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ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Bromeliad growth and stoichiometry: responses to atmospheric nutrient supply in fog-dependent ecosystems of the hyper-arid Atacama Desert, Chile

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Abstract Carbon, nitrogen, and phosphorus (C, N, P) stoichiometry influences the growth of plants and nutrient cycling within ecosystems. Indeed, elemental ratios are used as an index for functional differences between plants and their responses to natural or anthropogenic variations in nutrient supply. We investigated the variation in growth and elemental content of the rootless terrestrial bromeliad *Tillandsia landbeckii*, which obtains its moisture, and likely its nutrients, from coastal fogs in the Atacama Desert. We assessed (1) how fog nutrient supply influences plant growth and stoichiometry and (2) the response of plant growth and stoichiometry to variations in nutrient supply by using reciprocal transplants. We hypothesized that *T. landbeckii* should exhibit physiological and biochemical plastic responses commensurate with nutrient supply from atmospheric deposition. In the case of the Atacama Desert, nutrient supply from fog is variable over space and time, which suggests a relatively high variation in the growth and elemental content of atmospheric bromeliads. We found that the nutrient content of *T. landbeckii* showed high spatio-temporal variability, driven partially by fog nutrient deposition but also by plant growth rates. Reciprocal transplant experiments showed that transplanted individuals converged to similar nutrient content, growth rates, and leaf production of resident plants at each site, reflecting local nutrient availability. Although plant nutrient content did not exactly match the relative supply of N and P, our results suggest that atmospheric nutrient supply is a dominant driver of plant growth and stoichiometry. In fact, our results indicate that N uptake by *T. landbeckii* plants depends more on N supplied by fog, whereas P uptake is mainly regulated by within-plant nutrient demand for growth. Overall, these findings indicate that variation in fog nutrient supply exerts a strong control over growth and nutrient dynamics of atmospheric plants, which are ubiquitous across fog-dominated ecosystems.

Keywords Atmospheric deposition · Ephiphytes · Growth rate · Nitrogen · Nutrient ratios · Nutrient supply · Phosphorus

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Introduction

Nitrogen (N) and phosphorus (P) are often considered to be limiting nutrients for primary production in terrestrial ecosystems (Elser et al. 2007). Indeed, new empirical evidence indicates that the mass balance of multiple elements in biochemical reactions can constrain biological processes such as growth and reproduction and influence important physiological and ecological phenomena at several levels of biological organization (Sterner and Elser 2002; Moe et al. 2005). For example, stoichiometry of primary producers influences ecosystem processes via sequestration and storage of carbon (C) in living and dead biomass (Hessen et al. 2004), thus regulating nutrient transfer through food webs (Dodds et al. 2004) and the transport, storage, and recycling of nutrients within ecosystems (Evans-White and Lamberti 2006).

Spatial and temporal variation in autotroph biomass elemental content has both inter-and intra-specific components, with most variation resulting from the plastic physiological responses of plants to environmental changes (Güsewell 2004; Niklas et al. 2005). Previous studies have shown that the stoichiometric composition of terrestrial primary producers change with soil nutrient availability (Güsewell 2004). While Sterner and Elser (2002) hypothesize that autotroph N:P content should closely match N and P supplies, other researchers have documented that some producers exhibit limited response to natural and experimental nutrient gradients (Méndez and Karlsson 2005). The correspondence between biomass N:P ratios and the relative availability of N and P in the environment is not exact because of physiological mechanisms, such as homeostatic regulation by plants (Güsewell 2004), and nutrient recycling (Ballantyne et al. 2008).

In some coastal and montane ecosystems, fog water accounts for a large percentage of the total hydrological input (Ponnete-González et al. 2009). Although fog deposition can vary greatly across space and time due to topographic conditions, wind speed, and fog frequency (Weathers 1999), it may have strong ecological relevance where the fog/rainfall ratio is high. For instance, fog influences forest structure (Cavelier and Goldstein 1989; Graham and Andrade 2004; del-Val et al. 2006; Reyes-García et al. 2008), vegetation pattern formation in deserts (Borthagaray et al. 2010), plant growth (Cervantes et al. 2005), and water balance in plants with a crassulacean acid metabolism (Griffiths et al. 1989; Andrade 2003). Furthermore, fog provides ecologically significant inputs of chemical elements and pollutants for coastal and montane ecosystems (Weathers and Likens 1997; Weathers 1999; Weathers et al. 2006). Hence, fog influences ecosystem hydrology and nutrient cycling and can potentially affect the structure and functioning of ecosystems (del-Val et al. 2006; Ewing et al. 2009).

Epiphytic bromeliads are major vegetation components in montane fog-dependent ecosystems (Benzing 1990). Within this group, ‘atmospheric’ bromeliads are specialized plants that obtain most of their water and nutrients from atmospheric sources, such as fog or rain (Virzo de Santo et al. 1976; Benzing 1990). Despite important advances in understanding the role of nutrients supplied by fog on the survival and growth of epiphytic bromeliads that occur in many tropical cloud forests (Wania et al. 2002; Reich et al. 2003; Guevara-Escobar et al. 2010), fog–plant interactions in coastal deserts, such as the Namib and Atacama Deserts, have received far less attention. As with all deserts, these ecosystems have little or no rainfall; the water inputs supplied by fog are often greater than those provided by precipitation (Weathers 1999, Agam and Berliner 2006; Lange et al. 2006; Lange et al. 2007; Westbeld et al. 2009), allowing for the occurrence of sparse vegetation adapted to extremely low resource conditions (Rundel et al. 1991; Pinto et al. 2006; Lange et al. 2007).

