Which abiotic factors limit vegetative growth in a vascular epiphyte?

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Summary

1. Vegetative growth in vascular epiphytes is assumed to be severely limited by intermittent supply of water and nutrients, but experimental evidence for this notion is meagre. The effects of water, nutrient supply and light on growth were studied in an epiphytic bromeliad, *Vriesea sanguinolenta* Cogn. & Marchal (syn. *Werauhia sanguinolenta*) in a large forest gap in a lowland forest of Panama, in a full-factorial design. To investigate ontogenetic drift, three plant-size classes ($\approx$5, 15 and 35 cm leaf length) were included in the experiment.

2. Water supply had the strongest influence on growth, but the magnitude of this effect differed considerably among size classes. Nutrient supply affected growth only in small and intermediate-sized plants. More light (60% of direct irradiation) tended to decrease growth rates compared to 30% irradiation.

3. Small plants showed by far the highest potential to adjust their relative growth rate (RGR) in response to favourable growing conditions.

4. Despite these size-related differences, absolute RGRs were extremely low compared to studies with other plant groups, confirming the notion that vascular epiphytes are inherently slow-growing plants.

Key-words: growth, ontogenetic drift, Panama, rainforest, RGR

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Introduction

The lush, complex appearance of tropical rainforests is largely due to the many structurally dependent plants, primarily lianas, hemi-epiphytes and epiphytes (Richards 1996). The latter group may be particularly prominent, accounting for a large proportion – or even most – of the vascular species at a given site (Whitmore *et al*. 1985; Gentry & Dodson 1987a; Kelly *et al*. 1994). Despite their high local diversity and abundance, herbaceous epiphytes supposedly grow very slowly; available information suggests the time to reach maturity is about a decade or more (Benzing 1981; Larson 1992; Zotz 1995; Zotz 1998; Hietz *et al*. 2002; Schmidt & Zotz 2002).

Slow growth is assumed to be primarily because of short and irregular availability of water and nutrients (Benzing 1990; Zotz & Hietz 2001), but this notion is based almost entirely on indirect evidence. Studies using growth analyses are rare. In one of the few exceptions, Castro-Hernández *et al*. (1999) studied the effects of different light and nutrient levels on growth

in *Tillandsia guatemalensis*, and found a moderate-to-high increase of relative growth rates (RGR) in NPK-fertilized plants. However, as pointed out by Zotz & Hietz (2001), lack of inclusion of different levels of water supply as a factor in such experiments complicates an unambiguous interpretation of these results – under field conditions water scarcity may completely override any nutrient effect. There is one other manipulative study on epiphyte growth (Schmidt & Zotz 2002), but again the effects of nutrients and water were not separated. That study highlights the strongly divergent response of plants of varying size to experimental manipulation. While RGR in the smallest size class increased by about an order of magnitude under optimal resource supply, larger individuals showed only a moderate increase in growth. Although such an observation is not exceptional (cf. Poorter & Pothmann 1992; Adams *et al*. 1997; McConnaughay & Coleman 1999; or Bruhn *et al*. 2000), this kind of growth response of ontogenetic drift may be particularly pronounced in vascular epiphytes.

In addition to water and nutrient supply, irradiance is a third major ecological factor influencing plant growth (Adams *et al*. 1997; Lambers *et al*. 1998). To incorporate all these factors and ontogenetic drift in

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one study, we conducted an experiment with a full-factorial design in which light, water and nutrient supply were combined with plant size. We chose *Vriesea sanguinolenta* as study species for several reasons. First, its water-impounding tank facilitated the experimental manipulation of water and nutrient supply. Second, the already available ecological and physiological information (Zotz 1997; Schmidt & Zotz 2001), in particular the availability of a long-term data set on *in situ* growth for this species (Schmidt & Zotz 2002), allowed us to consider our experimental results in a broader ecological context.

Materials and methods

STUDY SITE AND ORGANISM

The present study was carried out on Barro Colorado Nature Monument (BCNM, 9°10′ N, 79°51′ W), Republic of Panama. The vegetation of this biological reserve is classified as tropical moist forest (Holdridge *et al*. 1971). Mean annual rainfall is ≈2600 mm with a pronounced dry season from late December to late April. During these 4 months, completely rainless periods regularly extend for several weeks (Windsor 1990). A detailed description of vegetation, climate and ecology is given by Leigh *et al*. (1982).

