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Original article

Foliar resorption in *Quercus petraea* subsp. *iberica* and *Arbutus andrachne* along an elevational gradient

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Abstract

• The resorption of nutrients (mainly N and P) from senescing leaves may be a key component of adaptive mechanisms that conserve scarce nutrients. Resorption may be expressed in two ways as resorption efficiency (RE) which is the ratio of the resorbed amounts of nutrient losses during leaf senescence in relation to its prior amount deposited in leaves and resorption proficiency (RP) is the level to which nutrient concentration per unit leaf mass is reduced in senescent leaves.

• There is still much debate whether or not different life-forms (i.e. deciduous and evergreen species) show different foliar resorption patterns. Two sympatric species, namely *Quercus petraea* (Mattuschka) Liebl. subsp. *iberica* (Steven ex Bieb.) Krassiln. (deciduous) and *Arbutus andrachne* L. (evergreen) along an elevational gradient were compared with each other to determine whether or not nitrogen and phosphorus resorption efficiency and proficiency varies along the elevational gradient and which leaf parameters were as related to RE and RP.

• NRE was found to be rather low in *Q. petraea* subsp. *iberica* compared to other deciduous species. Similarly, PRE in *A. andrachne* was rather low compared to other evergreen species. Mean residence time (MRT) measures how long a unit of nitrogen (MRT_N) and phosphorus (MRT_P) is present in the plant. MRT_N and MRT_P were found to be considerably higher in *A. andrachne* compared to *Q. petraea* subsp. *iberica*. In both species, the foliar N/P ratio was below 14 along the elevational gradient and, according to this threshold value, N-limitation occurred in the study area. Although both species in the present study show incomplete resorption deciduous species was more proficient as compared to evergreen one due to low N and P concentrations in senescent leaves. Based on the significant correlations ($p < 0.05$ and 0.01) between MRT and foliar resorption, it can be concluded that MRT could interfere with the mechanisms controlling nutrient resorption.

Mots-clés :
stratégies de Grime /
temps moyenne de résidence (MRT) /
rapport N/P /
efficience de la résorption /
capacité de résorption /
espèces sympatriques

Résumé – Résorption foliaire chez *Quercus petraea* subsp. *iberica* et *Arbutus andrachne* le long d'un gradient altitudinal.

• La résorption des éléments nutritifs (essentiellement N et P) par sénescence des feuilles peut être une composante clé des mécanismes d'adaptation qui permettent de conserver les rares éléments nutritifs. La résorption peut être exprimée de deux façons : l'efficience de résorption (RE) qui est le rapport entre la quantité résorbée des pertes d'éléments nutritifs au cours de la sénescence des feuilles par rapport à son montant déposé auparavant dans les feuilles et la capacité de résorption (RP) qui est le niveau auquel la concentration des éléments nutritifs par unité de masse de feuilles est réduite dans les feuilles sénescentes.

• Il reste encore beaucoup de débat pour déterminer si les différentes formes de vie (c'est-à-dire les espèces décidues et les espèces sempervirentes) présentent différents modes de résorption foliaire. Deux espèces sympatriques, à savoir *Quercus petraea* (Mattuschka) Liebl. subsp. *iberica* (Steven ex Bieb.) Krassiln. (décidue) et *Arbutus andrachne* L. (sempervirente), ont été comparées l'une à l'autre, le long d'un gradient altitudinal, afin de déterminer si l'efficience de résorption de l'azote et du phosphore et la capacité de résorption varient le long d'un gradient altitudinal et quels paramètres de la feuille sont liés à RE et RP.

