

SHORT COMMUNICATION

The resorption of phosphorus is greater than that of nitrogen in senescing leaves of vascular epiphytes from lowland Panama

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The epiphytic habitat is assumed to be nutrient deficient, although this generally held notion is based almost completely on circumstantial evidence (Zotz & Hietz 2001). Most studies on the nutrient relations of vascular epiphytes focus on nitrogen (Bergstrom & Tweedie 1998, Hietz & Wanek 2003, Stewart *et al.* 1995). Although nitrogen plays a key role in limiting plant growth worldwide, there is an on-going discussion whether nitrogen or rather phosphorus are more limiting in many tropical forests (Grubb 1989, Harrington *et al.* 2001, Vitousek & Howarth 1991). To identify which nutritional factor is most limiting for plant growth, nutrient ratios have been proposed as a very useful tool (Koerselman & Meuleman 1996). These authors stated that N:P ratios exceeding 16 are indicative of P limitation, while an N:P ratio < 14 suggests N limitation. Some reports of such ratios in the epiphyte literature indicate that phosphorus may indeed be limiting for epiphytes in tropical forests. For example, the N:P ratio of two field-grown bromeliads (*Tillandsia circinnata* and *T. usneoides*) decreased dramatically from 23.6 and 40.4, respectively, to 3.6 and 3.4, respectively, when fertilized with both N and P in the laboratory (Benzing & Renfrow 1974a). On the other hand, however, the average N:P ratios of mature leaves of 41 epiphyte species compiled from a number of papers did not appear particularly high (12.1 ± 10.5 , cf. Zotz & Hietz 2001).

Studies of the nutrient relations of vascular epiphytes deal almost exclusively with nutrient uptake (Benzing

1990, Benzing & Renfrow 1974b) and internal allocation, e.g. towards reproduction (Benzing & Davidson 1979, Zotz 1999), while virtually no attention has been given to nutrient retention before the abscission of plant organs. This neglect is surprising, because resorption of nutrients before leaf abscission is a keystone process in plant nutrient relations in most, if not all, ecosystems (Killingbeck 1996). Resorption allows the conservation of nutrients which otherwise have to be newly acquired. Such reduced dependence on nutrient uptake should be particularly important for canopy-dwelling plants. While ground-rooted flora can take up temporarily lost nutrients in the leaf litter after decomposition via their roots, litter input and decomposition rates are very low in the forest canopy (Nadkarni & Matelson 1991). Thus, epiphytes have to acquire nutrients from highly dilute and transitory canopy solutions. If epiphytes were more limited by phosphorus than by other nutrients, one could expect a particularly pronounced resorption proficiency for this element (*sensu* Killingbeck 1996), i.e. lower levels to which nutrients are reduced in senesced leaves. In consequence, this should lead to an increase in the N:P ratio of senesced vs. living organs. This expectation for leaves is also consistent with the earlier finding that the N:P ratios of the stems of the epiphytic orchid, *Dimerandra emarginata*, increase continuously with stem age from 11.8 to 25.9 (Zotz 1999).

In the present paper, I explore the above notions by studying the nutrient content of leaf material from 34 individual plants belonging to 20 species of vascular epiphyte (Table 1), which were growing naturally in the crowns of several tree species in the moist tropical lowland forest of Barro Colorado Island (Republic of Panama). With the exception of *Catasetum viridiflavum* (Zotz &

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Table 1. Mineral-element concentrations (mg g^{-1}) of mature (m) and senesced (s) leaves from 20 species of vascular epiphytes. Data are means of two replicates from two different plants (single determinations are indicated by *). Resorption efficiencies (%N, %P, %K) are only given for N, P and K. Also given are the N:P ratios of mature and senesced leaves and means \pm SD for each column. Species names follow D'Arcy (1987).