In the hyper-arid Atacama Desert in Chile, coastal areas located from 600 to 1,000 m a.s.l. are subjected to periodic but spatially and temporally variable fog events (see Cereceda et al. 2008). Fog moisture enables the establishment of terrestrial bromeliads in the coastal desert, known as ‘atmospheric’ bromeliads. These plants do not have functional roots (see Benzing and Renfrow 1980; Rundel et al. 1997; Pinto et al. 2006) and acquire all of their moisture (see Pinto et al. 2006)—and likely most nutrients (Weathers et al. 2000)—from fog deposition. The particular features of variable fog supply in the coastal Atacama Desert and the occurrence of discrete populations of a single bromeliad species, namely *Tillandsia landbeckii*, provide a unique opportunity to examine patterns of nutrient dynamics in terrestrial plants in general and the role of fog nutrient inputs in bromeliad growth and elemental content in particular. Further, since the atmosphere is the primary source of water and nutrients for this rootless plant, the system can be used to understand the direct effects of nutrient supply on plants without the complexities added by nutrient recycling in the soil and associated biotic feedbacks that may constrain plant stoichiometry (McGroddy et al. 2004; Ballantyne et al. 2008).

To date, studies of nutrient content variability in producer biomass have contributed to our understanding of autotroph stoichiometry and their ecological consequences, mainly in freshwater and marine ecosystems (Diehl et al. 2005; Dickman et al. 2006). Patterns and controls of intraspecific variation in nutrient content remain poorly investigated in terrestrial plants across terrestrial ecosystems. A major aim of the study reported here was to investigate the effects of fog nutrient supply on elemental stoichiometry in the terrestrial bromeliad *T. landbeckii*, the only primary producer in some coastal areas of the hyperarid Atacama Desert. We addressed the following questions: (1) how variable is plant-nutrient content across spatial and temporal gradients of atmospheric nutrient supplies from fog and (2) does *T. landbeckii* stoichiometry and growth reflect the atmospheric nutrient supply from the new environment after plants have been transplanted from where they originated? Specifically, we hypothesized that *T. landbeckii* nutrient content should display a plastic response to changes in nutrient supply from atmospheric deposition, with higher growth and biomass nutrient content under higher fog N and/or P supply. Such responsiveness and a strong reliance upon atmospheric nutrient supply, which in the case of the Atacama Desert is variable over space and time, might suggest a relatively high intraspecific variation in the growth and elemental content of atmospheric bromeliads. We also compared patterns of elemental content of these terrestrial bromeliads with those reported for other terrestrial plants, discussing potential mechanisms of inter-specific divergence.

Materials and methods

Study system

This study was carried out in the coastal Atacama Desert in northern Chile. The area is characterized by a relatively constant temperature (annual average 18.1°C, annual maximum 20.9°C, annual minimum 15.9°C), a mean annual rainfall of 1.7 mm over the last century (Dirección meteorológica de Chile), and by the occurrence of fog events, mainly during the austral winter (June–August; Cereceda et al. 2008). Fog originates from thick stratocumulus banks below 1,000 m which, when intercepted by isolated mountaintops or steep coastal slopes of the Coastal Cordillera, generate a fog immersion zone known as "garúa" in Peru and "camanchaca" in Chile (see Pinto et al. 2006; Cereceda et al. 2008). The increased air moisture and deposition in the fog zone is correlated with the development of isolated and diverse vegetation islands (Cereceda et al. 2008). This Lomas vegetation spreads inland through low elevation valleys or passes where fog is also frequent (Pinto et al. 2006). Several terrestrial bromeliad species of the genus *Tillandsia* inhabit Lomas formations of southern Peru and northern Chile, which depend exclusively on fog inputs as their primary water source (Pinto et al. 2006). The most noticeable one, *T. landbeckii,* invades sandy soils, covering vast areas and forming specialized communities called "tillandsiales" (Pinto et al. 2006).

We selected four *T. landbeckii* stand sites based on accessibility and geographical distribution. These four sampling sites were distributed geographically at 8, 15, 23, and 25 km inland from the coast, namely, Cerro Guanacos (G; 20°24′08.17″S, 70°05′11.41″W), Cerro Huantajaya (H; 20°13′48.24″S, 70°00′16.12″W), Cerro Pajonal (P; 20°43′38″S, 69°57′43″W), and Cerro Isla (I; 20°13′32.15″S, 69°54′46.24″W), respectively. The sites range in elevation from 944 to 1,212 m a.s.l. and were from 2 to 8 ha in size.