• NRE a été trouvé plutôt faible chez Q. *petraea* subsp. *iberica* par rapport à d'autres espèces décidues. De même, chez *A. andrachne* PRE a été plutôt faible par rapport à d'autres espèces

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sempervirentes. Le temps de résidence moyen (MRT) mesure combien de temps une unité d'azote (MRT_P) et de phosphore (MRT_P) est présente dans la plante. MRT_P et MRT_P étaient considérablement plus élevés chez *A. andrachne* par rapport à *Q. petraea* subsp. *iberica*. Chez les deux espèces, le ratio foliaire N/P était inférieur à 14 le long du gradient altitudinal, en fonction de la valeur de ce seuil, une limitation d'azote s'est produite dans la zone d'étude. Bien que les deux espèces, dans la présente étude, montrent une résorption incomplète, l'espèce décidue avait une meilleure capacité de résorption comparativement à l'espèce sempervirente en raison de la faible concentration de N et de P dans les feuilles sénescentes. Sur la base des corrélations significatives ($p < 0.05$ et 0.01) entre MRT et la résorption foliaire, il peut être conclu que MRT pourrait interférer avec les mécanismes de contrôle de la résorption des éléments nutritifs.

1. INTRODUCTION

Nutrient resorption is known to be one of the most important strategies employed by plants to conserve nutrients prior to senescence. The resorption of nutrients and their removal from senescent leaves, and their accumulation or storage in the perennial parts of trees is a common process. This resorption of nutrients may meet a significant demand of the nutritional requirements for the production of new biomass. Similarly, resorption is a beneficial process because the tree is less subject to losses due to a decrease in biomass decomposition (Regina and Tarazona, 2001). Nutrients which are resorbed from the plant during senescence are directly available for further plant growth, which makes a species less dependent on current nutrient uptake. Nutrients which are not resorbed, however, will be circulated through litterfall in the longer term. All of these factors have important implications for element cycling at the ecosystem level (van Heerwaarden et al., 2003).

The resorption of nutrients (mainly N and P) from senescing leaves may be a key component of adaptive mechanisms that conserve scarce nutrients (Niinemets and Tamm, 2005; Killingbeck, 1996).

Resorption can be expressed in two ways: as resorption efficiency and resorption proficiency. Resorption efficiency is most accurately calculated for any nutrient as the area-specific mass in green leaves minus the area-specific mass in senesced leaves divided by the area-specific mass in green leaves

$$[(\textit{Nutrient in live leaves} - \textit{Nutrient in senescent leaves})/ \textit{Nutrient in live leaves}] \times 100. \quad (1)$$

A new measure of resorption was introduced by Killingbeck (1996) as resorption proficiency. Killingbeck (1996) emphasized that resorption proficiency (the concentration of a nutrient in senesced leaves) over resorption efficiency is not subject to temporal variation in nutrient concentration in green leaves or the timing of sampling. Proficiency is simply the amount of a nutrient that remains in fully senesced leaves (Yuan et al., 2005a).

Two sympatric species along an elevational gradient were selected for this study. One of these species is deciduous (*Quercus petraea* subsp. *iberica*; deciduous), while the other is an evergreen species (*Arbutus andrachne*). Soil fertility and soil water content vary along the elevational gradient. Both species are canopy species and occurred along the elevational gradient. The present study addresses three main objectives: (a) to determine which leaf parameters were related to nitrogen and phosphorus efficiency (NRE and PRE) and proficiency (NRP and PRP); (b) to compare deciduous and evergreen species in terms of resorption efficiency and proficiency, leaf mass per area (LMA); and (c) to determine whether or not nitrogen and phosphorus resorption efficiency and proficiency varies along the elevational gradient in two sympatric species.

2. MATERIALS AND METHODS

2.1. Study Area and Collection of Samples

This study was carried out along an elevational gradient in Amasya, Yassıcal Mountain (1 148 m a s l), situated in the North of Turkey, where both species are widespread. Plots of 20 m × 20 m (400 m^2) were chosen at low (450 m a s l), middle (600 m a s l) and high (800 m a s l) altitudes from homogeneous places. Plots were chosen which had closed tree canopies. Chestnut soils which formed as a result of calcification were dominant along the catena (Turkish Ministry of Agriculture and Forestry, 1991). Average annual rainfall ranges from 24.2 mm (September) to 86.9 mm (June). January is the coldest month (0.9 °C) and July (21.3 °C) is the hottest month. The climate of the study area has a transitional character between semi-arid and humid Mediterranean climates (Turkish Ministry of Agriculture, 2002).

