Temporal variation in the demography of the clonal epiphyte *Tillandsia brachycaulos* (Bromeliaceae) in the Yucatán Peninsula, Mexico

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Abstract: Epiphytes are one of the most ubiquitous elements of tropical forest canopies, including seasonally dry tropical forests. Given the temporal variation in weather conditions in the latter, epiphyte populations may be subject to wide temporal variation in seedling recruitment, reproductive success, vegetative propagation and mortality rate. In this study, we use a 3-y demographic data set for *Tillandsia brachycaulos* to project its long-term population dynamics through the use of average and periodic matrices, as well as stochastic simulations. The results show that demographic behaviour varied over the 3 years of study, apparently in relation to rainfall. The first 2 years yielded a low λ value (0.79 and 0.80 – although only the former was significantly lower than unity), while the third year resulted in a $\lambda = 1.08$ (not significantly different from 1.0). When incorporating this demographic variation in an average matrix, a periodic matrix and stochastic simulations, the resulting overall λ was below unity in all three cases. The projections of the stochastic simulations suggest that the population would be able to persist in the long run only if the frequency of 'good' years (defined here as those with an August rainfall above 200 mm) was above 0.6, which appears unlikely given that global warming might result in a lower frequency of rainy years in tropical dry forests.

Key Words: Bromeliaceae, Dzibilchaltún National Park, elasticity analysis, matrix models, periodic matrices, population dynamics, stochastic simulations, *Tillandsia*, tropical dry forest

INTRODUCTION

Epiphytes are important elements of many tropical ecosystems. Particularly, they are ubiquitous in tropical rain and cloud forests, and many species occupy mangroves, tropical dry forests and even semi-arid shrublands (Gentry & Dodson 1987, Ibisch *et al.* 1996, Montaña *et al.* 1997, Olmsted & Gómez-Juárez 1996). It is known that epiphytic species depend on atmospheric humidity, which tends to be high and rather constant in tropical rain and cloud forests. However, in tropical dry forests precipitation is less abundant and falls unevenly throughout the year, with a marked dry season lasting for a varying number of months, and wide inter-annual variation in yearly rainfall amounts (Khurana & Singh 2001, Medina 1995). It is unclear how epiphytic species respond demographically to this temporally heterogeneous environment, which

severely limits photosynthesis during a substantial part of the year, and sometimes for several years in a row. Some epiphytes form small water reservoirs among their leaves, many show Crassulacean Acid Metabolism (CAM), and others rely on vegetative propagation as a means of persistence during unfavourable periods (Benzing 1990).

The epiphyte species that inhabit tropical dry forests must have evolved certain 'demographic adaptations' which allow populations to withstand the low and erratic water availability that characterizes these ecosystems. Species that are well adapted to these conditions should be able to adjust growth and reproduction patterns depending on water availability; thus, they may show some degree of demographic flexibility. The ability to propagate both sexually and vegetatively and, as noted above, the possibility of relying on one or the other for population maintenance depending on water availability, may indeed be one expression of such demographic plasticity.

Little is known about the demography of epiphytic species. A few have been studied through time-invariant demographic models (Hernández-Apolinar 1992, Mondragón *et al.* 1999, Tremblay 1997). However, since temporal variability in demographic behaviour of plant populations has been found to be the rule rather than the exception (Horvitz & Schemske 1995), especially for species that occupy highly seasonal habitats, it makes sense to utilize demographic models that incorporate yearly variation in population dynamics, which may be a result of temporal heterogeneity in environmental conditions (Bierzychudek 1982, Caswell & Trevisan 1994, Mandujano *et al.* 2001, Nakaoka 1996). In this study we analyse the temporal variation in the demographic behaviour of the clonal epiphyte *Tillansdia brachycaulos* Schltdl. in the tropical dry forest of the Dzibilchaltún National Park (Yucatán, Mexico). We use a 3-y demographic data set for this species to project its long-term population dynamics through the use of average and periodic matrices, as well as stochastic simulations; the latter were performed to explore the effect of climatic variation on long-term population dynamics, by simulating different probabilities of occurrence of years with different rainfall regimes.

A short-term demographic analysis on *T. brachycaulos* reported elsewhere yielded a declining population in which vegetative propagation was the main mechanism for the recruitment of new individuals (Mondragón *et al.* 1999). The study of the temporal variability in the demographic behaviour of this epiphytic species, which shows an ability to propagate either sexually or vegetatively, also offers the opportunity to analyse the way in which these two processes may contribute differentially to population growth rate as a result of environmental variation (Mandujano *et al.* 2001).

METHODS

The species

Tillandsia brachycaulos is an epiphytic bromeliad commonly found in tropical dry forests and semi-arid shrublands in southern Mexico and Central America (Isley 1987). Within the Yucatán Peninsula it may be found in all types of woody vegetation, although it is most abundant in tropical dry forests (Olmsted & Gómez-Juárez 1996). This plant is a stemless monocarpic rosette. In adult plants, leaves are 12–26 cm long and those near the inflorescence turn reddish during flowering. Flowering occurs between June and August (during the rainy season). Lilac-coloured flowers emerge from inflorescences born at the centre of the rosette; they have linear tubular petals 5–7 cm long. Fruiting takes place from August–September until January. Fruits are

4-cm-long cylindrical capsules which produce wind-dispersed seeds. Rosettes die just after fruiting, but they are able to propagate vegetatively. From each rosette one or two new rosettes (offshoots) may be formed from the axillary buds of the most basal leaves (Utley 1994). Seeds germinate and establish on different tree species. At the study site (see description below), *T. brachycaulos* usually establishes on *Gymnopodium floribundum* Rolfe (Polygonaceae), although it may also be found in *Phylostylon brasiliense* Capan. ex Benth & Hook. f. (Ulmaceae), *Acacia gaumeri* Blake (Mimosaceae) and *Pithecellobium dulce* (Roxb.) Benth. (Mimosaceae).

The study site

This study was carried out in the Dzibilchaltún National Park (21°05′N, 89°99′W), located in the state of Yucatán, south-eastern Mexico. The climate in this area is warm and subhumid, with a mean annual precipitation of 879 mm and mean annual temperature of 25.8 °C (Thien *et al.* 1982). The rainfall pattern is markedly seasonal, the rainy season falling between June and November. The vegetation at the site has been classified as a low, seasonally dry, deciduous forest with a maximum canopy height of 8 m (Campos-Ríos & Durán 1991). The most common tree species are *Bursera simaruba* (L.) Sarg., *Caesalpinia gaumeri* Greenm., *Piscidia piscipula* (L.) Benth. and *Gymnopodium floribundum*. The epiphytic community is composed of species in the Bromeliaceae, Cactaceae and Orchidaceae. Among the bromeliads, six species of *Tillandsia* are found in the area, with *T. brachycaulos* being the most abundant.

