Original article

Differences in vital demographic rates in three populations of the epiphytic bromeliad, *Werauhia sanguinolenta*

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Abstract

Since the response to differences in resource availability is most pronounced in smaller individuals of vascular epiphytes such as *Werauhia sanguinolenta* Cogn. et Marchal (Bromeliaceae), I expected variation in growth and survival of small individuals to play an important role in the dynamics of entire populations. Four annual censuses (2002–2005) of three study populations, which were located across the isthmus of Panama, allowed me to construct stage transition matrices, and to conduct growth analysis and elasticity analysis. Differences between populations were highly consistent through time, but, contrary to expectations, hardly related to the comportment of smaller plants. For example, although average mortality rates were highest at the driest site, close to the Pacific, small plants were not predominantly affected. Similarly, although the highest relative growth rates (RGR) of individuals and the highest population growth rates (λ) were found in the population with the highest moisture input, which was located close to the Atlantic coast, this was not due to a particularly strong stimulation of RGR in small plants. Elasticity analysis indicated rather small differences in the importance of the three demographic processes growth, survival, and reproduction for population growth in the three populations, but invariably identified the survival of large tanks as the single most important process determining λ.
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1. Introduction

Vascular epiphytes are a common component of most tropical forests. Although frequently highly abundant and locally diverse, available evidence suggests that epiphytes are growing extremely slowly and that the time to reach maturity is in the order of a decade or more in these herbaceous plants (Benzing, 1981; Larson, 1992; Zotz, 1998; Hietz et al., 2002). The major limitation to growth and reproduction is generally seen in the short and irregular supply of water and nutrients (Benzing, 1990; Zotz and Hietz, 2001), although direct evidence for this notion is surprisingly scarce. Recent experimental work with the epiphytic bromeliad *Werauhia sanguinolenta* (Schmidt and Zotz, 2002; Laube and Zotz, 2003) showed that improved resource supply primarily stimulated growth in smaller plants, while larger conspecifics showed little or no response. Long-term observational data from an on-going field study in Panama agreed with these results (Laube and Zotz, 2003): while the relative growth rates (RGR) of smaller individuals was highly correlated with the varying amounts of annual precipitation between 1997 and 2002, there was no such correlation for larger plants. Plant size will also directly affect the vulnerability to drought. Smaller plants have a higher surface to volume ratio than larger conspecifics (Zotz et al., 2001), and local differences in water supply should thus have a stronger effect on the mortality of juveniles than adults.

To date, the consequences of these size-related differences at the level of *individuals* for the dynamics of epiphyte *populations* have hardly been investigated. Due to their responsiveness to varying resource supply I expected that growth and survival of smaller individuals could strongly influence the dynamics in different populations. I chose three populations of the epiphytic bromeliad *W. sanguinolenta* for study that were located on the Atlantic slope of Panama (Coco

Solo), in central Panama (Barro Colorado Nature Monument), and on the Pacific slope (Lajas). These sites, where I monitored growth, survival, and recruitment from early 2002 to early 2005, differed in a number of respects, the most obvious differences being a decrease in moisture availability (from wetter to drier), different sets of host trees, and highly varying densities.

2. Material and methods

2.1. Study species

W. sanguinolenta (syn. *Vriesea sanguinolenta* Cogn. et Marchal; Grant 1995) is found from Costa Rica to Colombia and on various Caribbean islands in lowland to lower montane wet forests (Croat, 1978). This epiphytic bromeliad is polycarpic, but individual shoots flower only once. Flowering occurs in the rainy season and seeds are released in the late dry season. Since *W. sanguinolenta* is heteroblastic, the small juveniles, which appear in the early rainy season, resemble atmospherics (i.e. possess non-impounding rosettes of small, linear leaves, which are densely covered by the shields of foliar trichomes), whereas larger conspecifics form tanks (i.e. feature broad leaves, which overlap basally forming water-filled chambers, for illustrations see Zotz, 2004). Vegetative propagation, i.e. the production of offshoots, that is common in many other bromeliads (Benzing, 2000; Mondragón et al., 2004), was only observed in very few smaller tank individuals and will therefore not be considered in this paper. More detailed descriptions of its ecology can be found in Schmidt and Zotz (2000, 2002).

