

GROWTH AND SURVIVAL OF THE EARLY STAGES OF THE HETEROBLASTIC BROMELIAD *VRIESEA SANGUINOLENTA*

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Abstract. This 5-year study documents *in situ* growth and survival of the early life stages of a heteroblastic epiphyte, *Vriesea sanguinolenta* (Bromeliaceae), in a tropical lowland forest in central Panama. Growth was generally slow and negatively correlated with plant size. Mortality, which did not vary with size, averaged 28% per year and was mostly drought-related. Even 6 years after germination there were plants that had not completed the transition to the tank form. Using survival analysis it is estimated that 50% of all plants need more than 5 years to produce adult leaves. *Accepted 20 July 2003.*

Key words: Barro Colorado Island, bromeliads, El Niño, epiphytes, growth, heteroblasty, plant size, RGR.

INTRODUCTION

Many phytotelm bromeliads show heteroblasty: while juveniles resemble so-called atmospherics with leaves characterized by stout morphology and trichome-covered surfaces, broad adult foliage forms the typical water-impounding tank (Benzing 2000). Although this phenomenon has fascinated ecologists for more than a century (Morren 1873, Lieske 1914), there are very few studies on the life-history of heteroblastic species (Matos & Rudolph 1984), or on the possible adaptive significance of an atmospheric juvenile stage (Adams & Martin 1986b, c; see also Reinert & Meirrelles 1993). Adams & Martin (1986a) proposed that xeromorphic juveniles allow establishment on otherwise inhospitable substrates, for example at exposed sites in the canopies of rain forest trees. Although plausible, we lack sufficient physiological and life-history information to test this notion. To date only a single study has specifically addressed the duration and demographic characteristics of the life-history stages of a heteroblastic bromeliad. Matos & Rudolph (1984) report that the atmospheric stage of epiphytic *Tillandsia depeana* persists for more than a decade and that mortality during this part of the life cycle is much higher than later. Other demographic studies

sometimes include heteroblastic epiphytes, but do not address changes associated with a phase change in detail (e.g., Hietz 1997, Hietz *et al.* 2002).

Most vascular epiphytes are long-lived organisms and understanding possible bottlenecks in life history clearly demands long-term investigations. We initiated such a study with a population of the heteroblastic bromeliad, *Vriesea sanguinolenta* Cogn. & Marchal more than five years ago, in 1997 (Schmidt & Zotz 2002), in conjunction with a range of ecophysiological and ecological experiments (e.g., Schmidt & Zotz 2001, Stuntz & Zotz 2001, Zotz & Vollrath 2002). This multifaceted approach is intended to promote understanding of the mechanisms behind population processes. This is not of purely academic interest: the knowledge of the vital rates of epiphyte populations is also an essential prerequisite for efficient conservation measures under current conditions or in the wake of global climate change (Tremblay & Hutchings 2002).

MATERIALS AND METHODS

Habitat and study species. The study was carried out in the Barro Colorado Nature Monument (9°10'N, 79°51'W), Republic of Panama. The forest of this biological reserve, which is classified as a tropical moist forest (Holdridge *et al.* 1971), receives about 2600 mm of annual precipitation, with a pronounced dry season

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FIG. 1. Morphological characteristics of juvenile atmospheric (1 year old, upper panel), transition stage (ca. 4 years old), and young tank (ca. 7 years old) of *Vriesea sanguinolenta*. Whole plants were photographed *in situ* in Panama. Atmospheric feature linear leaves arranged in a non-impounding rosette, transition forms develop the first broad leaves with limited capacity for impoundment, while tank forms impound both water and detritus. The scale equals 1 cm.

from late December to late April. Detailed descriptions of vegetation, climate, and ecology are reported by Croat (1978).

Vriesea sanguinolenta (syn. *Werauhia sanguinolenta* Cogn. & Marchal; Grant 1995) ranges from Costa Rica to Colombia to various Caribbean islands in lowland to lower montane wet forests (Croat 1978). On Barro Colorado Island, it occurs high in the forest canopy on a number of tree species, but is particularly abundant on flood-tolerant, evergreen *Annona glabra* L. (Annonaceae, Zotz *et al.* 1999). More information on the physiology and ecology of this species can be found in Schmidt & Zotz (2002) and Zotz (1997).

