Inherently slow growth in two Caribbean epiphytic species: A demographic approach

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Abstract. In relation to the drought-prone and nutrient-poor habitat, vascular epiphytes are routinely referred to as inherently slow-growing plants, although actual evidence is rare. To test this notion we measured *in situ* growth of the understorey orchid *Aspasia principissa* and the tank bromeliad *Vriesea sanguinolenta*, and, for the latter species, also the growth under favourable conditions in the greenhouse. Using growth analysis we show: (1) that in an intraspecific comparison, small to intermediate individuals yield the highest relative growth rates (RGR) *in situ*: *A. principissa*: 1.6 10^{-3} d^{-1}; *V. sanguinolenta*: 3.3 10^{-3} d^{-1}; (2) that the bromeliad reaches maximum size after ca. 15 yr, while the orchid needs at least 20 yr; and (3) small *V. sanguinolenta* plants exhibit a highly plastic growth response to favourable conditions in the greenhouse, reaching an almost 10-fold increase in RGR. In spite of a substantial increase in growth under more favourable conditions, our results are consistent with the notion that epiphytes are *inherently* slow growing organisms.

Keywords: *Aspasia*; Epiphyte; Plant size; Panama; RGR; *Vriesea*.

Nomenclature: D'Arcy (1987).

Abbreviations: DM = Dry mass; LL = Length of the longest leaf of a plant; PPFD = Photosynthetic photon flux density; PsbL = Length of the most recent pseudobulb; RGR = Relative growth rate; SC = Size category.

Introduction

Vascular epiphytes represent a highly diverse group of plants regarding taxonomy, life form and physiology (e.g. Lüttge 1989; Benzing 1990), reflecting at least in part the heterogeneity of their common habitat, the forest canopy. Growing sites are distributed in three-dimensional space and characterized by a high variability in microclimatic conditions (Benzing 1990), and water and nutrient supply (Lesica & Antibus 1991). Moreover, the substrate, i.e. tree trunks, branches and canopy soil, is more unstable than most terrestrial systems (Benzing 1981), and hampers long-term survival.

Epiphyte habitats are mostly referred to as drought-prone and nutrient-poor (e.g. Benzing 2000). Epiphyte growth and development is thus generally considered to be very slow (e.g. Lüttge 1989; Benzing 1990, 2000), although only a few studies provide a quantitative basis for this conclusion. For example, in a study on the population structure of *Tillandsia circinnata,* Benzing (1981) estimated that this bromeliad requires 8-10 yr to reach reproductive size, and Larson (1992) predicts first flowering of the orchid *Encyclia tampensis* at an age of ca. 15 yr. For another epiphytic orchid, *Dimerandra emarginata*, Zotz (1995) modeled vegetative growth using annual size increments of specimens of varying sizes, concluding that a model plant takes ca. 10 yr to be potentially reproductive, and about 25 yr to reach maximum size. None of these studies used quantitative growth analysis (e.g. Hunt 1982), which makes their results difficult to compare with published data for other plant groups.

Using quantitative growth analysis in the current study we compared growth parameters of two epiphytic species, differing strongly in a number of physiological, morphological and life history characteristics. Growing in the exposed parts of the forest canopy, the tank bromeliad *Vriesea sanguinolenta* exhibits rather high rates of photosynthesis (Schmidt et al. 2001; Schmidt & Zotz 2001). During early ontogeny the bromeliad experiences a change in life form from 'atmospheric' (= obtaining water from the atmosphere by interception or condensation; cf. Benzing 2000), to a water-impounding plant which is able to draw on its own supply of externally stored water, i.e. is 'continuously supplied' (*sensu* Benzing 1990). In contrast, *Aspasia principissa*, an epiphytic understorey orchid featuring much lower photosynthetic rates (Schmidt et al. 2001), is 'pulse supplied' during rainfall events (*sensu* Benzing 1990). Generally, species with high rates of photosynthesis from sites with better resource availability tend to grow faster than taxa with low photosynthetic performance from resource poor habitats (e.g. Evans 1989; Poorter et al. 1990, Lambers et al. 1998). Thus, we expected pronounced differences in respect to *in situ* growth between the two species, possibly indicative of

the range of different growth rates among vascular epiphytes at our study site, a seasonal tropical lowland forest in Central Panama. Additionally, growth of *V. sanguinolenta* under favourable conditions in the greenhouse was studied to explore the plasticity of growth and test the notion of generally slow inherent growth in this group.

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 is classified as a tropical moist forest (Holdridge et al. 1971). Mean annual rainfall is ca. 2600 mm with a pronounced dry season from late December to late April (Windsor 1990). Detailed descriptions of vegetation, climate and ecology are reported by Croat (1978) and Leigh et al. (1982).

