

SHORT RESEARCH PAPER

Growth in epiphytic bromeliads: response to the relative supply of phosphorus and nitrogen

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ABSTRACT

Insufficient nitrogen (N) and phosphorus (P) frequently limit primary production. Although most nutrient studies on vascular epiphytes have focused on N uptake, circumstantial evidence suggests that P rather than N is the most limiting element for growth in this plant group. We directly tested this by subjecting a total of 162 small individuals of three bromeliad species (*Guzmania monostachia*, *Tillandsia elongata*, *Werauhia sanguinolenta*) to three N and three P levels using a full-factorial experimental design, and determined relative growth rates (RGR) and nutrient acquisition over a period of 11 weeks. Both N and P supply had a significant effect on RGR, but only tissue P concentrations were correlated with growth. Uptake rates of N and P, in contrast, were not correlated with RGR. Increased nutrient supply led to an up to sevenfold increase in tissue P concentration compared to natural conditions, while concentrations of N hardly changed or even decreased. All treatment combinations, even at the lowest experimental P supply, led to decreased N:P ratios. We conclude that P is at least as limiting as N for vegetative function under natural conditions in these epiphytic bromeliads. This conclusion is in line with the general notion of the prevalence of P limitation for the functioning of terrestrial vegetation in the tropics.

INTRODUCTION

Vascular epiphytes live in a habitat that is generally assumed to be nutrient deficient (Benzing 1990; Zotz & Hietz 2001). Until recently, the majority of studies dealing with the nutrient relations of vascular epiphytes focused on nitrogen, *i.e.* the element known to be most limiting worldwide for plant growth (*e.g.* Stewart *et al.* 1995; Bergstrom & Tweedie 1998; Endres & Mercier 2003; Hietz & Wanek 2003), but there is now an increasing body of evidence that suggests a similarly important, or even more limiting, role of a different macronutrient, phosphorus (*e.g.* Benzing & Renfrow 1974a,b; Zotz 1999, 2004). This shift in attention is due to a number of observations. For example, the N:P ratio of two field-grown bromeliads (*Tillandsia circinnata* and *Tillandsia usneoides*) decreased dramatically from >20 to about 3, when fertilized with both N and P in the laboratory (Benzing & Renfrow 1974a). Similarly, the N:P ratio increased drastically with

age in backshoots of the epiphytic orchid, *Dimerandra emarginata* (Zotz 1999). Since such nutrient ratios are believed to allow detection of the element most limiting for plant growth (Koerselman & Meuleman 1996), these findings suggest *in situ* phosphorus deficiency. The results of other studies dealing with other aspects of plant nutrient relations, *e.g.* resorption efficiency before leaf abscission (Zotz 2004) or allocation to reproductive structures (Zotz & Richter 2006), similarly suggest that P rather than N may be the most limiting element in the forest canopy. Noteworthy is that this proposition is in line with the on-going discussion on whether P rather than N is more limiting in tropical forests (*e.g.* Vitousek & Howarth 1991; Harrington *et al.* 2001; McGroddy *et al.* 2004; Benner & Vitousek 2007).

Although suggestive, none of the above studies has supplied actual experimental proof for the suggested crucial role of P in the nutrient relations of vascular epiphytes. The widely accepted method of demonstrating limitation

unambiguously is a 'well-controlled, well-replicated nutrient addition experiment' (Vitousek & Howarth 1991). Unfortunately, the few experimental studies that have directly investigated the growth response of epiphytic species to such nutrient additions (Castro-Hernández *et al.* 1999; Laube & Zotz 2003) used commercial NPK fertilizer, and thus provide no insight into the issue of the solo contribution of N and P. This motivated the current study, in which field-grown plants of three epiphyte species were transferred to a greenhouse and subjected to different regimes of N and P supply, while the remaining nutrients were not varied. This approach, which also included analysis of natural and experimentally altered tissue nutrient concentrations, should answer the question of how varying degrees of N and P deficiency might affect *in situ* growth of these epiphytic bromeliads.

MATERIALS AND METHODS

Plant material

Plant material of the three study species was obtained in January 2005 from natural populations growing on the tree *Annona glabra* (Annonaceae) in the Barro Colorado Nature Monument (BCNM, 9°10' N, 79°51' W), Republic of Panama (Leigh *et al.* 1982). All three bromeliads, *Tillandsia elongata* H.B.K. var. *subimbricata* (Bak.) L.B.Sm., *Guzmania monostachia* (L.) Rusby ex Mez. and *Werauhia sanguinolenta* (Linden ex Cogn. & Marchal) Grant form tanks, and the water and nutrients that accumulate in the overlapping leaf bases are taken up *via* absorbing scales (Benzing 2000).