Field methods

In November 1996 nine *G. floribundum* trees were chosen within three randomly selected plots (to cover spatial variability) and all individuals (i.e. rosettes or shoots) of *T. brachycaulos* established on them were tagged – with the exception of a few individuals that were left out of the sample because they were inaccessible. A total of 920 individuals were included in this initial sample. These individuals were followed for 3 y, until November 1999. We took bimonthly records of survival, plant height (from the base of the rosette to the tip of the tallest leaf), number of capsules, and shoot production through vegetative propagation. From these data we calculated the basic vital rates for demographic analyses, i.e. stage-specific survival, growth and reproduction.

Plants were classified into two major groups according to their origin, i.e. individuals arising from seeds, or individuals arising through vegetative propagation, which may easily be told apart. In turn, each group was

Table 1. Size categories based on rosette height and origin (i.e. from seed or vegetative propagation) of *Tillandsia brachycaulos* plants. n refers to the observed number of individuals in each category at the beginning of the study (November 1996)*

Category	Rosette height (cm)	n
Seedling (s)	>0.4	14
Infant (i)	0.5–2.4	78
Juvenile (j)	2.5–4.9	74
Adult 1 (a_1)	5–7.9	67
Adult 2 (a_2)	8–11.4	61
Adult 3 (a_3)	>11.5	18
Infant offshoot (io)	0.5–2.4	61
Juvenile offshoot (jo)	2.5–4.9	87
Adult 1 offshoot (ao_1)	5–7.9	171
Adult 2 offshoot (ao_2)	8–11.4	213
Adult 3 offshoot (ao_3)	>11.5	76

* Sample size for each category was lower in the second and third year due to plant mortality.

subdivided into several categories according to plant size (Table 1). The yearly records of plant fates allowed us to calculate the probabilities of plants in each category contributing or transiting to different categories from one year to the next. From this information we built three population projection matrices, one for each of the growth periods analysed (1997, 1998 and 1999). To construct these matrices, the transition probabilities were calculated as the proportion of individuals in each category that moved to another category, while stasis was calculated as the proportion of individuals that remained in the same category from one year to the next (Figure 1).

Fecundity was calculated as the average number of seedlings produced by an individual in each category. This was estimated from the data on the number of seeds produced per individual, the probability of successful dispersal and the germination probability, as follows:

$$F_{ij} = (c_j \times s \times d \times g)/n_j \qquad (1)$$

where F_{ij} is the contribution of an average individual in the *j*-th category to the seedling category between t and t + 1; c_j is the total number of capsules produced by all individuals in the *j*-th category; *s* is the mean number of seeds per capsule (150, n = 50); *d* is the probability of successful dispersal (0.0045, according to the results of field experiments carried out at the site during the dispersal seasons of 1998 and 1999 – Mondragón 2001); *g* is the germination probability (0.024, 0.031 and 0.042 for 1997, 1998 and 1999 respectively, according to the results of field experiments conducted at the site – Mondragón 2001); and n_j is the number of individuals in the *j*-th category. Finally, the contribution of individuals in each category to vegetative propagation was calculated as the total number of shoots produced by all individuals in each category, divided by the number of individuals in that category (Figure 1).

Numerical analysis

We built three 11×11 Lefkovitch matrices, corresponding to each of the three growth periods analysed. From
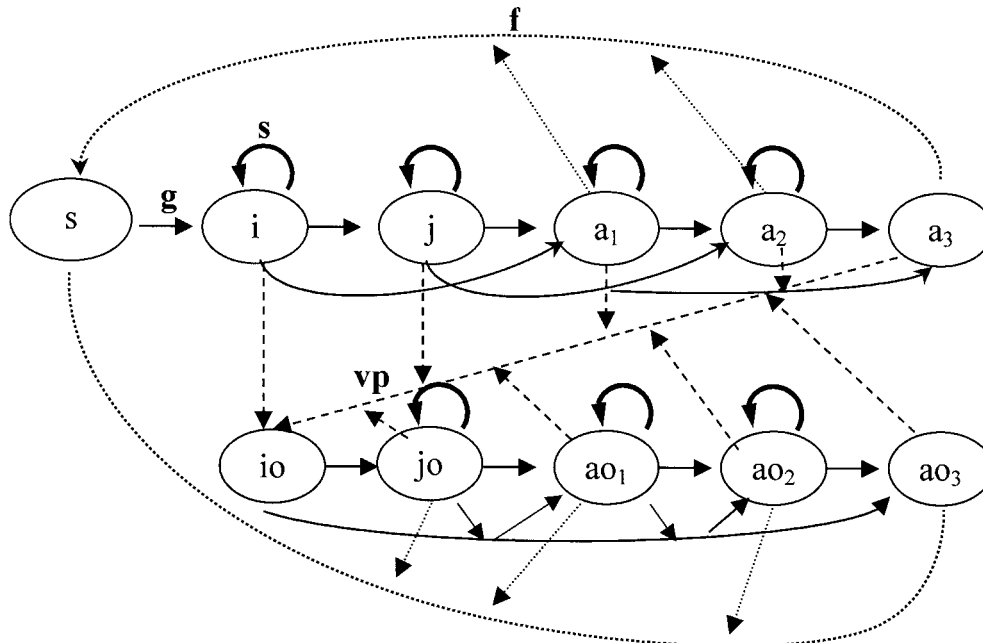

Figure 1. Life cycle of *Tillandsia brachycaulos.* Growth (g; solid lines) indicate the transition probability of individuals from one category to a larger category from one year to the next. Stasis (s; bold solid lines) show the probability of remaining in the same category. Fecundity (f; dotted lines) represent the number of seedling produced by an average individual in each category. Vegetative propagation (vp; dashed lines) indicate the average number of offshoots produced per individual in each category. Categories as in Table 1.

these matrices we obtained the finite population growth rate (λ), the stable size distribution (vector w) and the size-specific reproductive values (vector v) using the power method (Caswell 1989). Confidence intervals for the λ values were calculated according to the analytical methods proposed by Alvarez-Buylla & Slatkin (1991).

Elasticity matrices were constructed to evaluate the relative importance of each matrix entry to population growth rate. Each entry in the elasticity matrix was calculated as

$$e_{ij} = (\delta\lambda/\delta a_{ij})(a_{ij}/\lambda) = s_{ij}(a_{ij}/\lambda) \tag{2}$$

where s_{ij} is the absolute sensitivity of λ to changes in a_{ij}. The elasticity of each matrix entry (a_{ij}) measures the relative sensitivity of λ to relative changes in a_{ij}. Since the addition of all the entries in an elasticity matrix equals unity, the elasticity value of each entry may be interpreted as its relative contribution to the value of λ (de Kroon *et al.* 1986).

