

SEASONAL AND ALTITUDINAL CHANGES IN LEAF NUTRIENT CONCENTRATIONS
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RÉSUMÉ.— *Changements saisonniers et altitudinaux des concentrations foliaires en nutriments de Hedera helix L. (Araliaceae).*— La résorption est l'une des plus importantes stratégies d'utilisation des nutriments développées par les plantes. Le ratio de la surface foliaire à la masse sèche (SLA) est lié aux nutriments foliaires. Dans la présente étude, les changements de concentration en SLA, N et P, le rapport N/P et la teneur en C des feuilles de lumière et d'ombre de la liane sempervirente *Hedera helix* L. ont été étudiés au long de l'année sur un gradient altitudinal. L'efficacité (RE) et l'efficacité (RP) de la résorption foliaire ont également été calculées dans les feuilles de lumière et celles d'ombre. Les traits foliaires ont montré des changements significatifs entre les localités et au cours de l'année. Des différences significatives sont apparues entre les feuilles de lumière et celles d'ombre pour ce qui concerne le SLA, la concentration en N et la teneur en C, mais se sont avérées dépendantes des différences d'altitude. Toutefois, aucune différence significative de concentration en P n'a été trouvée entre les feuilles de lumière et celles d'ombre. Dans les feuilles, tant de lumière que d'ombre, le SLA augmentait à la fin du printemps et baissait après l'automne. D'une manière générale, la teneur en C augmentait en janvier. La concentration en N des feuilles, tant de lumière que d'ombre, était habituellement la plus faible en début d'été et croissait en octobre. Les plus fortes teneurs en P ont été observées entre décembre et janvier dans toutes les localités. N/P différait significativement selon les localités. L'interaction localité x temps était aussi significative sauf pour les concentrations en P foliaire et N/P. Des corrélations positives ont été notées entre les traits foliaires et ceux du sol comme le SLA, les N, P et C foliaires, l'humidité du sol, et les teneurs en N, P et C. La PRE (efficacité de la résorption du phosphore) et la NRP (efficacité de la résorption de l'azote) différaient de manière significative entre les localités mais pas entre les feuilles de lumière ou d'ombre. Cependant, la NRE (efficacité de la résorption de l'azote) et la PRP (efficacité de la résorption du phosphore) n'étaient pas significativement différentes. Les feuilles de lumière et celles d'ombre ont montré une résorption incomplète car, dans toutes les localités, les valeurs de NRP et de PRP étaient supérieures aux niveaux de référence.

SUMMARY.— Nutrient resorption is one of the most important nutrient use strategies developed by plants. The ratio of leaf area to dry mass (SLA) is related to leaf nutrients. In this study, the changes in SLA, N, P concentrations, N/P ratio and C content of sun and shade leaves of the evergreen liana *Hedera helix* L. were investigated over the year in an altitudinal gradient. Foliar resorption efficiency (RE) and proficiency (RP) were also calculated in sun and shade leaves. Leaf traits significantly changed among studied localities and over the year. There were statistically significant differences between sun and shade leaves regarding SLA, N concentration and C content, but these were dependent on the differences of altitude. However, no significant differences were found for P concentrations between sun and shade leaves. SLA increased in sun and shade leaves at the end of the spring and decreased after the fall. Leaf C content generally increased in January. Leaf N concentration in sun and shade leaves was usually lowest in early summer and increased in October. The highest leaf P content was found between December and January in all localities. N/P significantly differed between localities. Locality × time interaction was also significant except leaf P concentrations and N/P. Positive correlations were seen between leaf and soil traits such as SLA, leaf N, P and C, soil moisture, N, P and C. PRE (Phosphorus resorption efficiency) and NRP (Nitrogen resorption proficiency) were significantly different among the localities, but not among sun and shade leaves. However, NRE (Nitrogen resorption efficiency) and PRP (Phosphorus resorption proficiency) were not significantly different. Sun and shade leaves of *H. helix* showed incomplete resorption, because, in all localities, NRP and PRP values were above the benchmark levels.

Nutrient resorption is one of the most important strategies developed by plants to save nutrients (Killingbeck, 1986). In particular, N and P are withdrawn from the leaves before abscission, and used for the formation of new tissues (Aerts, 1996).

Nutrient resorption efficiency is known as the percentage of a nutrient withdrawn from mature leaves before abscission (Aerts 1996; Aerts & Chapin 2000). Resorption proficiency is described by Killingbeck (1996) as the minimum level to which a nutrient is reduced during senescence, and has also been used to quantify nutrient resorption. Resorption proficiency seems to be more responsive than resorption efficiency to nutrient availability (Renteria *et al.*, 2005).

Soil fertility is often considered as one of the most significant factors in controlling leaf nutrient resorption (Chapin, 1980). Some studies have shown that resorption may increase depending on soil nutrient availability (Sabaté *et al.*, 1995), while others found a negative relationship between foliar resorption and soil nutrient content (Boerner, 1984; Rejmánková, 2005). Other parameters such as the amplitude of the abscission period (Del Arco *et al.*, 1991), leaf mass and nutrients (Ralhan & Singh, 1987), higher-level taxonomic/phylogenetic variation (Killingbeck, 1996; Watanabe *et al.*, 2007) may influence foliar nutrient interactions and resorption (Trémolières *et al.*, 1999). Hoch *et al.* (2001) reported that shading of senescing leaves substantially reduced resorption efficiency and a relationship exists between the amount of available photosynthetic energy and resorption activity (Niinemets, 1997).

