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## Foliar N and P resorption and nutrient (N, P, C, and S) contents of *Vaccinium arctostaphylos* L. and *Vaccinium myrtillus* L. from East Black Sea region of Turkey

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**Abstract:** Phosphorus (P), nitrogen (N), carbon (C), and sulfur (S) contents of the leaves and specific leaf area (SLA), leaf mass per area (LMA), and N and P resorption were researched in *Vaccinium arctostaphylos* L. and *Vaccinium myrtillus* L., economically important for the East Black Sea region of Turkey. The leaves samples were collected from Solaklı Valley in Trabzon at 60 to 1800 m for *V. arctostaphylos* L. and 2100 to 2300 m for *V. myrtillus* L. The N, C, and S contents were determined by Dumas method and P concentration by the stannous chloride method. Nutrient contents, SLA, and LMA in leaves and N, P, organic matter, and pH in soil were measured. The foliar N, P, C, and S contents of the plants depending on the altitude gradient were statistically significant. N and S contents were significantly important during the growing season for both species. There were significant differences in terms of N and P proficiency for both species. Resorption values of *V. myrtillus* L. were found to be within the normal limits and the resorption efficiency values increased in parallel with the altitude changes. N resorption levels of *V. arctostaphylos* at lower (60 m) and higher (1800 m) altitudes were below the declared limits. It was also seen that while N proficiency showed significant increase, P proficiency decreased depending on the altitude. Both N and P proficiency for *V. myrtillus* decreased with the altitude increase.

**Key words:** Resorption, nutrient, *Vaccinium*, Solaklı Valley, Trabzon, Turkey

### 1. Introduction

Nutrient resorption is one of the major strategies used by plants to preserve minerals before senescence. Resorption and elimination of minerals from senescent leaf and their gathering or storage in the perennial parts of trees are common events. An important piece of the nutritional needs for the production of new biomass may be ensured by this resorption of nutrients. Similarly, resorption provides an advantageous continuum due to being less subject to losses from the reduction in biomass decomposition of trees (Regina and Tarazona, 2001). If minerals are restrictive, plants generally respond to P supplement with a positive reply in biomass and leaf P (de Campos et al., 2013). Plants may gather again minerals from leaves during senescence, and subsequently these minerals are transferred to pools, inclusive of thriving leaves (Veneklaas et al., 2012). Resorption of both nitrogen and phosphorus tends to increase with reducing leaf mineral status (Vergutz et al., 2012). The holding time of leaf minerals in a plant is mainly a function of leaf resorption (Escudero et al., 1992).

An effective mechanism of mineral protection in different plant species is nutrient retranslocation from

senescent leaves (Chapin, 1980; Killingbeck, 1996; Hagen-Thorn et al., 2006). Up to 80% of P and N foliar basins may be translocated again (Chapin and Kedrowski, 1983; Lambers et al., 1998; Hagen-Thorn et al., 2006). Though resorption of other minerals is less effective, it can still be quantitatively considerable for nutrient stocks of forest ecosystems (Hagen-Thorn et al., 2006). Resorption of minerals from senescent leaves is of vital adaptive importance because such minerals are directly available for further usage, making species less dependent on actual mineral uptake (Aerts and Chapin, 2000; Van Heerwaarden et al., 2003b). Most of the nitrogen and phosphorus from senescent leaves is withdrawn before abscission and used for new growth or stocked in vegetative tissue until the next growing season (Van Heerwaarden et al., 2003a).

The process of nutrient resorption decreases the possibility of mineral loss in litter fallen on the forest floor, and afterwards, the withdrawn nutrients are redeposited in developing tissues such as leaves or productive structures (like seeds), or stocked for further usage. Resorption is an integrated part of the well predicted process of leaf senescence and seems to occur in many species (Wright and Westoby, 2003).

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Mineral resorption parameters are essential for determining the correctness of ecological system and biogeochemical patterns (Vergutz et al., 2012; Liu et al., 2014). The usability of nitrogen (N) and phosphorous (P) is of special significance for the functioning of most terrestrial plant associations. These two minerals are critical constituents of plant nutriment and are considered those that most widely restrict plant growth in terrestrial ecosystems (Chapin, 1980; Ratnam et al., 2008). A common strategy used by plants in order to overcome the restrictions of N and P is to absorb again these minerals from senescent leaves before abscission. Since resorption contributes to decreasing a plant's dependence on available mineral supply, it could potentially be as substantial to a plant's mineral economy as absorption by roots and is one of the most significant strategies used by plants to preserve minerals (Chapin and Kedrowski, 1983; Aerts, 1996; Killingbeck, 1996; Aerts and Chapin, 2000; McGroddy et al., 2004; Ratnam et al., 2008). It is estimated that about 50% of leaf N and P is recycled through resorption across a broad range of perennial life models (Aerts, 1996; Aerts and Chapin, 2000; Ratnam et al., 2008).