2.2. Study populations

Spatiotemporal variation was studied in three different populations in the Republic of Panama. The first population, which is the object of an on-going long-term population study (Schmidt and Zotz, 2002; Zotz, 2004), is located in the Barro Colorado Nature Monument (BCNM). All individuals were growing on *Annona glabra*, a tree species restricted to the marshy shores of Lake Gatun. The second population occurred close to the Atlantic coast near Coco Solo, in a monotypic stand of *Avicennia germinans* (Verbenaceae). The third population grew on trees in pastures near the Pacific Ocean in Chiriqui Province, close to Lajas. There, *W. sanguinolenta* used a number of different host trees, e.g. large *Anacardium excelsum* (Anacardiaceae), which were possibly remnants of the original forest, but also other, mostly smaller trees, e.g. *Guazuma ulmifolia* or *Erythrina costaricensis*.

Rainfall data from the Panama Canal Authority for 1981–1995 indicate about 10% higher annual rainfall at the Coco Solo weather station compared to BCNM (2762 ± 874 mm vs. 2526 ± 641 mm, mean ± S.D.). No detailed rainfall data are available for the third site (Lajas), but the Atlas de Panama indicates average annual precipitation in a similar range (2000–2500 mm). However, since epiphytes were growing on isolated trees in pastures, which results in a much higher radiation load and higher evaporative demand (Sillett et al., 1995), this third site is treated as the drier end of the environmental gradient.

Plots were established in early 2002 in Coco Solo and Lajas, while those on BCNM had been established in 1997 (Schmidt and Zotz, 2002). Each plot consisted of a trunk or branch section (1–3.5 m in length) not more than 4 m above the ground. The available surface area of a plot, which was estimated as the surface of a cylinder in more or less vertical plots and as a semi-cylinder in more or less horizontal plots, ranged from 0.1 to 2.9 m^2. All plants > 10 cm maximum leaf length (LL) were labelled. Only a representative subset of smaller individuals (LL < 10 cm) was monitored individually, whereas the size of all unlabelled plants was estimated within the limits of seven size categories. At the end of the dry seasons of 2003–2005, I recorded again LL, fruiting events, and new establishments within the plots. The initial number of plots ranged from 15 (Coco Solo) and 17 (Lajas) to 25 (BCNM). The total number of individuals in any of the 4 years and sites ranged from a minimum of 336 (Lajas in April 2002) to a maximum of 1369 (BCNM in April 2002). Population densities of *W. sanguinolenta* were analysed for the year 2003. (Other epiphyte species were rarely present, and if so, in small numbers and are therefore ignored.) Because individual size varies by more than five orders of magnitude from < 1 mg dry mass in small atmospherics to > 100 g dry mass in large tanks (Schmidt and Zotz, 2002), averages of size classes are rather meaningless. Although I partly avoided this problem by confining density estimates to tanks, i.e. reducing the variation in dry mass to three orders of magnitude, they should still be taken as qualitative measures of population densities.

2.3. Matrix construction and data analysis

From the demographic data, stage transition matrices were constructed. Seven size classes were defined on the basis of developmental states (atmospherics vs. tank form, non-reproductive vs. reproductive) and plant size: atmospherics < 2 cm LL (*A1*, in part first year seedlings), larger atmospherics (*A2*), tanks with a LL of < 5 cm (*T1*), 5–10 cm (*T2*), 10–20 cm (*T3*), 20–40 cm (*T4*), and > 40 cm (*T5*, this group includes all potentially reproductive individuals, Schmidt and Zotz, 2002). Average fecundity was estimated by dividing the number of new seedlings in year t by the number of all potentially reproductive adults (T5) in year $t – 1$. A projection matrix ($\mathbf{B} = \{bij\}$, where $i, j = 1, 2, . . . , 7$) contains the transition probabilities and contributions (i.e. fecundity) of an average individual at different stages of the life cycle over a unit time interval, in our case a year. The matrix operates over a vector ($\mathbf{n}_t$) containing the distribution of individuals in the size structure of the population at a particular time t (Caswell, 2001).

The size of the population after one time interval is equal to the product of matrix **B** by vector $\mathbf{n}_t$ or

$$N_{t+1} = B_{n_t}.$$

The largest eigenvalue of matrix $\mathbf{B}(\lambda)$, is equivalent to the population's finite rate of increase, the right (**w**) and left (**v**) eigenvectors associated to λ are equivalent to the stable size distribution and the reproductive value distribution, respectively (Caswell, 2001).

