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# FOLIAR RESORPTION AND NUTRIENT CHANGES IN LEAVES AND SOILS OF *TILIA RUBRA* SUBSP. *CAUCASICA* (LINDEN) ALONG AN ALTITUDINAL GRADIENT DURING THE GROWING SEASON

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## ABSTRACT

This study was conducted (i) to explore variations in the foliar nitrogen (N) and phosphorus (P) resorption and nutrient dynamics of linden along with altitudinal gradient and during one growing season and their relationships with nutrient contents and (ii) to identify how the soil factors affect foliar N and P resorption. We measured nitrogen (N), carbon (C), sulphur (S), phosphorus (P) concentrations and SLA in both green and senescent leaves of the same individuals. We compared the resorption proficiency (RP) and efficiency (RE) of N and P, SLA values, N, C, S and P dynamics in plant leaves, besides comparing N and P concentrations in soils for different altitudes during the growing season and we investigated impacts of climate, soil and altitudinal variations. The N, C, S and P concentrations increase with increasing altitude. The N, C, S and P levels in green leaves were higher than those in senesced leaves. On average, the leaf N-RE and P-RE were 42 and 46%, respectively; and the corresponding N-RP and P-RP were 0.6 and 0.54%, respectively. N-RE and P-RE increase and N-RP and P-RP decrease with increasing altitude. The SLA, soil nutrient contents and pH significantly change along with the altitudinal gradient and during the growing season. These results support that plants growing in areas with high altitude or in areas with low soil N and P concentrations should have lower N-RP and P-RP and higher N-RE and P-RE. Our finding can improve the understanding of variations in N and P resorption and their response to global change.

## KEYWORDS:

carbon, nitrogen, phosphorus, resorption efficiency, resorption proficiency, soil, sulphur

## INTRODUCTION

The genus *Tilia* L. is a member of the family

Tiliaceae, represented by four species in Turkey: *Tilia cordata* Miller, *T. rubra* D.C., *T. platyphyllos* Scop., and *T. argentea* Desf.. *Tilia rubra* DC. subsp. *caucasica* (Rupr.) V. Engler especially spreads in the east of the Black Sea region [1]. The different parts of this species are consumed as medicine. Linden flowers are well known and widely used in folk medicine [2].

N and P concentrations, two of the important components of leaves, play critical roles in ecosystem function and dynamics [3]. It has long been known that N and P are crucial components of plant nutrition and these two elements generally limit plant growth in both terrestrial and aquatic ecosystems [4-6]. N and P are functionally coupled in biological systems, from cells to ecosystems [7]. The synergistic and interacting effects of N and P availability are widespread among different ecosystems [8,9]. Although most studies have focused on N and P resorption, in addition to these elements, sulphur and carbon are also necessary for plant growth and development. Sulphur is involved in protein synthesis and is a component of amino acids cysteine and thiamine. At the low level, plants can use atmospheric SO<sub>2</sub> as sulphur source [10]. Carbon partitioning in plants is controlled by a number of factors such as the source of photosynthate, the number and size of competing sinks [11].

Plants have developed different strategies to overcome nutrient shortages [12,13]. Nutrient resorption is one of the most important mechanisms of nutrient conservation, which enables a plant to reuse nutrients directly and to be less dependent on external nutrient supplies [14-17]. The nutrient status of a plant can be determined by the concentrations of nutrients in mature leaves [18]. Therefore, foliar analysis is a classic tool for determining nutrient use efficiencies and it has long been applied to forest trees, shrubs and herbs [19]. In a plant, most of the nutrients can be removed from the senescing tissues and transported to other parts through this process [17,20]. Nutrient use efficiencies can be improved within the plant, enhancing adaptability to environments where

nutrients are lacking [17,21,22].

Nutrient resorption parameters are essential to estimate biogeochemical patterns [23-26]. Nutrient resorption can be defined by nutrient resorption efficiency (the percentage of reduction in the nutrient concentration between green and senescing leaves) and nutrient resorption proficiency (the concentration of nutrient in senescent leaves) [27]. High nutrient resorption efficiency makes plants less dependent on the current nutrient uptake and increases plant adaptation, especially in nutrient-poor ecosystems [28,29]. In addition, nutrient resorption proficiency directly affects litter quality, litter decomposition rate and soil nutrient availability [27,30].

*Tilia rubra* subsp. *caucasica* is a relict species remained from tertiary period and also plays an important ecological role in Turkey. The principal objectives of this study are (i) to explore variations in the foliar nitrogen and phosphorus resorption and nutrient (N, C, S and P) dynamics of linden along with altitudinal gradient and during one growing season and their relationships with nutrient contents and (ii) to identify how the soil factors affect foliar N and P resorption.

## MATERIAL AND METHODS

**Study area and plant samples.** This study was conducted in Firtina Valley, located in the north eastern of Turkey, Rize. Average temperature and rainfall were 15 °C and 1722 mm for 2014 (Turkish Republic Ministry of Forest and Water Affairs, General Directorate of Meteorology 2014). The soil in the research area was acidic. *Tilia rubra* DC. subsp. *caucasica* (Rupr.) V. Engler was selected as the research material and plant samples were collected from Rize province. Three topographic positions were sampled over the elevation range (330, 679 and 974 m). Five (20 m × 20 m) plots were chosen in homogeneous places for each altitude (330 m N 41°00'753"/E 40°59'659", 679 m N 40°58'416"/E 40°57'521" and 974 m N 40°54'152"/E 40°56'743"). In each plot, five healthy plants were randomly selected and marked. Each plant was selected ≥2.5 m from the stems of neighboring canopy trees to avoid potential microsite variation [31]. Green leaf samples were collected in the first weeks from May to September 2014. Senescent leaves were collected in the first week of October. Senescent leaves were collected by shaking lightly the same branches from which green leaves were collected. Leaf samples were collected from five marked plants from the middle of the crown for each plant from the five replicate plots. The collected samples were mixed with each replicate plots and brought to the laboratory in polyethylene bags.