Fog water input and chemical analysis

Passive fog water collectors were used at each study site to quantify relative water inputs among the sites. Each collector consisted of four square 0.5 × 0.5-m panel frames

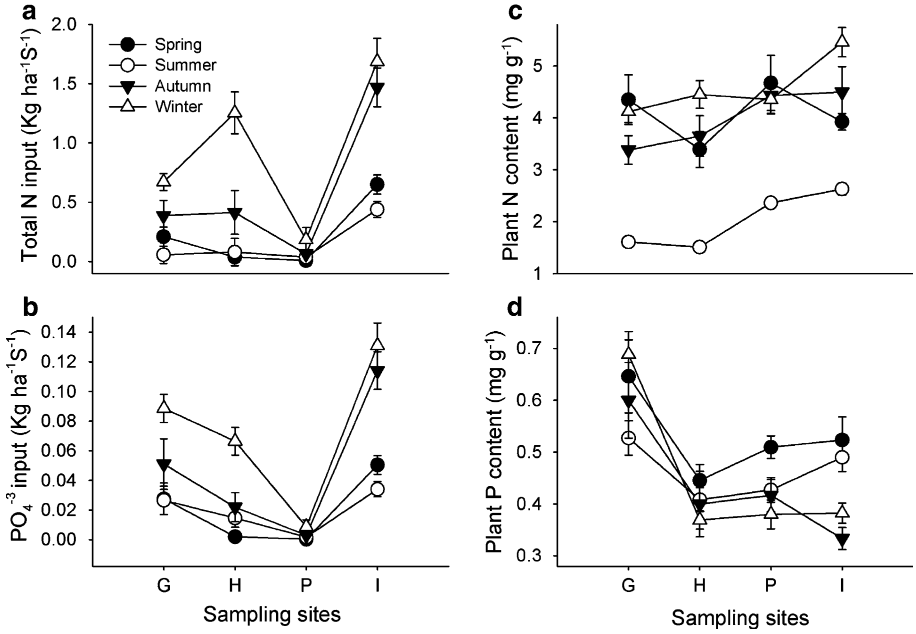

Fig. 1 Patterns of variation [mean ± standard error (SE)] in fog nutrient supply and *Tillandsia landbeckii* nutrient content in the sampling sites and seasons in the coastal Atacama Desert: **a** Total nitrogen (*N*) input measured in fog water, **b** Phosphate (PO_4^{-3}) input measured in fog water, **c** plant N content, **d** plant phosphorus (*P*) content. Sites: *G* Guanacos, *H* Huantajaya, *I* Isla, *P* Pajonal; seasons: austral autumn, winter, spring, and summer

with plastic mesh screening to capture fog droplets (e.g., Schemenauer and Cereceda 1991). A polypropylene trough attached to each collector was connected by tubing to a 10-L polypropylene container. Eight passive fog collectors were randomly placed at each site, at about 1.0 m above ground (similar to height of plants). Five drops of mineral oil were added to the collection bottles to prevent evaporation losses (e.g., del-Val et al. 2006). The containers were placed below ground and covered with sand as additional protection against evaporation losses. Monthly water volume was collected from December 2005 to December 2006. These data were pooled and expressed as the mean volume of water (mm) per site and season.

In addition, three fog water samples for chemical analysis were collected at approximately 2.0 m above the ground at each site using a CalTech Active Strand Cloudwater Collector after Weathers et al. (2000). Samples were stored in polyethylene bottles, fixed with 0.5 ml of reagent grade chloroform, and kept in the dark at 5°C until chemical analysis. Nitrogen (NO_3^-, NH_4^+ and total nitrogen) and P (PO_4^{-3}) were measured at the Cary Institute of Ecosystem Studies' Analytical Facility (Millbrook, NY) following the methods described in Weathers and Likens (1997) and Weathers et al. (2000). Total N was determined by persulfate digestion and standard wet chemical techniques, and organic N was determined by calculating the difference between total N and inorganic N (as in Weathers et al. 2000). Total annual nutrient inputs via fog (i.e., nutrient deposition) were calculated for each site and season as the product of the total amount of fog water deposited in the passive fog collector at each site, and the mean nutrient concentration.

Plant nutrient content variability and experimental transplants

To characterize the spatial and temporal changes in plant elemental stoichiometry, whole plants of *T. landbeckii* (stems and leaves) were collected from each of the four sampling sites over the four seasons between December 2005 and December 2006 ($n = 19$ plants per site and season). We did not include individuals with reproductive structures (i.e., flowers or fruits) in the analysis. In addition, to relate variation in plant growth and nutrient supply, we randomly selected 12 plants and marked their initial stem length; growth rate was quantified by recording stem elongation in millimeters every month during the study period.

Finally, to assess the plasticity of plant elemental content and plant growth in response to local variations in nutrient supply, we carried out reciprocal transplant experiments. Twelve individual plants were randomly selected and cross-transplanted between two sites. The reciprocal transplants were carried out at site Isla, an N-rich site, and site Guanacos, an N-poor site. Selection of rich and poor sites for this experiment were based on earlier samplings [Guanacos: 0.39 ± 0.13 kg N ha season^{-1} atmospheric deposition and 12.5 ± 1.23 plant N:P ratios; Isla: 0.78 ± 0.41 kg N ha season^{-1} atmospheric deposition and 21.1 ± 1.39 plant N:P ratios; analysis of variance (ANOVA) $P < 0.0001$, Tukey's Honestly Significant Difference (HSD) $P < 0.0001$]. Each site acted as both a source (where *T. landbeckii* was collected from) and a host site (to which *T. landbeckii* was transplanted). All collected plants were similar in size (length range 12–22 cm) and were transplanted by hand to the host site and placed over the sandy substrate. Twelve individuals were also transplanted within each source site as a control procedure. Plant growth rates of the 12 selected plants from each site were assessed as previously described. We also measured the number of leaves produced by each plant per site. The experiment was set up in March 2006, and all plant samples for nutrient analyses were collected in April 2007.

