Short communication

Population dynamics of the epiphytic bromeliad *Tillandsia butzii* in cloud forest

Tarin Toledo-Aceves [a],[*], Mariana Hernández-Apolinar [b]

[a] Red de Ecología Funcional, Instituto de Ecología, A.C., Carretera antigua a Coatepec no. 351, El Haya, CP 91070, Xalapa, Veracruz, Mexico
[b] Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito Exterior S/N Ciudad Universitaria, 04510, México, D.F., Mexico

ABSTRACT

Epiphytes are a major component of tropical montane cloud forests. Over-exploitation and forest loss and degradation affect remnant populations. In this study, we analysed the population dynamics of the epiphytic bromeliad *Tillandsia butzii* over a 2-y period in a tropical montane cloud forest fragment in southern Mexico. Matrix analysis revealed that the *T. butzii* population is likely to be stable at the study site. On average the λ value did not differ significantly from unity: λ (95% confidence interval) = 0.978 (0.936–1.001). λ was highly influenced by stasis, to a lesser extent by growth and only slightly by fecundity. Overall, adult plant stasis and phalanx growth habit played a fundamental role in population maintenance. *T. butzii* tolerance to xeric conditions may contribute to population stability in the studied region.

© 2016 Elsevier Masson SAS. All rights reserved.

1. Introduction

In tropical montane cloud forests (TMCF) epiphytes are considered highly vulnerable to habitat loss and climate change (Benzing, 1998; Wolf, 2005; Zotz and Bader, 2009). Populations of these plants peak in TMCF; epiphytes can represent up to 50% of the plant species present (Benzing, 1998; Gentry and Dodson, 1987; Kelly et al., 1994). However, TMCF rank among the most threatened ecosystems worldwide (Scatena et al., 2011) and plant populations in small forest remnants face high extinction risks because they are particularly vulnerable to environmental, demographic and genetic stochasticity (Menges, 1998; Turner et al., 1994; Young et al., 1996). In addition to the detrimental effects of forest transformation and climate change on epiphyte populations, over-exploitation also constitutes an important factor affecting remnant populations (Flores-Palacios and Valencia-Diaz, 2007; Toledo-Aceves et al., 2014a; Turner et al., 1994).

However, groups, or even species, within the same genus do not all respond equally to disturbance. Various bromeliad species have been found to increase in abundance and thus contribute greatly to the diversity of disturbed montane forests (Hietz et al., 2006; Krömer and Gradstein, 2003; Wolf, 2005) and on isolated trees in pasturelands (Flores-Palacios and García Franco, 2004). These findings contrast with the results of demographic analyses; approximately half of studied populations of epiphytic bromeliads display negative population growth rates, indicating the likelihood of decline (Mondragón et al., 2015). Such is the case of *Tillandsia brachycaulos* (Mondragón et al., 2004), *Catopsis sessiflora, Tillandsia deppeana, Tillandsia multicaulis, Tillandsia punctulata* (Toledo-Aceves et al., 2014a; Winkler et al., 2007), *Tillandsia flexulosa* (Wester and Zotz, 2010), *Tillandsia violacea* and *Tillandsia macdougallii* (Mondragón and Ticktin, 2011) and *Tillandsia imperialis* (Haeckel, 2009). However, average λ values greater than unity have been reported for other epiphytic bromeliads such as *Werauhia sanguinolenta* (Zotz et al., 2005) and *Tillandsia recurvata* (Valverde and Bernal, 2010). The analysis of population dynamics is a key tool with which to evaluate the likelihood of growth or decline in populations (Menges, 2000). In this study, we carried out a traditional demographic analysis of a population of the epiphytic bromeliad *Tillandsia butzii* Mez over a 2-y period in a TMCF of southern Mexico.

---

* Corresponding author.
E-mail address: tarintoledo@gmail.com (T. Toledo-Aceves).

2. Study area and methods

2.1. Study area

The study was carried out in a TMCF located in central Veracruz, Mexico (19°32′16″N, 96°59′57″W; 1660 m asl; mean annual temperature: 18 °C). The average annual precipitation for the region is 1650 mm (Williams-Linera et al., 2002); this value was 1567 mm and 1757 mm in the study years of 2010 and 2011, respectively (National Water Commission). The studied fragment area is 6.6 ha, immersed within a matrix of secondary forests. The dominant tree species in the studied forest are *Quercus delgadoana* S. Valencia, Nixon & M.L. Kelly, *Liquidambar styraciflua* L. and *Clethra macrophylla* M. Martens & Galeotti (Toledo-Aceves et al., 2014b). Harvesting of epiphytes had not taken place in the studied fragment; however, unplanned and illegal selective tree logging has occurred over the last 80 years. A more detailed description of the studied forest is presented elsewhere (Toledo-Aceves et al., 2014b).