Vriesea sanguinolenta (syn. *Werauhia sanguinolenta* Cogn. & Marchal; Grant 1995) is found from Costa Rica to Colombia and on various Caribbean islands in lowland to lower montane wet forests (Croat 1978). The species colonizes a number of host tree species high in the forest canopy, but is particularly abundant on floodtolerant, evergreen *Annona glabra* (*Annonaceae*; Zotz et al. 1999). Throughout the study we used maximum leaf length (LL, in cm) as a measure of size. This parameter is highly correlated with a more rigorous measure for size, i.e. plant dry mass (DM) *in situ*:

$$DM = 10^{\,2.87 \times \log LL - 2.84};\ r^2 = 0.99;\ n = 38;\ p < 0.001 \qquad (1)$$

(Pearson product-moment correlation, Schmidt & Zotz 2001), and under near-optimal conditions in the greenhouse:

$$DM = 10^{\,2.83 \times \log LL - 3.09};\ r^2 = 0.98;\ n = 6;\ p < 0.001. \qquad (2)$$

For more information on the biology of *V. sanguinolenta* see Schmidt & Zotz (2001).

Aspasia principissa occurs in central and eastern Panama, preferring the wetter forests of the region (Croat 1978). Most plants are found in the understorey, growing on trunks of various tree species, but may be encountered occasionally in higher strata of the forest. Again we chose a non-destructive measure of plant size (length of the most recent pseudobulb, PsbL, in cm) that allowed repeated size determinations in the field and is correlated closely with plant DM:

$$DM = 10^{\,2.66 \times \log PsbL + 0.69};\ r^2 = 0.95;\ n = 34;\ p < 0.001 \qquad (3)$$

(Pearson product-moment correlation).

Census data

In 1997, 25 plots with *V. sanguinolenta* were established in an area of ca. 1 ha. Each plot consisted of a branch section (1-2.5 m in length) within the crown of *A. glabra*, sometimes with more than one plot per tree. Due to its maximum height of 8 m, epiphytes on this tree were easily accessible. In 1997, 1998 and 1999, respectively, 313, 287 and 315 plants were monitored. Plants larger than 10 cm LL were all labelled, while only a representative subset of smaller individuals (LL < 10 cm) was monitored individually. The size of all unlabelled plants (1997: 2099 plants, 1998: 1443 plants, 1999: 1588 plants) was estimated, and then plants were assigned to size categories. Annually, at the beginning of the rainy season, we recorded LL, the total number of leaves, and fruiting events.

To determine the annual leaf production, the very tip of the youngest leaf was clipped as a marker for the next census. For plants that died between two observation intervals, the cause of death was noted. Categories were: (1) individuals that fell off the substrate for unknown reasons (missing); (2) plants still in the plot but dried (drought); (3) plants that died because trees fell or branches broke (branch/tree fall); and (4) dead specimens with more than 70% of the plant leaf area consumed (herbivory; for determination of relative leaf damage see Schmidt & Zotz 2000). To compensate for losses due to mortality we added an appropriate number of new specimens in the plots on additional *A. glabra* trees during each of the three annual census periods.

Similarly, we established 90 plots with *A. principissa* in 1997. Along 10.3 km of the forest's unformed trail system on Barro Colorado Island we recorded all individuals of *A. principissa* within 2.5 m to the left and right for each trail, thus covering a transect of 5.2 ha. Each plot was defined as the section of a tree stem from ground level up to 2 m in height, and in total contained 191 specimens. We determined the length of all pseudobulbs, leaves and bracts, and noted flowering and fruiting events. Missing or dead plants were classified as with *V. sanguinolenta*. All plants were re-censused annually, at the beginning of the rainy season. Extending our observation area along the trail system, we added plots annually to maintain a more or less constant number of individuals.

Determination of size categories

In the case of *V. sanguinolenta* we distinguished size categories (SC) corresponding to the ontogenetic stages: (1) atmospheric, non-impounding; (2) tank-forming, vegetative; and (3) tank-forming, reproductive. To subdivide the large category of vegetative tank-forming

bromeliads we used a procedure suggested by Vandermeer (1978). By these means a set of individuals is split into an optimal number of categories in such a way as to minimize distribution and sampling errors. Applying this method yielded four additional size categories (Table 1). In *A. principissa*, with no distinct step changes during ontogeny, the limits of all size categories were computed following Vandermeer (1978, Table 1).

Controlled environment experiment

Vriesea sanguinolenta plants ($n = 10$) were potted in hydroleca (a growing substrate without soil) and kept in the greenhouse in Würzburg, Germany for 2 yr. The length of the longest leaf was determined annually. Climatic conditions were mean integrated daily PPFD ca. 10 mol. m^{-2} d^{-1}; air temperature 24 to 26 °C; relative humidity 60 to 80%. Tanks were filled twice daily with a fertilizer solution (N: 10 μg g^{-1}, K: 10 μg g^{-1}, P: 7 μg g^{-1}, POLY CRESCAL-fertilizer, Aglukon Spezialdünger GmbH, Düsseldorf, Germany).

