



UvA-DARE (Digital Academic Repository)

Establishment of epiphytic bromeliads in successional tropical premontane forests in Costa Rica

Cascante Marin, A.; Wolf, J.H.D.; Oostermeijer, J.G.B.; den Nijs, J.C.M.

Published in:
Biotropica

DOI:
[10.1111/j.1744-7429.2008.00403.x](https://doi.org/10.1111/j.1744-7429.2008.00403.x)

[Link to publication](#)

Citation for published version (APA):

Cascante Marin, A., Wolf, J. H. D., Oostermeijer, J. G. B., & den Nijs, J. C. M. (2008). Establishment of epiphytic bromeliads in successional tropical premontane forests in Costa Rica. *Biotropica*, 40(4), 441-448.
<https://doi.org/10.1111/j.1744-7429.2008.00403.x>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.



Establishment of Epiphytic Bromeliads in Successional Tropical Premontane Forests in Costa Rica

Alfredo Cascante Marín¹, Jan H. D. Wolf, J. Gerard B. Oostermeijer, and Joannes C. M. den Nijs

Institute for Biodiversity and Ecosystem Dynamics (IBED), Universiteit van Amsterdam, Kruislaan 318, NL-1098 SM Amsterdam, The Netherlands

ABSTRACT

Plant community composition is the combined result of species-specific competitive abilities and the availability of propagules. For epiphytic plants, current hypotheses consider that dispersal-related factors are most important. By controlling seed dispersal constraints, we experimentally examined whether the community composition of epiphytic bromeliads in a tropical premontane area is determined during early phases of seedling recruitment. Also, we tested whether establishment success was related to eco-physiological traits of the species. A total of 7200 seeds were artificially affixed on several host trees in two secondary forest patches and in a mature forest stand. Four bromeliad species with differing physiological characteristics (CAM, C₃-CAM, and C₃) and habitat preference (secondary vs. primary forest) were selected. We found that differences in seed germination probability among habitats and species were not likely to influence community assembly. After 2 yr, seedling survival and plant development were relatively higher in the early-successional forest. Seedling establishment success was not associated with specific physiological and morphological adaptations or habitat preference of the studied species. Our results were not consistent with the described community composition and rates of population recruitment of the studied species in the same successional habitats. The results support the hypothesis that chance and historic events related to seed dispersal have an important influence on community assembly of epiphytic plants. In addition, differences in growth rates and reproductive turnover among species are expected to influence the relative abundance and recruitment rates in a particular habitat.

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

Key words: *Catopsis nutans*; colonization; dispersal limitation; forest succession; *Guzmania monostachia*; Monteverde; *Tillandsia fasciculata*; *Weraubia gladioliflora*.

ACCORDING TO RECENT HYPOTHESES ABOUT COMMUNITY ASSEMBLY OF VASCULAR PLANTS, recruitment limitation is more important than competitive differences among species (*i.e.*, the dispersal- vs. niche-assembly perspectives; Hurtt & Pacala 1995, Hubbell 2001). For terrestrial plant communities in different ecosystems, the limited ability of species to recruit in all available favorable sites (*i.e.*, recruitment limitation) is attributed to dispersal (Hubbell *et al.* 1999, reviewed by Turnbull *et al.* 2000, Svenning 2001, Tofts & Silvertown 2002). In epiphytic plant communities, there is controversy over which ecological factors, dispersal or niche specificity, are more important for community composition. From a niche perspective, several studies suggested that the species' ability to exploit the gradient of light exposure and humidity determine the distribution of epiphytic bromeliads in the canopy (*e.g.*, Pittendrigh 1948, Benzing & Renfrow 1971, ter Steege & Cornelissen 1989, van Leeuwarden *et al.* 1990, Freiberg 1996, Cardelús & Watkins 1998, Hietz & Briones 1998, Benzing 2000). For example, these studies showed that species with thick leaves, a dense trichome layer, and crassulacean acid metabolism (CAM) were mostly found in the exposed outer crown. The dispersal perspective (Hubbell 2001) proposes that for ecologically equivalent species, random events during seed dispersal determine the specific community composition. In this regard, several authors attributed a major role to propagule availability and dispersal in determining the colonization success and community assemblage of epiphytic species (*e.g.*, Benzing 1981, Yeaton & Gladstone 1982, Wolf 1994, van Dunné 2001). Ackerman

et al. (1996) reported the influence of seed supply and dispersal on the recruitment levels of *Tolumnia variegata*, an epiphytic orchid. Zotz and Vollrath (2002) argued that dispersal and germination were likely to explain the spatial distribution of some *Tillandsia* and *Vriesea* bromeliad species.

