FOLIAR RESORPTION IN NITROGEN-FIXING AND NON-FIXING SPECIES IN A SWAMP FOREST IN NORTHERN TURKEY

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RÉSUMÉ. — *La résorption foliaire des espèces fixatrices et non-fixatrices d'azote dans une forêt marécageuse du nord de la Turquie.* — La résorption foliaire des nutriments dans les végétaux est un facteur-clé de conservation des nutriments en particulier de l'azote (N) et du phosphore (P) et rend les plantes moins dépendantes des ressources nutritionnelles du sol. La question de savoir si les espèces fixatrices d'azote diffèrent ou non des non-fixatrices dans leurs stratégies d'utilisation de N et de P demeure fort débattue. Deux fixatrices d'azote (une actinorhize et une légumineuse) et quatre non-fixatrices ont été échantillonnées dans une forêt marécageuse du nord de la Turquie afin de comparer les fixatrices au non-fixatrices dans l'efficience (RE) et la capacité (RP) de leur résorption. Les espèces fixatrices (actinorhize et légumineuse respectivement) ont été *Alnus glutinosa* (L.) Gaertner subsp. *glutinosa* et *Robinia pseudoacacia* L. Les non-fixatrices étaient *Quercus hartwissiana* Stev., *Acer campestre* L. subsp. *campestre*, *Euonymus europaeus* L. et *Fraxinus excelsior* L. Il a été trouvé dans la présente étude que les fixatrices d'azote ont un plus faible NRE mais une plus grande capacité en P que les non-fixatrices (à l'exception de *F. excelsior*). De plus, les N/P ratios des fixatrices d'azote sont apparus plus élevés que ceux des non-fixatrices. La résorption foliaire ne s'est pas avérée de forte capacité tant chez les fixatrices que chez les non-fixatrices d'azote dans notre étude.

SUMMARY. — Foliar resorption of nutrients in plants is a key factor to conserve nutrients especially nitrogen (N) and phosphorus (P) and makes plant species less-dependent to soil nutrient status. There is much debate whether N-fixing and non-fixing species differ or not with respect to N and P usage strategies. Two N-fixing (one actinorhizal and one legume) and four non-fixing species were sampled in a swamp forest in northern Turkey to compare nitrogen-fixing and non-fixing species with respect to resorption efficiency (RE) and resorption proficiency (RP). Actinorhizal and legume species were *Alnus glutinosa* (L.) Gaertner subsp. *glutinosa* and *Robinia pseudoacacia* L., respectively. Non-fixing species were *Quercus hartwissiana* Stev., *Acer campestre* L. subsp. *campestre*, *Euonymus europaeus* L. and *Fraxinus excelsior* L. It has been found that N-fixing species had lower NRE than non-fixing species in the present study, while N-fixing species were more P-proficient than non-fixing species (except for *F. excelsior*). Additionally, N/P ratios of N-fixing species were higher than those of non-fixing species. Foliar resorption was not highly proficient in both N-fixing and non-fixing species in the present study.

Foliar resorption is an important mechanism of nutrient conservation and up to 80 % of nitrogen (N) and phosphorus (P) foliar pools can be re-translocated and expressed as resorption efficiency (RE) and resorption proficiency (RP) (Chapin & Kedrowski, 1983; Lambers *et al.*, 1998). RE is the difference between the nutrient concentration in green leaves and senescent

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Rev. Écol. (Terre Vie), vol. 69, 2014.

leaves, given as a percentage (Distel *et al.,* 2003), whilst RP is the absolute value by which nutrients are reduced in senescent leaves (Yuan *et al.,* 2005; Lima *et al.,* 2006). Higher levels of resorption proficiency correspond to lower final nutrient concentrations in senescent leaves, thus the lower concentration of a nutrient in senescent leaves indicates greater resorption proficiency (Killingbeck, 1996; van Heerwarden *et al*., 2003).

