Proceedings of the International Academy of Ecology and Environmental Sciences, 2014, 4(4): 162-175

Article

Dynamics of 35 trace elements throughout plant organs in the subalpine broad leaf evergreen shrub *Rhododendron ferrugineum*

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Received 14 July 2014; Accepted 20 August 2014; Published online 1 December 2014

Abstract

Increased atmospheric deposition and climate change might affect soil biogeochemical processes and release potentially toxic trace elements in the soil solution. The dynamics and the distribution among plant organs of many trace elements are nevertheless still poorly documented, especially in evergreen species. Here,we measured the concentration of 35 trace elements in roots, stems, as well as in current, 1 yr-old and 2 yr-old leaves (respectively L0, L1 and L2) of the subalpine evergreen shrub *Rhododendron ferrugineum*. In every plant compartment, concentrations decreased with increasing atomic number. Based on a PCA analysis and the distribution of elements among the different plant compartments at least two groups of elements could be distinguished: i) elements with a high retention factor (RF) in the root compartment and accumulating in leaves with leaf aging, resulting in concentrations decreasing in the order Roots >> Stems > L2 > L1 > L0; and ii) elements with a low RF resulting in leaf concentrations higher or close to those in roots and stems. However, in contrast with elements from the first group, the dynamics in the leaf compartment of elements from the second group was erratic, with concentrations increasing, decreasing or remaining constant with leaf aging.

Keywords *Rhododendron ferrugineum*; trace elements; retention factor; translocation; subalpine heathland.

Proceedings of the International Academy of Ecology and Environmental Sciences
ISSN 2220-8860
URL: http://www.iaees.org/publications/journals/piaees/online-version.asp
RSS: http://www.iaees.org/publications/journals/piaees/rss.xml
E-mail: piaees@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Global warming and increased nitrogen and sulphur atmospheric depositions are known to alter biogeochemical cycles by impacting physical, chemical and biological processes occurring in soils (Campbell et al., 2009; Zhang and Liu, 2012). Atmospheric deposition has resulted in increasing soil acidity which can increase the release and the mobility in the soil solution of metals potentially toxic like Al, Pb or Cd (Blake and Goulding, 2002; Ediagbonya et al., 2013). The fate of these elements depends on several factors such as soil properties and environmental conditions, which control their mobility in the soil and their phytoavailability (e.g., pH, cation exchange capacity, clay and organic matter contents) (Greger, 2004). It also depends on the ability of plants to take up and then translocate these elements from roots to the other plant compartments (Perronnet et al., 2003; Anim et al., 2012). The uptake, translocation or accumulation of trace elements across the different plant organs partly depend on their physicochemical properties (e.g. solubility, mobility in the phloem) and roles in plant physiology, as well as on plant genetics and environment (Greger, 2004).

Numerous studies have focused on the uptake, translocation and storage of major elements (e.g. N, P, Ca) in both agro- and ecosystems, but much less is known about trace elements (Watanabe et al., 2007). Yet, their dynamics in the plants (e.g. uptake, translocation, storage) can have an impact on their cycling rate and on the cycling of major elements representing large proportions of plant biomass (e.g., C, N, Ca). The uptake of some key elements can actually impact the growth or the longevity of plant organs, particularly leaves and roots. For instance, it has been shown that N plant uptake affected both the kinetics of leaf N resorption and leaf life span in *Rhododendron ferrugineum* (Marty et al., 2009), that high Al accumulation in roots accelerated root turnover in *Abies amabilis* (Vogt et al., 1987a, 1987b), that Cd decreased leaf longevity in wheat (Ouzounidou et al., 1997), and that Cd and Zn inclusions in the soil stimulated root proliferation in *Thlaspi caerulescens* (Schwartz et al., 2003), while other heavy metals can inhibit root elongation and growth of herbaceous species (Baker et al., 1994; Bakkaus et al., 2005). It is therefore important to investigate element dynamics in the plants in order to predict their cycling in the soil-plant system. Translocation of toxic elements from roots to aboveground biomass could for instance result in their accumulation in the upper soil horizons through leaf shedding and their dispersion through the food chain through herbivory.

Here, we measured the concentration of 35 trace elements in different plant compartments (roots, stems and current, 1 yr-old and 2 yr-old leaves) during the growing season of a widespread evergreen plant in the Pyrenean subalpine belt, *Rhododendron ferrugineum*. This species dominates most ericaceous heathlands of European mountains and contrary to most evergreen species of high altitude habitats *R. ferrugineum* is characterized by broad leaves. These oligotrophic ecosystems are particularly at risk because the parental material is depleted in base cations and as a consequence have a low buffering power. Soils may therefore acidify in response to even low atmospheric deposition. The aim of this study was to describe and compare the distribution and dynamics of these 35 elements in the different plant organs and try to group them according to their distribution patterns among plant organs.

2 Materials and Methods

2.1 Study site

The study was conducted in the central French Pyrenees in the vale of Estaragne. This valley (42° 48’ N; 0°9’ E) is oriented North-east /South-west (opening to the north) and stretches over 3 km between 1850 and 2500 m a.s.l. The vegetation is composed of a mosaic of meadows, shrubs and trees (*Pinus uncinata* Ram.) with long heathland/meadow ecotones. Heathlands are mainly composed of *Rhododendron ferrugineum* L. and *Vaccinium myrtillus* L. (Ericaceae). *Nardus stricta* L. and *Festuca eskia* Ram. are the main dominating species (Poaceae) of the meadows.The subalpine climate prevailing in the site is relatively mild due to Ibero-Mediterranean influences. Snow cover usually persists from late October till early June. The average annual precipitation amounts to 1500 mm. The geological substrate is mainly granite, amphibole and schist. Soils are acidic (pH = 4.7 ± 0.1, SD; total N: 0.5% ± 0.044, SD; bulk density: 0.65 ± 0.099, SD). This site has been intensively studied

(Marty et al., 2009, 2010; Pornon and Lamaze, 2007). Soil field capacities and organic matter contents are respectively 0.8 ± 0.1 g g^{-1} DW and 11.7 ± 1.3 %.

