab
1,800	12.0 \pm 2.0 AB	12.9 \pm 2.1 ab	45 \pm 14 A	102 \pm 20 a	227 \pm 35 A	347 \pm 14 a
2,000	8.9 \pm 1.4 B	6.6 \pm 1.6 c	49 \pm 7 A	26 \pm 10 c	199 \pm 36 AB	174 \pm 39 b
2,200	11.6 \pm 2.6 AB	18.5 \pm 1.3 a	38 \pm 14 A	80 \pm 13 ab	132 \pm 35 B	265 \pm 26 ab
	$\delta^{15}\text{N}$ (‰)		P_{total} (mg/g)		$P_{\text{inorg-avail}}$ ($\mu\text{g/g}$)	
	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate
1,200	-3.60 \pm 0.21 C	0.09 \pm 0.60 a	0.58 \pm 0.03 C	1.14 \pm 0.03 a	120 \pm 37 B	154 \pm 49 a
1,400	-3.63 \pm 0.31 C	-3.17 \pm 0.36 b	0.64 \pm 0.04 C	0.76 \pm 0.12 c	151 \pm 20 A	160 \pm 53 a
1,600	-0.61 \pm 0.66 B	-2.46 \pm 0.64 b	1.00 \pm 0.02 B	0.72 \pm 0.08 c	58 \pm 13 C	103 \pm 25 b
1,800	-0.95 \pm 0.53 B	-2.47 \pm 0.50 b	0.93 \pm 0.02 B	1.04 \pm 0.13 ab	50 \pm 15 CD	174 \pm 34 a
2,000	1.91 \pm 0.45 A	0.08 \pm 0.29 a	1.13 \pm 0.06 B	0.60 \pm 0.08 c	33 \pm 5 D	29 \pm 10 c
2,200	1.05 \pm 0.69 A	-0.40 \pm 0.45 a	1.35 \pm 0.08 A	0.84 \pm 0.03 bc	45 \pm 22 CD	43 \pm 6 c
	$P_{\text{org-avail}}$ ($\mu\text{g/g}$)		C_{total} (%)		N:P	
	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate
1,200	16 \pm 2 D	105 \pm 12 a	40.4 \pm 2.3 A	28.6 \pm 4.3 ab	25.2 \pm 1.6 A	10.6 \pm 0.8 c
1,400	28 \pm 4 C	43 \pm 24 c	41.4 \pm 1.6 A	22.2 \pm 6.8 b	22.1 \pm 1.6 A	13.5 \pm 2.0 bc
1,600	38 \pm 6 B	37 \pm 17 c	30.2 \pm 4.2 B	27.2 \pm 6.9 ab	14.7 \pm 1.4 B	18.4 \pm 3.8 ab
1,800	42 \pm 5 B	76 \pm 42 b	27.4 \pm 3.8 BC	28.3 \pm 3.3 ab	12.8 \pm 1.4 BC	12.4 \pm 1.5 bc
2,000	87 \pm 17 A	92 \pm 24 a	17.8 \pm 3.0 C	15.6 \pm 2.6 b	7.9 \pm 1.0 D	10.5 \pm 1.3 c
2,200	47 \pm 7 B	64 \pm 10 b	22.3 \pm 5.5 BC	38.9 \pm 3.2 a	9.0 \pm 2.7 CD	22.2 \pm 2.6 a
	C:N		C:P		pH	
	Carbonate	Silicate	Carbonate	Silicate	Carbonate	Silicate
1,200	28.0 \pm 0.7 A	23.8 \pm 2.5 ab	702 \pm 37 A	254 \pm 43 b	5.46 \pm 0.08 A	5.28 \pm 0.14 a
1,400	29.8 \pm 1.0 A	18.5 \pm 2.3 b	664 \pm 64 A	265 \pm 62 b	5.43 \pm 0.09 A	5.26 \pm 0.14 ab
1,600	20.3 \pm 1.4 B	20.1 \pm 2.1 ab	304 \pm 46 B	361 \pm 70 ab	5.26 \pm 0.11 A	5.00 \pm 0.13 ab
1,800	23.2 \pm 2.1 B	22.7 \pm 1.8 ab	298 \pm 38 B	280 \pm 36 b	5.21 \pm 0.19 A	4.72 \pm 0.11 b
2,000	19.6 \pm 1.2 B	26.0 \pm 3.4 a	155 \pm 22 C	261 \pm 25 b	5.63 \pm 0.08 A	5.43 \pm 0.07 a
2,200	19.8 \pm 2.5 B	21.3 \pm 1.0 ab	176 \pm 58 C	463 \pm 34 a	5.49 \pm 0.09 A	5.00 \pm 0.13 ab

Note. In each column, the means followed by different letters (capital letters for carbonate bedrock and small letters for silicate bedrock) differ significantly ($p < 0.05$) from each other based on Fisher's LSD post hoc tests.