2.2. Study species

T. butzii presents an atmospheric morphology and produces rosettes that reach 20–35 cm in height (Espejo-Serna et al., 2005). Individuals (genets) have a phalanx growth form, composed of a succession of closely packed rosettes united by a short rhizome. The leading rosette dies after fruiting, but the genet keeps growing by producing new rosettes. A single rosette can produce as many as four new rosettes per year, which are always attached to the polycarpic genet. Individual rosettes may decrease in size as a result of herbivory, leaf senescence and/or desiccation. A fertile rosette bears only one inflorescence that produces 84.8 ± 23 seeds (mean $\pm$ SE, N = 11; Toledo-Aceves et al., 2012) and a genet may comprise up to 19 rosettes. Fruits mature in about 11 mo and the seeds are wind-dispersed during the dry season (October–May; Toledo-Aceves et al., 2012). *T. butzii* is relatively common in the region; in the studied forest it presented 7.47% of relative abundance among epiphytic bromeliads (Toledo-Aceves et al., 2014b).

2.3. Field methods

Since *T. butzii* never spread through independent ramets, we used a plant categorization method based on genet size to analyse its population dynamics. To obtain total plant size, we measured and summed the length of all the rosettes that comprised a genet (Clark-Tapia et al., 2005). Rosette size was measured with a calliper as the length from base to tip of the longest leaf. An initial sample of 93 genets (making a total of 238 rosettes) were tagged in 2009 and monitored for 2 y. These were established on the branches and trunk (main trunk = 78%, branches = 22%) of three randomly selected trees in the centre of the fragment. Trees were chosen from those that fulfilled the following criteria: they could be scaled using single-rope techniques (Jepson, 2000), they did not have overlapping crowns, they belonged to *Q. delgadoana*, the dominant species of the forest studied (Toledo-Aceves et al., 2014b), and

presented a dbh $\geq$30 cm. Plants were grouped into five categories based on total plant size and reproductive status (Table 1). The limit between infants and juveniles was established following Winkler et al. (2007). The presence of inflorescences was used to define the adult category; the lowest size at which plants were fertile was 35 cm of rosette height.

2.4. Demographic analysis

We constructed two 5×5 Lefkovitch matrices (periods 2009–2010 and 2010–2011) in order to characterize the population dynamics. These Lefkovitch matrices summarize the survival, growth and fecundity rates of the different life-cycle stages into which populations are structured. Size-specific stasis and growth were calculated from the proportion of individuals in each size class that died, remained in the same size class (stasis), grew to the following size class (growth) or regressed to a previous size (retrogression) from one year to the next.

In addition to growth and survival, the contribution of adult individuals to the first size-category, i.e. fecundity rate, was estimated as the average number of seedlings in year t + 1 produced by an individual of each adult category (A1 and A2) in year t (Mondragón et al., 2004) as:

$$F_j = (c_j \times s \times d \times g) / n_j$$

where F_j is the fecundity of an average individual in the j-th category; c_j is the total number of capsules produced by all individuals in the j-th category; s = mean number of seeds per capsule (32.8; n = 12); d = probability of successful dispersal (we used a value of 0.037, reported for *T. deppeana* in TMCF; García-Franco and Rico-Grey, 1988); g = germination probability based on the results of field experiments (0.10; Toledo-Aceves et al., 2012) and n_j is the number of individuals in the j-th category.

We used seed germination and seedling establishment data from experiments carried out in the field to obtain estimates of survival and transition probabilities for the life-cycle stages from Toledo-Aceves et al. (2012). Transition probabilities from the seedling to infant categories were calculated based on the results of seedling survival and growth from emergence up to one year old from Toledo-Aceves et al. (2012).

Elasticity analysis evaluates the relative contribution of different matrix elements to the population growth rate (λ) by providing information on the potential impact on λ of relatively small changes in matrix elements (de Kroon et al., 1986). The elements of the elasticity matrices were calculated as:

$$e_{ij} = (v_i w_j / <w, v>) * (a_{ij} / \lambda)$$

where w and v represent the vectors corresponding to the stable size-class distribution and size-specific reproductive values, respectively. Since entries in an elasticity matrix sum to unity (De Kroon et al., 1986), they may be used to calculate the relative contribution to λ made by the different size-classes and the

Table 1
Categories defined according to individual size (cumulative height: see text) in order to analyse the population dynamics of *Tillandsia butzii*. The average number of rosettes per category ($\pm$s.e.) was obtained from data collected over a period of two years. Categories are: S = seedling, I = infant, J = juvenile, A1 = adult 1, and A2 = adult 2.

Category	Cumulative height (cm)	Average number of individuals per category	Average number of rosettes per genet
S	<1.5	120	1 ± 0
I	1.5–8	36.5	1 ± 0
J	8–35	20.5	1.98 ± 1.10
A1	35–150	15.5	2.64 ± 1.41
A2	>150	14.5	7.54 ± 4.34