2.2 Vegetation sampling

The species studied, *Rhododendron ferrugineum*, is an evergreen shrub, with well-branched trailing stems that reaches a height of 70-80 cm. It is widely distributed in the Alps and the Pyrenees between 1600 and 2200 m a.s.l. (Ozenda, 1985)where it can dominate plant communities especially in areas where grazing pressure has subsided. Chemical analyses were conducted on five compartments: roots (R), stems (S) and current, 1 yr-old and 2 yr-old leaves (respectively L0, L1 and L2). Every compartment was collected three times in the vegetation period on mature shrubs: mid-June, mid-August and end-October. These periods match with the beginning of the vegetation period, the end of shoot growth and the end of the vegetation period respectively. Ten sub-areas (50 m^2 each) were delimited. Inside each sub-area, plant compartment samples were collected on four shrubs and pooled together so that we obtained ten replicates of each compartment from forty individuals three times during the whole vegetation period. Samples were immediately refrigerated before they were meticulously rinsed with ultrapure water (Milli-Q integral system) in the laboratory. Then, they were oven-dried for 72h at 60°C and ground in fine powder (Ø<10µm) in an agate mortar.

2.3 Multi-elementary analysis

For each plant sample, series of oxidizing acid attacks (bidistilled HNO_3, HF and HCl) were conducted on 100 mg powder in Teflon reactors (Savillex®). Details about the whole procedure are elsewhere (Viers et al., 2007). The dry residual was then weighted and diluted in bi-distilled nitric acid (2%) for multi-elementary analyses.

Trace elements were analyzed by inductively coupled plasma mass spectrometry (ICP-MS; 7500 CE, Agilent Technologies).

2.4 Calculations and statistics

Differences in elements concentrations among plant compartments were tested with one-way ANOVA followed by a Turkey post hoc analysis (R core Development Core Team, 2009). A principal component analysis (PCA) was performed to analyze data on the concentrations of 35 elements in the different plant compartments using R package ade4 (Dray and Dufour, 2007). For each element, a retention factor (RF) was calculated as the ratio between the concentration in roots and that in stems (R-S), 2-yr old leaves (R-L2), 1-yr old (L1) and current-year leaves (R-L0).

Annual translocation from roots to the foliage (AT) was estimated for each element. Some elements like barium have been shown to accumulate in *R. ferrugineum*’s leaves with leaf aging while others like rubidium are partly resorbed from leaves over their life span (Marty et al., 2014). Therefore, for elements with decreasing concentrations with leaf age (concentrations decreasing in the order L0>L1>L2), AT was estimated as the amount of the element in the L0 cohort at the end of the growing season minus the amount of the element resorbed from the L1 and L2 cohorts (eqn 1). In contrast, for elements with increasing concentrations with leaf age (concentrations decreasing in the order L0<L1<L2), the amount of element accumulated in the remaining L1 and L2 leaves must be accounted and AT was estimated as shown in eqn 2.

$$AT_j = mL0_j \times CL0_j - mL0\left(CL0_j - CL1_j\right) - mL1\left(CL1_j - CL2_j\right) \qquad (1)$$

$$AT_j = mL0 \times CL0_j + mL1\left(CL1_j - CL0_j\right) + mL2\left(CL2_j - CL1_j\right) \qquad (2)$$

where, AT_j is the annual translocation to leaf biomass (µg m^{-2}) of the element *j*, *mL0* and *mL1* are the biomasses of the L0 and L1 cohorts (g DW) at the end of the growth period respectively, and $CL0_j$, $CL1_j$ and $CL2_j$ (µg g^{-1}) are the concentrations of the element *j* in L0, L1 and L2 cohorts, respectively.

Leaf biomass values for the L0, L1 and L2 cohorts (mL0, mL1 and mL2, respectively) were estimated as the product of leaf surface area for L0 (S, m^2) with the LMA and the proportion (p_i) of leaves from the L0 cohort still attached after respectively one and two years provided in Marty et al. (2009):

$$mL_i = S_{L0} \times LMA_i \times p_i \tag{3}$$

The AT values were multiplied by branch density (number of branches m^{-2} of shrub) to have a value of AT by m^{-2} of shrub. Annual leaf surface area production (S, m^2) and leaf mass area (LMA; g m^{-2}) for L0 as well as leaf shedding patterns data were extracted from Marty et al. (2009) and Marty et al. (2010). Branch density (number of branches m^{-2}) was measured on 40 shrubs within a frame of 35cm x 35cm.

3 Results

Concentrations in plant tissues decreased with increasing element atomic numbers in all plant compartments (Fig. 1). The correlation was slightly stronger for leaves (especially current-year leaves, L0) than for roots and stems.

The two first axes of a principal component analysis (PCA) explained about 70% of the total variation in elemental concentrations (Fig 2 top panel). On the very left side of the first axis (PC1 values<-0.92), was found a group of 16 elements including all analyzed lanthanides with the exception of Eu (La, Ce, Pr, Nd, Sm, Gd, Tb, Dy, Ho, Er and Yb), as well as Al, Ti, V, Fe and U. Between PC1=-0.91 and PC1=-0.56, was found another group including Th, Eu, Pb, Co, Cr and Sb. For PC1>-0.55, the 13 other elements were spread on the first axis and no group could be clearly distinguished. On the second axis, most elements were included in the interval -0.25<PC2<0.25. However, Ba, Sr, Mn and Ni had PC2 values>0.5 while Cu and Rb had PC2 values<-0.5.

When plant compartments were projected on the principal component axes, roots (R) were located on the left side of the PC1 axis whereas the three leaf cohorts (L0, L1 and L2) were located at the right extremity of the PC1 axis, and stems (S) in between these two compartments (Fig. 2 bottom panel). Current year leaves (L0) were opposite to older leaves (L1 and L2) on the PC2 axis.