Resorption proficiency is a parameter used for measuring nutrient resorption. Resorption proficiency appears to be more responsive than resorption efficiency to mineral availability. Some studies revealed that N fertilization resulted in higher N contents in the litter of many species (Van Heerwaarden et al., 2003b). These studies also demonstrated that N fertilization led to lower N resorption proficiencies (Van Heerwaarden et al., 2003b).

*V. arctostaphylos* and *V. myrtillus* occur naturally and are cultivated in a large part of the East Black Sea region of Turkey; they have an economic importance for the country. We selected these species in order to reveal

differences between nutrient dynamics of *Vaccinium* species in subalpine and alpine zones that belong to the same genus. The objectives of this study are to determine probable differences in the use of macronutrient elements in deciduous *V. arctostaphylos* and *V. myrtillus* species, the annual changes in dynamics of N and P, the change and the reasons of leaf resorption according to the altitude gradient, and the effect of soil factor upon leaf resorption.

## 2. Materials and methods

### 2.1. Plant samples

*V. arctostaphylos* and *V. myrtillus* (Ericaceae) species were collected from Solaklı Valley in Trabzon, the northeastern part of Turkey at an altitude ranging from 60 to 1800 m for *V. arctostaphylos* L. (A8) and from 2100 to 2300 m for *V. myrtillus* L. (A8). Five (20 m × 20 m) plots were chosen in homogeneous places at altitudes of 60 m, 300 m, 800 m, 1100 m, 1300 m, 1600 m, 1800 m, 2100 m, and 2300 m (Table 1). In each plot, at least five plant samples were randomly selected and flagged. The green leaf samples of *V. arctostaphylos* were collected from May to September 2009 and of *V. myrtillus* from June to September. Senescent leaves of both species were collected directly from plants in October.

### 2.2. Chemical analyses

Leaf samples were dried at 60 °C until constant weight, then ground and sieved. Five plants were selected and the results of each plant were cross-checked three times. N (%), C (%), and S (%) analyses of samples were determined by an NCS Analyzers (Thermo Scientific FLASH 2000 Series) device based on the Dumas method (Jiménez and Ladha, 1993).

P (%) was determined colorimetrically by using molybdate and metavanadate after wet digestion in nitric and perchloric acid. The absorbance was measured

**Table 1.** Localities and coordinates belong to species.

Species	Localities (m)	Coordinates
<i>V. arctostaphylos</i>	60	40°55'306"N, 40°16'648"E
	300	40°36'995"N, 40°18'094"E
	800	40°49'561"N, 40°16'048"E
	1100	40°38'784"N, 40°16'283"E
	1300	40°36'991"N, 40°18'096"E
	1600	40°36'720"N, 40°17'982"E
	1800	40°35'694"N, 40°18'344"E
<i>V. myrtillus</i>	2100	40°17'480"N, 40°36'700"E
	2300	40°36'700"N, 40°17'280"E

at 430 nm with a Biochrom Libra S70 Double Beam Spectrophotometer (Allen et al., 1986).

N and P (g/dm<sup>2</sup>) were calculated according to the following formula:

$$\text{N contents} = \Sigma (\text{LDW (g)} \times \text{crude N concentration} / \text{SLA}$$

$$\text{P contents} = \Sigma (\text{LDW (g)} \times \text{crude P concentration} / \text{SLA}$$

Leaf area of each species was measured with a leaf-area meter (LI-3000, LICOR-USA). Specific leaf area (SLA) and leaf mass per area (LMA) were calculated according to Cornelissen et al. (1997):

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

$$\text{LMA} = \Sigma (\text{LDW (g)} / \Sigma (\text{LA (dm}^2))$$

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

LDW: Leaf dry weight (g)

Resorption efficiency was calculated as the percentage of nitrogen (N-RE) and phosphorus (P-RE) and it was recovered from senescing leaves (Orgeas et al., 2002; Rejmankova, 2005):

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

Nitrogen resorption proficiency (N-RP) and phosphorus resorption proficiency (P-RP) were the concentration of nutrient in senescent leaves (Killingbeck, 1996).