Plant nutrient content analyses

Plants were rinsed with deionized water to remove dust and particles before grinding/analyzing, and then analyzed for total C, N, and P content (Laboratory for Soil and Plant Analyses, Universidad de Concepción, Chile). Nitrogen content was determined by a micro-Kjeldahl procedure using direct nesslerization and spectrophotometry; C content was measured using a combustion method followed by colorimetric determination, using a segmented flow auto-analyzer (Sadzawka et al. 2001); P content was determined by colorimetric quantification of the phosphomolybdate complex (Sadzawka et al. 2001). Nutrient content of whole-plant samples (leaves and stems) from each site and season were expressed as the mean mass (mg g^{-1}) based on dry mass. The nutrient ratios were calculated on a molar basis to facilitate the comparison with those previously reported for other ecological stoichiometry studies in terrestrial and freshwater ecosystems.

Statistical analyses

Differences in fog nutrient inputs and plant biomass nutrient content over seasons were analyzed using generalized linear models (GLMs) and one-way repeated-measures ANOVA with sites as the main effect and all seasons as the time effect, followed by a posteriori multiple comparison tests (Tukey's HSD). Plant nutrient content and plant growth differences between the reciprocal transplants (host and source plants) were analyzed by a two-way ANOVA. The C:N, C:P, and N:P ratios were analyzed by a multivariate ANOVA (MANOVA), and if the overall MANOVA model was significant, each elemental ratio was analyzed using univariate ANOVA. When necessary, data were log-transformed to meet ANOVA assumptions of homogeneity of variances. All mean values are shown ± 1 SE.

GLMs with plant nutrient content as the response variable were performed to examine whether variation in plant nutrient content was associated with variation in fog nutrient input. Site was included as the categorical variable, and fog nutrient input and growth rate were treated as covariables. We tested for interactions between site and fog nutrient input, and growth rate in all GLMs.

Results

Fog water input and nutrient deposition

The amount of fog water collected varied significantly across sites (Table 1). The highest fog mean water input (13.0 ± 2.4 mm year^{-1}) was recorded at site Isla, whereas the lowest fog water input was recorded at site Pajonal (2.1 ± 0.8 mm year^{-1}) [Electronic Supplementary Material (ESM) 1]. Repeated-measures ANOVA also revealed a significant seasonal effect (Table 1), primarily because of the increase in water input during the winter season (15.1 ± 2.2 mm season^{-1}). The interaction between site and season was not significant (Table 1).

Total annual nutrient concentration of fog was dominated by inorganic N, while organic N (calculated by difference) was not a significant proportion of N in these samples. Inorganic N was primarily NO_3–N and secondarily NH_4-N, with fog concentrations ranging from 1.09 to 9.07 mg L^{-1} NO_3–N and 1.24 to 5.32 mg L^{-1} NH_4–N, representing 38–73% (NO_3–N) and 27–60% (NH_4–N) of the inorganic N in fog samples. Fog N chemistry was significantly different among sites (Huantajaya > Isla = Guanacos = Pajonal; $F_{3,9} = 7.264$, $P < 0.05$) (ESM 1). Total N deposition was significantly different among sites, with the highest N input at site Isla (Isla ≥ Huantajaya > Guanacos = Pajonal), particularly during winter, as shown by the significant season effect in the repeated-measures ANOVA (Table 1, Fig. 1a). There was also a significant interaction of site and season (Table 1).

Fog P concentration was not significantly different among sites ($F_{3,9} = 1.273$, $P = 0.348$) (ESM 1). However, phosphate (PO_4^{-3}) deposition differed significantly among sites, with higher inputs at site Isla than other sites (Isla > Guanacos > Huantajaya > Pajonal), in particular during the austral winter (Table 1, Fig. 1a). Site and season showed a significant interaction (Table 1).

Variation in fog nutrient input, plant growth, and nutrient content

The mean N content of plant tissue was 4.1 ± 0.1 mg N g^{-1} (4.4 ± 0.2 mg N g^{-1} in leaves and 3.6 ± 0.3 mg N g^{-1} in stems). The plants at site Isla had a significantly higher N content than those growing at other sites (Fig. 1c). Plant N content followed the sequence Isla ≥ Pajonal > Guanacos ≥ Huantajaya. Repeated-measures ANOVA also showed a significant seasonal effect (Table 1), primarily because of the increase in plant N

Table 1 Repeated-measures ANOVA results for the effect of site, season, and their interaction on fog nutrient input and plant nutrient content in the Atacama Desert, Chile

Variable	Site			Season			Site × season		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Fog nutrient input									
Water input	15.817	3	0.001	22.786	3	<0.001	1.6323	9	0.162
Nitrogen input	19.832	3	<0.001	23.747	3	<0.001	3.1691	9	0.012
Phosphate input	23.655	3	<0.001	21.771	3	<0.001	2.5552	9	0.032
Plant nutrient content									
Plant N content	14.06	3	<0.001	39.76	3	<0.001	6.022	9	<0.001
Plant P content	13.309	3	<0.001	4.272	3	0.008	1.32	9	0.246
Plant C content	13.7	3	<0.001	101.71	3	<0.001	4.24	9	<0.001
Plant C:N ratios	21.117	3	<0.001	76.596	3	<0.001	6.865	9	<0.001
Plant C:P ratios	8.329	3	<0.001	9.66	3	<0.001	0.788	9	0.628
Plant N:P ratios	18.169	3	<0.001	18.909	3	<0.001	1.8302	9	0.081

The *F* values for each factor in the analysis of variance (ANOVA) are indicated

C Carbon, *N* nitrogen, *P* phosphorus content during the winter season. There was also a significant interaction of site and season on plant N content (Table 1).