Elements were sorted according to their PC1 values and their concentrations in the different plant compartments are displayed on Fig. 3. For the 22 elements with the lowest PC1 values and europium (Eu), concentrations decreased in the order: Roots > Stems > L2 > L1 > L0. In contrast, the 12 remaining elements displayed various patterns. However, for most of them concentrations in the different leaf cohorts were higher or close to those in roots and stems (e.g. Li, B, Ni, and Zn). The four most abundant elements among analyzed plant compartments were Mn, Al, Fe and Ba. In stems, L2, L1 and L0, Mn was the most abundant element, followed by Al, Fe and Ba (Supplementary material). In roots, Al was the most abundant element (1040 µg g^{-1}) followed by Mn (675 µg g^{-1}) and Fe (650 µg g^{-1}). Barium concentration in roots was comparatively very low (53 µg g^{-1}). In comparison, other elements had very low concentrations, most of them with concentrations lower than 1 µg g^{-1}(Supplementary material).

The retention factor (RF), i.e. the ratio between the concentration in roots and that in the other compartments, widely varied among elements and compartments (Fig. 5). Between roots and stems, RF ranged from 0.8 for boron (B) and 11.1 for cobalt (Co). However, the value for Co was excessively high compared to the other elements since the second highest value reached only 5.2, and 75% of the values were included in the interval 0.8-3.8. This RF was not correlated with elements' atomic numbers (R=0.18; P=0.29).

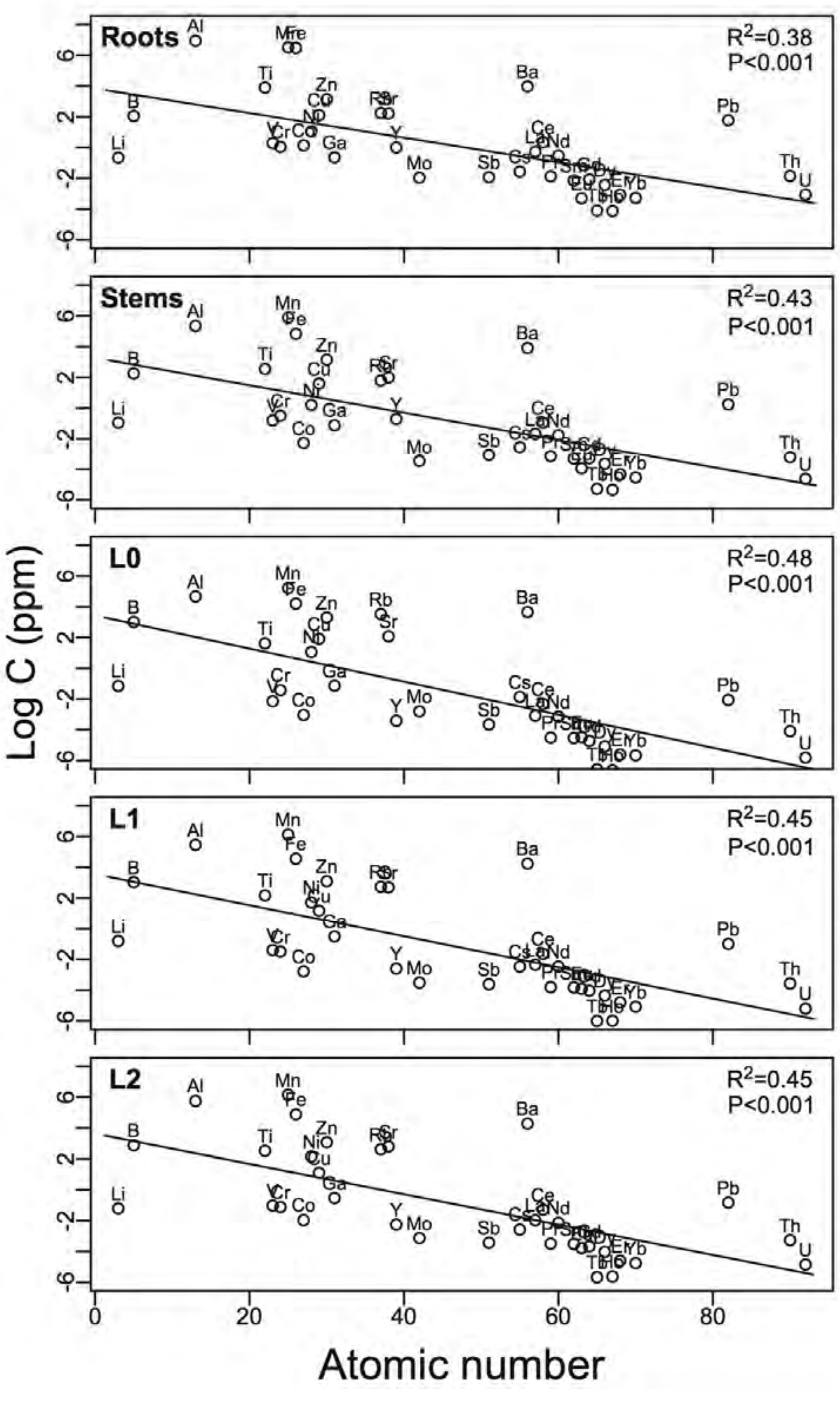

Fig. 1 Relationship between log-transformed concentrations of 35 trace elements in *R. ferrugineum* tissues and their atomic numbers. For each element, value is the mean of 30 analyses (10 sub-areas × 3 sampling periods). See materials and methods for details.