In addition to the analysis of individual matrices representing different years, an average matrix was constructed in which each individual entry was calculated as the average of the three relevant matrix entries. In this way, the temporal variation in the vital rates was integrated in a single matrix that represents the average demographic behaviour of the 3 years of study (Mandujano *et al.* 2001). Average population growth rate (λ_A) was obtained from this matrix according to the power method.

Also, periodic matrices were built using the three yearly matrices described above. Periodic matrices also incorporate the temporal variability in demographic behaviour assuming that this variability presents itself in a cyclic form (Caswell & Trevisan 1994). Periodic matrices were obtained by multiplying the three yearly matrices as follows:

$$n_{t+3} = [A^{(1)}A^{(2)}A^{(3)}]n_t = A'n_t \tag{3}$$

Depending on the order in which the three individual matrices are multiplied, a different periodic matrix, A', may be obtained. However, the population growth rate (λ_P) for all the resulting periodic matrices is the same.

An additional way to incorporate temporal variability in demographic behaviour is to use stochastic simulations, in which a randomly chosen matrix is selected for each iteration (Bierzychudek 1982, Valverde *et al.* 2003). The probability of choosing each matrix may be weighted according to its actual probability of representing the population dynamics each particular year. In this case, to decide the probability with which each matrix would be chosen during the iteration process, we explored the frequency of occurrence of years with different weather patterns, and used the following line of reasoning:

(1) First, we obtained the weather records for the study area for 1997, 1998 and 1999, and explored several

weather variables to look for a relationship between them and the population growth rates (λ) obtained for each year. The λ values obtained varied in a parallel manner with two particular weather variables (see Results below): total annual precipitation (854 mm for 1997; 1121 mm for 1998 and 1188 mm for 1999), and the August precipitation (146 mm for 1997, 174 mm for 1998 and 227 mm for 1999). Of these two, the latter resulted in a better correlation with population growth rate ($r^2 = 0.901$, P = 0.202). The amount of rain falling during August appears to be critical in determining seedling establishment success. Seeds germinate every year in early June, at the start of the rainy season; the fate of germinated seedlings must depend on water availability during the following months, particularly August, during which a short dry interval (locally known as 'canícula') frequently takes place. Thus, years with a severe canícula (i.e. low August precipitation) apparently result in poor seedling establishment, whereas years with a mild canícula (i.e. high August precipitation) render much higher seedling survival.

(2) We subdivided the observed August precipitation values of the last 11 y (range: 49–270 mm) to characterize 'good' years (those with an August precipitation above 200 mm) and 'bad' years (those with an August precipitation below 200 mm), and calculated the relative frequency of occurrence for these two (0.36 and 0.64, respectively). The study years corresponded to two 'bad' years (1997 and 1998) and one 'good' year (1999).

(3) Using a spreadsheet program, we assigned these probabilities to each of the transition matrices (0.32, 0.32 and 0.36, for 1997, 1998 and 1999, respectively) to generate 30 series of 200 matrix iterations each. For each series we calculated the stochastic population growth rate (λ_s) by plotting the natural logarithm of the number of individuals against time (iterations) and fitting a linear regression line; the slope of the fitted line was considered a measure of the intrinsic rate of population increase (r), from which λ_s could be calculated ($\lambda = e^r$) (Bierzychudek 1982, Valverde *et al.* 2003).

As will be noted below, our initial stochastic simulations (i.e. the base run) resulted in a λ_s value significantly lower than unity when we used the observed probability of occurrence of 'good' and 'bad' years (Figure 3). Therefore, we changed the value of the probability of occurrence of the most favourable year (corresponding to the 1999 matrix, that rendered a λ value above unity) to evaluate the conditions under which a long-term $\lambda_s > 1$ would be obtained. Since we calculated 30 λ_s values in each run, we were able to report an average λ_s value (plus confidence intervals) as well as to estimate the 'persistence probability' of the overall population according to its projected long-term numerical behaviour over a period of 200 y. The latter was defined as the relative frequency with which population numbers fell

Table 2. Transition matrices and main demographic results for the *Tillandsia brachycaulos* population studied for 3 consecutive years. Categories as in Table 1. Confidence intervals (95%) for the obtained λ values are given in the left-hand column. Other symbols are: q_x = mortality rate, v = size-specific reproductive values; w = stable size distribution.

		s	i	j	a_1	a_2	a_3	io	jo	ao_1	ao_2	ao_3	v	w
	1997													
λ = 0.79	s	0	0	0	0.007	0.017	0.036	0	0.001	0.011	0.024	0.035	0.026	0.01
±0.20	i	0.28	0.167	0	0	0	0	0	0	0	0	0	0.068	0.01
	j	0	0.330	0.189	0	0	0	0	0	0	0	0	0.085	0.00
	a_1	0	0.103	0.378	0.134	0	0	0	0	0	0	0	0.082	0.00
	a_2	0	0	0.081	0.179	0.066	0	0	0	0	0	0	0.094	0.00
	a_3	0	0	0.014	0	0.082	0	0	0	0	0	0	0.094	0.00
	io	0	0.039	0.108	0.448	0.754	0.940	0	0.300	0.507	0.985	1.243	0.074	0.53
	jo	0	0	0	0	0	0	0.033	0.570	0	0	0	0.119	0.03
	ao_1	0	0	0	0	0	0	0.148	0.183	0.035	0	0	0.115	0.12
	ao_2	0	0	0	0	0	0	0.180	0.207	0.193	0.037	0	0.115	0.17
	ao_3	0	0	0	0	0	0	0.115	0.126	0.175	0.066	0	0.124	0.13
	q_x	0.71	0.397	0.338	0.687	0.852	1.000	0.525	0.425	0.596	0.897	1.000		
	1998													
λ = 0.80	s	0	0	0	0	0.008	0.050	0.002	0.006	0.014	0.041	0.035	0.009	0.02
±0.29	i	0.22	0.310	0	0	0	0	0	0	0	0	0	0.021	0.01
	j	0.56	0.230	0.286	0.187	0	0	0	0	0	0	0	0.044	0.01
	a_1	0	0	0.286	0.343	0	0	0	0	0	0	0	0.078	0.00
	a_2	0	0	0	0.062	0.500	0	0	0	0	0	0	0.146	0.00
	a_3	0	0	0	0	0.060	0	0	0	0	0	0	0.095	0.00
	io	0	0	0	0.244	0.500	1.000	0	0.245	0.573	0.586	0.793	0.075	0.40
	jo	0	0	0	0	0	0	0.22	0.161	0.063	0	0	0.157	0.15
	ao_1	0	0	0	0	0	0	0.148	0.225	0.101	0.098	0	0.14	0.15
	ao_2	0	0	0	0	0	0	0.032	0	0.24	0.279	0	0.158	0.09
	ao_3	0	0	0	0	0	0	0	0.664	0.087	0.311	0	0.075	0.18
	q_x	0.21	0.462	0.429	0.406	0.440	1.000	0.593	0.548	0.506	0.311	1.000		
	1999													
λ = 1.08	s	0	0	0	0.375	0.714	2.000	0	0.245	0.220	1.345	2.35	0.030	0.23
±0.20	i	0.66	0	0	0	0	0	0	0	0	0	0	0.048	0.14
	j	0	0.375	0.273	0	0	0	0	0	0	0	0	0.048	0.07
	a_1	0	0.250	0.454	0.235	0	0.167	0	0	0	0	0	0.068	0.08
	a_2	0	0	0	0.294	0.428	0	0	0	0	0	0	0.093	0.04
	a_3	0	0	0	0	0.143	0	0	0	0	0	0	0.094	0.00
	io	0	0.375	0.182	0.421	0.571	0.667	0	0.326	0.341	1	1.157	0.045	0.24
	jo	0	0	0	0	0	0	0.033	0.041	0.015	0.011	0	0.104	0.08
	ao_1	0	0	0	0	0	0	0.111	0.204	0.118	0.034	0.025	0.131	0.05
	ao_2	0	0	0	0	0	0	0	0.204	0.412	0.310	0.225	0.183	0.06
	ao_3	0	0	0	0	0	0	0	0.143	0.176	0.322	0	0.155	0.03
	q_x	0.33	0.375	0.273	0.471	0.429	0.833	0.556	0.408	0.279	0.322	0.750		