Data analysis

Calculating relative growth rate (RGR) required a conversion of our non-destructive size measurements (LL, PsbL) into DM via the regression equations given above. *In situ* and in the greenhouse, RGR was then calculated as:

$$RGR = (\log_e (DM_{year\ n+1}) - \log_e (DM_{year\ n})) / \Delta_{time} \qquad (4)$$

(Hunt 1982). The significance of differences in RGR was tested with a *t*-test for independent samples.

Growth simulation

In order to visualize growth kinetics and to explore how long it might take a small epiphyte to reach maturity or maximal size we simulated growth in both species. Starting with a minimum plant size of 0.5 cm (LL; PsbL) we estimated daily size increments from the mean RGR for the smallest size category. After reaching the threshold size to the next size category RGR was adjusted and changed for every subsequent size category in a stepwise fashion. Simulations ended when the maximum size of plants in the natural populations was reached.

Results

Phenology

The life cycle of *Vriesea sanguinolenta* is comprised of 3 distinct life stages: (1) an atmospheric stage; (2) a vegetative, tank-forming stage; and (3) a reproductive tank-forming stage. The smallest size in the late dry season (i.e. ca. 10 mo after germination) was ca. 0.5 cm maximum leaf length (LL). Atmospheric seedlings on average reached ca. 2 cm (maximum 4 cm) LL before undergoing a shift in life form. During the subsequent tank-forming stage, each leaf base forms a water tight chamber resulting in a multi-tank rosette. Larger plants (> 60 cm LL) may produce one tall inflorescence (up to 2 m in height, Table 1) bearing 44 ± 29.1 (mean ± SD, $n = 7$) capsules, each containing 1008 ± 323 seeds (mean ± SD, $n = 6$). Plants are polycarpic, but individual shoots flower only once.

Table 1. Life history and morphological characteristics (means ± SD) of *Vriesea sanguinolenta* and *Aspasia principissa*. Numbers for annual probability of fruiting are means of 2 observation periods. For *V. sanguinolenta* we determined 6 size categories (SC), using maximum leaf length (LL) as a measure for plant size. Proportion of leaves replaced annually (mean % ± SD, *n*) individuals per SC. For *A. principissa* ($n = 3$ yr) the limits of the 7 SCs are given as the length of the most recent pseudobulb (PsbL).

		SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7
Vriesea sanguinolenta								
LL (cm)		< 2.0	2.1 - 7.0	7.1 - 13.0	13.1 - 25.0	25.1 - 60.0	> 60.0	–
DM (g)		< 0.0003	0.0003 - 0.39	0.40 - 2.31	2.32 - 15.13	15.14 - 187.9	> 188.0	
	1997/1998	n.d.	82 ± 26.1	89 ± 30.0	79 ± 25.3	68 ± 11.4	45 ± 6.1	–
Proportion + SD and *n* of leaves replaced annually (%)			(63)	(22)	(31)	(19)	(3)	
	1998/1999	n.d.	93 ± 38.6	77 ± 36.5	83 ± 35.1	81 ± 31.4	83 ± 3.5	–
			(47)	(30)	(25)	(16)	(2)	
Probability of fruiting (%)		0	0	0	0	4	58	–
Aspasia principissa								
PsbL (cm)		< 1.5	1.6 - 2.5	2.6 - 4.0	4.1 - 6.0	6.1 - 8.0	8.1 - 11.0	> 11,0
DM (mg)		< 14.3	14.4 - 55.5	55.6 - 193.7	193.7 - 569.1	569.1 - 1222.7	1222.8 - 2850.5	> 2850.6
Pseudobulbs per plant		1.5 ± 0.24	2.3 ± 0.19	2.9 ± 0.37	3.5 ± 0.27	3.5 ± 0.67	3.8 ± 0.41	4.1 ± 0.26
Leaf longevity (yr)		1.2 ± 0.07	1.5 ± 0.16	1.8 ± 0.18	2.0 ± 0.12	2.2 ± 0.10	2.5 ± 0.05	2.9 ± 0.05
Bract longevity (yr)		1.0 ± 0.01	1.2 ± 0.14	1.2 ± 0.12	1.4 ± 0.05	1.5 ± 0.02	1.7 ± 0.13	2.0 ± 0.10
Probability of fruiting (%)		0	0	0	0	2 ± 2.9	10 ± 4.3	11 ± 6.4

Aspasia principissa grows sympodially. At the end of the dry season (March to April), a new shoot emerges from the base of the previous shoot, growing continuously during most of the rainy season. While the shoot morphology is almost identical in differently sized specimens (each pseudobulb has mostly two leaves at the apex and is sheathed by up to 3 leafy bracts), the absolute number of living shoots (or parts thereof) depends on plant size (Table 1). Large plants may comprise up to 8 pseudobulbs, while leaf longevity ranged from roughly 1 yr in SC 1 to almost 3 yr in SC 7 (Table 1). Although bracts were almost identical in morphology, anatomy, and physiology (unpubl. data), they were shed earlier than the apical leaves, i.e. their life spans ranged from 1 to 2 yr (Table 1). Once reaching a pseudobulb length (PsbL) of ca. 7 cm plants became mature, i.e. they potentially can produce flowers and fruits (Table 1).