Vriesea sanguinolenta Cogn. & Marchal (syn. *Werauhia sanguinolenta*; Grant 1995) is a tank-forming bromeliad with a geographic distribution from Costa Rica to Colombia, including various Caribbean islands. Also found in the forest canopy throughout BCNM, it is particularly abundant on the flood-tolerant tree *Annona glabra* L. (Annonaceae) along the shore of Lake Gatun (Croat 1978; Schmidt & Zotz 2002).

GROWTH EXPERIMENT

The effects of light, nutrients and water supply on plant growth were studied for 124 days, from late May until October 2001, in an experiment with a full-factorial design. Each factor had two levels, each replicated for three different size classes (size was expressed as maximum leaf length, LL_{max}; Table 1). These size classes were chosen to include both the smallest tanks (after the shift from a non-impounding, juvenile stage) and the largest non-reproductive plants

(cf. Schmidt & Zotz 2001). In early May 2001 we collected 255 plants growing in *A. glabra*. Although the roots had to be severed to remove plants from their original substrate, no influence on experimental results was expected because roots serve these bromeliads only as holdfasts (Benzing 2000); there was little root regrowth during the experiment. After thoroughly rinsing the plants to remove accumulated humus, initial plant dry weight (DW) was determined for a subset of five individuals per size class (7 days at 60 °C). The remaining plants were labelled individually, and eight groups of 10 randomly chosen plants per size class were put on a large metal rack, which was set up in the open near the laboratory building on Barro Colorado Island. There they were subjected to a combination of treatments as described below. To avoid an edge effect, plants were regularly moved at random. Two members of the largest size class died during the study.

Plants were exposed to either high light (L+; ≈60% of direct sunlight) or low light (L–; ≈30% of direct sunlight) conditions. At noon, direct sunlight reached 2100 µmol m^{-2} s^{-1} photon flux density (PFD). L+ and L– conditions were created with shade cloths, the average integrated PFD being, respectively, ≈18·5 mol m^{-2} day^{-1} (L+) and ≈9·2 mol m^{-2} day^{-1} (L–). L– conditions were similar to natural light in the centre of the crown of *A. glabra*, where integrated PFD amounted to 26·7 ± 6·4% (mean ± SD) of the direct light above the trees (*n* = 6 days in April 2002).

While a full tank was maintained continuously in one group (W+ treatment), the other (W–) was alternately watered and left dry. This was achieved by watering the plants for 2 days, emptying the tank, and filling it again after 2 days. In all other cases, tank water was completely renewed each day. We used water from Lake Gatun, which is very nutrient-poor (B. Stallard, US Geological Survey, personal communication).

For the two nutrient treatments we used an NPK fertilizer (Substral Universaldünger 18-14-18, Scotts Celaflor, Ingelheim, Germany) which contains both ammonium and nitrate. Nievola *et al*. (2001) have shown that this combination of nitrogen sources maximized growth in congeneric *Vriesea fosteriana*. Plants were supplied with fertilizer once a week. The high-nutrient solution (N+) contained 0·5 g fertilizer l^{-1}, while the low-nutrient solution (N–) contained only 1% of this amount. The NH_4^+ concentration in the N+ solution was 38·5 mg l^{-1}; that of NO_3^- was 51·5 mg l^{-1}.

Plant size, expressed as maximum leaf length (LL_{max}, in cm), was determined for all individuals at the beginning and end of the experiment. This parameter is strongly and positively correlated with plant DW ($r^2 = 0.99$; cf. Schmidt & Zotz 2002), which allowed the conversion of LL_{max} to DW and the subsequent calculation of mean RGR (in mg g^{-1} day^{-1}), following Hunt (1982):

Table 1. Size classes of *Vriesea sanguinolenta* in the growth experiment (SC = size class; LL_{max} = maximum leaf length); sample size = 80 in each SC

| Parameter | LL_{max} (cm) | | |
	SC1	SC2	SC3
Range	4·5–5·8	13·1–17·1	30·4–39·8
Mean	5·4	15·4	37·7

$$RGR = (\ln DW_{t+1} - \ln DW_t)/\Delta t \qquad \text{eqn 1}$$

Such a non-destructive approach to growth analysis could be problematic if our population differed from that of Schmidt & Zotz (2002), or if the correlation between LL_{max} and DW changed with treatment conditions. We addressed the first possibility by comparing the 15 determinations of initial DW with the calculated DW: the regression coefficient was not significantly different from 1 ($P < 0.05$). The second possible problem was addressed by harvesting a subset of 48 plants (six per treatment combination) at the end of the experiment, determining LL_{max} and DW (7 days at 60 °C). The relationship of LL_{max} *vs* log(DW) was invariably the same (data not shown). Thus we could reliably derive DW from LL_{max} (cf. Villar *et al*. 1998).