Species	Family	N _m	N _s	%N	P _m	P _s	%P	K _m	K _s	%K	Mg _m	Mg _s	Ca _m	Ca _s	N _m :P _m	N _s :P _s
<i>Anthurium brownii</i>	Araceae	12.3	8.4	32	1.28	0.49	61	23.5	18.4	22	3.7	6.4	17.7	36.9	9.6	17.0
<i>Anthurium clavigerum</i>	Araceae	30.7	20.9	32	1.36	0.59	57	18.9	12.5	34	7.5	7.6	24.6	31.7	22.6	35.3
<i>Anthurium friedrichsthali</i>	Araceae	13.0	7.7	41	1.32	0.61	54	32.0	25.3	21	7.5	7.6	39.4	41.4	9.8	12.6
<i>Anthurium scandens</i> *	Araceae	7.5	5.5	27	0.47	0.27	43	15.1	5.3	65	9.4	7.5	21.8	19.0	16.1	20.6
<i>Clusia uvitana</i>	Clusiaceae	7.6	6.7	12	0.38	0.31	21	11.7	10.7	9	5.8	5.2	39.2	34.7	19.8	21.9
<i>Aspasia principissa</i>	Orchidaceae	14.6	8.4	42	0.73	0.32	57	20.7	19.3	7	1.1	0.7	19.0	20.1	20.0	26.6
<i>Catasetum viridiflavum</i>	Orchidaceae	10.8	6.7	38	0.58	0.09	85	17.4	11.4	35	6.3	4.8	20.7	16.7	18.4	74.8
<i>Caularthron bilamellatum</i>	Orchidaceae	12.7	7.8	39	0.61	0.09	85	29.1	16.9	42	3.2	2.1	15.2	7.1	21.0	84.3
<i>Dimerandra emarginata</i>	Orchidaceae	9.4	4.3	54	0.94	0.30	68	18.3	6.8	63	1.9	1.7	19.5	18.5	10.0	14.2
<i>Encyclia chimborazoensis</i> *	Orchidaceae	13.4	7.1	47	0.61	0.17	73	10.0	1.7	83	2.3	2.7	10.2	11.9	22.1	42.4
<i>Epidendrum imatophyllum</i> *	Orchidaceae	15.5	8.5	45	2.11	0.62	71	33.7	19.2	43	6.4	4.4	23.3	8.1	7.3	13.7
<i>Epidendrum nocturnum</i>	Orchidaceae	11.4	6.8	40	0.54	0.08	84	2.3	0.7	68	6.5	5.9	22.4	19.7	21.2	81.4
<i>Epidendrum rigidum</i> *	Orchidaceae	11.3	6.8	40	0.51	0.07	87	2.6	1.8	31	9.4	8.8	26.4	15.5	22.0	101.6
<i>Gongora quinquenervis</i> *	Orchidaceae	25.8	13.4	48	3.09	0.75	76	34.4	7.7	78	6.1	7.9	13.0	34.3	8.3	17.9
<i>Maxillaria friedrichsthali</i>	Orchidaceae	9.8	6.5	33	0.45	0.21	52	7.4	6.1	18	2.5	2.6	10.8	9.8	21.9	30.6
<i>Oncidium ampliatum</i> *	Orchidaceae	11.4	10.9	5	0.85	0.52	38	3.4	2.8	19	8.6	10.2	28.8	11.7	13.4	20.8
<i>Polystachia foliosa</i>	Orchidaceae	20.8	10.5	49	1.02	0.43	58	20.9	13.9	34	5.2	5.2	20.7	27.1	20.4	24.6
<i>Sobralia suaveolens</i>	Orchidaceae	13.4	11.6	13	0.75	0.50	33	11.7	10.7	9	1.3	1.6	14.5	8.4	17.8	23.0
<i>Trigonidium egertonianum</i>	Orchidaceae	12.4	7.3	41	0.85	0.24	71	8.3	1.3	85	1.7	3.0	5.5	10.1	14.6	30.2
<i>Peperomia macrostachya</i>	Piperaceae	11.2	8.7	22	2.27	0.60	73	43.0	39.6	8	5.4	9.1	30.1	40.3	4.9	14.4
Mean		13.7	8.7	35.1	1.04	0.36	62.3	18.2	11.6	38.6	5.1	5.3	21.1	21.1	16.1	35.4
SD		5.8	3.6	13.4	0.71	0.21	18.5	11.6	9.7	26.3	2.7	2.8	8.8	11.5	5.8	27.2

Winter 1994), all species were evergreen, although members of some species (e.g. *Polystachya foliosa* or *Trigonidium egertonianum*) may frequently lose all leaves during particularly severe dry seasons. I sampled one senesced leaf and, for comparison, one mature green leaf per plant. The latter was comparable in size, exposure and age to the senesced leaf. Confining sampling activity to the dry season, which lasts from early January to April (Leigh *et al.* 1982), allowed me to exclude possible leaching of senescing leaves as a complicating factor. Only senesced leaves that were not affected by herbivory or pathogen attack and that were just about to abscise were used. Species in which senesced leaves do not abscise (e.g. most species of bromeliads and ferns) were excluded. After collection, leaves were dried at 60 °C for 7 d and mineral nutrient concentrations were subsequently determined with an ICP spectrometer (JY 70 plus; ISA, Munich, Germany) and a CHN-O element analyser (Heraeus, Hanau, Germany) at the University of Würzburg, Germany.