imply higher NRE and/or PRE at low altitudes that was not the case in our study. Although we did not measure soil water content, previous studies showed that soil moisture had negligible if any importance, in affecting ecological patterns across the two gradients (Gerdol, Iacumin, & Tonin, 2018; Gerdol et al., 2017). So, soil chemistry appeared the main cause responsible for variations in nutrient resorption efficiency across the two gradients. Both NRE and PRE increased more or less regularly with increasing

altitude on both bedrock types, which would give support to hypothesis #1. Higher NRE at high-altitude sites was not associated with lower N mineralization rates but was rather related to low levels of $N_{\text{org-avail}}$ and higher, that is less negative soil $\delta^{15}\text{N}$ signature. Indeed, NRE always was greater at high altitude where less N was available in organic form and the soil $\delta^{15}\text{N}$ was higher which suggests that the substrate became enriched in the heavy N isotope because of isotope fractionation during N cycling in the soil

TABLE 4 Pearson's correlation coefficients of nutrient resorption efficiencies and their ratio with foliar chemistry, litter chemistry and leaf growth (N = 12)

	N _{leaf}	N _{litter}	δ ¹⁵ N _(leaf-soil)	P _{leaf}	P _{litter}	N:P _{leaf}	N:P _{litter}	Leaf growth
Nitrogen resorption efficiency	0.28	-0.67*	-0.83**	-	-	-	-	0.62*
Phosphorus resorption efficiency	-	-	-	-0.44	-0.81**	-	-	0.66*
N:P RE	-	-	-	-	-	-0.01	0.25	0.32

Note. Significant values in bold character (***p* < 0.01; **p* < 0.05; †*p* < 0.10).

TABLE 5 Summary of stepwise multiple regressions of nutrient resorption efficiencies and their ratio on soil chemistry variables

	B	<i>p</i>
Nitrogen resorption efficiency (<i>R</i> ² = 0.848; <i>p</i> = 0.02*)		
N _{org-avail}	-0.078	0.01*
δ ¹⁵ N	1.664	0.02*
N _{total}	0.632	0.09†
N _{inorg-avail}	0.139	0.11
C:N	0.334	0.24
pH	N.E.	-
Phosphorus resorption efficiency (<i>R</i> ² = 0.902; <i>p</i> = 0.006**)		
P _{inorg-avail}	-0.084	<0.001**
C:P	0.026	0.005**
P _{total}	10.829	0.009**
P _{org-avail}	0.028	0.35
pH	N.E.	-
N:P RE (<i>R</i> ² = 0.607; <i>p</i> = 0.02**)		
C:P	-0.0002	0.006**
pH	0.032	0.33
N:P	N.E.	-
C:N	N.E.	-

Note. Significant values in bold character (***p* < 0.01; **p* < 0.05; †*p* < 0.10). N.E. not entered in the stepwise procedure.

(Callesen et al., 2013). Three processes can lead to ¹⁵N enrichment in the soil: nitrification (Högberg, 1997), humification with consequent stabilization of soil organic matter (Kramer, Sollins, Sletten, & Swart, 2003) and transfer of N from soil to plants by mycorrhizal fungi (Hobbie & Ouimette, 2009). Nitrification did not seem to be responsible for ¹⁵N enrichment in the soil because nitrate concentrations always were negligible. Should higher δ¹⁵N signature in high-altitude soils be derived by microbial processes associated with humification, this would imply consistently lower C:N at high altitudes (Schulten & Leinweber, 2000). However, the altitudinal pattern of soil C:N varied in relation to bedrock type while the soil δ¹⁵N increased across the altitudinal gradients on both bedrock types (Table 3). Hence, isotope discrimination through mycorrhizal N transfer appeared to represent the cause of ¹⁵N enrichment in our soils. Plants shift from inorganic to organic forms as source of N uptake with decreasing temperatures (Averill & Finzi, 2011).

Decreasing concentrations of N_{org-avail} across the altitudinal gradients may reflect stronger competition for organic N sources by soil microbes. Our results suggest that lower availability of organic N forms at high-altitude sites is counterbalanced by more efficient N resorption and/or by higher rates of N transfer from mycorrhizal fungi to the plants.