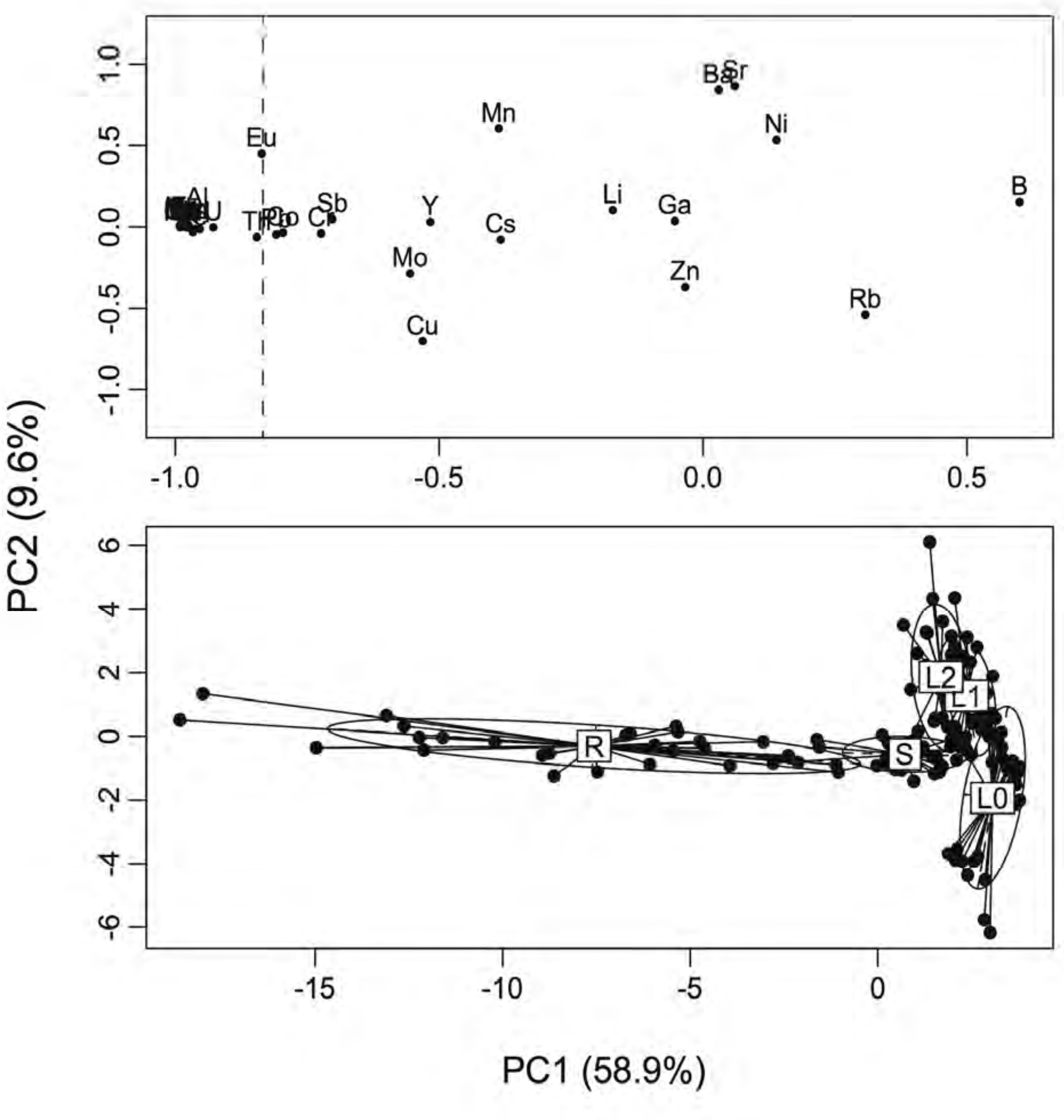

Fig. 2 Principal component analysis (PCA) of concentrations of 35 elements in plant compartments. *Top:* Projection of the different elements analyzed in the two principal axes space. *Bottom:* Projection of the different plant compartments in the two principal axes space. Each ellipse is a graphic résumé of the point cloud, the centre of which representing the gravity centre.

