

Long-term population dynamics of the epiphytic bromeliad, *Werauhia sanguinolenta*

Gerhard Zotz, Stefan Laube and Gerold Schmidt

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The population dynamics of the epiphytic bromeliad, *Werauhia sanguinolenta*, growing in the moist tropical forest of Barro Colorado Island, Panama, was studied for seven years from 1997 through 2004. In contrast to the generally held notion of the great importance of moisture availability for growth and survival of vascular epiphytes, no demographic process showed a significant correlation with the amount of annual precipitation or the varying number of rainy days per year. Most deaths, for example, were rather related to substrate instability (tree falls, branch breakage, or flaking bark) in all but the smallest size classes. We found evidence for both competition and facilitation. Elasticity analysis revealed that the finite rate of population increase, which invariably exceeded unity, was mostly influenced by survival (stasis) and to a lesser extent by growth, and very little by fecundity. In contrast to earlier reports on disastrous outbreaks of herbivores in this epiphyte species, the long-term impact of herbivory on the population dynamics of *W. sanguinolenta* was negligible. Being at least facultatively autogamous, reproduction seems to be controlled by resource availability alone: this is suggested by long intervals between reproductive events, and a decrease in size and an increased mortality after reproduction. We conclude that the demography of this epiphytic bromeliad is probably influenced at least as much by biotic factors (i.e. the dynamics of the substratum) as by abiotic limitations.

G. Zotz (gerhard.zotz@unibas.ch), Botanisches Inst. der Univ. Basel, Schönbeinstrasse 6, CH-4056 Basel, Switzerland. – S. Laube, Fachber. Biologie, Abt. Allgem. Botanik 13/274, D-67653 Kaiserslautern, Germany. – G. Schmidt, digiTus iT-services, Am Kesselhaus 5, D-79596 Weil am Rhein, Germany.

Vascular epiphytes form a major component of many tropical forests. Their ecology has attracted much interest in recent years, and there is a rapidly growing body of information on population and community structure of vascular epiphytes (Benzing 1981, Hietz and Hietz-Seifert 1995, Hietz 1997, Zotz et al. 1999, Nieder et al. 2000, Barthlott et al. 2001, Vandunné 2002). Major advances from purely descriptive studies of the past (e.g. “classics” such as Went 1940 or Johansson 1974) are attempts to understand the underlying mechanisms of the structure and dynamics of populations and assemblages using a number of approaches. For example, there are efforts to determine the role of host tree species in seedling establishment (Benzing 1978a,

Callaway et al. 2002), to identify the ontogenetic stage (e.g. seed dispersal or seedling establishment) when vertical distributions within host trees are actually determined (Zotz and Vollrath 2002), or to link vertical distributions of mature plants with their physiological characteristics (Griffiths and Smith 1983, Hietz and Briones 1998, Griffiths and Maxwell 1999). Available evidence suggests that most vascular epiphyte species are long-lived plants characterised by very slow growth and late maturation (Benzing 1981, Larson 1992, Schmidt and Zotz 2002). However, a common weakness of almost all of these studies to date is their brief duration. Although the need and the importance of long-term studies is almost unanimously acknowledged by biolo-

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gists when working with long-lived organisms (Rees et al. 2001), our knowledge of long-term changes in populations and assemblages of vascular epiphytes is almost completely circumstantial and stems, for example, from comparisons of epiphyte assemblages in orchards of different age (Catling et al. 1986). This scarcity of information contrasts sharply with an on-going global effort to document and analyse long-term changes in populations of the woody plants of tropical forests (Hubbell et al. 1999) or with the relative wealth of such data for plants from the temperate zone (Tamm 1972, Silvertown et al. 2002). This motivated the present study, which followed the fate of a population of the epiphytic bromeliad, *Werauhia sanguinolenta*, for seven years. Apart from a purely descriptive approach we also conducted some experiments to analyse certain aspects of plant demography, e.g. the impact of herbivores on plant performance or the effect of density on growth and survival.

Methods

Study species

Werauhia sanguinolenta (syn. *Vriesea sanguinolenta*; see Grant 1995) is found from Costa Rica to Colombia and on various Caribbean islands in lowland to lower montane wet forests (Croat 1978). Flowering occurs in the rainy season and seeds are released in the late dry season. Observations in the greenhouse in Würzburg, Germany, suggested that the species is at least facultatively autogamous (Zotz and Schmidt unpubl.). Since *Werauhia 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). A detailed analysis of the demography of the atmospheric stage has already been published (Zotz 2004).

