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FOLIAR RESORPTION OF NUTRIENTS IN SELECTED SYMPATRIC TREE SPECIES IN GALLERY FOREST (BLACK SEA REGION)

ABSTRACT: Gallery forests in Central Black Sea Region are dominated by *Platanus orientalis* L. The studies were performed in four sites (Mert River, Adalar, Kurupelit and Taflan Regions) located in V-shaped river valleys and differing with soil conditions. Nutrient concentrations were measured in green and senescent leaves in selected sympatric tree species. Foliar nutrient resorption efficiency (RE; as the ratio of the resorbed amounts of nutrient losses during the leaf senescence to its prior amount deposited in the leaves) and proficiency (RP; the level to which nutrient content per unit leaf mass, mg g^{-1}, has been reduced in senescent leaves) were examined in several sympatric species. The high nitrogen resorption efficiency (N-RE) (62%) were found in *Hedera helix* L., while the lowest (40%) – in *Salix alba* L. The phosphorus resorption efficiency (P-RE) ranged between 35% (*Rubus discolor* Weithe and Nees) and 50% (*S. alba*) and that of potassium (K-RE) ranged between 49% (*S. alba*) and 62% (*Robinia pseudoacacia* L.). The different trend was observed in the values of proficiency (RP). The high nitrogen resorption proficiency (N-RP) ranged between 10 mg g^{-1} (*Clematis vitalba* L.) and 18 mg g^{-1} (*R. discolor*). The high phosphorus resorption proficiency (P-RP) was found in *R. discolor* (0.5 mg g^{-1}) similar to N-RP. The lowest P-RP was found in *R. pseudoacacia* (0.3 mg g^{-1}) like K-RP (5 mg g^{-1}). The high K-RP (10 mg g^{-1}) was found in *H. helix*. There is no significant difference between four study sites. Soil N, P and organic matter concentrations were significantly correlated with green-leaf N, P and K concentrations. Significant correlations were also found between K-RP and soil nutrient concentrations and soil moisture. However, no significant correlations were found among green-leaf nutrient concentrations, RE, RP and soil nutrient concentrations and moisture.

KEY WORDS: Gallery forests, resorption efficiency, resorption proficiency, soil moisture, soil nitrogen, soil phosphorus, soil potassium, sympatric tree species

1. INTRODUCTİON

The process of nutrient resorption reduces the likelihood of nutrient loss in litter dropped on the forest floor and subsequently, the withdrawn nutrients are redeposited in developing tissues such as leaves or reproductive structures (like seeds), or stored for later use. It is an integrated part of the highly predicted process of leaf senescence and appears to occur in most species. Nutrient resorption allows the foliar nutrients to be reused rather than lost with leaf fall, thus increasing the mean residence time of nutrients in the plant (Wright and Westoby 2003).

Nitrogen and phosphorus are largely withdrawn from senescent leaves before abscission, and used for new growth or stored in vegetative tissue until the next growing season (van Heerwaarden *et al.* 2003). Especially nitrogen is one of the most important nutrients that determines plant productivity and rates of carbon cycling inside the ecosystem (Yuan *et al.* 2005a). The efficiency of nutrient resorption (RE) is meant as the ratio of the resorbed amounts of nutrient losses during the leaf senescence to its prior amount deposited in the leaves.

There is a discussion whether nutrient resorption is related to soil fertility or not (Martínez-Sánchez 2005). For example, Kost and Boerner (1985), Tanner (1985) and Minoletti and Boerner (1994) demonstrated that nutrient resorption efficiency is higher on fertile and lower on infertile soils, respectively. However, Aerts (1996) found that nutrient resorption efficiency (RE) is not correlated with nutrient availability. Because species phenology differs in multi-species forest stands, species-specific nutrient resorption and leaf fall kinetics may play an important role in modifying total nutrient return to the soil as well as in determining the overall variability in litter chemistry; thereby it can strongly affect the performance of the forest community (Niinemets and Tamm 2005).

Gallery forests are forest formations which occur along stream margins with the canopy of trees from both margins touching each other, thus forming a gallery. They oc-cur in deep valleys, with the rivers running over rocks, others develop in concave valleys with low slopes with the streams running over sand banks. Because of their microclimate and water retention capacity they are important refuge areas, as well as food and water resources for the local fauna (Scheuber *et al.* 1997; Schiavini 1997).