For each population I constructed two types of transition matrices: (1) annual matrices, based on the data for each growing season, and (2) mean matrices, constructed by averaging the class-specific transition values for the two matrices at each site. In addition, I explored population trajectories by running stochastic models, which included both demographic and environmental stochasticity. The latter was approximated by sampling the elements of the transition matrix (survival rates and fecundities) at each time step from random distributions created from the mean matrices and the standard deviation matrix derived from the annual matrices such that the mean and variance were the same as those observed in the past. For each population I ran 1000 replications of the model with a duration of 20 years each.

The relative contribution of individual life cycle transitions to population growth rate was analysed with elasticity analysis (De Kroon et al., 1986; Caswell, 2001). This analytical tool quantifies the proportional change in λ resulting from an infinitesimal proportional change in a matrix transition aij:

$$e_{ij} = \delta(\log\lambda)/\delta(\log a_{ij}) = a_{ij}/\lambda \times \delta\lambda/\delta a_{ij}.$$

All elasticities of a transitions matrix sum up to unity, and elasticities of transitions of similar type (e.g. survival = stasis and retrogression [L], growth [G], reproduction [F]) may be added. These characteristics allow the comparison of the relative importance of different types of transitions between populations of the same or different species (for an extensive discussion see Silvertown et al., 1993). RAMAS Ecolab 2.0 (Applied Biomathematics, Setauket, NY, USA) was used to calculate λ, **w**, **v**, **e**, and to run the stochastic models.

Further data analysis was done with STATISTICA 5.0 (Statsoft Inc., Tulsa, OK, USA). Possible differences in the demographic fates of vegetative plants between years and populations were analysed with log-linear analyses (Horvitz and Schemske, 1995; Caswell, 2001), considering stage (stage$_t$) (seven stage classes, as above), year (2002–2003 and 2003–2004), population (at three locations, as above), and fate (stage$_{t+1}$) (seven stage classes and dead) as categorical variables. Fates were analysed for each state separately and for the entire state-by-fate transition probability table (compare Horvitz and Schemske, 1995). In the first set of analyses I tested the null hypothesis that the fate of an individual was independent of site and year using a different three-way contingency Table for each state (factors year (T), site (P), and fate (F)). The second analysis was based on a four-way contingency Table defined by the factors year (T), site (P), state

(S), and fate (F) and tested the null hypothesis that conditional on its initial state, the fate of an individual is independent of site and year. Log-linear analyses were also used to test for significant differences in size class distributions.

In situ growth in the three population was also analysed via the comparison of RGR. The calculation of RGR followed Hunt (1982):

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

The conversion of LL as a non-destructive measure of size to dry weight (DW) was possible due to the very tight correlation of LL and DW ($r^2 = 0.99$). More details are given in Schmidt and Zotz (2002). Growth data were analysed with a three-way ANOVA with the factors year, site, and size class. Mortality and leaf damage in 2005, which did not allow me to determine LL exactly, decreased the number of individuals in T3 available for this analysis. To allow the use of a complete ANOVA design, I combined T1 and T2 in the group "small tanks" and T3 and T4 in "medium-sized tanks".

3. Results

Plant densities of individual plots at Coco Solo, BCNM, and Lajas varied considerably among and within populations. While I found 52 ± 7.6 tanks m^{-2} bark surface (mean $\pm$ S.E.) growing at the BCNM site (range 5–174 tanks m^{-2}), densities in the other two populations were significantly lower (ANOVA with log-transformed data, $F_{2,54} = 22.9$, $P < 0.001$): 15.4 ± 3.6 tanks m^{-2} at Coco Solo (range: 4–45 tanks m^{-2}) and, respectively, 9.2 ± 1.9 tanks m^{-2} (2–32 tanks m^{-2}) at Lajas. There was also a significant difference in the stage class distributions among populations (log-linear analysis, $P < 0.001$, Fig. 1). All stage classes analysed individually yielded significant differences as well, but variation was particularly pronounced in the smallest stage class (A1): small atmospherics accounted for up to 76% of the entire population (4-year average: 63%) at BCNM, while on the other extreme the contribution of A1 was as low as 12% at Coco Solo in 2004 (4-year average: 30%). Temporal variation was also substantial in the overall SC distributions (Fig. 1), but this time not only due to smaller individuals. In Coco Solo, for example, the proportion of atmospherics (A1, A2) decreased by 25% during the duration of the study, while that of adults (T5) almost doubled (+ 86%). Adults also increased in BCNM (+ 50%), whereas the proportion of atmospherics varied little between 2002 and 2005 (82–88% of the population). In Lajas, both the proportion of atmospherics and that of adults showed no obvious temporal trend. The overall temporal variation across sites in larger tanks (T3–T5) was not significant ($P > 0.05$).