Van Heerwaarden et al. (2003) proposed that current measures of nutrient resorption efficiency lead to a substantial underestimation of the real resorption efficiency, due to changes in leaf mass or leaf area during senescence. These authors suggested pre-selection of leaves in order to minimize the risk of comparing green and senescent leaves of different cohorts (Rentería et al., 2005). Ten trees for each species were pre-selected and marked. Leaf samples from throughout the midcrown of each individual were taken and consisted of leaves with no evidence of insect attack. Individuals were selected ≥ 2.5 m. from the stems of neighboring canopy trees to avoid potential microsite variation (Boerner and Koslowsky, 1989). Senesced leaves were obtained from near the marked trees. Fifteen to twenty leaf samples were taken from each individual for both species and each altitude at each sampling date.

Green leaf samples of *Q. petraea* subsp. *iberica* were sampled in mid-June, whilst senesced leaf samples were collected in October. Green leaves of *A. andrachne* were sampled in mid-April, while senesced leaf samples were collected in June. Foliar nutrient concentrations are most stable in mid-June and mid-April in deciduous and evergreen species, respectively (Fig. 1). When fully senesced, leaves

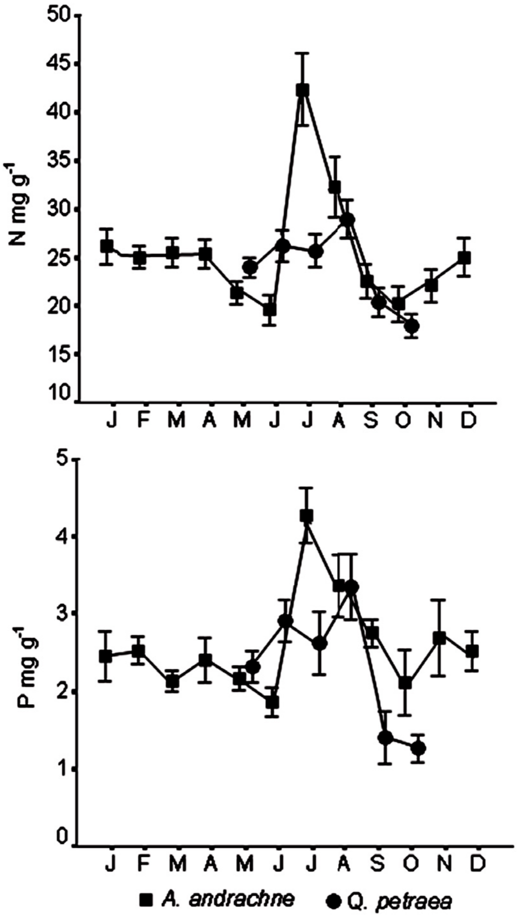

Figure 1. Nitrogen and phosphorus dynamics across time for the two studied species.

of *Q. petraea* subsp. *iberica* become light brown and dry, and those of *A. andrachne* become yellow and readily fall off when touched. Resorption efficiency (%) was calculated as the percentage of N, P and recovered from senescing leaves (Rejmánková, 2005):

- Leaf samples of both species were scanned and the leaf area was calculated by using Net Cad software (Anonymous, 1999). Leaf samples of both species were oven dried at 70 °C until they reached a constant weight, and then weighed.
- Leaf mass per area (LMA) of fully expanded leaves and senescence leaves was calculated from dry leaf mass (oven-dried 48 h at 60 °C). Grime's CSR (C: competitive; S: stress-tolerant; R: ruderal) strategies were used to compare both sympatric species in terms of N and P usage strategies by using a program developed in Microsoft Excel. Canopy height, dry matter content, flowering period, the onset of flowering, lateral spreading, dry leaf weight and specific leaf area were used to determine which Grime's category the studied species belonged (Hodgson et al., 1999).

The mean residence time (MRT, years) of a unit of N (MRT_N) and P (MRT_P) in the leaf was estimated as MRT = leaf life span × $1/(1 - r)$ where r is the nutrient resorption efficiency and leaf life span is expressed in years (Aerts and Chapin, 2000).

Table I. The comparison of two sympatric species regarding leaf traits by one-way ANOVA.

