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# Foliar Nutrient Dynamics and Foliar Resorption in *Quercus brantii*Lindley along an Elevational Gradient

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**Abstract:** Foliar mass per area (mg dm<sup>-2</sup>) -based nitrogen and phosphorus concentrations, specific leaf mass (mg dm<sup>-2</sup>) and absolute and proportional resorption in *Quercus brantii* was investigated along a topographic gradient from 450 to 850 m altitude. Foliar N and P concentrations in *Q. brantii* exhibited significant differences with respect to topographic position and sampling dates in all of the studied parameters. A sharp decrease was observed from April to September in terms of Specific Leaf Mass (SLM) values. However, mass per area-based absolute and proportional N resorption was lowest at 450 m, while absolute and proportional P resorption was lowest at 850 m. Significant correlations were found between mass per area-based leaf nutrient concentration and foliar resorption except for the correlations between absolute P resorption and foliar P concentrations at 450, 650 and 750 m during full-leaf expansion and 850 m during senescence, respectively.

Key words: Absolute resorption, proportional resorption, foliar nutrient dynamics, Fagaceae, Quercus brantii

### INTRODUCTION

The resorption of nutrients prior to leaf fall is one of the key processes by which plants conserve them. This process reduces the likelihood of nutrient loss in litter dropped on the forest flor and subsequently, the withdrawn nutrients are redeployed in new tissues, such as leaves and reproductive structures or stored for later use. The resorption accompanied by a reduction in nutrient restitution (through leaf litter) and requirements, affords the ecosystem a certain independence from the soil and the possibility of good management of the available elements (Singh *et al.*, 2005).

Forest trees and shrubs retranslocate sizeable portions of the nutrient contents of leaves before leaf senescence. One of the most important methods to measure nutrient use efficiency in plants is to determine foliar resorption, the process of nutrient translocation from the leaves into storage tissues during senescence (Killingbeck, 1986; Killingbeck and Costigan, 1988). Nutrient resorption reduces nutrient loss with annual litterfall, so that it reduces dependence on soil nutrient supply (Xue and Luo, 2002).

Both endogenous and exogenous factors, cause foliar nutrients to vary in time and space (Del Arco *et al.*, 1991). The main cause of spatial variation is topography, vegetation, structure and disturbance. Temporal variation is primarily regulated by leaf age and growth, overall plant phenological state and weather (Chabot and Hicks, 1982; Oleksyn *et al.*, 2002).

Grime (2002) suggested that mineral nutrients, especially nitrogen and phosphorus should be considered as the major regulating factors of vegetation processes at scales ranging from the individuals to ecosystems. Oleksyn *et al.* (2002) concluded that intraspecific genetic differences exist in foliage nutrient concentrations among diverse populations and if nutrient availability were limited as a result of interactions between temperature, litter quality and mineralization, a tendency toward higher foliage concentrations of macronutrients can be adaptive feature enhancing plants metabolic activity in their native habitats.

In deciduous species, foliar nutrient concentrations will remain relatively constant from the time of full leaf expansion to the beginning of senescence, then decrease rapidly as nitrogen and phosphorus are resorbed prior to abscission (Hevia *et al.*, 1999).

Foliar nutrient content is widely recognized as an effective measure of the nutritional status of plants because leaves are the primary sites of physiological activity including photosynthesis, respiration, transpiration, gas exchange and nutrient storage (Oleksyn *et al.*, 2002).

Quercus L. comprises 531 tree and shrub species distributed among contrasting phytoclimates in the Northern Hemisphere, from temperate and subtropical deciduous forests to Mediterranean evergreen woodlands (Corcuera et al., 2002). Quercus brantii Lindley is a deciduous shrub or small tree up to a height of 6-10 m belonging to Fagaceae and distributed in Irano-Turanien

phytogeographic region (Davis, 1982). We selected this species for our investigation because it occurs along the entire topographic gradient and it is a typical species of the Irano-Turamen phytogeographic region forming pure stands.

The main aim of this study is to examine whether mass per leaf area (mg dm<sup>-2</sup>) -based nitrogen and phosphorus concentrations, specific leaf mass (mg dm<sup>-2</sup>) and absolute and proportional resorption changed the topographic position.