The objective of this study is a) to examine the leaf nutrient resorption efficiency (RE) and proficiency (RP) in sympatric tree species which occured in a *Platanus orientalis* gallery forest in different sites in Central Black Sea Region and b) to show the interactions among resorption efficiency and proficiency and leaf and soil parameters.

2. MATERIALS AND METHODS

The studies were performed in four sites (Mert River, Adalar, Kurupelit and Taflan Regions) located in V-shaped river valleys and differing to soil conditions. The study area is located in the Central Black Sea Region, in the north of Turkey (Fig. 1).

The area has a humid Mediterranean climate (Kutbay and Kılınç 1995). The years of observation of the annual temperature and annual precipitation lasted from 1941 to 2004. The highest and the lowest mean annual precipitation and mean annual temperatures were observed in Kurupelit and Adalar Regions (Table 1). The mean annual precipitation is extended from 664.2 mm in Adalar to 722.08 in Kurupelit and the mean temperature is extended from 10.5 in Ada-

Table 1. General characters of the gallery forests in the river valleys (see Fig 1).

River Locality[1]	Mean annual temperature (°C)	Mean annual precipitation (mm)	River bed width (m)	Average flow rate ($m^3 s^{-1}$)	Soil	Composition of the gallery forest
Mert	14.3	712	80	1.84	Slightly basic	*P. orientalis* dominates, others[1] are abundant.
Adalar	10.5	664	70	1.44	Slightly basic	*P. orientalis* dominates, others are abundant.
Kurupelit	14.3	722	35	2.42	Basic	*P. orientalis* dominates, others are abundant.
Taflan	13.6	750	20	2.51	Basic	*P. orientalis* dominates, others are abundant.

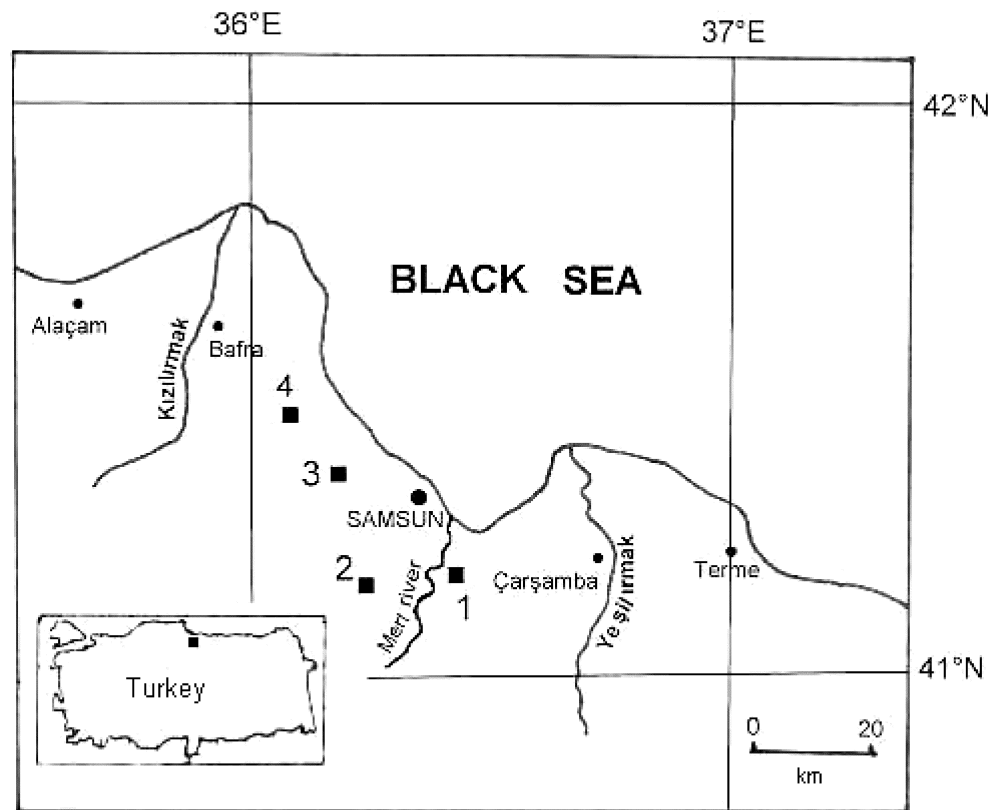[1] Others: *R. pseudoacacia, S. alba, R. discolor, H. helix, C. vitalba.*