Soil samples (0–30 cm depth) were collected with an auger per altitude at each sampling date. The soil samples were air-dried and then sieved to pass through a 2-mm screen. Soil texture was determined by the Bouyoucos hydrometer method and pH values (1:1) were measured by pH-meter. Soil nitrogen was determined by Kjeldahl method, soil phosphorus by extraction with ammonium acetate, and organic matter content by Walkley–Black method spectrophotometrically.

### 2.3. Statistical analyses

Statistical analysis was performed by using SPSS 21. One-way analysis of variance (ANOVA) was performed in order to reveal whether foliar N, P, C, and S concentrations were significant. ANOVA and independent samples t-test were also performed for resorption efficiency and proficiency changes with respect to species and altitude. Pearson's correlation coefficient was computed to infer the pattern of relationships among altitude, pH, N, P, and organic matter in soil. The best regression model was selected according to R<sup>2</sup> values. Tukey's honestly significant difference (HSD) test was used to rank means following the analysis of variance by SPSS (SPSS Inc., 1999).

### 3. Results

There were significant differences between green and senesced leaves of *V. arctostaphylos* and *V. myrtillus* with respect to altitudes. The calculated values for each element at different altitudes through the sampling period and these significant differences can be seen in Tables 2 and 3.

P content of *V. arctostaphylos* showed significant differences in terms of altitude, but there were no significant differences in N content. The situation was opposite in terms of months. For *V. arctostaphylos*, the highest N and P (g/dm<sup>2</sup>) contents were found in May and August, and the October, respectively (Figure 1). The highest and lowest leaf N contents were measured at 1600 m and 300 m, respectively. The highest and lowest P values for *V. arctostaphylos* were at 1300 m and 1800 m (Table 2). N and P contents of *V. arctostaphylos* decreased from May to October, save for August. In addition, P contents were close to each other in June and July. In terms of sampling intervals, N content of *V. myrtillus* showed statistically

**Table 2.** N, P, C, and S values of leaves for studied species according to altitude (mean ± standard error). Different letters denote significant differences between the groups according to Tukey's HSD test in *V. arctostaphylos* (rejection level: 0.05).

Species	Altitude (m)	N		P		C (%)	S (%)
		(%)	(g/dm <sup>2</sup> )	(%)	(g/dm <sup>2</sup> )		
<i>V. arctostaphylos</i>	60	1.63 ± 0.03 (d)	1.00 ± 0.1 (a)	0.038 ± 0.005 (b)	0.006 ± 0.002 (bc)	48.95 ± 0.25 (ab)	0.09 ± 0.01 (d)
	300	1.78 ± 0.06 (d)	0.90 ± 0.1 (a)	0.055 ± 0.0008 (a)	0.008 ± 0.0007 (ab)	48.46 ± 0.37 (ab)	0.13 ± 0.01 (c)
	800	2.07 ± 0.12 (cd)	1.12 ± 0.1 (a)	0.057 ± 0.0007 (a)	0.009 ± 0.001 (ab)	48.44 ± 0.33 (ab)	0.13 ± 0.01 (bc)
	1100	2.64 ± 0.19 (ab)	1.43 ± 0.3 (a)	0.062 ± 0.001 (a)	0.01 ± 0.001 (ab)	47.25 ± 0.64 (bc)	0.16 ± 0.01 (b)
	1300	2.33 ± 0.06 (abc)	1.50 ± 0.2 (a)	0.063 ± 0.0007 (a)	0.012 ± 0.001 (a)	49.36 ± 0.35 (a)	0.14 ± 0.01 (bc)
	1600	2.78 ± 0.08 (a)	1.55 ± 0.1 (a)	0.010 ± 0.0006 (c)	0.0017 ± 0.0001 (c)	46.25 ± 0.53 (c)	0.20 ± 0.01 (a)
	1800	2.29 ± 0.09 (bc)	1.09 ± 0.1 (a)	0.011 ± 0.0001 (c)	0.0015 ± 0.0002 (c)	47.75 ± 0.30 (abc)	0.14 ± 0.01 (bc)
<i>V. myrtillus</i>	2100	1.70 ± 0.09	0.01 ± 0.01	0.009 ± 0.0005	0.001 ± 0.0001	47.51 ± 0.36	0.09 ± 0.01
	2300	1.69 ± 0.11	0.011 ± 0.01	0.008 ± 0.0005	0.002 ± 0.0003	47.61 ± 0.42	0.11 ± 0.01

**Table 3.** Comparison of green and senesced leaves of *V. arctostaphylos* and *V. myrtillus* on the basis of N, C, S, and P according to altitude (NS = not significant; \*P < 0.05; \*\*P < 0.01).