Senesced leaves showed consistent reductions in the concentrations of nitrogen (N), phosphorus (P) and potassium (K), while the concentrations of magnesium (Mg), calcium (Ca), manganese (Mn), iron (Fe) and zinc (Zn) were comparable in green and senesced leaves (Table 1; data for Mn, Fe and Zn are not shown). Nitrogen concentrations in the senesced leaves varied about 5-fold from 4.3 mg g⁻¹ (*Dimerandra emarginata*) to 21 mg g⁻¹ (*Anthurium clavigerum*), the P concentrations varied 11-fold from 0.07 mg g⁻¹ (*Epidendrum rigidum*) to 0.75 mg g⁻¹ (*Gongora quinquenervis*), while the K concentrations varied more than 50-fold (0.7 mg g⁻¹ in *Epidendrum nocturnum* to 40 mg g⁻¹ in *Peperomia macrostachya*; Table 1). The average concentrations in senesced leaves of the 20 epiphyte species were 8.7 ± 3.6 mg g⁻¹ (N, mean ± SD; n = 20), 0.36 ± 0.21 mg g⁻¹ (P) and 11.6 ± 9.7 mg g⁻¹ (K). The average resorption efficiency, which is defined as the amount of nutrients resorbed during senescence given as a percentage of the amount prior to senescence, was highest for P (62%) and rather similar for N (35%) and K (39%). Resorption efficiencies for N, P, and K were all significantly correlated with each other (P < 0.05, r² between 0.2 and 0.46). The resorption efficiency for P was significantly higher than that for N (Wilcoxon Matched Pairs Test, P = 0.0004). As a result, the average N:P ratio increased significantly from 16.1 in green leaves to 35.4 in senesced leaves. The N:K ratio, on the other hand, did not differ in mature and senesced leaves (Table 1, Wilcoxon Matched Pairs Test, P = 0.52). Similar to findings of other studies of the nutrient relations during leaf senescence (Aerts 1996), resorption efficiencies were not correlated with the nutrient status of green leaves prior to senescence (P = 0.11, 0.49, and 0.87; for N, P and K, respectively).

Table 2. Mean mineral element concentrations (mg g⁻¹) of senesced leaves from a number of tropical tree species (n = number of species) growing on sites with infertile soils. Given are concentration means ± SD and the average resorption efficiencies for N and P.

N _s	%N	P _s	%P	n	Location
12.3 ± 2.5	37	0.51 ± 0.11	53	6	Maracá Island, Brazil ¹
12.1 ± 4.1	43	0.34 ± 0.14	62	9	San Carlos de Rio Negro, Venezuela ²
10.2 ± 2.6	48	0.72 ± 0.24	45	6	Renukoot Forest, India ³

Sources: ¹ Scott *et al.* (1992), ² Reich *et al.* (1995), ³ Lal *et al.* (2001).

A comparison with nutrient resorption efficiencies of leaves from tropical tree species growing on nutrient-poor soils indicates that the average resorption efficiency of these epiphytes for N (35%) was rather low, while that for P (62%) was relatively high (compare Table 1 and 2). Retranslocation of N and P prior to leaf fall at two Amazonian sites amounted to 37 and 53% (Maracá Island, Brazil, Scott *et al.* 1992), and 43 and 62%, respectively (San Carlos de Rio Negro, Venezuela, Reich *et al.* 1995), that reported for a dry forest in India (Renukoot Forest, India, Lal *et al.* 2001) was 48 and 43%. Unfortunately, resorption data for other life forms from the same locations are not available. Considering the strong variation in tree leaves from different sites (Table 2), the question whether epiphytes differ from ground-rooted flora in their resorption efficiencies can currently not be answered unambiguously.

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 and introduced the concept of resorption proficiency. He called those plants highly proficient that reduce nitrogen and phosphorus in their senescing leaves to concentrations below 7 mg g⁻¹ and 0.5 mg g⁻¹, respectively. The ultimate potential resorption in a sample of 89 woody species resulted in concentrations of 3 mg g⁻¹ for nitrogen and 0.1 mg g⁻¹ for phosphorus (Killingbeck 1996). Applying these categories, only seven epiphyte species (35% of all species) were highly proficient in respect to nitrogen resorption, but almost twice as many (13 species or 65% of the total) in respect to phosphorus resorption. No epiphyte sample came close to the presumed potential for N resorption (3 mg g⁻¹), while final P values in senesced leaves of four epiphyte species were even lower than 0.1 mg g⁻¹. Similarly, few tropical trees from infertile sites showed high proficiency in the resorption of nitrogen, while their proficiency in the resorption of phosphorus was pronounced (Table 2). The average P concentrations of senesced leaves from San Carlos de Rio Negro were comparable with those of the epiphytes of this study (Reich *et al.* 1995), although no tree reached the extremely low concentrations observed in four epiphytes (< 0.1 mg g⁻¹; Table 1).

In summary, this paper is the first to study nutrient resorption during leaf senescence in vascular epiphytes in an attempt to identify which nutritional factor is most limiting for growth in this group of plants. Consistent with the general notion that phosphorus may be limiting in many tropical forests, the indirect measures of this study, i.e. resorption efficiency and resorption proficiency, and the resulting changes in N:P ratios during senescence consistently indicate that phosphorus is cycled much more efficiently than nitrogen in vascular epiphytes. This finding in turn suggests that phosphorus may be more important than nitrogen in limiting growth and reproduction in these canopy-dwelling plants.

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