Fig. 1. Map of the study area (1: Mer River 2: Adalar 3: Kurupelit 4: Taflan)

lar to 14.3°C in Kurupelit. The mean annual precipitation and the mean annual temperature is 712 mm and 13.6 and 14.3°C in Taflan and Mert River, respectively (Table 1). The highest temperature occurs in July (24.9°C; Kurupelit), the lowest in January (6.8°C; Adalar), the highest precipitation occurs in November (79.49 mm; Kurupelit), the lowest in July (33.88 mm; Adalar) (Quézel et al. 1980; Kutbay and Kılınc 1995).

The tree species are mainly separated into two classes as canopy and subcanopy species. Canopy status is represented by *P. orientalis*, while the other species belong to the subcanopy species. Ten 20 × 20 m (400 m²) plots were chosen from homogeneous places; one plot per locality. Plots were selected to have closed tree canopies.

Platanus orientalis L. is the widespread species around river corridors in Black Sea Region and formed gallery forest in valley bottoms and alluvial soils rich in pebbels (Davis 1982). Nutrient concentrations were measured in green and senescent leaves of

following sympatric tree species; *Platanus orientalis* L, *Salix alba* L., *Robinia pseudoacacia* L. and *Rubus discolor* Weithe and Nees, *Hedera helix* L., and *Clematis vitalba* L. Taxonomic nomenclature followed that of Brummitt and Powell (1992).

Van Heerwaarden et al. (2003) proposed that current measures of nutrient resorption efficiency lead to a substantial underestimation of the real resorption efficiency due to changes in leaf mass or leaf area during senescence. These authors suggested preselection of leaves in order to minimise the chance of comparing green and senescent leaves of different cohorts (Rentería et al. 2005). Leaf samples were taken from mid-crown part of individual to avoid effects of crown position and without insect attack. Five individuals of each species were randomly selected and flagged from each locality per plot. Individuals were selected ≥ 2.5 m from the stems of neighboring canopy trees to avoid potential microsite variation (Boerner and Koslowsky 1989). The

leaf samples were taken in monthly intervals from April 2005 to September 2005.

Green and senescent leaves were collected in each plot. Senescent leaves were collected as dead leaves that were ready to abscise. These leaves are easily to identify as they are generally of different colour from live leaves and can be removed by a gentle flicking of the branch. Senescent leaves (often yellow) were collected directly from plants (Yuan *et al.* 2005b). Leaves of climbers like *H. helix* and *C. vitalba* were taken by using extendible pruning poles from a secure perch in the canopy (Ingram and Lowman 1995).

Nutrient resorption efficiency (RE) was calculated on a per-leaf basis as percent ratio of the differences between nutrient content in green leaves minus the content in senescent leaves to the content in green leaves (Orgeas *et al.* 2002; van Heerwaarden 2004; Rejmánková 2005). In other words, RE is the percentage of leaf N, P and K that is resorbed during senescence and is named respectively as N-RE, P-RE and K-RE.

Because leaf abscission does not occur simultaneously in all species the senescent leaves were collected in different months (Rentería *et al.* 2005). Green leaves of deciduous plants were taken in June, whereas senescent leaves of deciduous plants were collected during September. Green and senescent leaves of evergreen *H. helix* were taken in August and May, respectively.

Resorption proficiency (RP) is the level to which nutrient content per unit leaf mass (mg g^{-1}) has been reduced in senescent leaves. Resorption proficiency is considered a more stable indicator of the plant capacity to reuse nutrients than resorption efficiency (Killingbeck 1996, 2004; Lima *et al.* 2006). Killingbeck (1996) argued that the absolute levels to which nutrients are reduced constitutes a more objective measure of the degree to which selection has acted to minimize nutrient loss. It is because proficiency is not the subject to temporal variation in nutrient concentration in green leaves and timing of sampling (Zotz 2004; Kobe *et al.* 2005). In other words, resorption proficiency is defined as the amounts of nutrients left in unit mass of senescent leaf (Yasumura *et al.* 2005; Yuan *et al.* 2005b).