The demographic fates of individual plants did not vary with time. A log-linear analysis of the annual matrices of the three study sites yielded no significant time effect ($P = 0.99$), but a significant site effect ($P < 0.001$). Consequently, only matrices with averages of the three transitions between
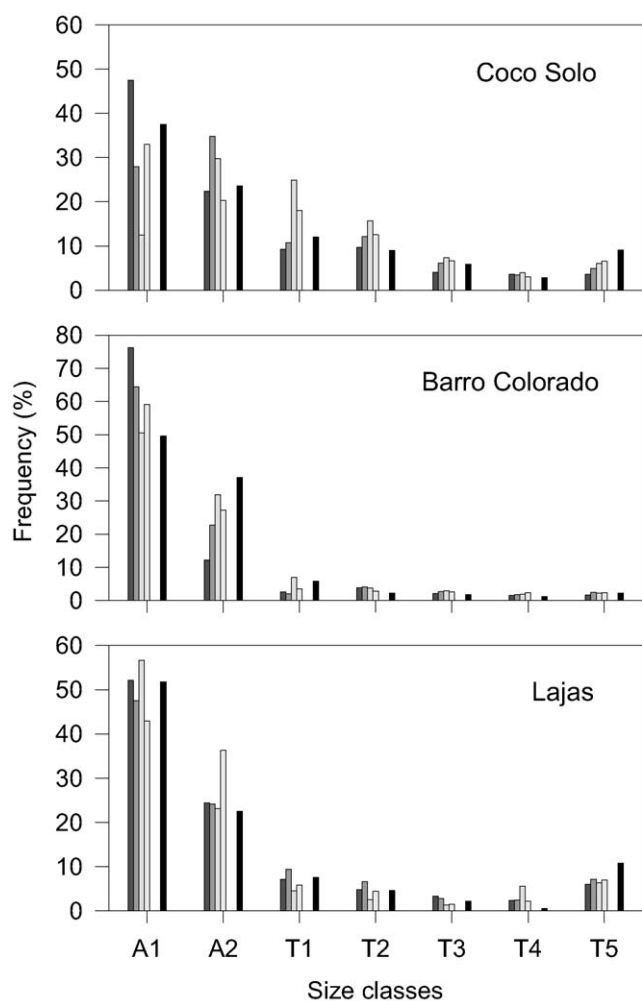
Fig. 1. Size class distribution of three populations of *W. sanguinolenta*. For each population the four distributions in April 2002–2005 (grey bars) are given along with the stable size class distributions (black bars) as determined from the analyses of the average matrices.

2002 and 2005 are presented in the following. When analysing all size classes individually, significant variation in demographic fates between sites was apparent in most size classes, although differences were most pronounced in larger atmospherics (A2) (Table 1). At Coco Solo, more than 40% of all large atmospherics changed to tank form annually (Table 2). This exceeded the transition rates in BCNM and Lajas five-

Table 1
Results of log-linear analyses of effects of site and year on fates of *W. sanguinolenta* stages

Stage	Null fit?	Year	Population
A1	0.97	0.70	0.98
A2	0.003	0.22	< 0.001
T1	0.49	0.17	0.04
T2	0.97	0.92	0.03
T3	0.79	0.86	0.002
T4	0.88	0.24	0.01
T5	0.99	0.99	0.60

It is indicated whether the null hypothesis fits and whether the incremental change in the log-likelihood χ^2 for the added (conditional) effects of plot or year were significant ($P < 0.05$).

fold and twofold, respectively. Moreover, 8% of all large atmospherics at Coco Solo even changed to the second tank class (T2) within a given year, which was never observed in the two other populations. Consistent with these findings from the analysis of transition matrices, the RGRs were highest in Coco Solo for all but the largest tanks (Table 3 and Fig. 2). The significant interaction of site and stage class (Table 3) was mostly due to the largest tanks, which did not differ in RGR among sites (planned comparison, $P = 0.27$).