Species	Nutrient	n	Green leaves	Senesced leaves
<i>V. arctostaphylos</i>	N (%)	15	2.30 ± 0.05**	1.79 ± 0.07**
	C (%)	15	48.26 ± 0.17**	47.07 ± 0.54 NS
	S (%)	15	0.15 ± 0.004**	0.12 ± 0.007**
	P (%)	15	0.04 ± 0.002**	0.043 ± 0.005**
	N (g/dm <sup>2</sup> )	15	1.29 ± 0.08 NS	0.90 ± 0.13 NS
	P (g/dm <sup>2</sup> )	15	0.007 ± 0.001**	0.005 ± 0.001**
<i>V. myrtillus</i>	N (%)	15	1.79 ± 0.07 NS	1.28 ± 0.03 NS
	C (%)	15	47.39 ± 0.27 NS	48.22 ± 0.8 NS
	S (%)	15	0.10 ± 0.004 NS	0.08 ± 0.005*
	P (%)	15	0.009 ± 0.001*	0.007 ± 0.001 NS
	N (g/dm <sup>2</sup> )	15	0.011 ± 0.002 NS	0.008 ± 0.001 NS
	P (g/dm <sup>2</sup> )	15	0.002 ± 0.001 NS	0.001 ± 0.001 NS

important differences, while there were no significant differences in terms of altitude. The highest N and P contents for *V. myrtillus* were observed in July at 2300 m and the lowest in September (Figure 1). N and P contents of *V. myrtillus* decreased from June to September, save for July and October. According to Tukey's HSD test results, the data showing the statistical differences are given in Figure 1.

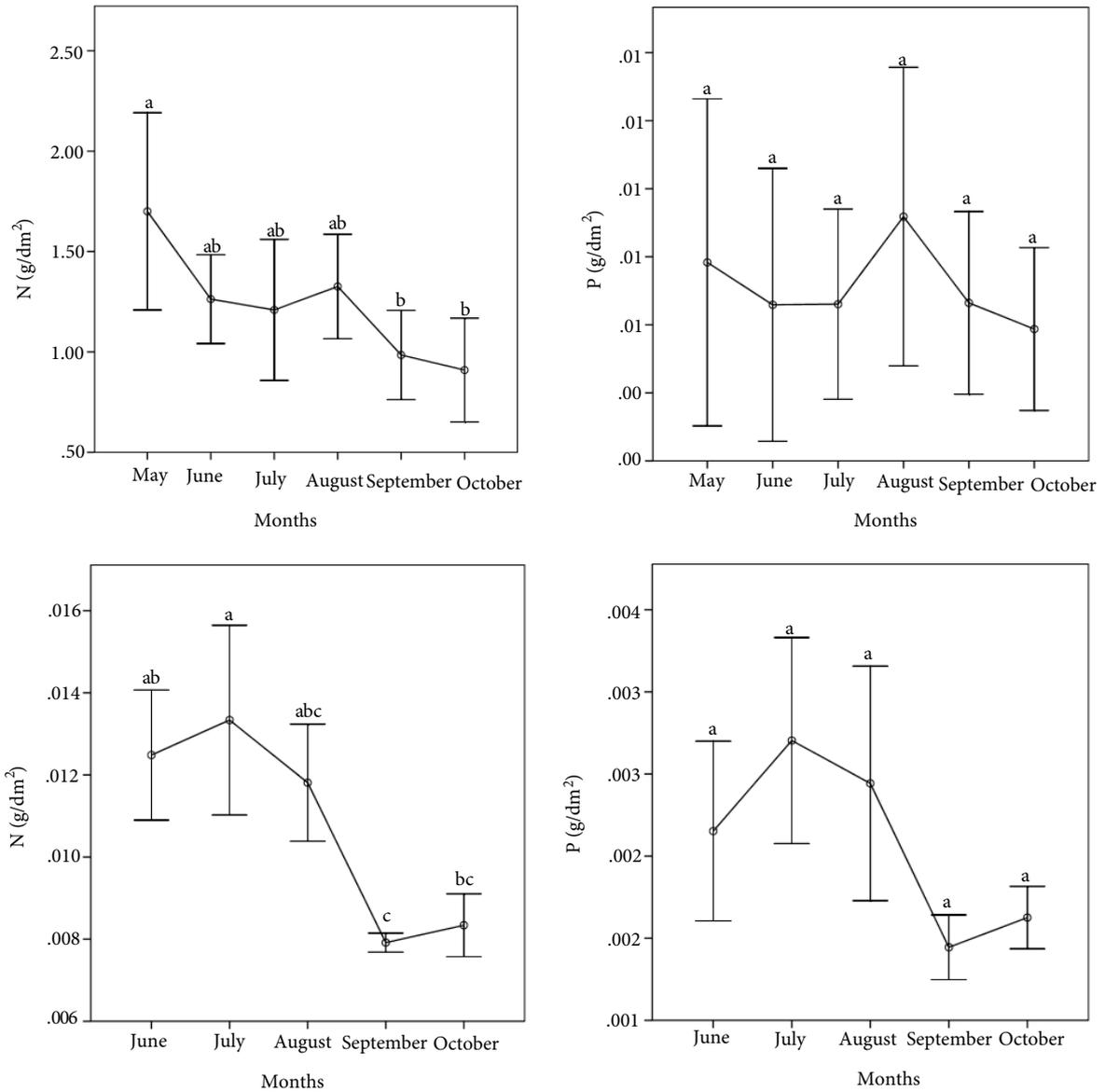
The highest and the lowest LMA values (g/dm<sup>2</sup>) of *V. arctostaphylos* were found in May and June at 60 and 1600 m, respectively. For *V. myrtillus*, the highest LMA (g/dm<sup>2</sup>) was observed in July at 2300 m and the lowest LMA (g/dm<sup>2</sup>) in June at 2100 m. The highest and lowest SLA (dm<sup>2</sup>/g) were found in October and August and the values of the other months were similar to each other. The highest and lowest SLA values (dm<sup>2</sup>/g) of *V. arctostaphylos* were found at 1600 m and 60 m, respectively. The highest and lowest SLA values (dm<sup>2</sup>/g) for *V. myrtillus* were measured in June at 2100 m and August at 2300 m, respectively (Table 4). N-RE, N-RP, P-RE, and P-RP values ranged from 9.37% to 43.57%, 0.0079% to 1.38%, 2.32% to 50.00%, and 0.001% to 0.059%, respectively. The measured resorption efficiency and proficiency for *V. arctostaphylos* and *V. myrtillus* at different altitudes can be seen in Table 5.

