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NITROGEN AND PHOSPHORUS RESORPTION IN SOME SYMPATRIC PLANT SPECIES IN THE NORTH OF TURKEY

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RÉSUMÉ.— *Résorption de l'azote et du phosphore chez quelques espèces végétales dans le nord de la Turquie*.— Les concentrations foliaires de nutriments (N et P) en été et en automne, ainsi que l'efficience (RE) et la proficience (RP) de la résorption foliaire, ont été étudiées dans le nord de la Turquie chez quelques espèces végétales décidues sympatriques sur sols à faible teneur en phosphore. Les NRE et PRE trouvées sur les espèces étudiées se situaient dans les éventails de valeurs rapportés par d'autres études. Les concentrations en N et P les plus fortes, rapportées tant à la masse qu'à la surface, ont été observées chez *Acer hyrcanum* subsp. *sphaerocaryum.* Les plus fortes NRE ont également été trouvées chez *Acer hyrcanum* subsp. *sphaerocaryum* alors que les plus grandes PRE ont été décelées chez *Sorbus umbellata* var. *umbellata*. Toutefois la tendance inverse est apparue quand, pour ces deux espèces, la correction MLCF a été appliquée. L'espèce la plus N- et P-proficiente était *Cerasus mahaleb* en raison des plus faibles concentrations en N et P trouvées dans les feuilles sénescentes. Cependant, l'espèce la plus N-proficiente était *S. umbellata* var. *umbellate* pour ce qui concerne la NRP basée sur la masse. Les rapports N/P des feuilles vertes des espèces étudiées s'étalaient entre 22,95 et 35,25 sur la zone d'étude, ce qui indiquait une limitation en P au niveau local. Chez toutes les espèces, les rapports N/P sont apparus s'accroître durant la sénescence et, au niveau de la plante, le statut de N et P n'était pas strictement contrôlé par les concentrations en N et P des feuilles, vertes et sénescentes ; toutes les espèces ont montré une résorption complète en fonction de valeurs-seuils. Nos résultats impliquent que la PRE joue un rôle plus important dans la conservation du P que la NRE dans celle de N. Ainsi, dans notre zone d'étude, les deux espèces *A. hyrcanum* subsp. *sphaerocaryum* avec sa plus forte PRE (basée tant sur la masse que sur la surface) et *C. mahaleb* qui est l'espèce la plus P-proficiente, ont de meilleurs avantages compétitifs que les autres espèces à utiliser efficacement P dans les sols qui en sont pauvres.

SUMMARY.— In the North of Turkey, foliar nutrient concentrations during summer and autumn and foliar resorption efficiency (RE) and proficiency (RP) were investigated in some sympatric deciduous plant species occurring on soils with low phosphorus availability. NRE and PRE were found to be within the ranges reported by other studies for the same studied species. The highest mass and area-based N and P concentrations were found in *A. hyrcanum* subsp. *sphaerocaryum*. The highest mass and area-based NRE were also found in *A. hyrcanum* subsp. *sphaerocaryum*, while the highest mass and area-based PRE were found in *S.umbellata* var. *umbellata*. However, the opposite trend was found when MLCF correction was used for both species. The most N and P-proficient species was *C. mahaleb* because the lowest N and P concentrations were found in its senesced leaves. However, the most N-proficient species was *S. umbellata* var. *umbellata* regarding mass-based NRP. N/P ratios of green leaves of the studied species ranged from 22.95 to 35.25 in the study area and this indicated that P limitation may occur at a local level. It has been found that N/P ratios were increased during senescence in all species. Plant N and P status was not strictly controlled by N and P concentrations of green and senesced leaves in the studied species; all of these show complete resorption according to threshold values. Our results implied that PRE has a much important role in conservation of P as compared to NRE conservation of N. In the study area, compared to other species, *A. hyrcanum* subsp. *sphaerocaryum* with the highest both mass- and area-based PRE and *C. mahaleb* which is the most P-proficient species, have competitive advantages for an effective use of P in P-poor soils.

Nitrogen (N) and phosphorus (P) are the primary nutrients that limit growth in natural environments (Vitousek & Howarth, 1991; Marschner, 1995; Koerselman & Meuleman, 1996;

Aerts & Chapin, 2000). They are largely withdrawn from senescent leaves before abscission, and used for new growth or stored in vegetative tissue until the next growing season. Especially N deficiency promotes drastic consequences during plant development period. P is a component of important macromolecules like nucleic acids and phospholipids and important especially for energy transfer and metabolism (Miatto *et al.*, 2016).