Understanding nutrient resorption efficiency requires previous knowledge about natural levels of nutrient content in functional leaves. Internal and external factors affecting the nutrient content of leaves vary in time and space (Craine *et al.*, 2009). Leaf nutrient concentration may be different depending on altitude, leaf age, phenology and soil formation phases (Vitousek *et al.*, 1995; Oleksyn *et al.*, 2002; Wright *et al.*, 2002; Kutbay *et al.*, 2005). There are fundamental physiological and ecological differences for obtaining and using nutrients and light energy between sun and shade leaves in the plants (Givnish, 1988). Sun leaves generally contain higher amounts of proteins and lower amounts of soluble nitrogen when compared with shade leaves (Meleti-Christou *et al.*, 1994). Nitrogen resorption per leaf area unit is slightly lower in shade leaves than in sun leaves of *Liquidambar styraciflua* L. (Herrick & Thomas, 2003).

Ivy, *Hedera helix* L., has two different types of leaves. Some of the leaves grow on the ground surface, while the other leaves climb on the supporting structures (i.e. tree stems or walls and fences). Therefore, it can be considered that *H. helix* has got both sun and shade leaves (Roderick & Cochrane, 2002). *H. helix*, the most abundant liana in temperate forests of Europe and Asia minor, is an evergreen and also a good colonizer. Evergreen species mitigate nutrient circulation in forests because they immobilize nutrients in leaves for longer periods of time than do deciduous species (Thomas & Grigal, 1976). Since evergreenness prolongs the use of nutrients in leaf biomass, it has been interpreted as an adaptation contributing to improved nutrient use efficiency (Escudero & Mediavilla, 2003). N resorption tends to be higher in deciduous species than in evergreen ones, and higher in trees than in shrubs, while P resorption is generally higher in evergreen than deciduous species (Yuan & Chen 2009). In temperate regions, where plants are exposed to dynamic seasonal changes in climate, plants exhibit significant seasonal changes in their activity (Ueda *et al.*, 2011). Seasonal variations are particularly effective on evergreen species, because leaf nutrients may vary in response to the different growth phases, the life cycle, the age of leaf and development, and a continuously changing environment throughout the year (Núñez *et al.*, 1996).

There is little information about the nutrient resorption efficiency and proficiency of sun and shade leaves of *H. helix* (Özbucak *et al.*, 2008). Besides, there are very few studies which examine the nutrient resorption efficiency and proficiency according to the elevation gradient in temperate regions. For these reasons, the objectives of this study are (1) to determine the seasonal change of foliar N, P, C concentrations, SLA and leaf N/P in sun and shade leaves of *H. helix*, (2) to assess the differences between nutrient resorption efficiency and proficiency of sun and shade leaves, and (3) to examine whether or not there are relationships between soil moisture, soil and leaf N, P, C concentrations, leaf N/P ratio concentrations, SLA and N, P resorption proficiency (NPR, PRP) and efficiency (NRE, PRE) in sun and shade leaves in an elevation gradient in a temperate region.

MATERIALS AND METHODS

SITE DESCRIPTION

Three localities along an elevation gradient were selected in Samsun province in the north of Turkey. The first locality (41° 15' 01.15" N, 36° 31' 28.47" E) is 10 m, the second (41° 14' 33.59" N, 36° 23' 25.68" E) is 200 m, and the third (41° 14' 04.97" N, 36° 23' 10.74" E) is 400 m above sea level.

The first locality is a *Fraxinus angustifolia* subsp. *oxycarpa* M.Bieb. ex Wiold. swamp forest. The second and third localities were characterized by *Quercus cerris* L. var. *cerris* forests. In all three localities, *H. helix* L. shows a wide distribution in the forest surface, on the trees and shrubs.

Annual rainfall of the first locality is 895.10 mm and annual mean temperature is 13.73°C (Anonymous, 2010). Annual rainfall of the second locality is 904.10 mm and annual average temperature is 13.60°C. Annual rainfall in the third locality is 913.10 mm and average temperature is 12.60°C. Temperature and precipitation values of the second and third locality were calculated by interpolation from data of Samsun State Meteorological Station (Erinç, 1965; Doğan, 1977; Kılınç *et al.*, 2006).

LEAF AND SOIL SAMPLING

Leaf samples were collected from mid April 2010 to mid April 2011 for morphological and chemical analyses. At each locality, five individuals were selected at least 2.5 m from the stems of neighbouring canopy trees to avoid potential microsite variation (Boerner & Koslowsky, 1989). Monthly, three pairs of sun and shade leaves per individual were harvested, choosing leaves as similar in size, shape and location as possible. Undamaged mature and senesced leaves were sampled. Chemical analyses, SLA and resorption calculations were made separately for each individual.

After harvesting, petioles were removed, leaves were scanned by using a BenQ 7650T scanner and the leaf area was determined by a software developed by University of Sheffield (Kılınç *et al.*, 2010). After that, leaves were dried in an oven at 70°C to a constant weight; and dry weight was measured. Later, they were grinded and stored in polyethylene bags until chemical analysis.

On each sampling date, plant and soil samples were obtained simultaneously. Since nutrients are concentrated mainly on the topsoil (Trémolières *et al.*, 1999), we sampled only the upper 20 cm of the A1 horizon. Throughout the study, a total of 180 soil samples (five samples per month) were taken at each locality, as close to the *H. helix* individuals as possible. The soil samples were air dried for 48-72 h and sieved through a 2 mm sieve before the chemical analyses (Allen *et al.*, 1986; Kacar & Inal, 2008).

CHEMICAL ANALYSES

In the leaf and soil samples, N and C analyses were done with Thermo Scientific FLASH 2000 Series - CHNS/O Analyzers instrument following Dumas (1831) method (Allen *et al.*, 1986). P determination was carried out by the vanadomolibdophosphoric yellow color method in leaf samples (Kacar & Inal, 2008).

Moisture content (%), total N (%), C (%) and extractable P (%) concentrations of soil samples were also determined. For the determination of soil moisture, fresh weight of soil samples belonging to the upper 20 cm of the A1 horizon were collected, and a subsample was dried for 48 h at 105°C to calculate wet to dry mass ratios. These values were used to calculate soil moisture (gravimetric method). In order to determine soil extractable P, the following protocol was followed. Firstly, soil pH was measured for a soil / pure water (1:1) mixture using a pH meter. After that, soil extractable P was assessed according to Olsen *et al.* (1954) for basic soils (soils in the second and third localities), while soil extractable P was determined according to Bray & Kurtz (1945) for acidic soils (the first locality).