The lowest P (0.006%) and N (0.095%) contents of soil were observed at 60 m, while the highest values (0.014% and 0.755%, respectively) were at 1600 m. Similar results were also obtained for organic matter content (%). The lowest value (2%) of organic matter was at 60 m and this accounts for the moderate level. The highest value of

organic matter was at 1600 m (15%) and this accounts for the very high level. Soil was acidic and usually nutrient-rich at all altitudes except for 60 m (Table 6). Considering the soil parameters, we performed regression analysis only for P and a cubic linear regression fitted between P (x-axis = P) and altitude (y-axis = meters) ( $y = 5995.234 + 1,351,257.215 x - 5.7 \times 10^{-7} x^2$ ,  $R^2 = 0.928$ ) for *V. arctostaphylos* (Figure 2). There was no correlation for *V. myrtillus*.

#### 4. Discussion

In general, macroelement concentrations (especially nitrogen) are strongly linked to photosynthetic capacity, which is clearly known to reduce in the process of senescence (Feller and Fischer, 1994; Kutbay et al., 2005), during which remobilization of mineral nutrients (except calcium and manganese) from leaves to woody parts takes place (Marschner, 1995). We found that, on average, N, C, S, and P (%) values were 2.21%, 48.06%, 0.14%, and 0.04% for *V. arctostaphylos* and 1.69%, 47.56%, 0.10%, and 0.008% for *V. myrtillus*, respectively. N, P, C, and S levels in senesced leaves of both species were generally lower. However, C (%) concentration of *V. myrtillus* and P (%) concentration of *V. arctostaphylos* increased in the senescence period. N and P resorption mechanisms are more effective due to the higher N and P concentrations before senescence (Milla et al., 2004). Turkis and Ozbucak (2010) determined that mature leaf nutrients were higher than in senescent leaf and N concentrations increased in the senescence period. Similarly, Ozbucak et al. (2009)



**Figure 1.** N and P (g/dm<sup>2</sup>) contents of *V. arctostaphylos* and *V. myrtillus* depending on months. Different letters denote significant differences between the groups according to Tukey's HSD test (rejection level: 0.05).

demonstrated that N and P contents were decreased in senescent leaves. These differences may be due to local microclimatic factors in *V. arctostaphylos* and *V. myrtillus* associations (i.e. seepage due to precipitation during early spring) (Ozbucak et al., 2009).