Forest trees and shrubs resorbed sizeable proportions of nutrients from leaves before leaf abscission and resorption increases the control of the individual plant over the nutrient resources and allows the plant to reutilize them (Kutbay *et al*., 2003; Van Heerwaarden *et al.*, 2003; Yuan *et al*., 2005a). There is a large gap in understanding the scale and the mechanisms of intraspecific variation in nutrient behaviour in plants, especially in long-lived plants such as trees (Oleksyn *et al.,* 2002; Brant & Chen, 2015). Foliar resorption of nutrients is a key process in ecosystem nutrient cycling because it makes plants less dependent on current nutrient uptake (Aerts & Chapin, 2000; Hagen-Thorn *et al.,* 2006; Covelo *et al.,* 2008).

Foliar resorption can be expressed in two ways as resorption efficiency and proficiency. Foliar resorption process is commonly quantified as resorption efficiency and is defined as the percentage of a nutrient recovered from a senescing leaf (Aerts, 1996; Aerts & Chapin, 2000; Hoch *et al*,. 2003). Resorption proficiency (RP) is defined as the residual nutrient concentration in senesced leaves (Killingbeck, 1996).

Mixed temperate deciduous forests include many sympatric species which have different forms (i.e climbers, shrubs, etc.) and these sympatric species show some differences with respect to foliar nutrient use strategies (Kutbay, 2001). Mass and area-based nitrogen and phosphorus concentrations during summer and autumn and nitrogen and phosphorus efficiency and proficiency (NRE, PRE, NRP and PRP) were investigated in a mixed deciduous forest in some sympatric species in the north of Turkey. This study is aimed at: (a) determining whether significant differences among deciduous sympatric species with respect to NRE, PRE, NRP and PRP are or not present in a mixed deciduous forest in Northern Turkey; (b) examining the relationships between foliar resorption and N/P ratios; and (c) finding which species among co-occurring ones are the most efficient for the use of N and P on P-poor soils in a mixed deciduous forest.

MATERIALS AND METHODS

THE STUDY AREA AND THE COLLECTION OF SAMPLES

The studied species were collected in the north of Turkey from a mixed deciduous forest around the slopes of Abaci Mountain (35° 56' 00" - 36° 10' 30" N and 40° 39' 58" - 40° 44' 45" E; 700 m a.s.l.) which includes many characteristic deciduous woody species of Euro-Siberian phytogeographical region. Sedimentary and ultrabasic rocks are widespread in the study area which has highly curled and cracked tectonic structure (Kurter & Yildiz, 1986). The mean annual temperature and precipitation are respectively 13.5ºC and 449.6 mm in the study area; Q (Emberger's pluviothermic quotient) value is 48.4 and the area belongs to semiarid cold Mediterranean bioclimate (Akman, 1999; Kaya *et al*,. 2010).

Five 20 x 20 m plots were sampled. They were selected to have closed tree canopies on southwest-facing slopes. Five dominant species were selected from canopy (*Acer hyrcanum* Fisch. & Mey subsp. *sphaerocaryum*) and subcanopy (*Sorbus umbellata* (Desf.) Fritsch var. *umbellata*, *Cerasus mahaleb* (L.) Miller var. *mahaleb*, *Quercus pubescens* Willd., and *Cionura erecta* (L.) Griseb.). The individuals were selected ≥ 3 m from the stems of neighbouring canopy trees to avoid potential microsite variation (Boerner & Koslowsky, 1989) and they were flagged. Since sun and shade leaves may differ in foliar nutrient concentrations, only outer sun leaves were collected (Kutbay & Kilinc, 1994). Green and senesced leaves were taken from four individual plants and they were pooled for nutrient analysis (Zhang *et al*., 2015) during August and November 2008, respectively for each plot (Fig. 1). When a leaf or at least two-thirds of its area turned yellow or brown, it was considered senesced (Williams-Linera, 2000). Determination of the measurement basis can be done by preselecting mature leaves that are to be collected when they have senesced. Preselection also minimises the chance of comparing green and senesced leaves of different cohorts (Van Heerwaarden *et al.*, 2003).

Taxonomic nomenclature for plant species followed that of Guner *et al*,. (2012).

Species	Months											
	1	2	3	4	5	6	7	8	9	10	11	12
A. hyrcanum	NG		FL	FL	FR	FR	FR	FLE	FR	FR	SEN	SD
C. mahaleb	NG		FL	FL	FL	FR	FR	FLE	FR	FR	SEN	SD
C. erecta	NG	NG		FL	FL	FL	FR	FLE	FR	FR	SEN	SD
Q. pubescens	NG	NG						FLE	FL	FR	SEN	SD
S.umbellata	NG	NG	NG			FL	FR	FLE	FR	FR	SEN	SD

Vegetative phase	
Flowering phase	FL
Full leaf expansion	FLE
Fruiting phase	FR
Seedling phase	SD
Senescence	SEN
No growth	NG

Figure1.— Phenological calendar of the studied species.

