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Germination and Establishment of *Tillandsia eizii* (Bromeliaceae) in the Canopy of an Oak Forest in Chiapas, Mexico

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ABSTRACT

We assessed the effectiveness of repopulating the inner canopy and middle canopy of oak trees with seeds and seedlings of the epiphytic bromeliad *Tillandsia eizii.* Canopy germination was 4.7 percent, considerably lower than *in vitro* (92%). Of the tree-germinated seedlings, only 1.5 percent survived 6 mo. In contrast, 9.3 percent of transplanted laboratory seedlings survived 15 mo. To repopulate trees, we recommend transplanting laboratory-grown seedlings, as large as practically possible, to branches in the middle canopy.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: bromeliads; epiphytes; forest canopy; non-timber forest product; reintroduction; seedling survival.

VASCULAR EPIPHYTES CAN CONTRIBUTE MORE THAN 30 PERCENT to the species richness of a tropical florula (reviewed in Wolf & Flamenco 2003). They are significant contributors in biogeochemical cycles and productivity (*e.g.*, Nadkarni 1986, Hofstede *et al.* 1993) and are also an important source of food and habitat for animals (*e.g.*, Nadkarni & Matelson 1989, Benzing 1990).

Tree-dependent epiphytes are threatened by loss, degradation, and fragmentation of the forest. In the Highlands of Mexico, deforestation between 1990 and 2000 proceeded at an alarming average annual rate of 4.8 percent (Cayuela *et al.* 2006). The conversion of oak forest into pine forest (González-Espinosa *et al.* 2001) furthermore reduces epiphytes since oaks are better host trees for epiphytes than pines (Castro-Hernández *et al.* 1999). Compared to trees, the epiphytic life form appears particularly vulnerable to disturbance of the forest (*e.g.*, Hietz & Hietz-Seifert 1995, Padmawathe *et al.* 2004, Wolf 2005). However, some bromeliad species may increase in abundance and contribute greatly to the diversity of disturbed montane forests in Mexico (Hietz *et al.* 2006). In contrast, Krömer and Gradstein (2003) reported that bromeliads were among the most affected by the forest disturbance in Bolivia.

In addition to the reduction and alteration of the habitat, the over-extraction of epiphytes for trade and traditional uses has a deleterious effect on populations. In Mexico, the volume of illicitly traded epiphytes in local markets exceeds legal exports and comprises many species (Flores-Palacios & Valencia-Díaz 2007). In the Highlands of Chiapas, particularly *Tillandsia eizii* L.B. Smith is collected from the wild by local indigenous inhabitants (Beutelspacher 1989, Breedlove & Laughlin 1993). As a result, in some areas this species has totally disappeared and in most areas it is now rare. Similar patterns have been reported for other bromeliad species in Mexico and Guatemala (Schippmann & Zizka 1994 in Hietz *et al.* 2002).

The recovery of epiphyte populations may be promoted by sparing large remnant 'rescue' trees during logging which would boost local recruitment (Wolf 2005). In the present study, we address another possibility: the manual repopulation of trees. Trees may be repopulated with seeds, seedlings, or adult plants. The reintroduction of seeds or seedlings offers possibilities to incorporate many genotypes. It has been noted that the introduction of few adults may be less effective since it does not restore genetic variation (Oostermeijer *et al.* 2003). The aim of this study is to compare the effectiveness of repopulating host trees with seeds, with that of transplanting seedlings. Since canopy position may influence the performance in terms of germination and survivorship (Winkler *et al.* 2005), germination and seedling survival were studied at inner and middle positions within the treecrown.

METHODS

STUDY AREA.—The study was conducted in the 136-ha protected area 'Reserva Ecologica Huitepec' (REH) in Chiapas, Southern Mexico (16°44′38″ N, 92°40′15″ W; 2230 m asl). The dominant vegetation type is oak forest (*sensu* Breedlove 1981). Tree species include *Quercus rugosa*, *Q. laurina*, and *Q. crassifolia* (Ramírez-Marcial *et al.* 1998). Mean annual temperature is 14–15°C and mean annual precipitation is 1057 mm (May–October: 933 mm and November–April: 125 mm; Comisión Nacional del Agua, pers. comm.).