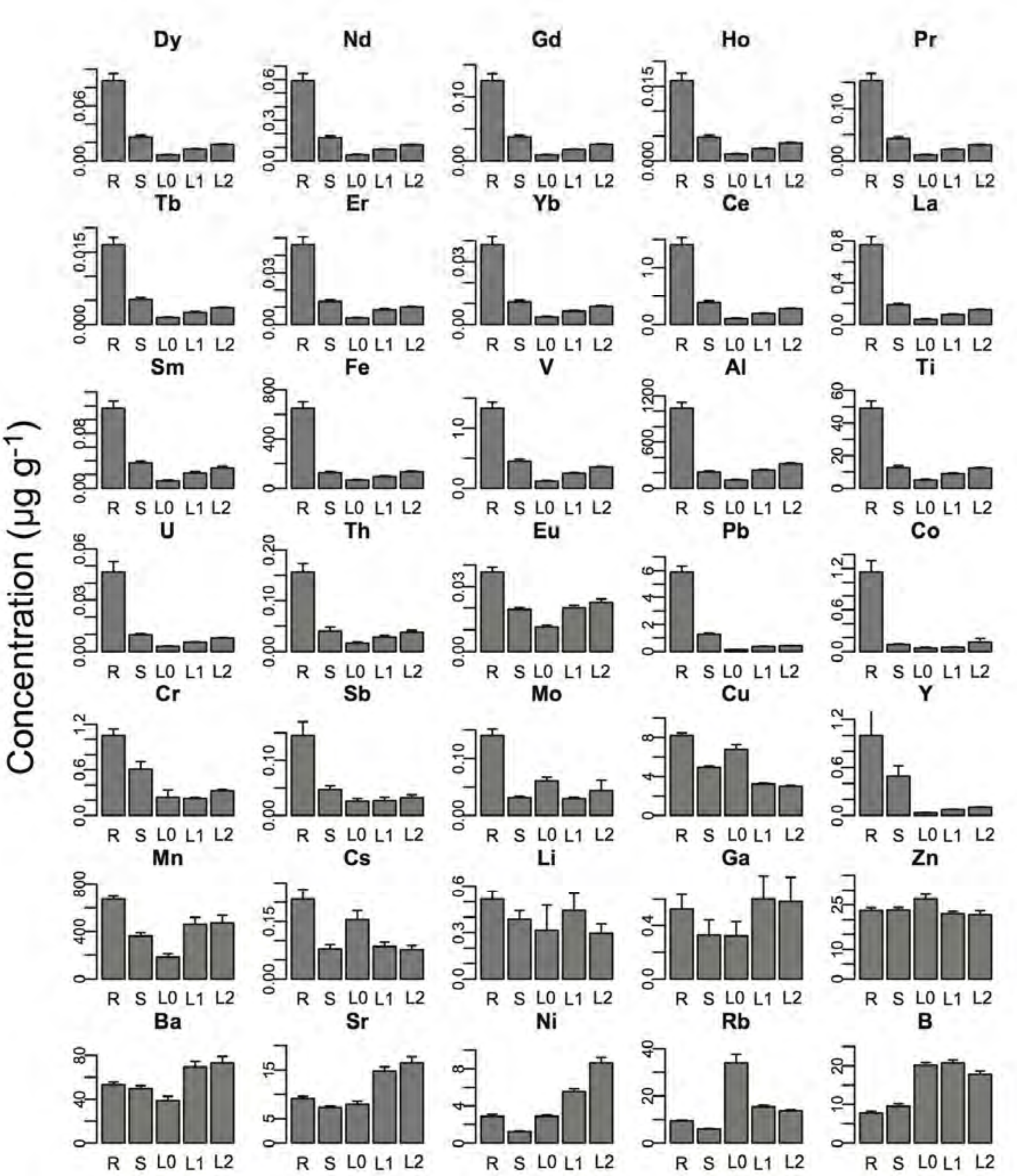

Fig. 3 Mean concentrations (µg g^{-1}) of the 35 analyzed trace elements in *R. ferrugineum*'s compartments. Elements are sorted as a function of their coordinate on the first axis of the PCA presented on Fig 2. PC1 values increase from right to left and from top to bottom. Errors bars are SE.

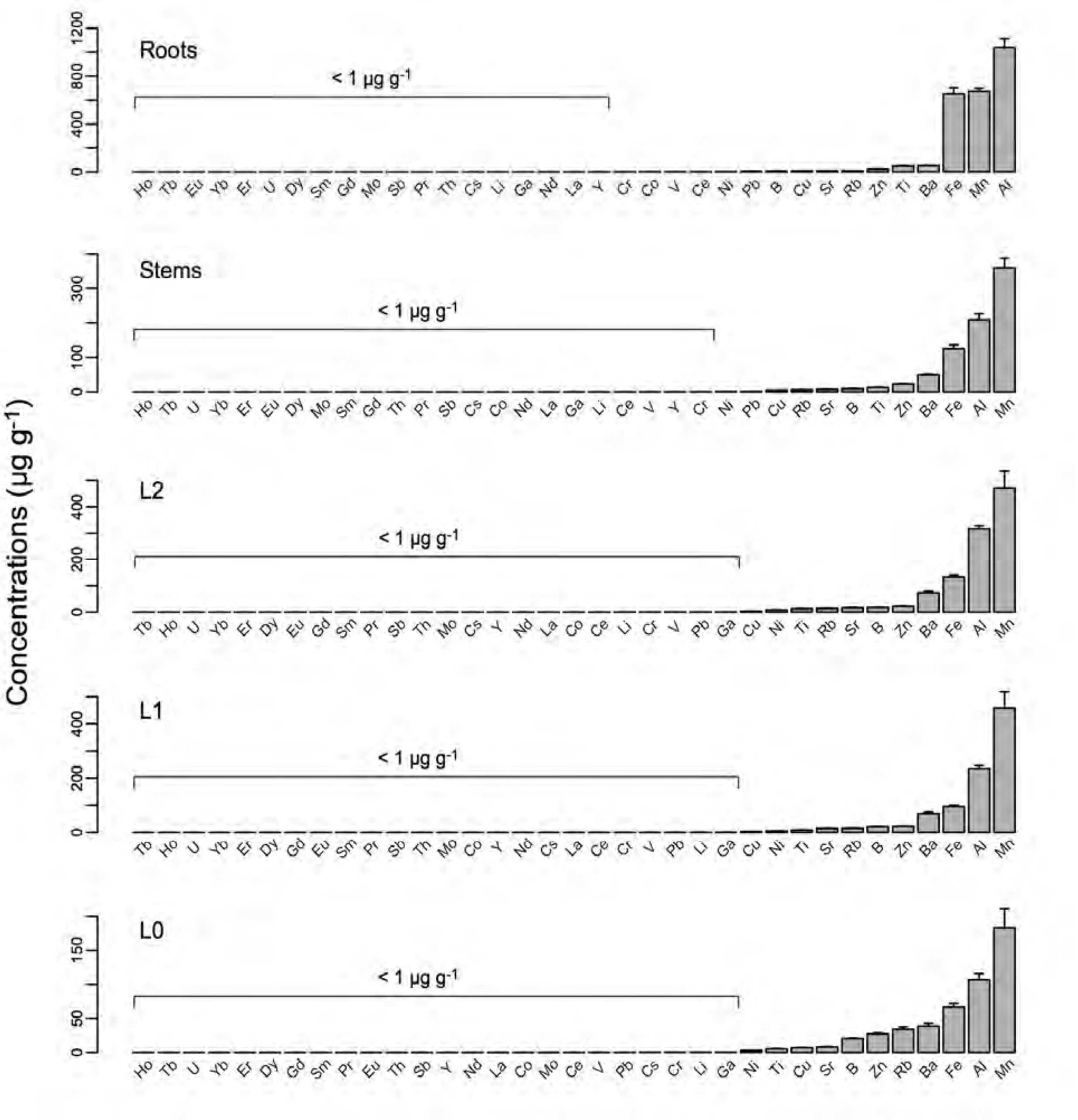

Fig. 4 Mean concentrations (μg g^{-1}) of the 35 analyzed trace elements in *R. ferrugineum*'s roots, stems, 2-yr old leaves (L2), 1-yr old leaves (L1) and current-yr leaves (L0). Errors bars are SE.