Census data. In 1997, 25 plots containing *Vriesea sanguinolenta* were set up in an area of about 1 ha. Each plot consisted of a branch section (1–2.5 m in length) within the crown of *Annona glabra* (Schmidt & Zotz 2002). Due to its maximum height of only ca. 8 m, epiphytes on this tree are easily accessible. A total of 126 plants were marked individually with thumb tacks. Annually, at the beginning of the rainy season, we recorded the length of the longest leaf (LL) and the total number of leaves.

For plants that died between successive observations, cause of death was noted. Categories were: 1) plants still in place but desiccated (“drought”), 2) plant missing with part of the substrate at the former attachment site (“detached bark”), 3) mortality because a tree fell or branches broke (branch/tree fall), and 4) individuals that simply disappeared (missing). To compensate for mortality, we marked additional specimens in new plots on additional *Annona glabra* trees after each of the five censuses. With these replacements this study reports observations on a total of 444 individuals in the atmospheric stage and 55 young individuals equipped with tanks. For some analyses, I defined four size classes (SC 1: < 1 cm; SC 2: 1–2 cm; SC 3: 2–3 cm; SC 4: > 3 cm) for atmospheric plants only.

Growth and survival analysis. Calculating relative growth rate (RGR) required conversion of our non-destructive size measurements (LL) into plant dry mass (DM). The relationship between LL and DM in atmospheric was: $DM \text{ (mg)} = 5.19 \text{ LL} - 2.49$, $r^2 = 0.87$, $n = 6$; range 0.5–1.00 cm LL; and $DM \text{ (mg)} = 14.50 \text{ LL} - 10.49$, $r^2 = 0.84$, $n = 16$; range 1.01–4.5 cm LL. RGR was then calculated as $RGR = (\ln(DM_{\text{year } n+1}) - \ln(DM_{\text{year } n})) / \Delta\text{time}$ (Hunt 1982).

For small tanks after transition I used the regression equation given by Schmidt & Zotz (2001). In addition, seed mass was determined for a sample of 78 seeds. The seed coat was assumed to account for 30% of the average mass of $0.505 \text{ mg seed}^{-1}$. Thus, $0.35 \text{ mg seed}^{-1}$ was used to estimate the RGR between germination and first census.

The time period between germination and the development of a tank, i.e., the length of the atmospheric stage, was analyzed with STATISTICA's survival analysis module (STATISTICA 5.1, StatSoft Inc., Tulsa, USA). Survival analysis is designed to compare times to the occurrence of a given event, typically death, among populations of individuals, accounting for three problems usually associated with such an analysis: skewed distributions of transition times, loss of individuals prior to the end of the study for other reasons (in this case death), and the possibility of individuals remaining "alive" past the end of the study (in this case, without performing a phase change until 2002). The latter two are types of cen-

soring, or truncation. A total of 176 observations (27 complete and 149 censored) were available for a Kaplan-Meier Analysis.

Data analysis. Statistical analysis was done with STATISTICA software. Before analysis of variance variables were tested for normality and homoscedasticity. Percentages were arcsine square root transformed (Sokal & Rohlf 1995). The RGR before and after the transition, which could be studied in 35 cases, had to be analyzed by a non-parametric Wilcoxon Matched Pairs Test. Before analyzing the relationship of annual growth rates and precipitation, RGRs were weighted by LL.

RESULTS

From atmospheric to tank. Individuals in the atmospheric stage ranged in size from 0.5 cm to 4.5 cm (Fig. 1). Maximum leaf length in the late dry season, approximately 10 months after germination, was $0.8 \pm 0.02 \text{ cm}$ (mean \pm SE, $n = 102$). The average size of