Study population

Spatiotemporal variation was studied in a large population in the southern part of the Barro Colorado Nature Monument (BCNM, Republic of Panama). All individuals were growing on *Annona glabra*, a tree species restricted to the marshy shores of Lake Gatun. The maximum height of ca 8 m makes epiphytes easily accessible in this tree. Although *Werauhia sanguinolenta* is particularly abundant in *Annona glabra*, it is also found in a large number of other tree species high in the forest canopy (Croat 1978). Plots were established in 1997 in the Vriesealandia area (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 0.65 m². 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 each dry season, we recorded LL, fruiting events, and new establishments within the plots. If possible, the cause of mortality was noted, distinguishing 1) drought (plants desiccated with no or little sign of herbivory), 2) herbivory (>2/3 leaf loss, the major herbivore being a Riodinid caterpillar; Schmidt and Zotz 2000), and 3) substrate failure (flaking bark, or branch or tree fall). Other, rare or unknown causes of death were combined in a fourth category (“other/unknown”). The total number of individuals in the eight censuses ranged from a minimum of 1131 (April 1999) to a maximum of 2707 (April 2004), the number of plots varied from 25 to 31. To compensate for mortality losses, an appropriate number of specimens in additional plots in other *Annona* trees was added during each census. Although other epiphyte species occurred in some of the plots (e.g. the bromeliad *Tillandsia fasciculata*, the fern *Niphidium crassifolium*, or the orchids *Dimerandra emarginata* or *Catasetum viridiflavum*), their low densities make an interaction with the focal species very unlikely.

Climate data were obtained for BCNM from the Smithsonian Tropical Research Inst., Panama <<http://striweb.si.edu/esp/>>. We used annual rainfall between census dates, the number of rainy days, and the length of the dry season as explanatory variables. The influence of leaf loss due to herbivory, and the effect of high population density on growth and survival was studied in an adjacent area of Aojeta Bay (BCNM). Herbivory, which may reach a high level in *Werauhia sanguinolenta* (Schmidt and Zotz 2000), was simulated by removing, respectively, 25 and 50% of total leaf area in early 2003. Plants were monitored again 12 months later. The relative difference of LL in 2003 and 2004 (in % of 2003 LL) was used as a measure of growth. Possible facilitation or competition by neighbouring atmospherics was investigated by comparing growth and survival of 41 small atmospherics growing in groups with growth and survival of 41 others growing alone (controls). In late 2002, we located dense groups of atmospherics on 41 branches in 19 trees. Each atmospheric in the centre of this group (consisting of 10–43 individuals in densities of 0.5–1.5 plants cm⁻²) was paired with another atmospheric of similar size (range 0.5–2.3 cm) growing alone on the same branch, the distance to the nearest conspecific being 14 ± 7 cm

(mean \pm SD). Growth and survival were determined 12 months later. Finally, the frequency of reproduction in mature individuals was quantified in more detail by following the fate of a large cohort of plants that had fruited in early 2001 during the following four years.

Matrix construction and data analysis

Seven stage classes were defined on the basis of developmental states (atmosphorics vs. tank form, non-reproductive vs. reproductive) and plant size: atmosphorics <2 cm LL (in part first year seedlings), larger atmosphorics, tanks with a LL of <5, 5–10, 10–20, 20–40, and >40 cm (the latter group including all potentially reproductive individuals, Schmidt and Zotz 2002). Individual plots did frequently not contain all of these size classes. Therefore, the combined demographic data of all plots were used to construct stage transition matrices. Average fecundity (transition T5–A1) 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 stage projection matrix ($B = \{b_{ij}\}$, where $i, j = 1, 2, \dots, 7$) 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. This Lefkovich matrix operates over a vector (n_t) containing the distribution of individuals in the size structure of the population at a particular time t (Caswell 2001). Population size after one time interval is equal to the product of matrix B by vector n_t or

$$N_{t+1} = Bn_t \quad (1)$$

The largest eigenvalue of matrix $B(\lambda)$ 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).

We constructed two types of transition matrices: 1) annual matrices, based on the data for each growing season, and 2) a mean matrix, constructed by averaging the class-specific transition values for all annual matrices.