LONG-TERM CENSUS

Permanent census plots were established in early 1997 in an area of *c*. 0·5 ha in Aojeta Bay, BCNM, and were revisited annually at the beginning of the rainy season (cf. Schmidt & Zotz 2002). Each of the 40 plots consisted of a branch section (1–2·5 m long) within the crown of an *A. glabra* specimen; on a few occasions there was more than one plot per tree. More than 300 plants of *V. sanguinolenta*, ranging from 1 to 90 cm maximum leaf length (LL_{max}), were labelled individually. During each census maximum leaf length was measured, and dead or missing specimens were replaced by plants of similar size. Average daily RGRs over 1 year were estimated only for individuals of similar size to those used in the experiment (SC1: 4·0–5·9 cm; SC2: 13·1–16·6 cm; SC3: 27·2–45·2 cm; Table 1). Sample size was consistently largest in SC1 (16–29 plants) and smallest in SC3 (7–14 plants) during the five study periods.

DATA ANALYSIS

Data were analysed with STATISTICA (Statsoft Inc., Tulsa, OK, USA). A four-factor ANOVA was performed to test the effects of light, water supply, nutrient supply, and plant size on plant growth. Because of the non-normality of the data we log-transformed RGR before analysis (Sokal & Rohlf 1995). The significance of size-related differences in RGR under field conditions was examined with a one-way ANCOVA, using rainfall as a covariate. To explore possible differences in the range of RGR under experimental conditions from that for natural variation in the field, the years with the lowest and highest *in situ* growth rates (1997 and 1999, respectively) were contrasted with the extreme RGRs under experimental conditions (N+W+ and N–W–) for each size class using STATISTICA's planned comparison option. All correlations are parametric (Pearson Product moment correlations).

Results

The growth response of *V. sanguinolenta* depended strongly on plant size, and the observed RGR varied by more than an order of magnitude, from 0·6 mg g^{-1} day^{-1} in large plants (SC3) in treatment L+W–N– to 8·4 mg g^{-1} day^{-1} in small plants (SC1) in treatment L–W+N+ (Table 2). Both increased water and increased nutrient supply had a highly significant positive effect on RGR (Table 3; Fig. 1), contrasting with the effect of light: RGR was almost 20% lower under L+ conditions, although this trend was not significant ($P = 0.068$). Improved water supply increased RGR in all size classes, while for nutrient supply this was true only for small and intermediate-sized plants (Fig. 1). The nutrient effect on RGR also depended on water supply. In small plants, in particular, the increase in RGR under N+ conditions was much more pronounced when plants were well watered. The difference between RGR under poor (W–, N–) and good resource supply (W+, N+) was almost 700% in small plants, almost 300% in intermediate-sized plants, but minor in large plants (+60%) (Fig. 1).

Table 2. Maximum leaf length (LL_{max}) of *Vriesea sanguinolenta* at the end of the experiment (duration 124 days) and relative growth rate (RGR) in response to eight treatments: two levels each of the abiotic factors light (L), water (W) and nutrient supply (N)

	Treatment							
	L+				L–			
	W+		W–		W+		W–	
Parameter	N+	N–	N+	N–	N+	N–	N+	N–
LL_{max} (cm)								
SC1	7·5	6·1	5·8	5·6	7·9	6·1	5·8	5·5
SC2	18·2	16·0	16·5	16·6	18·2	18·1	17·5	16·3
SC3	36·4	38·1	35·7	36·8	36·9	37·3	35·7	36·8
RGR (mg g^{-1} day^{-1})								
SC1	7·58	3·84	2·57	1·24	8·41	3·21	2·69	1·22
SC2	3·52	1·56	1·60	1·36	4·17	4·06	3·02	1·58
SC3	1·23	1·69	0·79	0·56	1·45	1·21	0·80	1·15

+, Treatments with high level of a given factor; –, low level.
Data are means (*n* = 10 per treatment and size class; nine each in L+W+N+ and L–W–N– of SC3).