Leaf trait	df	F-value	p
N mg/g	647	113.12	0.001**
P mg/g	647	64.36	0.003**
LMA mg/dm^2	647	242.23	0.001**
N/P	647	1.028	0.141NS
NRE	647	36.29	0.003**
PRE	647	3.28	0.162NS
NRP	647	9.40	0.006**
PRP	647	17.60	0.004**
MRT_N	647	109.63	0.001**
MRT_P	647	30.08	0.003**

NS: Not significant; df: degrees of freedom; ** $p < 0.01$.

2.2. Chemical analyses

Leaf samples were digested in a mixture of nitric and perchloric acids, with the exception of samples for N analysis. Nitrogen was determined by the micro Kjeldahl method with a Kjeltec Auto 1030 Analyzer (Tecator, Sweden) after digesting the samples in concentrated H_2SO_4 with a selenium catalyst. P was determined with the stannous chloride method using a Jenway spectrophotometer (Allen et al. 1986).

Five soil samples of 0–60 cm depth were collected using an auger at each elevation and each sampling date. The soil samples were air-dried and then sieved to pass through a 2-mm screen. The pH values were measured in deionized water (1:1). Soil nitrogen (g/kg) was determined by the micro Kjeldahl method. Soil phosphorus (g/kg) was determined spectrophotometrically following extraction by ammonium acetate. Organic matter (g/kg) concentration was determined using the Walkley-Black method (Allen et al., 1986). For the determination of soil moisture (cm^3 H_2O/100 cm^3 soil), samples of approximately 250–300 g were placed in soil pins, weighed fresh, dried at 105 °C for 48 h, then weighed dry; Soil moisture was then calculated on a volume basis (Boerner 1984). Soil nutrient concentrations were determined according to Allen et al. (1986).

Taxonomic nomenclature for plant species followed that of Brummitt and Powell (1992).

2.3. Statistical analyses

One and two-way analysis of variance (ANOVA) and a multivariate General Linear Models procedure were carried out using SPSS Version 10.0 (Anonymous 1999). Dependent and independent variables were foliar nutrient concentrations and foliar resorption, and species, growth period and localities, respectively. Following analysis of variance, Tukey's honestly significant difference (HSD) test was used to rank means. Pearson correlation coefficients among leaf and soil traits were also calculated.

3. RESULTS

Annual changes in N and P concentrations were similar in both species (Fig. 1). There were statistically significant differences between the two sympatric species regarding leaf traits, except for N/P ratio and PRE (Tab. I). Leaf N concentration in both species was different at 600 m compared with 450 m and 800 m respectively. Similarly, leaf P concentration was significantly different at 800 m in both species (Tab. II). No significant differences were found in *A. andrachne* along the elevational gradient in terms of N/P ratio. However, N/P ratio at 800 m was significantly different along the elevational gradient in *Q. petraea* subsp. *iberica*. N/P ratio in *Q. petraea* subsp. *iberica* was higher than that of *A. andrachne* and ranged from 10.10–11.61. N/P ratio varied between 8.00–12.00 in *A. andrachne*. LMA values were significantly different along the elevational gradient in both species ($p < 0.01$) and higher in *A. andrachne*. Similarly MRT_N and MRT_P in *A. andrachne* were also considerably higher than those of *Q. petraea* subsp. *iberica*. MRT_N and MRT_P did not significantly change along the elevational gradient except for MRT_N in *A. andrachne*, which varied significantly along the elevational gradient (Tab. II).

P concentrations and NRP varied significantly along the elevational gradient in *Q. petraea* subsp. *iberica* ($p < 0.01$). However, N concentrations, NRE, PRE and PRP were not significantly changed in either species. (Tab. II).

Significant correlations ($p < 0.01$) were found between green leaf N concentrations and NRE and PRE in both species. There were negative correlations between NRP and NRE and also between PRE and PRP, respectively in both species. Statistically significant correlations ($p < 0.01$) were also found between MRT_N and NRE and also between MRT_P and PRE, respectively. However, NRP and PRP were negatively correlated with MRT_N and MRT_P in both species (Tabs. III and IV).

Both soil nitrogen and organic matter concentrations were at medium level, whereas soil phosphorus concentrations were rather low. Total nitrogen, available phosphorus, soil water content and soil organic matter increased along the elevational gradient. However, soil pH decreased along the elevational gradient (Tab. V).