Smaller individuals are known to show a much stronger growth response to changes in environmental conditions compared to larger conspecifics (Zotz 2000). Hence, we intentionally used smaller plants (initial size *c.* 7 cm maximum leaf length in *Werauhia* to *c.* 10 cm in *Tillandsia* and *Guzmania*) to document the maximum response potential. The initial dry weight (DW) ranged from 0.15 ± 0.07 g (mean \pm SD, $n = 54$) in *Guzmania*, 0.15 ± 0.09 g in *Werauhia* to 0.23 ± 0.08 g in *Tillandsia*.

Immediately after collection, plants were cleaned of any detritus accumulated in their leaf bases and remaining roots were removed if necessary. After transfer *via* air-plane to the University of Basel on 21 January 2005, plants were put on plastic racks and kept in a growing house for 2 weeks before the beginning of the experiment. A subset (5–6 individuals per species) were dried at 60 °C for 72 h in a drying oven to establish a correlation between plant fresh weight (FW) and dry weight (DW, $r^2 = 0.96$ – 0.99 , depending on species). Twice daily, plants were watered by completely filling the tank with deionised water. Environmental conditions in this pre-treatment period were similar to those of the later experiment in the same growing house, except that plants were not fertilized: daytime temperature *c.* 25 °C, nighttime temperature *c.* 20 °C, natural light supplemented by artificial light sources to ensure a *c.* 12-h light period with

c. $10 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ PFD, air humidity *c.* 60%. These conditions are within the range of conditions experienced in the field (Zotz & Winter 1994).

Growth experiment and data analysis

In the afternoon before the beginning of the growth experiment, we determined the initial fresh weight of all plants. During the experiment, which lasted for 77 days, we continued to water the plants twice daily, while nutrients were supplied once every 5 days by filling the tanks completely with one of nine different nutrient solutions. Each species had six replicates per treatment ($n = 9 \times 6$ individuals per species). The full-factorial design had three different levels of N and P concentration, which varied by one and two orders of magnitude, while the overall supply of all other nutrient elements was kept nearly constant by appropriate blending of 14 different inorganic salts, and was equivalent to half-strength Hoagland solution (Jones 1982). For example, the concentrations of K and Ca in the nutrient solutions ranged from 1.0–1.2 to 0.43–0.55 mM, respectively. Concentrations of N, on the other hand, supplied in the form of nitrate and ammonium, were 0.01, 0.14 and 1.35 mM, and those of P, which was supplied as phosphate, were 0.01, 0.08 and 0.88 mM.

The major response variable in the growth experiment was relative growth rate (RGR, $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), which is defined as:

$$\text{RGR} = (\ln \text{DW}_{\text{final}} - \ln \text{DW}_{\text{initial}}) / \Delta t \quad (1)$$

in which DW is plant dry weight and Δt is the duration of the experiment in days (Evans 1972). The initial DW was estimated from the measured fresh weight using the tight correlation between FW and DW; the final DW was directly determined gravimetrically. In a few cases, new roots had grown during the study and were excluded. All plants were dissected and total leaf area determined from digital photographs using the histogram function of Photoshop (Adobe Photoshop 6.0; Adobe, San Jose, CA, USA). Leaves and stems were dried separately to allow calculation of the components of RGR necessary for growth analysis. This technique can be used to analyse the causes of variation in growth rate by factorizing RGR in its components, *i.e.* leaf area ratio (LAR, $\text{m}^2 \cdot \text{kg}^{-1}$) and net assimilation rate (NAR, $\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) as follows (Lambers *et al.* 1998; Poorter & Van der Werf 1998):

$$\text{RGR} = \text{NAR} \times \text{LAR} \quad (2)$$

Variation in NAR, defined as the increase in plant mass per unit leaf area, reflects the balance between leaf photosynthesis and respiratory losses, which was not analysed here, while LAR, leaf area per unit plant weight, was further analysed as the product of leaf weight ratio (LWR, $\text{g} \cdot \text{g}^{-1}$), the fraction of total plant weight invested in leaves, and specific leaf area (SLA, $\text{m}^2 \cdot \text{kg}^{-1}$), the leaf area per unit leaf weight.

