

GROWTH IN THE XEROPHYTIC EPIPHYTE *TILLANDSIA FLEXUOSA* SW. (BROMELIACEAE)

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Abstract. Vegetative growth of the xerophytic epiphyte *Tillandsia flexuosa* was studied both *in situ* and under controlled conditions in a growth chamber. Realized growth rates under natural conditions in the dry Peninsula de Azuero (Panama) were similar to those of previously studied epiphytes from wetter habitats. Near-optimal *ex situ* conditions stimulated growth only in smaller individuals. Field-collected plants were initially not nutrient starved, which can be deduced from the lack of a growth response to fertilization in contrast to a substantial irrigation effect. After several months, both increased water and nutrient availability had a strong effect on growth. A likely explanation for this finding is luxury consumption of nutrients.

Resumen. Se estudió el crecimiento del xerófito, *Tillandsia flexuosa*, *in situ* y bajo condiciones controladas en una cámara de crecimiento. Las tasas de crecimiento relativas (RGR) bajo condiciones naturales en la Península de Azuero (Panamá) fueron similares a las de epífitas de bosques más lluviosos. Condiciones casi óptimas *ex situ* causaron una estimulación de RGR solamente en plantas pequeñas. Plantas colectadas en el campo no sufrían de un bajo almacenamiento de nutrientes, lo que se deduce de una falta de respuesta a la fertilización, mientras la irrigación tenía un efecto inmediato y sustancial al crecimiento. Después de varios meses, tanto mejor almacenamiento con agua como con nutrientes causaron un aumento en RGR. La explicación más probable es el “consumo de lujo” de nutrientes bajo condiciones naturales. Accepted 30 April 2009.

Key words: luxury consumption, pastures, plant growth, RGR, tropical dry forest.

INTRODUCTION

Vascular epiphytes are a prominent component of tropical forests (Benzing 1990), being most conspicuous in wet montane settings, where these structurally dependent plants can make up more than 50% of the flora (Kelly *et al.* 2004) and constitute an important part of above-ground biomass (Nadkarni *et al.* 2004). In a classic study, Gentry & Dodson (1987) documented a steep decline in species numbers and abundance in this life form with decreasing precipitation, indicating that vascular epiphytes are much more affected by low moisture availability than trees, shrubs, or herbs. On the other hand, tropical dry forests are not at all devoid of epiphytes (e.g. Murphy & Lugo 1986, Reyes-García *et al.* 2008), although epiphytes from moist or wet tropical forests have received far more attention by physiological ecologists than those from drier vegetation (Zotz &

Hietz 2001; but see, e.g. Andrade 2003, Cervantes *et al.* 2005).

Epiphytes from wetter forests commonly show extremely low *in situ* relative growth rates ($< 5 \times 10^{-3}$ day⁻¹; Hietz *et al.* 2002, Schmidt & Zotz 2002, Zotz 2005), remaining very low even under near optimal conditions in the greenhouse (c. 10×10^{-3} day⁻¹; Castro-Hernández *et al.* 1999, Schmidt & Zotz 2002). Some information exists on epiphyte growth in dry forests (Cervantes *et al.* 2005), but an experimental study using growth analysis is not available. Thus it remains unclear how representative our present understanding of epiphyte growth is for more xerophytic taxa. *Tillandsia flexuosa* is the most xerophytic epiphytic bromeliad in many countries of Central America and the Caribbean, e.g. in Trinidad (Smith *et al.* 1986) or Panama (Zotz, pers. obs.), and was therefore a natural choice for such a study. I started the study with a number of hypotheses: 1) Considering the drought-prone natural habitat, I expected a larger discrepancy in achieved *in situ*