Plant size and vegetative growth

The size category distribution of individual *V. sanguinolenta* plants (Fig. 1) illustrates that the majority (> 65%) of the population were atmospheric. While the smallest tank-forming size (SC 2) still represented roughly 20% of the sample, members of larger SCs became increasingly rare: fewer than 1% of all plants were potentially reproductive individuals (SC 6). This pattern remained relatively constant during the study period (Fig. 1 A-C). The SC distribution of *Aspasia*

principissa was similar over the 3 years, but trends were less pronounced; while the smallest SC represented about 20% of all individuals, the largest SC still accounted for ca. 7% (Fig. 1 D-F).

Annual measurements of maximum leaf length (LL) in *V. sanguinolenta* revealed only subtle size increments from 1997 to 1998, while during the following year most plants increased considerably in size (Fig. 2A, B), with about doubled relative growth rates compared to the preceding year (RGR; Fig. 3A). When analysed for all specimens, mean RGR differed between years, and although there was an element of non-independence in the RGR calculations, due to the repeated use of the 1998 census data, the statistical probability was robust enough to render the conclusion valid: $p < 0.001$, df = 421 (*t*-test for independent samples) with RGR:
1997/1998: $1.1\ 10^{-3} \pm 1.4\ 10^{-3}\ d^{-1}$ (mean ± SD; $n = 208$);
1998/1999: $2.5\ 10^{-3} \pm 1.8\ 10^{-3}\ d^{-1}$ (mean ± SD, $n = 215$).
Flowering shoots died, but plants produced a new, smaller rosette (Fig. 2A, B). Irrespective of plant size, almost the entire leaf set was replaced between two observations (Table 1). Growth was also studied on individuals under controlled greenhouse conditions: under high resource availability mean RGR was significantly higher than *in situ*:
in situ: $1.8\ 10^{-3} \pm 1.8\ 10^{-3}\ d^{-1}$;
greenhouse: $6.9\ 10^{-3} \pm 3.9\ 10^{-3}\ d^{-1}$; $p < 0.001$, df = 438, *t*-test for independent samples. This effect was mainly attributable to small tank plants (SC 2), where RGR increased from $1.3\ 10^{-3}\ d^{-1}$ to $11.2\ 10^{-3}\ d^{-1}$, i.e. by
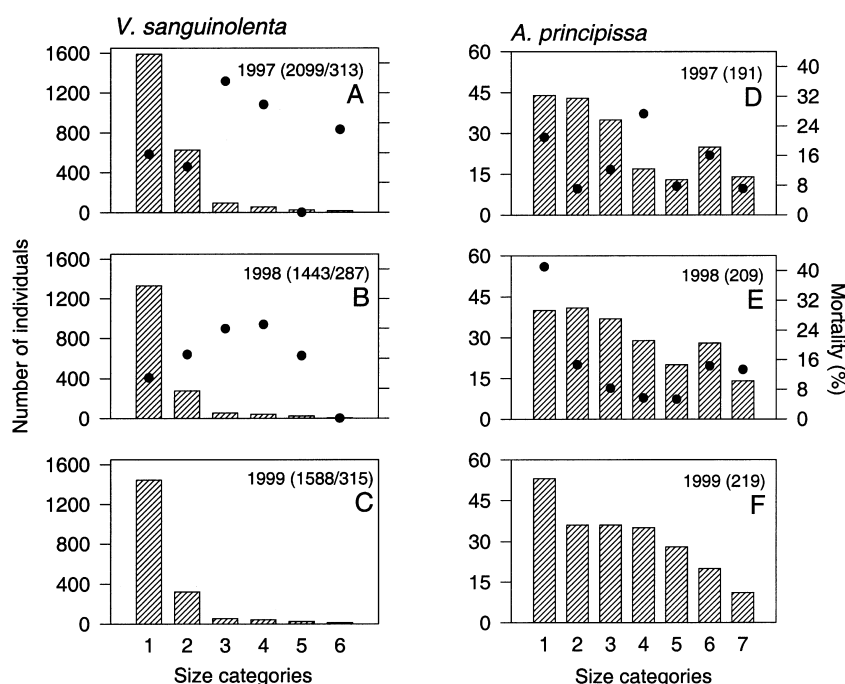