Mineral nutrient analysis

The LWR averaged 0.89 for the three species and we did not analyse nutrient concentrations separately for different compartments, only for entire plants. Nitrogen concentrations were determined with a CHN-S element analyser (Flash EA; Thermo Electron, Milan, Italy), while P concentrations were analysed following the protocol outlined in Chen *et al.* (1956).

Statistical analysis

All statistical analyses were done with R 2.6.0. (R Development Core Team 2007). All error terms are standard deviations. Growth data were analysed with a three-way analysis of variance (ANOVA) with the factors species, N and P level. Possible effects of these factors on SLA and LAR were explored in separate ANOVAs. The effects of SLA, LAR, LWR, NAR, P and N tissue concentrations on RGR were analysed with linear regression models. Nutrient uptake rates ($\mu\text{g}\cdot\text{g}_{\text{DW}}^{-1}\cdot\text{d}^{-1}$) were derived from the differences in total plant P and N content of the two harvests and the initial dry weight (using final DW gave highly consistent results; r^2 between 0.96–0.99). In two ANCOVAs, we then analysed the relationships of (i) these uptake rates and (ii) final N and P tissue concentrations and species with RGR.

RESULTS

The growth rates of the three species included in this study were consistently low, the highest single value of RGR being only $13.0\text{ mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ in a *Guzmania* plant. All species responded to increased nutrient supply with faster growth (Table 1, Fig. 1). We found a significant main effect of species N supply and P supply on RGR (Table 1), but the magnitude of the effects of both N and P were quite moderate: a rise in the supply of these macronutrients by two orders of magnitude raised RGR, on average, only 15–33% (Fig. 1). Even when comparing RGRs of the extreme cases (the combinations $N_{(\text{low})}$, $P_{(\text{low})}$ versus $N_{(\text{high})}$, $P_{(\text{high})}$) for individual species the increases in RGR were never very high, at about +40% (*Guzmania*), +62% (*Tillandsia*) and +99% (*Werauhia*).

Table 1. Results of a full-factorial ANOVA on the effects of the factors species, nitrogen level and phosphorus level on relative growth rate (RGR).

effect	df	F	P-level
species (S)	2, 143	38.3	<0.001
nitrogen (N)	2, 143	12.8	<0.001
phosphorus (P)	2, 143	16.4	<0.001
S × N	4, 143	1.2	0.31
S × P	4, 143	1.1	0.35
N × P	4, 143	2.0	0.10

df = degrees of freedom. F-values and significance levels (P).