The present study showed that *V. arctostaphylos* had high leaf N, C, S, and P (%) values and *V. myrtillus* had low N, C, S, and P (%) values. Lajtha (1987) and Kobe et al. (2005) suggested that higher leaf nutrient status was generally related to lower resorption efficiency within species. The lower nutrient concentration in living tissues leads to a greater nutrient resorption during senescence (Yuan A et al., 2005). In our study, the lowest N and P

concentrations and the highest N-RE and P-NE were found in *V. myrtillus*. The study also confirmed that N and S concentrations (%) of *V. arctostaphylos* and *V. myrtillus* showed significant differences ( $P < 0.01$ ) in terms of months. P (%) values of *V. myrtillus* were statistically ( $P < 0.05$ ) important depending on months and altitudes. There were significant differences ( $P < 0.01$ ) between N, C, S, and P (%) of *V. arctostaphylos* in terms of altitude. Bilgin et al. (2004) reported that the foliar N and P concentrations varied along the elevation gradient and significant changes were observed along the topographic gradient. Ozbucak et al. (2011) determined that leaf N and P concentrations were subject to significant changes during the growing season,

**Table 4.** LMA (g/dm<sup>2</sup>) and SLA (dm<sup>2</sup>/g) values of *V. arctostaphylos* and *V. myrtillus* according to altitude and months.

		n	<i>V. arctostaphylos</i>		<i>V. myrtillus</i>	
			LMA	SLA	LMA	SLA
Altitude (m)	60	15	0.635 ± 0.02 (a)	1.54 ± 0.09 (c)		
	300	15	0.582 ± 0.04 (ab)	1.75 ± 0.11 (abc)		
	800	15	0.422 ± 0.01 (ab)	2.38 ± 0.08 (ab)		
	1100	15	0.536 ± 0.09 (ab)	1.90 ± 0.27 (abc)		
	1300	15	0.631 ± 0.04 (a)	1.78 ± 0.20 (abc)		
	1600	15	0.386 ± 0.01 (b)	2.49 ± 0.17 (a)		
	1800	15	0.618 ± 0.05 (a)	1.68 ± 0.15 (bc)		
	2100	15			0.610 ± 0.02	1.87 ± 0.05
	2300	15			0.669 ± 0.01	1.64 ± 0.06
Months	May	15	0.580 ± 0.08 (a)	1.89 ± 0.26(a)		
	June	15	0.516 ± 0.03 (a)	1.99 ± 0.12 (a)	0.587 ± 0.05 (a)	1.75 ± 0.11 (a)
	July	15	0.545 ± 0.06 (a)	2.01 ± 0.24 (a)	0.681 ± 0.01 (a)	1.48 ± 0.04 (a)
	August	15	0.563 ± 0.05 (a)	1.71 ± 0.18 (a)	0.675 ± 0.05 (a)	1.47 ± 0.13 (a)
	September	15	0.540 ± 0.04 (a)	1.82 ± 0.12 (a)	0.612 ± 0.03 (a)	1.65 ± 0.09 (a)
	October	15	0.521 ± 0.05 (a)	2.16 ± 0.20 (a)	0.643 ± 0.007(a)	1.54 ± 0.02 (a)

**Table 5.** N and P resorption efficiency and proficiency (%) in studied species at the altitude changes (mean ± standard error). Different letters denote significant differences between the groups according to Tukey's HSD test in *V. arctostaphylos* (rejection level: 0.05).

