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Effect of Canopy Position on Germination and Seedling Survival of Epiphytic Bromeliads in a Mexican Humid Montane Forest

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• *Background and Aims* Seeds of epiphytes must land on branches with suitable substrates and microclimates to germinate and for the resulting seedlings to survive. It is important to understand the fate of seeds and seedlings in order to model populations, but this is often neglected when only established plants are included in analyses.
• *Methods* The seeds of five bromeliad species were exposed to different canopy positions in a Mexican montane forest, and germination and early seedling survival were recorded. Additionally, the survival of naturally dispersed seedlings was monitored in a census over 2·5 years. Survival analysis, a procedure rarely used in plant ecology, was used to study the influence of branch characteristics and light on germination and seedling survival in natural and experimental populations.
• *Key Results* Experimental germination percentages ranged from 7·2 % in *Tillandsia deppeana* to 33·7 % in *T. juncea*, but the seeds of *T. multicaulis* largely failed to germinate. Twenty months after exposure between 3·5 and 9·4 % of the seedlings were still alive. There was no evidence that canopy position affected the probability of germination, but time to germination was shorter in less exposed canopy positions indicating that higher humidity accelerates germination. More experimental seedlings survived when canopy openness was high, whereas survival in census-seedlings was influenced by moss cover. While mortality decreased steadily with age in juveniles of the atmospheric *Tillandsia*, in the more mesomorphic *Catopsis sessiliflora* mortality increased dramatically in the dry season.
• *Conclusions* Seedling mortality, rather than the failure to germinate, accounts for the differential distribution of epiphytes within the canopy studied. With few safe sites to germinate and high seedling mortality, changes of local climate may affect epiphyte populations primarily through their seedling stage.

Key words: Bromeliaceae, *Catopsis*, epiphytes, germination, habitat heterogeneity, Mexico, seedling establishment, survival analysis, *Tillandsia*.

INTRODUCTION

Tree crowns impose a powerful set of constraints upon epiphytes, offering a fragmented and stressful habitat with substantial rates of patch turnover (Benzing, 1990). Epiphytes experience tree crowns as a mosaic of suitable and unsuitable habitats, with the suitable type occurring in relatively small and discrete patches (Hanski and Gilpin, 1997). Seed size in epiphytes rarely exceeds 2 mm regardless of the dispersal mechanism, and 84 % of epiphyte species are adapted to wind dispersal either by dust-like diaspores or by winged or plumed seeds (Madison, 1977). Small seed size is advantageous for epiphytes as the potential habitat can be showered with numerous seeds, increasing the chance that an adequate number will fall onto safe sites. Furthermore, small seeds are more likely to slip into cracks in bark and their large surface-to-volume ratio favours the rapid uptake of water (Madison, 1977). On the other hand, small seeds provide few resources for seedlings to succeed on bark substrates (Benzing, 1990). Some epiphytes have developed special devices for transport and attachment to bark (van der Pijl, 1972). For instance, members of the bromeliad subfamily Tillandsioideae disperse via small seeds equipped with coma hairs extending from one or both ends of the integument (Benzing, 2000). These constitute more than half of the aggregate seed mass in epiphytic species, providing buoyancy and holdfast to substrates (Benzing, 2000). Seedling mortality can be expected to be high because of small seed size and high proportional investment in the dispersal apparatus (Howe and Smallwood, 1982; Jakobsson and Eriksson, 2000).

Germination and seedling establishment tend to be the most vulnerable stages in the life cycle of plants because seedling mortality is often high (Harper, 1997). However, germination ranks among the least-studied aspects of bromeliad reproduction (Benzing, 2000; but see Benzing, 1978, 1981; Mondragón, 2000). Studies on seedling survival report high mortality in the first year and that survival increases with plant size. Drought and/or branchfall were the most important causes of death (Benzing, 1978, 1981; Hietz, 1997). The implications of spatial heterogeneity on germination and survival are well known for other plants (e. g. Augspurger, 1984; Kobe, 1999; Daws *et al*., 2002; Beckage and Clark, 2003; Castro *et al*., 2004), but have rarely been studied in epiphytes. Zotz (1997), studying

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the distribution of three epiphytic bromeliads, found no evidence for differential seedling mortality between growing sites and suggested that the spatial distributions of these epiphytes may be determined at the time of germination although survival was higher in the tree periphery and stem base than on intermediate branches, and on the sides rather than at the top or underside of branches in exposed seedlings of these bromeliads. However, this site-specific survival was not related to and could not help explain the distribution of older individuals (Zotz and Vollrath, 2002).