Total P content of *T. landbeckii* showed even larger differences among sites than N content (Fig. 1d). Overall, plant P content followed the sequence Guanacos > Pajonal ≥ Isla ≥ Huantajaya, and the analysis revealed a significant seasonal effect on *T. landbeckii* P content, principally because of the increased biomass P content during the spring compared to the other seasons (Fig. 1d, Table 1). There was no significant effect of a site × season interaction on plant P content. Plant C content was significantly different among sites (Table 1), with the highest C content in plants from site Guanacos during the summer. There was a significant effect of a site × season interaction on plant C content. Nutrient ratios also showed differences among sites, and C:N ratios were lowest at site Isla (Huantajaya ≥ Guanacos ≥ Pajonal > Isla; Fig. 2a). The repeated-measures ANOVA also showed a significant effect of season on plant C:N ratios (Fig. 2a; Table 1). There was a significant interaction effect between site and season on plant C:N ratios but not on plant C:P and N:P ratios (Table 1). The N:P ratios showed a significant effect of site (Fig. 2b) and followed the sequence Isla ≥ Pajonal ≥ Huantajaya > Guanacos; the analysis showed a significant seasonal effect on *T. landbeckii* N:P ratios principally because of the increased biomass P content during the spring. The interaction between site and season was not significant (Table 1).

The GLMs showed a significant effect of fog N input on plant N content and C:N ratios ($r^2 = 0.519$, $P < 0.05$ and $r^2 = 0.274$, $P < 0.05$, respectively), whereas the effect of growth rate on plant N content was not significant ($P = 0.324$). There was a non-significant effect of fog PO_4^{-3} input on plant P content ($P = 0.937$), but a positive significant relationship was found between growth rate and P content ($r^2 = 0.304$, $P < 0.05$; Fig. 3a). The N:P ratios were significantly related to fog N input ($r^2 = 0.362$, $P < 0.01$) but not to growth rate ($P = 0.683$) or fog P input ($P = 0.136$). There was a non-significant effect of fog N

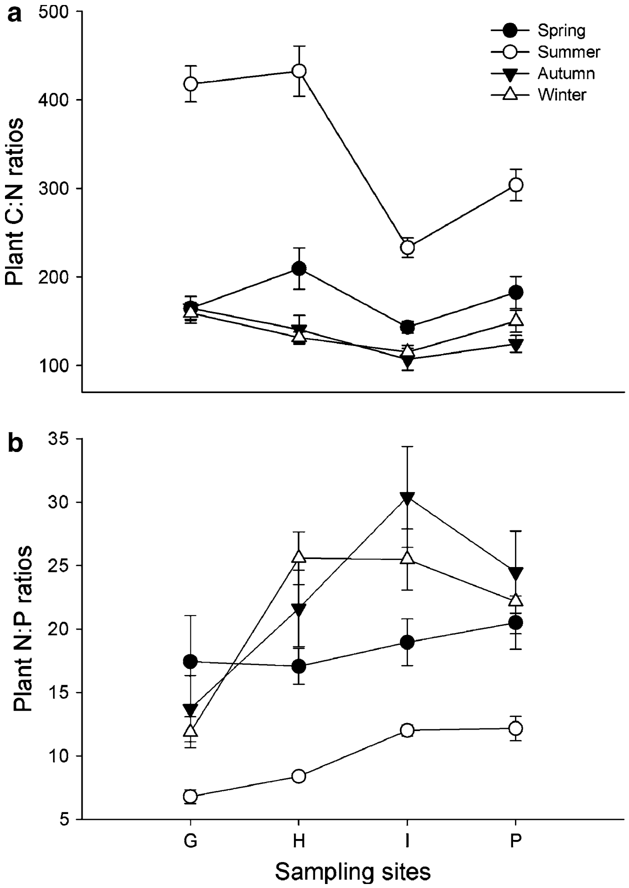

Fig. 2 Patterns of variation (mean ± SE) in nutrient ratios in *T. landbeckii* plants in the sampling sites and seasons in the coastal Atacama Desert, Chile: **a** plant C:N ratios, **b** plant N:P ratios. Sites and seasons are as in Fig. 1