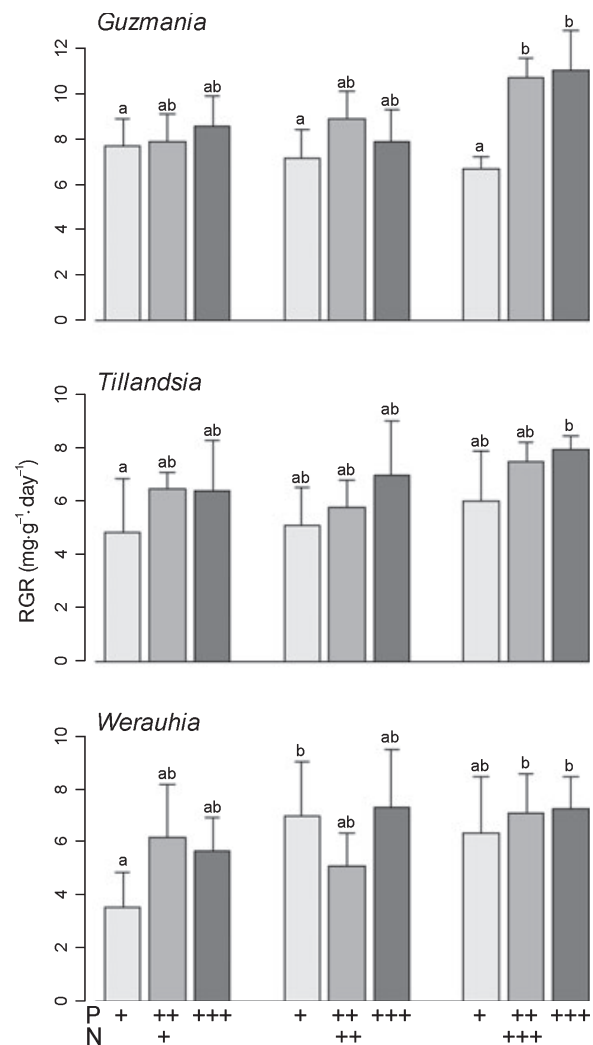


Fig. 1. Effect of increased levels of N and P supply on relative growth rates (RGR) of three species of epiphytic bromeliad. Data are means \pm SD ($n = 6$). Nutrient supply levels varied by two orders of magnitude from low (+), intermediate (++) to high (+++). The main effects of species, N supply and P supply were all significant (three-way ANOVA, $P < 0.001$, compare Table 1). Different letters indicate significant differences among treatments within a species (Tukey post-hoc test, $P < 0.05$).

Differences in nutrient supply did not have a statistically detectable effect on specific leaf area (SLA) nor on the leaf area ratio (LAR), and neither SLA nor LAR were correlated with RGR (Fig. 2A). LWR did not vary with treatment nor change compared to initial conditions, and SLA and LAR were highly correlated with each other when analysed separately for each species ($r = 0.76$ – 0.96), but varied significantly among species (two one-way ANOVAs, $F_{2,143} > 389$, $P < 0.001$, Table 2). In contrast to these variables, NAR was closely correlated with RGR in all species and explained up to 88% of the variation (Fig. 2B).

Nutrient concentrations of the field-collected plants were consistently low, averaging $0.7\text{ mg}\cdot\text{P}\cdot\text{g}_{\text{DW}}^{-1}$ and

Table 2. Morphological characteristics of three epiphytic bromeliads that are related to growth analysis.

species	SLA	LAR
<i>Guzmania monostachya</i>	34.9 ± 4.5 ^a	32.5 ± 5.4 ^b
<i>Tillandsia elongata</i>	17.3 ± 2.1 ^b	15.3 ± 2.4 ^a
<i>Werauhia sanguinolenta</i>	19.1 ± 1.8 ^c	16.8 ± 1.6 ^a

Data are means ± SD (n = 54). Different letters in the same column indicate significant differences (one-way ANOVA, Scheffé test, $P < 0.5$).

7.0 mg·N·g_{DW}⁻¹ (Fig. 3), the resulting N:P ratios being around 11 in all species. The highest treatment P supply resulted in a 5–7 fold increase in P in plant tissue during the course of the experiment, but even fertilizer with the lowest P concentration (0.01 mM) led to an almost doubled tissue P. This general pattern was identical in all species (two-way ANOVA, interaction term 'species × P': $P = 0.71$). In contrast, fertilization with different N

concentrations had relatively little effect on tissue N. Remarkably, tissue N concentrations from the field were significantly *higher* than those of the N_(low) treatment (Fig. 3, Tukey *post-hoc* test, $P < 0.05$). Consequently, the significant decrease in N:P ratios with improved nutrient supply was exclusively due to changes in tissue P.

Species identity and final P concentration had a significant effect on RGR (ANCOVA, $P < 0.01$), while N concentrations did not (ANCOVA, $P = 0.77$). However, the final concentration of P alone explained relatively little of the overall variation in RGR (Pearson product moment correlation, $r^2 = 0.07$). The calculated uptake rates of N and P, on the other hand, did not correlate significantly with RGR (ANCOVA, $P > 0.09$). These averaged 25 ± 23 - $\mu\text{g} \cdot \text{P} \cdot \text{g}_{\text{DW}} \cdot \text{d}^{-1}$ (mean ± SD, n = 162) and 17 ± 16 - $\mu\text{g} \cdot \text{N} \cdot \text{g}_{\text{DW}} \cdot \text{d}^{-1}$ (mean ± SD, n = 162). Maximum values were $106 \mu\text{g} \cdot \text{P} \cdot \text{g}_{\text{DW}} \cdot \text{d}^{-1}$ and $110 \mu\text{g} \cdot \text{N} \cdot \text{g}_{\text{DW}} \cdot \text{d}^{-1}$, respectively.