**Laboratory analyses.** The leaf samples were dried at 60 °C until the constant weight, then grounded and sieved. N, C and S (%) concentrations of samples were determined by an NCS Analyzer (Thermo Scientific FLASH 2000 Series) device based on the method of Dumas [32]. P (%) concentration was determined colorimetrically by using molybdate and metavanadate after wet digestion in nitric and perchloric acid. The absorbance was measured at 430 nm with a Biochrom Libra S70 Double Beam Spectrophotometer [33].

Soil samples taken from a depth of 0-30 cm, were also collected from each altitude during the growing season. On each sample date, soil and plant samples were taken from each altitude simultaneously during the growing season. The soil samples were air-dried and then sieved to pass through a 2-mm screen. Soil pH values (1:1) were measured by pH-meter (Thermo Scientific Orion 3 Star, Singapore). Soil nitrogen and phosphorus content was spectrophotometrically determined by Kjeldahl method, by extraction with ammonium acetate, respectively.

**Calculation of specific leaf area (SLA), nutrient contents, resorption efficiency and proficiency.** Leaf area of each species was measured with a leaf-area meter (LI-3000, LICOR-USA). Specific leaf area (SLA) was calculated according to Cornelissen et al. [34]:

$$SLA = \sum LA \text{ (dm}^2\text{)} / \sum LDW \text{ (g)}$$

LA: Leaf area (dm<sup>2</sup>)

LDW: Leaf dry weight (g)

N, C, S and P (g dm<sup>-2</sup>) were calculated according to the following formulas.

$$N \text{ contents} = \sum LDW \text{ (g)} \times \text{crude N concentration} / SLA = \text{g dm}^{-2}$$

$$C \text{ contents} = \sum LDW \text{ (g)} \times \text{crude C concentration} / SLA = \text{g dm}^{-2}$$

$$S \text{ contents} = \sum LDW \text{ (g)} \times \text{crude S concentration} / SLA = \text{g dm}^{-2}$$

$$P \text{ contents} = \sum LDW \text{ (g)} \times \text{crude P concentration} / SLA = \text{g dm}^{-2}$$

Resorption efficiency (RE) and resorption proficiency (RP) were calculated for N and P. Resorption efficiency was calculated as the percentage of nitrogen (N-RE) and phosphorus (P-RE) and it was recovered from senescent leaves [35,36]:

$$RE = [(\text{Nutrient in mature leaves} - \text{Nutrient in senescent leaves}) / \text{Nutrient in mature leaves}] \times 100$$

Nitrogen resorption proficiency (N-RP) and phosphorus resorption proficiency (P-RP) were the concentrations of nutrient in senescent leaves [27].

**Statistical analyses.** Statistical analysis was performed by using SPSS version 21 (IBM SPSS Statistics for Windows, Armonk, NY). One-way analysis of variance (ANOVA) was performed in order to reveal whether foliar N, P, C and S concentrations, resorption efficiency and proficiency changed with respect to months and altitudes. Tukey's honestly significant difference (HSD) test was used to rank means following the analysis of variance.

## RESULTS

There were significant differences between green (from May to October) and senesced leaves (October) of linden with respect to all altitudes. The foliar nutrient concentrations in green leaves were higher than those in senescent leaves. These significant differences and the calculated values for each element at different altitudes through the sampling period can be seen in Table 1A, B, C and Table 2A, B, C.

**TABLE 1A**  
The comparison of the monthly changes in N, C, S and P (%) values of *Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.

Parameters		Sum of Squares	df	Mean Square	F	Sig.
N	Between Groups	21.225	5	4.245	42.421	0.000**
	Within Groups	4.803	48	0.100		
	Total	26.028	53			
C	Between Groups	1542.490	5	308.498	70.503	0.000**
	Within Groups	210.032	48	4.376		
	Total	1752.522	53			
S	Between Groups	0.038	5	0.008	25.519	0.000**
	Within Groups	0.014	48	0.000		
	Total	0.053	53			
P	Between Groups	16.826	5	3.365	24.019	0.000**
	Within Groups	6.725	48	0.140		
	Total	23.552	53			

\*P< 0.05 \*\*P< 0.01

**TABLE 1B**  
The comparison of the elevation gradients in N, C, S and P (%) values of *Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.

Parameters		Sum of Squares	df	Mean Square	F	Sig.
N	Between Groups	0.991	2	0.495	1.009	0.372 <sup>NS</sup>
	Within Groups	25.037	51	0.491		
	Total	26.028	53			
C	Between Groups	38.204	2	19.102	0.568	0.570 <sup>NS</sup>
	Within Groups	1714.317	51	33.614		
	Total	1752.522	53			
S	Between Groups	0.005	2	0.002	2.624	0.082 <sup>NS</sup>
	Within Groups	0.048	51	0.001		
	Total	0.053	53			
P	Between Groups	3.926	2	1.963	5.101	0.010*
	Within Groups	19.626	51	0.385		
	Total	23.552	53			

\*P< 0.05 \*\*P< 0.01 NS: Not Significant

**TABLE 1C**  
**Nitrogen, carbon, sulphur and phosphorus values of *Tilia rubra* subsp. *caucasica* depending on altitudes and months by using Tukey's HSD test (Mean±SE).**