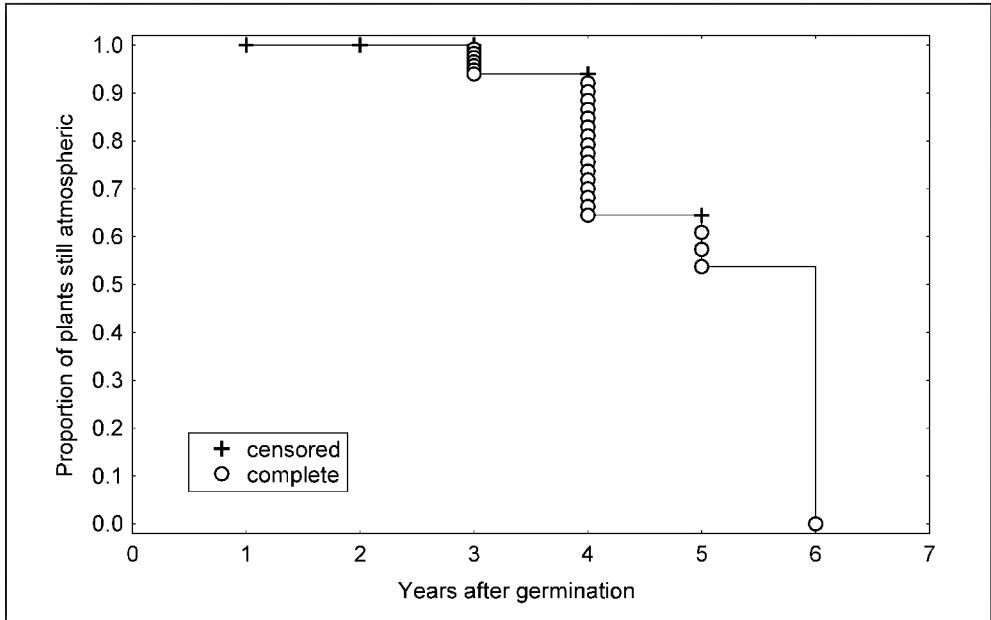


FIG. 2. Relationship of time since germination and the proportion of plants still in the atmospheric stage. Given is the survival function of a Kaplan-Meier analysis with different symbols for censored and non-censored data points.

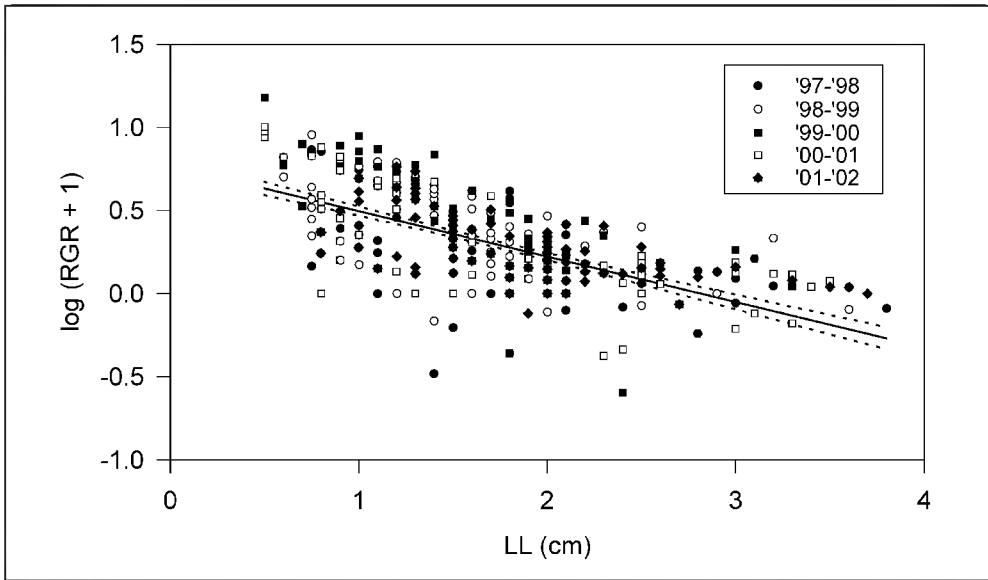


FIG. 3. Changes of relative growth rates with plant size in atmospheric individuals. The regression equation is $\log(\text{RGR} + 1) = 0.77 - 0.27 \text{ LL}$. $r^2 = 0.41$, $p < 0.001$ (RGR in $\text{mg g}^{-1} \text{ d}^{-1}$). LL = length of the longest leaf.

plants that changed life form in a subsequent year was $2.7 \pm 0.7 \text{ cm}$ ($n = 53$). The complete cycle from germination until transition to tank form took 3–6 years in the 27 cases that could be followed from first-year seedling to tank. However, a number of plants monitored since May 1997 remained atmospheric in 2002, i.e., a transition had not occurred almost 6 years after germination. A Kaplan-Meier Product-Limit Analysis suggests that 50% of all plants need more than 5 years to start producing adult leaves that impound water (Fig. 2).