DATA PROCESSING

Specific leaf area (SLA) was calculated ($\text{dm}^2 \text{g}^{-1}$) by using the equation:

$$\text{SLA} (\text{dm}^2 \text{g}^{-1}) = \text{Leaf area} / \text{Dry leaf weight} \quad (1)$$

Leaf nitrogen, phosphorus and carbon contents on an area basis (N_{area} , P_{area} and C_{area}) were calculated as mean leaf N, P, C_{weight} / mean SLA (Cornelissen *et al.* 1997).

Area-based nutrient resorption efficiency was calculated as:

$$\text{Nur}_{\text{eff}} (\%) = (\text{Nu}_{\text{max}} - \text{Nu}_{\text{sen}}) / \text{Nu}_{\text{max}} \times 100 \quad (2)$$

where Nu_{max} is the maximum leaf nutrient content (on a per area basis, $\text{g} \cdot \text{dm}^{-2}$), and Nu_{sen} ($\text{g} \cdot \text{dm}^{-2}$) is the nutrient content of fully senesced leaves. The maximum leaf nutrient content (Nu_{max}) and the nutrient content of fully senesced leaves (Nu_{sen}) were considered in December and May for nitrogen and phosphorus in all localities, respectively. Henceforth, NRE and PRE will be referred to as nitrogen and phosphorus resorption efficiency, respectively.

N and P resorption proficiency were calculated as the lowest nutrient concentrations in the senesced leaves. Hereinafter, NRP and PRP will be referred to as nitrogen and phosphorus resorption proficiency, respectively. In other words, terminal N and P contents ($\mu\text{g} \cdot \text{cm}^{-2}$ of leaf surface) in senesced leaves were used directly as an indicator of the NRP and PRP. The nutrient content ($\mu\text{g} \cdot \text{cm}^{-2}$) was calculated as the amount per unit area in senesced leaves as the NRP and PRP (Killingbeck, 1996).

TABLE I

The comparison of SLA ($dm^2.g^{-1}$), N ($g.dm^{-2}$), C ($g.dm^{-2}$), P ($g.dm^{-2}$) and N/P values using three-way ANOVA between the shade and sun leaves, the localities and time. ($n = 5$ individuals)

Dependent Variable	Source	Sum of Squares	df	Mean Square	F	Sig.
SLA	Locality	4.26	2	2.13	64.35	<0.01*
	Time (Month)	8.09	11	0.73	22.19	<0.01*
	Leaf type (Sun and Shade)	2.86	1	2.86	86.26	<0.01*
	Locality*Time	1.73	22	0.07	2.38	<0.01*
	Locality*Leaf type	1.17	2	0.58	17.65	<0.01*
	Time*Leaf type	0.24	11	0.02	0.67	0.76
	Locality*Time*Leaf type	0.27	22	0.01	0.37	0.99
	Error	9.48	286	0.03		
Total	971.48	358				
C	Locality	0.20	2	0.10	78.91	<0.01*
	Time (Month)	0.46	11	0.04	31.85	<0.01*
	Leaf type (Sun and Shade)	0.11	1	0.11	87.51	<0.01*
	Locality*Time	0.09	22	0.00	3.19	<0.01*
	Locality*Leaf type	0.05	2	0.02	19.08	<0.01*
	Time*Leaf type	0.01	11	0.00	0.86	0.57
	Locality*Time*Leaf type	0.01	22	0.00	0.66	0.87
	Error	0.37	286	0.00		
Total	32.96	358				
N	Locality	0.00	2	0.00	160.90	<0.01*
	Time (Month)	0.00	11	8.372E-005	33.85	<0.01*
	Leaf type (Sun and Shade)	4.316E-005	1	4.316E-005	17.45	<0.01*
	Locality*Time	0.00	22	5.791E-006	2.34	<0.01*
	Locality*Leaf type	3.495E-005	2	1.747E-005	7.06	<0.01*
	Time*Leaf type	3.342E-005	11	3.038E-006	1.22	0.26
	Locality*Time*Leaf type	4.237E-005	22	1.926E-006	0.77	0.75
	Error	0.00	286	2.473E-006		
Total	0.04	358				
P	Locality	1.034E-005	2	5.168E	16.65	<0.01*
	Time (Month)	1.171E-005	11	1.065E	3.43	<0.01*
	Leaf type (Sun and Shade)	5.368E-007	1	5.368E	1.73	0.18
	Locality*Time	4.616E-006	22	2.098E	0.67	0.86
	Locality*Leaf type	4.087E-006	2	2.043E	6.58	<0.01*
	Time*Leaf type	1.408E-006	11	1.280E	0.41	0.95
	Locality*Time*Leaf type	1.885E-006	22	8.569E	0.27	1.00
	Error	8.875E-005	286	3.103E		
Total	0.00	358				
N/P	Locality	2455.38	2	1227.69	4.18	0.01**
	Time (Month)	4192.08	11	381.09	1.29	0.22
	Leaf type (Sun and Shade)	463.59	1	463.59	1.57	0.21
	Locality*Time	4802.72	22	218.30	0.74	0.79
	Locality*Leaf type	395.48	2	197.74	0.67	0.51
	Time*Leaf type	2706.05	11	231.02	0.78	0.65
	Locality*Time*Leaf type	83971.75	22	123.00	0.41	0.99
	Error	2455.38	286	293.60		
Total	182299.66	358				

* $P < 0.01$, ** $P < 0.05$

Statistical analysis was performed using a SPSS (21.0 version) software (Anonymous, 2012). Data were analysed for normality by using Kolmogorov-Smirnov test, and square root transformation of the data was used for normal distribution before performing the ANOVA tests.