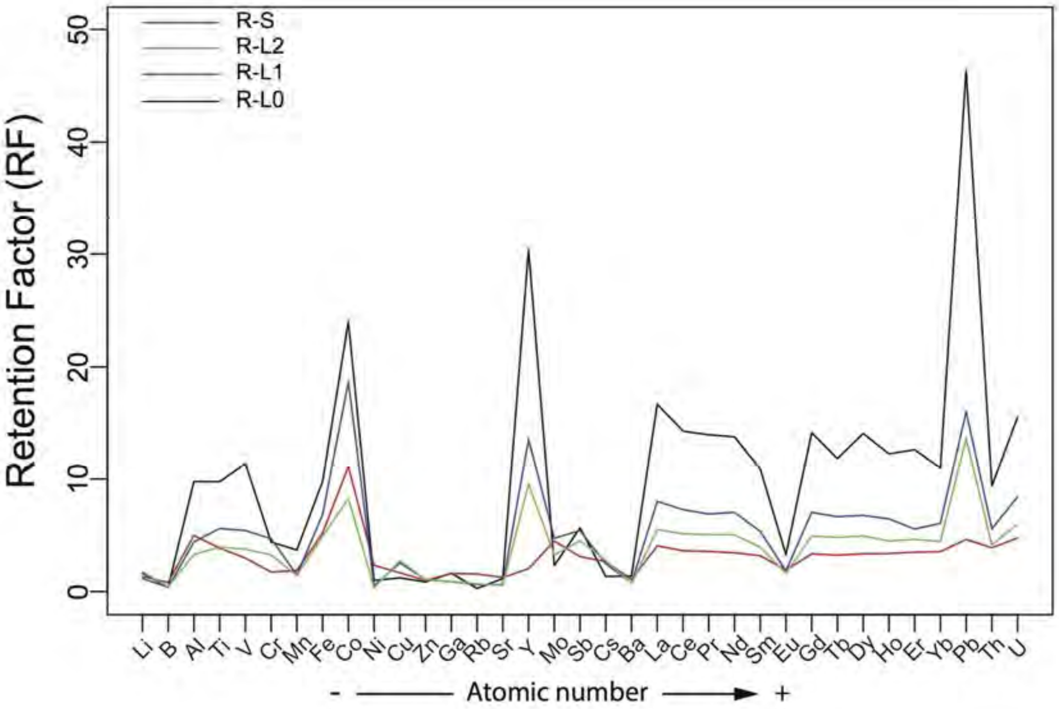

Fig. 5 Retention factor (RF) between roots and stems (R-S), 2-yr old leaves (R-L2), one yr-old leaves (R-L1) and current-year leaves (R-L0) for 35 trace elements. The retention factor is calculated as the ratio between the concentration in roots and that in the other compartments. Elements' atomic number increases from the left to the right of the x-axis.

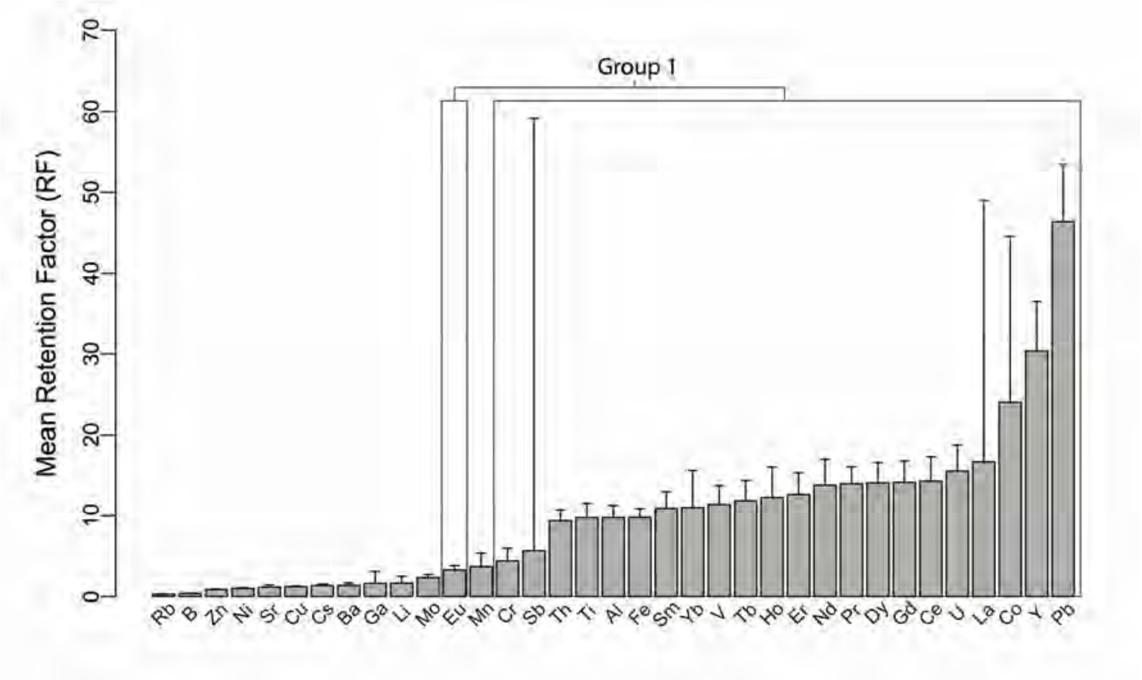

Fig. 6 Mean Retention Factor (+ SE) for the 35 analyzed elements. The group of elements characterized by a low PC1 value as well as by concentrations decreasing in the order R>S>L2>L1>L0 (Group 1) is shown.