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STUDY SPECIES.—*Tillandsia eizii* is distributed between 1200 and 2400 m altitude in Chiapas (Mexico) and Guatemala (Smith & Downs 1977, Utley 1994). Oak trees are colonized in larger quantities than pines (Castro-Hernández *et al.* 1999, pers. obs.). Individual plants can have a pendent inflorescence of 1.5 m and leaves of 50–70 cm in length (Smith & Downs 1977). Interestingly, we observed that individual monocarpic rosettes of *T. eizii* (genets) only rarely produce side shoots (ramets). This makes the species particularly vulnerable to the removal of the inflorescence. The inflorescence starts to develop in November and flowers between March and April; the seeds mature in about 11 mo and are wind dispersed at the end of the dry season. A single inflorescence of *T. eizii* with 28 spikes produces 61,370 seeds (± 9580; mean ± 1 SE; $N = 3$).

GERMINATION ON HOST TREES.—Seeds of eight *T. eizii* individuals were collected from a forest near to REH and pooled. To evaluate seed germination *in vitro*, ten seeds were placed in six closed Petri dishes (60 seeds) with filter paper under natural light conditions, frequently sprayed with distilled water, and kept at 19.5 ± 1.7°C. Germination was recorded when the hypocotyl reached about 0.5 mm and weekly for 2 mo.

Seed germination *in situ* was investigated in the rainy season (August). To evaluate the effect of the position within the canopy on seed germination, five *Q. rugosa* canopy trees were selected at REH. On each tree, five branches were sown with 60 seeds equally divided over two different positions, using a total of 1500 seeds. One position was the inner canopy near to the trunk, and the other was 2 m toward the canopy exterior, *i.e.*, in the middle canopy. To reduce environmental variation, we selected trees close to each other and branches of similar diameter (5–20 cm) and inclination (0 ± 40°). The seeds were glued to the bark by their plumed appendages using a nontoxic glue (® Resistol 850), following Benzing (1978). A preliminary test indicated no negative effect of the glue on germination. Seeds were placed at 1 cm from each other. Germination was recorded after 3, 5, 7, and 10 mo. Tree canopies were accessed using single rope climbing techniques (Mitchell *et al.* 2002).

The effect of the position within the tree canopy on the proportion of germinated seeds was analyzed with a general linear model with the position as a fixed factor and the tree as a random factor (Quinn & Keough 2002). The proportion of germinated seeds was transformed with the Box–Cox transformation procedure in order to normalize the residuals (Crawley 2002).

SEEDLING SURVIVORSHIP AND GROWTH ON HOST TREES.—To quantify the survivorship and growth of seedlings in the canopy, seeds from the same pool as in the *in situ* germination experiment were germinated on wet filter paper in closed Petri dishes. Fungicide ('Captan'® Bayer 0.03 g/l) was applied once to the seedlings at the beginning of the experiment. Seedlings were grown under natural light for 6 mo before transplanting to the trees, which occurred toward the end of the rainy season (November 1996). At that time, they were 5.0 mm (± 0.05) in height. On each of six branches in one *Q. rugosa* tree, 70 seedlings were affixed with nontoxic glue, equally divided over two cohorts within the branch, one in the inner canopy and the other in the middle canopy, at an underlying distance of 1 cm. Thus, there were 420 seedlings in total (35 seedlings × two positions × six branches). Survivorship and size were recorded approximately every 2 mo after transplanting and for a total of 15 mo.

To analyze the effect of the position within the tree on seedling survivorship we used the Kaplan–Meier model to estimate the survival rate at 0, 2, 4, 6, 9, 12, and 15 mo after transplanting (Crawley 2002). Next, we compared survival rates between the two positions on the tree with the Log-rank statistic, which assumes a chi-square distribution. The survivorship analyses were carried out using SPSS 13.0 (SPSS Inc. 2004). The final size of the plants was compared between the two positions in the canopy with the Student's *t*-test in MINITAB Statistical Software (version 14.12).

RESULTS

GERMINATION, SURVIVORSHIP AND GROWTH OF *TILLANDSIA EIZII* SEEDLINGS.—Of the 1500 seeds in the canopy, only 71 (4.7%) germinated after 3 mo in comparison with 92 percent germination in the laboratory after 3 weeks. Since germination was first recorded 3 mo after sowing, some seeds that germinated and consequently died may have escaped detection. No newly germinated seeds were observed after 5 and 7 mo, but after 10 mo, at the beginning of the second rainy season, seven more seeds germinated in the middle canopy. The germination rate neither differed between the two positions on the crown (37 seeds germinated in the inner canopy and 34 in the middle canopy; $\mathrm{df} = 1$, $F = 0.10$, $P > 0.05$), nor was it affected by the individual tree ($\mathrm{df} = 4$, $F = 2.5$, $P > 0.05$). Many of the germinated seeds failed to survive and after 10 mo there were only 23 living seedlings; one in the inner canopy and 22 in the middle canopy. Most seeds remained affixed to the branch by the end of the experiment (91 and 80% in the inner and middle canopy, respectively).