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 a_{ij} :

$$e_{ij} = \delta (\log \lambda) / \delta (\log a_{ij}) = a_{ij} / \lambda \times \delta \lambda / \delta a_{ij} \quad (2)$$

All elasticities of a transition matrix sum up to unity, and elasticities of transitions of similar type can be added. These characteristics allow the comparison of the relative importance of different types of transitions

between populations of the same species or among species. Types of transition are, e.g. stasis and retrogression (to remain in the same or lower stage class), growth (change into a higher one), or reproduction (recruitment of seedlings from current seed production) (for an extensive discussion see Silvertown et al. 1993). RAMAS Ecolab (Applied Biomathematics, Setauket, NY, USA) was used to calculate λ , w , v , and e . For further data analysis we used STATISTICA 5.0 (Statsoft, Tulsa, OK, USA).

Differences in the demographic fates of vegetative plants between years were analysed with log-linear analyses (Horvitz and Schemske 1995, Caswell 2001), considering stage ($stage_t$) (seven stage classes, as above), year (seven transitions), 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 we tested the null hypothesis that the fate of an individual was independent of year using a different two-way contingency table for each state (factors year (T) and fate (F)). The second analysis was based on a three-way contingency table defined by the factors year (T), state (S), and fate (F) and tested the null hypothesis that conditional on its initial state, the fate of an individual is independent of year. Log-linear analyses were also used to test for significant differences in stage class distributions.

Population densities

Population densities were analysed in those 16 of the original plots that were not totally or partially destroyed between 1997 and 2004. Because individual size varies over more than five orders of magnitude in *Werauhia sanguinolenta* from <1 mg dry mass (<1 cm leaf length) in small juveniles (Zotz 2004) to >100 g dry mass in large mature plants (>100 cm leaf length) (Schmidt and Zotz 2002), average densities would be rather meaningless. Therefore, local densities were calculated for each plot and each size class separately for each of the eight censuses.

Results

Size/stage class distribution

Different from many other bromeliads (Benzing 2000), vegetative reproduction plays no important role in the life cycle of *Werauhia sanguinolenta*: the production of offshoots was rare and only observed in a few smaller tank individuals and is thus not considered further in this paper. Recruitment following sexual reproduction, on the other hand, yielded a large number of seedlings in

all years, and the two atmospheric size classes were numerically dominating the population structure (Fig. 1). The size class distribution of the population fluctuated over time, which was particularly pronounced in the smaller size classes: the proportion of small atmospherics (A1) in the entire population varied, e.g. from 26 to 53% (log-linear analysis, $G^2 = 1663$, $DF = 48$, $p < 0.001$).

We constructed Lefkovich matrices for each of the seven annual transitions. The finite rates of population increase (λ) varied from 1.01 (1997–1998 period)–1.20 (1998–1999 period), averaging 1.09 ± 0.07 (SD). Annual rainfall between censuses varied more than two-fold in the study period from 1389 mm (1997–1998) to 3326 mm (1999–2000), corresponding to the driest year and the second most rainy year of the last 50 yr, but the seven λ s correlated with neither annual rainfall nor the length of the dry season nor the number of rainy days (days with rainfall > 3 mm, $p \geq 0.41$). Thus, we only report the average transition matrix for the entire study period (Table 1). The demographic fates of individual plants also varied temporally in the 7 yr of this study (log-linear analysis, $G^2 = 344$, $DF = 294$, $p < 0.025$), which was mostly due to the smaller size classes (A1–T2, Table 2). Relating the amount of annual rainfall to the probabilities of the plants of a given size class to 1) stay in the same size class for the next 12 months (stasis), to change into a higher one (growth), or 3) to die (mortality) showed a consistent, but mostly not significant trend: smaller plants, in particular, were more likely to change into higher size classes in years with higher rainfall. Mortality rates, on the other hand, did not decrease in years with higher rainfall. On the contrary, the only significant relationship (T1) indicated a positive correlation of precipitation and mortality rate. Considering the lack of a clear relationship between annual moisture availability and demographic processes we used the average elasticity matrix to analyse the relative

importance of the demographic processes growth, survival and sexual reproduction for population growth (Table 3). By far the most important process was stasis, accounting for 56% (including 1% retrogression), followed by growth (38%), and fecundity (7%).