Leaf samples were dried at 60°C until constant weight, ground, and sieved and digested in a mixture of nitric and perchloric acids with the exception of samples for nitrogen analysis. Nitrogen (N) was determined by the micro Kjeldahl method with a Kjeltec Auto 1030 Analyser (Tecator, Sweden) after digesting the samples in concentrated H$_2$SO$_4$ with a selenium catalyst. Phosphorus (P) was determined with stannous chloride method by using a Jenway spectrophotometer. Potassium (K) was determined using a Perkin-Elmer 2280 atomic absorption spectrophotometer, using an air/acetylene flame (Allen *et al.* 1986).

Three soil samples of 0–60 cm depth were collected using an auger per locality at each sampling date. The soil samples were air-dried and then sieved to pass through a 2-mm screen for the determination of the soil texture with Bouyoucus hydrometer method. pH values were measured in deionized water (1:1). One soil subsample was ground to pass through a 0.5–mm screen for analyzing soil nitrogen and phosphorus. Soil nitrogen (mg g^{-1}) was determined by the micro Kjeldahl method. Soil phosphorus (mg g^{-1}) was determined spectrophotometrically following the extraction by ammonium acetate. Soil potassium (mg g^{-1}) was determined by using a Petracourt PFP-7 flame photometer after wet digestion in nitric acid. Organic matter (mg g^{-1}) concentration was determined by Walkley-Black method (Allen *et al.* 1986; Kutbay and Kılınc 1995). For the determination of soil moisture (cm^3 H$_2$O 100 cm^{-3} soil) about 250–300 g samples were placed in soil pins, weighed fresh, dried at 105°C for 48 h, then weighed again. The soil moisture was calculated on a volume basis (Boerner 1984). Soil nutrient concentrations were evaluated according to Allen *et al.* (1986) and Kılınc *et al.* (2006).

Statistical analysis was performed using SPSS 10.0 (1999) software. One-way analysis of variance (ANOVA) was also performed to show the differences among localities in terms of soil pH, soil nutrient and organic matter concentrations. Two-way analysis of variance (ANOVA) test was performed to reveal whether or not foliar N, P and K concentrations and resorption efficiency and proficiency changed with respect to species and localities using the multivariate General

Linear Models procedure. Data set was normally distributed. Foliar nutrient concentration and foliar nutrient resorption efficiency and proficiency and, species and localities, were dependent and independent variables, respectively. Tukey's significant difference (HSD) test was used to rank means following analysis of variance by using SPSS 10.0 version. Pearson correlation coefficients were also calculated by using SPSS 10.0 (1999) software.

3. RESULTS

Significant differences were found among selected sympatric species in the studied gallery forests in terms of both RE and RP.

The highest N concentrations in green leaves i.e. 23 mg g^{-1} were found in *S. alba*. The highest P and K concentrations in green leaves were noted in *H. helix* and amounted 1.2 and 27 mg g^{-1}, respectively. The lowest N and P concentrations in green leaves were found in *C. vitalba* being 0.6 and 15 mg g^{-1}, respectively, whereas the lowest K concentrations (12 mg g^{-1}) in green leaves were found in *R. pseudoacacia* (Fig. 2).

The high nitrogen resorption efficiency (N-RE) i. e. 62% was found in *Hedera helix*, while the lowest one (40%) in *Salix alba*. The phosphorus P-RE ranged between 35% (*Rubus discolor*) and 50% (*S. alba*) and that of potassium (K-RE) between 49% (*S. alba*) and 62% (*Robinia pseudoacacia*). The different trend was observed in the values of proficiency (RP). The high nitrogen resorption proficiency (N-RP) ranged between 10 mg g^{-1} (*Clematis vitalba*) and 18 mg g^{-1} (*R. discolor*). The high phosphorus resorption proficiency (P-RP) was found in *R. discolor* (0.5 mg g^{-1}) similar to N-RP. On the contrary, the lowest P-RP was found in *R. pseudoacacia* (0.3 mg g^{-1}) like K resorption proficiency (5 mg g^{-1}). The high potassium resorption proficiency (10 mg g^{-1}) was found in *H. helix* (Fig. 3). There is no significant difference between four study sites.