## MATERIALS AND METHODS

The study area and the collection of samples: *Q. brantii* specimens were collected from Batman city in the southeastem part of Turkey (41°29' E, 38°23'N) from plots located at altitudes from 450 to 850 m. The plots are located at the B8 square according to the grid system of Davis (1982). *Q. brantii* formed pure stands in the study area. Mean annual temperature in the study area is 15.8°C and mean annual precipitation 552.2 mm. Maximum temperature in the hottest month; July (M) is 44.1°C and minimum temperature for the coldest month; January (m) -19.4°C. Pluviometric quotient (Q) is 33.43. Mean annual relative humidity in summer and winter are 80 and 31%, respectively. According to these data the study area has a continental climate (Anonymous, 1994).

Plots of  $20\times20$  m were sampled along a topographic gradient altitudes from 450 to 850 m (450, 550, 650, 750 and 850 m) above sea level. Plots were selected to have stands with closed tree canopies on southwest facing slopes. From each topographic position five *Q. brantii* individuals ( $\geq 4.5$  m tall) were randomly selected and flagged. Individuals were selected a  $\geq 3$  m distance from the stems of neighboring canopy trees to avoid potential microsite variation (Boerner and Koslowsky, 1989). Since sun and shade leaves may differ in foliar nutrient concentrations, only sun leaves were collected (Grubb, 1977).

Deciduous forest species usually reach full-leaf expansion phase during earlysummer to midsummer (Diaz and Cabido, 1997). Mature leaves were preselected and they are to be collected when they have senesced. Preselection also minimises the chance of comparing green and senesced leaves of different cohorts (Van Heerwarden et al., 2003). Five fresh leaves from throughout the midcrown per individual were collected to avoid effects of crown position at the beginning of leaf expansion (at the second half of April 2000) and at the full-leaf expansion (mid-growing season) leaves (at the first half of July 2000). Senesced leaves (five leaves) were also collected at the second half of September 2000. Leaf area of specimens was measured with a leaf area meter (LI-3000, LI-COR, USA). Leaf dry mass was

determined after oven-drying at 70°C for at least 3 days. After that specific leaf mass (SLM as mg dm<sup>-2</sup>) was calculated as the leaf dry mass per unit leaf area.

From each topographic position five soil samples were taken at a depth of 30 cm with a soil corer. Each sample from each topographic position was a composite of five subsamples collected at random beneath the plant specimens. Soil samples were air-dried and sieved to pass through a 2 mm mesh prior to analysis. Because soil parameters changed very little during both sampling period soil samples belonging to both sampling period were pooled.

**Methods of chemical analysis:** Leaf samples were dried at 70°C until constant weight, ground, sieved and digested in a mixture of nitric and perchloric acids with the exception of samples for N analysis. Nitrogen (N) and phosphorus (P) analysis were made by standard methods (Allen *et al.*, 1986).

Foliage nutrient concentrations were multiplied by leaf mass and absolute resorption was calculated as the difference between the concentration×leaf mass of the nutrient in fresh and senesced-leaves (Staaf, 1982; Wright and Westoby, 2003). As leaves can lose as much as 30 % their total dry weight during senescence and resorption estimates based on the quantity of nutrient per unit leaf area are more accurate than those determined on a mass basis. Proportional resorption was then calculated as the percentage reduction in leaf N and P per unit leaf area from fresh to senesced-leaves (Lusk and Contreras, 1989; Wright and Westoby, 2003).

Soil pH, soil nitrogen (g kg<sup>-1</sup>) and soil phosphorus (g kg<sup>-1</sup>) were determined by standard methods. For the determination of soil moisture (cm³ H<sub>2</sub>O/100 cm³ soil) about 250-300 g samples were placed in soil pins, weighed fresh, dried at 105°C for 48 h; then weighed dry and then soil moisture was calculated on a volume basis (Boemer, 1984). The results of soil analysis were explained according to Bayraklı (1987).

**Statistical analyses:** One-way ANOVA test was performed to determine whether or not SLM (mg dm<sup>-2</sup>) change with respect to leaf growth stage by using SPSS 10.0 version (Anonymous, 1999; Schaefer and Anderson 1989). Two-way ANOVA test was also performed to determine whether or not N, P and SLM change in terms of leaf growth stage and elevation by using MINITAB 12.1 version (Anonymous, 1998). Dependent and independent variables were N and P concentrations and SLM and leaf growth stages and elevation, respectively.

Multiple comparisons among pairs of means were performed using Duncan's multiple range test when a significant ANOVA result occurred.