Mortality

Only in ca 70% of all cases could we unambiguously identify the cause of mortality (Table 4). While drought was the most important cause in smaller plants, mortality in large plants (T4 and T5) could never be related to drought. Severe herbivory could be linked to mortality in smaller tanks in a few cases (Table 4), but its overall impact was quite low. Flaking bark or branch breakage, or tree falls, on the other hand, caused the death of more individuals than drought. The highest levels of mortality occurred in the 1999/2000 interval, when four out of 31 plots (=13% of all plots) vanished. Reanalysing the relationship between mortality rates and annual precipitation for each size class without the losses due to substrate instability or herbivory did not yield a significant relationship with moisture availability either (data not shown).

Reproduction

In the 2000 dry season, we surveyed all reproductive individuals of a large *Werauhia sanguinolenta* population in Aojeta Bay, close to the study population. The smallest individual with fruits measured 40 cm LL, the largest 114 cm. The number of capsules of an infructescence approximately followed a cubic function of plant size (Fig. 2). This increase in capsule numbers actually underestimates the total mass of capsules because their average size increased with plant size as well (average

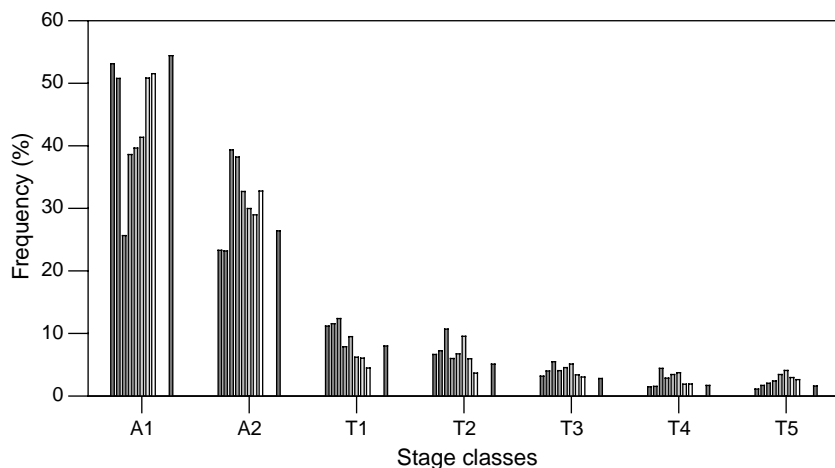


Fig. 1. Stage class distribution of *Werauhia sanguinolenta*. Shown are the eight distributions from April 1997 through 2004 (grey bars) along with the stable stage class distributions (rightmost, black bars) as determined from the analysis of the average Lefkovich matrix. Stage classes are defined in Table 1.

Table 1. Average transition probability matrix for a *Werauhia sanguinolenta* population in Barro Colorado National Monument. Data are averages \pm SD of seven annual matrices. Size classes are defined in brackets. Also given are average reproductive value (RV) and mortality rate for each size class.

Stage at year t+1	Stage at year t							RV
	A1	A2	T1	T2	T3	T4	T5	
A1 (atmospherics <2 cm)	0.51 \pm 0.17	0.01 \pm 0.04					19.4 \pm 12.1	1
A2 (atmospherics \geq 2 cm)	0.28 \pm 0.09	0.52 \pm 0.19						1.8
T1 (tanks <5 cm)	0.02 \pm 0.02	0.17 \pm 0.08	0.39 \pm 0.18	0.01 \pm 0.01				4.7
T2 (tanks 5–10 cm)		0.02 \pm 0.03	0.33 \pm 0.13	0.47 \pm 0.17	0.02 \pm 0.01			9.5
T3 (tanks 10–20 cm)			0.01 \pm 0.03	0.32 \pm 0.10	0.47 \pm 0.14	0.02 \pm 0.02	0.02 \pm 0.03	18.3
T4 (tanks 20–40 cm)				0.01 \pm 0.01	0.30 \pm 0.12	0.60 \pm 0.11	0.01 \pm 0.02	33.9
T5 (tanks \geq 40 cm)				0.01 \pm 0.01	0.01 \pm 0.02	0.21 \pm 0.09	0.85 \pm 0.06	81.5
Mortality rate	0.20	0.27	0.26	0.19	0.20	0.18	0.11	