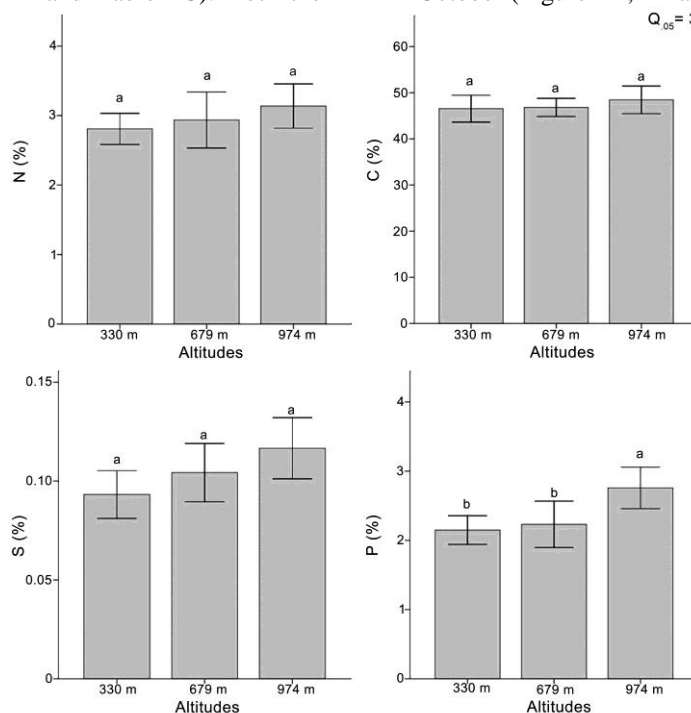
	n	N		C		S		P	
		%	(g dm <sup>-2</sup> )	%	(g dm <sup>-2</sup> )	%	(g dm <sup>-2</sup> )	%	(g dm <sup>-2</sup> )
Altitudes	330 m	2.80±0.11 <sup>a</sup>	0.51±0.02 <sup>b</sup>	46.56±1.48 <sup>a</sup>	8.41±0.75 <sup>b</sup>	0.099±0.007 <sup>a</sup>	0.018±0.002 <sup>b</sup>	2.14±0.10 <sup>b</sup>	0.39±0.02 <sup>b</sup>
	679 m	2.93±0.2 <sup>a</sup>	0.65±0.02 <sup>b</sup>	46.82±1.01 <sup>a</sup>	10.98±0.56 <sup>b</sup>	0.104±0.007 <sup>a</sup>	0.024±0.001 <sup>b</sup>	2.23±0.17 <sup>b</sup>	0.48±0.16 <sup>b</sup>
	974 m	3.13±0.16 <sup>a</sup>	1.26±0.12 <sup>a</sup>	48.46±1.53 <sup>a</sup>	20.52±1.95 <sup>a</sup>	0.110±0.007 <sup>a</sup>	0.035±0.002 <sup>a</sup>	2.75±0.15 <sup>a</sup>	1.20±0.02 <sup>a</sup>
Q <sub>05</sub> = 3.42									
Months	May	3.12±0.07 <sup>b</sup>	0.90±0.19 <sup>ab</sup>	50.40±0.96 <sup>b</sup>	14.53±3.43 <sup>ab</sup>	0.097±0.005 <sup>bc</sup>	0.018±0.002 <sup>bc</sup>	2.28±0.06 <sup>cd</sup>	0.99±0.24 <sup>a</sup>
	June	4.04±0.2 <sup>a</sup>	1.14±0.20 <sup>a</sup>	56.31±1.06 <sup>a</sup>	20.47±2.88 <sup>a</sup>	0.135±0.006 <sup>a</sup>	0.030±0.002 <sup>a</sup>	3.16±0.12 <sup>a</sup>	1.11±0.27 <sup>a</sup>
	July	3.08±0.04 <sup>b</sup>	0.88±0.19 <sup>ab</sup>	47.07±0.5 <sup>c</sup>	12.70±1.58 <sup>ab</sup>	0.134±0.006 <sup>a</sup>	0.036±0.002 <sup>a</sup>	2.89±0.12 <sup>ab</sup>	0.70±0.13 <sup>ab</sup>
	August	2.98±0.07 <sup>b</sup>	0.72±0.05 <sup>ab</sup>	46.93±0.4 <sup>c</sup>	12.53±2.44 <sup>ab</sup>	0.117±0.020 <sup>ab</sup>	0.029±0.002 <sup>ab</sup>	2.52±0.10 <sup>bc</sup>	0.54±0.04 <sup>ab</sup>
	September	2.53±0.05 <sup>c</sup>	0.68±0.04 <sup>ab</sup>	43.98±0.3 <sup>d</sup>	11.76±0.74 <sup>ab</sup>	0.078±0.005 <sup>cd</sup>	0.025±0.003 <sup>abc</sup>	1.84±0.18 <sup>de</sup>	0.53±0.04 <sup>ab</sup>
	October	1.97±0.04 <sup>d</sup>	0.51±0.03 <sup>b</sup>	38.97±0.4 <sup>e</sup>	7.82±0.62 <sup>b</sup>	0.065±0.005 <sup>d</sup>	0.016±0.002 <sup>c</sup>	1.56±0.10 <sup>e</sup>	0.30±0.03 <sup>b</sup>

Q<sub>05</sub>= 4.21

\*Different letters in the same column indicate statistically significant differences among parameters (N, C, S and P) for the mean of both altitudes and months. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

There were notable differences ( $P < 0.01$ ) in N, C, P and S (%) concentrations of linden in terms of months. Depending on altitudes, only P (%) concentration showed a difference ( $P < 0.05$ ) (Table 1A and 1B). The N, C, S and P concentrations increased with increasing altitude. N, C, P and S (%) concentrations were higher in June and lower in October (Figure 1A, 1B and Table 1C). Both the

altitudinal gradient and the growing season significantly affected the N, C, S and P (g dm<sup>-2</sup>) contents (Table 2A and 2B). The N, C, S and P contents increased with increasing altitude. While the highest N, C and P contents were observed in June, the highest S content was determined in July. The lowest values of these elements were found in October (Figure 2A, 2B and Table 1C).