In the transplanting experiment, 39 (9.3%) seedlings were alive after 15 mo, mostly in the middle canopy (Fig. 1). During the experiment, 206 (49.1%) of the transplanted seedlings vanished from the branch. These dislodged seedlings were recorded as having died for the purpose of our experiment. Seedling mortality was the highest at the beginning of the experiment. The survivorship probability in the middle canopy was significantly higher than in the inner canopy ($\chi^2 = 6.6$, $\mathrm{df} = 1$, $P = 0.01$). During the first 6 mo there was little growth, but during the following rainy season the plants approximately doubled in size (Fig. 1). Canopy position had no effect on growth after 15 mo ($t = 1.14$, $P = 0.32$).

DISCUSSION

GERMINATION.—The proportion of *T. eizii* seeds that germinated in the canopy (4.7%) was considerably lower than under laboratory conditions (92%). The low *in situ* germination rate is in agreement with that of other *Tillandsia* species. For example, in Florida only *ca*

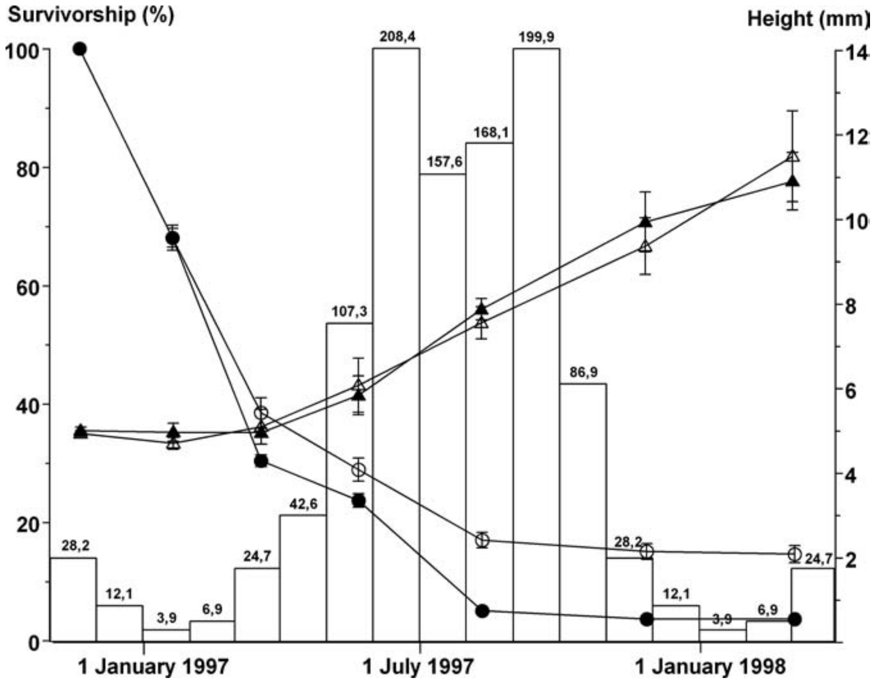

FIGURE 1. The fate of *Tillandsia eizii* seedlings, in terms of survivorship (left axis, circles, mean ± SE) and growth (right axis, triangles, mean ± SE), transplanted to a *Quercus rugosa* tree in an oak forest in southwest Mexico. Seedling survivorship was higher on the six branches in the middle canopy (open symbols) than on those in the inner canopy (closed symbols) ($P = 0.01$). Also given is the average monthly rainfall in millimeters (columns); data from 1978 to 1995, Estación La Cabaña, San Cristóbal de Las Casas (Comisión Nacional del Agua, pers. comm.).

3 percent of *Tillandsia paucifolia* seeds survived the first year after sowing on host trees, despite high germination rates *in vitro* (Benzing 1978). Mondragón *et al.* (2004) report 2–4 percent germination for *T. brachycaulos* in a seasonally dry deciduous forest and Winkler *et al.* (2005) found 0.2–33 percent germination in four *Tillandsia* species in a humid montane forest. Nevertheless, in a pine-oak forest close to our study site nearly all seeded *Tillandsia guatemalensis* seeds (93–100%) germinated (Castro-Hernández *et al.* 1999). In contrast to our study and the studies cited above, these seeds were not sown under exposed conditions but in the understory of the forest where the relative humidity is higher (Freiberg 1997). In addition to species differences, the proportion of germinated seeds is likely to be influenced by the availability of water, which would also explain why a larger proportion of *T. eizii* seeds germinated in the Petri dishes. Germination rates did not differ between the inner canopy and middle canopy, confirming earlier results (Winkler *et al.* 2005). Our results suggest that the water availability in the canopy limits seed germination to the same extent in the inner and middle parts of the crown.