DISCUSSION

This study shows that increased supply of both N and P independently stimulate vegetative growth in these epiphytes, a pattern observed in all three species (Table 1). However, even at the highest nutrient supply, the RGRs of these epiphytes were very low, even when compared with slow-growing woody species (e.g. Grime & Hunt 1975; Poorter 1999). This finding adds support to the notion that vascular epiphytes as a group are inherently extremely slow-growing (Schmidt & Zotz 2002). Similar to plants from other nutrient-poor habitats (Chapin 1980), the potential for increased growth is quite limited in these canopy-dwelling plants: a 100-fold increase in either N or P supply resulted in a meagre increase in RGR of just 15–33% (Fig. 1).

Although growth was stimulated independently by both N and P supply in our experiment, the observations that natural tissue P concentrations were lower than at the lowest experimental level, while *in situ* tissue concentrations of N were similar or significantly *higher* than those of treated plants (Fig. 3), are highly suggestive that P is the nutrient element most limiting for growth in these epiphytic bromeliads in the field. Unfortunately, all other evidence leaves room for interpretation, because plants are known to take up nutrients in excess of the minimum requirement for current growth (Güsewell 2004; Ågren 2008). Such 'luxury consumption' affects the interpretation of the significant correlation of P with RGR, as well as interpretation of the stoichiometry of N and P. For example, the highest P concentrations and associated low N:P ratios <2.5, which we observed in all three species at the highest experimental P supply (Fig. 3), are not necessarily equivalent to optimal P concentrations or an optimal element ratio (Ågren 2008). Similarly, the relatively low N:P ratios in the tissues of field-grown individuals of our study species (Fig. 3) cannot be taken as unambiguous evidence that N rather than P is most limiting, although N:P ratios of <16.0 are frequently interpreted in that way (Koerselman & Meuleman 1996;

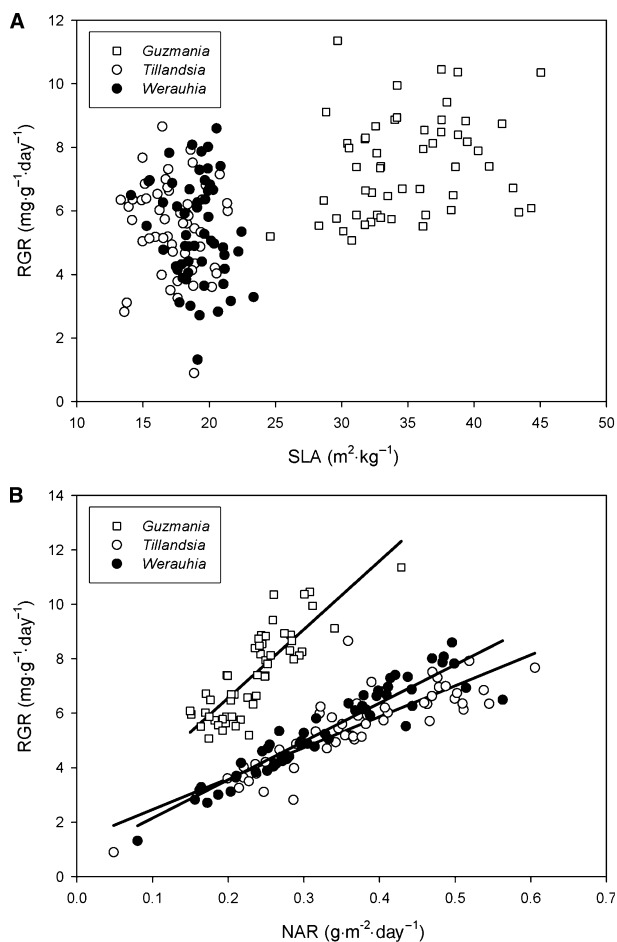


Fig. 2. Relative growth rates (RGR) of three epiphytic bromeliad species as a function of specific leaf area (SLA, plot A) and net assimilation rate (NAR, plot B). Solid lines indicate significant linear regressions: $\text{RGR} = 0.028 \text{ NAR} + 0.028$, $r^2 = 0.70$ (*Guzmania*); $\text{RGR} = 0.064 \text{ NAR} + 0.016$, $r^2 = 0.73$ (*Tillandsia*); $\text{RGR} = 0.063 \text{ NAR} - 0.008$, $r^2 = 0.88$ (*Werauhia*); all $P < 0.001$.