**FIGURE 1A**

**Nitrogen, carbon, sulphur and phosphorus (%) concentrations in leaves of *Tilia rubra* subsp. *caucasica* depending on altitudes.**

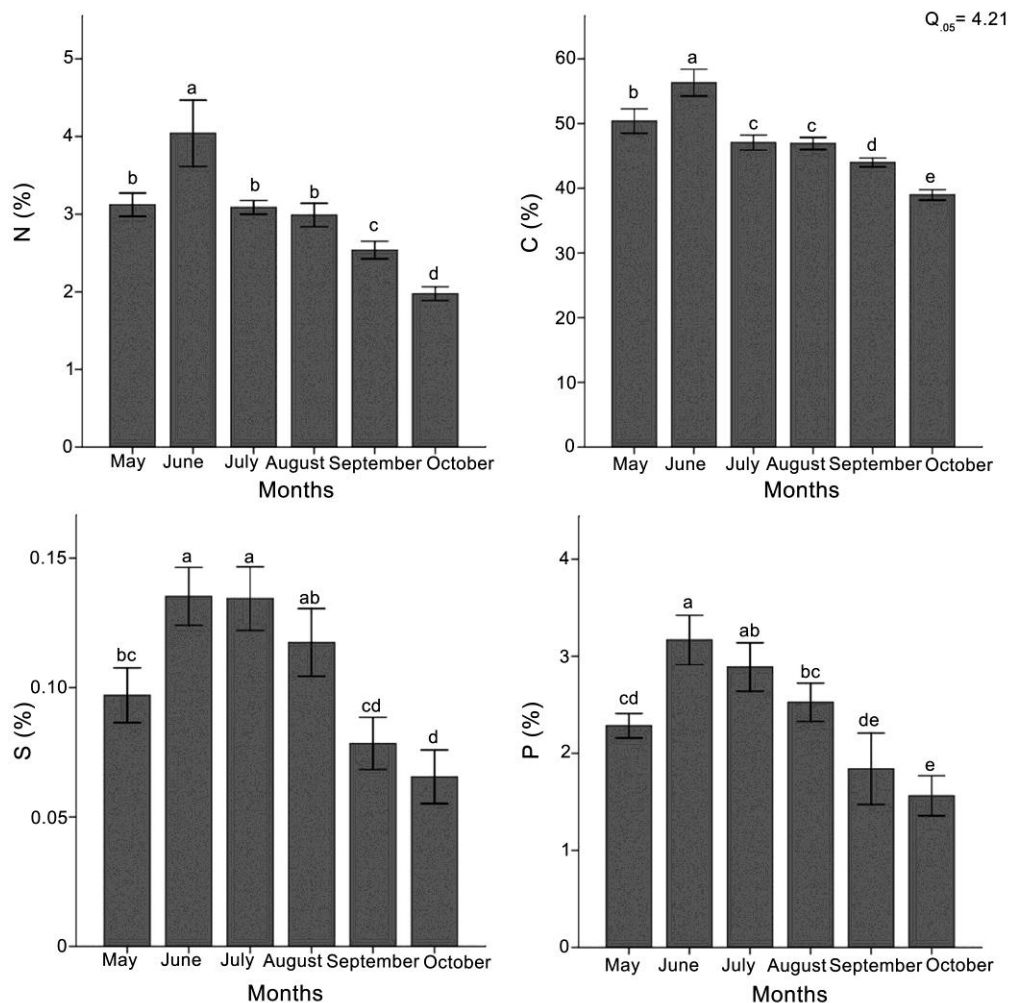


FIGURE 1B

Nitrogen, carbon, sulphur and phosphorus (%) concentrations in leaves of *Tilia rubra* subsp. *caucasica* depending on months.

TABLE 2A

The comparison of the monthly changes in N, C, S and P (g dm<sup>-2</sup>) values of *Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.

Parameters		Sum of Squares	df	Mean Square	F	Sig.
N	Between Groups	2.108	5	0.422	2.292	0.060*
	Within Groups	8.827	48	0.184		
	Total	10.935	53			
C	Between Groups	775.521	5	155.104	3.497	0.009**
	Within Groups	2128.835	48	44.351		
	Total	2904.356	53			
S	Between Groups	0.003	5	0.001	7.787	0.000**
	Within Groups	0.003	48	0.000		
	Total	0.006	53			
P	Between Groups	4.192	5	0.838	3.504	0.009**
	Within Groups	11.483	48	0.239		
	Total	15.674	53			

\*P < 0.05 \*\*P < 0.01

**TABLE 2B**  
**The comparison of the elevation gradients in N, C, S and P (g dm<sup>-2</sup>) values of *Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.**

Parameters		Sum of Squares	df	Mean Square	F	Sig.
N	Between Groups	5.696	2	2.848	27.726	0.000**
	Within Groups	5.239	51	0.103		
	Total	10.935	53			
C	Between Groups	1465.257	2	732.629	25.964	0.000**
	Within Groups	1439.099	51	28.218		
	Total	2904.356	53			
S	Between Groups	0.003	2	0.001	19.175	0.000**
	Within Groups	0.003	51	0.000		
	Total	0.006	53			
P	Between Groups	7.092	2	3.546	21.070	0.000**
	Within Groups	8.583	51	0.168		
	Total	15.674	53			

\*P < 0.05 \*\*P < 0.01

**TABLE 2C**  
**Comparison of green and senesced leaves of *Tilia rubra* subsp. *caucasica* on the basis of nitrogen, carbon, sulphur and phosphorus across all the altitudes by using One-Way ANOVA (Mean±SE).**