below five individuals among the 30 series of 200 iterations performed for each run. Also, an estimated time to extinction (the time needed for population size to collapse below five individuals) was calculated for each series.

RESULTS

Tillandsia brachycaulos shows a complex life cycle that includes a diverse array of potential transitions between size categories (Figure 1). Plants may either remain in the same size category from one year to the next, or grow one to several categories; they may also contribute to the seedling stage through reproduction or may produce vegetative offshoots; these in turn may display equivalent demographic fates to those observed in sexually recruited plants. Each arrow in the life-cycle graph in Figure 1 represents a matrix entry in Table 2. In the transition matrices, the first six columns show the vital rates for sexually recruited plants, while the last five columns refer to vegetative offshoots. It may be noticed that the contribution to seedling recruitment of both offshoots and sexually recruited plants is similar, although offshoots may reproduce at a smaller size than sexually recruited plants. In both types of plants fecundity was higher as

plant size increased and a higher fecundity was observed in the third year (1999, the year with the highest August and total precipitation) than in the previous two.

Offshoots show a larger number of positive transitions than plants derived from seeds, which implies that they may contribute to several categories within one year, basically due to their high growth rate. Mortality was high during the early stages of development (particularly in sexually recruited plants) and decreased as plant size increased. The main cause of death of sexually derived seedlings and infants was the falling of individuals due to dislodging or branch breakage (Mondragón 2001). On the other hand, the death of larger plants (of both sexual and vegetative origin) was caused mainly by the loss of their apical meristem due to the attack of a curculionid larva. The largest adults died after fruiting, which is shown by the high mortality values of these stages (Table 2); however, some of them survived after the third year, which implies that they did not set fruit during 1999.

Population growth rate (λ) was below unity in 1997 and 1998, and above unity in 1999. However, the confidence intervals for λ indicated that population growth rate was significantly lower than 1.0 only in 1997; both the 1998 and 1999 λ values were indistinguishable from unity (Table 2). In general, stable population structures (i.e. those that would be expected after a large number of years of the particular demographic behaviour represented by each matrix) included a high proportion of small offshoots, and the majority of the population composed basically of vegetatively recruited plants. Only for the 1999 matrix did the population structure expected at equilibrium include a relatively larger proportion of seedlings and plants originated by seed (Table 2).

Stage-specific reproductive values (i.e. the present value of the future offspring of individuals in each category – Caswell 1989) generally increased with increasing plant size, and they were consistently larger in offshoots than in the equivalent sexually derived size-categories (Table 2).

Elasticity matrices (Table 3) showed a distinct pattern in relation to the λ value of the relevant transition matrix: for transition matrices with an absolute λ value below unity (i.e. 1997 and 1998) the highest elasticities were concentrated in the entries representing rapid growth of young offshoots and vegetative propagation by large offshoots. This implies that these transitions are largely responsible for the λ value observed, and that relative changes in these transitions would result in a great relative impact on λ. In contrast, in the matrix with a λ value above unity (i.e. 1999) the highest elasticity values correspond to the growth of small offshoots and to seedling recruitment (Table 3).
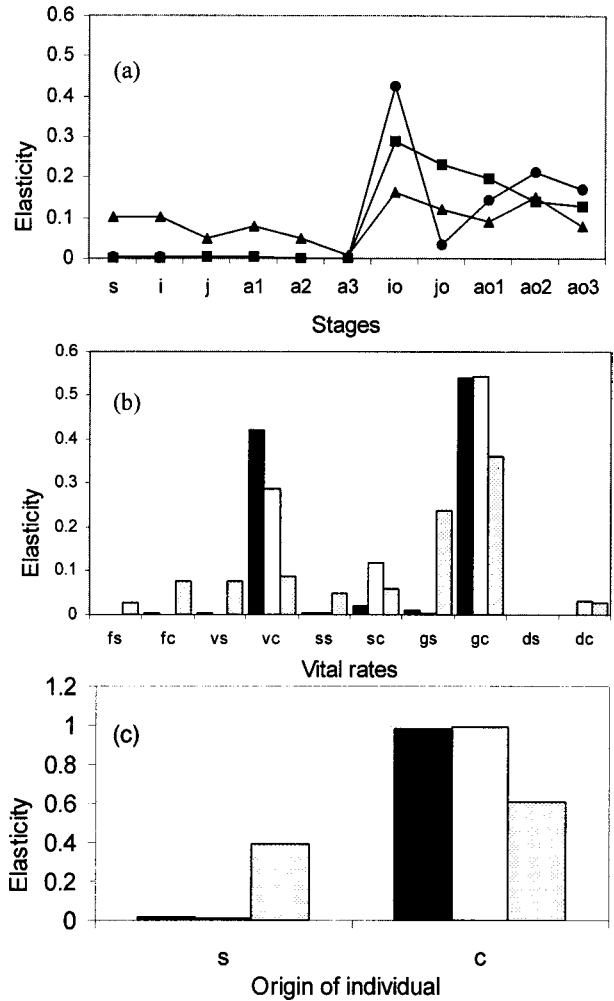

Figure 2. Added elasticity values (a) by category, for 1997 (circles), 1998 (squares) and 1999 (triangles), categories as in Table 1; (b) by vital rate – nomenclature: the first letter represents the demographic processes, i.e. f: fecundity, v: vegetative propagation, s: stasis, g: growth and d: retrogression; the second letter represents plant origin, i.e. s: from seed, c: from clonal propagation. For example, fs is the sum of the fecundity elasticity values for all categories derived from seed; black bars = 1997; dotted bars = 1998; dashed bars = 1999. (c) by origin (bars as in b).