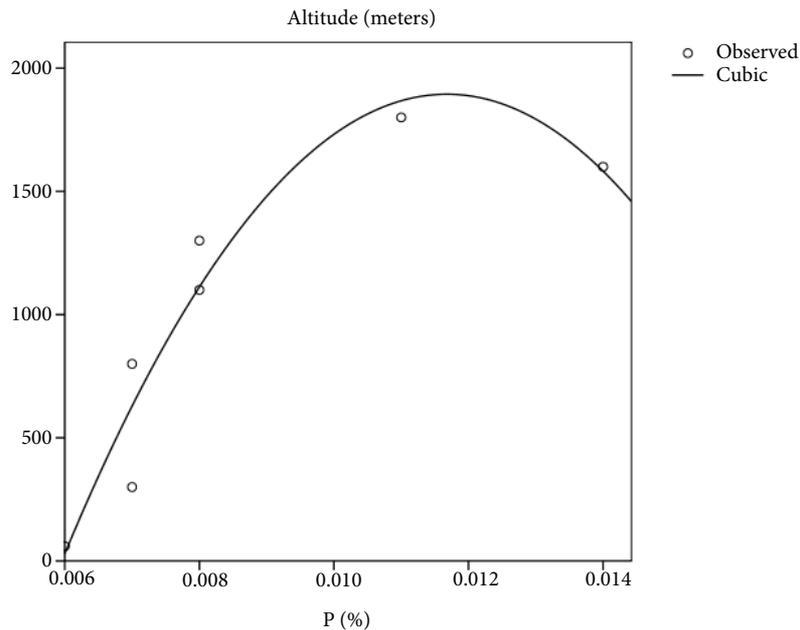
	Altitude (m)	N-RE (%)	N-RP (%)	P-RE (%)	P-RP (%)
<i>V. arctostaphylos</i>	60	9.37 ± 0.15 (g)	0.58 ± 0.05 (f)	7.81 ± 0.80 (e)	0.059 ± 0.0005 (a)
	300	26.82 ± 0.80(e)	0.6 ± 0.05 (e)	20.87 ± 0.23 (d)	0.0072 ± 0.0001 (cd)
	800	34.32 ± 0.20 (c)	0.55 ± 0.08 (f)	45.45 ± 0.90 (a)	0.006 ± 0.0001 (d)
	1100	34.88 ± 0.16 (b)	0.84 ± 0.05 (d)	2.32 ± 0.08 (c)	0.0084 ± 0.0001 (c)
	1300	33.93 ± 0.14 (d)	1.09 ± 0.03 (c)	38.38 ± 0.70 (b)	0.01 ± 0.0008 (b)
	1600	38.86 ± 0.14 (a)	1.29 ± 0.08 (b)	5.88 ± 0.20 (f)	0.001 ± 0.0001 (e)
	1800	15 ± 0.40 (f)	1.38 ± 0.06 (a)	5.29 ± 0.08 (g)	0.0015 ± 0.0001 (e)
<i>V. myrtillus</i>	2100	33.33 ± 0.03	0.008 ± 0.0001	26.08 ± 0.02	0.0017 ± 0.0001
	2300	43.57 ± 0.01	0.0079 ± 0.0003	50.00 ± 0.04	0.0015 ± 0.0002

and leaf P concentrations also significantly changed along the topographic gradient. Zhao et al. (2015) reported that both altitude changes and leaf age significantly affected the leaf C and N content, and leaf C and N values decreased with increasing altitude below 3000 m a.s.l. but increased above 3000 m a.s.l. Kutbay et al. (2003) pointed out that C

contents significantly differed with respect to leaf growth stage and species. There was a significant interaction between species and leaf growth stage for C. Vergutz et al. (2012) determined that there was lower average resorption (23.2%) in C and there was a decrease in resorption with increased nutrient status. Wang et al. (2014) reported

**Table 6.** Mean values of soil characteristics for different altitudes.

	Altitude (m)	pH	N (%)	P (%)	Organic matter (%)
<i>V. arctostaphylos</i>	60	5.55	0.095	0.006	2
	300	4.62	0.298	0.007	6
	800	4.89	0.146	0.007	3
	1100	4.53	0.305	0.008	6
	1300	5.03	0.457	0.008	9
	1600	4.27	0.755	0.014	15
	1800	4.98	0.410	0.011	8
<i>V. myrtillus</i>	2100	4.7	0.525	0.007	10
	2300	4.9	0.528	0.007	11

**Figure 2.** Soil P (%) cubic regression curve for *V. arctostaphylos*.

that C contents in senesced leaves was significantly lower and C resorption efficiency was 27% in *Chamaedaphne calyculata*. Liu et al. (2014) reported that most of the lowest concentrations of S in green and senesced leaves were in grasses or evergreen species with only a very low RE of S (12.5%) in deciduous trees; consequently, S did not show resorption or accumulation. Juszczuk and Ostaszewska (2011) revealed that elemental S levels were 2.29 and 2.36 mg/g dry weight in young and old leaves, respectively.

Aerts (1996) pointed out that mean nutrient resorption efficiency was 40%–75% and 30%–70% for N and P in deciduous species, respectively. N and P resorption

efficiencies were within the ranges of 26%–64% and 56%–71% in deciduous forests, too (Boerner, 1985; Côte et al., 2002). N resorption efficiency in some deciduous species like *Quercus suber*, *Populus nigra*, and *Frangula alnus* was found to be 47.9%, 62.6%, and 61.6%, respectively (Escudero et al., 1992; Turkis and Ozbuca, 2010). In our study, N resorption efficiency values of both species were between 9.37% and 43.57%, and P resorption efficiency values were between 2.32% and 50.00%. Resorption efficiency values of *V. myrtillus* were found to be within normal limits and resorption efficiency values increased in parallel with the altitude increase. However, N

resorption efficiency of *V. arctostaphylos* at lower (60 m) and higher (1800 m) altitudes were below the declared limits. P resorption efficiency for *V. arctostaphylos* was within the normal limits at 800 and 1300 m. It was seen that the plants of both species effectively used N and P at high elevations. The reason for this may be due to the increase in the concentration of N and P in the soil. Kilic et al. (2010) reported that resorption was affected by the altitude gradient, and, as a result, resorption efficiency and proficiency altered depending on altitude. Killingbeck (1996) and Vergutz et al. (2012) argued that water availability, timing of abscission, leaf nutrient status, or shade could cause the variations between resorption efficiencies.