capsule fresh mass [g] = $0.052 \times \text{LL} + 2.15$, $p = 0.02$, $r^2 = 0.66$, $n = 7$, Pearson Product Moment). The proportion of plants in T5 of the *Vriesealandia* population that fruited annually from 1997 through 2004 ranged from 14 to 29% showing no correlation with the amount of rainfall in the preceding 12 months ($r = 0.21$, $p = 0.65$, $n = 7$ yr). The number of new recruits in year t per infructescence in year $t - 1$, however, showed a positive trend with higher rainfall ($r = 0.60$, $p = 0.14$). To obtain a better estimate of the frequency of reproduction, we measured and marked an additional cohort of 172 fruiting plants in early 2001, and followed their fate for the next 4 yr (Fig. 3). The largest proportion (38%) fruited again after 2 yr (2003), while <10% had fruited in 2002, the year after the initial census. More than 5% had not fruited again until 2005, i.e. within 4 yr. Almost one fourth of all plants died between 2001 and 2005 without reproducing again. Including those individuals that reproduced again before dying the average annual mortality rate was 11%. Mortality immediately after reproduction was clearly related to plant size. Reproductive plants dying in the 12 months after the initial census were significantly smaller than those surviving for at least another year (82 vs 75 cm LL; t -test, $t = -2.46$, $DF = 186$, $p = 0.015$): almost 40% of small plants <70 cm LL died, but only 13% of those >90 cm LL. Most members of the cohort reproduced only one more time in the following four years, but there were 45 plants that flowered and fruited twice. The average fruiting

frequency of the individuals surviving until 2005 was 2.3 ± 0.6 times in five years (mean \pm SD; $n = 108$ plants).

Herbivory

Werauhia sanguinolenta is known to be attacked by the larvae of *Napaea eucharilla* (Riodinidae, Lepidoptera) (Schmidt and Zotz 2000). During the seven years of this study, we invariably observed some leaf damage in T4 and T5 plants, although no plant suffered damage of >10% total leaf area. Damage in smaller tanks was less consistent, but occasionally exceeded 25% of the total leaf area. Possibly lethal damage to small tanks was observed in only about one plant per census (Table 4). We simulated the effect of herbivory on subsequent growth and reproduction by the experimental removal of, respectively, 25 and 50% of total leaf area in plants differing in size and fruiting status (Table 5). While the removal of 25% total leaf area invariably yielded no effect, losing 50% leaf area led to a significant reduction of growth in small tank plants during the following year (ANOVA, Newman-Keuls test, $p < 0.05$). The likelihood of reproduction in larger plants in the following year, on the other hand, was not reduced by the two levels of experimental leaf loss ($\chi^2 = 2.01$, $DF = 2$, $p = 0.37$).

Population density

The density of *Werauhia sanguinolenta* on the studied branch sections (plots) varied from 4 to 1442 plants m^{-2} bark surface for small atmospherics (A1), from 0 to 505 plants m^{-2} bark surface for large atmospherics (A2), while maximum densities of large plants (T5) reached up to 17 plants m^{-2} bark surface. On average, densities of atmospherics varied temporally more than tenfold in individual plots (12.1 ± 1.9 ; mean \pm SE), but maximum densities exceeded minima in some cases almost 30-fold, both in A1 and in A2. Averaged over all 16 plots, temporal variation in the density of A1 was mirrored by fluctuations in A2 (Fig. 4). While small and intermediate-sized tanks also showed considerable oscillations

Table 2. Results of log-linear analyses of a temporal effect on fates of *Werauhia sanguinolenta*. It is indicated whether the null hypothesis fits and whether the incremental change in the log-likelihood χ^2 for the added effects of plot or year were significant (asterisks).

Stage	G ²	DF	p-value
A1	133	48	<0.001***
A2	110	48	<0.001***
T1	91	48	<0.001***
T2	68	48	0.03*
T3	41	48	0.75
T4	40	48	0.78
T5	64	48	0.07

Table 3. Average elasticity matrix. Size classes are the same as in Table 1.

Stage in year t+1	Stage in year t						
	A1	A2	T1	T2	T3	T4	T5
A1	0.059	0.001					0.067
A2	0.057	0.051					
T1	0.011	0.046	0.031	0.001			
T2		0.011	0.053	0.048	0.001		
T3			0.004	0.062	0.051	0.001	0.001
T4				0.002	0.060	0.074	0.001
T5				0.001	0.007	0.062	0.239

through time, there was a steady and significant increase in the density of large, potentially mature plants (T5, Pearson Product Moment correlation, $p > 0.001$): their density increased >4-fold during the seven years of this study.