A major constraint for the statistical analysis of seedling survival is that observations are often incomplete or censored, e.g. the birth or death of individuals is not observed, and data are generally non-normally distributed. Survival analysis is a powerful tool to analyse such data where the response variable is the time until occurrence of some event (Hosmer and Lemeshow, 1999; Klein and Moeschberger, 2003). The study of events involving an element of time has a long history in statistical research and practice, especially in clinical studies in medicine (e.g. Crowley and Hu, 1977; Breslow and Day, 1980, 1987; Goldberg *et al*., 1988). In ecological research, the use of survival analysis has only recently become more widespread, particularly the use of complex regression analysis of survival data (e.g. Greipsson and Davy, 1994; Beckage and Clark, 2003; Castro *et al*., 2004; Vange *et al*., 2004).

Microsite-specific germination or seedling survival could explain the observed distribution of individuals, but these are only two factors affecting the community structure of epiphytes. In this study, germination and survival experiments with five epiphytic bromeliad species on branches in different canopy positions in a Mexican montane forest were conducted and *in situ* germination and seedling survival in relation to habitat characteristics were studied. Special attention was paid to differences in germination and seedling survival between canopy strata, branch inclinations, light and moisture conditions, and to seasonal variations in mortality.

MATERIALS AND METHODS

Study area and species

This study was conducted in a small forest reserve adjacent to the Instituto de Ecología, 2·5 km south of Xalapa, in central Veracruz, Mexico (19°31′N, 96°57′W), at 1350 m elevation. Average temperature is 19 °C, and annual precipitation is 1500 mm, most of which falls in the June–October wet season. According to the Holdridge life-zone system (Holdridge, 1967), the forest is at the transition between premontane and lower montane moist forest. In Mexico, it is commonly classified as 'bosque mesófilo de montaña' (mesophilous montane forest) following Rzedowski (1986). Description of the forest structure is given by Williams-Linera (1997), and that of the epiphyte community by Hietz and Hietz-Seifert (1995).

Germination and seedling survival were recorded in the epiphytic bromeliads *Catopsis sessiliflora* (Ruiz and Pav.) Mez, *Tillandsia deppeana* Steud., *T. juncea* (Ruiz and Pav.) Poir., *T. multicaulis* Steud. and *T. punctulata* Schltdl. and Cham. All *Tillandsia* juveniles and adults of *T. juncea* exhibit the atmospheric habit, meaning that they possess narrow leaves that do not hold water but display confluent layers of absorbing trichomes. *Catopsis sessiliflora* of all sizes and intermediate-to-adult *T. multicaulis* and *T. deppeana* have broad thin leaves that form tanks, and *T. punctulata* is an atmospheric–tank intermediate species.

Germination experiments

Seeds were collected in spring 2002 and stored dry at room temperature until used for the germination experiments. The viability of the seeds was not tested prior to exposure, but to minimize possible maternal effects, the seeds of several plants were mixed. For each study species, 20 randomly selected seeds were tied to 30 woody twigs (approx. 30 cm long, 5 cm diameter) with a thin thread. As bromeliad germination can be affected by substrate (Benzing, 1978; Merwin *et al*., 2003), which is primarily a consequence of different water-holding capacities of the bark (Callaway *et al*., 2002), we used wood limbs of homogenous size with the surface free from bryophytes and lichens. Lichens were removed because they can be allelopathic (Lawrey, 1986) and can also affect abiotic characteristics of the substrate (Hawkes and Menges, 2003) by absorbing and retaining moisture (Riefner and Bowler, 1995). The twigs were tied to branches on 11 trees, representing the range of canopy strata colonized by the species studied. According to their height of attachment relative to total tree height and distance to the trunk relative to the crown radius, branches were assigned to one of three canopy positions (trunk and inner crown, intermediate crown, outer crown). Canopy openness (using a convex spherical densiometer, Ben Meadows, Atlanta, GA), inclination, and circumference at the position of attachment were measured and percent bryophyte cover was estimated for each branch.

The twigs were exposed in May (*C. sessiliflora*), June (*T. deppeana*) and July (*T. juncea*, *T. multicaulis*, *T. punctulata*) 2002, at the times the seeds of the respective species are dispersed. Twigs were examined for seed germination and seedling survival approximately every tenth week after exposure until February 2003, and additionally at the end of the dry season in May 2003 and in February 2004.

Census of natural populations

In August 1999 and 2001, 186 branch sections between 10 and 250 cm long and distributed throughout the crowns of nine trees were selected and marked. The same branch parameters as for the germination experiments were measured and bryophyte and lichen cover were estimated. Natural germination and seedling survival of the study species were monitored twice a year until February 2003, and in February 2004. Fifty-eight seedlings of *C. sessiliflora* were recorded. As seedlings of *Tillandsia* species can not normally be determined to species level, the 368 seedlings were assigned to the group '*Tillandsia* juveniles'. In cases where mass germination of seedlings was observed close to the fruiting mother plant, 388 seedlings of *T. deppeana* and 859 of *T. multicaulis* could be assigned to a species.