SEEDLING SURVIVORSHIP AND GROWTH.—Low seedling survival rates are commonly found in epiphytes. For example, less than 15 percent of naturally established *Tolumnia variegate* (Orchidaceae) seedlings survived over a 2-yr period (Ackerman *et al.* 1996). For *Dimerandra emarginata*, another orchid, less than 50 percent of the seedlings survived the first dry season after germination (Zotz 1998). In natural populations also, 39 percent of *Tillandsia brachycaulos* seedlings and 34.5 percent of *T. guatemalensis* seedlings survived the first year (Castro-Hernández *et al.* 1999, Mondragón *et al.* 2004). Average survivorship of *Tillandsia* seedlings < 2 cm on oak trees was 67 percent (Hietz 1997). Planted seedlings mostly fare worse. Only 19.4 percent of *T. guatemalensis* seedlings that developed from seed sown on pieces of bark in the understory survived to 7 mo (Castro-Hernández *et al.* 1999). In Florida, survivorship of *T. paucifolia* seedlings in one cohort of 470 seedlings was 30.9 percent after 21 mo and in another cohort of 430 seedlings 25.4 percent after 16 mo (Benzing 1978). Different cohorts of the same species may show different survivorship curves in different places or at different times (Crawley 1997). In our study, *T. eizii* seedling survivorship increased with age of the seedlings (Fig. 1). Increased survivorship with size is commonly observed in plants (*e.g.*, Begon *et al.* 1996) and also in epiphyte populations (Hietz 1997, Mondragón *et al.* 2004, Zotz & Schmidt 2006, Winkler *et al.* 2007).

Seedling growth did not vary with position in the canopy but survivorship was highest in the middle canopy. Seedlings that developed from seeds sown in the canopy showed a similar pattern. Although we made no light measurements, it is likely that the middle canopy receives more photosynthetic active radiation than the inner canopy (Freiberg 1997), which presumably benefits *Tillandsia* seedlings (Hietz 1997). Three other Mexican *Tillandsia* species, growing in a similar forest type, also showed lower seedling mortality on sun-exposed branches in comparison with shaded ones despite the presumed benefit of higher amounts of canopy soil and available water (Winkler *et al.* 2005).

The highest mortality occurred 6–9 mo after transplanting. An initial small reduction in plant size indicates that plants suffered from the transplant, and during the following dry season seedling growth was minimal, irrespective of their position in the canopy. At the advent of the rainy season, seedling growth and survivorship both increased. In the second dry season, the surviving seedlings were well established showing continuous growth and low mortality.

Plant mortality is the combined result of desiccation, herbivory, disease, and dislocation. Although we did not quantitatively separate these factors, we observed that dislodgement affected nearly half of all seedlings. Falling from branches may be an important cause of death for young bromeliads (Hietz 1997, Castro-Hernández *et al.* 1999, Mondragón *et al.* 2004). Animal activity, torrential rains, and high winds may all contribute to the dislodging of young germinated seedlings that have few anchoring roots. A separate cause of epiphyte mortality may be when supporting branches, or parts thereof, fall to the ground. Branchfall in oaks, however, is relatively rare for branches with a diameter < 12 cm (Hietz 1997).

REPOPULATION OF *TILLANDSIA EIZII*.—We have shown that the transplanting of seedlings is preferred over the seeding of trees due to low *in situ* germination rates. Seedling mortality directly after transplanting was nevertheless high, despite the relatively favorable conditions near the end of the rainy season. Average seedling size in our experiments was 5.0 mm (± 0.05) and, to reduce posttransplant stress, we recommend transplanting closer to the beginning of the rainy season and using larger seedlings. *Tillandsia eizii* seedlings develop slowly after germination, but the initial growth rate may be increased tenfold in tissue culture propagation (Pickens *et al.* 2003). While several bromeliad species are already clonally propagated in tissue culture, this protocol starts of with seeds so that genetic diversity is not lost.

Seedling growth did not vary with position in the canopy but survivorship was highest in the middle canopy. The middle canopy branches that were suitable for transplanting were relatively exposed, comparatively stable (diameter >10 cm), and nearly horizontal. Even though the latter factor was not analyzed, plants on horizontal branches may capture more rainfall and the upper surface may offer better anchoring points. The latter is important since seedling dislodgement was a major cause of mortality. Accordingly, we also recommend testing other, and potentially better, methods of securing seedlings to branches. Finally, we recommend using trees that are well distributed over the reserve to enhance the recovery by reducing dispersal limitation.

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