Foliar nutrient resorption can vary depending on soil fertility (Stachurski & Zimka, 1975), leaf nutrient status (Del Arco *et al.*, 1991), time span of senescence (Nordell & Karlson, 1995; Côté *et al.*, 2002), and symbiotic relationships (Richardson *et al.*, 2008). It has been suggested that patterns in foliar nutrient resorption may offer new insights into plant nutrient status and limitation for example nutrient conservation by withdrawing from senescing tissues and sequestering them for future use especially in stressful habitats (Hongua *et al.*, 2011; Reed *et al.*, 2012; Yilmaz *et al.*, 2013).

Wetlands cover one third of the Earth's surface and 60 % of these areas are swamp forests. Swamp forests are ecosystems restricted to hydromorphic soils which are subject to the presence of surface water due to upwelling of groundwater. The water table is at or near the land surface, and this causes anaerobic conditions within the root zone of plants and as a result of this, swamp forests show a slower rate of nutrient cycling, mainly due to low litter nutrient quality and slower litter decomposition rate (Calhoun, 1999; Yalcin *et al.,* 2004; Shah, 2006; Reef *et al.,* 2011). It has been stated that nitrogen-fixing plants are key constituents in many natural ecosystems throughout the world and provide the major source of N that enters the N cycle in these ecosystems (Plassmeyer, 2008). However, several authors concluded that plants which perform symbiotic N-fixation presented lower N-resorption proficiency (NRP), and N-resorption efficiency (NRE) than non-fixing species (Killingbeck, 1996; Stewart *et al*., 2008).

This study addresses the following objectives: (i) Co-occurring nitrogen-fixing (N-fixing) and non-fixing deciduous species in a swamp forest in northern Turkey were compared to find whether co-occurring N-fixing and non-fixing species differed or not regarding N and P usage strategies. (ii) Nutrient ratios (N/P ratio) were investigated to find whether the two functional groups N- or P-limited differ or not in the studied swamp forest. (iii) The interactions among plant species and soil traits were investigated by multivariate methods.

MATERIAL AND METHODS

STUDY AREA

The study was carried out in a swamp forest called "Hacı Osman Forest" (41°18' N; 36°55' E) in Central Black Sea Region of Turkey (Fig. 1). This forest covers an 86 ha area and is located 4 m a.s.l. Hacı Osman Forest has been defined as unique and endangered alluvial ecosystems on a world-wide basis and declared as a Nature Protection Area by the Turkish General Directorate of Forestry. The study area has a rather closed canopy (90 %) and is characterized by hydromorphic alluvial soils and includes later successional shade-tolerant species (Kutbay, 2001). Co-occurring tree and shrub species in this studied swamp forest are *Fraxinus excelsior, Alnus glutinosa* subsp. *glutinosa*, *Robinia pseudoacacia*, *Euonymus europaeus, Quercus hartwissiana,* and *Acer campestre* subsp. *campestre*. All species have winter deciduous leaf habit.

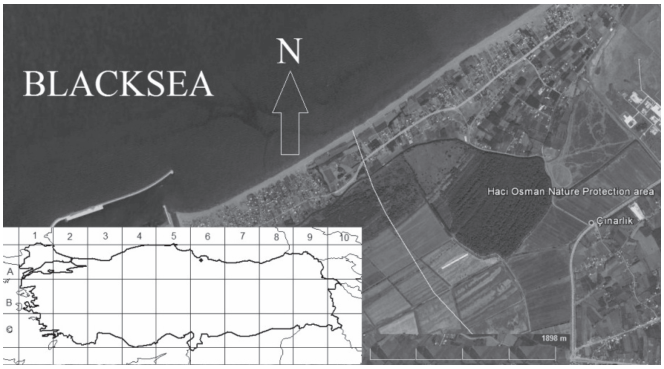

Figure 1. — Map of the study area (Google Earth Software, 2012).