Statistical methods

Logistic regression was used to determine which of the following factors affect seed germination probabilities: species identity, position in the host tree, inclination, bryophyte cover, and canopy openness. Several models of different complexities were explored using the GLM function for binomial responses with logit-link in S-Plus (Anonymous, 1999). The optimal model chosen was the one that minimized the Akaike information criterion (AIC = −2 log likelihood minus the number of parameters in model; Agresti, 1990). To analyse time from exposure to germination and to seedling death, survival analysis was applied (Hosmer and Lemeshow, 1999; Klein and Moeschberger, 2003). Our survival data are right-censored because many individuals were still alive at the end of the observation, and interval-censored as survival time is only known to be between two observation times. The non-negative random variable T measures survival time. The survivor function $S(t)$ measures the probability that an individual will survive beyond time t: $S(t) = P[T \geqslant t]$.

The Kaplan–Meier estimator $S(t)$ was used to calculate non-parametric estimates of the survivor function:

$$\hat{S}_{(t)} = \prod_{j=1}^{s}\left(1-\frac{d_j}{n_j}\right)$$

where d_j is the number of individuals that experienced the event in a given interval and n_j is the number at risk. Survival curves are monotone non-increasing step functions equal to 1 at time zero, and 0 as time approaches infinity. Statistical differences between survival curves were calculated using the log-rank test. Because this test cannot be calculated for interval-censored data, the mid-point of each interval was used in this case.

To account for explanatory variables, parametric regression models of the form

$$f(T) = \beta_0 + \beta^t x + \sigma\varepsilon$$

were fitted to the data using the censorReg function in S-plus 2000 (Anonymous, 1999), where f() is a model-dependent link function, β_0 is the intercept, β^t is a transposed vector of regression coefficients, x is a vector of explanatory variables, σ is the scale parameter and ε is the model-dependent error distribution. Explanatory variables were position, inclination, bryophyte cover and canopy openness. Covariates were included in the models following the purposeful selection procedure proposed by Hosmer and Lemeshow (1999). All covariates significant at the 20 % level in the bivariate analysis were included in an initial multivariable model. The values of the Wald tests were used to identify non-significant covariates, which were removed one by one from the model. Following the fit of the reduced model, we assessed if removal of a covariate produced a change of more than 20 % in the coefficients of the variables remaining in the model. If the variable excluded was an important confounder it was added back into the model. This process continued until no more covariates could be deleted from the model. In the next step, all two-way interactions from the main terms were added to the main effects model. All interactions significant at the 5 % level (likelihood ratio test) were then added jointly to the model. Interactions that were still significant remained in the model. A frailty term was incorporated to account for unmeasured 'random' effects of the branches.

Models with different error distributions were explored (normal and logistic with an identity link; Weibull, exponential, extreme, logistic, log-logistic and log-normal which have a natural log link) and compared using the Akaike information criterion statistic. The model with the smallest AIC value was chosen as the best fitting final model. The coefficient values, their standard error, 95 % confidence interval, significance and time ratio (Hosmer and Lemeshow, 1999) are reported. The time ratio (e^{β}) reflects how a change in covariate values changes survival time (e.g. when time ratio for a dichotomous covariate with $x = 0$ and $x = 1$ is 2·0, the interpretation is that survival times of subjects with $x = 1$ is twice that of individuals with $x = 0$).

Daily mortality in the rainy season 2002 (June–October), in winter 2002/2003 (November–February), in the dry season 2003 (March–May) and between May 2003 and February 2004 (rainy season plus winter) was calculated as

$$m = 1 - (N_1/N_0)^{1/t}$$

where N_0 and N_1 are seedling counts at the beginning and end of the census interval t (Sheil *et al.*, 1995).

All statistical analyses were calculated using S-plus 2000 (MathSoft Inc., Seattle, 1988–1999).

RESULTS

Germination experiments

The best logistic regression model was the null model without explaining variables, thus germination probabilities were not affected by any of the observed parameters. Out of 3000 seeds 524 germinated, most of them (65·8 %) within the first 10 weeks after exposure (Table 1). Most of the seeds of *T. multicaulis* failed to germinate. The median time to germination was 37 d in *T. punctulata* and *T. juncea*, 40 d in *C. sessiliflora* and 62 d in *T. deppeana*. According to the log-gaussian parametric survival model, time to germination was species-specific and affected by position in the crown (Table 2A), with seeds exposed in the outer crown taking longer to germinate. The median time to germination in the inner, intermediate and outer crown was 37, 40 and 44 d, respectively. *Tillandsia juncea* seeds germinated sooner on steeply inclined branches; in the other species the interaction with branch inclination was not significant (Table 2A).