Average annual mortality rates of the seven size classes at Lajas ($37 \pm 12\%$, mean ± S.D., Table 2) were about twice as high as those at the other two sites (Coco Solo: $21 \pm 8\%$; BCNM: $19 \pm 9\%$). Invariably, the lowest mortality rates were observed in mature plants (T5), but the relative site differences in mortality rates varied little with stage class.

The proportion of large plants (T5) that fruited in a given year differed between sites as well. On average, the proportion of reproductive plants was more than twice as high at BCNM ($23 \pm 6\%$ of T5; $N = 4$ years) than at Coco Solo ($10 \pm 3\%$), with intermediate values at Lajas ($18 \pm 10\%$). This observation partly explains the large site differences in the reproductive values of large plants (Table 2).

Population growth rates (λ) were above unity in Coco Solo (1.08 ± 0.06; $N = 3$ years) and BCNM (1.05 ± 0.02), but below 1 in Lajas (0.92 ± 0.12). Stochastic simulations (not shown) suggest that the first two populations will continue to grow in the coming years, although the average λ in 20 years is slightly lower than in the averages of the deterministic matrix models. Not surprisingly, the stochastic model indicated a decline in population size at Lajas, with the probability of extinction in the next 20 years being ca. 40%.

The expected stable size class distributions at BCNM and Lajas were dominated by atmospherics (A1 and A2), where they account for about 85% of the populations. The expected proportion of atmospherics at Coco Solo is only 61%. These projections are very close to the actual percentages observed at the three sites between 2002 and 2005 (Fig. 1; Coco Solo: $57 \pm 14\%$; BCNM: $85 \pm 3\%$; Lajas: $74 \pm 4\%$, mean ± S.D.).

Overall, the three populations differed rather little in the relative contributions of the three demographic processes 1) growth (G), 2) survival (L), and 3) sexual reproduction (F) to λ (Table 4). Survival (mostly stasis, particularly in mature individuals) ranged from 0.55 to 0.73, while *F* scores were invariably low (0.04–0.07). Invariably, the largest single contribution was survival of the largest tanks.

4. Discussion

The expectation that differences in growth and survival of smaller individuals would explain a considerable proportion of the variation in the dynamics of populations was not fulfilled. Although the observed differences in stage structure (Fig. 1), RGR of individuals (Fig. 2), population growth rates, and mortality rates (Table 2) were consistent with the key importance of water availability in the epiphytic habitat, little

Table 2
Average transition probability matrices for three *W. sanguinolenta* populations

Stage at year $t + 1$	Stage at year $t + 1$							
	A1	A2	T1	T2	T3	T4	T5	v
Coco Solo	(23)	(23)	(22)	(22)	(15)	(15)	(29)	
A1	0.28	0	0	0	0	0	3.26	1
A2	0.44	0.36	0	0	0	0	0	1.7
T1	0	0.36	0.35	0	0	0	0	2.6
T2	0	0.08	0.44	0.27	0	0	0	3.9
T3	0	0	0.01	0.48	0.30	0	0	6.5
T4	0	0	0	0	0.34	0.36	0	13.7
T5	0	0	0	0	0.01	0.47	0.92	20.5
Mortality	0.26	0.18	0.18	0.23	0.33	0.15	0.07	
BCNM	(34)	(62)	(45)	(43)	(46)	(40)	(62)	
A1	0.39	0	0	0	0	0	14.6	1
A2	0.31	0.63	0	0	0	0	0	2.1
T1	0	0.08	0.49	0.01	0	0	0	10.0
T2	0	0	0.24	0.42	0.00	0	0	23.1
T3	0	0	0	0.36	0.60	0.01	0	35.2
T4	0	0	0	0	0.26	0.64	0	59.3
T5	0	0	0	0.01	0	0.21	0.92	111.2
Mortality	0.28	0.27	0.26	0.18	0.12	0.12	0.06	
Lajas	(22)	(18)	(14)	(12)	(11)	(12)	(24)	
A1	0.34	0	0	0	0	0	4.29	1
A2	0.30	0.35	0	0	0	0	0	1.7
T1	0	0.20	0.31	0	0	0	0	4.4
T2	0	0	0.26	0.17	0	0	0	9.7
T3	0	0	0	0.29	0.3	0	0	24.5
T4	0	0	0	0	0.3	0.31	0	49.0
T5	0	0	0	0	0	0.37	0.85	81.6
Mortality	0.35	0.43	0.41	0.52	0.4	0.31	0.14	