Hacı Osman Forest has an oceanic type climate with a mean annual precipitation of 885.2 mm (P); summer drought is not observed in the area. Mean annual temperature is 13.8 °C. Summer rainfall (PE) is 152.2 mm. Mean maximum for the hottest month (M) and mean minimum for the coldest month (m) are 27.7 and 2.1 °C, respectively. The precipitation regime in this forest is East Mediterranean-type (Autumn, Winter, Spring, Summer; Au, Wi, Sp, Su) (Kutbay, 2001; Yalcın *et al.*, 2011; Huseyinova *et al.*, 2013).

Species and sampling

Taxonomic nomenclature for plant species followed is that of Brummitt & Powell (1992). Two functional groups were selected in the study area as N-fixing and non-fixing species (Tab. I). N-fixing species are represented by *A. glutinosa* and *R. pseudoacacia,* while non-fixing ones are represented by *A. campestre*, *F. excelsior*, *E. europaeus*, and *Q. hartwissiana*.

Leaf samples were collected monthly from May to November 2009. For each species five trees were pre-selected and marked. Leaf samples were taken from throughout the mid-crown of each individual and consisted of leaves with no evidence of insect attack. At least ten leaves per plant were collected. Individuals were selected from 4 to 10 m (only *R. pseudoacacia* individuals were taken ≥ 2.5 m because individuals were located very close to each other in the studied swamp forest) from the stems of neighbouring canopy trees to avoid potential microsite variation (Boerner & Koslowsky, 1989). When a leaf or at least two-thirds of its area turned yellow or brown, it was considered senesced (Williams-Linera, 2000; Kilic *et al.*, 2012).

Chemical analysis

Leaf samples were scanned and leaf area was calculated by using a Netcad software (Anonymous, 1999) and then leaves were dried at 70 ^{o}C for 24 h. Leaf samples were digested in a mixture of nitric acid and perchloric acid, with the exception of sample for N analysis. Nitrogen was determined by the Kjeldahl method. P concentration was determined with the stannous chloride method using a Jenway spectrophotometer (Allen *et al.*, 1986).

Ten soil samples of 0-30 cm depth were collected using an auger from May to November 2010. Then the soil samples were air-dried and sieved to pass through a 2-mm screen. The pH values were measured in deionised water (1:1). Soil nitrogen (%) was determined by the micro Kjeldahl method. Soil available phosphorus (ppm) was determined spectrophotometrically following extraction by ammonium acetate. $CaCO_3$ % was determined by Scheibler calcimeter method. Soil moisture was calculated on a volume basis by soil pins (Allen *et al*., 1986; Kacar, 2009). The results of soil analysis were evaluated according to Kacar (2009).

Calculations

RE was defined as the percentage of N and P removed from senescing leaves and calculated as the difference between peak foliar N and P and senesced leaves. Nitrogen and phosphorus resorption efficiency (NRE and PRE) (%) was calculated as the percentage of N, P and recovered from senescing leaves and calculated by: NRE = (N mature green - N senescent) / N mature green × 100 %, where: N mature green = N in mature green leaves, N senescent = N in senescent leaves. PRE = (P mature green - P senescent) / P mature green × 100 %, where: P mature green = P in mature green leaves, P senescent = P in senescent leaves (Kilic *et al.*, 2010). Green and senescent leaves were sampled in August and November, respectively.

Vergutz *et al.* (2012) stated that mass loss should be taken into account for calculation of RE and RE was calculated using the following formulas:

$$\text{Nutrient RE} = \left(1 - \frac{\text{Nutrient in senescent leaves}}{\text{Nutrient in green leaves}}\text{MLCF}\right) \times 100 \left(\text{Vergutz } et.\ al., 2012\right)$$

$$\text{MLCF} = \frac{\text{Senescent leaves mass (g)}}{\text{Green leaves mass (g)}} \left(\text{van Heerwaarden } et.\ al., 2003\right)$$

where MLCF is the mass loss correction factor. MLCF is ratio of dry mass of senesced leaves and the dry mass of green leaves (van Heerwaarden *et al.*, 2003).