In the leaf samples, SLA ($\text{dm}^2 \text{g}^{-1}$), N (g dm^{-2}), C (g dm^{-2}), P (g dm^{-2}) and N/P values were subjected to three-way ANOVA. Meanwhile, we assigned those SLA, N, C, P and N/P as dependent variables; locality, time and type of leaf were assigned as fixed factors.

NRE, PRE, NRP and PRP values of sun and shade leaves and studied localities were also compared by two-way ANOVA. In this case, NRE, PRE, NRP and PRP were dependent variables; locality and type of leaf were assigned as fixed factors.

One-way ANOVA was also performed to show the difference among localities in terms of soil moisture and nutrient availability. Soil traits and localities were assigned as the dependent and independent variables, respectively.

Tukey's significant difference (HSD) test was used to rank means following the analysis of variance. Probable relationships between leaf and soil variables, and leaf traits and nutrient resorption efficiency and proficiency were assessed by using Pearson correlation.

RESULTS

DIFFERENCES IN LEAF TRAITS ACROSS ELEVATIONS, MONTHS AND LEAF TYPES

All leaf traits significantly differed between the studied localities and between months excepting N/P where there was significant differences between localities only (Tab. I). Sun and shade leaves were significantly different with respect to SLA, N and C content (Tab. I). Locality \times time interaction was significant except for leaf P concentrations and N/P. Locality \times leaf type interaction was significant for all leaf traits except N/P. There was no significant time \times leaf type and locality \times time \times leaf type interactions (Tab. I).

We generally found higher SLA values in shade than in sun leaves. SLA was significantly lower in the third locality for sun and shade leaves. SLA ($\text{dm}^2 \text{g}^{-1}$) in sun and shade leaves peaked in June in the first and third localities and was lowest in April. No significant temporal differences in SLA were found in the second locality (Fig 1).

The highest leaf C content (g dm^{-2}) was generally found between March and April except for sun leaves in the second locality. After that time, leaf C content gradually decreased at the end of the summer, then remained relatively constant during the fall and generally increased again in January. Mean C content was generally higher in sun leaves than in shade leaves (Fig 2).

Leaf N concentration (g dm^{-2}) in sun and shade leaves significantly changed over the year and it was usually lowest in late spring (May) or early summer (June) and increased in October. We have found slightly higher N concentrations in sun leaves than in shade leaves in the same locality (Fig 3).

Leaf P concentration (g dm^{-2}) significantly changed for shade leaves in the third locality over the year. The highest leaf P content was found between December and January, and after January it decreased toward June for sun shade leaves in all localities. Mean P contents were slightly higher in shade and sun leaves in the third locality, compared to the first and second locality (Fig 4). There was generally the same pattern of leaf C, N and P content in relation to localities and leaf types. This interaction was due to differences among localities in the existence of significant differences between leaf types for C, N and P content.

Leaf N/P significantly differed only between localities (Table I). Mean N/P decreased from 18.69 ± 1.78 through 14.19 ± 1.33 to 12.25 ± 1.41 from the first to third locality.

SOIL VARIABLES AND THEIR RELATIONSHIP WITH LEAF TRAITS

All soil traits determined were statistically different between the three localities: soil moisture was highest and significantly decreased with elevation in the first, soil C content was lowest in the second, soil N and P concentrations were highest in the third (Tab. II).

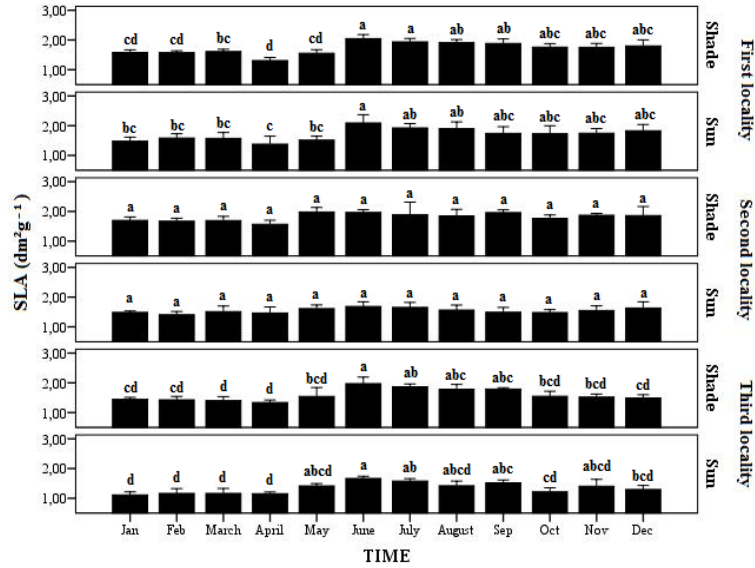


Figure 1.— Seasonal variation of specific leaf area (SLA) between type of leaves and localities. Data are mean and ± 1 SE. The difference in letters above bars indicates the significant difference ($P < 0.05$) between means according to Tukey's (HSD) test among months for each locality.

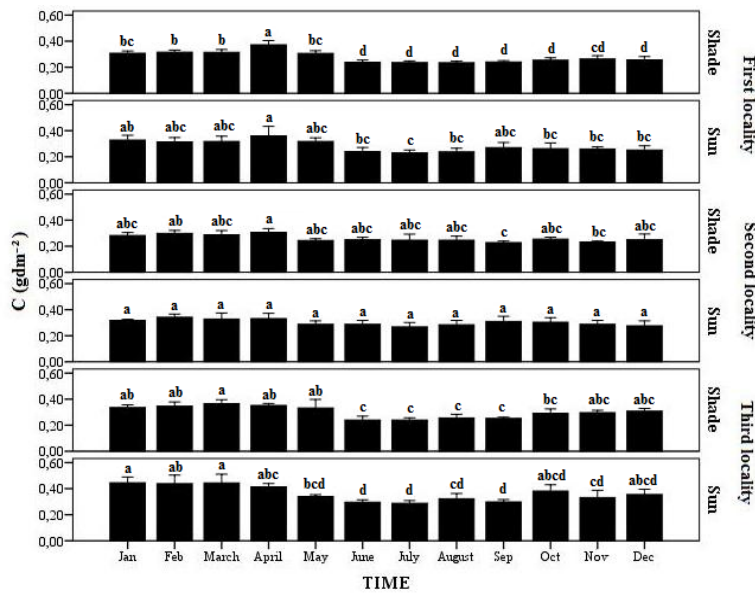


Figure 2.— Seasonal variation of leaf carbon concentration between type of leaves and localities. Data are mean and ± 1 SE. The difference in letters above bars indicates the significant difference ($P < 0.05$) between means according to Tukey's (HSD) test among months for each locality.