Stage classes are described in Section 2. The average numbers of plants per stage class at the beginning of each annual census period are given in parentheses. Also given is the reproductive value (v) for each stage class.

of the variation between the three populations could be explained with the comportment of smaller individuals. For example, mortality rates were not particularly elevated in A1 on isolated trees in pastures (Lajas), although average mortality rates in this population were indeed much higher than in BCNM and Coco Solo (Table 2). I expected increased drought to affect primarily the smallest individuals (Zotz et al., 2001). Indeed, drought is almost unanimously reported as the prime cause of mortality in juveniles (Benzing, 1981; Zotz, 1998; Mondragón et al., 2004). However, there is other,

conflicting evidence of a limited effect of even severe drought on the survival of juvenile epiphytes: in a 5-year field study, Zotz (2004) found no significant variation in the mortality

Table 3
Results of a three-way ANOVA of the effects of year (2002–2003, 2003–2004, 2004–2005), site (Coco Solo, BCNM, Lajas), and size class (small atmospherics [A1], large atmospherics [A2], small tanks [T1; T2], medium-sized tanks [T3; T4], and large tanks [T5]) on the RGR of *W. sanguinolenta*

Factor	df	F	P-level
Year	2	2.2	0.12
Site	2	54.3	< 0.001
Size class	4	44.2	< 0.001
Year × Site	4	1.8	0.13
Year × Size class	8	0.9	0.54
Site × Size class	8	9.7	< 0.001
Error	1000		

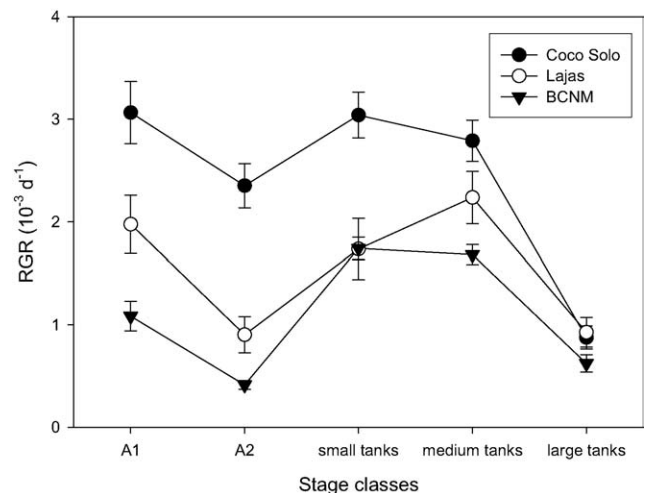Given are degrees of freedom (df), F values and significance levels (P).

Fig. 2. RGR as function of site (Coco Solo, BCNM, Lajas) and plant size (small atmospherics [A1], large atmospherics [A2], small tanks [T1; T2], medium-sized tanks [T3; T4], and large tanks [T5]). Data mean ± S.D. Compare Table 3 for detailed statistical results.

Table 4
Average elasticity matrices for three *W. sanguinolenta* populations

Stage at year $t + 1$	Stage at year t						
	A1	A2	T1	T2	T3	T4	T5
Coco Solo							
A1	0.024	0	0	0	0	0	0.067
0A2	0.067	0.034	0	0	0	0	0
T1	0	0.051	0.025	0	0	0	0
T2	0	0.017	0.047	0.022	0	0	0
T3	0	0	0.003	0.065	0.026	0	0
T4	0	0	0	0	0.062	0.031	0
T5	0	0	0	0	0.005	0.062	0.39
BCNM							
A1	0.030	0	0	0	0	0	0.050
A2	0.049	0.075	0	0	0	0	0
T1	0	0.049	0.044	0.001	0	0	0
T2	0	0	0.050	0.034	0.0004	0	0
T3	0	0	0	0.044	0.058	0.001	0
T4	0	0	0	0	0.044	0.069	0
T5	0	0	0	0.007	0	0.043	0.350
Lajas							
A1	0.029	0	0	0	0	0	0.038
A2	0.039	0.024	0	0	0	0	0
T1	0	0.038	0.020	0	0	0	0
T2	0	0	0.038	0.009	0	0	0
T3	0	0	0	0.037	0.019	0	0
T4	0	0	0	0	0.037	0.019	0
T5	0	0	0	0	0	0.021	0.614

Stage classes are the same as in Table 2.

rates of juvenile, atmospheric *W. sanguinolenta* in spite of a more than twofold variation in annual precipitation (from < 1400 mm to > 3300 mm).