Seedling survival was similar among species (Fig. 1A, Table 3). About two-thirds of newly germinated seedlings were dead at the following census (*T. juncea*, 56·9 %; *T. punctulata*, 67·1 %; *T. deppeana*, 72·1 %; *C. sessiliflora*, 77·2 %). Less than 20 % of the seedlings or 3 % or less of the seeds were still alive about 1 year after exposure (Table 1). The most-parsimonious parametric survival model was the log-logistic model (Table 2B). Seedling survival time was influenced by position in the crown and canopy openness

TABLE 1. *Percentage of germinated seeds within 10, 20 and 30 weeks of exposure and percentage of seedlings that survived 7, 12 and 20 months in the experiments*

	% germinated within			% seedlings alive		
	10 weeks	20 weeks	30 weeks	approx. 7 months	approx. 12 months	approx. 20 months
Catopsis sessiliflora	16·5	18·5	18·8	14·0	7·0	3·5
Tillandsia deppeana	4·2	6·4	7·2	27·9	11·6	4·7
T. juncea	31·5	33·7	33·7	24·8	17·8	9·4
T. multicaulis	0·2	0·2	0·2	0·0	0·0	0·0
T. punctulata	25·8	27·1	27·3	16·5	10·4	4·9
Total	15·7	17·2	17·5	20·0	12·6	6·3

TABLE 2. *Parametric survival models for interval and right-censored data of (A) germination, (B) seedling death in experiments and (C) seedling death in the census populations. The coefficient values (β), the standard error, Z and P-value of the Wald test and time ratio are listed. The time ratio reflects the amount by which median survival time is changed by a factor (e^{β}) or a 10-unit increase ($e^{\beta*10}$) in a continuous covariate. The frailty term accounts for unmeasured random effects of the branches. Factor variables are split into 0–1 coded dummy variables according to their number of factor levels. The first (= reference) level has a coefficient value of 0 and time ratio is 1. The reference levels in the variable species are* C. sessiliflora *in the experiments, and unidentified* Tillandsia *juveniles in the census survival model, respectively. In the covariate position, 'inner crown' is the reference level*

	Coefficient	s.e.	*Z*	*P*	Time ratio
(A) Time to germination (log-gaussian, n = 523)					
Intercept	0·441	0·138	3·20	0·001	
Species: *Td*	0·287	0·078	3·68	0·000	1·33
Species: *Tj*	−0·307	0·073	−4·20	0·000	0·74
Species: *Tp*	−0·065	0·034	−1·89	0·059	0·94
Position: intermediate	0·154	0·068	2·28	0·023	1·17
Position: outer crown	0·111	0·041	2·69	0·007	1·12
Inclination	−0·003	0·002	−1·35	0·176	1·00
Frailty (branch)	−0·010	0·004	−2·74	0·006	
Td × Inclination	0·002	0·003	0·78	0·438	1·02
Tj × Inclination	−0·006	0·002	−3·17	0·002	0·94
Tp × Inclination	0·001	0·001	0·75	0·457	1·01
(B) Seedling survival experiment (log-logistic, n = 523)					
Intercept	1·656	0·118	13·98	0·000	
Species: *Td*	0·166	0·049	3·41	0·001	1·18
Species: *Tj*	0·014	0·021	0·69	0·494	1·01
Species: *Tp*	−0·018	0·014	−1·29	0·197	0·98
Position: intermediate	0·048	0·030	1·59	0·111	1·05
Position: outer crown	0·069	0·025	2·82	0·005	1·07
Inclination	−0·002	0·001	−2·01	0·045	0·98
Bryophyte	−0·001	0·001	−1·11	0·267	0·99
Canopy openness	0·010	0·004	2·52	0·012	1·11
Frailty (branch)	−0·004	0·002	−2·38	0·017	
(C) Seedling survival census (log-gaussian, n = 1673)					
Intercept	2·385	0·105	22·73	0·000	
Species: *Cs*	−0·405	0·154	−2·62	0·009	0·67
Species: *Td*	−0·228	0·076	−3·01	0·003	0·80
Species: *Tm*	0·092	0·035	2·65	0·008	1·10
Inclination	−0·002	0·001	−1·20	0·230	0·98
Bryophyte	0·012	0·002	7·00	0·000	1·12
Frailty (branch)	−0·006	0·001	−6·64	0·000	
Cs × Bryophyte	0·010	0·003	3·37	0·001	1·10
Td × Bryophyte	0·001	0·001	0·85	0·393	1·01
Tm × Bryophyte	−0·005	0·001	−7·05	0·000	0·95
Cs × Inclination	−0·007	0·003	−2·64	0·008	0·93
Td × Inclination	0·002	0·001	1·65	0·099	1·02
Tm × Inclination	0·002	0·001	3·93	0·000	1·02

Cs, *Catopsis sessiliflora*; *Td*, *Tillandsia deppeana*; *Tj*, *T. juncea*; *Tm*, *T. multicaulis*; *Tp*, *T. punctulata*.