Resorption proficiency is considered to be a stable indicator of the plant capacity to reuse minerals rather than resorption efficiency (Killingbeck, 1996, 2004). Killingbeck (1996) argued that the absolute levels at which nutrients are diminished constitute a more objective criterion of the degree that acted to minimize mineral loss, since proficiency was not subject to the temporal changes in mineral concentration in the green leaves and sampling time (Kobe et al., 2005). Complementing the above argument, Yuan ZY et al. (2005) described resorption proficiency as the amounts of nutrients left in unit mass of senescent leaf. Killingbeck (1996) further reported that resorption was extremely proficient in plants in which nitrogen and phosphorus concentrations decreased below 0.7% and 0.05%, respectively, during their senescence stages. Statistically significant differences were found among species in respect to N and P resorption efficiency and proficiency. N resorption proficiency increased while P resorption proficiency decreased with the altitude increase in *V. arctostaphylos*. On the contrary, Tang et al. (2013) determined that N resorption proficiency decreased as altitude increased for all woody species and for the different plant groups. P resorption proficiency values of *V. arctostaphylos* were sufficient at all altitudes except for 60 m. However, N resorption proficiency values were only sufficient at 60, 300, and 800 m. N and P resorption proficiency values of *V. myrtillus* were also below the declared limits. *V. myrtillus* in the present study showed full resorption in all altitudes with respect to threshold values as described by Killingbeck (1996).

In this study, the LMA values increased for both species until August and then showed a significant decrease for the rest of the season. However, significant differences were only observed in LMA values of *V. arctostaphylos* in terms of altitudes. The increase in LMA can be explained by the high concentrations of N and P in these months.

Diminution of LMA also brings potential short-term benefits of lower leaf structure costs per area, and lower maintenance costs (i.e. respiration rates per area) (Lusk et al., 2008; Kilic et al., 2010). SLA is the rate of leaf area and leaf dry matter, and it is one of the most significant leaf characteristics (Liu et al., 2008; Ozbucak et al., 2011). We found that SLA values for *V. arctostaphylos* had only significant differences with respect to altitude. There were no significant differences in SLA values of *V. myrtillus* depending on months and altitude. Similarly, Bilgin et al. (2004) reported that there were no important differences in SLA between mid-growing season and senesced leaf samples in either basal or stem leaves. Ozbucak et al. (2011) revealed that the SLA and LMA significantly changed along with the topographic gradient and during the growing season.

N and P (%) contents of soils were significantly different from upper and lower localities. This may be due to the differences between the localities in terms of altitude, temperature, precipitation, and other abiotic factors. Topographic variables are more important than the vegetation types in explaining the soil data. In our study, soil N and P (%) contents generally increased with increasing altitude. Kilic et al. (2010) also reported that total N, available P, soil water content, and soil organic matter increased along with the altitudinal gradient. Other researchers found that there were positive correlation coefficients between soil and plant nutrient levels (Powers, 1984; Johnson et al., 1987). Likewise we determined that there was high N resorption efficiency in soils that had high N concentration. Soil N concentrations affected plant N concentration and this feedback may also alter plant growth, net primary productivity, and ecosystem productivity (Yuan ZY et al., 2005).

In conclusion, according to the values of our study, P resorption proficiency of *V. arctostaphylos* was sufficient at all altitudes except for 60 m. However, N resorption proficiency values were only sufficient at 60, 300, and 800 m. N and P resorption proficiency values of *V. myrtillus* were also below the declared limits at all altitudes. In the present study, *V. myrtillus* showed full resorption with respect to threshold values as described by Killingbeck (1996). The primary reason for this result may be low soil N and P values at these altitudes. The study also revealed that nutrient (N, C, S, and P) concentrations and contents in a subalpine zone are higher than in alpine zones. Furthermore, green leaf nutrients of both species were higher than in senescent leaf. The SLA and LMA significantly changed along with the topographic gradient and during the growing season.

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