Both small and intermediate-sized plants showed a significant correlation between *in situ* growth rate and annual precipitation, while no such trend was detected for the largest size class (Fig. 2). For example, compared to the El Niño year 1997, with less than 1400 mm of
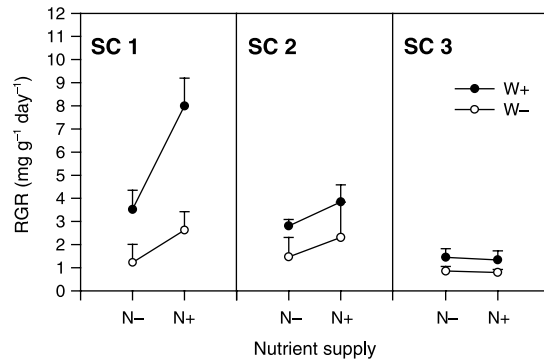
Fig. 1. Effect of water (W), nutrients (N) and plant size class (SC) on relative growth rate (RGR) in *Vriesea sanguinolenta*; + and – indicate two levels of resource supply. Data are means ± SD ($n = 20$) and are averaged across light treatments.
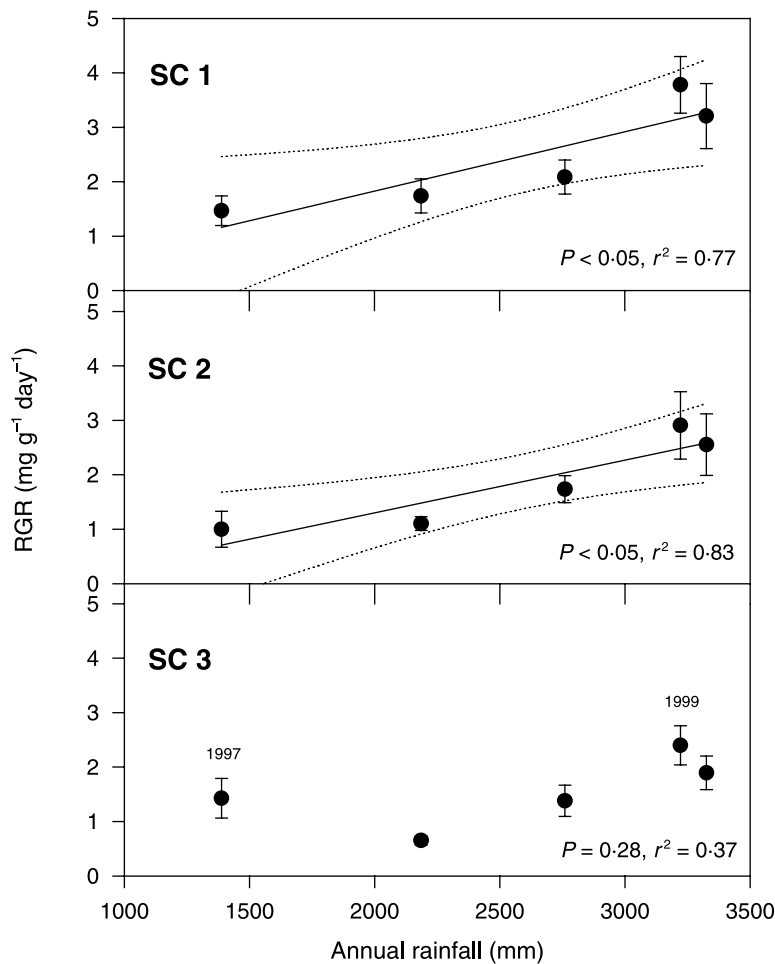
Fig. 2. Relationship of annual precipitation and relative growth rates (RGR) in *Vriesea sanguinolenta*. Data are means ± SE ($n = 7$–29 in 5 years from 1997 to 2002). Solid lines are linear regressions, dotted lines 95% confidence intervals. Years with extreme RGRs (1997 and 1999) are marked in the lower plot.