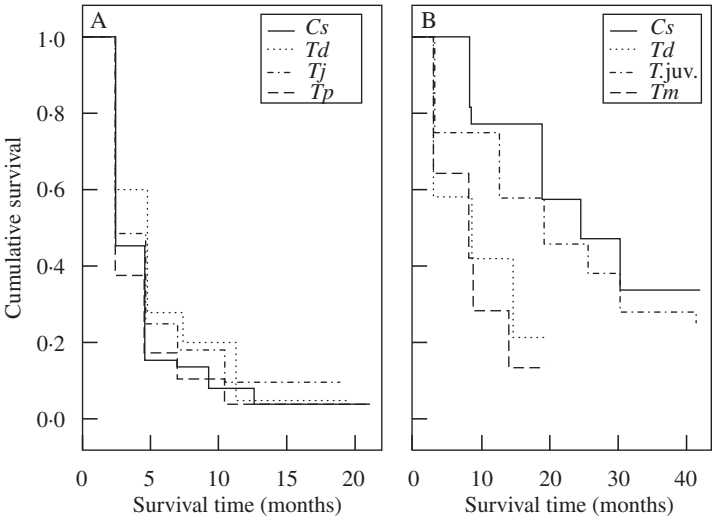

FIG. 1. Seedling survival in epiphyte species based on Kaplan–Meier estimates in (A) experiments and (B) census populations. Differences in survival curves are significant (log-rank test, $P < 0.001$). *Cs*, *Catopsis sessiliflora*; *Td*, *Tillandsia deppeana*; *Tj*, *T. juncea*; *T.* juv., *Tillandsia* juveniles not identified to species level; *Tm*, *T. multicaulis*; *Tp*, *T. punctulata*.

TABLE 3. *Median survival time in experimental and census populations*

	Median survival time (d)	
	Experiments	Census
Catopsis sessiliflora	132	778
Tillandsia deppeana	143	354
T. juncea	137	–
T. multicaulis	–	256
T. punctulata	125	–
Tillandsia juveniles	–	558

Tillandsia juveniles could not be identified to species level.

(Table 2B, Fig. 2A): in outer and intermediate crown positions, the survival time was longer. An increase in canopy openness of 10 % increased seedling survival time by the factor 1·11. Compared to the reference species *C. sessiliflora*, median survival time was significantly higher for *T. deppeana* seedlings (Table 2B).

Daily mortality decreased with increasing seedling age (Fig. 3). The *Tillandsia* species showed an almost parallel monotonic decline in mortality. In contrast, daily mortality in *C. sessiliflora* seedlings increased dramatically in the dry season. For every species except *C. sessiliflora* daily mortality was higher on shaded than on sun-exposed branches (Table 4).

Census of natural populations

Seedlings that had germinated naturally on branches survived longer than those attached to the twigs (Fig. 4), and survival time differed between species (Fig. 1B, Table 3). Pooling all species, survival was higher on steep branches and when bryophyte cover was high (Fig. 2B, Table 2C). A log-gaussian survival model revealed that the interaction between species and bryophyte cover and between species and inclination significantly influenced survival time (Table 2C). In *C. sessiliflora* and *T. deppeana*, median survival time increased with bryophyte cover (although not significantly in the latter), whereas in *T. multicaulis* survival time was shorter on branches with strong bryophyte cover. Steeper branches were favourable for the seedling survival of *T. deppeana* and *T. multicaulis*, but not for *C. sessiliflora*.

DISCUSSION

Germination experiments

Seeds were exposed as the capsules of all five species opened during the dry season or at the beginning of the rainy season (M. Winkler *et al.*, unpubl. data). Many anemochorous epiphytes disperse their seeds during the dry season when deciduous trees lose their foliage and movement through canopies is thus not hindered by the leaves of trees (Madison, 1977). However, in the study forest most of the dominant trees shed their foliage in winter, and by the beginning of the dry season new leaves are expanding (Williams-Linera and Tolome, 1996). The fact that precipitation tends to mat the comas of these seeds also favours dry-season dispersal, as does dry air itself (Bonn and Poschlod, 1998).