Growth. Measured relative growth rates of individual plants ranged from slightly negative ($-0.7 \text{ mg g}^{-1} \text{ d}^{-1}$) to a maximum of $14.1 \text{ mg g}^{-1} \text{ d}^{-1}$. Estimating growth rates during the approximately 10 months from germination in the early wet season until the first census by comparing seed dry mass and the estimated DM of new seedlings in the study plots yielded an average RGR of $5.2 \pm 0.3 \text{ mg g}^{-1} \text{ d}^{-1}$ (mean \pm SE, $n = 102$). During the atmospheric stage, RGR decreased continuously from the smallest to the largest individuals (Fig. 3). While RGR between the first and second census (initial plant size 0.8 cm) averaged $3.4 \pm 0.3 \text{ mg g}^{-1} \text{ d}^{-1}$ (mean \pm SE, $n = 81$), growth in

plants $> 3 \text{ cm}$ LL was reduced to less than 10% of this rate ($0.3 \pm 0.06 \text{ mg g}^{-1} \text{ d}^{-1}$, mean \pm SE, $n = 26$). Accounting for these size-related differences in RGR in an analysis of co-variance, I found significant inter-yearly variation in growth rates (ANCOVA, $F_{4,435} = 3.80$, $p = 0.004$, with LL as co-variate). RGR tended to increase in years with higher rainfall, but this trend was not significant ($p = 0.11$). Immediately after the phase shift, RGR increased again (Fig. 4, Wilcoxon Matched Pairs Test, $n = 35$, $p = 0.001$). RGR among plants with tanks decreases continuously as size increases (Schmidt & Zotz 2002).

Mortality. The causes of mortality could not be determined reliably for a large proportion of the lost plants (Table 1). Without clear evidence of substrate failure (i.e., when entire branches or larger parts of bark were missing), or desiccated plants still in place, I left the cause of mortality open (missing/unknown). Mortality rates for the atmospheric individuals did not differ among size classes (ANOVA, $F_{3,16} = 1.21$, $p = 0.33$), but significant variation was found between years (ANOVA, $F_{4,15} = 3.60$, $p = 0.03$). The second finding was caused by the exceptional mortality between May 1999 and April 2000, when almost 50% of the atmo-

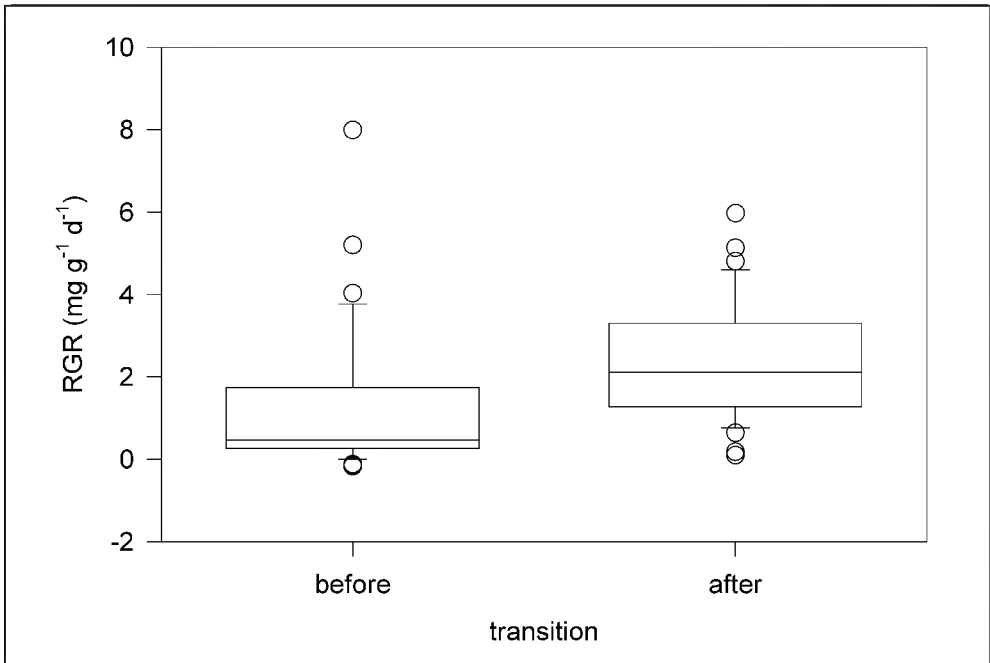


FIG. 4. Relative growth rates in the year before and the year after the transition from atmospheric stage to tank form. Shown are box plots with 25–75 percentiles (box), the median (horizontal line), and the 10TH and 90TH percentiles. Individual data points outside the latter percentiles are shown as circles.