We repeatedly observed negative interactions as a result of high density. For example, growth in the rain shadow of a large plant was frequently associated with death due to desiccation (accounting for a large proportion of the drought-related mortality in T2 and T3, Table 4). In other cases, smaller plants were physically squeezed between vertical tree branches and a large bromeliad. However, we also found positive interactions. Seeds often stick together with their coma, which leads to dense clusters of juveniles. We compared growth and survival of 41 small atmospherics (initial size 1.5 ± 0.3 cm LL) growing in the centre of such a cluster with others growing alone. The plant density in the clusters was 0.9 ± 0.05 plants cm^{-2} (mean \pm SE; range 0.5 – 1.5 cm^{-2}). The focal individuals did not differ in annual mortality rates (12.5% in clusters vs 10.5% alone, $\chi^2 = 0.06$; $p = 0.78$), but showed significantly higher growth rates in clusters (t-test for dependent samples, $t = -2.94$, $p < 0.01$).

Discussion

Although water supply is generally identified as the most important limitation to the growth and survival of

vascular epiphytes (Benzing 1990, Zotz and Hietz 2001), the results of this study meet expectations only to some extent. In *Werauhia sanguinolenta*, we found significant interannual variation in virtually all demographic processes (e.g. Table 2), but correlations of these demographic processes with annual rainfall or other measures of water availability such as the number of rainy days were rather poor. Whenever an effect of varying moisture availability was detected, it was largely confined to smaller plants (e.g. Table 4), which agrees with the results of recent experimental studies (Schmidt and Zotz 2002, Laube and Zotz 2003). The rather consistent but mostly not significant trends towards higher recruitment per infructescence and towards higher growth in smaller plants with increased annual rainfall did not result in a significant correlation of rainfall and population growth rates. This was, however, not surprising in view of the low influence of growth and survival of smaller individuals on λ as indicated by low elasticity scores (Table 3). Taken together: in spite of substantial variation in the amount of annual rainfall during this study from a minimum of ca 1400 in an El Niño year to >3300 mm, only a rather small portion of the variation in demographic processes can be attributed unambiguously to annual differences in moisture availability. This suggests in turn that other factors and processes are strongly influencing the demography of structurally dependent flora.

Herbivores, which sometimes cause severe leaf loss, and even mortality, in *Werauhia sanguinolenta* (Schmidt

Table 4. Causes of mortality in *Werauhia sanguinolenta*. Given are proportional losses due to desiccation, herbivory, substrate failure, and for other or unknown reasons (all in %). Data are means \pm SE of 7 yr. Size classes are the same as in Table 1.

Size class	Cause of death			
	drought	herbivory	substrate failure	other/unknown
A1	51 ± 5	0	17 ± 6	31 ± 9
A2	42 ± 4	0	26 ± 9	30 ± 8
T1	30 ± 8	0	35 ± 10	35 ± 9
T2	32 ± 7	6 ± 3	39 ± 8	23 ± 5
T3	20 ± 6	4 ± 3	51 ± 11	24 ± 4
T4	0	2 ± 1	45 ± 12	51 ± 11
T5	0	0	83 ± 7	16 ± 7

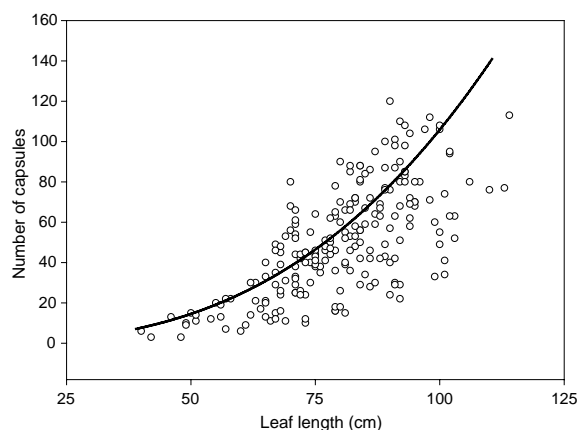


Fig. 2. Relationship of plant size (LL, cm) and the number of capsules of an infructescence. The regression line is: capsule number = $0.0002 \text{ LL}^{2.86}$, $R^2 = 0.58$.

and Zotz 2000), can hardly explain the observed variation in growth and survival either. Their impact on mortality was generally low (Table 4, see also Winkler et al. 2005). Moreover, our experiment showed that given the generally low levels of damage in situ and the lack of an effect of leaf loss below 50% total leaf area (Table 5), neither growth, survival, nor future reproduction are likely to be much affected by the natural levels of herbivory in this population. This finding is at odds with the frequent observation that even low rates of leaf loss can have a negative impact on plant fitness (Coley and Barone 1996), although other studies are consistent with our results (Lubbers and Lechowicz 1989).