CHEMICAL ANALYSES

Leaf area of each species was measured with a leaf-area meter (LI-3000, LI-COR, USA) (Kutbay *et al.,* 2003; Kilic *et al.,* 2010). Leaf samples were dried at 70°C until constant weight, ground, and sieved. They were then extracted with a mixture of concentrated HCl and HNO_3 (3:1) with the exception of samples for N analysis. This digest was filtered through a Whatman filter paper no. 42. Nitrogen was determined by the micro Kjeldahl method with a Kjeltec Auto 1030 Analyser (Tecator, Sweden) after digesting the samples in concentrated H_2SO_4 with a selenium catalyst. P was determined with stannous chloride method by using a Jenway 6105 ultraviolet/visible spectrophotometer (Allen *et al.,* 1986). Nutrient concentrations in leaves were expressed on a leaf mass (mg g^{-1}) and area (mg/dm^2) basis.

Nitrogen resorption efficiency (NRE) was calculated as the percentage reduction in leaf nutrient from green to senesced leaves (Killingbeck, 1996; Miatto *et al.,* 2016). Nitrogen and phosphorus resorption efficiency was calculated by the following formulas:

$$NRE = (N_g-N_s)/N_g * 100 \qquad PRE = (P_g-P_s)/P_g * 100$$

where N_g and P_g = N and P concentration in mature green leaves, Ns and Ps = N and P concentrations in senesced leaves (Lima *et al.,* 2006; Miatto *et al*., 2016).

Foliar resorption was also calculated as resorption proficiency (RP). RP Proficiency is simply the amount of a nutrient that remains in fully senesced leaves (*sensu* Killingbeck, 1996).

Vergutz *et al.* (2012) emphasized that if a mass loss correction factor was not used RE would be underestimated due to the loss of dry mass during senescence. Mass loss correction factor (MLCF) is defined as the ratio of dry mass of senesced leaves to the dry mass of green leaves. So nitrogen and phosphorus resorption efficiency (NRE and PRE) (%) was also calculated by using MLCF (van Heerwaarden *et al.,* 2003; Vergutz *et al*., 2012).

Five soil samples of 0-30 cm depth were collected in each forest using an auger. 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 was determined by the micro Kjeldahl method. Soil available phosphorus (g.kg^{-1}) was spectrophotometrically determined by Olsen method following extraction by sodium bicarbonate. Organic matter concentration was determined using the Walkley-Black method (Allen *et al.,* 1986).

Soil pH are slightly alkaline. Soil N and organic matter concentrations of soil are high, while soil phosphorus concentration is rather low (Tab. I).

TABLE I

Soil properties in the study area

Soil trait	Mean ± SD	Significance
pH	7.71 ± 0.05	0.001**
Soil total N concentration	0.26 ± 0.02	0.001**
Available phosphorus	1.93 ± 1.07	0.001**
Organic matter (%)	4.23 ± 0.87	0.002**

*P<0.01 SD: Standard deviation.

STATISTICAL ANALYSES

Repeated multivariate analyses of variance (R-MANOVA) were applied to leaf traits to show significant differences among the studied species. Multivariate General Linear Models procedure were used. Regression between green and senesced leaf N/P ratio and N and P concentrations of green and senesced leaves were also calculated. R-MANOVA and regression were carried out by using SPSS Version 10.0 (IBM Corp. 2012). Dependent and independent variables were foliar nutrient concentrations and foliar resorption, and species, and localities, respectively. Following analysis of variance, Tukey's honestly significant difference (HSD) test was used to rank means. Data were tested for normality using the Kolmogorov–Smirnov test.

RESULTS

There were significant differences among the studied species regarding leaf traits except for SLA and P concentrations of senescence leaves and green leaf N/P ratio. Regression between green and senesced leaf N/P ratios and green and senesced leaf N and P concentrations were not found to be significant (Tabs II & III). It has been found that N/P ratios were increased during senescence (Tab. IV).

TABLE II

R-MANOVA test for leaf traits

Source	Dependent Variable	df	Mean Square	F-value	Significance
	Green Leaf weight g	4	1.84	8.34	0.001**
	Green Leaf Area dm^2	4	1.96	6.52	0.003*
	Green Leaf SLA	4	0.31	5.67	0.050*
	Green Leaf N %	4	0.65	10.56	0.001**
	Green Leaf N mg/g	4	19.77	12.41	0.001**
	Green Leaf N g/dm^2	4	14.82	6.91	0.002**
	Green Leaf P %	4	0.01	31.8	0.440*
	Green Leaf P mg/g	4	0.03	5.69	0.005**
	Green Leaf P g/dm^2	4	0.10	5.95	0.004**
	Green Leaf N/P	4	19.23	0.57	0.690NS
	Senescence Leaf weight g	4	1.92	4.17	0.018*
Species	Senecence Leaf area dm^2	4	1.94	3.32	0.039*
	Senecence Leaf SLA	4	0.02	0.77	0.560NS
	Senescence Leaf N%	4	0.28	16.92	0.001**
	Senescence Leaf N mg/g	4	2.98	7.10	0.002**
	Senescence Leaf N g/dm^2	4	2.33	4.57	0.013*
	Senescence Leaf P %	4	0.01	0.31	0.865NS
	Senescence Leaf P mg/g	4	0.001	0.74	0.581NS
	Senescence Leaf P g/dm^2	4	0.002	1.28	0.322NS
	Senescence Leaf N/P	4	0.01	5.95	0.004*