Parameters	n	Green Leaves	n	Senesced Leaves
N (%)	45	3.15±0.08 <sup>NS</sup>	9	1.97±0.045**
F-value		1.420		14.818
C (%)	45	48.94±0.7 <sup>NS</sup>	9	38.97±0.4**
F-value		1.075		12.753
S (%)	45	0.11±0.004 <sup>NS</sup>	9	0.06±0.005**
F-value		0.793		15.200
P (%)	45	2.54±0.08**	9	1.56±0.104**
F-value		8.981		159.616
		Q <sub>05</sub> = 3.44	Q <sub>05</sub> = 4.34	
N (g dm <sup>-2</sup> )	45	0.86±0.07**	9	0.52±0.03**
F-value		40.124		18.290
C (g dm <sup>-2</sup> )	45	14.40±1.13**	9	7.82±0.62**
F-value		42.036		38.775
S (g dm <sup>-2</sup> )	45	0.028±0.001**	9	0.017±0.002**
F-value		24.014		14.376
P (g dm <sup>-2</sup> )	45	0.77±0.08**	9	0.30±0.03**
F-value		26.571		102.245
		Q <sub>05</sub> = 3.44	Q <sub>05</sub> = 4.34	

\*P < 0.05 \*\*P < 0.01 NS: Not Significant

P-RP was remarkably varied with altitudes ( $P < 0.01$ ). However, there were no significant differences in N-RE, N-RP and P-RE (Table 3A). N-RE and P-RE increased and N-RP and P-RP decreased with increasing altitudes (Table 3B). Statistically significant differences ( $P < 0.01$ ) were found in SLA (dm<sup>2</sup> g<sup>-1</sup>) values in terms of months and altitudes (Table 4A and 4B). SLA increased in parallel with the altitudinal changes. The measured SLA values according to different altitudes and months are demonstrated in Table 4C.

The differences in N, P and pH values of soils according to both altitudes and months were suggestive. The highest soil N and P values were 0.30 and 0.31% at 330 m, respectively; the lowest N and P values were 0.16 and 0.24 % at 974 m, respectively. The soil N and P concentrations were higher in October, while the soil N and P were lower in June. N (%), P (%) and pH values decreased with increasing altitude. Soils in all altitudes were acidic (Table 5A, 5B and 5C).

**TABLE 3A**  
The comparison of the elevation gradients in N-RE, N-RP, P-RE, P-RP (%) values of *Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.

Parameters		Sum of Squares	df	Mean Square	F	Sig.
N-RE	Between Groups	20.394	2	10.197	2.187	0.193 <sup>NS</sup>
	Within Groups	27.979	6	4.663		
	Total	48.373	8			
N-RP	Between Groups	0.087	2	0.044	4.080	0.076 <sup>NS</sup>
	Within Groups	0.064	6	0.011		
	Total	0.152	8			
P-RE	Between Groups	70.014	2	35.007	2.455	0.166 <sup>NS</sup>
	Within Groups	85.566	6	14.261		
	Total	155.580	8			
P-RP	Between Groups	0.172	2	0.086	17.795	0.003 <sup>**</sup>
	Within Groups	0.029	6	0.005		
	Total	0.201	8			

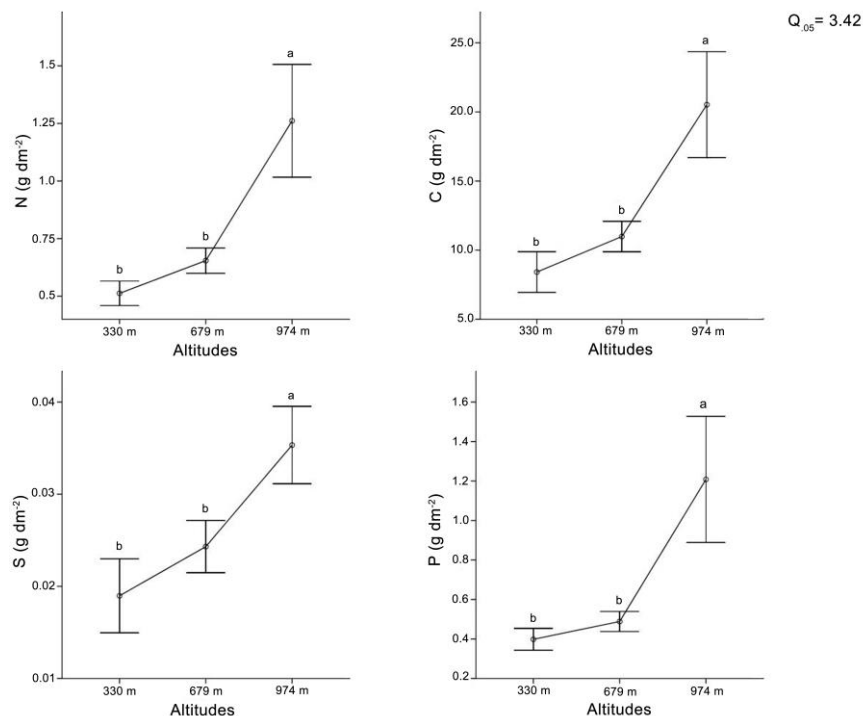
\*P < 0.05 \*\*P < 0.01 NS: Not Significant

**TABLE 3B**  
Nitrogen and phosphorus resorption efficiency and proficiency (%) in *Tilia rubra* subsp. *caucasica* across all the altitudes by using Tukey's HSD test.