Contrary to hypothesis #2, the altitudinal pattern of PRE was much the same on the two bedrock types in spite of strong differences in terms of P_{total} concentrations. The negative correlation between PRE and P_{inorg-avail} means that the plants resorbed more P when the concentrations of readily available inorganic P forms in the soil were lower. Overall, the supply of inorganic P in soils principally derives from bedrock weathering and consequent diffusion to the soil solution. However, physical-chemical processes of rock weathering dominate in deep mineral soil horizons while microbial processes leading to P mineralization prevail in the upper organic soil horizon. While deeply rooting plants can exploit available inorganic P in deep soil layers (Achat, Bakker, Augusto, & Morel, 2013), the roots of the plants investigated in this study are all confined to the uppermost soil horizon (R. Gerdol, personal observation) where the P_{inorg-avail} supply depends on microbial processes. Microbial P mineralization is depressed by cold temperature with minor influence of soil chemistry (Vincent, Sundqvist, Wardle, & Giesler, 2014). So, the availability of readily accessible inorganic P primarily depended on temperature-dependent control of microbial activity rather than on the influence of bedrock geology on physical-chemical processes of rock weathering. Phosphorus resorption was not enhanced by low levels of total soil P content as PRE was even positively related to P_{total}. Hence, total soil P content need not represent an index of P availability for plants at the local scale, in contrast with previous studies reporting negative correlations between PRE and P_{total} at the regional scale (Achat et al., 2018; Augusto et al., 2017). Inorganic phosphate represents the most biologically available form of soil P (Turner, 2008) while most of P_{total} consists of stable organic or inorganic forms, for example sorbed to the surface of Al and Fe oxides or occluded in mineral compounds (Turner, 2008). The plants investigated probably were capable of accessing sparingly soluble forms of organic and/or inorganic forms of soil P, either directly or with the aid of mycorrhizal associates (Gerdol et al., 2017). Utilizing stable P forms requires energy associated with the release of organic acids or phosphatases for solubilizing recalcitrant inorganic or organic P forms (Cairney, 2011). Ali, Louche, Legname, Duchemin,

and Plassard (2009) observed that P uptake by mycorrhizal fungi is not sufficient to fulfil the P requirement of the host when $P_{\text{inorg-avail}}$ levels are too low. Our results suggest that P resorption represents a cost-effective strategy to cope with P deficiency when the $P_{\text{inorg-avail}}$ content in the soil is low. N:P RE values <1 demonstrate higher efficiency in resorbing P with respect to N, as observed in most studies (Jiang et al., 2012; Vergutz et al., 2012). A possible explanation resides in the different mobility of N and P, with a larger proportion of N than of P locked in structural compounds (Jónsdóttir, Khitun, & Stenström, 2005). While at the global scale N:P resorption ratios reflect soil N and P stoichiometry (Reed, Townsend, Davidson, & Cleveland, 2012), we did not observe any significant relationship between N:P RE and soil N:P. This suggests that at the local scale, the differential efficiency in resorbing nutrients is determined more by the relative cost of resorbing nutrients than by the absolute soil nutrient levels and their stoichiometric ratio (Tang et al., 2013; Wright & Westoby, 2003). The negative correlation between N:P RE and soil C:P means that the plants resorbed proportionally more P than N when the soil C:P was higher. A possible explanation consists of higher fraction of microbial P immobilization under high soil C:P (Zheng et al., 2018).

The strong negative correlations between nutrient resorption efficiencies (NRE and PRE) and nutrient concentrations in senescing leaves (N_{litter} and P_{litter} , respectively) mean that nutrient resorption efficiency mirrored nutrient resorption proficiency, that is the concentrations of nutrients in litterfall (Killingbeck, 1996). The poor correlations between nutrient resorption efficiency and nutrient concentration in green leaves suggest that foliar N or P concentrations are primarily determined by species-specific features so that they cannot always be used as an indicator of nutrient status (Achat et al., 2018). Increasing $\delta^{15}\text{N}_{(\text{leaf-soil})}$ values across altitudinal gradients demonstrate that the plants utilized increasing fractions of organic N at higher altitudes especially through associated mycorrhizal partners (Amundson et al., 2003). The negative correlation between NRE and $\delta^{15}\text{N}_{(\text{leaf-soil})}$ suggests that improved efficiency in absorbing organic N and higher N resorption represented a common strategy for coping with N limitation at high altitude. The positive correlations of NRE and PRE with leaf growth indicate that resorbing both nutrients was effective to improve the growth potential of the plants investigated. Conversely, the N:P RE was unrelated to leaf growth, thus suggesting that the plants were unable to regulate the relative importance of NRE and PRE, in relation to the availability of N and P, for optimizing growth potential.

5 | CONCLUSION

Variation in nutrient resorption efficiency across altitudinal gradients need not be determined by changes in species composition across the gradients, but can derive from adaptation of co-existing species to varying environmental conditions. The main process regulating nutrient resorption was a negative feedback to soil nutrient availability. The negative feedback of nutrient resorption efficiency

to soil nutrient status was unrelated to total soil nutrient contents but depended on concentrations of organic N forms for NRE and on inorganic P forms for PRE. While we hypothesized that the resorption of P, as a principally rock-derived nutrient, depended on physical-chemical processes affected by soil chemistry, our results showed that microbial P mineralization was the main source of inorganic P supply to the plants. Both NRE and PRE were effective to improve the growth potential of plants, but there was no evidence of stoichiometric adaptations of N:P RE to nutrient ratio in the soil.

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AUTHORS' CONTRIBUTIONS

R.G. designed the study. R.G. and L.B. conducted the fieldwork. P.I. conceived the analyses and interpreted the data on stable isotope discrimination. All three authors made substantial contributions to the development of ideas and the subsequent writing of the text. The authors gave final approval for publication.

DATA ACCESSIBILITY

Data are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.jb677gv> (Gerdol, Iacumin, & Brancaloni, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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