spherics died (LSD test, $p < 0.05$). Drought is not likely the cause of mortality because the year 2000 was a particularly wet year. However, branch and tree falls eliminated four entire study plots during that period. Ignoring these losses, the annual differences were no longer significant (data not shown). For the entire study period of five years, annual mortality rates aver-

aged 28%. The relationship between mortality rates and annual precipitation was not significant (Spearman Rank, $p > 0.05$). Mortality was elevated immediately after the phase shift: more than half of the plants (29 of 55 cases) that I observed shifting from atmospheric to tank-forming plant died during the subsequent year. However, compared to the overall

TABLE 1. Causes of mortality in atmospheric *Vriesea sanguinolenta* during a 5-year period. Given are the total number of individuals that died (n) and the proportional losses due to desiccation, detached bark, branch or tree fall, and unknown reasons (all in %).

period	drought	detached bark	branch or tree fall	Missing/unknown	n
'97-'98	76.9	23.1	0	0	13
'98-'99	37.5	25	25	12.5	16
'99-'00	16.4	0.0	42.6	37.7	61
'00-'01	39.3	3.6	0.0	57.1	28
'01-'02	59.1	0.0	4.5	36.4	22

mortality during the atmospheric stage (144 out of 444 plants) this increase was only marginally significant ($\chi^2 = 3.66$, $p = 0.055$).

DISCUSSION

There are few anecdotal statements and even fewer data on the duration of the atmospheric stage in heteroblastic bromeliads. Matos & Rudolph (1984) presented a model of the entire life history of *Tillandsia deppeana* based on data from a montane forest in Guatemala. The first adult leaves did not appear earlier than 10–12 years after germination in this population. Another decade passed before the first flowering. Quite in contrast, Hietz *et al.* (2002) estimated only 11 years for the entire period from germination to reproduction for the same species in a montane forest in Mexico. My results with a different species in a moist lowland habitat fall between these extremes: 50% of all plants complete the atmospheric stage within 5 years (Fig. 2), and at least 10 more years pass before reproduction starts (Schmidt & Zotz 2002). Mortality rates during the early atmospheric stage can only be compared with those reported by Matos & Rudolph (1984), yielding a surprisingly similar 28% annually in both studies. Consistent with other studies on epiphytes, mortality was caused primarily by drought and substrate failure. What proportion of a newly germinated cohort of *Vriesea* plants survive to produce adult leaves? Assuming a similar mortality rate between germination and first census compared to older atmospheric (28% year⁻¹) and a maximum of 7 years until phase change, I estimate that almost 30% of successfully germinated plants should go through this phase change. Interestingly, mortality increased immediately after this transition. Considering Adams & Martin's (1986a) argument on the adaptive significance of the atmospheric stage and the size-dependence of the utility of water-impounding tanks in bridging rainless periods (Zotz & Thomas 1999), this finding was actually expected. The transition seems to be a typical life-history bottleneck, with plants lacking the xerophytic features of atmospheric without yet benefiting from a fully functional tank.

Compared to terrestrial plants, even to those from low-productivity habitats (Figs. 3 and 4; compare for example Grime & Hunt 1975 or Khan *et al.* 2000), growth was very slow in these epiphytic atmospheric. This is, however, not an idiosyncrasy of this ontogenetic stage: extremely slow growth rates seem to be

typical for vascular epiphytes (Sieber 1955, Castro-Hernández *et al.* 1999, Hietz *et al.* 2002, Schmidt & Zotz 2002). In fact, average *in situ* RGRs of first-year atmospheric (3.4 mg g⁻¹ d⁻¹) and small individuals with tanks (3.3 mg g⁻¹ d⁻¹; compare Schmidt & Zotz 2002) were very similar, while growth decreased as plants became larger within both the atmospheric and tank stages. Benzing's (2000) suggestion that atmospheric grow slowly, while faster growth is associated with the development of foliar impoundment, is therefore only partially valid. While this notion is obviously incorrect for the entire life cycle, it agrees with the data on growth immediately before and after the phase shift (Fig. 4). Remarkably, neither growth or survival were significantly affected by annual variation in rainfall: RGRs in a very dry El Niño were comparable to those in a year with average precipitation. Overall, there was at least a suggestive trend ($p = 0.11$).

In summary, I report life-history data on the early stages of the heteroblastic epiphytic bromeliad, *Vriesea sanguinolenta*. Consistent with theoretical considerations, the change to the tank form seems to represent a life-history bottleneck with increased mortality immediately after transition. Before generalizations about the adaptive significance of heteroblasty in the Bromeliaceae are possible, similar information for other species is needed. This also applies to a detailed analysis of the morphological and physiological changes during transition.

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