Differences in growth rates were not restricted to smaller plants either (Fig. 2). Moreover, while growth was highest at Coco Solo in all but the largest tanks (Fig. 2 and Table 3), RGRs tended to be lowest in the BCNM population rather than in Lajas. Host tree species, which were not identical across sites, are known to differ in their suitability for epiphyte colonisation and subsequent growth (Callaway et al., 2002) and may provide a possible explanation. Alternatively, populations of *W. sanguinolenta* may differ in their ecophysiological characteristics, but only the population at BCNM has been studied to date in that respect (e.g. Laube and Zotz, 2003). Common garden experiments could identify possible ecophysiological differentiation among populations.

I can only speculate on the differences in fecundity (Table 2). There was certainly no lack of available bark surface for the establishment of recruits in all but the most populated plots at BCNM. While the low fecundity in Lajas meets expectations for the driest site, the even lower average fecundity at Coco Solo is puzzling. In part, this reflects the used definition of fecundity as the ratio of recruits in year t to *all* potentially reproductive individuals (T5) in year $t – 1$ (Table 2) and a low proportion of fruiting adults in Coco Solo (as low as 4% in 2003). However, even when relating recruitment to the number of fruiting individuals in the previous year, recruitment was poorest at Coco Solo. Again, host tree identity may provide an explanation. Conceivably, the flaking bark of *Avi-*

cennia constitutes a poor substrate for establishment. Alternatively, germination and/or growth and survival of seedlings may be affected by salt input in the *Avicennia* stand, in contrast to plants with a tank as long as high precipitation dilutes and removes salt loads (Gómez and Winkler, 1991). Conversely, *Annona* may be a particularly good substrate for germinating *Werhauia sanguinolenta*, but such suggestions await a rigorous experimental examination.

Stage class distributions are frequently used as an indicator of the health of plant populations, with a large proportion of young individuals typical for "dynamic", a large proportion of adult stages typical for "regressive" populations (e.g. Oostermeijer et al., 1994; Sosa and Platas, 1998; Hegland et al., 2001). Our results are at odds with this concept, because the population with the lowest average proportion of small atmospherics (Coco Solo) was also the one with the highest λ (Fig. 1). However, inferring population growth rates from size class distributions alone is known to be problematic (Condit et al., 1998): high growth rates of juveniles and high survival at any size will also produce size distributions with relatively few smaller individuals. Indeed, atmospherics and all but the largest tanks at Coco Solo are characterised by substantially higher growth rates than those at the two other sites (Fig. 2 and Table 3). Stage class distributions varied significantly with time (Fig. 1), but transition probabilities did not (Table 2). This suggests that temporal changes in size class distributions were mostly driven by annual variation in fecundity.

At all three sites, the finite rate of population increase (λ) was primarily influenced by growth (G) and survival (L) of

individual plants, while sexual reproduction (F) contributed very little to λ (Table 4). In agreement with the previous discussion, the scores of smaller individuals were not particularly high, the most important being the survival of adult individuals. Particularly high scores of L coupled with very low scores of *F* are typical for long-lived terrestrial herbs (Silvertown and Franco, 1993; Franco and Silvertown, 2004). A growing body of information (e.g. Hernandez Apolinar, 1992; Tremblay, 1997; Mondragón et al., 2004) suggests that the relative importance of demographic processes (G, L, F) of long-lived vascular epiphytes is very similar to that of long-lived terrestrial herbs. Differences in F in *W. sanguinolenta* could not be related to increased moisture availability, unlike the 65% change in the importance of G from 0.23 in Lajas to 0.38 in Coco Solo (Table 4).

In conclusion, this study could not confirm that growth and survival of smaller individuals plays a particularly important role for the population dynamics of vascular epiphytes as expected from earlier ecophysiological work. In contrast, the survival of large individuals seems to be the single most important process influencing λ. Although most findings are consistent with the notion the moisture availability is a key variable for demographic processes of these epiphytes, other biotic and abiotic factors (e.g. host tree characteristics) may strongly modify or even over-compensate the influence of precipitation.

Acknowledgements

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