Table 3. Results of a four-way ANOVA of the effects of light (L), water (W), nutrients (N) and plant size (S) on the relative growth rate in *Vriesea sanguinolenta* measured over 124 days' growth

Factor	df	F	P
L	1	3·21	0·07
W	1	59·71	<0·001***
N	1	25·15	<0·001***
S	2	39·22	<0·001***
L × W	1	0·06	0·81
L × N	1	0·12	0·72
W × N	1	4·56	0·03*
L × S	2	2·21	0·11
W × S	2	15·01	<0·001***
N × S	2	12·41	<0·001***
L × W × N	1	0·02	0·89
L × W × S	2	0·47	0·63
L × N × S	2	0·43	0·65
W × N × S	2	3·97	0·02*
L × W × N × S	2	2·09	0·13
Error	214		

rain, RGRs in SC1 and SC2 increased almost threefold in wet years with more than 3000 mm of rain (1998, 1999). However, the correlation between RGR and the number of rainy days (>1 mm rain day^{-1}) was invariably not significant ($P = 0·3$–$0·7$). Consistent with the results of the growth experiment (Table 2; Fig. 1), RGR under field conditions was highest in small plants (ANCOVA, $F_{2,252} = 7·69$, $P < 0·001$): the average growth rate of 2·3 mg g^{-1} day^{-1} in SC1 was almost 40% higher than in SC3 (Tukey's HSD test, $P < 0·05$). With the exception of SC3, the maximum *in situ* RGR observed during 5 years was intermediate between the extremes under different experimental conditions (Table 4). In the largest plants, field and experimental RGR did not differ significantly. The lowest RGR in the growth experiment (W–N–) in small and intermediate-sized plants was comparable with those observed during El Niño year 1997.

Discussion

Improved water and improved nutrient supply strongly stimulated growth in *V. sanguinolenta* (Fig. 1). However, the effect of the former was more pronounced (Table 3) and – in contrast to the latter – detectable in all size classes. Increased light, on the other hand, tended to decrease RGR ($P = 0·07$, Table 3). Due to the pronounced self-shading in leaf rosettes (Zotz *et al.* 2002), we had anticipated the opposite effect. This unexpected finding may be due to partial stomatal closure at high vapour pressure deficits under high light. This notion is supported by the observation of a pronounced midday depression of CO_2 uptake, even under well watered conditions (Schmidt & Zotz 2001). Invariably, smaller plants responded more strongly to increases in water and nutrient supply,

Table 4. Comparison of lowest and highest RGR (mg g⁻¹ day⁻¹) under field and experimental conditions. Field RGRs are from the El Niño year 1997 and the wet year 1999 (cf. Fig. 2). RGR from the growth experiment (W–N– and W+N+) include only L-treatments (Table 2) which are comparable to the light conditions *in situ*. Statistics refer to three one-way ANOVAs and subsequent contrast analyses

Size class	Field	Experiment	df	F	P	Contrast
			ANOVA results			
SC1			3,58	21·67	<0·001	
	RGR min	RGR min				0·8
		RGR max				<0·001***
	RGR max	RGR min				0·02*
		RGR max				<0·001***
SC2			3,52	7·28	<0·001	
	RGR min	RGR min				0·3
		RGR max				<0·001***
	RGR max	RGR min				0·19
		RGR max				0·04*
SC3	–	–	3,46	1·43	0·24	–

which is consistent with other recent reports about growth in epiphytic bromeliads and orchids (Hietz *et al.* 2002; Schmidt & Zotz 2002).

Lasting for 4 months, our experiment was short in comparison to the plants' life span. According to the growth simulations of Schmidt & Zotz (2002), the plants of the three size classes were approximately 7, 12 and 14 years old, respectively. Bromeliads are known for luxury consumption of nutrients (Benzing & Renfrow 1974). This important mechanism for obtaining scarce nutrients in pulse-supplied environments (Lambers *et al.* 1998) could impede an unequivocal interpretation of the results of a short-term experiment (Fig. 1; Table 3): the insensitivity of larger plants to differences in nutrient supply could simply be the consequence of previous nutrient storage. However, several observations counter this argument. First, an earlier greenhouse study over 2 years (Schmidt & Zotz 2002) yielded similarly low RGR under high-nutrient conditions in large *V. sanguinolenta* plants. Second, while both small and intermediate-sized plants showed a significant increase in RGR under experimental N+W+ conditions compared to the highest growth rates observed *in situ*, this was not the case in the largest individuals (Table 4). Third, large plants did not react to annual differences in water supply (Fig. 2), although higher water input should be coupled with an improved nutrient supply (Benzing 1990).