Elasticity values may be added up either across different demographic processes (Silvertown *et al.* 1993) or across different life-cycle stages. In relation to the different demographic processes that compose the life cycle of *T. brachycaulos*, it may be noticed that λ was dependent mainly on the growth of vegetatively recruited plants, followed by the recruitment of new offshoots (Figure 2b). Yet, the pattern was slightly different in 1999: the relative importance of demographic processes of sexually derived individuals increased when compared with the previous 2 y (Figures 2b and 2c). The same is apparent when analysing the relative contribution of the different life-cycle categories to the value of λ: in the first 2 y all the elasticity was concentrated in the offshoots,

Table 3. Elasticity matrices for the *Tillandsia brachyaulos* population. The three highest values in each matrix are in bold typescript. Categories as in Table 1.

	s	i	j	a_1	a_2	a_3	io	jo	ao_1	ao_2	ao_3
1997											
s	0	0	0	0	0	0	0	0	0.001	0.002	0.002
i	0.004	0.001	0	0	0	0	0	0	0	0	0
j	0	0.003	0.001	0	0	0	0	0	0	0	0
a_1	0	0.001	0.002	0.001	0	0	0	0	0	0	
a_2	0	0	0	0.001	0	0	0	0	0	0	0
a_3	0	0	0	0	0	0	0	0	0	0	0
io	0	0	0	0.002	0.001	0	0	0.008	0.063	**0.181**	**0.169**
jo	0	0	0	0	0	0	0.030	0.002	0	0	0
ao_1	0	0	0	0	0	0	0.129	0.008	0.007	0	0
ao_2	0	0	0	0	0	0	**0.157**	0.009	0.037	0.011	0
ao_3	0	0	0	0	0	0	0.109	0.006	0.036	0.020	0
1998											
s	0	0	0	0	0	0	0	0	0	0	0.001
i	0.001	0.001	0	0	0	0	0	0	0	0	
j	0.001	0.001	0.001	0	0	0	0	0	0	0	0
a_1	0	0	0.002	0.001	0	0	0	0	0	0	0
a_2	0	0	0	0.001	0.001	0	0	0	0	0	0
a_3	0	0	0	0	0	0	0	0	0	0	0
io	0	0	0	0.001	0	0	0	0.034	0.077	0.049	**0.129**
jo	0	0	0	0	0	0	**0.166**	0.047	0.018	0	0
ao_1	0	0	0	0	0	0	**0.100**	0.058	0.025	0.015	0
ao_2	0	0	0	0	0	0	0.024	0	0.067	0.049	0
ao_3	0	0	0	0	0	0	0	0.092	0.012	0.026	0
1999											
s	0	0	0	0.012	0.010	0.004	0	0.008	0.004	0.031	0.034
i	**0.103**	0	0	0	0	0	0	0	0	0	0
j	0	0.036	0.012	0	0	0	0	0	0	0	0
a_1	0	0.034	0.028	0.017	0	0.001	0	0	0	0	0
a_2	0	0	0	0.030	0.019	0	0	0	0	0	0
a_3	0	0	0	0	0.007	0	0	0	0	0	0
io	0	0.034	0.008	0.021	0.013	0.002	0	0.016	0.010	0.035	0.025
jo	0	0	0	0	0	0	**0.115**	0.005	0.001	0.001	0
ao_1	0	0	0	0	0	0	0.048	0.029	0.010	0.003	0.002
ao_2	0	0	0	0	0	0	0	0.040	**0.049**	0.044	0.020
ao_3	0	0	0	0	0	0	0	0.024	0.018	0.039	0

particularly in the smallest ones, while in the third year the contribution of sexually recruited plants showed a dramatic increase (Figure 2a).

When the temporal variability in demographic behaviour was incorporated through the use of periodic matrices, a $\lambda_P = 0.85$ was obtained, which was slightly lower than the value obtained for the average matrix ($\lambda_A = 0.92$). In the absence of confidence intervals for these values, it is difficult to conclude whether they actually represent a clearly declining population. Yet, the result of the stochastic simulation (base run – 0.36 probability for 'good' years and 0.64 probability for 'bad' years) yielded a $\lambda_s = 0.92 \pm 0.02$ ($\pm 95\%$ confidence intervals), which suggests an overall declining trend for this population.