4. DISCUSSION

NRE was found to be higher in *A. andrachne*, whereas PRE was higher in *Q. petraea* subsp. *iberica*. Huang et al. (2007) found that PRE was lower in evergreen species than deciduous species. The negative effect of this low resorption efficiency is outweighed by the positive effect of increased leaf longevity on mean residence time (Escudero et al., 1992). MRT_N and MRT_P were found to be considerably higher in *A. andrachne* compared to *Q. petraea* subsp. *iberica*. Long leaf lifespan prolonged MRT_N and MRT_P by increasing the retention time of N and P (Silla and Escudero, 2004). MRT_N and MRT_P were significantly correlated with NRE and PRE, respectively in deciduous species. Similarly, MRT was significantly correlated with PRE in evergreen species. Plants with low LMA have leaves with a short lifespan and high nitrogen concentration and this relationship would be important in mixed species stands containing species differing in leaf longevity (Wright and Westoby, 2003). It can be argued that such a relationship was not completely the case in the two studied species, because the leaf lifespan in *Q. petraea* subsp. *iberica* and *A. andrachne* were found to be 180 and 420 d, respectively. Deciduous species has low LMA, whereas it had low leaf nitrogen concentrations than that of the evergreen one. It has been concluded that LMA varies over about two orders of magnitude across the species, and this variation is thought to represent a key trade-off between the performance and persistence of leaves. Reduction of LMA also brings potential short-term advantages of lower leaf construction costs per area, and lower maintenance costs (i.e. respiration rates per area) (Lusk et al., 2008).

Some researchers reported a positive correlation between NRE and green-leaf nutrient concentrations (del Arco et al., 1991; Escudero et al., 1992), while other researchers stated that such a relationship was not found between NRE and green-leaf nutrient concentrations (Huang et al., 2007; Niinemets and Tamm, 2005; Yuan et al., 2005a). Ratnam et al. (2008) stated that both NRE and PRE decreased as nutrient concentrations in green leaves increased. However, significant correlations were found among green-leaf N and P concentrations and NRE and PRE, respectively in both species although no significant correlations were exist among NRE, PRE and N/P ratio. Ratnam et al. (2008) also emphasized that specific patterns of resorption and the functional relationships between nutrient concentrations in green and senesced leaves varied depending on the nutrient and plant life form.

PRE in *Q. petraea* subsp. *iberica* was similar to that of other deciduous species. However, NRE was found to be rather low compared to other deciduous species (Tab. VI). Norby et al. (2000) found low resorption efficiency values in *Quercus alba* and NRE was much lower than that of *Acer* sp. According to Norby et al. (2000), this may have been related to high levels of phenolic compounds in *Quercus* sp. Phenolic compounds can bind proteins and interfere with their hydrolysis into smaller, mobile compounds (Pugnaire and Chapin, 1993). NRE in *A. andrachne* were similar to those of other evergreen species. However, PRE was found to be 39.2%, which is rather low compared to other evergreen species (Tab. VI).

PRE in *Q. petraea* subsp. *iberica* was similar to those of other deciduous species. However, NRE was found to be rather low compared to other deciduous species. NRE in *A. andrachne* was similar to that of other evergreen species. However, PRE was found to 39.2%, which is was rather low compared to other evergreen species (Tab. VI). Several researchers (Aerts and Chapin, 2000; Huang et al., 2007) concluded that nutrient resorption efficiency did not differ among growth-forms (e.g. deciduous versus evergreen species). However, statistically significant differences ($p < 0.01$) were found regarding NRE between the studied sympatric species. Significant negative correlations ($p < 0.01$) between NRE and NRP and PRE and PRP, respectively were found in both species, indicating that resorption efficiency was controlled by nutrient concentration in senescent leaves (NRP and PRP), and was distinct from leaf longevity, which leads to resource conservation (Haddad et al., 2004).