Soil N and P concentrations for different sites varied from low to moderate levels, while the levels of soil K concentrations were rather high. Organic matter concentrations were at moderate levels like soil moisture. Soil pH was neutral. Adalar is nutrient-poor
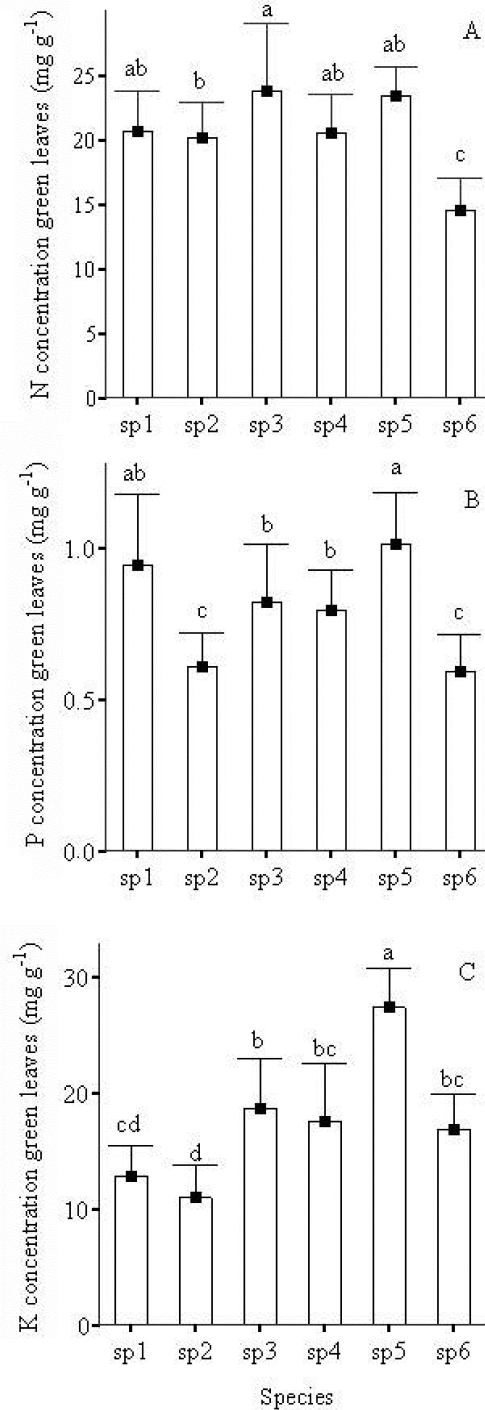