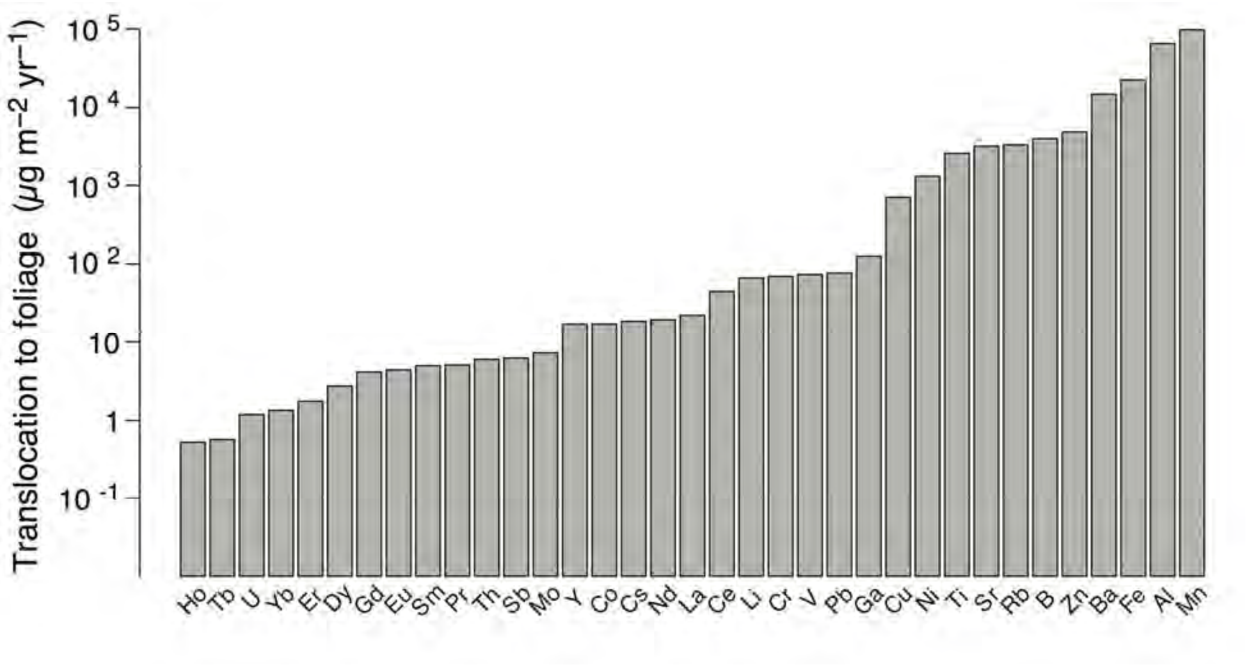

Fig. 7 Annual translocation to the foliage (µg m^{-2} yr^{-1}) for each analyzed element.

The RF between roots and all leaf cohorts was high and similar for all elements with an atomic number higher than 57 (at the right of lanthanum on Fig. 5) with the exception of europium (Eu) for which RF for all leaf cohorts was only slightly higher than for stems. The RF between roots and leaves was particularly high for lead (Pb), yttrium (Y) and cobalt (Co) with RF_{R-L0} averaging 46, 30 and 24, respectively. For most elements, RF decreased with leaf age (R-L0>R-L1>R-L2) with the exception of 12 elements: Li, B, Mn, Ni, Cu, Zn, Ga, Rb, Sr, Mo, Cs and Ba. For these elements, the RF for leaves was similar, slightly higher or even lower than for stems. The RF for L0, L1 and L2 was positively correlated with elemental atomic number (R=0.42, P<0.05; R=0.35, P<0.05; R=0.44, P<0.01, respectively).

The amount of element annually translocated from roots to the foliage varied by several orders of magnitude (Fig. 7), from ~0.5 µg m^{-2} yr^{-1} for homium (Ho) and terbium (Tb) to ~100 mg m^{-2} yr^{-1} for manganese (Mn). Only ten elements had annual translocation higher than 1 mg m^{-2} yr^{-1} (Ni < Ti <Sr<Rb< B < Zn <Ba< Fe < Al <Mn). Most elements had an annual translocation to the foliage <10 µg m^{-2} yr^{-1}.

4 Discussion

4.1 Elements retention in the root compartment

As expected we found a large discrepancy in concentrations among elements and plant compartments. In every compartment, concentrations decreased with elements' atomic number which is in line with Watanabe et al. (2007) who observed the same patterns on 670 species of terrestrial plants, sampled from 29 sites in four countries. The fact that roots and the three leaf cohorts were opposite on the PC1 axis reflected the markedly different chemical composition of these compartments. Concentrations were generally higher in roots than in leaves, especially for the 22 elements with the lowest PC1 coordinate (Fig. 3). These elements with yttrium (Y) could be assembled in one group (hereafter Group 1) characterized by high retention factors (RF) (Fig. 6) and a slight accumulation in leaves as they aged which resulted in the following concentration pattern: R>>S>L2>L1>L0 (Fig. 3). For this group of elements, concentration was on average i) 3.8 times higher in roots than in stems with a range of 1.7 times for chromium (Cr) to 11.1 times for cobalt (Co); ii) 14.1times higher in roots than in L0 with a range of 3.3 to 46.3 for europium (Eu) and lead (Pb), respectively; iii) 2.6 times higher in L2 than in L0 with a range of 1.2 to 3.4 for antimony (Sb) and lead (Pb), respectively. The 12 remaining elements (hereafter Group 2) including molybdenum (Mo), copper (Cu), manganese (Mn), cesium (Cs), lithium (Li), gallium (Ga), zinc (Zn), barium (Ba), strontium (Sr), nickel (Ni), rubidium (Rb) and boron (B) showed various concentration patterns but were all characterized by low RFs (Fig. 6). This generally resulted in relatively high concentrations in leaf cohorts compared to elements from Group 1.

Although RF tended to increase with atomic number some elements with a relatively low atomic number had a high RF (e.g., Al, V, Co) and some with a high atomic number had a low RF (e.g., Ba, Rb, Sr, Eu). Elements like aluminum (Al) and cobalt (Co) are known to be toxic for plants. High retention of these elements in the roots corroborates the hypothesis that in acidic soils, root biomass plays an important role in sequestration of toxic trace elements (Vogt et al., 1987b). This accumulation followed by root senescence and death could actually avoid the toxicity to propagate in all the biological components. However, despite its toxicity and its high RF, Al was the second most abundant trace element in the foliage after Mn (Supplementary material). This might result from its high concentration in the soil solution in phytoavailable form (see below). In contrast, barium (Ba) and strontium (Sr), two alkaline earth elements, as well as rubidium (Rb), an alkali element, had a low RF. This probably resulted from their physico-chemical properties (Aberg et al., 1990), which are similar to those of calcium (Ca) for the two firsts and potassium (K) for the latter, and which confer them similar dynamics in the plant-soil system (see below).