Plant densities may be high enough for intraspecific competition or facilitation to play a role in demographic processes. We show, e.g. that dense clusters of juveniles can have a positive impact on plant performance. Plants in the centre of such a cluster are probably slightly buffered against rapid water loss by their neighbours, allowing longer periods of photosynthetic activity, which in turn explains increased growth rates. But increased growth in the centre of dense clusters is bound to lead to asymmetric competition later, unless mortality related to

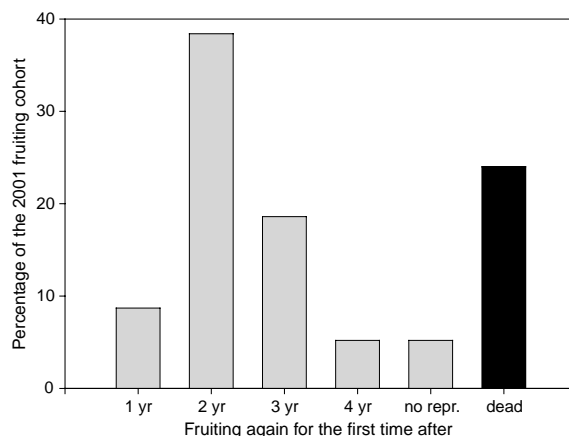


Fig. 3. Fate of 172 large individuals fruiting in 2001 during subsequent years. Given are the proportions of this cohort that fruited again for the first time in the four following years, those still alive in 2005 without further reproduction ("no repr.") and those that died during the same period without further reproduction.

other factors decreases plant densities. Clearly, the importance of positive and negative intraspecific interactions relative to other factors merits a more rigorous, experimental analysis. Substrate instability, the third factor to be considered, is of unequivocal importance (Hietz 1997, Zotz 1998, Mondragón et al. 2004). Flaking bark, breaking branches, or tree falls accounted for a higher percentage of total mortality than drought-related deaths in our study system (Table 4). This statement probably still underestimates the impact of substrate instability on the demography of *Weruuhia sanguinolenta*: while drought primarily affects smaller plants, substrate instability kills those larger plants with the greatest influence on population growth as indicated by their elasticity scores (Table 3).

The poor correlation between most demographic processes and annual variation in rainfall contrasts to some extent with the results of a recent comparative study with the same species (Zotz 2005) that took advantage of a gradient in moisture availability across

Table 5. Annual change in plant size [$(\text{LL}_{2004} - \text{LL}_{2003}) / \text{LL}_{2003}$ in %] and proportion of subsequently fruiting plants after experimental removal of, respectively, 25 and 50% of total leaf area. Given are means \pm SE for growth and percentages for fruiting, $n = 10$ plants. Letters identify significant differences in growth within lines (Newman-Keuls test, $p < 0.05$). No plant fruiting in 2003 fruited again in 2004.

Stage	Growth		
	controls	25% leaf loss	50% leaf loss
Size Class 1 (8–15 cm LL)	24.5 ± 5.7^a	20.6 ± 4.9^a	3.9 ± 4.9^b
Size Class 2 (25–42 cm LL)	26.0 ± 2.8^{ab}	33.6 ± 5.2^b	14.1 ± 6.3^a
Size Class 3 – non-fruiting (67–90 cm LL)	1.8 ± 3.8^a	4.9 ± 2.7^a	5.1 ± 2.8^a
– fruiting in following year	40%	50%	20%
Size Class 3 – fruiting (70–93 cm LL)	-3.1 ± 2.0^a	-2.3 ± 3.3^a	0.6 ± 3.8^a