Fig. 2. Mean values of nutrient concentration in green leaves (data for all sites and study period) A – N concentration B – P concentration and C – K – concentration. Different lowercase letters indicate significant differences between sites. Vertical lines indicate standart error.
sp1. *P. orientalis*, sp2 *R. pseudo-acacia*, sp3 *S. alba*, sp4. *R. discolor,* sp5 *H. helix,* sp6 *C. vitalba*
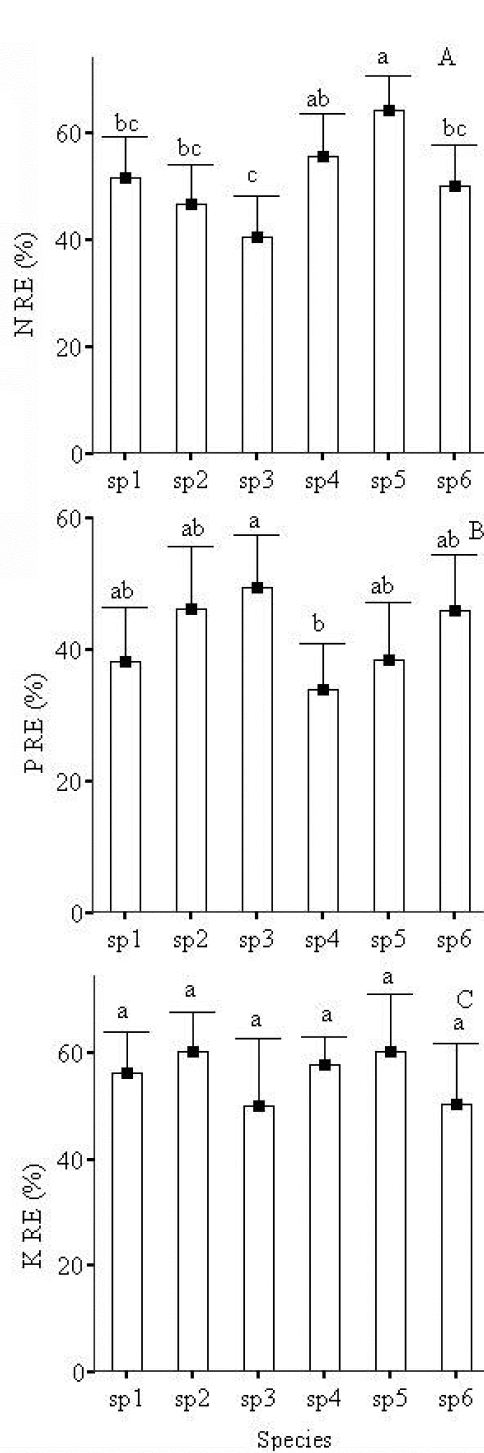
Fig. 3. Mean % values of nutrient resorption efficiency (see Table 3 for explanation) (data for all sites and study period) A – N resorption efficiency B – P resorption efficiency and C – K resorption efficiency. Different lowercase letters indicate significant differences between sites. Vertical lines indicate standart error.
sp1. *P. orientalis,* sp2 *R. pseudo-acacia,* sp3 *S. alba,* sp4 *R. discolor,* sp5 *H. helix,* sp6 *C. vitalba*
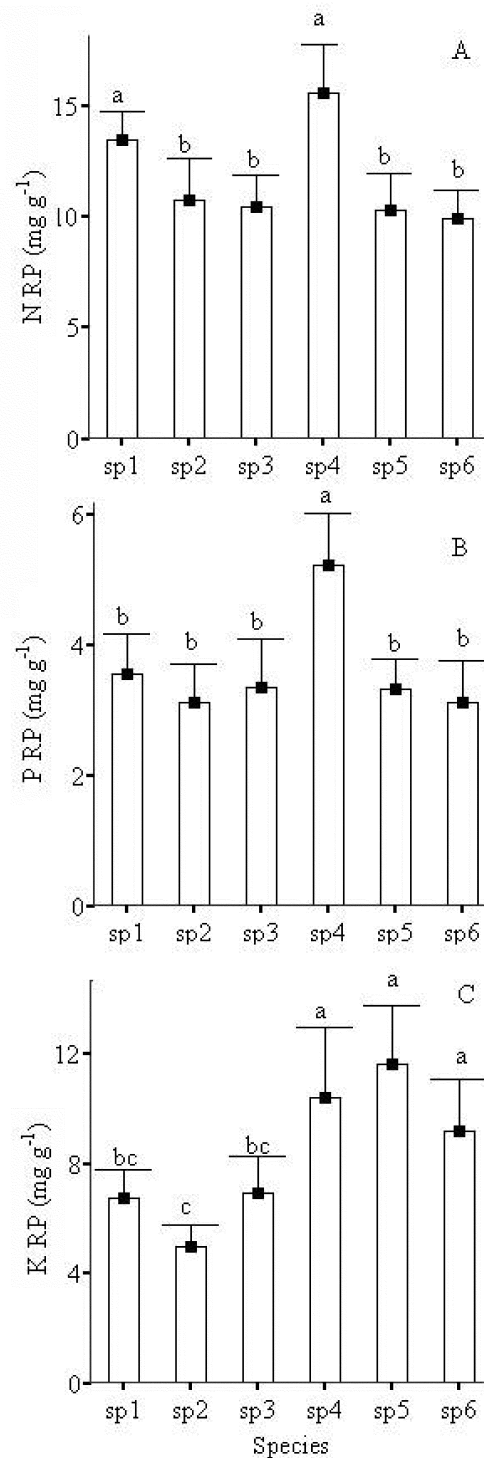

Fig.4. Mean values of nutrient resorption proficiency (RP-see table 3 for explanation) (data for all sites and study period) A – N resorption proficiency B – P resorption proficiency and C – K resorption proficiency. Different lowercase letters indicate significant differences between sites. Vertical lines indicate standart error.
sp1. *P. orientalis,* sp2 *R. pseudo-acacia,* sp3 *S. alba,* sp4 *R. discolor,* sp5 *H. helix,* sp6 *C. vitalba*

Table 2. Mean values (± S. E.) of soil characteristics (N=18) for diferent localities (see Fig. 1). Different lowercase letters indicate significant differences among localities.