Epiphyte communities in secondary and mature forests differ in their diversity and composition and these differences are presumably related to structural and microclimatic variation of the habitat (Dunn 2000, Barthlott *et al.* 2001, Krömer & Gradstein 2003, Merwin *et al.* 2003, Wolf 2005). Nevertheless, there is little experimental evidence to support that view. Secondary forests undergo a series of structural and microclimatic changes as the habitat succession proceeds toward the more stable conditions of a mature forest (Brown & Lugo 1990). Light and moisture, microclimatic variables considered critical for epiphyte establishment (Benzing 2000), are expected to change along the forest successional stages. Following the niche hypothesis, the epiphyte community in a determined forest successional stage is expected to exhibit adaptations to exploit the prevalent microclimatic conditions, other aspects (seed availability and dispersal) remaining constant.

In a previous study, we found marked differences in the composition of epiphytic bromeliad communities of contiguous secondary and mature premontane forests (Cascante Marín *et al.* 2006a). We suggested that the low recruitment rates and abundance of bromeliads in the mature forest were the result of limited dispersal and seed availability rather than habitat preferences of the species. In this study, we explicitly test whether dispersal and seed availability or habitat specificity determines community assemblages by examining the establishment success of four epiphytic bromeliads in two secondary forests of different age and a mature forest stand.

Received 17 October 2006; revision accepted 31 October 2007.

¹Corresponding author; current address: Departamento de Historia Natural, Museo Nacional de Costa Rica, Apartado Postal 749-1000, San José, Costa Rica; e-mail: hnatural@museocostarica.go.cr

Bromeliads represent an important component of the local diversity (Gentry & Dodson 1987) and biomass (Wolf 2005) of epiphyte communities in several tropical montane forests. CAM in Tillandsioid bromeliads is most frequent among shade-intolerant species and C_3 is mainly found in shade-tolerant species (Medina 1974, Griffiths & Smith 1983). Several bromeliad species constitute an important part of indigenous cultures in tropical American countries (Bennett 2000) and represent a potential source of exotic ornamental plants for the international market. However, habitat destruction and uncontrolled harvesting are threatening many local populations (Wolf & Konings 2001). Secondary forests in tropical regions are increasing (FAO 1993), thus conservation practices designed for the recovery or sustainable use of epiphytic communities in successional forests can benefit from the knowledge of the factors affecting their establishment.

In this experimental study, we artificially sowed seeds of a series of species in field conditions, and thus controlled for the constraints imposed by seed availability and dispersal. We recorded germination and monitored seedling survivorship and development over a 2-yr period. We specifically tested: (1) whether germination rates and seedling establishment of epiphytic bromeliads is related to the forest successional stage; (2) whether establishment success is related to specific morphological and physiological characteristics of the species regarding the general microclimatic conditions at each habitat; and (3) whether establishment success correlates with existing population abundance and species presence in the studied secondary and mature forest.

METHODS

STUDY SITE AND SPECIES.—The upper watershed of the San Luis River Valley is located on the Pacific slope of the Tilarán mountain range in the Monteverde area, Province of Puntarenas, Costa Rica (10°17'10" N, 84°47'40" W), at 1100 m asl. The forest is seasonal and classified as premontane wet forest, according to Holdridge's Life Zone System (Haber 2000). Average annual rainfall is 3282 (\pm 489) mm and nearly 80 percent of the vertical rainfall is collected from May to November. Annual temperature fluctuates between 17°C and 25°C (Records from the Ecological San Luis and Research Station).