Table 1: Variance analysis in terms of mass (mg g<sup>-2</sup>) and mass per area (mg dm<sup>-2</sup>)-based N and P concentrations and SLM (mg dm<sup>-2</sup>) of *Q. brantii* leaves with respect to elevation and months by two-way ANOVA

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Parameters		10	99	3.50	P. 1	D 1 139	a: :e
$(mg dm^{-2})$	Source	df	SS	MS	F-value	Probability	Significance
N	Elevation	4	0.07121	0.01780	5.68	0.001	\$4 sh
N	Months	2	0.73366	0.36683	117.13	0.000	***
N	Error	60	0.01879	0.00313	-	-	-
P	Elevation	4	2.28100	0.57000	6.89	0.005	ste ste
P	Months	2	3.49000	0.23600	42.15	0.000	ste ste
P	Error	60	3.31100	0.08200	-	-	-
SLM	Elevation	4	87.69000	21.92000	4.26	0.004	ole ole
SLM	Months	2	4079.89000	2039.94000	396.87	0.000	\$4 sh
SLM	Error	60	308.41000	5.14000	-	-	-

df:: Degrees of freedom, SS: Sum of Squared, MS: Mean Square, \*: p<0.05 \*\*: p<0.01

### RESULTS

Foliar N and P concentrations in O. brantii exhibited significant differences with respect to topographic position and sampling dates in all of the studied parameters (Table 1). Mass per leaf area-based N concentrations were higher at 850 m while the lowest mass per leaf area-based N concentrations were found at 450 m. The highest and the lowest mass per leaf area-based P concentrations were found at 550 and 850 m, respectively. In summary, Mass per leaf area-based N concentrations were increased with altitude, while mass per leaf area-based P concentrations were decreased with altitude. The highest and the lowest SLM values were observed at 550 and 850 m, respectively like mass per leaf area-based P concentrations (Fig. 1-4). SLM values were slightly increased from April to July. However, a sharp decrease was observed during September. According to the results of Duncan's multiple range test upland and bottomland positions were significantly different from each other in terms of N and P (mg dm<sup>-2</sup>) concentrations and SLM (mg dm<sup>-2</sup>) (Table 2).

Leaves showed a maximum N and P concentrations and SLM in April and nutrient concentrations and SLM rapidly dropped from April to June (Table 3).

Significant differences were observed along the topographic gradient with respect to absolute and proportional foliar resorption. According to the results of Duncan's multiple range test upland positions (850 m) were significantly different from bottomland positions (450 m). Mass per leaf area-based proportional N resorption was lowest at 450 m, while proportional P resorption was lowest at 850 m (Table 4).

Significant correlations were found between mass per leaf area-based leaf nutrient concentration and foliar resorption. However, the correlations between mass per leaf area-based absolute P resorption and foliar P concentration at 550 and 650 m during full-leaf expansion and 750 and 850 m during senescence were not statistically significant (Table 5 and 6).

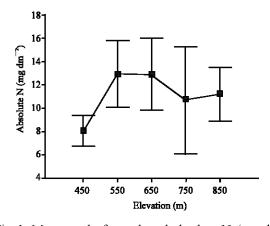


Fig. 1: Mass per leaf area-based absolute N (mg dm<sup>-2</sup>) resorption along the topographic gradient

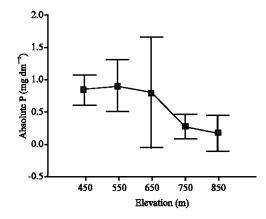


Fig. 2: Mas per leaf area-based absolute P (mg dm<sup>-2</sup>) resorption along the topographic gradient

Soil N and P concentrations were low to medium levels at 450, 550 and 850 m although soil P and N concentrations were higher at slope positions (650 and 750 m, respectively). Similarly soil moisture were higher at slope positions (650 and 750 m). There were significant differences in all of the soil parameters along the topographic position except for soil pH (Table 7).