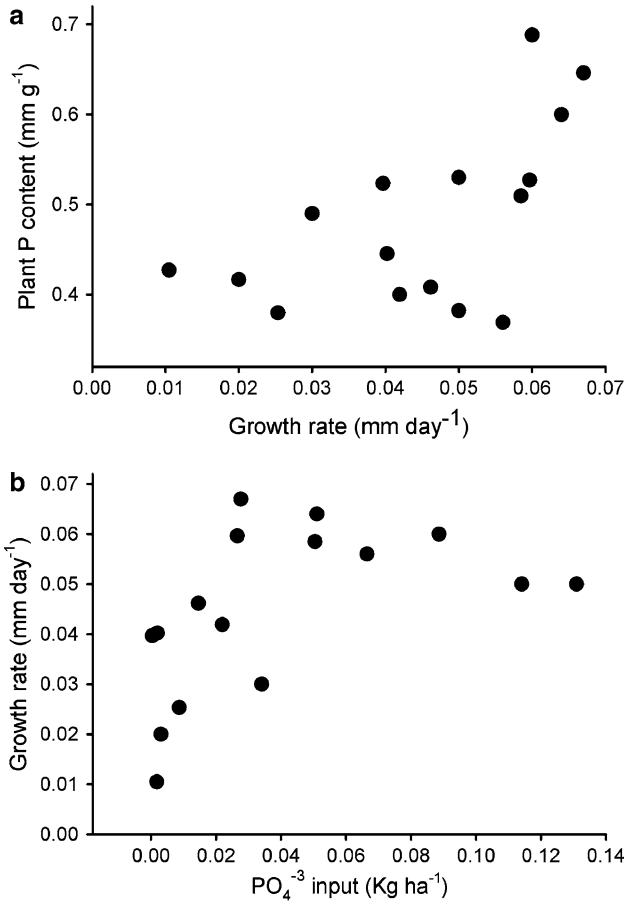

Fig. 3 Patterns of variation in *T. landbeckii* P content and growth rate (**a**) and *T. landbeckii* growth rate and fog PO_4^{-3} input (**b**)

Table 2 Effects of source site[a], host site[b], and their interactions on tissue N and P content, nutrient ratio, growth rate, and leaf production of *Tillandsia landbeckii* plants, Atacama Desert, Chile, 1 year after plants had been transplanted

Variable	Source sites			Host sites			Source × host sites		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Plant N content	0.499	1	0.485	12.15	1	0.001	0.646	1	0.427
Plant P content	0.024	1	0.878	12.75	1	<0.001	0.661	1	0.661
Plant C:N ratios	2.216	1	0.145	16.76	1	<0.001	0.111	1	0.740
Plant C:P ratios	0.545	1	0.464	13.455	1	<0.001	2.102	1	0.154
Plant N:P ratios	0.079	1	0.780	14.619	1	<0.001	0.018	1	0.894
Plant growth rate	2.89	1	0.096	139.106	1	<0.001	0.027	1	0.869
Plant leaf production	0.912	1	0.345	11.63	1	0.001	0.168	1	0.684

F values for each factor in the ANOVA are indicated

[a] Site from where *T. landbeckii* plants came from

[b] Site to which *T. landbeckii* plants were transplanted

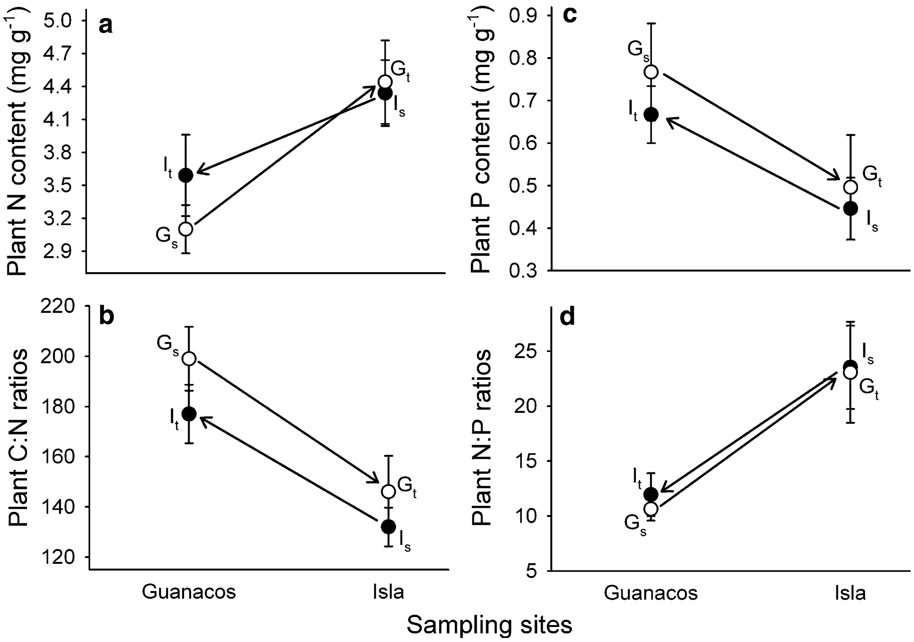

Fig. 4 Mean changes (±SE) in the element content of *T. landbeckii* plants after the reciprocal transplants: **a** N content, **b** C:N molar ratios, **c** P content, **d** N:P molar ratios. Transplant groups: I_s Isla source site, I_t Isla plants transplanted to Guanacos, G_s Guanacos source site, G_t Guanacos plants transplanted to Isla. *Filled circles* plants from Isla, *open circles* plants from Guanacos, *arrows* indicate relative changes in *T. landbeckii* nutrient content from the source site to the transplanted site

input on plant growth rate ($P = 0.181$). In contrast, fog P input had a positive significant effect on the plant growth rate ($r^2 = 0.239$, $P < 0.05$; Fig. 3b).