Fig. 1. Size category distribution (dashed bars) and subsequent annual mortality rates (closed circles) in 1997, 1998 and 1999 in *Vriesea sanguinolenta* (**A - C**) and *Aspasia principissa* (**D - F**). Numbers in brackets are the total number of plants at the beginning of the period. For *V. sanguinolenta* the numbers of plants assigned to SCs by estimation is represented by the first number in brackets. The second number in brackets refers to all labeled and measured plants, from which data on mortality were derived as well. All individuals of *A. principissa* were labeled and measured.
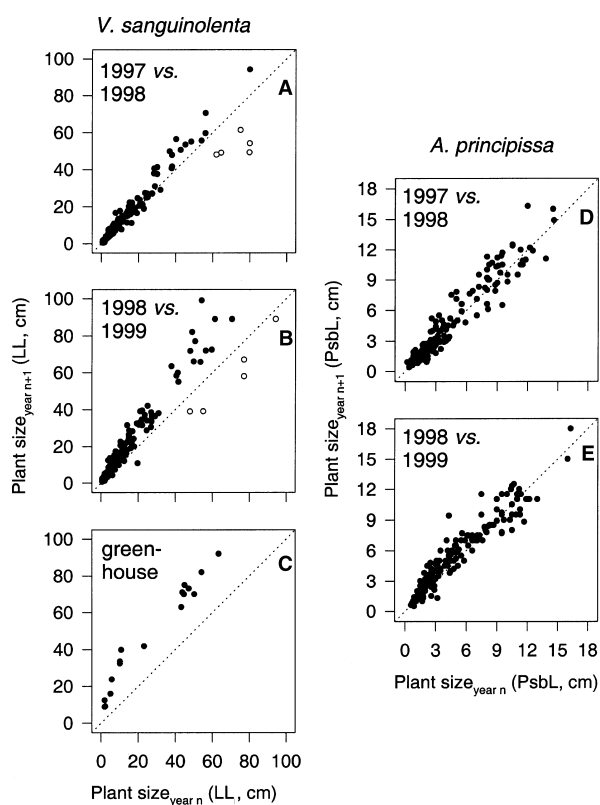
Fig. 2. Vegetative growth in the two epiphytes, as size increments of plants in two consecutive years. Vegetative (closed symbols) and reproductive individuals (open symbols) were distinguished in *Vriesea sanguinolenta*. Dotted lines indicate zero annual increment.

Fig. 3. Relative growth rates (RGR) of differently sized *Vriesea sanguinolenta* (**A**) and *Aspasia principissa* (**B**). Values are means + SD for the observation periods 1997-1998 (open bars) and 1998-1999 (grey bars). For *V. sanguinolenta* RGR was also determined under favourable conditions in the greenhouse (circles).

almost one order of magnitude compared to field conditions during 1997 (Fig. 3A). Conversely, larger plants (SC 4, 5 and 6) grew at similar rates under favourable greenhouse conditions and *in situ* (Fig. 2A-C and 3A). In *A. principissa* annual size increments in situ were also significantly lower in the first vs. the second observation period:

1997: $0.43\ 10^{-3} \pm 1.8\ 10^{-3}\ d^{-1}$ (mean $\pm$ SD, $n = 156$);
1998: $0.92\ 10^{-3} \pm 1.8\ 10^{-3}\ d^{-1}$ (mean $\pm$ SD, $n = 173$; Figs. 2D, E and 3B).

On the basis of RGR, we simulated growth starting with the size of a seedling (*V. sanguinolenta*, LL = 0.5 cm; *A. principissa*, PsbL = 0.5 cm) until the maximum size of the two species was reached (LL: ca. 100 cm; PsbL: ca. 11 cm). As shown in Fig. 4A a model bromeliad would need more than 40 yr to reach maximum size assuming the growing conditions of 1997 throughout its entire life. Given the conditions of 1998 the same plant would need only ca. 17 yr to attain a comparable size. In the greenhouse under high resource supply, development is accelerated: plants need only 5 to 6 yr from seedling to maximum size (Fig. 4A). For *A.*
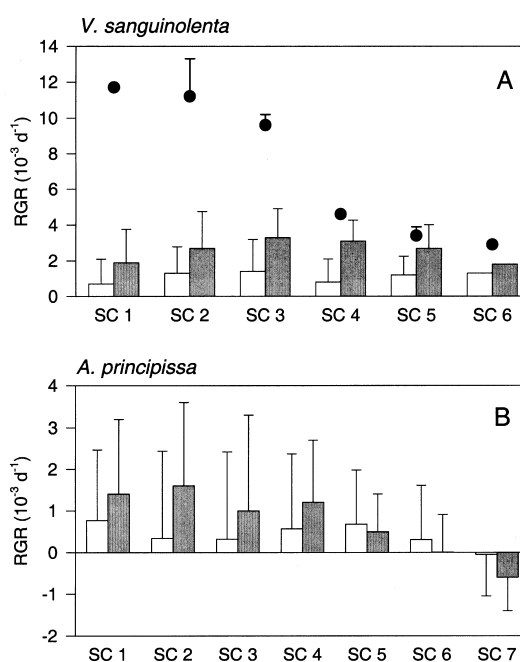
principissa the model calculations yielded similar year-to-year differences. Subjected to the growing conditions of 1997 a model plant would need ca. 50 yr to complete development, while under the growing conditions of 1998 comparable size would be reached after ca. 20 yr (Fig. 4B).