Altitudes	N-RE (%)	N-RP (%)	P-RE (%)	P-RP (%)
330 m	41.63±1.70 <sup>a</sup>	0.82±0.06 <sup>a</sup>	42.48±1.27 <sup>a</sup>	0.70±0.05 <sup>a</sup>
679 m	41.74±0.04 <sup>a</sup>	0.66±0.06 <sup>a</sup>	47.12±0.88 <sup>a</sup>	0.56±0.02 <sup>a</sup>
974 m	44.88±1.32 <sup>a</sup>	0.58±0.05 <sup>a</sup>	49.14±3.45 <sup>a</sup>	0.36±0.02 <sup>b</sup>

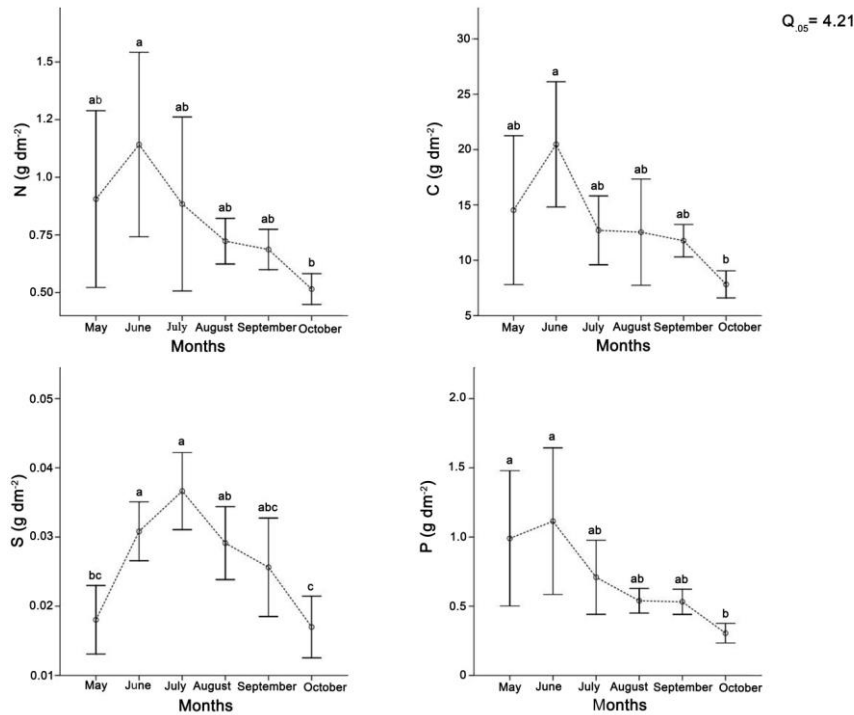
$Q_{.05} = 4.34$

\*Different letters in the same column indicate statistically significant differences among parameters (N-RE, N-RP, P-RE and P-RP) for the mean of both altitudes. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.



**FIGURE 2A**  
Nitrogen, carbon, sulphur and phosphorus (g dm<sup>-2</sup>) contents in leaves of *Tilia rubra* subsp. *caucasica* depending on altitudes.





**FIGURE 2B**  
Nitrogen, carbon, sulphur and phosphorus (g dm<sup>-2</sup>) contents in leaves of *Tilia rubra* subsp. *caucasica* depending on months.

**TABLE 4A**  
The comparison of the monthly changes in specific leaf area (SLA) values of *Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.

Parameters		Sum of Squares	df	Mean Square	F	Sig.
SLA	Between Groups	1.683	5	0.337	4.674	0.001**
	Within Groups	3.457	48	0.072		
	Total	5.140	53			

\*P < 0.05 \*\*P < 0.01

**TABLE 4B**  
The comparison of the elevation gradients in specific leaf area (SLA) values of *Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.

Parameters		Sum of Squares	df	Mean Square	F	Sig.
SLA	Between Groups	1.081	2	0.540	6.791	0.002**
	Within Groups	4.059	51	0.080		
	Total	5.140	53			

\*P < 0.05 \*\*P < 0.01

**TABLE 4C**  
**SLA (dm<sup>2</sup> g<sup>-1</sup>) values of *Tilia rubra* subsp. *caucasica* depending on altitudes and months**  
**by using Tukey's HSD test.**

		n	SLA
Altitudes	330 m	18	1.60±0.05 <sup>b</sup>
	679 m	18	1.73±0.08 <sup>ab</sup>
	974 m	18	1.95±0.05 <sup>a</sup>
<b>Q<sub>.05</sub>= 3.42</b>			
Months	May	9	2.08±0.10 <sup>a</sup>
	June	9	1.58±0.06 <sup>b</sup>
	July	9	1.59±0.08 <sup>b</sup>
	August	9	1.66±0.06 <sup>b</sup>
	September	9	1.82±0.04 <sup>ab</sup>
	October	9	1.84±0.13 <sup>ab</sup>
<b>Q<sub>.05</sub>= 4.21</b>			

\*Different letters in the same column indicate statistically significant differences among parameter (SLA) for the mean of both altitudes and months. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

**TABLE 5A**  
**The comparison of the monthly changes in N, P (%) and pH values in soils of**  
***Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.**

Parameters		Sum of Squares	df	Mean Square	F	Sig.
N	Between Groups	0.234	5	0.047	9.250	0.000**
	Within Groups	0.243	48	0.005		
	Total	0.476	53			
P	Between Groups	0.029	5	0.006	3.717	0.006**
	Within Groups	0.075	48	0.002		
	Total	0.103	53			
pH	Between Groups	2.362	5	0.472	6.916	0.000**
	Within Groups	3.278	48	0.068		
	Total	5.640	53			

\*P< 0.05 \*\*P< 0.01

**TABLE 5B**  
**The comparison of the elevation gradients in N, P (%) and pH values in soils of**  
***Tilia rubra* subsp. *caucasica* by using One-Way ANOVA.**

Parameters		Sum of Squares	df	Mean Square	F	Sig.
N	Between Groups	0.191	2	0.096	17.108	0.000**
	Within Groups	0.285	51	0.006		
	Total	0.476	53			
P	Between Groups	0.043	2	0.022	18.359	0.000**
	Within Groups	0.060	51	0.001		
	Total	0.103	53			
pH	Between Groups	3.070	2	1.535	30.468	0.000**
	Within Groups	2.570	51	0.050		
	Total	5.640	53			