NS: Not significant * $p<0.05$ ** $p<0.01$ df:Degrees of freedom.

TABLE III

Regression analysis between green leaf N/P ratio and senescence leaf N and P concentrations

Model		Std. Error	t-value	Significance
Dependent Variable: Green Leaf N/P	(Constant)	3.80	6.437	0.001
	Sen*.N (mg/g)	7.31	-0.515	0.614
	Sen.N (g/dm2)	7.66	0.592	0.563
	Sen.P (mg/g)	18.07	0.408	0.689
	Sen.P (g/dm2)	20.18	-0.366	0.719
Dependent Variable: Senescence Leaf N/P	(Constant)	18.72	1.585	0.134
	Green*.N (mg/g)	2.68	0.531	0.603
	Green.N (g/dm2)	3.47	-0.133	0.896
	Green P (mg/g)	36.25	0.148	0.884
	Green .P (g/dm2)	36.23	-0.518	0.612

* $p < 0.05$; ** $p < 0.01$; Sen: Senescence

TABLE IV

N/P ratios of green and senesced leaves of the studied species

		Green		Senescence	
	N	Mean	SD	Mean	SD
A. hyrcanum	4	26.90	0.83	43.615	7.767
C. mahaleb	4	21.57	1.30	24.347	7.295
C. erecta	4	15.90	7.17	31.280	5.002
Q. pubescens	4	24.20	0.98	37.312	5.092
S.umbellata	4	22.84	2.52	23.223	2.821

SD: Standard deviation.

Green leaf SLA was significantly changed among species, while senesced leaf SLA was not (Fig. 2).

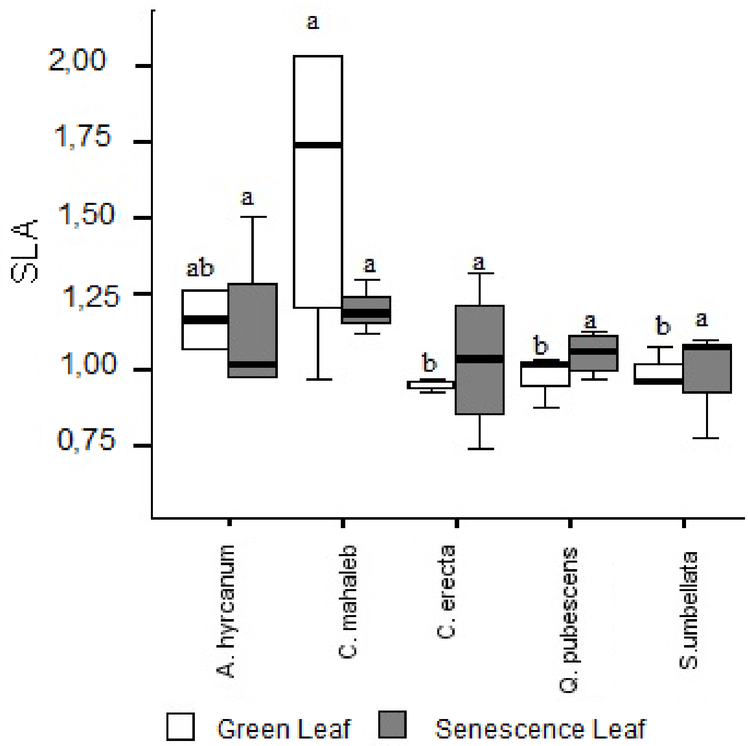

Figure 2.— Boxplots of specific leaf area (SLA (dm^2/g) values of the studied species.
Bars indicate standard deviation of means. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

The highest mass and area-based N and P concentrations were found in *A. hyrcanum* subsp. *sphaerocaryum* (Figs. 3 & 4).