Nutrient RP = Nutrient concentration in the senesced leaves (mg/g).

Statistical analysis

Statistical analyses were performed by SPSS software version 17.0 (SPSS Inc., 2007). The differences among species and sampling months regarding leaf traits and leaf nutrient concentrations were investigated by two-way ANOVA. Dependent variables were N and P concentrations, NRE, PRE, NRP, PRP and N/P ratio, respectively. Independent variables were functional groups and species. Tukey's honestly significant difference (HSD) test was used to rank means. The relationships between plant species and some soil traits were investigated by Canonical Correspondence Analysis (CCA) (Jongman *et al.*, 1995) using the ECOM version 1.33 (Henderson & Seaby, 2001).

RESULTS

Statistically significant differences were found among the studied species with respect to NRE. The highest PRE was found in nitrogen-fixing *A. glutinosa* and non-fixing *F. excelsior*. There were statistically significant differences between N-fixing and non-fixing species with respect to NRP and PRP. NRE was lower in N-fixing species than that of non-fixing species. NRE values of N-fixing species were similar. The highest NRE was found in *A.campestre* subsp. *campestre*, while the highest PRE was found in *A. glutinosa*. N-fixing species were lowest NRP like NRE. The most N- proficient species was *F. excelsior* because this species had the lowest N concentration in their senescent leaves, while the most P-proficient species was *A. glutinosa* (Tab. I; Fig. 2).

TABLE I

Mean resorption proficiency and efficiency of nitrogen (N) and phosphorus (P) (Mean ± SE)(MLCF: Mass loss correction factor). Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test

Group, family and species	NRP (mg/g)	PRP (mg/g)	NRE (%)	PRE (%)	NRE (%)	PRE (%)
			Vergutz *et al*., 2012		RE values without MLCF factor.	
Nitrogen-fixing species						
Actinorhizal:						
Betulaceae:						
Alnus glutinosa	20.86±2.0a	0.51±0.03c	49.35±1.5d	84.21±0.9a	36.12±1.95	75.94±1.49
N-fixing legume species:						
Fabaceae						
Robinia pseudoacacia	24.00±0.8a	0.91±0.01b	42.34±1.3e	67.80±1.7b	33.17±1.52	63.36±2.03
Non-N-fixing species:						
Celastraceae						
Euonymus europaeus	15.21±0.5b	1.32±0.13a	59.35±0.7c	68.69±2.3b	43.49±0.98	56.47±3.29
Oleaceae						
Fraxinus excelsior	11.71±0.7b	0.80±0.06b	64.56±0.9b	79.87±1.0a	55.71±1.14	74.84±1.35
Fagaceae:						
Quercus hartwissiana	12.32±1.1b	1.10±0.04b	62.23±0.3b	64.21±0.8b	58.02±0.36	60.23±0.93
Aceraceae:						
Acer campestre	12.03±0.4b	1.06±0.05b	70.83±0.6a	65.74±2.1b	65.61±0.73	59.60±2.49

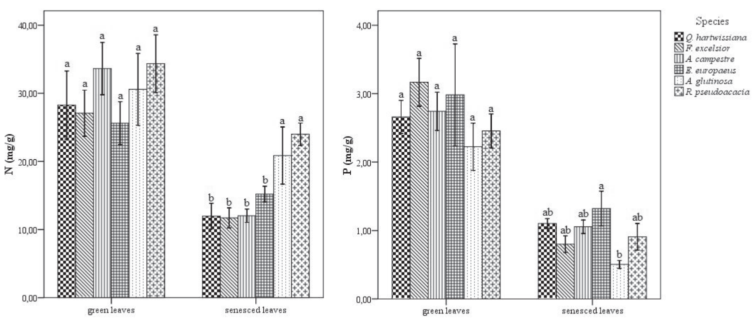

Figure 2. — N and P concentrations in green and senesced leaves of nitrogen-fixing and non-fixing species (Mean ± SE; $p < 0.001$).