The failure of the planted seeds of *Tillandsia multicaulis* to germinate is surprising considering its abundance at the study site. It is possible that the seeds, collected from seven plants, were not viable or that the species has particular germination requirements, although the latter appears unlikely as this species is found growing on a wide range of branch types and positions. In the other species, germination ranged from 7·2 to 33·7 %. These values may be underestimates as it is possible that some seeds germinated and died between two observation intervals, but they are still in the upper range observed in other bromeliad or epiphyte species. Benzing (1978, 1981) obtained 6–35 % germination

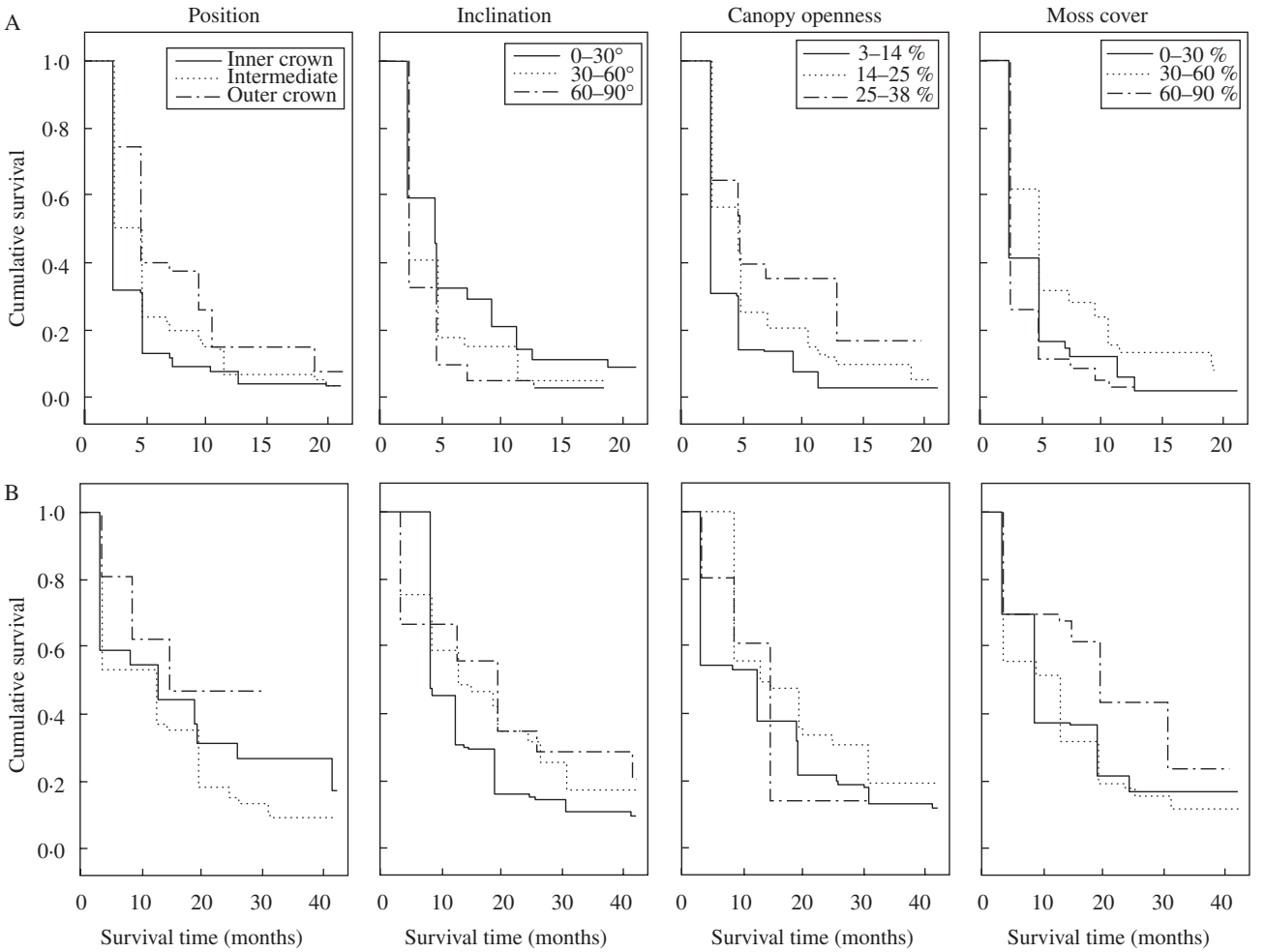

FIG. 2. The effect of the branch parameters position, branch inclination, canopy openness and bryophyte cover on seedling survival in (A) experiments and (B) census populations. Survival functions were based on Kaplan–Meier estimates. Differences in survival curves are significant (log-rank test, $P < 0.001$).