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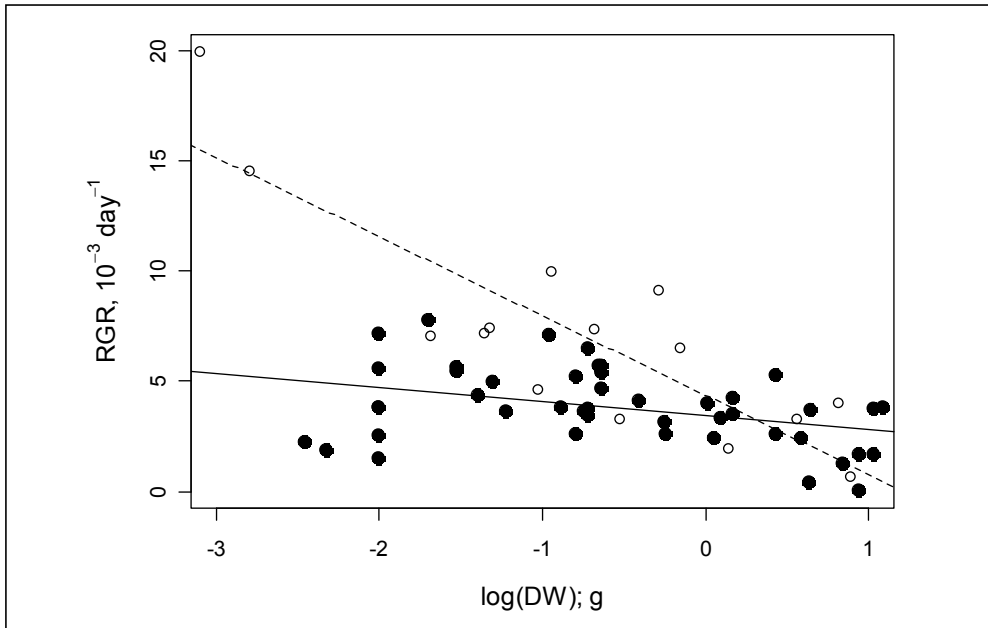


FIG. 1. Relationship of plant size (dry mass in g) and relative growth rate (RGR, in 10^{-3} day^{-1}) in the field and under near optimal conditions in a growth chamber. Closed symbols represent field data, open circles are from growth chamber measurements. The two regressions (solid lines) are: $\text{RGR}(\text{field}) = -1.09(\log \text{DW}) + 4.9$, $r^2 = 0.18$, $p < 0.01$; $\text{RGR}(\text{growth chamber}) = -3.6(\log \text{DW}) + 4.3$, $r^2 = 0.74$, $p < 0.001$.

growth and potential growth under nearoptimal conditions compared with species from wetter forests. 2) Even in moist forests, water seems to be more limiting for plant growth than nutrient supply (Laube & Zotz 2003), and I expected a similar or even higher relative importance of water for a xerophyte. As a corollary, this should imply luxury consumption of nutrients (*sensu* Chapin 1980) under natural conditions (Benzing & Renfrow 1974). These expectations were addressed both experimentally and descriptively by studying *T. flexuosa* both in the field under natural conditions and in the laboratory.

MATERIALS AND METHODS

Study sites. *In situ* growth was monitored in natural populations of *Tillandsia flexuosa* Sw. (Bromeliaceae) in the eastern part of the Peninsula de Azuero (Republic of Panama, Herrera and Los Santos Provinces). The annual rainfall in the region averages less than 1300 mm (Anonymous 1988). The original

plant cover has been replaced by pastures, scattered planted shade trees, or a few remnant trees of the original vegetation. Typical species are *Byrsonima crassifolia* (Malpighiaceae), *Guazuma ulmifolia* (Sterculiaceae), or *Enterolobium cyclocarpum* (Fabaceae). The only other common vascular epiphyte species in this driest part of Panama, besides the studied bromeliad, is *Brassavola nodosa* (Orchidaceae) (Zotz, pers. obs.).