Locality	Total N (mg g^{-1})	Available P (mg g^{-1}×10^3)	Available K (mg g^{-1}× 10^3)	Organic matter (mg g^{-1})	Moisture (cm^{3}H$_2$O 100 cm^{-3} soil)	pH
Mert River	2.50±0.05 a	12.00±2.07 a	57.00±0.26 ab	2.11±1.13 ab	50±2.13 b	7.15±0.34 a
Adalar	1.00±0.07 b	2.00±0.61 b	61.00±0.10 ab	1.05±0.52 ab	55±0.94 b	7.35±0.38 a
Kurupelit	2.30±0.05 a	2.00±0.75 b	61.00±0.09 ab	3.43±0.58 a	62±2.97 a	6.80±0.20 b
Taflan	2.50±0.04 a	4.00±0.60 b	71.00±0.32 a	1.85±1.55 b	62±1.57 a	7.10±0.33 a
F-value	5.546 **	2.475*	2.724 *	4.110 **	2.092 *	2.472 *

*P <0.05 **P <0.01

Table 3. Pearson correlation coefficients among soil variables and green-leaf nutrient (N, P, K) concentrations, and nutrient resorption efficiency[1] and proficiency[2] (Data for all species and sites).

	N	P	K	N-RE	P-RE	K-RE	N-RP	P-RP	K-RP
Soil Moisture	0.297	0.331	0.068	−0.221	−0.094	−0.369	−0.134	−0.270	0.927 **
Soil N	0.532 *	0.548 *	0.598 *	0.291	−0.264	0.375	0.176	0.010	−0.830 **
Soil P	0.521 *	0.542 *	0.552 *	0.123	−0.367	0.335	0.234	−0.057	0. 660 **
Soil K	0.245	0.234	0.447	0.485	0.049	0.310	0.429	0.371	0.841 **
Organic matter	0.526 *	0.542 *	0.595 *	0.301	−0.259	0.377	0.176	0.017	−0.698 **

*P <0.05 **P <0.01

[1] RE: the ratio of the resorbed amounts of nutrient losses during the leaf senescence to its prior amount deposited in the leaves.
[2] RP: the level to which nutrient content per unit leaf mass (mg g^{-1}) has been reduced in senescent leaves.

site because soil nitrogen and phosphorus concentrations were rather low as compared to other localities, while the other regions are usually nutrient-rich. However, soil phosphorus concentration was low in Kurupelit, whereas soil potassium concentration was highest (Table 2).

Soil N, P and organic matter concentrations were significantly correlated with green-leaf N, P and K concentrations. Significant correlations were also found between K-RP and soil nutrient concentrations as well as soil moisture. However, no significant correlations were found among green-leaf nutrient concentrations, RE, RP and soil nutrient concentrations and soil moisture (Table 3).

4. DISCUSSION

Bigelow (1993) stated that the climbers have a competitive advantage in light capture by allocating resources (i.e, nutrients, mainly N and P) to maximize elongation rates. Phil-lips *et al.* (2005) and Cai and Bongers (2007) also found clear evidence in favour of a novel mechanism whereby climber species may influence the ecosystem. However, Aerts (1996) stated that nutrient resorption does not differ greatly between growth forms. Statistically significant differences were found only between the values of N-RE for climber *H. helix* and the other species. Therefore, relative importance of RE and RP among plant functional groups is still highly controversial.

Aerts (1996) reported that mean nutrient resorption efficiency was 40–75% and 30–70%, respectively for nitrogen and phosphorus in deciduous species. Boerner (1984) and Côte *et al.* (2002) reported a range of 26–64% and 56–71 for N and P resorption efficiency, in deciduous forests too. Nitrogen and phosphorus resorption efficiency values in the present study were similar to the values reported for the other deciduous species. Similarly, Aerts and Chapin (2000) reported mean foliar concentrations 15–25

mg g^{-1} and 1–2 mg g^{-1}, respectively for N and P of deciduous species. Foliar N concentrations in the studied gallery forest were found to be higher than that reported by Aerts and Chapin (2000), whereas foliar P concentrations were found within the range reported by Aerts and Chapin (2000).

It is assumed that higher leaf nutrient status is usually associated with lower resorption efficiency within species (Lajtha 1987; Kobe *et al.* 2005). However, only N-RE in *S. alba* supported that hypothesis because the highest green-leaf N concentration and the lowest N-RE was found in this species. On the contrary to *S. alba*, both green-leaf N concentrations and N-RE were high in *H. helix*. So we conclude that this hypothesis is not a general trend.