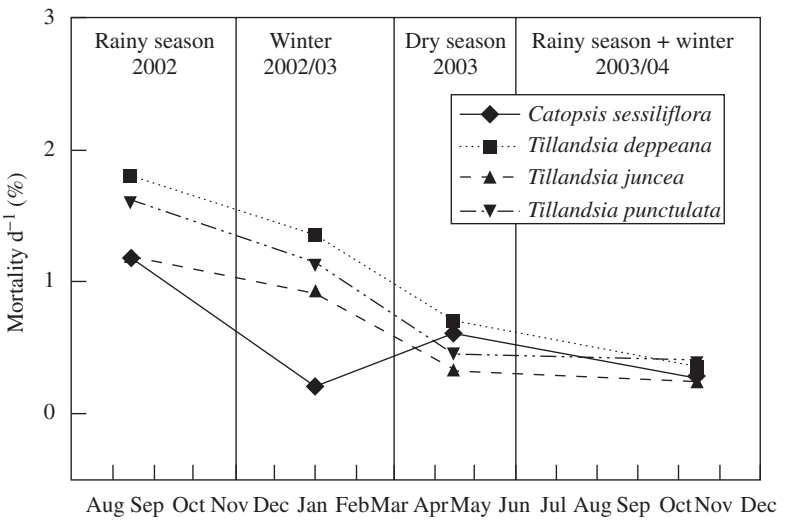

FIG. 3. Percent mortality per day in epiphyte species in different seasons.

TABLE 4. *Percent seedling mortality per day on shady branches, where canopy openness is below the mean of all branches (<17 %), and sunny branches (canopy openness ⩾17 %) in different seasons. Differences between branch types are not significant (Mann–Whitney* U*-test,* P > *0·05)*

Species	Branch type	% mortality d^{-1} (*n*)			
		Rainy season 2002	Winter 2002/03	Dry season 2003	Rainy season+winter 2003/04
Catopsis sessiliflora	Shady	1·35 (54)	0·00 (14)	0·89 (15)	0·11 (9)
	Sunny	1·55 (45)	0·49 (14)	0·18 (13)	0·35 (12)
Tillandsia deppeana	Shady	2·27 (20)	1·61 (14)	0·79 (8)	0·42 (3)
	Sunny	0·73 (5)	0·90 (6)	0·56 (4)	0·27 (2)
T. juncea	Shady	1·67 (116)	1·04 (39)	0·37 (19)	0·37 (13)
	Sunny	0·65 (73)	0·83 (55)	0·29 (31)	0·19 (23)
T. punctulata	Shady	2·01 (110)	1·34 (33)	0·61 (13)	0·33 (7)
	Sunny	0·94 (45)	0·88 (24)	0·33 (14)	0·47 (10)

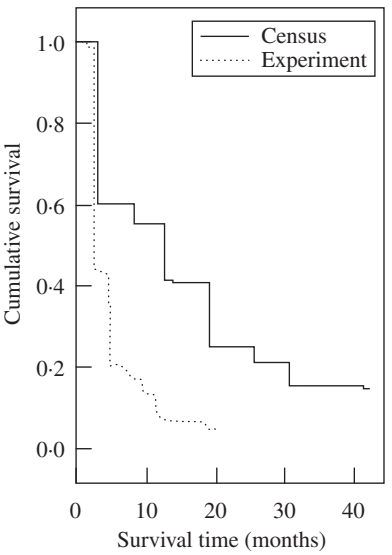

FIG. 4. Survival of all seedlings based on Kaplan–Meier estimates under experimental and natural (census) conditions. Differences in survival curves are significant (log-rank test, $P < 0.001$).

of *Tillandsia paucifolia* after 14 weeks in greenhouse experiments with regular misting, but less than 4 % in the field. In a Mexican dry forest, planted *Tillandsia brachycaulos* seeds germinated at 2·4, 3·1 and 4·2 % in three consecutive years (Mondragón, 2000). Nearly 100 % of the seeds of the epiphytic orchid *Laelia speciosa* (Hernández-Apolinar, 1992) germinated *in vitro*, but results in the field were far below 1 % ($4{\cdot}8 \times 10^{-5}$ to $2{\cdot}2 \times 10^{-4}$). Between 9 and 41 % of the seeds of hemiepiphytic *Ficus stupenda* germinated on different substrate types in Borneo (Laman, 1995).

Whether or not germination occurred was not influenced by any of the investigated parameters. However, lower germination rates *in situ* compared to in the laboratory in several *Tillandsia* species (Benzing, 1978, 1981; García-Franco, 1990; Mondragón, 2000) show that some factors must be responsible for sub-optimal germination conditions in the field. About 90 % of germination events were observed within 10 weeks of exposure. A single seed germinated after 30 weeks and the remaining seeds appeared to be dead or were never viable. Our findings thus support the notion that epiphyte seeds are non-dormant and do not build seed banks (Benzing, 1990). In laboratory experiments, all of the seeds of *Tillandsia deppeana* that germinated did so within 7 d (García-Franco, 1990). Seeds of all species germinated earlier in the less exposed zones of the canopy where branches are moister, suggesting that insufficient humidity delays germination in the field.