Table 2: The comparison of mass per leaf area (mg dm<sup>-2</sup>) based N and P concentrations and SLM (mg dm<sup>-2</sup>) of Q. brantii leaves on the basis of elevations

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Parameters (mg dm <sup>-2</sup> )	450 m	550 m	650 m	750 m	850 m
N	11.02c	12.52b	12.97b	13.24ab	14.13a
P	4.56a	4.95a	3.46ab	3.15ab	2.19b
SLM	28.66a	30.95a	29.78a	28.80a	27.68a

Means followed by the same letter(s) are not significantly different at the 0.05 level using Duncan's multiple range test

Table 3: The comparison of mass per leaf area (mg dm<sup>-2</sup>) based N and P concentrations and SLM (mg dm<sup>-2</sup>) of *Q. brantii* leaves on the basis of months

Parameters (mg dm <sup>-2</sup> )	April	July	September
N	20.20a	9.07b	9.06b
P	7.88a	2.12b	1.00b
SLM	39.50a	25.34b	22.74c

Means followed by the same letter(s) are not significantly different at the p<0.05 level using Duncan's multiple range test

Table 4: Mass per leaf area-based absolute and proportional N and P resorption along topographic gradient in Q. brantii. Standard errors were given in parenthesis

Parameters	450 m	550 m	650 m	750 m	850 m	F-value	Probability
Absolute N resorption	8.05 (0.48)b	12.90 (1.04)a	12.85 (1.12)a	10.65 (1.64)ab	11.19 (0.81)ab	3.313	0.031*
Proportional N resorption	45.91 (1.41)b	55.37 (2.14)ab	59.54 (3.06)ab	51.95 (5.73)ab	61.81 (3.72)a	3.170	0.036*
Absolute P resorption	0.83 (0.09)ab	0.89 (0.14)a	0.79 (0.30)ab	0.25 (0.07)ab	0.16 (0.10)b	4.394	0.010**
Proportional P resorption	87.72 (2.29)a	69.18 (6.11)ab	81.88 (11.26)a	77.35 (5.97)ab	48.32 (8.67)b	4.183	0.013*

Means followed by the same letter(s) are not significantly different at the 0.05 level using Duncan's multiple range test. \*: p<0.05 \*\*:p<0.01

Table 5: Pearson correlation coefficients between mass per leaf area-based absolute and proportional resorption and foliar N and P concentrations during full-leaf expansion

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Parameters	450 m	550 m	650 m	750 m	850 m
Absolute N resorption-Foliar N concentration	-0.976**	0.654**	-0.901**	-0.870**	-0.530**
Proportional N resorption-Foliar N concentration	0.989**	0.991**	0.973**	0.889**	0.970**
Absolute P resorption-Foliar P concentration	-0.385 <sup>NS</sup>	-0.641**	$0.105^{NS}$	-0.203 <sup>NS</sup>	-0.546**
Proportional P resorption-Foliar P concentration	0.996**	0.944**	0.940**	0.920**	-0.546**

\*\*: p<0.01, NS: Not Significant

Table 6: Pearson correlation coefficients between mass per leaf area-based absolute and proportional resorption and foliar N and P concentrations during senescence

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Parameters	450 m	550 m	650 m	750 m	850 m
Absolute N resorption-Foliar N concentration	-0.689**	0.654**	0.775**	0.225 <sup>NS</sup>	0.831**
Proportional N resorption-Foliar N concentration	0.944**	0.991**	0.986**	0.933**	0.982**
Absolute P resorption-Foliar P concentration	0.935**	0.725**	0.632**	$0.479^{NS}$	-0.241 <sup>NS</sup>
Proportional P resorption-Foliar P concentration	0.996**	0.945**	0.941**	0.920**	0.657**

\*\*: p<0.01, NS: Not Significant

Table 7: Mean values for soil parameters along the topographic position and the comparison of soil parameters by one-way ANOVA test. Standard errors are given in parenthesis

Parameters	450 m	550 m	650 m	750 m	850 m	F-value	Sig.
Extractable N (g kg <sup>-1</sup> )	0.47 (0.07)a	0.45 (0.09)a	0.45 (0.04)a	0.78 (0.16)b	0.34 (0.06)a	7.351	*
Extractable P (g kg <sup>-1</sup> )	0.008 (0.25×10 <sup>-3</sup> )a	$0.008 (0.19 \times 10^{-3})a$	0.015 (0.05)b	0.009 (0.003)a	0.009 (0.002)a	7.230	*
Moisture cm <sup>3</sup> H <sub>2</sub> O/100 cm <sup>3</sup> soil	60 (2.20)a	65 (2.14)a	71 (3.30)b	71 (1.74)b	66 (3.25)a	8.105	*
pH	7.50 (0.05)a	7.40 (0.06)a	7.65 (0.20)a	7.50 (0.11)a	7.45 (0.05)a	1.770	NS

Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test. \*: p<0.05 NS: Not Significant Sig.: Significance

Table 8: Proportional (%) N and P foliar resorption for some deciduous and evergreen species

Species	Leaf habit	N	P	Locality	Source
Quercus brantii	Deciduous	54.9	66.2	Northeastern Turkey	Present study
Q. ilicifolia	Deciduous	70.0	59.1	Rhode Island	Killingbeck and Costigan (1988)
Q. rubra	Deciduous	70.0	55.0	Southern Québec	Côté et al. (2002)
Q. lobata	Deciduous	46.5	-18.6	California	Knops and Koenig (1997)
Q. douglasii	Deciduous	59.2	-27.4	California	Knops and Koenig (1997)
Q. kellogii	Deciduous	81.1	-0.8	California	Knops and Koenig (1997)
Viburnum cotinifolium	Deciduous	55.7	48.5	India	Ralhan and Singh (1987)
Fagus sylvatica	Deciduous	72.0	70.0	Sweden	Staaf (1982)
F. grandifolia	Deciduous	62.0	77.0	Southern Québec	Côté et al. (2002)
F. orientalis	Deciduous	73.4	72.9	Northeastern Turk <i>e</i> y	Kutbay et al. (2003)
Acer saccharum	Deciduous	66.0	78.0	Southern Québec	Côté et al. (2002)
Fraxinus americana	Deciduous	59.0	54.0	Southern Québec	Côté et al. (2002)
Populus grandidentata	Deciduous	68.0	60.0	Southern Québec	Côté et al. (2002)
Corylus avellana	Deciduous	39.6	14.0	Poland	Zimka and Stachurski (1992)
Lonicera maackii	Deciduous	33.6	40.2	Ohio	Demars and Boerner (1997)
Vaccinium vacillans	Deciduous	25.7	29.1	Rhode Island	Killingbeck and Costigan (1988)

Table 8: Continued

Species	Leaf habit	N	P	Locality	Source
V. arctostaphylos	Deciduous	28.5	51.7	Northeastern Turkey	Kutbay et al. (2003)
Nothofagus pumilio	Deciduous	62.7	43.8	Central Chile	Hevia et al. (1999)
Rhododendron luteum	Deciduous	55.8	79.7	Northeastern Turkey	Kutbay et al. (2003)
D. pontica	Evergreen	51.1	57.3	Northeastern Turkey	Kutbay et al. (2003)
Quercus ilex	Evergreen	33.0	43.0	Spain	Mayor and Rodà (1992)
Q. chrysolepis	Evergreen	51.9	32.4	California	Knops and Koenig (1997)
Q. agrifolia	vergreen	43.3	17.3	California	Knops and Koenig (1997)

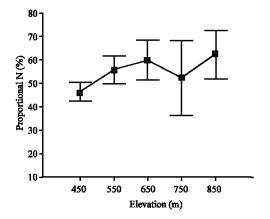


Fig. 3: Mass per leaf area-based proportional N (%) resorption along the topographic gradien

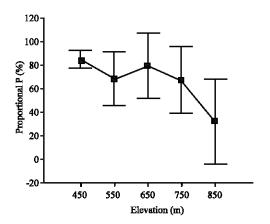


Fig. 4: Mass per leaf area-based proportional P (%) resorption along the topographic gradient

There were some differences between proportional resorption values of *Q. brantii* and the other deciduous species (Table 8).

# DISCUSSION

The first sampling date (at the beginning of leaf expansion) was significantly different from the other sampling dates with respect to foliar N and P concentrations. Nitrogen and phosphorus in particular are highly influenced by seasonal variations (Escudero *et al.*,

1992). Similar differences were also observed in some other deciduous species, e.g., canopy and subcanopy species in a *Fagus orientalis* Lipsky forest and a *Quercus cerris* L. var. *cerris* forest (Kutbay and Kılınc, 1994; Kutbay *et al.*, 2003).

Temporal variation which primarily regulated by leaf age and growth is found to be the most important factor on foliar nutrient contents during biological cycles of leaves (Chabot and Hicks, 1982; Mayor and Rodà, 1992; Orgeas *et al.*, 2002). The vegetative cycle of deciduous forest species undergoes three stages of development: the first is of rapid growth, the second refers to maturation and the third involves senescence. During full-leaf expansion nutrient concentrations increase rapidly and decrease through senescence (Regina and Tarazona, 2001).