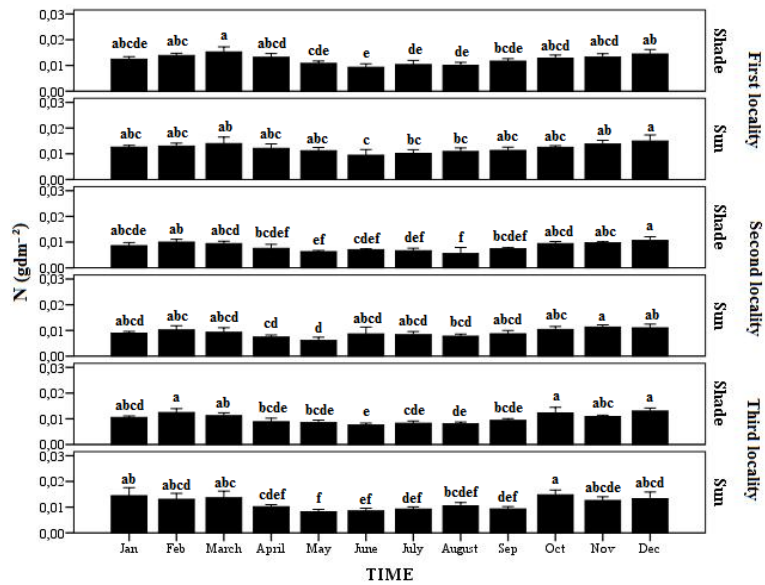


Figure 3.— Seasonal variation of leaf nitrogen concentration between type of leaves and localities. Data are mean and ± 1 SE. The difference in letters above bars indicates the significant difference ($P < 0.05$) between means according to Tukey's (HSD) test among months for each locality.

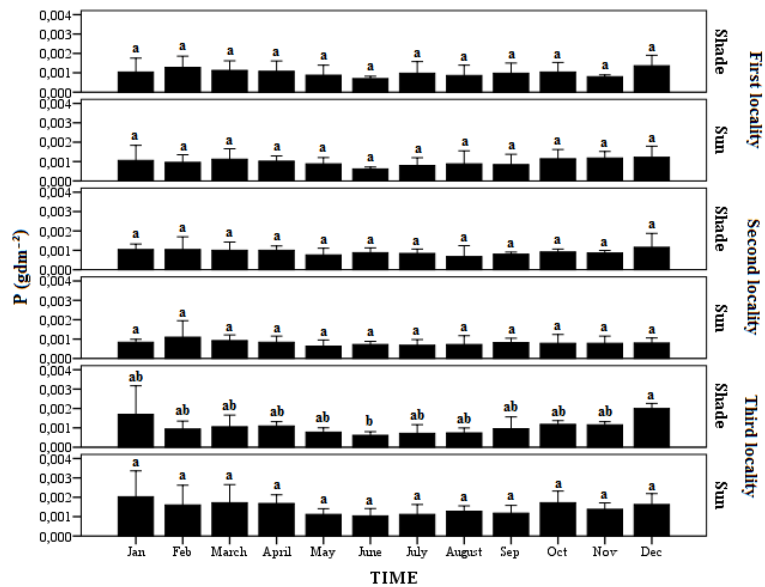


Figure 4.— Seasonal variation of leaf phosphorus concentration between type of leaves and localities. Data are mean and ± 1 SE. The difference in letters above bars indicates the significant difference ($P < 0.05$) between means according to Tukey's (HSD) test among months for each locality.

TABLE II

The mean values of the soil traits in the localities and their comparison with ANOVA test. BG: Between Groups; WG: Within Groups; E: Error

Traits	Localities	N	Mean	Std. Dev.	Sum of Squares	df	Mean Square	F	Sig.
Moisture (%)	First	60	28.25 a	16.45	2122.11 (BG)	2 (BG)	1061.05 (BG)	7.85	<0.01*
	Second	60	23.90 b	7.90	23911.61 (WG)	177 (WG)	135.09 (WG)		
	Third	60	19.84 c	8.48	26033.73 (E)	179			
N (%)	First	60	0.26 b	0.15	5.13 (BG)	2 (BG)	2.56 (BG)	3.68	0.02**
	Second	60	0.19 c	0.51	123.54 (WG)	177 (WG)	0.69 (WG)		
	Third	60	0.58 a	1.34	128.68 (E)	179			
C (%)	First	60	3.85 a	1.96	115.83 (BG)	2 (BG)	57.91 (BG)	11.32	<0.01*
	Second	60	2.10 b	1.82	905.25 (WG)	177 (WG)	5.11 (WG)		
	Third	60	3.76 a	2.85	1021.08 (E)	179			
P (%)	First	60	0.08 b	0.12	15.65 (BG)	2 (BG)	7.82 (BG)	100.84	<0.01*
	Second	60	0.13 b	0.15	13.74 (WG)	177 (WG)	0.07 (WG)		
	Third	60	0.73 a	0.44	29.40 (E)	179			

* $P < 0.01$, ** $P < 0.05$; the difference in letters indicates significant difference ($P < 0.05$) between means according to Tukey's (HSD) test among localities.