Measurements in situ. A total of 53 plants ranging in size from 1 to 38 cm (LL), and growing on six different trees, was measured and marked in March 2006. The sites were revisited in 2007 and 2008. Only 25 plants were still alive in 2008. The dry weight (DW) of 13 additional individuals (LL 1–40 cm) excluding roots was determined by keeping them in a drying oven (80°C) for 5 days. The correlation between the length of the longest leaf (LL, cm) and plant dry weight (DW) was very high:

$\text{DW} = -0.000006 \times \text{LL}^4 + 0.0005 \times \text{LL}^3 - 0.0021 \times \text{LL}^2 + 0.008 \times \text{LL}$; $r^2 = 0.999$.

The correlation between LL and DW allowed the determination of *in situ* relative growth rates (RGR) in $\text{g g}^{-1} \text{day}^{-1}$ following Hunt (1982):

$$\text{Equation 1 } \text{RGR} = (\ln \text{DW}_{t+1} - \ln \text{DW}_t) / \Delta t$$

Measurements in the growth chamber. In 2006 I collected individuals of *Tillandsia flexuosa* of varying size and transferred them to the greenhouse in Oldenburg. In a first experiment, I determined the relationship of plant size and maximum RGR for 15 plants (LL 0.5–35 cm). Plants were kept in a growth chamber (Microclima 1750 E, Snijder Scientific, Tilburg, The Netherlands) under the following conditions: photon flux density (PFD): $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 12 hours, air temperature: 26°C day, 20°C night; relative air humidity: 60% day, 85% night; external CO_2 concentration $c. 370 \mu\text{l l}^{-1}$. Although climate data for the natural growing sites are lacking, the chamber conditions are quite similar to the situation of tropical lowlands and should allow near-maximal carbon gain since photosynthesis of most bromeliads is almost light-saturated at the chosen PFD (Stuntz & Zotz 2001). Plants were watered daily by immersing them in deionized water for 15 minutes, with added fertilizer twice weekly (Flory 3: 10-15-10, Euflo, Munich, Germany). The nitrogen concentration was 200 mg l^{-1} (30% NO_3^- , 70% NH_4^+). Plant fresh weight (FW) was determined four hours after watering, which allowed a consistent estimation of plant dry weight: there was a close, reproducible relationship of plant dry / plant fresh weight, with an average value of $16.7 \pm 0.4\%$ (mean

$\pm \text{SE}$, $n = 60$). Knowing the slow growth rates in other vascular epiphytes, I ran the experiment for eight weeks.

The effect of varying water and nutrient supply on plant growth was studied in a second experiment, using 54 relatively small individuals (mean DW: $0.14 \pm 0.01 \text{ g}$), which are known to show the strongest response to changes in resource availability (Laube & Zotz 2003). The conditions in the climate chamber were identical to Experiment 1, but the irrigation and fertilization regimes differed. In a full factorial design, plants were either watered twice daily (W^+), every other day (W^0), or only once in four days (W^-). Plants were fertilized once every eight days with one of three concentrations of a commercial fertilizer (Flory; as above), which, e.g., represented nitrogen concentrations of $200 \text{ (N}^+)$, $20 \text{ (N}^0)$, and $2 \text{ mg N l}^{-1} \text{ (N}^-)$. The experiment lasted almost 12 weeks. Plant fresh weight was determined at the onset of the experiment and again after two weeks, and converted to plant dry mass as described above. To exclude the possibility that the relationship between DW and FW changes with watering frequency, we determined this ratio repeatedly for another group of plants that were watered only every fourth day: there was no significant change over 72 days (Pearson product moment correlation, $r = 0.01$, $p = 0.79$, $n = 7$). In addition, both fresh and dry weight of all individuals were determined at the end of the experiment. All statistical analyses were done with R 2.6.0. (R Development Core Team 2007).