Mortality

In *V. sanguinolenta* patterns of mortality were similar for the two observation periods: annual mortality rates ranged from 0 up to 35% depending on the size category, with highest losses in medium sized individuals (Fig. 1A, B). The average mortality rate for all individuals during the entire study period was 16.5%. A third of the dead bromeliads could not be relocated after one year, i.e. they either had lost contact with the substrate, fell off with peeling bark, or were torn down by falling tree parts or by animals. Calculated for the entire population 36% of plants that died between two observations were found dry (Table 2). However, drought related death was never encountered in SCs 5 and 6. About 17% died because of branch or tree fall (Table 2). Herbivory and other causes of death (i.e. plants squeezed between branches) each accounted for less than 10% of the overall mortality (Table 2).
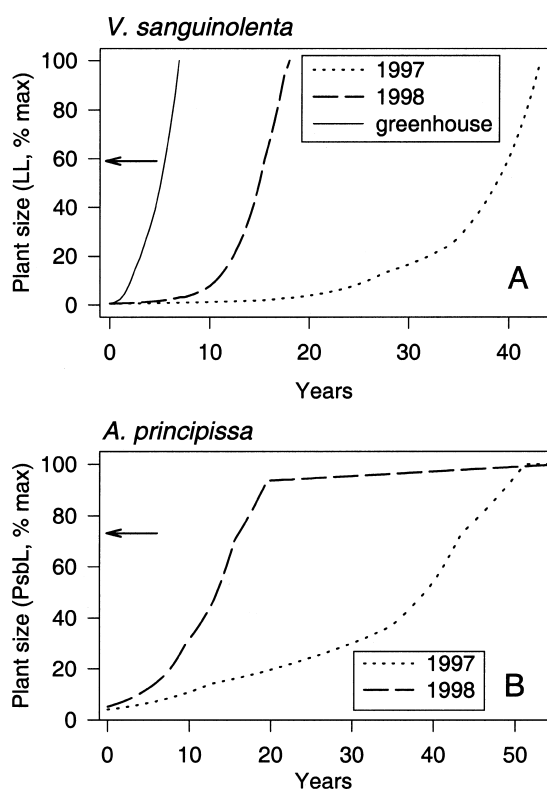
Fig. 4. Simulated growth for *Vriesea sanguinolenta* and *Aspasia principissa*, computed with daily RGR of the different size categories. Plant size is expressed relative to maximum plant size (ca. 100 cm LL; 11 cm PsbL). Model calculations with size increments are from 1997-1998 (dotted lines), 1998-1999 (dashed lines), and for *V. sanguinolenta* only under greenhouse conditions (solid line). Arrows indicate the minimum size of reproductive individuals.

Average mortality in *A. principissa* was similarly high (ca. 15%), but there was no trend towards increased mortality rates at a specific ontogenetic stage (Fig. 1D, E). Again, the fate of a high proportion of individuals remains unclear: 55% were missing at the subsequent census (Table 2). Drought-related death was somewhat less important in the understorey orchid *A. principissa* (26%) compared to the bromeliad, but it was likewise restricted to small to intermediate SCs (data not shown). Branch or tree fall accounted for ca. 17% of death cases (Table 2). Herbivory was encountered frequently, but never reached a lethal level, while pathogens caused irregular growth and finally death in one specimen (categorized as 'other' causes of mortality in Table 2).

Discussion

Population structure and dynamics differed greatly in the two epiphytic taxa. In *Vriesea sanguinolenta* most of the specimens found in the plots were atmospheric seedlings (Fig. 1A-C). Mortality, however, was comparatively low in this SC. Featuring slow growth and low mortality the annual probability of atmospherics completing the shift towards small tank plants is rather low *in situ,* and plants remain atmospheric for several years. Small and intermediate tanks had higher growth and mortality rates (Figs. 1A and 3A). In *Aspasia principissa* small individuals were not as numerically dominant as they were in the bromeliad population (Fig. 1). The highest growth rates were encountered in small to medium sized plants, while rates declined in larger individuals of SC 5 to 7 (Fig. 3B), coinciding with increasing potential for reproduction (Table 1; see also Zimmerman & Aide 1989).

Under natural conditions, values of RGR in *V. sanguinolenta* were about twice those of *A. principissa* (Fig. 3), corresponding to similar differences in photosynthetic capacity (Schmidt et al. 2001). In spite of these interspecific differences, *in situ* RGR in both species was very low compared to those of forbs from more productive habitats (e.g. Grime & Hunt 1975; Poorter et al. 1990), but rather similar to those of other life forms such as tree seedlings, growing in the understorey of other moist lowland forests (e.g. Poorter 1999). Although RGR of small bromeliads increased substantially under greenhouse conditions, these plants still grew slowly (Fig. 3A). Thus, we conclude that our results are consistent with the notion that vascular epiphytes are inherently slow growing plants (Benzing 1990; Zotz 1995).