The N/P ratio of green leaves is considered as an important indication of nutrient availability (Güsewell, 2005). A foliar N/P ratio below 14 indicated N limitation and foliar N/P ratio below 12.5 indicated an optimal P nutrition (Aerts and Chapin 2000). The N/P ratio in *Q. petraea* subsp . *iberica* was found to be slightly higher than that of *A. andrachne* and ranged from

Table II. Leaf traits and NRE (%), PRE (%), NRP (mg g^{-1}) and PRP(mg g^{-1}) along the elevational gradient (±SE). Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

Species	*A. andrachne*						*Q. petraea*					
Elevation	450 m		600 m		800 m		450 m		600 m		800 m	
		CV		CV		CV		CV		CV		CV
N (mg/g)	23.91 ± 0.63 a	39.88	26.86 ± 0.63 a	28.67	26.13 ± 0.63a	29.76	22.60 ± 0.89a	26.94	24.70 ± 0.89a	21.48	24.35 ± 0.89a	24.24
P (mg/g)	2.57 ± 0.09a	41.71	2.71 ± 0.09a	41.62	2.51 ± 0.09a	41.25	2.52 ± 0.13a	62.21	2.24 ± 0.13b	43.44	2.14 ± 0.13b	51.58
LMA	1.90 ± 0.02ab	15.50	1.91 ± 0.02a	20.70	1.72 ± 0.02b	21.25	1.36 ± 0.03b	11.57	1.50 ± 0.03a	16.96	1.42 ± 0.03b	14.57
N/P	10.30 ± 0.45a	42.30	11.54 ± 0.45a	45.45	11.46 ± 0.45a	36.87	11.24 ± 0.64a	74.83	12.58 ± 0.64a	54.40	12.67 ± 0.64a	56.17
NRE (%)	59.14 ± 3.89a	24.51	47.56 ± 3.89a	35.90	45.77 ± 3.89a	30.40	31.61 ± 3.89a	41.48	36.07 ± 3.89a	30.46	42.42 ± 3.89a	32.76
PRE (%)	56.93 ± 5.34a	24.44	53.24 ± 5.34a	32.10	52.12 ± 5.34a	32.18	62.76 ± 5.34a	37.90	54.01 ± 5.34a	38.27	59.31 ± 5.34a	34.85
NRP (mg/g)	17.71 ± 1.11a	26.01	20.22 ± 1.11a	18.77	20.69 ± 1.11a	23.04	16.23 ± 1.11b	23.87	19.71 ± 1.11a	17.15	17.992 ± 1.11ab	19.33
PRP(mg/g)	1.82 ± 0.14a	30.68	1.45 ± 0.14a	23.02	1.94 ± 0.14a	30.58	1.08 ± 0.14a	55.56	1.35 ± 0.14a	41.31	1.34 ± 0.14a	40.14
MRT_N	2.92 ± 0.24a	35.20	2.89 ± 0.24a	32.40	1.89 ± 0.24b	23.22	0.66 ± 0.03a	16.25	0.68 ± 0.03a	18.32	0.76 ± 0.03a	17.45
MRT_P	0.67 ± 0.07a	36.51	0.68 ± 0.07a	43.92	0.73 ± 0.07a	35.96	0.19 ± 0.04a	60.39	0.28 ± 0.04a	55.47	0.25 ± 0.04a	47.44

CV: Coefficient of variation (the variability among leaves in terms of leaf traits), SE: Standard error.

Table III. Pearson correlations among leaf traits in *Q. petraea* subsp. *iberica*.

	N/P	NRE	PRE	NRP	PRP	Green leaf N	Green leaf P	Green leaf LMA	Senescence leaf LMA	MRT$_{\text{N}}$	MRT$_{\text{P}}$	Leaf longevity
N/P	–											
NRE	0.15	–										
PRE	0.16	0.36*	–									
NRP	–0.04	–0.89**	–0.28	–								
PRP	–0.49**	–0.20	–0.70**	0.19	–							
Green leaf N	0.29	0.43**	0.21	0.02	–0.07	–						
Green leaf P	–0.49**	0.24	0.38*	–0.21	0.29	0.08	–					
Green leaf LMA	–0.01	–0.04	0.13	–0.01	0.05	–0.08	0.19	–				
Senescence leaf LMA	–0.02	–0.29	0.01	0.31	0.16	–0.02	0.20	0.16	–			
MRT$_{\text{N}}$	0.16	0.98**	0.36*	–0.89**	–0.20	0.40*	0.24	–0.01	–0.26	–		
MRT$_{\text{P}}$	0.18	0.50**	0.67**	–0.48**	–0.47**	0.13	0.38*	0.20	–0.08	0.51**	–	
Leaf longevity	0.17	0.18	0.22	–0.13	0.04	0.14	0.22	–0.15	0.01	0.20	0.28	–

* $p < 0.05$; ** $p < 0.01$.