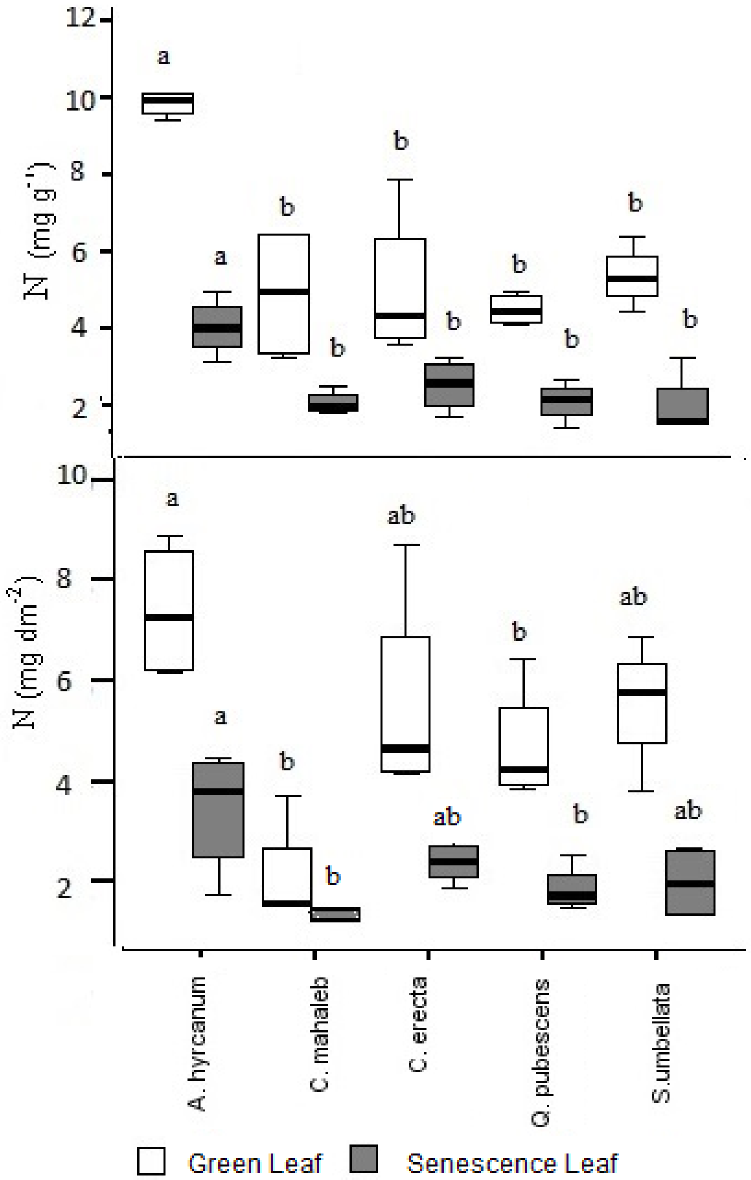

Figure 3.— Boxplots of mass (mg/g) and area-based (mg/dm^2) N concentrations of the studied species. Bars indicate standard deviation of means. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

The highest mass and area-based NRE were also found in *A. hyrcanum* subsp. *sphaerocaryum*, while the highest mass and area-based PRE were found in *S.umbellata* var. *umbellata*.