In addition to the overall trend in population growth rate given by the different methods used to incorporate the temporal variability in demographic behaviour, the stochastic simulations also offer the possibility of incorporating the relative frequency of occurrence of years with different rainfall patterns, as well as the chance to analyse the transient dynamics of the population in the short and medium term. Figure 3 shows the projected numerical behaviour of the population for a period of 50 y, given the current probabilities of occurrence of 'good' and 'bad' years. These theoretical results suggest that under these conditions the *T. brachycaulos* population may show a declining trend (Figure 3a). This projected population decline would be apparent in all size categories considered, although in some of them the decrease would be steady, i.e. in individuals arising through vegetative propagation (Figure 3c), while in others, particularly in individuals arising from seed, fluctuating numbers would be expected (Figure 3b). The first category to be lost would be the
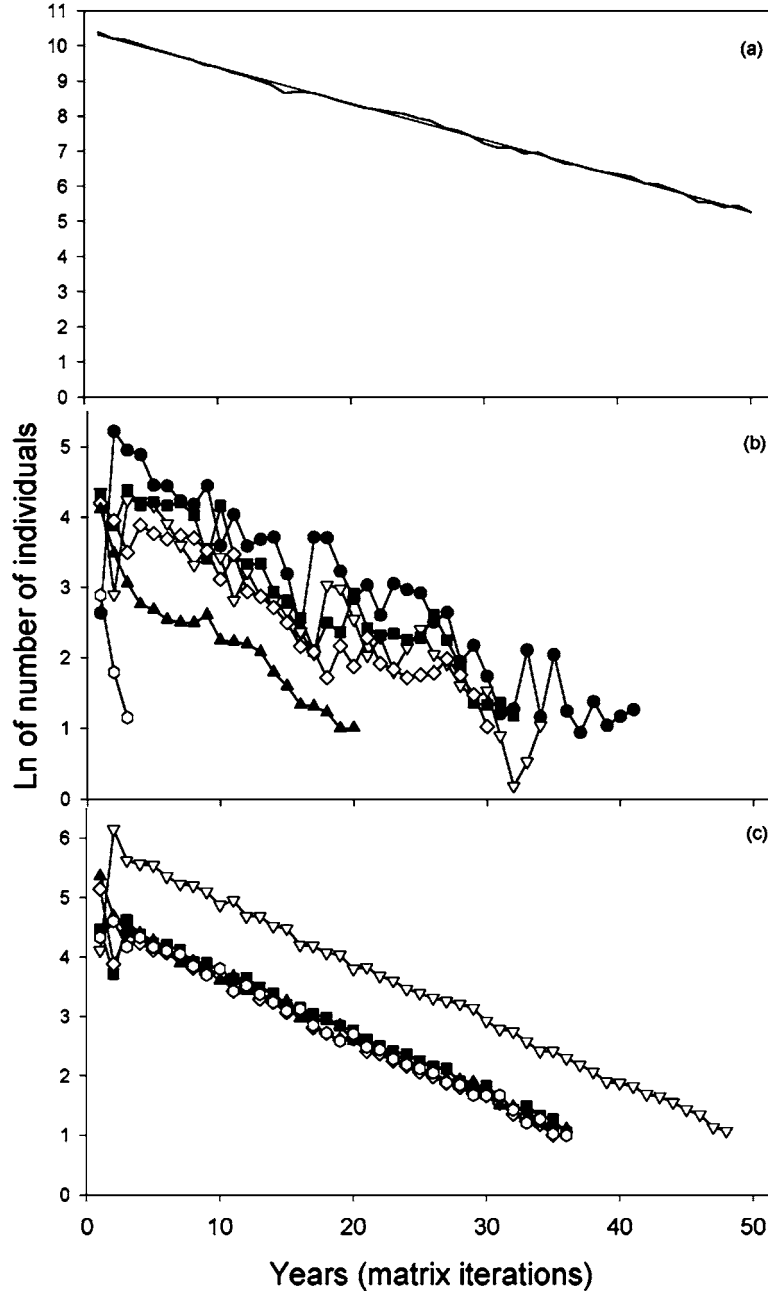
Figure 3. Stochastic behaviour of the *Tillandsia brachycaulos* population, using 1997, 1998 and 1999 annual matrices, with a probability of occurrence of 0.32, 0.32 and 0.36 respectively (see text for details). (a) Average total number of individuals (ln transformed, $n = 30$) for the first 50 y of stochastic simulations; linear regression line is shown. (b) Average number of individuals in different life cycle stages (ln transformed, $n = 30$) for the first 50 iterations (only individuals emerging from seed are included); categories are: black circle = s, white triangle = i , black square = j , white rhombus = a_1, black triangle = a_2, white circle = a_3. (c) Average number of individuals arising through vegetative propagation in different life cycle stages (ln transformed, $n = 30$) for the first 50 iterations (category nomenclature as in b).

largest sexually derived adults; juvenile offshoots would take the longest to be lost, and their decline would be steady through time.

According to the modelling approach used in the stochastic simulations, the overall population trend would depend on the frequency of 'good' years (those with high August rainfall, which coincide with the largest λ value) relative to the frequency of 'bad' years (with relatively lower August rainfall and a lower λ value). When we carried out several simulations with different probabilities of occurrence of 'good' and bad' years, the results yielded a λ_s value significantly higher than unity
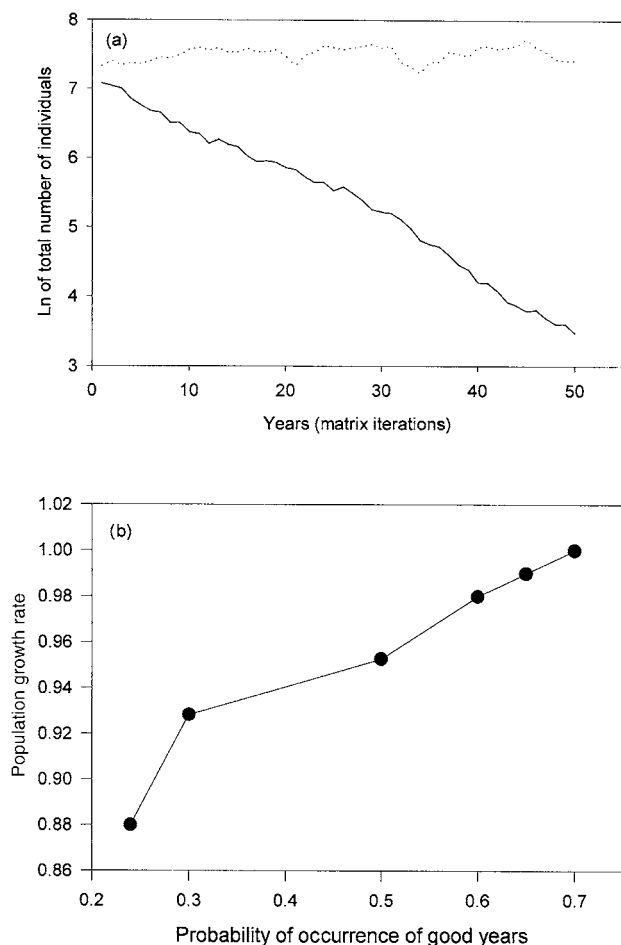
Figure 4. (a) Long-term numerical behaviour of the *T. brachycaulos* population projected over 50 y with different probabilities of occurrence of 'good' years: continuous line = 0.5, broken line = 0.7; (b) λ_s values obtained in stochastic simulations with increasing probabilities of occurrence of 'good' years.

only when the probability of occurrence of 'good' years was above 0.6 (Figure 4a and b; Table 4). Even with this high frequency of 'good' years, the population extinction risk would still be quite high (40%; Table 4).

The results of different stochastic simulation exercises performed with different probabilities of 'good' and 'bad' years project that even with a frequency of occurrence of 'good' years of 40%, population extinction risk is 1 and

the estimated time to extinction is around 70 y. Under the current weather pattern (i.e. that observed in the last 11 y), the population is expected to go extinct within 70 y (Table 4).

DISCUSSION

The *T. brachycaulos* population at the Dzibilchaltún National Park is composed of a high proportion of vegetatively recruited individuals. However, in contrast with other clonal species in which the recruitment of sexually derived individuals is rare (García-Franco 1990, Mendoza & Franco 1998), in *T. brachycaulos* the high number of seedlings observed in the study site, as well as the fecundity values (via seedling recruitment) recorded during the study period, suggest that seedling recruitment occurs frequently in this population. In other epiphytic species seedling recruitment has also been reported to occur frequently, although in rather low numbers (Hernández-Apolinar 1992, Larson 1992, Tremblay 1997, Zotz 1998), which could also be the case for *T. brachycaulos*; high pulses of seedling recruitment may occur only during particularly favourable years, as suggested by the results of the 1999 period.