Reciprocal transplants

Results of experimental transplants showed that the local environment determined the mineral element content and growth of bromeliads (Table 2). After 1 year, plants transplanted from the site with lower N and higher P levels (site Guanacos) to that with higher N and lower P levels (site Isla) had increased N content (Fig. 4a) and a lower C:N ratio (Fig. 4b). The total P content also decreased (Fig. 4c) while the N:P ratios increased in plants grown under high N and low P conditions (Fig. 4d). Similarly, plants from site Isla transplanted to site Guanacos had a lower N content (Fig. 4a) but a higher C:N ratio (Fig. 4b) than plants grown at their source site. Moreover, their P content increased (Fig. 4c), and their N:P ratio decreased (Fig. 4d) when they were grown under low N and high P conditions. During the 'transplantation' year, plants growing at site Guanacos had a higher growth rate than those growing at site Isla (Fig. 5a). The analysis showed a significant effect of host site on plant growth rate, but the interaction between source and host site was not significant (Table 2). Further, plants transplanted to site Guanacos had a higher leaf production than those growing at site Isla (Fig. 5b). The interaction between source and host site was not significant (Table 2). In general, we found that transplanted individuals converged to a similar mean nutrient

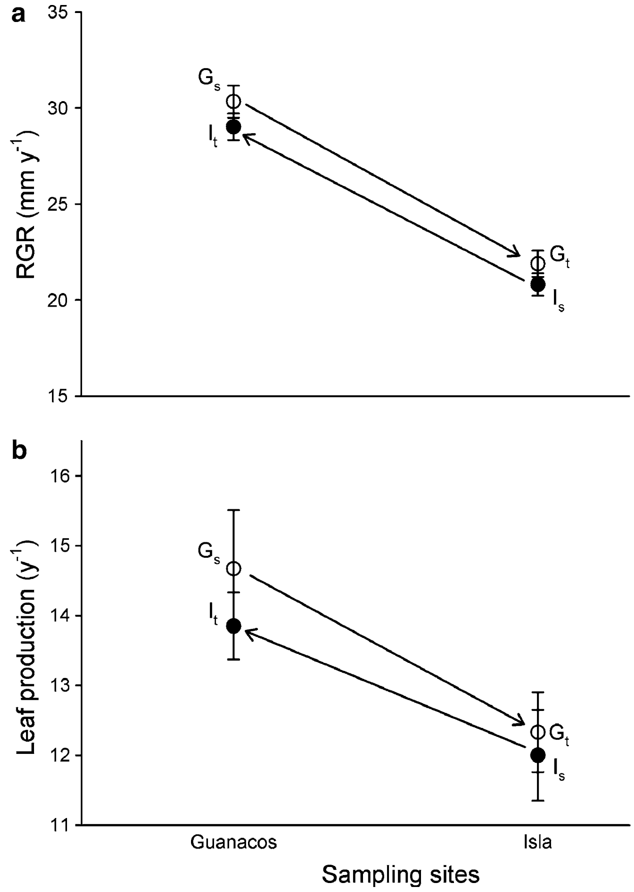

Fig. 5 Mean changes (±SE) in the growth rate of *T. landbeckii* after the reciprocal transplants: **a** stem elongation, **b** leaf production. Transplant groups are as indicated in Fig. 4

content, growth rate, and leaf production of resident plants at each host or source site.

Discussion

Overall nutrient content in *T. landbeckii*

In this study, the N contents of the desert bromeliad *T. landbeckii* were found to be lower than those recorded for most other terrestrial plants (see Elser et al. 2000; McGroddy et al. 2004; Reich and Oleksyn 2004). However, low N contents have been reported for epiphytic bromeliads in general, mainly because of their nutrient sources and physiology (Benzing and Renfrow 1974; Husk et al. 2004). Overall, these plants exhibit biochemical and physiological features corresponding to stress-tolerant species adapted to nutrient-poor conditions (Grime 2001). Therefore, we speculate that the strong reliance of *T. landbeckii* upon atmospheric N sources via fog water may have led to the evolution of a high N use efficiency, as suggested by the high C:N ratios found in their vegetative tissues (Zotz and Hietz 2001).

Interestingly, *T. landbeckii* had a higher P content than commonly reported for other *Tillandsia* species (see Benzing and Renfrow 1974; Husk et al. 2004), which may represent a combination of high P in fog (e.g., Weathers et al. 2000; Vitousek 2004) and desert dust deposits on plant surfaces that can dissolve in fog water and thus become available to plants. Although we did not measure dust deposition, we noted that desert dust is often a rich source of PO_4^{-3} (Ridame and Guieu 2002). Fluxes of N and P via atmospheric fog or desert dust are therefore important nutrient inputs to arid-land ecosystems; they may contribute to soil formation and plant biomass accumulation (Herut et al. 2002; Okin et al. 2004; Ewing et al. 2006). The hyper-arid soils of the Atacama Desert have been shown to have a high N content as well, dominated by NO_3^-, which is a function of long-term atmospheric sources (Michalski et al. 2004; Ewing et al. 2006). Dry nutrient deposition via dusts and marine aerosols are also a major sources of solutes (Derry and Chadwick 2007). In fact, the results of a recent study in the atmospheric *T. capillaries* suggest that the chemical material retained in its leaf surface influences its tissue nutrient content (Abril and Bucher 2009). Therefore, as noted above, in the presence of fog water, a portion of the particulate inorganic P and N, as well as other nutrients associated with these particles, may become labile and assimilated by plants via roots or, in this case, leaves (Herut et al. 2002; Ridame and Guieu 2002).

