

Original article

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

Gerhard Zotz<sup>a,b,\*</sup>

<sup>a</sup> *Botanisches Institut der Universität Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland*

<sup>b</sup> *Smithsonian Tropical Research Institute, Apdo 2072, Balboa, Panama*

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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 compartment 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 ( $\lambda$ ) 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  $\lambda$ .

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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

\* Fax: +41 61 267 3504.

E-mail address: [gerhard.zotz@unibas.ch](mailto:gerhard.zotz@unibas.ch) (G. Zotz).

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 ( $2762 \pm 874$  mm vs.  $2526 \pm 641$  mm, mean  $\pm$  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<sup>2</sup>. 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 ( $\mathbf{B} = \{b_{ij}\}$ , 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. 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).

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