High NRE and PRE values were found in both N-fixing and non-fixing species when mass loss correction factor was used (Tab. I). Leaf P concentrations of N-fixing species and N and P concentrations of non-fixing species were significantly changed over the growing season. However, no significant changes were found in leaf N concentrations of N-fixing species from May to October. However, leaf N concentration was decreased in November in N-fixing species (Table II). Significant differences were found between N-fixing and non-fixing species with respect to N/P ratio of green leaves. N/P ratios of N-fixing species were found to be higher than that of non-fixing ones (Tab. III).

TABLE II

Foliar N and P concentrations in N-fixing and non-fixing species over the growing season. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test

	Growing seasons						
Functional group	May	June	July	August	September	October	November
N-fixing species							
N (mg/g)	25.53 a	27.08 a	28.65 a	28.69 a	26.41 a	24.87 a	18.04 b
P (mg/g)	2.36 a	1.92 ab	2.13 ab	1.89 ab	1.72 abc	1.33 bc	0.91 c
Non-fixing species							
N (mg/g)	28.66 a	26.48 ab	26.07 ab	24.53 ab	22.86 b	18.02 c	11.99 d
P (mg/g)	2.73 a	2.23 ab	1.94 bc	1.92 bc	1.84 bc	1.43 cd	0.96 d

TABLE III

Mean nitrogen/ phosphorus ratio in green and senescent leaves in N-fixing and non-fixing species. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test

	Green leaves
Group, species	N/P ratio
Nitrogen-fixing species	
Alnus glutinosa	13.27a
Robinia pseudoacacia	12.86ab
Non-fixing species:	
Euonymus europaeus	8.92c
Fraxinus excelsior	8.10c
Quercus hartwissiana	9.26bc
Acer campestre	9.97abc

No significant differences were found in N and P concentrations of green leaves, while there were significant differences among senescent leaves with respect to N and P concentrations (Fig. 2). N-fixing species have higher SLA than non-fixing species (Fig. 3).

Soil pH was slightly alkaline. Soil N concentration was high, while soil P concentrations were found to be low, while $CaCO_3$ content was at medium level in studied swamp forest (Tab. IV). The cumulative percentage of variance explained by the first and axis accounted for 25.56 and 5.42 %, respectively. Species environment scores were found to be significant ($p < 0.01$). According to canonical coefficients soil N concentration and $CaCO_3$ content were significant in the first axis, while none of the soil traits were significant in the second axis (Tab. V). CCA diagram revealed that only *Q. hartwisiana* associated with $CaCO_3$ content, while the other species were not associated with soil traits, *F. excelsior*, *A. campestre* and *E. europaeus* were found in the negative side of axis 1, while the other species occurred in the positive side. (Fig. 4).

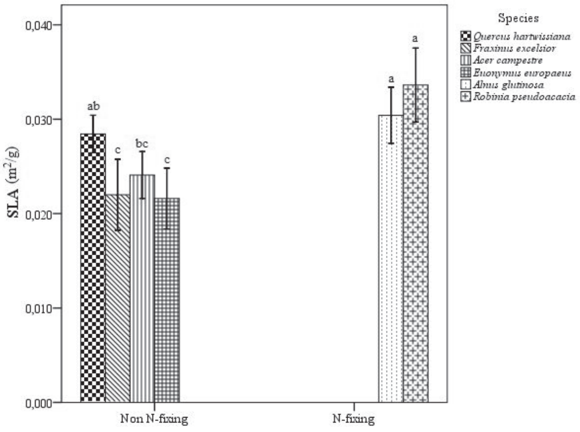

Figure 3. — SLA in nitrogen-fixing and non-fixing species (±SE; p<0.001).