With regards to the mortality pattern, we observed that the early stages of sexually derived individuals were the most vulnerable, as is the case with most vascular plants. In particular, the mortality of early stages among epiphytes has been reported to be between 30 and 50% (Benzing 1981, Hietz 1997, Tremblay 1997, Zotz 1998). The mortality rates for *T. brachycaulos* seedlings were above 70% for the first 2 y, and around 30% for the more favourable year of 1999. Thus, although seedlings emerged yearly, significant recruitment occurred only during the most favourable year. Several authors have reported that drought is the main cause of death during the early phases of development of epiphytic species (Benzing 1981, Larson 1992). Our results support this idea, since seedling mortality was highest in those years in which August rainfall was low – apparently the most critical month for seedling establishment and growth, as explained earlier. In addition to drought, the falling of individuals due to dislodging or branch

Table 4. Projected λ_s values, extinction risks, and time to extinction for the *Tillandsia brachycaulos* population studied, using different probability of occurrence of 'good' years (exemplified by the 1999 matrix) and 'bad' years (given by the 1997 and 1998 matrices, with equal probabilities). Extinction risk refers to the relative frequency with which population numbers fell below five individuals among the 30 series of 200 iterations performed for each run. Estimated time to extinction refers to the time in which projected population size was below five individuals. For λ_s and time to extinction, average and confidence intervals are given (n = 30 series of 200 matrix iterations each).

	Probability of occurrence of 'good' years					
	0.30	0.40	0.50	0.60	0.65	0.70
λ_s value	0.917 ± 0.01	0.927 ± 0.02	0.954 ± 0.02	0.978 ± 0.02	0.994 ± 0.02	1.004 ± 0.02
Extinction risk	1.00	1.00	0.967	0.400	0.003	0.000
Time to extinction (y)	64.0 ± 26.1	70.7 ± 31.8	108 ± 56.4	217 ± 113	458 ± 334	< 1000

breakage (particularly of thin branches, on which most *T. brachycaulos* individuals establish) was an important cause of death of young individuals.

In the third year of this study, we noticed a general decrease in the number of individuals at our study site. Our matrix results agree with this observation. The λ value for the first year (i.e. 1997) was significantly lower than unity, and in the following 2 y population growth rate did not differ significantly from one. In addition, the different overall λ values calculated (average, periodic and stochastic) all depict a population that appears to be declining. This apparent decline may be accounted for by an overall high seedling and adult mortality that was not compensated by the recruitment of new – sexually or vegetatively derived – individuals, even though the 'good' year allowed some short-term recuperation of population numbers. Clearly, the evaluation of population dynamics for this species must incorporate the temporal variability in demographic patterns, since its numerical behaviour during one particular year may be completely atypical and long-term projections from this type of data may be totally misleading. It is noticeable that the overall λ values obtained through the different methods in which we incorporated this temporal variability (average, periodic and stochastic) were similar, as has been observed by other authors (Golubov *et al.* 1999, Mandujano *et al.* 2001). However, we consider the results of the stochastic analysis the most interesting, since they have the advantage of allowing the analysis of the transient dynamics, as well as incorporating the effect of weather patterns on the long-term population behaviour. Of course, the value of the stochastic analysis is limited by the assumptions on which it rests, namely that temporal variability in demographic behaviour may be adequately represented by our 3-y data-set, and that the relative frequency of years with a high August precipitation is the main factor determining which of these projection matrices will characterize population dynamics each particular year. Yet, the assumptions of this type of analysis appear more realistic than those on which the periodic or the average matrices rest, precisely because the former may incorporate the effect of weather patterns, which in tropical dry forests are clearly determinant of a host of population and community processes.

The results of the projections of our stochastic analysis suggest that under the current rainfall patterns (i.e. 0.36 probability if occurrence of 'good' years) the *T. brachycaulos* population would show a decreasing trend. Note that when we refer to the current rainfall patterns we are actually including the trend of only the last 11 years (1990–2000). We decided to take into account only this short time period to characterize the relative frequency of 'good' and 'bad' years, since weather patterns have altered dramatically in recent times and a summary

of the last 50 y, for instance, might not accurately represent the current situation. Anyway, despite the precise current frequency of 'good' and 'bad' years, our projections suggest that the population might not be able to persist in the long run unless the frequency of 'good' years was substantially high (i.e. above 60%). Yet, this possibility appears remote, since the current trends in global climate change predict higher frequency of dry years for the tropical dry forests in Mexico (Villeres-Ruíz & Trejo-Vázquez 1997). If this is the case, many populations of long-lived species of seasonally dry environments whose population growth depends on occasional favourable years will be dramatically affected.

The results of this study show that during unfavourable years the *T. brachycaulos* population is maintained by vegetative propagation. Elasticity analyses show that the demographic behaviour of this population is strongly determined by the fate of vegetatively derived individuals. The high survival probability of these offshoots may be related to the fact that they remain attached to the parent rosette for some time, during which the translocation of photosynthates from parent to offshoot probably takes place (Callaghan 1984, Hartnett & Bazzaz 1983, Mendoza & Franco 1998, Price & Hutchings 1996). This results in a high growth rate which allows the offshoot to reach the reproductive size in only 1 y, in addition to avoiding the mortality risks associated with dispersal, establishment and early growth. However, note that this offshoot production is mainly a means by which successful genets perpetuate themselves, rather than a source of actual population growth, since most rosettes barely replace themselves through offshoot production (Table 2). This explains why in the absence of seedling recruitment (i.e. during unfavourable years) the absolute λ values were below unity. Even though the population may show some 'demographic plasticity' in its vital rates in response to changing environmental conditions, which allows it to withstand harsh periods, seedling recruitment is still essential for population growth. Despite the low elasticity values of fecundity entries (Table 3), which appear to suggest that they do not have a strong impact on population growth rate, the high seedling recruitment of 1999 (i.e. high fecundity values, resulting in turn from relatively higher germination probability compared to the previous 2 y) was the main determinant of a higher λ value for this period.

Finally, the results of this paper emphasize the need for long-term studies to adequately describe the demographic patterns of long-lived species. The demographic behaviour of these populations may be dramatically different between years, and it is fundamental to sample the potential span of demographic behaviours, as well as to have some idea of the relative frequency with which the different behaviours occur, in order to be able to

project their potential long-term dynamics. The later point requires us to understand the factors that determine population dynamics at any given point in time. In the case of seasonally dry environments, such as our study site, it is of paramount importance that we address the effect of weather patterns, especially in relation to rainfall (which is the most limiting factor in this case), on the demographic behaviour of plant populations, particularly since those rainfall patterns are likely to change in the years to come as a result of global warming and might produce important changes in the dynamics of plant populations and communities.