We chose four species of epiphytic bromeliads in the subfamily Tillandsioideae with putatively different physiologies and morphologies and a wide range of geographic distribution, from South Florida and Mexico to Colombia, Ecuador, and Brazil and some Caribbean islands (Smith & Downs 1977). *Catopsis nutans* (Sw.) Griseb. has C_3 photosynthesis and thin leaves sparsely covered by trichomes; *Guzmania monostachia* (L.) Rusby ex Mez is facultatively C_3 -CAM and has thin leaves with a moderate trichome layer; *Tillandsia fasciculata* Sw. has CAM and thick leaves covered by a dense trichome layer (Benzing & Renfrow 1971, Medina & Throughton 1974, Martin 1994, Benzing 2000), and *Werauhia gladioliflora* (H. Wendl.) J. R. Grant likely has C_3 and has thin leaves and a sparse trichome layer. All species have a moderate to well-developed phytotelm and small seeds with a hairy appendage or coma adapted for anemochory (Smith & Downs 1977). Disper-

sal at the study site occurs during the dry season, from February through April (A. Cascante, pers. obs.).

FOREST SUCCESSIONAL STAGES.—We selected three forest areas of different successional stages located within a radius of 700 m: early-successional, late-successional, and mature forest. The early-successional vegetation is an abandoned pasture, 8–12 yr, and ca 3 ha with a scattered vegetation cover composed of a herbaceous understory beneath a low canopy, 5.5–6.0 m tall, where *Acnistus arborescens* (Solanaceae), *Psidium guajava* (Myrtaceae), and *Sapium glandulosum* (Euphorbiaceae) are the predominant trees. *Guzmania monostachia* and *C. nutans* are the dominant bromeliad species, with high recruitment rates, whereas the *T. fasciculata* population is mainly composed of juvenile plants. The late-successional vegetation patch is an abandoned shaded coffee plantation, 35–40 yr, and ca 1 ha in size. The understory contains a.o. *Heliconia* sp. (Heliconiaceae) and shrubs and treelets of *Hamelia patens* and *Randia calycosa* (Rubiaceae), while the canopy, 12–16 m tall, is dominated by *Beilshmiadia brenesii* (Lauraceae), *Cordia eriostigma* (Boraginaceae), *Dendropanax arboreus* (Araliaceae), *Hasseltia floribunda* (Flacourtiaceae), and *Lonchocarpus oliganthus* (Fabaceae) trees. This area is also dominated by the aforementioned bromeliad species and additionally comprises *T. tricolor*. The mature forest is over 100-yr old, ca 20 ha fragment surrounded by pastures and secondary vegetation. The understory and subcanopy is well developed. Characteristic canopy trees, 18–22 m tall, are *Billia colombiana* (Hippocastanaceae), *Exothea glabra* (Sapindaceae), *Diospyros conzatii* (Ebenaceae), *Ficus pertusa* and *F. tuerckheimii* (Moraceae), *Nectandra salicina* (Lauraceae), *Ormosia cruenta* (Fabaceae), and *Sideroxylum stenospermum* (Sapotaceae). *Tillandsia fasciculata* and *T. tricolor* are the dominant bromeliads there, but exhibit low rates of recruitment, whereas the populations of *G. monostachia* and *C. nutans* are much reduced. *Werauhia gladioliflora* does not occur at any of the studied forest sites, but is present at scattered early- to late-successional locations in the surroundings. Hereafter, the studied species are referred to by their genus name.

EXPERIMENTAL DESIGN.—We collected all seeds from five to seven fruits from each of 10–15 individual plants per bromeliad species. Seeds were collected from multiple successional forests in the area during February and March 2002. The seeds of each species were pooled to avoid maternal effects on germination and survival. We selected six host-trees within each successional forest stage based on accessibility, either by using an aluminum ladder or single-rope climbing techniques (Perry 1978a), and randomly regarding tree species identity. On each tree, we established eight rectangular quadrats, 100–140 cm², on the main trunk or on a large branch in the inner crown. If present, we removed all vascular plants from the quadrats. Since the presence of bryophytes and lichens on the bark is suggested to influence the establishment of vascular epiphytes (Nadkarni 2000), we included this variable in our experiment. Two substrate types were defined: (a) presence of a natural bryophyte and lichen cover; and (b) absence of it, either by selecting a naturally bare area or by manually removing the bryophytes and lichens. In total, we had four quadrats with bryophytes and lichens and four bare per tree.