The greenhouse experiment illustrated the potential of small *V. sanguinolenta* to respond to differences in resource availability, while larger plants grew at similar rates in both the greenhouse and *in situ* (Fig. 3A). This prompted us to hypothesize that small bromeliads are strongly limited by resource availability in their natural environment, while an increase in size alleviates these external limitations. This notion is concordant with earlier findings. Tanks of larger *V. sanguinolenta* are increasingly more effective in bridging rainless periods (Schmidt & Zotz 2001), i.e. they can continue to draw on their externally stored water while smaller plants

Table 2. Proportions of individuals (% of all death cases) that died for a specific reason during the entire observation period from 1997 to 1999, and *n* = sample size.

Species	Missing	Drought	Branch/tree fall	Herbivory	Other	*n*
Vriesea sanguinolenta	33.3	36.4	17.2	8.1	5.1	99
Aspasia principissa	55.0	26.7	16.7	0	1.7	60

Table 3. Comparison of climatic data for different years for Barro Colorado Island (provided by the Smithsonian Tropical Research Institute). Average values are means ± SD, $n = 7$ yr (excluding the dry 1997 year).

Year	Precipitation (mm)	Days with rain	Evaporation (mm)	PPFD (kmol m^{-2} yr^{-1})
Average 1991- 1998	2685 ± 320	163 ± 11	1314 ± 120	11.8 ± 1.1
1997	1700	120	1454	15.2
1998	2684	154	1359	12.6

become water-limited. However, even the larger tank bromeliads are not independent of the natural variability in annual climate in the study area. As shown in Fig. 3A, RGR of all SCs were reduced in 1997. That year was characterized by an El Niño event during which both annual precipitation and the number of rain events were reduced, while the evaporative demand and radiation intensity were elevated (Table 3). Conversely, climatic conditions of 1998 were close to average (Table 3). This suggests that the measured slow growth during the El Niño year (in both species) is exceptional, while plant growth during 1998 may be more appropriate for long-term *in situ* growth scenarios. Consequently, both species are expected to need ca. 15 yr to reach reproductive size (*V. sanguinolenta*: 60 cm LL; *A. principissa*: 7 cm PsbL; compare Fig. 4), which is even longer than published estimates for other epiphytic taxa (Benzing 1981; Larson 1992; Zotz 1995). However, these estimates are only valid for specimens in the study area, which is the southern distribution border of *V. sanguinolenta*. Across the isthmus to the north annual precipitation increases towards the Atlantic coast (max. 3500 mm, S. Paton, STRI, pers. comm.), and here *V. sanguinolenta* is highly abundant (pers. obs.). If a decrease in annual precipitation during the El Niño year (1997) retarded growth in *V. sanguinolenta* in our study area, the greater precipitation towards the Atlantic coast would probably produce greater growth and thus reduce the risk of dying before reaching reproductive size.

Simulating growth for model plants revealed species specific patterns; irrespective of growing conditions *V. sanguinolenta* featured hyperbolic growth curves (Fig. 4A), while those of *A. principissa* were sigmoid (Fig. 4B). Growth in *V. sanguinolenta* is not reduced substantially in late ontogeny, when approaching maximum size (Fig. 4, but also Figs. 2 and 3). The most likely explanation is that reproduction is a singular event in the

life of a shoot of *V. sanguinolenta* and plants grow until an unknown cue triggers a presumably high investment into reproduction (compare Benzing & Davidson 1979). When the fruiting ramet finally dies, a dormant meristem develops a new shoot. Notably, there is a ca. 30% reduction in expected plant size, i.e. in LL, after fruiting compared to a non-fruiting plant of similar initial size (Fig. 2). Probably as a consequence of substantial costs of reproduction plants do not flower in subsequent years; not a single *V. sanguinolenta* was encountered flowering twice during the three years of observation. Conversely, reduced growth rates in larger conspecifics of *A. principissa* (Fig. 3) led to a sigmoid simulation curve of size versus age (Fig. 4B). Larger plants may slow in growth for a number of reasons (e.g. a decreasing ratio of photosynthetic and non-photosynthetic tissue), but this may also be the consequence of continuously increasing investment into reproduction with increasing size. Indeed, Zimmerman & Aide (1989) found that both flower production and fruit length were positively correlated with shoot length in this orchid. Moreover, similar to observations in other epiphytic orchids (Zotz 1998), the annual probability of fruiting also increased with plant size (Table 1), although flower production was reduced in subsequent years (Zimmerman & Aide 1989). Like *V. sanguinolenta*, this orchid showed a reduction in plant size after a reproductive event, but the effect was less pronounced (Table 4).

Combining growth analysis and aspects of population biology in the two epiphytic taxa illustrates their different strategies for coping with their habitat conditions. Reduced growth of larger *A. principissa* and repeated, but moderate investment into reproduction, contrast with the higher growth rates in large *V. sanguinolenta*, with a presumably high energetic input into monocarpic shoots (Benzing 2000). Similarly, growth of non-reproductive plants differed between the two

Table 4. Comparison of annual changes in plant size (*Vriesea sanguinolenta*: LL; *Aspasia principissa*: PsbL) for non-reproductive and reproductive plants of similar size. Size differences were calculated as: $\log_e (\text{size}_{\text{year n}+1}) - \log_e (\text{size}_{\text{year n}})$ to allow comparison with Zimmerman & Aide (1989).