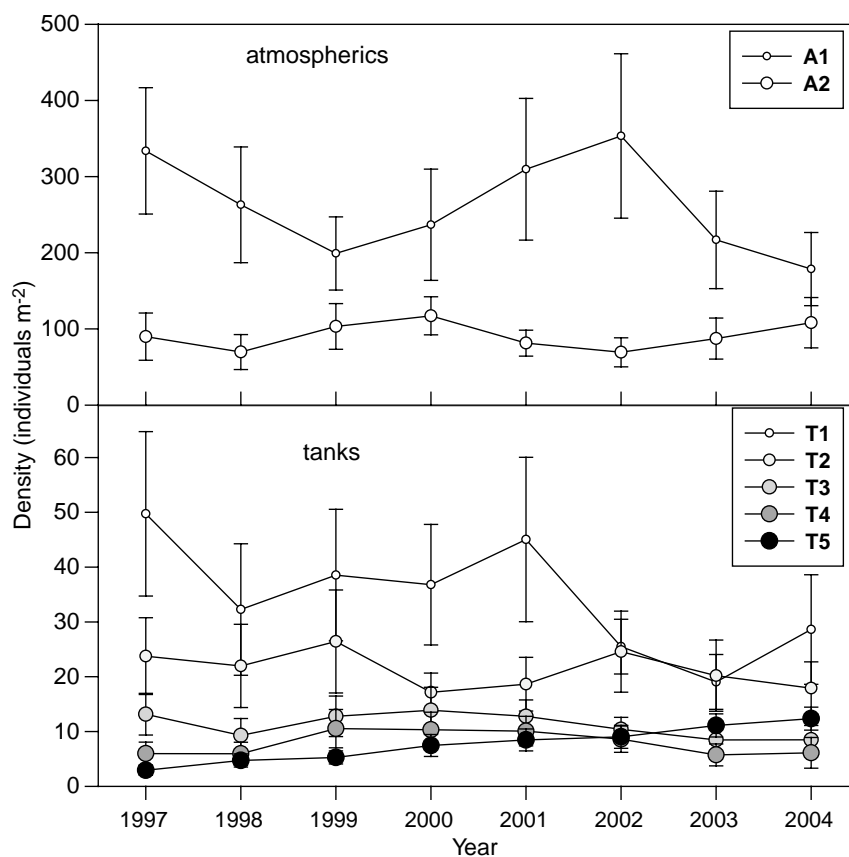


Fig. 4. Temporal changes in epiphyte density in *Werauhia sanguinolenta* in 16 plots from 1997–2004. Data are means \pm SE for each stage class separately. Stage classes (SC) are defined in Table 1.

the isthmus of Panama. Although the variation in rainfall across Panama is much smaller than the 7-yr variation in the present study, the population of *Werauhia sanguinolenta* growing at the wet end of the gradient had the highest individual and population growth rates, while mortality rates were highest in the population at the dry end. Consistent with the present report, however, growth stimulation was highest in smaller individuals (A2) and, moreover, a large proportion of variation could not be explained by differences in rainfall, but was probably related to, e.g. characteristics of the different host trees or other uncontrolled factors co-varying with moisture availability between sites. Without common garden experiments, which may identify local differences in the norm of reaction, we can only speculate on the reasons for the observed discrepancy in the response to moisture availability within and among populations.

Considering the rather unstable substratum of most vascular epiphytes, these plants are expected to show a high investment into reproduction which is, on the other hand, severely restricted by low nutrient availability (Benzing 1978b, 1990, Zotz and Hietz 2001). We observed a strong trade-off between early reproduction and survival in *Werauhia sanguinolenta*. A large propor-

tion of relatively small reproductive plants that fruited in 2001 died in the subsequent 12 months. There was also a negative effect on vegetative growth after reproduction that was already observed by Schmidt and Zotz (2002): plant size generally decreased after reproduction (Table 5). In contrast to large plants in the greenhouse which, when fertilised and watered regularly, reproduce each year (Zotz unpubl.) only a small percentage of plants fruited in consecutive years under natural conditions (Fig. 3). To summarise, increased mortality in smaller adults after reproduction, a generally negative effect on future growth, long intervals between reproductive events, and the significant relationship of plant and infructescence size (Fig. 2) all indicate a considerable cost of reproduction in this species.

The epiphytic habitat is generally characterised by high environmental stress and frequent disturbance (Benzing 1990). Although water availability is certainly correctly identified as the major abiotic limitation to individual growth, the relative importance of drought vs. the dynamics of the host tree for the comportment of entire epiphyte populations under natural conditions is much less obvious. The present study suggests that the demography of dependent flora may well be at least as much affected by biotic as by abiotic factors.

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