Seedling establishment was low, only one eighth of them survived after 1 year and only half of these were still living after 20 months. The early stages of the cycle are the most vulnerable in epiphytes, as in most other vascular plants (Silvertown and Lovett-Doust, 1993). For instance, first-year survival in seedlings of *Tillandsia paucifolia* was only between 0·46 and 3·35 % in seedling cohorts of four consecutive years (Benzing, 2000). Mondragón *et al*. (2004) report annual seedling mortalities between 21–71 % in three years for *Tillandsia brachycaulos*. The low survival rates contrast with a previous study that found survival probabilities of about 70 % for *Catopsis* and *Tillandsia* plants <2 cm length at the same forest site (Hietz, 1997). However, that study was based on the analysis of photographs taken annually, where all individuals that germinated and died between two observations were left out, and these seedlings were larger and probably less vulnerable than the seedlings described in the present study.

Survival times were longer in the outer canopy and in locations where canopy openness was high. In the atmospheric seedlings of *Tillandsia* spp, mortality steadily decreased with age, but in the more mesomorphic *C. sessiliflora* mortality increased in the dry season. By contrast, dry season mortality was lowest in *T. juncea* seedlings, the only species utilizing CAM (Hietz *et al*., 2002). Furthermore, *Tillandsia* seedling mortality was lower on sunny branches during all seasons. This is surprising as drought constitutes the major threat to early juveniles because they desiccate faster than adults due to their less-favourable surface-to-volume ratio and small size (Benzing, 1990; Hietz, 1997; Schmidt and Zotz, 2001; Zotz *et al*., 2001; Mondragón *et al*., 2004). Seedlings of the soft-leafed, tank-forming Tillandsioideae are equipped with denser layers of insulating and absorbing trichomes than during the later life stages (Madison, 1977; Adams and Craig, 1986). The trichomes aid in water uptake and reduce water loss, but hinder photosynthesis (Adams and Craig,

1986) when the wet leaf surface impedes gas exchange (Benzing *et al*., 1978). Thus, atmospheric species, as well as atmospheric seedlings of species that as adults have broad leaves with only scattered trichomes on their surface, may be favoured by exposed conditions, not only because they require more light, but also because they are damaged by excessive humidity.

Census of natural populations

The longer survival times among the natural populations compared to those exposed for the experiments may in part be a consequence of longer observation intervals, which were mostly 6 months for the census but 2 months for the experimental population. Thus, any seed that germinated and died between two observations was not recorded. High early stage mortality (only 14–28 % of the experimental seedlings survived for 7 months) largely explains the difference in survival between natural and experimental seedlings (Fig. 4). Additionally, the twigs with rather smooth bark and few cryptogams used in the experiments may also have been less suitable than the live branches that supported the census population.

Most seedlings were anchored near what could have been their parents. Spatial distribution of seeds is usually clumped because few of them travel more than short distances from their parents (Silvertown and Lovett-Doust, 1993). About half of the seeds of wind-dispersed *Tillandsia deppeana* remained near the mother plant, and for more mobile seeds the probability of reaching a branch decreased with the distance travelled (García-Franco and Rico-Gray, 1998). Of 8500 seeds used in their experiments only 2 % were recovered from one of the six downwind traps that covered in total 3·4 m^2. Seventy-two seeds per square metre were captured at a distance of 8·8 m from the experimental 'mother plant', 54 at 14·4 m, and 44 at 28 m distance, respectively (García-Franco and Rico-Gray, 1998).

On branches *in situ*, which had a more diverse bark structure and cryptogam cover than the experimental twigs, bryophyte cover was more important for survival than light. Survival times of seedlings of *C. sessiliflora* and *T. deppeana* increased with bryophyte cover. These species occur in more exposed canopy strata (Hietz *et al*., 2002) where the humidity, and possibly protection against excess radiation provided by cryptogams, may favour seedling success. On the other hand, on the thicker and shadier branches preferred by *T. multicaulis* (Hietz *et al*., 2002), bryophyte cover negatively affected seedling survival, probably because of excessive humidity or shading of seedlings.

Conclusions

The heterogeneity of the habitat in a sampled forest canopy, which presumably influences the distribution of epiphytes growing there, affected seedling success, but not germination percentage. Given the scarcity of safe sites in epiphytic habitats and the high initial mortality, germination and early survival can be bottlenecks determining epiphyte population sizes and growth rates, but further research is needed to confirm this. Because epiphyte seedlings are sensitive to differences in microclimate and their mortality is typically high, it may be expected that global climate change will affect epiphytes primarily during their seedling stage. If tropical wet mountains get drier, as has been predicted and in part already observed (Pounds *et al*., 1999), epiphytes may be the most adversely impacted group (Benzing, 1998; Foster, 2001). We expect many epiphytes to survive only in relatively protected positions within the habitats they occupy now, and possibly to colonize higher elevation sites if such forests are present in an area and if migration is fast enough.

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