During the end of April and early May 2002, 50 randomly selected seeds from each species were manually affixed on each quadrat by gluing their coma to the bark surface with a small droplet of nontoxic transparent glue (Resistol®). A total of 7200 seeds from the four study species were distributed among the three forest habitats. A seed was recorded as having germinated when hypocotyl elongation was visible to the naked eye. Germination and seedling survival was recorded monthly during the first year and then at the 18th and 24th month, in the second year. We recorded seedling development at the end of the experiment as: (1) plant size measured as the length of the largest leaf to the nearest 0.5 mm; and (2) number of leaves per plant.

STATISTICAL ANALYSIS.—We modeled the probability of germination and seedling survival after 2 yr using forward stepwise logistic regression (Hosmer & Lemeshow 2000). The explanatory variables of habitat, species, substrate type, and all possible interactions, were selected for the initial inclusion in the model at the $\alpha = 0.05$ level. We arbitrarily selected as reference values of the variable intercepts the following categories: mature forest (habitat), *Guzmania* (species), and absence of bryophytes (substrate type). We used the Hosmer and Lemeshow's goodness-of-fit test to assess the fit of the logistic model to the data. The statistical significance of the parameter estimates was evaluated with a Wald's χ^2 test. We estimated the odds ratios between the model's reference category and the respective categories of the significant parameters and the 95% CI (SAS; SAS Institute Inc. 2001). When the confidence interval includes the value 1, it indicates that the categories compared are similar. In this case, the variable may add information to the overall logistic model but does not make a strong contribution to distinguish between categories.

We described the effect of forest habitat on the survival probabilities of germinated seeds of each bromeliad species over time by using the Kaplan–Meier product-limit function, $S(t)$ (Klein & Moeschberger 1997). The function $S(t)$ measures the survival probability at time t and is calculated as follow: $S(t) = \prod_{t(j) \leq t} (1 - \frac{d_j}{n_j})$, where d_j is the number of individuals that failed in time t and n_j is the number of individuals that entered in that time. The date of sowing represents time = 0. We excluded seeds that disappeared during the first month and of which the germination status was unknown. Our survival data are right-censored because several individuals were alive at the end of the experiment and interval-censored as survival time is known only to occur between the monitoring intervals. Since the Kaplan–Meier product-limit function cannot calculate interval-censored data, we used the endpoint of each interval. Then, we compared the survival curves for each species among forest habitats with the log-rank test, a nonparametric method that follows a χ^2 distribution, with $n - 1$ degrees of freedom ($n =$ number of curves being compared) (Statistica; StatSoft Inc. 2000). The effect of the tree on seed germination rates and seedling survivorship could not be evaluated since this type of analysis does not allow the inclusion of that source of variation in a nested fashion.

We examined the effects of habitat and species on bromeliad growth and leaf number with a multivariate analysis of variance (MANOVA, Statistica; StatSoft Inc. 2000). Substrate was not in-

cluded in the analysis because of missing data. This time, we could not examine the effect of trees within habitats with a nested model because not all replicates contained all species, rendering the design incomplete. Data on seedling size and leaf number were square root and \log_{10} transformed, respectively, in order to increase normality and reduce heteroscedasticity (Zar 1999). We used Tukey's Honest Significant Differences (HSD) test for post hoc comparisons between main factors after detecting significant ANOVAs ($P < 0.05$). Differences among habitats for each species and among species for each habitat were analyzed with Contrast Analyses.