ACKNOWLEDGEMENTS

LITERATURE CITED

ALVAREZ-BUYLLA, E. R. & SLATKIN, M. 1991. Finding confidence limits on population growth rates. *Trends in Ecology and Evolution* 6:221–224.

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. 354 pp.

BIERZYCHUDEK, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* 52:331–351.

CALLAGHAN, T. V. 1984. Growth and translocation in a clonal southern hemisphere sedge – *Uncida meridensis. Journal of Ecology* 72:529–546.

CAMPOS-RÍOS, G. & DURÁN, R. 1991. *Vegetación de la Península de Yucatán. El Jardín Botánico como herramienta didáctica.* Colunga, P., Orellana, R., Ayora, N., Arellano, J. & Campos, G. (eds). Centro de Investigación Científica de Yucatán, México. 66 pp.

CASWELL, H. 1989. *Matrix population models: construction, analysis and interpretation.* Sinauer, Sunderland. 328 pp.

CASWELL, H. & TREVISAN, M. C. 1994. Sensitivity analysis of periodic matrix model. *Ecology* 75:1299–1303.

DE KROON, H., PLAISIER, A., VAN GROENENDAEL, J. V. & CASWELL, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427–1431.

GARCÍA-FRANCO, J. 1990. *Biología reproductiva de Tillandsia deppeana Steudel (Bromeliaceae).* Masters thesis. Facultad de Ciencias. UNAM. México. 80 pp.

GENTRY, A. H. & DODSON, C. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19:149–156.

GOLUBOV, J., MANDUJANO, M., FRANCO, M., MONTAÑO, C., EGUIARTE, L. E. & LOPEZ-PORTILLO, J. 1999. Demography of invasive woody perennial *Prosopis gladsulosa* (honey mesquite). *Journal of Ecology* 87:955–962.

HARTNETT, D. C. & BAZZAZ, F. A. 1983. Physiological integration among intraclonal ramets in *Solidago canadensis. Ecology* 64:779–788.

HERNÁNDEZ-APOLINAR, M. 1992. *Dinámica poblacional de* Laelia speciosa *(H.B.K.) Schltr. (Orchidaceae).* Bachelor thesis. Faculdad de Ciencias. UNAM. México. 86 pp.

HIETZ, P. 1997. Population dynamics of epiphytes in a Mexican humid montane forest. *Journal of Ecology* 85:767–775.

HORVITZ, C. C. & SCHEMSKE, D. W. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs* 65:155–192.

IBISCH, P. L., BOEGNER, A., NIEDER, J. & BARTHLOTT, W. 1996. How diverse are neotropical epiphytes? An analysis based on the "Catalogue of the flowering plants and Gymnosperms of Peru". *Ecotropica* 2:13–28.

ISLEY, P. T. 1987. *Tillandsia.* Botanical Press. Gardena, California. 210 pp.

KHURANA, E. & SINGH, J. S. 2001. Ecology of seed and seedling growth for conservation and restoration of dry forest. *Conservation Biology* 28:39–52.

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

MANDUJANO, M. C., MONTAÑA, C., FRANCO, M., GOLUBOV, J. & FLORES-MARTÍNEZ, A. 2001. Integration of demographic annual variability in a clonal desert cactus. *Ecology* 82:344–359.

MEDINA, E. 1995. Diversity of life forms of high plants in Neotropical dry forest. Pp. 221–242 in Bullock, S. H., Mooney, H. A. & Medina, E. (eds). *Seasonally dry forest.* Cambridge University Press, Cambridge.

MENDOZA, A. E. & FRANCO, M. 1998. Sexual reproduction and clonal growth in *Reinhardtia gracilis* (Palmae), an understory tropical palm. *American Journal of Botany* 85:521–527.

MONDRAGÓN, D. 2001. *Dinámica poblacional de* Tillandsia brachycaulos *Schltdl. en el Parque Nacional de Dzibilchaltún, Yuc.* Ph.D. thesis. Centro de Investigación Ciénifica de Yucatán, México. 92 pp.

MONDRAGÓN, D., DURÁN, R., RAMÍREZ, I. & OLMSTED, I. 1999. Population dynamics of *Tillandsia brachycaulos* Schltdl. (Bromeliacae) in Dzibilchaltun national park, Yucatán. *Selbyana* 20:250–255.

MONTAÑA, C., DIRZO, R. & FLORES, A. 1997. Structural parasitism of an epiphytic bromeliad upon *Cercidium praecox* in an intertropical semiarid ecosystem. *Biotropica* 29:517–521.

NADKARNI, N. M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* 16:249–256.

NAKAOKA, M. 1996. Dynamics of age- and size-structured populations in fluctuating environments: applications of stochastic matrix models to natural populations. *Researches on Population Ecology* 38: 141–152.

OLMSTED, I. & GÓMEZ-JUÁREZ, M. 1996. Distribution and conservation of epiphytes in the Yucatan Peninsula. *Selbyana* 17:58–70.

PRICE, E. A. & HUTCHINGS, M. J. 1996. The effects of competition, growth and form in *Glechoma hederacea. Oikos* 75:279–290.

SILVERTOWN, J., FRANCO, M., PISANTY, I. & MENDOZA, A. 1993. Comparative plant demography - relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennial. *Journal of Ecology* 81:465–467.

THIEN, L. B., BRADBURN, A. S. & WELDEN, A. L. 1982. *The woody vegetation of Dzibilchaltún, a Maya archaeological site in Northwest Yucatan, Mexico.* Middle American Research Institute. Tulane University, New Orleans. 24 pp.

TREMBLAY, R. L. 1997. *Lepanthes caritensis*, an endangered orchid: no sex, no future? *Selbyana* 18:160–166.

UTLEY, J. F. 1994. Bromeliaceae. Pp. 89–156 in Davidse, G., Sousa, M. & Chater, A. (eds). *Flora Mesoamericana vol. 6.* Universidad Nacional Autónoma de México – Instituto de Biología, Missouri Botanical Garden & Natural History Museum (London). UNAM. México.

VALVERDE, T., QUIJAS, S., LÓPEZ-VILLAVICENCIO, M. & CASTILLO, S. 2003. Population dynamics of *Mammillaria magnimamma* Haworth (Cactaceae) in a lava-field in central Mexico. *Plant Ecology* (in press).

VILLERES-RUIZ, L. & TREJO-VÁZQUEZ, I. 1997. Assessment of the vulnerability of forest ecosystems to climate change in Mexico. *Climate Research* 9:87–93.

ZOTZ, G. 1998. Demography of the epiphytic orchid, *Dimerandra emarginata. Journal of Tropical Ecology* 14:725–741.