TABLE III

The comparison of nitrogen and phosphorus resorption efficiency (%) and proficiency ($\mu\text{g cm}^{-2}$) using Two-Way ANOVA between leaf type and localities ($n = 5$ individuals)

Dependent Variable	Source	Sum of Squares	df	Mean Square	F	Sig.
NRE	Locality	765.80	2	382.90	1.89	0.17
	Leaf type (Sun and Shade)	104.53	1	104.53	0.51	0.47
	Locality*Leaf type	764.06	2	382.03	1.89	0.17
	Error	4846.40	24	201.93		
	Total	80882.00	30			
PRE	Locality	1907.26	2	953.63	11.73	<0.01*
	Leaf type (Sun and Shade)	0.03	1	0.03	0.00	0.98
	Locality*Leaf type	120.86	2	60.43	0.74	0.48
	Error	1950.80	24	81.28		
	Total	114271.00	30			
NRP	Locality	5083.02	2	2541.51	13.54	<0.01*
	Leaf type (Sun and Shade)	11.00	1	11.00	0.05	0.81
	Locality*Leaf type	64.78	2	32.39	0.17	0.84
	Error	4501.75	24	187.57		
	Total	192238.28	30			
PRP	Locality	0.68	2	0.34	0.13	0.87
	Leaf type (Sun and Shade)	0.39	1	0.39	0.15	0.69
	Locality*Leaf type	12.16	2	6.08	2.48	0.10
	Error	58.81	24	2.45		
	Total	1465.23	30			

* $P < 0.01$

For shade leaves, significant relationships between soil and leaf traits were found ($P < 0.05$) only for the second site. SLA was positively related to soil moisture (0.97) and negatively related to soil P (-0.99). Leaf C content was positively related to soil C (0.94) and P (0.98), and negatively related to soil N content (-0.95). For sun leaves ($P < 0.05$), a positive correlation was found between leaf N/P and soil P in the second locality (0.89), a negative relationship between soil P and leaf C (-0.96) and a positive relationship between soil P and SLA in the third locality (0.96).

DIFFERENCES IN LEAF NUTRIENT RESORPTION EFFICIENCY AND PROFICIENCY ACROSS ELEVATIONS AND LEAF TYPES

There were significant differences among the studied localities in PRE and NRP (Tab. III). PRE was highest in the third locality (Tab. IV), NRP was highest in the first locality and lowest in the second locality (Tab. IV).

TABLE IV

The mean resorption efficiency (%) and proficiency ($\mu\text{g cm}^{-2}$) of N and P for sun and shade leaves among localities. A difference in letters indicates significant difference ($P < 0.05$) between means according to Tukey's (HSD) test.

	Locality	Leaf type	Mean	Std. Deviation	N
PRE	First	Sun	55.60 b	7.46	5
		Shade	55.20 b	14.13	5
	Second	Sun	52.00 b	4.79	5
		Shade	57.20 b	3.03	5
	Third	Sun	74.20 a	12.69	5
		Shade	69.60 a	6.22	5
NRP	First	Sun	93.19 a	14.40	5
		Shade	94.64 a	24.73	5
	Second	Sun	63.28 c	5.01	5
		Shade	60.78 c	14.36	5
	Third	Sun	75.73 b	8.33	5
		Shade	80.42 b	2.32	5

RESORPTION EFFICIENCY AND PROFICIENCY OF N AND P, AND THEIR RELATIONSHIP WITH LEAF TRAITS AND SOIL VARIABLES

For shade leaves ($P < 0.05$), PRP was positively correlated with leaf P content (0.90), while negatively correlated with leaf N/P ratios (-0.89) in the second locality. Negative correlations were seen between PRE and soil moisture (-0.93), N (-0.94), C (-0.95) content in the first locality, while PRE negatively correlated to soil N content (-0.91) only in the third locality.

For the sun leaves, PRP ($P < 0.05$) and NRP ($P < 0.01$) negatively correlated with leaf N content in first (-0.91) and third (-0.98) locality, respectively. A positive correlation ($P < 0.05$) was only seen between PRE and soil C content (0.90) in the first locality. In the first locality, PRE showed a positive correlation with soil C content (0.90).

DISCUSSION

DIFFERENCES IN LEAF TRAITS ACROSS ELEVATIONS, MONTHS AND LEAF TYPES

In this study, there were significant differences in locality, time and locality \times leaf type interactions for all leaf traits except N/P. The sun and shade leaves in *H. helix* have different physiological and ecological features in obtaining nutrients and light energy and using them (Givnish, 1988; Evans & Poorter, 2001). Besides, there were significant differences with regard to soil nutrients and moisture, altitude and forest type, among the three localities.

Specific leaf area (SLA) has a major role on growing and development of the plant and is also important in capturing the light (Valladares *et al.*, 2011). In this study, we found that SLA values of *H. helix* individuals differed over the year and the highest SLA values were found during summer when the canopy was rather closed. Shipley & Almeida-Cortez (2003) stated that low light levels cause a remarkable rise in SLA. In the deciduous forests, the evergreen plants which

cover the forest ground are exposed to high light levels during the fall. However, photosynthetic capacities of evergreen plants decrease gradually during the winter due to low temperatures (Oberhuber & Bauer, 1991). During the spring photosynthetic activity increases again owing to the increase in light levels and temperatures (Fischer & Feller, 1994). In the present study, leaf dry weight increased and SLA decreased during the spring.

When compared to sun leaves, higher SLA values of shade leaves were found in the second and third localities. This can be due to tolerance to deep shade in shade leaves (Sack & Grubb, 2002). The leaf traits that have the greatest plastic response could be more important for leaf functioning in different light environments (Rozendaal *et al.*, 2006). Markesteijn *et al.* (2007) observed that the correlation between SLA and leaf traits occur at different light levels, this might have led to a different detected plasticity among habitat types. The differences in SLA may have originated through habitat differences among the studied localities (Koike, 1988). The first locality (swamp forest) particularly is wetter than the other localities which are semiarid. We found that SLA gradually decreased along the elevational gradient and this is a morphological and physiological adaptation of *H. helix* individuals in the second and third localities (Körner *et al.*, 1989). Soil water content and nutrients are two important elements affecting plant development and morphology (Lower & Orians, 2003). Statistically positive correlation was found between soil moisture and SLA in this study.