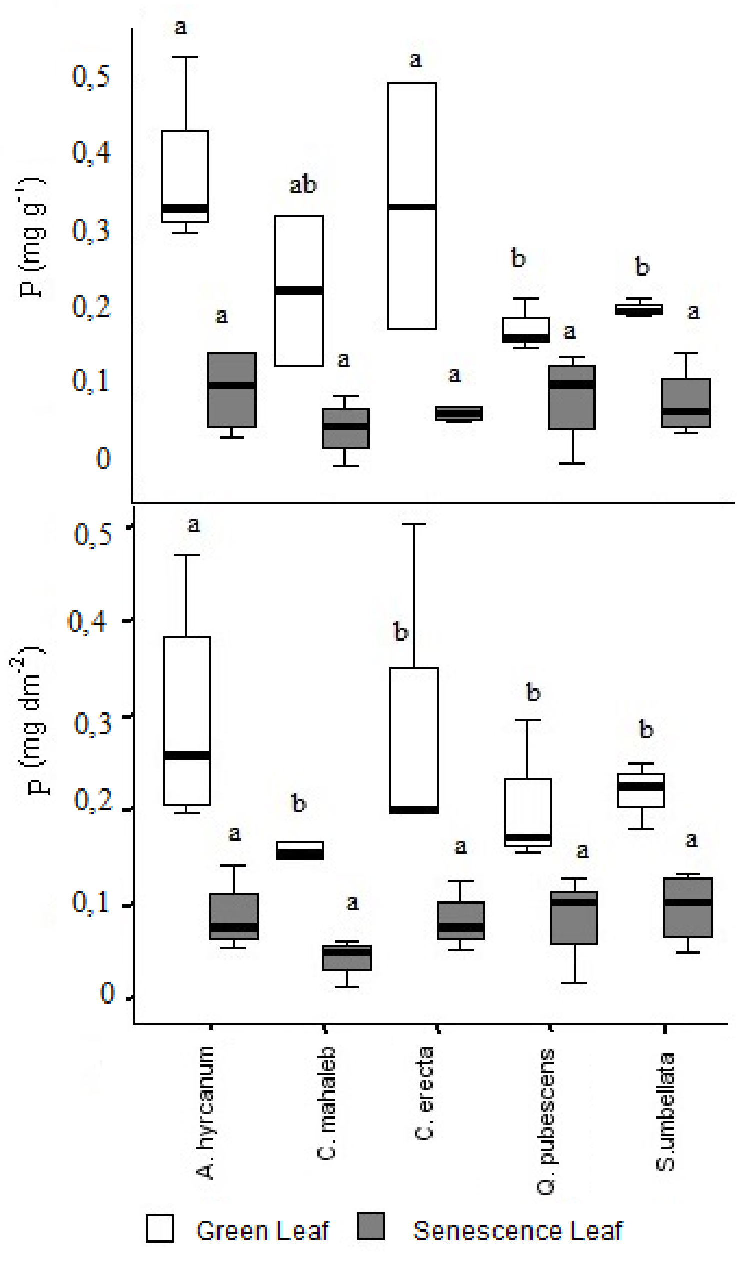

Figure 4.— Boxplots of mass (mg/g) and area-based (mg/dm^2) P concentrations of the studied species. Bars indicate standard deviation of means. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

However, the opposite trend was found when MLCF correction was used for both species (Figs. 5 & 6).

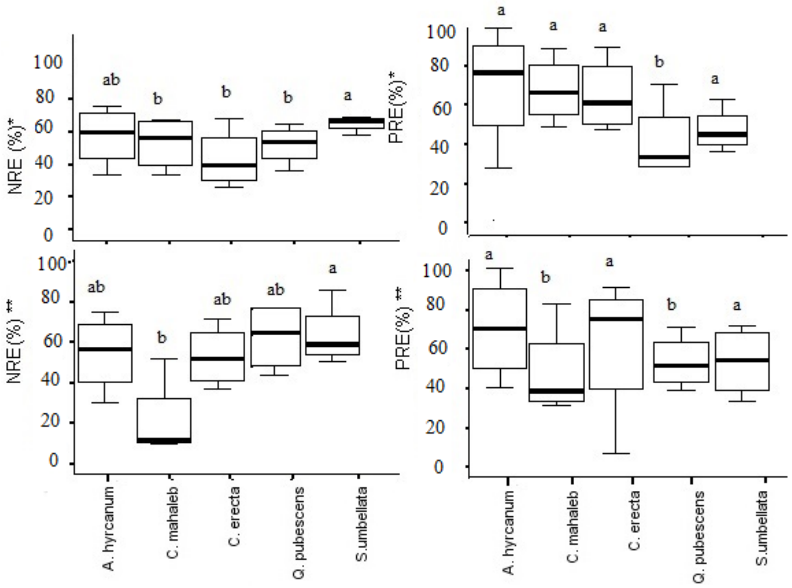

Figure 5.— Boxplots of mass (mg/g) and area-based (dm^2/mg) NRE and PRE of the studied species. Bars indicate standard deviation of means. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test (*=mg/g. **= mg/dm^2).

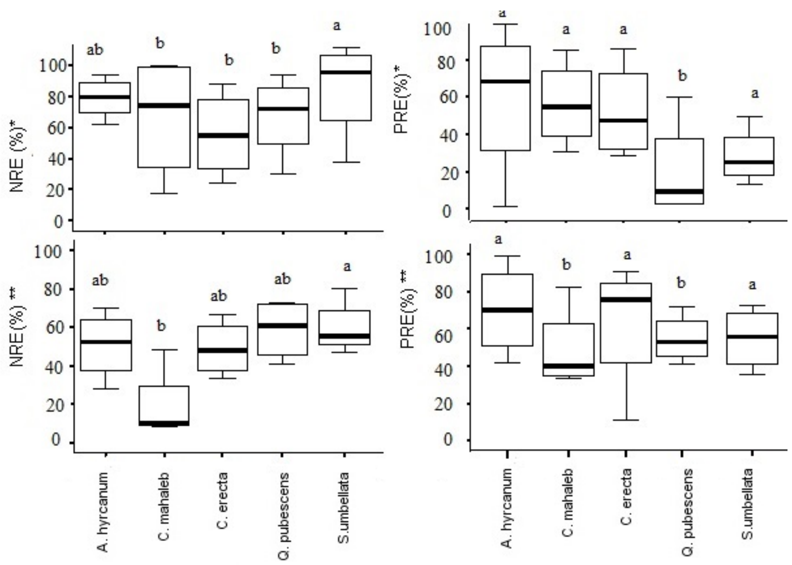

Figure 6.— Boxplots of RE values of the studied species with mass loss correction factor (MLCF). (*=mg/g. **= mg/dm^2).