Table IV. Pearson correlations among leaf traits in *A. andrachne*.

	N/P	NRE	PRE	NRP	PRP	Green leaf N	Green leaf P	Green leaf LMA	Senescence leaf LMA	MRT$_{\text{N}}$	MRT$_{\text{P}}$	Leaf longevity
N/P	–											
NRE	0.08											
PRE	0.23	–										
NRP	0.22	–0.72**	0.17									
PRP	–0.30	0.05	–0.58**	0.03	–							
Green leaf N	0.20	0.68**	0.23	–0.02	0.15	–						
Green leaf P	–0.05	0.18	0.65**	0.10	0.14	0.45**						
Green leaf LMA	–0.05	0.53**	0.31	–0.07	0.16	0.76**	0.57**	–				
Senescence leaf LMA	–0.02	–0.01	–0.19	–0.03	0.17	–0.06	–0.08	–0.15	–			
MRT$_{\text{N}}$	0.04	0.94**	–0.01	–0.72**	0.06	0.64**	0.16	0.48**	–0.01	–		
MRT$_{\text{P}}$	0.19	0.13	0.91**	0.04	–0.58**	0.26	0.69**	0.33*	–0.27	0.10	–	
Leaf longevity.	0.20	0.14	–0.03	0.07	0.13	0.26	0.19	0.02	0.36*	0.15	0.03	–

* $p < 0.05$; ** $p < 0.01$.

Table V. Soil traits along the elevational gradient (±SE). Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

Elevation	450 m	600 m	800 m
Total nitrogen (%)	0.17 ± 0.01*a*	0.19 ± 0.01*a*	0.23 ± 0.01*a*
Available phosphorus (ppm)	10.15 ± 0.96*a*	11.15 ± 0.96*a*	13.96 ± 0.96*a*
Soil water content (%)	42.08 ± 2.16*b*	63.00 ± 2.16*a*	63.83 ± 2.16*a*
Soil organic matter (%)	0.96 ± 0.18*b*	3.26 ± 0.18*a*	3.73 ± 1.18*a*
pH	7.96 ± 0.03*a*	7.80 ± 0.03*ab*	7.64 ± 0.03*a*

9.53–11.49, whereas the N/P ratio varied between 9.46 and 10.55 in *A. andrachne*. In both species, the foliar N/P ratio was below 14 along the elevational gradient and, according to this threshold value, N-limitation occurred in the study area. Plants with low leaf-nutrient concentrations tend to minimize nutrient loss through leaf shedding and are good examples of stress-tolerators (Milla et al., 2005). Güsewell (2005) stated that CS species which have low P concentration and high N/P ratios partly reflect slow growth, and partly their efficient internal cycling of P. *Q. petraea* subsp. *iberica* has low leaf P concentration and belongs to the C/CS (competitor/competitor stress-tolerant) transitional type strategy, whilst *A. andrachne* has high leaf P concentration, and belongs to the C (competitor) strategy. However, there were no statistically significant differences between the two sympatric species regarding N/P ratio, although the N/P ratio is slightly higher in deciduous species. NRE and PRE are poorly predicted by foliar N/P ratios. However, this is in contrast to NRP and PRP, which appear to be

Table VI. N and P resorption efficiency values in some deciduous and evergreen species.