The highest leaf C value was usually observed during spring in this study, as usual in evergreen plants for non-structural carbohydrate concentration (Zotz *et al.*, 2006; Muller *et al.*, 2011). In this study, the lowest leaf content was found during the summer because of higher canopy closure.

The highest C content was also found in sun and shade leaves of *H. helix* individuals in the third locality where canopy closure was lower than the other localities. The sun leaves *H. helix* had higher C content than shade leaves because they receive higher amount of light (Frank *et al.*, 2001; Taguchi & Wada, 2001; Schnitzler & Heuze, 2006). The evergreen or semievergreen leaf lifespan provides the possibility for significant C gain during parts of the winter in which temperatures are suitable for gas exchange and enzyme activity (Minoletti & Boerner, 1993). We also found significant correlations among soil N content and leaf C concentrations, soil C content and leaf C concentrations and, soil P content and leaf C contents, SLA and N/P ratios. Similar results were also reported by Özbucak *et al.* (2008). The feedback among soil and plant nutrient contents may change plant growing phases and productivity of ecosystem (Bassirrad, 2000).

Nitrogen is defined as a structural element, and plays an important role in all enzymatic activities (Aerts & Chapin, 2000). The nitrogen content of sclerophyll leaves of evergreen plants in temperate zones is subjected to seasonal fluctuations (Núñez *et al.*, 1996). During the winter, higher amount of light due to lower canopy closure, together with milder air temperature, stimulate the synthesis of nitrogen compounds in leaves (Hikosaka, 2005). For that reason, the highest leaf N concentrations were found in all localities during winter. Parker (1962) also found the same pattern and suggested that this increase depending on time was closely related to a sharp increase in total sugar as well as in anthocyanins. More than half of the leaf nitrogen is being invested into photosynthetic elements (Hikosaka, 2004). RUBISCO content mediates leaf N budgets during shade-sun acclimation (Seemann *et al.*, 1987). On the contrary, during the summer the forest ground receives minimum light due to high canopy closure (Muller *et al.*, 2011) and, thus, the lowest leaf N concentrations were found during the summer.

We found generally higher N concentrations in sun than shade leaves in the same locality. Leaf nitrogen shows a positive correlation to photosynthetic activity (Schnitzler & Heuze, 2006; Gratani *et al.*, 2006). Sun leaves of *H. helix* individuals had high N concentrations as compared to shade leaves because the leaves on a plant receive maximum amount of light, and as a result of this they have high photosynthetic capacity. Higher N concentrations in sun leaves of *H. helix* individuals as altitude increases agree with previous findings (Taguchi & Wada, 2001), as a result

of the increase in leaf dry weight (Körner, 1989). But, increasing leaf dry weight decreased SLA in sun leaves in this study. However, some studies showed that high foliar N concentrations were found in more fertile sites and lower foliar N in nutrient poor sites (Killingbeck & Costigan, 1988; Luken, 1988; Côte *et al.*, 2002); our results did not support this hypothesis, because, the percentage of soil nitrogen was highest in the highest locality. Furthermore, factors such as vegetation structure, topography and disturbance level also influence leaf nutrient concentrations (Oleksyn *et al.*, 2002). In temperate forests, the availability of P typically declines in old highly weathered soils, thus P may limit biological processes and regulate N cycling (Vergutz *et al.*, 2012).

In this study we found that P concentrations of shade leaves showed seasonal variability in the third locality. Leaves of *H. helix* senesced in May and P concentration rapidly decreased (Özbucak *et al.*, 2008; Aerts & Chapin, 2000). The lowest P concentrations in both sun and shade leaves were found during the summer because canopy closure was rather high and photosynthetic activity was rather low. Evergreen species tend to have lower P nutrient concentrations in both senesced and green leaves (Ares & Gleason, 2007). However, the highest leaf P concentrations were found during the winter. Milla *et al.* (2004) stated that evergreen leaves have more capacity of using nutrients than deciduous ones.

The highest leaf P concentrations were found in the third locality. P content per unit leaf area has increased along the elevational gradient (Körner, 1989). There was only N-limitation in the third locality. High foliar P concentrations reflected soil P availability (Del Arco *et al.*, 1991), but sometimes no correlations were obtained (Minoletti & Boerner, 1994).

Koerselman & Meuleman (1996) proposed the use of the N/P mass ratio in plant tissues as an indicator of the type of nutrient limitation. They suggested that at N/P ratios > 16, there was P-limitation; at N/P ratios < 14, plant growth was N-limited, and at N/P ratios between 14 and 16, co-limitation by N and P occurred. In this study, P-limitation was found in the first locality, whereas N-limitation was found in the third locality. N and P co-limitation is found in the second locality. All traits determined in the soil were statistically different, which can affect the levels of nutrient dynamics and resorption in the leaves at the three localities.