RESULTS

In natural populations of *Tillandsia flexuosa*, relative growth rates averaged $3.7 \times 10^{-3} \text{ d}^{-1}$ in 2006–2007 and $3.9 \times 10^{-3} \text{ d}^{-1}$ in the second year, minima being close to zero and with a maximum of $7.7 \times 10^{-3} \text{ d}^{-1}$, with size explaining 19% (2006–2007) or 29% (2007–2008) of the variation (Fig. 1). Growth under near optimal conditions in a climate chamber was elevated only in smaller individuals. Overall, growth was not significantly increased (ANCOVA, $p = 0.18$), but the slopes of the two regression lines were highly significantly different (ANCOVA, $p < 0.001$).

The effect of varying water and nutrient supplies on plant growth changed during the duration of the study. Initially, only the increase in water supply had a significant effect on plant growth (Table 1, Fig. 2). Over the entire course of three months, however, both water (W) and nutrient supply (N) affected

Table 1. Results of two one-way ANOVAS on the effects of water (W) and nutrients (N) on the relative growth rate of *T. flexuosa*.

Factor	df	F-value	P-value
First two weeks			
W	2	26.86	< 0.001 ***
N	2	0.712	0.50
W:N	4	1.62	0.19
Residuals	45		
Entire study			
W	2	29.07	< 0.001 ***
N	2	17.68	< 0.001 ***
W:N	4	3.82	0.009**
Residuals	45		