Orgeas et al. (2002) stated leaf ageing was more important during the early stages of leaf development, as it was a result of nutrient dilution with leaf growth whereby the rate of nutrient input was less than rapid leaf growth. They also found temporal variation which is regulated by leaf ageing processes was much more important in mineral nutrition than spatial variation which is regulated mainly by disturbance. Leaf senescence is a complex, highly regulated developmental phase in the life of a leaf that results in the coordinated degradation of macromolecules. Nitrogen resorption is the physiological process by which plants withdraw nitrogen from senescing leaves, making it available for investment in new structures (Cartaxana and Catarino, 2002). These supported by Boerner (1984), findings are also Boerner (1985), Eckstein et al. (1999), Feller and Fischer (1994) and Minoletti and Boerner (1994).

Mass per leaf area-based N concentrations were increased with altitude, while mass per leaf area-based P concentrations were decreased with altitude. Tanner *et al.* (1998) found conflict results in terms of N and P concentrations of tropical montane trees. However, P concentrations of tropical montane trees were decreased with altitude.

SLM is a good indicator of relative adaptability to shade (Bigelow, 1993; Jurik, 1986; Kutbay, 2001). SLM values in the present study were similar to other *Quercus* L. species. *Q. brantii* may be classified as a

shade-intolerant species because SLM values were rather low as in other *Quercus* species (Abrams and Kubiske, 1990; Lusk and Contreras, 1989).

Demars and Boerner (1997) and Kutbay and Ok (2003) hypothesized foliar resorption probably reflected topographic differences in soil moisture than in soil fertility. However, the present study was not fully support that hypothesis. The highest soil moisture was observed at 650 and 750 m. Although the highest absolute N resorption was found at 650 m, the highest proportional N resorption and absolute and proportional P resorption was not found at 650 and 750 m.

Demars and Boerner (1997) also hypothesized foliar resorption would be greater in the lower fertility sites. Our results were consistent with that hypothesis except for absolute N resorption. Proportional N resorption was higher at 850 m where soil N concentration was lowest. Soil P concentration was lowest at 450 and 550 m and proportional and absolute P resorption was highest at 450 and 550 m, respectively.

Although, Aerts (1996) pointed out that relations between leaf nutrient status and leaf nutrient resorption were very weak, Hevia et al. (1999) showed such a relationship does exist, at least for N. The observation of significant positive and negative correlations between foliar N and P concentrations and absolute and proportional resorption during both full-leaf expansion and senescence indicated there were some relations between leaf nutrient status and leaf nutrient resorption in Q. brantii. Côté et al. (2002) stated the resorption generally increased with a decrease in leaf N and P concentration. The negative correlations between mass per area based foliar N and P concentrations and absolute and proportional N and P resorption were explained in this way. Côté et al. (2002) also suggested resorption increases with leaf nutrient concentrations in some cases and the increase is more pronounced for leaf P. High and positive correlations were usually found between foliar P concentration and proportional P resorption in the present study.

There were some differences between proportional resorption values of *Q. brantii* and the other deciduous species although N and P resorption values were usually within the ranges reported by Aerts and Chapin (2000) and Schulze *et al.* (1994). For instance, proportional P resorption was usually higher than the other *Quercus* species and P resorption in *Q. brantii* was more efficient than the other *Quercus* species. P is a very mobile within the plant and most of the phosphorus was resorbed during senescence (Ralhan and Singh, 1987). In addition to this, P resorption was more efficient than N resorption in *Q. brantii* in agreement with other studies

(Kost and Boemer, 1985; Mayor and Rodà, 1992; Xue and Luo, 2002; Kutbay and Ok, 2003). In other words, *Q. brantii* translocates greater percentage of P out of leaves before senescence Knops and Koenig (1997) stated evergreen species had higher P resorption than the deciduous species on the contrary to the present study. In addition to this, being a deciduous species proportional N resorption value of *Q. brantii* was similar to evergreen *Q. chrysolepis* and *Q. agrifolia* and lower than the other deciduous *Quercus* species. Future research should be done to more precise explanation of leaf nutrient status and leaf nutrient resorption in deciduous and evergreen species.

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