\*P< 0.05 \*\*P< 0.01

**TABLE 5C**  
**The comparison of the monthly changes and the elevation gradients in soil characteristics of *Tilia rubra* subsp. *caucasica* by using Tukey's HSD test.**

		n	pH	N (%)	P (%)
Altitudes	330 m	18	6.65±0.55 <sup>a</sup>	0.30±0.02 <sup>a</sup>	0.31±0.007 <sup>a</sup>
	679 m	18	6.44±0.51 <sup>b</sup>	0.21±0.01 <sup>b</sup>	0.27±0.008 <sup>b</sup>
	974 m	18	6.07±0.52 <sup>c</sup>	0.16±0.01 <sup>b</sup>	0.24±0.008 <sup>c</sup>
<b>Q<sub>0.05</sub>= 3.42</b>					
Months	May	9	6.67±0.08 <sup>a</sup>	0.16±0.02 <sup>bc</sup>	0.26±0.02 <sup>ab</sup>
	June	9	6.63±0.08 <sup>a</sup>	0.12±0.01 <sup>c</sup>	0.23±0.01 <sup>b</sup>
	July	9	6.39±0.10 <sup>ab</sup>	0.23±0.02 <sup>ab</sup>	0.28±0.01 <sup>ab</sup>
	August	9	6.33±0.06 <sup>ab</sup>	0.24±0.01 <sup>ab</sup>	0.27±0.007 <sup>ab</sup>
	September	9	6.25±0.10 <sup>b</sup>	0.25±0.01 <sup>ab</sup>	0.28±0.003 <sup>ab</sup>
	October	9	6.07±0.07 <sup>b</sup>	0.32±0.03 <sup>a</sup>	0.31±0.01 <sup>a</sup>
<b>Q<sub>0.05</sub>= 4.21</b>					

\*Different letters in the same column indicate statistically significant differences among parameters (pH, N, P) for the mean of both altitudes and months. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

## DISCUSSION

SLA is the ratio of leaf area to leaf dry matter, which is one of the most significant leaf characteristics [37,38]. In our study, SLA values significantly varied along with the altitudinal gradient and the growing season. When evaluating monthly changes of SLA, the highest value was in May, then there was a decrease until September and an increase after this month. When the plants started to sprout, leaves were light, quite thin and also contained the excess amount of water. SLA values showed a decline until the beginning of senescence depending on the nutrient and tissue growth as a result of photosynthesis. The leaf weight decreased because of the realization of resorption in senescence. During this period, SLA increased due to an expansion in leaf area in parallel with the rainfall increase. Some researchers [39] reported that SLA values showed a decrease until October. In this study, SLA values increased with increasing altitude. Similarly, Zhao et al. [40] stated that SLA increased with increasing altitude below 3000 m a.s.l.. Ozbucak et al. [38] pointed out that the SLA showed changes with regard to the topographic gradient and the growing season.

In this study, we found that N, C, P and S (%) ranged from 1.97 to 4.04, 38.97 to 56.31, 1.56 to 3.16 and 0.06 to 0.14, respectively. N, C, P and S (g dm<sup>-2</sup>) ranged between 0.51-1.26, 7.82-20.52, 0.30-1.20 and 0.016-0.036, respectively. N, P, C and S levels in senesced leaves of linden were lower than those in mature leaves. Similarly, Turkis and Ozbucak [41] stated that nutrients in mature leaves were higher than those in senescent leaves. Singh [42] reported that in leguminous species, the foliar nitrogen concentration in mature and senesced leaves ranged between 2.08-2.26% and 1.14-1.45%, respectively. The senescence period may give rise to resorption.

In our study, there were notable seasonal and altitudinal variations in N, C, P, S values ( $P < 0.01$ ). N, C, P and S concentrations increased in parallel with the altitudinal changes. It may be caused by the decrease of soil moisture along the elevational gradient. In addition to this, another factor may be that N and P mechanisms are activated [43]. The high N content of high-altitude plants could be a passive consequence of the lower degree of dilution of the plant's N content under cold conditions than that under warm conditions, particularly if low temperatures and short growing seasons restrict shoot growth more than how much they restrict N uptake by the roots, concentrating leaf N content at high altitudes [40]. In addition, the high N content could be also a result of the way high-altitude plants adapt to low resource availability through higher biomass allocation to the root system and increased fine root production [38,44]. As for the recent studies on this topic in last few years, Bilgin et al. [19] reported that the foliar N and P concentrations varied along the elevational gradient and significant changes were observed along the topographic gradient. Ozbucak et al. [38] pointed out that leaf N and P concentrations were subjected to important changes during the growing season and leaf P levels also changed considerably along the altitudinal gradient. Similarly, some researchers [41,45,46] stated that N and P concentrations increased along an elevation gradient. Zhao et al. [40] reported that leaf C and N values decreased with increasing altitude below 3000 m a.s.l., but increased above 3000 m a.s.l. In the present study, N, P, C and S concentrations in the leaves of linden increased until the mature period and then showed a decrease after this period. This is probably due to the resorption of N compounds (nitrate, ammonium, and amino acids) and P compounds (nucleic acids, phospholipids of membranes, Pi, ATP, and sugar phosphates) from leaves of perennial plant parts at

the end of the mature leaf period [38].