The most N and P-proficient species was *C. mahaleb* because the lowest N and P concentrations were found in senesced leaves of *C. mahaleb*. However, the most N-proficient species was *S. umbellata* var. *umbellata* regarding mass-based NRP (Fig. 7).

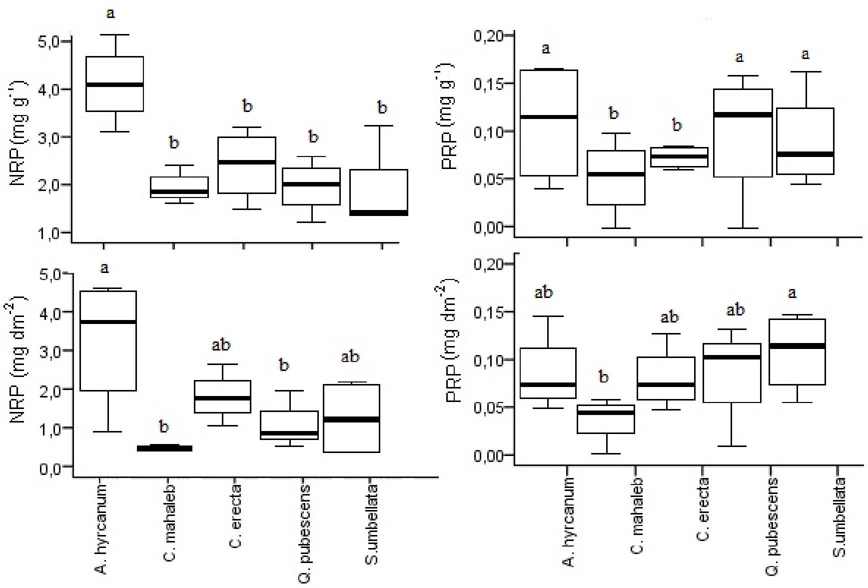

Figure 7.— Boxplots of mass (mg/g) and area-based (mg/dm^2) NRP and PRP of the studied species.
Bars indicate standard deviation of means. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

N/P ratio of senesced leaves were significantly changed, while N/P ratios of green-leaves were not (Fig. 8).

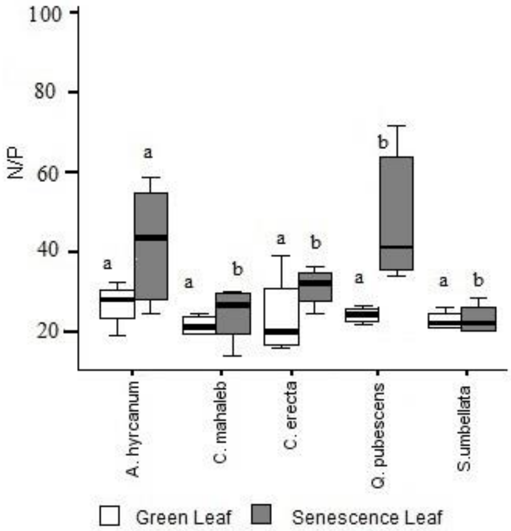

Figure 8.— Boxplots of N/P ratios of green and senesced leaves.
Bars indicate standard deviation of means. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

DISCUSSION

Aerts (1996) reported that the mean resorption efficiency in deciduous species is 54.0 %. It has been reported that NRE and PRE range 26-61 % and 56-71 %, respectively in deciduous species (Boerner, 1984; Côte *et al.,* 2002). Brant & Chen (2015) suggested NRE and PRE are 70.2 and 59.0, respectively in woody deciduous species. NRE and PRE in our studied species fall within the ranges reported by other studies.

Mass and area-based PRE was found to be higher than NRE in *A. hyrcanum* subsp. *sphaerocaryum*, *C. mahaleb* and *C.erecta*. Leaf P compounds is readily resorbed, while resorption of leaf N compounds is a bit slow and PRE is of great importance with respect to nutrient use efficiency (Aerts & Chapin, 2000; Covelo *et al*., 2008; Salazar *et al.,* 2011; Yilmaz *et al.,* 2014). Our study area is severely P-limited and it has been reported that species growing in P-limiting conditions would be more favoured by high resorption efficiency and that in P-poor soils phosphorus is more limiting than nitrogen (Covelo *et al.*, 2008; Kilic *et al.*, 2012; Miatto *et al.,* 2016). It has also been stated that limiting nutrients are usually more resorbed than non-limiting ones and species on infertile soils rely more on foliar resorption as compared to species on fertile soils (Yilmaz *et al.,* 2014; Brant & Chen 2015; Miatto *et al.*, 2016).