TABLE IV

Soil traits in studied swamp forest (Mean±SE).

pH	7.31 ± 0.072
P(ppm)	6.10 ± 0.011
$CaCO_3$ (%)	4.67 ± 0.74
N(%)	0.29 ± 0.03
Soil Moisture (%)	88.05±8.07

TABLE V

Canonical coefficients of soil traits for axis 1 and axis 2

Soil trait	Axis 1	Axis 2
pH	-0.35	0.38
N	0.89	0.02
P	-0.13	0.26
$CaCO_3$	0.80	-0.03
Soil Moisture	0.29	-0.07

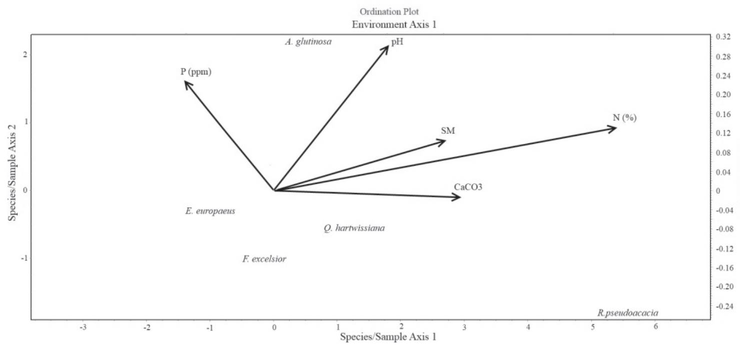

Figure 4. — CCA diagram of soil traits in studied swamp forest (SM: Soil moisture).

DISCUSSION

Several authors reported that NRE and PRE ranged from 20 to 70 % and 50 to 85 % respectively in N-fixing species (Aerts, 1996; Lima *et al.*, 2006; Ozbucak *et al.*, 2008, 2009). NRE and PRE in N-fixing species were similar to those reported in other studies in the present study. Van Heerwaarden *et al.* (2003) and Vergutz *et al.* (2012) implied that ignoring mass loss leads to an underestimation of nutrient resorption by 10 %. We found RE was increased about 10 % when we used mass loss correction factor. Vergutz *et al.* (2012) found that NRE values for deciduous angiosperms and N-fixing deciduous angiosperms namely 59.7 % and 49.5 %, respectively.

Foliar resorption was not highly proficient in both N-fixing and non-fixing species. Killingbeck (1996) stated that resorption is highly proficient in plants that have reduced N and P during their senescent stages to concentrations below 7.0 mg g^{-1} and 0.5 mg g^{-1}, respectively. N and P concentrations were above 7.0 mg g^{-1} and 0.5 mg g^{-1}, respectively in all of the species in the present study. Stewart *et al.* (2008) also found that low NRP vales for N-fixing species.

It has been reported that N-fixing plants have usually lower NRE than non-fixing species and this suggests that a trade-off between these two functional groups occurred (Stewart *et al.*, 2008; Drenovsky *et al.*, 2013). *Alnus* species and other actinorhizal plants have been found to resorb less foliar N in fall than non-fixing deciduous woody angiosperms (Kaelke & Dawson, 2003). N-fixing species had lower NRE than non-fixing species in the present study. They were also not N-proficient because they had high N concentrations in their senescent leaves. Continued N_2 fixation may lead to high senescent leaf N concentrations and rapid ecosystem incorporation of fixed N (Uliassi & Ruess, 2002). Unlike many shrub and tree species, actinorhizal plants typically retain a large amount of nutrients in their leaves during senescence instead of reabsorbing them into stem or other biomass (Stewart *et al.*, 2008; Vincent, 2011). Drenovsky *et al*. (2013) also found that N resorption in actinorhizal species were incomplete mainly due to environmental factors and phenotypic plasticity.