Species	Proportional changes in plant size over time		Source
	Vegetative	Reproductive	
V. sanguinolenta	+ 0.25 ± 0.16	− 0.30 ± 0.18	This study
A. principissa	− 0.07 ± 0.20	− 0.32 ± 0.24	Zimmerman & Aide (1989)

study species; irrespective of high, size-dependent intraspecific variability, maximum growth rates were ca. 100% higher in the bromeliad. In conclusion, while epiphytes seem to be inherently slow-growing plants, species are very variable, and smaller individuals may react with great plasticity to changes in environmental conditions (Figs. 3 and 4). Future work should explore the consequences of this plasticity for the dynamics of epiphyte populations, e.g. in forests differing in resource supply.

References

Benzing, D.H. 1981. The population dynamics of *Tillandsia circinnata* (Bromeliaceae): cypress crown colonies in Southern Florida. *Selbyana* 5: 256-263.

Benzing, D.H. 1990. *Vascular epiphytes: General biology and related biota*. Cambridge University Press, Cambridge, UK.

Benzing, D.H. 2000. *Bromeliaceae – Profile of an adaptive radiation*. Cambridge University Press, Cambridge, UK.

Benzing, D.H. & Davidson, E.A. 1979. Oligotrophic *Tillandsia circinnata* Schlecht (Bromeliaceae): an assessment of its patterns of mineral allocation and reproduction. *Am. J. Bot.* 66: 386-397.

Croat, T. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, CA.

D'Arcy, W.G. 1987. *Flora of Panama: Checklist and Index*. Missouri Botanical Gardens, St. Louis, MS.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* 78: 9-19.

Grant, L. 1995. Bromelienstudien. *Trop. Subtrop. Pflanzenwelt* 91: 1-57.

Grime, J.P. & Hunt, R. 1975. Relative growth rate: its range and adaptive significance in a local flora. *J. Ecol.* 63: 393-422.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. 1971. *Forest environments in tropical life zones: A pilot study*. Pergamon Press, Oxford, UK.

Hunt, R. 1982. *Plant growth curves – the functional approach to plant growth analysis*. Edward Arnold, London, UK.

Lambers, H., Chapin, F.S. & Pons, T.L. 1998. *Plant physiological ecology*. Springer, New York, NY.

Larson, R.J. 1992. Population dynamics of *Encyclia tampensis* in Florida. *Selbyana* 13: 50-56.

Leigh, E.G., Jr., Rand, A.S. & Windsor, D.M. (eds.) 1982. *The ecology of a tropical forest: Seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, DC.

Lesica, P. & Antibus, R.K. 1991. Canopy soil variability – potential significance to epiphyte species richness in wet tropical. *Natl. Geogr. Res. Explor.* 7: 156-165.

Lüttge, U. (ed.) 1989. *Vascular plants as epiphytes: Evolution and ecophysiology*. (Ecological Studies) Springer Verlag, Heidelberg, DE.

Poorter, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Funct. Ecol.* 13: 396-410.

Poorter, H., Remkes, C. & Lambers, H. 1990. Carbon and nitrogen economy of 24 wild species differing in Relative Growth Rate. *Plant Physiol.* 94: 621-627.

Schmidt, G. & Zotz, G. 2000. Herbivory in the epiphyte, *Vriesea sanguinolenta* Cogn. & Marchal (Bromeliaceae). *J. Trop. Ecol.* 16: 829-839.

Schmidt, G. & Zotz, G. 2001. Ecophysiological consequences of differences in plant size - *in situ* carbon gain and water relations of the epiphytic bromeliad, *Vriesea sanguinolenta* Cogn. & Marchal. *Plant Cell Environ.* 24: 101-112.

Schmidt, G., Stuntz, S. & Zotz, G. 2001. Plant size – an ignored parameter in epiphyte ecophysiology? *Plant Ecol.* 153: 65-72.

Vandermeer, J. 1978. Choosing category size in a stage projection matrix. *Oecologia* 32: 79-84.

Windsor, D.M. 1990. *Climate and moisture variability in a tropical forest: Long-term records from Barro Colorado Island, Panamá*. Smithsonian Institution, Washington, DC.

Zimmerman, J.K. & Aide, T.M. 1989. Patterns of fruit production in a neotropical orchid: pollinator vs. resource limitation. *Am. J. Bot.* 76: 67-73.

Zotz, G. 1995. How fast does an epiphyte grow? *Selbyana* 16: 150-154.

Zotz, G. 1998. Demography of the epiphytic orchid, *Dimerandra emarginata*. *J. Trop. Ecol.* 14: 725-741.

Zotz, G., Bermejo, P. & Dietz, H. 1999. The epiphyte vegetation of *Annona glabra* on Barro Colorado Island, Panama. *J. Biogeogr.* 26: 761-776.