Aerts [28] pointed out that the mean nutrient resorption efficiency was 40-75% and 30-70% for nitrogen and phosphorus in deciduous species, respectively. N and P resorption efficiency was in the range of 26-64% and 56-71% in deciduous forests, respectively too [47-49]. N resorption efficiency in some deciduous species such as *Quercus suber*, *Populus nigra*, *Frangula alnus*, *Prunus spinosa*, *Corylus avellana*, *Quercus rubra*, *Quercus petraea* subsp. *iberica*, *Clethra brammeriana*, *Populus yunnanensis*, *Alnus nepalensis* and *Fagus orientalis* was found to be 47.9, 62.6, 61.6, 24.3, 39.6, 70, 73.4, 10.2, 34.7, 17.7 and 28.3%, respectively [41,48,50-54]. P resorption efficiency in some deciduous species like *Corylus avellana*, *Viburnum acerifolium*, *Quercus rubra*, *Nothofagus pumilio*, *Fraxinus excelsior*, *Betula alnoides* and *Tilia cordata* was estimated as 14, 37.2, 55, 43.8, 37, 25.4 and 59%, respectively [45,48,51,54-56]. In this experiment, N and P resorption efficiency average values are 42 and 46%, respectively; and they are consistent with values observed in the literature for deciduous trees [28]. These results indicate that linden effectively resorbs N and P in all altitudes in general. The greater resorption efficiencies for both nitrogen and phosphorus in the present study in all altitudes clearly indicate that plants growing on habitats deficient in nitrogen and phosphorus have greater efficiencies for nitrogen and phosphorus resorption. The greater nitrogen and phosphorus resorption efficiencies in the study suggest that effective resorption is a mechanism in plants to overcome the problem of nutrient poverty. Moreover, we found that N-RE and P-RE show an increase with increasing altitude, because the environmental variables (e. g. climate and soil attributes) may change in a more complex manner along elevation [57], which is similar to the findings of the studies of Kilic et al. [53] and Tang et al. [57] on changes in NE and NP along the altitudes. Bilgin et al. [58] claimed that water availability, timing of abscission, leaf nutrient status, or shade could cause the variations among resorption efficiencies.

Resorption proficiency is more effective than resorption efficiency in determining nutrient availability [36]. Killingbeck [27] reported that during their senescence stages, if nitrogen and phosphorus concentrations are below 0.7% and 0.05%, respectively, resorption is extremely proficient in plants. In this study, we estimated that N resorption proficiency values are averagely 0.6%. Based on the threshold values [27], N resorption proficiency is biochemically completed in linden. However, P resorption proficiency ranges from 0.36 to 0.70%. According to the above values, linden is not P-proficient, having values higher than 0.05% P in senescent leaves of deciduous species. Similarly, Kilic et al. [53] and Han et al. [13] pointed out that

resorption proficiency was incomplete according to the threshold values defined by Killingbeck [27] in their study. Drenovsky and Richards [59] stated that *Chrysothamnus nauseosus* subsp. *consimilis* and *Sarcobatus vermiculatus* were proficient at resorbing N and P, respectively. Diehl et al. [60] observed that *Nothofagus antarctica* and *Nothofagus pumilio* were N-proficient and any of these species was not P-proficient. High resorption proficiency implies low concentrations because a low N concentration in senesced parts is the evidence of high proficiency, and vice versa [61]. Similar to the results of Tang et al. [57], N-RP and P-RP decreased with the increase of altitude in our study.

Soil N and P (%) concentrations varied along altitudinal gradients and the growing period of plants. Soil N, P and pH values decreased with increasing altitudes. This may have been due to the differences among the altitudes, temperature, precipitation, soil nutrient content and other abiotic factors [58]. Similar to the results of the study of Koontz et al. [62], soil pH values significantly changed along both altitudes and months in this study. Soil nutrient content can also affect plant nutrient resorption. In this report, soil N and P concentrations negatively related to leaf N and P. Leaf N, C, S and P of linden were negatively related to soil pH, conforming to the research results by Liu et al. [63]. Our results also showed that N-RP increased and N-RE decreased with increasing total soil N, while P-RP increased and P-RE decreased with increasing total soil P. These complex response models may reflect the various habitat conditions such as soil water and temperature, total soil nutrient level, and various plant species with different green leaf nutrient levels, which will cause different relative costs of nutrients withdrawn from soil versus senescing leaves [57]. Although there are many studies on this negative interaction between nutrient resorption efficiency and soil nutrient availability [64-66], there are also some studies on a connection between soil fertility and nutrient resorption. Aerts et al. [67] examined the results of some studies on nutrient resorption with relation to soil factor and concluded that nutrient proficiency patterns show a stronger relation to soil fertility, which means one can find the highest proficiency in an infertile area.

## CONCLUSION

Overall, both altitudinal changes and the growing season significantly affected the leaf nutrient dynamics, resorption, SLA, soil nutrient contents and soil pH. The nutrient dynamics, SLA, N-RE and P-RE increased with increasing altitude while N-RP, P-RP, soil pH, N and P decreased with increasing altitude. The SLA and nutrient dynamics

significantly differed with respect to leaf growth stage. The study also revealed that green leaf nutrients are higher than in senescent leaf. As the key strategy for plants responding to environmental nutrient stress, nutrient resorption traits should be influenced by factors that affect environmental nutrient supplies. About half of the green leaf N and P are resorbed before leaf abscission in linden. Linden showed full resorption with respect to N depending on threshold values as described by Killingbeck [27]. The SLA and nutrient dynamics decreased with increasing soil nutrient content. Soil nutrient content can also influence plant nutrient resorption. N-RE and P-RE decreased with increasing soil total N and P, while N-RP and P-RP increased. Furthermore, N-RE and P-RE increased with increasing leaf nutrient content while N-RP and P-RP decreased. These results support the hypothesis that linden growing in N and P limited areas (high altitudes) should have lower N-RP and P-RP and higher N-RE and P-RE. Our finding can improve the understanding of variations in N and P resorption and their response to global change.

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