DIFFERENCES IN LEAF NUTRIENT RESORPTION EFFICIENCY AND PROFICIENCY ACROSS ELEVATIONS AND LEAF TYPES

NRE and PRE values were almost consistent with the literature survey by Aerts (1996). However, for sun and shade leaves of *H. helix*, NRE was lower and PRE was higher than in Özbucak *et al.* (2008) that reported 62 % (N) and 39 % (P) for leaves of *H. helix* in a temperate deciduous gallery forest in the north of Turkey, respectively. In this study, PRE values were found to be higher than in previous studies (Mayor & Roda, 1992; Aerts, 1996; Hevia *et al.*, 1999; Cai & Bongers, 2007). Furthermore, PRE values were also higher than NRE values. It has been reported that PRE contributes more to nutrient use efficiency than NRE (Aerts & Chapin, 2000), because phosphorus compounds are more readily resorbed than nitrogen compounds (Covelo *et al.*, 2008; Salazar *et al.*, 2011; Yilmaz *et al.*, 2014). Phosphorus is a critical element in the production of ribosomes (Ågren, 2008). Although there were significant differences in the leaf N content and soil traits between localities and leaf type, we found neither significant differences between localities, leaf type (sun and shade) and their interaction for NRE, nor significant correlation with soil traits. Our NRE results do not support previous hypotheses about the effects of soil traits on the resorption efficiency and proficiency (Chapin, 1980; Boerner, 1984; Sabaté *et al.*, 1995).

Several authors suggested that high PRE usually indicates less soil P availability (Martinez-Sánchez, 2005; Yilmaz *et al.*, 2014). The interaction between low soil P availability and PRE may be controversial according to our results for sun leaves in the third locality. However, PRE shows negative significant correlation with some soil traits such as moisture, N and P for shade leaves in the first and third localities. P-limitation was found at the first locality and N and P co-limitation

was found at the second locality; our results for shade leaves mostly supported the hypothesis that P resorption efficiency was greater with lower soil P availability in temperate forest ecosystems (Killingbeck & Costigan, 1988; Minoletti & Boerner, 1994; Renteria *et al.*, 2005). PRE was positively correlated with soil C content for sun leaves in the first locality. High organic matter accumulation, and consequently organic nutrient accumulation, may be important in controlling total soil nutrient concentrations in swamps (Verhoeven, 1986). Our finding is supported by the fact that nutrient efficiency in swamps was partially controlled by organic matter content in the soil and soil nutrient availability (Bedford *et al.*, 1999) and high nutrient-use efficiency was observed in highly organic seasonally flooded forest (Gann *et al.*, 2005). It has been stated that soil water content is inversely proportional to resorption efficiency (Özbucak *et al.*, 2008). PRE values of *H. helix* individuals were lower in the first locality that had high soil water content (%); but, there were negative correlations between PRE and soil moisture, as compared to the other localities.

Resorption leaf N and P proficiency in *H. helix* was high in this study. NRP was higher than PRP for sun and shade leaves. These results supported the generalization that evergreens are more proficient at reducing P than N in their senescing leaves (Killingbeck, 1996; Lal *et al.*, 2001; Richardson *et al.*, 2005).

It has been stated that resorption is complete if N and P concentrations of senesced leaves are below 50 $\mu\text{g cm}^{-2}$ and 3.0 $\mu\text{g cm}^{-2}$, respectively (Killingbeck, 1996). According to these benchmark levels, sun and shade leaves of *H. helix* individuals showed incomplete resorption because NRP and PRP values were calculated above the benchmark levels in all localities. Incomplete resorption was also documented by Özbucak *et al.* (2008) in a temperate deciduous gallery forest in the north of Turkey. These values were higher than those obtained by Killingbeck (1996) in *Cyrilla racemiflora* L. and *Lyonia lucida* (Lam.) K. Koch in temperate ecosystems. Boerner (1986) hypothesized that the inverse relationship between nutrient uptake efficiency (via mycorrhizae) and nutrient use efficiency (resorption) exhibited by the forest understory plants, may be related to low-light limitation of energy reserves in the forest understory. *H. helix* has got vesicular-arbuscular mycorrhizal relationships (Maremmani *et al.*, 2003; Songachan *et al.*, 2011) which may be one of the reasons for incomplete resorption in sun and shade leaves. However, Takashima *et al.* (2004) found that evergreen species allocated two-fold more nitrogen to SDS-insoluble proteins (SDS; sodium dodecyl sulfate) than deciduous species. SDS-insoluble proteins are tightly bound to cell walls (Reiter, 1998) and are thus a recalcitrant N fraction that cannot be largely broken down and resorbed from senescing leaves (Yasumura *et al.*, 2005). So, in this study, we may not have seen the completed N-resorption proficiency in the sun and shade leaves of *H. helix*.

NRP significantly differed between localities, but PRP did not. NRP and PRP did not have significant difference between sun and shade leaves, and with regard to locality \times leaf type interactions. Sardans & Peñuelas (2013) suggested that the strategy of allocation in response to different availability of resources can be different from the strategy in response to different ecological roles. Because there were significant differences on account of soil traits, forest type and elevation between localities, different nutrient resorption patterns may have happened in this study. NRP showed negative correlation with soil N content for sun leaves in the third locality. This result is consistent with N resorption proficiency reflecting relative soil N availability (Hobbie & Gough, 2002; Renteria *et al.*, 2005). Our results did not indicate P resorption proficiency reflecting relative soil nutrient availability. This consequence complies with previous studies (Lal *et al.*, 2001; Renteria *et al.*, 2005). Such inconsistent results have been reported previously and attributed to differences in sampling, large annual variations and the response to soil nutrient availability over a narrow range (Côte *et al.*, 2002; Salazar *et al.*, 2011).

To conclude, our study showed that the sun and shade leaf nutrients of *H. helix*, a conspicuous climbing evergreen plant in temperate deciduous forests, vary temporally in different

localities. There were differences in terms of altitude, forest type, and consequently canopy openness between localities. There were significant differences in leaf traits, soil nutrients and moisture between localities. We found significant correlations between soil and leaf traits among localities. In accordance with existing literature (Killingbeck, 1996; Lal *et al.*, 2001, Richardson *et al.*, 2005), PRE was higher than NRE, while NRP was higher than PRP for sun and shade leaves. N and P resorption in the sun and shade leaves of *H. helix* were incomplete. Several reasons could explain incomplete resorption in the sun and shade leaves but we have not found significant differences in terms of resorption efficiency and proficiency between sun and shade leaves. These results could partly support that *H. helix* was a successful competitor in the different temperate forest ecosystems.

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