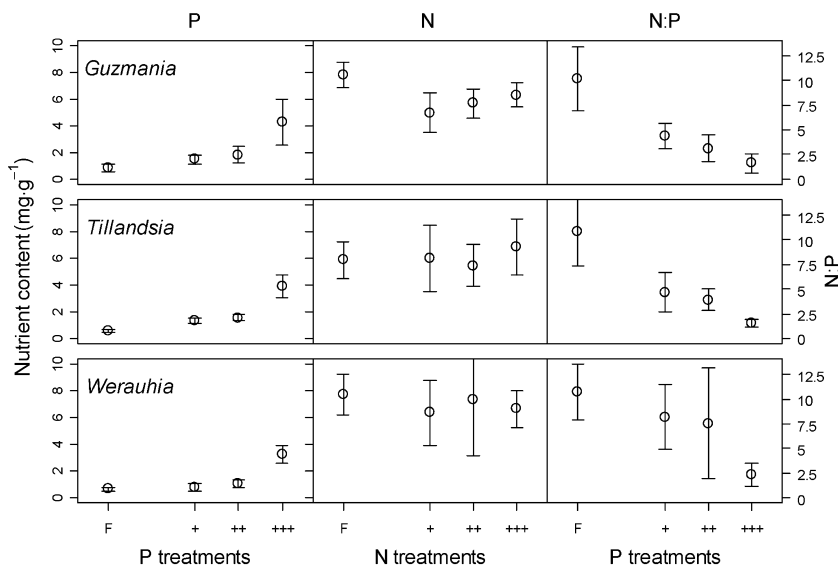


Fig. 3. Nutrient concentrations and N:P ratios in tissue of three epiphytic bromeliads in response to experimental growth conditions (low, +; intermediate, ++; high, +++ supply of N and P) and compared to concentrations in field-collected plants (F). Data are means \pm SD; $n = 5$ –6 for field-collected plants and $n = 18$ for each treatment.

Westoby & Wright 2006). Other reports on N:P ratios in epiphytes are inconsistent: while an earlier review summarized the data of 41 epiphyte species with an average foliar N:P ratio of 12.1 ± 10.5 (Zotz & Hietz 2001), a more recent study encompassing 20 species yielded N:P ratios of 16.1 ± 5.8 (Zotz 2004).

Nutrients in general are in short supply for most epiphytes (Zotz & Hietz 2001). Hence, it is not surprising that efficient uptake has been demonstrated for various N compounds (e.g. Endres & Mercier 2001; Inselsbacher *et al.* 2007), although luxury consumption of N has not been investigated in detail for this plant group. If P is indeed even more limiting than N or other nutrient elements in epiphytic plants, one would expect similar efficiency in P uptake, and we recently showed this for a number of epiphytic bromeliads (Winkler & Zotz 2009). We have also demonstrated that the larger proportion of newly acquired P is not used immediately in metabolism, e.g. in ribosomes or phospholipids, but is rather stored as phytin (Winkler & Zotz 2009). This suggests that the increase in the P concentrations observed in the current study (Fig. 3) is indeed at least partly due to luxury consumption. Considering the intermittent supply of water and nutrients in the epiphytic habitat, both highly efficient uptake and substantial storage capacity for nutrients in excess of current needs seem to be essential physiological characteristics, but available evidence is restricted to very few nutrient elements and a rather biased taxonomic subset of species studied to date (Zotz & Hietz 2001). For example, bromeliads had particularly low levels of N in a comparative study with other important taxa of vascular epiphytes, e.g. orchids, ferns and aroids (Stuntz & Zotz 2001), indicating that any generalization of nutrient deficiencies in vascular epiphytes would still be premature. Members of other taxonomic groups should be included in future studies.

The results of the current study are in line with a number of previous reports, which suggest a prevalent role of P in limiting growth *in situ*. These studies used different

approaches but reached quite similar conclusions (Benzing & Renfrow 1974a; Zotz 1999, 2004). Moreover, there are also first indications for the importance of P supply at the community level. Benner & Vitousek (2007) studied the response of epiphytes to long-term fertilization in a montane forest in Hawaii. Although this community was largely dominated by non-vascular epiphytes, the results are consistent with our conclusions: supplementing with P led to dramatic increases in species abundance, while N fertilization had no effect.

In summary, we demonstrated that both N and P addition independently stimulate vegetative growth in epiphytic bromeliads. A comparison of foliar nutrient concentrations under natural conditions and after experimental treatment suggests, however, that P may be limiting growth more than N under natural conditions.

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