Trace elements that are known to be essential for plants are boron (B), iron (Fe), zinc (Zn), copper (Cu), manganese (Mn), cobalt (Co), nickel (Ni) and molybdenum (Mo) (Graham and Stangoulis, 2003; Marschner, 1995). With the exception of Fe and particularly Co that had a very high RF and were characterized by the pattern R>>S>L2>L1>L0, all these essential elements were weakly retained in the roots (RF ranging from 0.4 for B to 2.3 for Mo). However, despite its high RF, Fe concentrations in the leaves were very high compared to the other essential elements (Fig. 3), suggesting that their high retention in the roots resulted from high element availability compared to leaf requirements. In contrast, Co concentrations in the roots and leaves were very low suggesting that the high retention of this element in the roots resulted from the very small amounts required by the plants and from its toxicity at high concentrations. Cobalt concentrations in plants are actually generally as low as 0.1–10 $\mu g g^{-1}$ (Palit et al., 1994) although concentrations can quickly increase in some crops, especially in roots, with increasing concentrations in the soil solution (Bakkaus et al., 2005). Concentrations of these essential elements were generally higher in roots than in the other plant compartments, with the exception of Zn, Ni and B (Fig. 3). In many soils, B can be taken up as a neutral molecule, which is highly permeable across cellular membranes (Stangoulis et al., 2001). Its transport throughout the plant is facilitated when external concentrations are low like in acidic alpine soils. Its passive uptake and its high transport ability could explain why B concentration is significantly higher in leaves than in stems and roots, which was not the case for most of the studied trace elements.

4.2 Elements dynamics in the leaf compartment

As mentioned above, concentration in leaves increased with leaf age for all elements from Group 1. This trend was also observed for some elements from Group 2: Mn, Ga, Ba, Sr and Ni. In contrast, concentrations in Cu, Zn, Cs and Rb tended to decline with leaf age. These different dynamics probably contributed to the opposite locations of these two groups of elements on the second axis of the PCA (Fig. 2). Indeed, Mn, Na, Sr and Ni had high positive PC2 values, while Cu, Zn and Rb had low negative PC2 values. These different patterns might result from elements' physico-chemical properties (e.g. lack of mobility in the phloem) and their physiological roles in the plant. For instance, root uptake is thought to not distinguish between Rb and K because of close ionic radii and similar valences (Marschner, 1995). These similarities in atomic properties could explain Rb high concentrations in leaves since K^+ optimal cytosolic concentration is in the range of 100 mM (Ashley et al., 2006), which makes K^+ the most abundant cation in the cytosol (Véry and Sentenac, 2003). In addition, K high solubility in the cytosol makes its retranslocation from senescent leaves through the phloem possible (Véry and Sentenac, 2003). These similar physico-chemical properties might explain the very close dynamics of these two elements in *R. ferrugineum* (Marty et al., 2014). The retranslocation process might therefore explain the decrease in the concentration of Rb and other elements like Cu and Zn with leaf age, as the latter are also known to be efficiently retranslocated from leaves, at least in crops (Marschner, 1995). As it has been shown for nitrogen, this resorption process might contribute to annual growth in *R. ferrugineum* (Marty et al., 2009, 2010; Pasche et al., 2002). In contrast, Sr and Ba accumulated in leaves with time and were shown to have the same dynamics as Ca in *R. ferrugineum* (Marty et al., 2014), resulting from similar physico-chemical properties. Strontium's ionic radius is close to that of Ca (1.00 and 1.18 Å for Ca and Sr, respectively), which can give these elements similar dynamics in the soil-plant system (Aberg et al., 1990; Poszwa et al., 2000). Barium, another alkaline-earth with a close ionic radius (1.35 Å), can also have a similar dynamics in soil-plant system (Suwa et al., 2008). Although Ca is one of the most abundant elements in plant tissues, cytosolic concentration is maintained at submicromolar levels because of a low solubility (White and Broadley, 2003). These properties prevent Ca and hence Sr and Ba from being translocated from leaves to other organs via the phloem and result in Ca, Sr and Ba accumulation with leaf age. Such low solubility in the cytosol and therefore low mobility in the phloem could be responsible for the accumulation of all elements from group 1.

Annual translocation to the foliage strongly varied among the analyzed trace elements. The four elements with the highest concentrations in the analyzed plant compartments (Mn, Al, Fe and Ba) were also the elements with the highest annual translocation to the foliage, which ranged from 10 to 100 mg m^{-2} yr^{-1}. The annual translocation to the foliage of Sr, Rb, B and Zn was >1 mg m^{-2} yr^{-1}. With the exception of Al, all these elements are either essential elements (B, Zn, Fe and Mn) or analogs of essential elements (Sr, Rb and Ba). Aluminum can be abundant in the parental rock and occur in the soil solution in nonphytotoxic forms, which might explain the high concentrations in roots (Fig 3). Nevertheless, the high translocation of Al is surprising since Al is known to be highly toxic for plants even at low concentrations (Delhaize and Ryan, 1995). This annual translocation to the foliage might result in the incorporation of a similar amount of element into the top layer of the soil through litter production. The amount of Al returning to the soil annually through litter (65 mg m^{-2} yr^{-1}) is nevertheless very low compared to major elements. Indeed, using concentrations values provided in Marty et al. (2014), we estimated that Ca and K annual translocation to the foliage was 1.9 g m^{-2} yr^{-1} and 0.9 g m^{-2} yr^{-1}, respectively. Therefore, it takes approximately 20 times longer to bring up a given amount of Al from the mineral soil to the top layer compared to Ca through this process.

5 Conclusion

The present data allowed us to distinguish at least two groups of elements among the 35 analyzed based on their distribution throughout the plant organs. The first group included 23 elements characterized by a high retention in the roots and accumulation in leaves with leaf aging. There was a positive relationship between retention in the roots and atomic number but this latter did not appear to be the only determinant factor since some elements with low atomic number (e.g., Al, Co) were highly retained in the roots. This retention might be an adaptation to impede the propagation of toxic elements to other plant organs. On the other hand, we found elements, most of them being essential for plants, which were weakly retained in the root compartment and distributed to the leaves where they either accumulated or were resorbed with leaf aging. More research should be conducted to verify whether the observed patterns in *R. ferrugineum* are universal or related to phylogenetic, functional or ecologic characteristics as it has been previously shown for leaf element composition (Watanabe et al., 2007). In addition, the different dynamics of the two groups of elements may impact element distribution throughout the soil profile. Concentrations of elements with high retention in the roots might remain very low in the upper horizons while those of elements with low retention could accumulate in the upper horizons through litter inputs.

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