Spatial and seasonal differences in C content can reflect variations in non-structural carbohydrates. Previous work on carbohydrate content from other terrestrial plants indicates that non-structural carbohydrate stores are used during dry periods, with a subsequent decrease in C content (Cruz and Moreno 2001; Zotz and Richter 2006). These results are consistent with our observations, which showed a drop in C stores immediately after the dry season (i.e., summer). According to Zotz and Richter (2006), tropical epiphytes show seasonal changes in total non-structural carbohydrate contents related to a C gain during the wet season, which is immediately allocated to the development of new tissues (Zotz 1999).

Variation in fog nutrient input, plant growth, and biomass nutrient content

The observed strong variability in the elemental content and growth among *T. landbeckii* plants in the study area indicates that fog nutrient supply—and associated dissolved particles—varied broadly across the coastal desert sites during our study period. Although limited data are available on terrestrial plants, similar trends of variation have been found in studies across plant species (Schlesinger and Marks 1977; Sterner and Elser 2002; Troxler 2007; Elser et al. 2010). Such results indicate that plant stoichiometry in general is strongly responsive to variations in local nutrient supply. Although our results show that plant nutrient content did not match exactly the relative supply of nutrients by fog, the discrepancy may be due to the physiological regulation of nutrient content by plants to maintain cell function under reduced nutrient availability or to avoid toxic effects with excessive increases in nutrient supply (Sterner and Elser 2002; Güsewell 2004; Hall et al. 2005).

Few studies have investigated the role of atmospheric nutrient inputs on the nutrient dynamics of atmospheric bromeliads (but see Richardson et al. 2000; Abril and Bucher 2009) and the plasticity of bromeliad biomass nutrient content under natural conditions. Our transplant assays of *T. landbeckii* between sites showed that when plants from different source populations were grown under similar conditions of nutrient availability, the plants adjusted their elemental stoichiometry to the new environmental conditions by increasing nutrient uptake. These results suggest that *T. landbeckii* respond to their local environment in a similar way as phytoplankton and other terrestrial plants across environmental gradients (see Güsewell 2004; Hall et al. 2005; James and Richards 2006; Bott et al. 2008; Gradowski and Thomas 2008). Phenotypic plasticity may optimize plant functioning in a given environment by influencing the plant's ability to acquire new resources and grow successfully under various nutrient regimes (Sardans et al. 2006; Nicotra et al. 2007).

Atmospheric bromeliads live in low-water and nutrient-poor ecosystems (Benzing 2000). Water is a resource that typically limits primary productivity in arid regions (Corbin et al. 2005; James et al. 2005). In the Atacama Desert, nutrient supply is intrinsically linked to fog water input; as such, it may be very difficult to separate the effects of water and nutrient inputs on plant responses. We observed that nitrogen content in *T. landbeckii* increased under higher N inputs from fog; however, there was no apparent relationship between plant growth rate and N content in the plants, suggesting the occurrence of N luxury consumption (vs. N for immediate growth) by *T. landbeckii* when N becomes available. This phenomenon has been widely reported in epiphytes, which are generally slow-growing plants (Benzing and Renfrow 1974; Benzing and Renfrow 1980; Benzing 2000) and is consistent with the high uptake of a particular nutrient to levels beyond its immediate needs, which has been reported for other plants in nutrient-poor ecosystems (Chapin 1980). Such luxury consumption makes it difficult to interpret the relationships between nutrient input, plant stoichiometry, and growth (Zotz and Asshoff 2010). Consequently, the tissue nutrient content of wild plants in general is not a good indicator of environmental nutrient availability (Chapin 1980).

The plastic responses in terms of tissue P content of *T. landbeckii* in both the natural variation and transplant experiments are a reflection of a tight link between P availability, growth rates, and P uptake. Previous studies on diverse *Tillandsia* species have suggested that P is the most limiting element for growth and reproduction in natural ecosystems (Schlesinger and Marks 1977; Benzing 1990; Zotz and Hietz 2001; Zotz and Richter 2006). The biochemical and physiological responses of *T. landbeckii* to nutrient input by fog reflect results from earlier studies by Benzing and Renfrow (1974); Zotz and Hietz (2001); Zotz and Richter (2006), and Zotz and Asshoff (2010) in tropical epiphytes. Despite habitat- and taxon-specific differences, the conclusions these authors reached are similar regarding the dominant role of P for epiphytic bromeliad growth. Overall, the inconsistent patterns of variation in *T. landbeckii* N and P contents suggest that N uptake depends more on its availability, and thus by fog N input, whereas P uptake is mainly regulated by demand.

The results of this study advance our understanding of the environmental and physiological basis for elemental stoichiometry variation in atmospheric bromeliads. This study also highlights the role of fog in influencing ecological function in coastal desert plant communities in the Atacama Desert. More research is needed, however, to assess how elemental content varies in different plant species and in other fog-dominated ecosystems. Moreover, because the elemental stoichiometry of plants probably determines the extent to which N and/or P are limiting for higher trophic levels, such information can provide important clues on how autotrophic and heterotrophic organisms respond to nutrient supply gradients or to human disruption of biogeochemical cycles, particularly in ecosystems that are driven by fog nutrient deposition.

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