Species	Leaf habit	N%	P%	Source
Quercus petraea **(Mattuschka) Liebl. subsp. *iberica* (Steven ex Bieb.) Krassiln.**	**Deciduous**	**27.9**	**50.4**	**Present study**
Quercus alba L.	Deciduous	38.5	59.0	Boerner (1984)
Quercus prinus L.	Deciduous	49.2	44.5	Boerner (1984)
Quercus ilicifolia Wang.	Deciduous	70.0	59.1	Killingbeck and Costigan.(1988)
Quercus pyrenaica Willd.	Deciduous	46.4	–	Escudero et al. (1992)
Quercus faginea Lam.	Deciduous	44.9	–	Escudero et al. (1992)
Betula pubescens Ehrh.	Deciduous	69.2	–	Escudero et al. (1992)
Populus nigra L.	Deciduous	62.6	–	Escudero et al. (1992)
Frangula alnus P. Mill.	Deciduous	61.6	–	Escudero et al. (1992)
Sambucus nigra L.	Deciduous	49.6	–	Escudero et al. (1992)
Fraxinus angustifolia Vahl	Deciduous	39.7	–	Escudero et al. (1992)
Crataegus monogyna Jacq.	Deciduous	37.1	–	Escudero et al. (1992)
Prunus spinosa L.	Deciduous	24.3	–	Escudero et al. (1992)
Quercus rubra L.	Deciduous	70.0	55.0	Côté et al. (2002)
Acer rubrum L.	Deciduous	65.0	74.0	Côté et al. (2002)
Populus grandidentata Michx.	Deciduous	56.0	65.2	Côté et al. (2002)
Fagus grandifolia Ehrh.	Deciduous	62.0	77.5	Côté et al. (2002)
Fagus orientalis Lipsky	Deciduous	73.4	72.9	Kutbay et al. (2003)
Rhododendron luteum Sweet	Deciduous	55.8	79.7	Kutbay et al. (2003)
Hypericum androsaemum L.	Deciduous	44.1	50.8	Kutbay et al.(2003)
Vaccinium arctostaphylos L.	Deciduous	28.5	51.7	Kutbay et al. (2003)
Quercus faginea Lam.	Deciduous	45.0	43.0	Mediavilla and Escudero (2003)
Quercus pyrenaica Willd.	Deciduous	47.0	51.0	Mediavilla and Escudero (2003)
MEAN	DECIDUOUS	50.77 ± 14.39	59.55 ± 12.29	
Arbutus andrachne **L.**	**Evergreen**	**49.2**	**39.7**	**Present study**
Vaccinium vacillans Torr.	Evergreen	25.7	29.1	Killingbeck and Costigan (1988)
Quercus coccifera L.	Evergreen	31.0	–	Escudero et al. (1992)
Quercus ilex L.	Evergreen	29.7	–	Escudero et al. (1992)
Ilex aquifolium L.	Evergreen	46.7	–	Escudero et al. (1992)
Daphne pontica L.	Evergreen	51.1	57.3	Kutbay et al. (2003)
Quercus suber L.	Evergreen	47.9	–	Escudero et al. (1992)
Quercus suber L.	Evergreen	49.0	55.9	Mediavilla and Escudero (2003)
Quercus coccifera L.	Evergreen	32.0	42.9	Mediavilla and Escudero (2003)
Quercus rotundifolia Lam.	Evergreen	31.0	33.2	Mediavilla and Escudero (2003)
MEAN	EVERGREEN	39.33 ± 10.15	43.01 ± 11.58	

more responsive to N/P ratios (Ratnam et al., 2008). Only PRP was negatively correlated with N/P ratio in deciduous species and the other correlations among RE and RP and N/P ratio were not significant in the present study (Tabs. III and IV).

Killingbeck (1996) stated that resorption is highly proficient in plants that have reduced nitrogen and phosphorus during their senescent stages to concentrations below 7 mg g^{-1} and 0.5 mg g^{-1}, respectively. Both species in the present study show incomplete resorption according to threshold values defined by Killingbeck (1996). Huang et al. (2007) found that N concentration in senesced leaves was lower in species with longer leaf lifespan. High resorption proficiency implies low concentrations because a low N concentration in senesced parts is the evidence of high proficiency, and vice versa (Yuan et al., 2005a). Deciduous species was more proficient because low N concentrations were found in senescent leaves.

In summary, based on the significant correlations between MRT and foliar resorption, it can be concluded that MRT could interfere with the mechanisms controlling nutrient resorption. Deciduous species was more proficient as compared to evergreen one due to low N and P concentrations in senescent leaves.

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