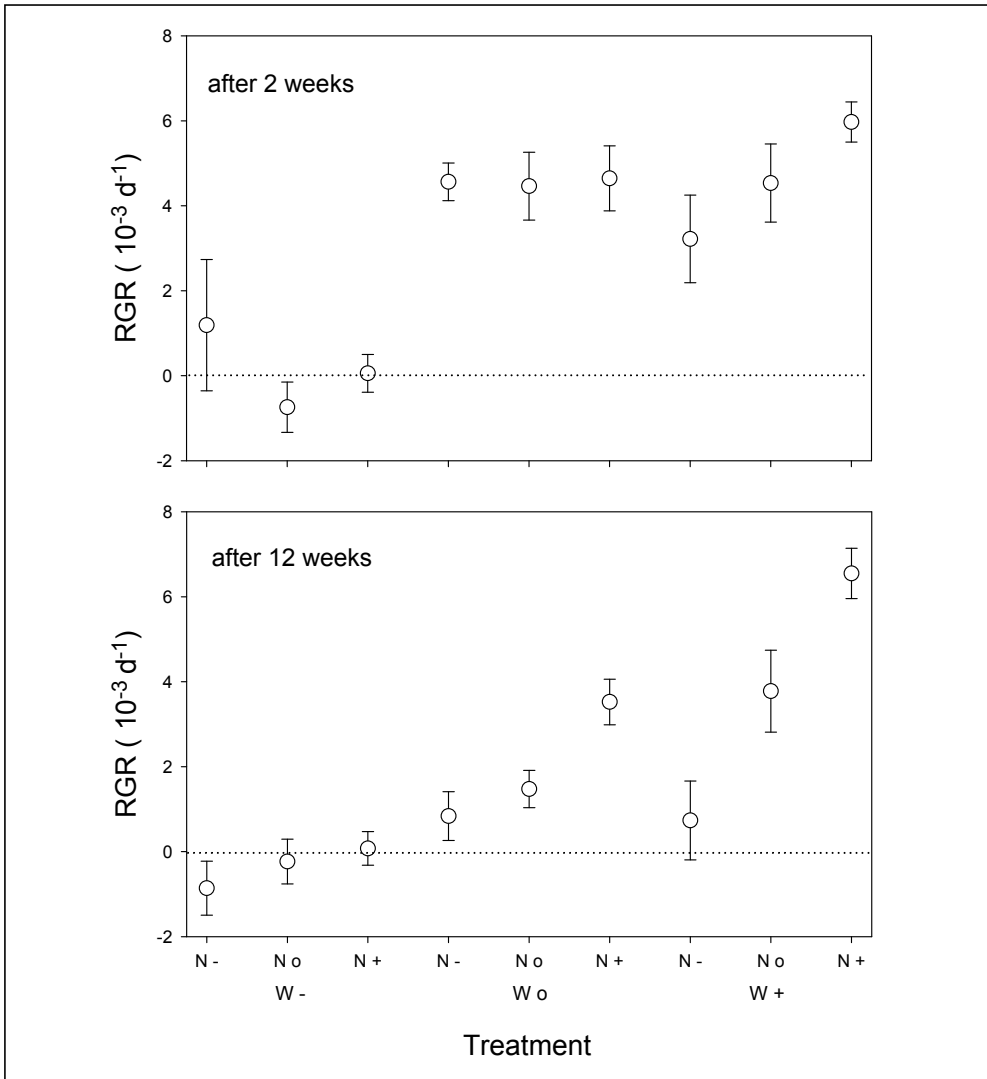


FIG. 2. Response of relative growth rates (RGR, in 10^{-3} day^{-1}) to varying levels of water (W) and nutrient (N) supply. Data are means \pm SD, $n = 6$. The three levels of resource supply are indicated as low (-), medium (o), and high (+). The results of the statistical analysis are given in Table 1.

growth, with a significant interaction between them: at the lowest levels of either N or W, relative growth rate (RGR) was not significantly different from zero, irrespective of the level of the other resource. In contrast, at intermediate and high levels of either N or W, an increase in the other resource led invariably to a substantial increase in RGR.

DISCUSSION

The observed *in situ* growth rates of the studied xerophyte, averaged over an entire year, were in the range of other vascular epiphytes from wetter habitats, such as moist lowland forests or wet montane forests (Hietz *et al.* 2002, Schmidt & Zotz 2002, Zotz

2005). Consistent with earlier findings from other species, there was a strong size-dependency in the achieved RGRs: smaller seedlings grew about 10 times faster than larger conspecifics under near optimal conditions (Fig. 1), but the highest growth rates in the present study are still very low when compared with other terrestrial plants (Grime & Hunt 1975, Hunt & Cornelissen 1997). Only smaller individuals showed increased growth rates under near optimal conditions in the climate chamber, which is consistent with earlier observations with the tank bromeliad *Werauhia sanguinolenta* from a moist lowland forest (Laube & Zotz 2003), where increased water and nutrient supply did not have an effect on growth of larger individuals either. In contrast to my expectation, the discrepancy between realized and potential growth in smaller individuals was only about two-fold in *Tillandsia flexuosa*, and thus not as pronounced as expected. On the contrary, species from wetter lowland forests, such as *Werauhia sanguinolenta* (Laube & Zotz 2003) or *Catopsis sessiliflora* (Zotz & Laube 2005), grew about 3–4 times faster under near optimal compared with natural conditions.

Which resource stimulates growth most in small individuals? At least initially, additional nutrients did not increase RGR in field-collected specimens as opposed to improved water supply (Fig. 2). Over three months, however, both water and nutrients led to increased RGRs. This finding is consistent with the concept of “luxury consumption” of nutrients, which is found in many stress-tolerant plants (Chapin 1980) and has been suggested for epiphytic bromeliads before (e.g. Benzing & Renfrow 1974, Endres & Mercier 2003). In such habitats, plants normally tune their nutrient uptake capacities towards the highly efficient capture of short pulses, and the temporal accumulation of reserves is simply a consequence of the combination of high uptake potential for nutrients and slow growth (Winkler & Zotz 2009). The present study provides evidence that field-collected epiphytes are not necessarily nutrient-starved, although favorable growth conditions, as given in our experiment, can lead to nutrient demands for sustained growth within a few weeks.

In conclusion, the results of this study only partly fulfilled the original expectations. The xerophytic epiphyte *Tillandsia flexuosa* shows a smaller rather than a greater capacity to take advantage of increased resource supply compared with epiphytes from wetter habitats. Water supply, on the other hand, is indeed more limiting than nutrient supply for growth, but only over rather brief periods.

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