The higher N-RE compared to those for P-RE might indicate that in the studied gallery forest N is probably more limiting to plant growth than P (Teklay 2004).

It has been concluded that nutrient resorption probably reflect more topographic differences in soil moisture than in fertility (De Mars and Boerner 1997). Water and nutrient availability would interact in effect on plant growth and leaf quality. Mineral nutrients are delivered from the root to the shoot along the transpirational stream, and therefore soil water deficits can limit nutrient transport simply by reducing the volume of water that moves into the plant (Lower and Orians 2002). However, nutrient RE and RP was negatively correlated with soil water content but Pearson correlation coefficients were not statistically significant. Soil water content was only significantly correlated with K-RP. Similar results were reported by Yuan *et al.* (2005c). These contradictory results may indicate the difficulty in differentiating between phenotypic and genotypic responses of plants to soil fertility and soil water content (Nambiar and Fife 1991; Kutbay and Ok 2003; Yuan *et al.* 2005c).

Positive correlations were found among soil N, P, K and organic matter concentrations and green-leaf N, P and K concentrations. Soil N concentrations affected plant N concentration and this feedback may also change plant growth, net primary, and ecosystem productivity (Yuan *et al.* 2005b). Tree species can exert a strong control on N

cycling in forest ecosystems that appears to be mediated through the quality of soil organic matter (Lovett *et al.* 2004).

The lower nutrient concentration in living tissues leads to the greater nutrient resorption during senescence (Yuan *et al.* 2005a). In the present study, the lowest K concentration and the highest K-RE were found in *R. pseudoacacia*. Similarly, green leaves of *R. pseudoacacia* has the lowest P concentration, and one of the highest P-RE. However, N did not follow this trend.

K is needed probably to increase the water passage to senescent leaves, thereby providing the appropriate cell hydration to conduct senescence adequately. Therefore, it is likely that K is retained in the leaf during most of the senescence phase. On the other hand, species with short period of leaf senescence are less prone to suffer the effects of environmental fluctuations and to these species the retention of K might not be such a priority (Milla *et al.* 2005). K-RP was not considerably high as compared to N-RP, because leaf senescence period was short in studied species (Ozbucak *et al.* in press).

Statistically significant differences were found among species with respect to N-RE and P-RE. Chapin (1980) indicated that terrestrial plants have developed some strategies to reduce nutrient stress, such as luxury consumption, reduced leaching and nutrient uptake by leaves. Often, one or more of these strategies co-occur with nutrient resorption. It is likely that different species make use of different strategies, or that a species may shift between strategies, which in turn could affect the interspecies variability of resorption efficiency (Stapel and Hemminga 1997).

Interspecific differences in terms of RP would likely result in altered species composition over time if continued over the long period (May *et al.* 2005). Resorption of N is highly proficient in vegetation that reduces N concentrations in its senescent leaves below 7 mg g^{-1} (Killingbeck and Costigan 1988; Killingbeck 1996; Schilling and Lockaby 2006). Low N-RP may be the result of rapid leaching. In many gallery forests, regular deposition of nutrient-rich sediment is necessary for forest maintenance because the soils are nutrient poor or because they experience rapid leaching associated with high

water tables (Naiman *et al.* 1998). Low N-RP in most species confirmed that a strong N conservation mechanism does not ocur in the study area (Martínez-Sánchez 2005).

On the contrary, a strong P conservation mechanism is present in the studied gallery forest because almost all of the studied species were highly P-proficient. Vegetation resorption of P is highly proficient when concentrations in senescent leaves are lower than 0.5 mg g^{-1} (Killingbeck 1996; Schilling and Lockaby 2006). As emphasized by Nambiar and Fife (1991) there is no single explanation for the resorption. It can be concluded that the relationship between vegetation strata with respect to nutrient concentrations and the relationships between nutrient concentrations in a leaf and its resorption may be the very complex process (Kutbay 2001; Kutbay *et al.* 2003).

There were significant differences among species in terms of RP. Statistically significant correlations were found between K-RP and soil N, P and K concentrations and soil organic matter concentrations. RP are species-specific and change due to the phenotypic plasticity of individual species and also depend on site conditions (Richardson *et al.* 2005).

Significant correlations were found among K-RP and soil N, P, K and organic matter concentrations and soil moisture. However, N-RE, P-RE and K-RE were not significantly correlated with soil nutrient concentrations and soil moisture.

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