The maxima of RGR observed *in situ* in small and intermediate-sized *V. sanguinolenta* specimens (Fig. 2) were significantly below those under high experimental water and nutrient supply (Table 4). Although comparable to reported growth rates of other epiphytes (bromeliads, Castro-Hernández *et al.* 1999; Hietz *et al.* 2002; Sieber 1955; orchids, Schmidt & Zotz 2002), even the highest RGRs observed in small individuals (8·4 mg g⁻¹ day⁻¹, Table 2) were extremely low compared to members of other plant groups. For example,

RGR in terrestrial perennials from more productive habitats may exceed 300 mg g⁻¹ day⁻¹ (Lambers *et al.* 1998), and seedlings of slow-growing temperate and tropical woody species may still grow faster (by about an order of magnitude) than these herbaceous epiphytes (Grime & Hunt 1975; Poorter 1999; Bruhn *et al.* 2000).

Under poor resource supply, size-related differences in RGR were relatively small (Table 2; Fig. 2). Although even the most adverse experimental conditions were probably more benign than conditions during the El Niño year, minimum RGR in the field in 1997 and during the experiment did not differ (Table 4). An increase in RGR in years with higher precipitation was expected, but was found only in small and intermediate-sized plants (Fig. 2). Moreover, RGR correlated only with total precipitation, not with the number of rainy days. This is surprising because it is generally assumed that rainfall distribution matters more than total precipitation for growth and survival of epiphytes (Gentry & Dodson 1987b; Benzing 1990). The significantly stronger growth response of small plants to improved resource availability could be highly adaptive. Larger plants are much less prone to desiccation than smaller conspecifics. For example, no plant of >25 cm LL_{max} died due to drought in the extremely dry year 1997 (Schmidt & Zotz 2002). Thus relatively fast growth in small plants under favourable conditions may minimize mortality. Alternatively, ontogenic drift may simply be the consequence of architectural and structural changes. For example, the leaf mass ratio of field-grown plants decreases with size from 0·82 g g⁻¹ in small individuals to 0·54 g g⁻¹ in the largest tanks in *V. sanguinolenta* (Schmidt 2000). Yet another possible reason for size-related changes in RGR is the storage of assimilates for future reproduction in larger plants. Individuals of >40 cm LL_{max} may flower and fruit (Schmidt & Zotz 2002), and reproductive effort is high in vascular epiphytes (Benzing & Davidson 1979; Benzing & Ott 1981; Zotz 1999).

Although leaf-level photosynthesis and growth are rarely strongly correlated (Körner 1991), it is striking that size-related trends in leaf gas exchange (Schmidt & Zotz 2001) and growth (this study) are actually divergent in *V. sanguinolenta*. The maximum rate of net CO_2 uptake of field-grown plants *increases* by almost 50% in plants of 5 and 30 cm LL_{max}, respectively (Schmidt & Zotz 2001), while maximum RGR *decreases* by more than 30% (Fig. 2). While scaling from leaf to plant is obviously problematic in *V. sanguinolenta*, it is possible from leaf to entire foliage: the area-based carbon gain of the entire green foliage was positively correlated with plant size, despite greater self-shading in larger plants (Zotz *et al.* 2002). The same reasons as proposed for differences in responsiveness to resource availability – differences in allocation patterns and plant structure (storage of assimilates and nutrients, changes in leaf mass ratio) – must explain this discrepancy.

Ours is the first experimental study to investigate simultaneously the effects of the most important abiotic determinants of growth in a vascular epiphyte, and also includes the analysis of ontogenetic drift. Within the range of experimental conditions, the factor 'water' explained more of the variation in RGR than any other factor. A more drastic reduction in water supply, simulating drier years, may have shown (as suggested by Zotz & Hietz 2001) that nutrient supply is even less limiting for vegetative growth in vascular epiphytes *in situ*. The present study cannot provide a definitive answer to this question. Although our experiment covered the range of RGR observed in a natural population (Table 4; Fig. 2), the use of only two different levels per factor for water, nutrients and light for logistical reasons limits interpretations. A follow-up study will focus on the smallest plants, and on water and nutrients only.

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