However, N-fixing species were more P-proficient than non-fixing species (except for *F. excelsior*) because they had low P concentrations in their senescent leaves. The highest PRE was found in *A. glutinosa*. Alders (*Alnus* species) resorbed high amount of P (Uliassi & Ruess, 2002). However, the lowest PRE was found in *Q. hartwissiana*. Oak species has been known as the highest indicators of P supply (i.e. available soil P), and lowest foliar resorption and this suggests that oak species may be less reliant on internally recycled P and more dependent on uptake (Weand *et al.*, 2010). It has been found that there were significant differences among functional types with respect to foliar P concentrations. P has been known as a critical limiting nutrient for microbial process. For example, P is very important for nodulation and N-fixation. Low P level inhibits plant growth, nodulation and N fixation processes (Almeida *et al.*, 2000; Novotny *et al.*, 2007). Honghua *et al.* (2001) and Mitchell & Ruess (2009) indicated that N-fixing plants have high P demands and high capacity for PRE. Mao *et al.* (2011) reported that mean PRE in nitrogen-fixing species was 67 %, while Vergutz *et al.* (2012) found PRE values for deciduous N-fixing angiosperms and non-fixing species of 59.6 and 54.5 % respectively, and indicated that N-fixing species should resorb less nitrogen than non-N-fixing species and potentially resorb proportionally more P and that high PRE in N-fixing species is probably due to their high P requirement.

It has been found that N/P ratios of N-fixing species were found to be higher than that of non-fixing ones in studied swamp forest. Novotny *et al.* (2007) and Kurokawa *et al.* (2010) found that N-fixers had higher N /P ratios than did non N-fixers in co-occurring woody species. It has been reported that foliar N/P ratio below 14 indicated N-limitation (Aerts & Chapin, 2000; Güsewell & Koerselman, 2002; Rejmankova, 2005). Koerselman & Meuleman (1996) indicated that N/P ratios below 16 indicate P-limitation, while Finzi *et al.* (2004) stated that N/P ratios >12.5 indicate P-limitation. N-limitation was found in all of the species, while nitrogen-fixing species were P-limited in the present study. Neatrour *et al.* (2008) showed colimitation by N and P in swamp forests. Vitousek *et al.* (2010) stated that the main cause of N-limitation in ecosystems is demand-independent losses, and constraints to N fixation can control the ecosystem level mass balance of N. N/P ratios may be an inconclusive indicator of nutrient limitation. However, high PRE and high PRP in nitrogen-fixing species showed that these species were particularly P-limited. Low biological activity in swamp forests may inhibit nutrient uptake and cycling (Rodríguez-González *et al.*, 2010; Anderson & Lockaby, 2011).

SLA has been considered a key variable to explain differences in leaf traits among different functional groups and it has been found to be involved in an efficient conservation of nutrients (Garnier *et al.*, 2001; Vilar & Merino, 2002). Plants with high SLA have leaves with high nitrogen concentration and this relationship would be important in mixed species stands (Wright & Westoby, 2003). However, such a trend is not found with respect to N concentrations, while it has been found that N-fixing species were more P-proficient than non-fixing species and high SLA of these species may contribute to optimal using of leaf P.

In conclusion, we found foliar N and P resorption in N-fixing and non-fixing species were incomplete. However, N-fixing species were more P-proficient, while non-fixing species were more N-proficient. In addition to these, N/P ratio was higher in N-fixing species. It has been emphasized that N-fixing species have some positive effects on co-occurring non-N-fixers in N-limited environments (Mason *et al.*, 2012). We found N-limitation in all of the species, whilst N-fixing species were P-limited. The differences between two functional groups with respect to foliar resorption patterns i.e. high PRP in N-fixing species vs. non-fixing ones may be interpreted on the basis of some positive effects against N- or P-limitation among co-occurring species in a swamp forest. Foliar resorption was not greatly influenced by soil traits because many of the species (except *Q. hartwissiana*) were not associated with soil traits in the studied swamp forest.

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