Fife *et al.* (2008) indicated that the nutrient concentration of a leaf is strongly influenced by its mass which varies among species. Significant differences were indeed found among our studied species with respect to mass-based N concentrations. There were also significant differences among our studied species with respect to mass-based green leaf N concentrations, while mass-based P concentrations of senesced leaves were not significantly changed.

Several researchers (Jurik, 1986; Popma & Bongers, 1988; Bigelow, 1993) found that SLA declined from the top to the bottom of the canopy. However, this trend was not found for our studied species. Kutbay (2001) also did not find such a trend with respect to SLA. It has also been suggested that subcanopy species have lower foliar resorption values than canopy species in the same area (De Mars & Boerner, 1997). However in the present study, some of the subcanopy species had higher NRE and PRE than canopy species. There were some evidences in favour of a novel mechanism whereby climber species have some competitive advantages for an economical use of nutrients (Cai & Bongers, 2007).

Wood *et al.* (2011) found that species with low SLA tended to resorb more P relative to N, while opposite trend was found for the species with high SLA. In other words, the species with high SLA tended to resorb more N relative to P. *C. erecta* had the lowest SLA. Mass and area-based PRE without MLCF correction were found to be higher than NRE in *C. erecta*. The highest SLA was found in *C. mahaleb*. However, only mass-based NRE was found to be higher than PRE in *C. mahaleb* when MLCF correction was used. It was also supported by high N/P ratio during senescence. It has been found that N/P ratio was increased during senescence. This suggests preferential resorption of P relative to N.

The overall elemental composition of plants in a particular ecosystem is simultaneously determined by sympatric species and by the physiological status of the dominant species (Ågren, 2008). Güsewell (2004) reported a broader range for N- (< 10) and P-limitation (> 20). N/P ratios above 16 indicate P deficiency, whilst N/P ratios below 14 indicate N deficiencies, and foliar N/P ratio below 12.5 indicate an optimal P nutrition (Aerts & Chapin, 2000; Finzi *et al.*, 2004; Haridasan, 2008). Koerselman & Meuleman (1996) suggested that threshold values for P-limitation was 16. N/P ratios of green leaves of our studied species ranged from 22.95 to 35.25 and this indicated that P limitation may occur at a local level (Rentería *et al.*, 2005). The highest N/P ratio was found in *A. hyrcanum* subsp. *sphaerocaryum* and this species had the highest PRE with and without MLCF. However, the highest PRP was found for *C. mahaleb*. Diehl *et al.,* (2008) and Du *et al.,* (2011) suggested that the critical values of N/P ratio and N- and P-limitation would vary extensively with plant species and leaf growth phases (green or senesced leaves). Highly proficient P resorption was responsible for the divergence in leaf N/P ratios on P-poor soils. These results emphasize the significance of proficient nutrient resorption as an advantageous plant trait for nutrient conservation on P-poor soils (Richardson *et al.,* 2008). *A. hyrcanum* subsp. *sphaerocaryum* had the highest both mass- and area-based PRE and *C. mahaleb* is the most P-proficient species and these two species have competitive advantages as compared to other species with respect to an effective use of P.

No significant relationships were found between green and senesced leaf N/P ratio and green and senesced leaf N and P concentrations and it may concluded that plant N and P status was not strictly controlled by green and senesced leaf N and P concentrations in studied species (Drenovsky *et al.,* 2013).

Foliar resorption is regarded as 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 (Killingbeck, 1996). All of our studied species show complete resorption in this respect. *C. mahaleb* was the most N- and P-proficient species because the lowest N and P concentrations were found in its senescent leaves. Higher proficiencies correspond to lower final nutrient concentrations in senesced leaves (Rentería *et al.,* 2005 ; Kilic *et al.,* 2010). The differences with respect to RP directly affect the residual nutrients contained in senesced leaves and inter-specific variability in RP could have important consequences for leaf decomposition rates and the return of a particular nutrient to the available soil nutrient pool (Wood *et al.,* 2011).

Our results in the studied mixed deciduous forest imply that PRE has a much more important role in the conservation of P as compared to that of NRE for the conservation of N (cf. See *et al.,* 2015). The highest N/P ratio was found in *A. hyrcanum* subsp. *sphaerocaryum,* and this may probably indicate that this species has the highest capacity to resorb N and P for the conservative use of nutrients (cf. Esteves & Suzuki, 2013). We also found some differences among co-occuring species with respect to mass- and area-based NRE and PRE with and without MLCF correction in a deciduous forest in northern Turkey. Although it has been stated that the variations in NRE are mainly due to plant functional types (Brent & Chen, 2015) interspecific differences were also found in deciduous species particularly regarding foliar traits (Kurokawa *et al.,* 2010). More research is still needed on nutrient use and resorption patterns in co-occuring plants in deciduous forests.

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