RESULTS

GERMINATION.—Thirteen percent (12.8%) of the experimentally affixed seeds disappeared by the first month's census without knowledge of their germination and were thus eliminated from the data set. The bulk of seed germination, 59.6 percent (3741 seeds), occurred at the onset of the rainy season in May with a few *Werauhia* seeds germinating in the second month. Germination values over habitats and species ranged from 51 to 67 percent (Fig. 1). Our logistic regression of the germination probability indicated a significant effect of habitat ($P = 0.033$), substrate type ($P < 0.001$), species ($P = 0.0027$), and the habitat \times species interaction ($P < 0.001$). The fit of the model to the data was near the acceptance limit (Hosmer & Lemeshow test; $P = 0.048$).

The odds ratio estimates indicated that overall germination probabilities were slightly higher in the mature forest than in the late successional forest (Table 1). Seeds on the substrate with bryophytes and lichens were 1.3 times more likely to germinate than seeds on bare bark. While germination odds for *Catopsis* and *Werauhia* were about 1.2 times higher than for *Guzmania*. However, those general trends were affected by the interaction between species and habitat type (Table 1; Fig. 1).

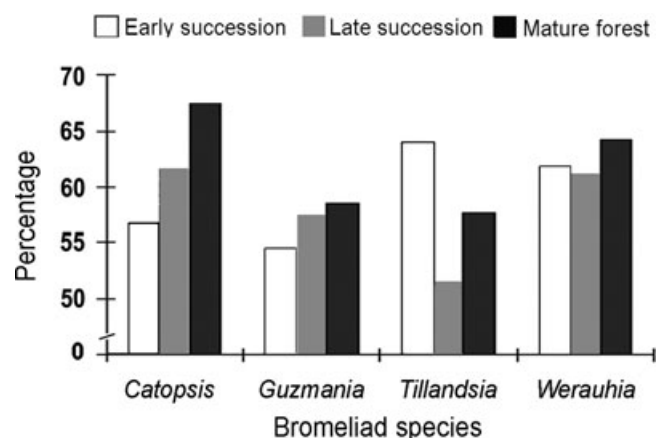


FIGURE 1. Percent germination of epiphytic bromeliad seeds in three successional premontane forests in Costa Rica.

TABLE 1. Parameter estimates of the logistic regression model for seed germination of epiphytic bromeliads in successional premontane forests in Costa Rica.

Parameter	Estimate (SE)	Wald's χ^2 ^a	P-value	Odds ratio ^b	95% CI
Intercept	0.398 (0.026)	235.1	<0.001		
Habitat					
Early succession	-0.019 (0.036)	0.28	0.60	0.90	0.79, 1.02
Late succession	-0.074 (0.037)	4.05	0.04	0.85	0.75, 0.96
Mature forest	0				
Substrate type ^c					
Presence	0.133 (0.026)	26.3	<0.001	1.30	1.18, 1.44
Absence	0				
Species					
<i>Catopsis</i>	0.095 (0.045)	4.35	0.037	1.22	1.06, 1.41
<i>Tillandsia</i>	-0.082 (0.044)	3.46	0.063	1.04	0.91, 1.20
<i>Werauhia</i>	0.108 (0.046)	5.64	0.018	1.26	1.10, 1.46
<i>Guzmania</i>	0				
Habitat × species					
Early succession					
<i>Catopsis</i>	-0.200 (0.062)	10.4	0.001		
<i>Tillandsia</i>	0.281 (0.062)	20.5	<0.001		
<i>Werauhia</i>	-0.007 (0.063)	0.01	0.91		
<i>Guzmania</i>	0				
Late succession					
<i>Catopsis</i>	0.054 (0.064)	0.71	0.40		
<i>Tillandsia</i>	-0.180 (0.062)	8.42	0.004		
<i>Werauhia</i>	0.024 (0.064)	0.14	0.70		
<i>Guzmania</i>	0				

^aThe Wald's χ^2 test evaluates the null-hypothesis about the parameter estimate ($\beta = 0$).

^bOdds ratio estimates compare the parameter category against the reference category.

^cBryophyte and lichen cover.

SEEDLING SURVIVAL.—Fifteen percent (14.8%) of the seedlings from the four bromeliad species survived after the first year and 7.8 percent (290) survived by the end of the second year. The percentage of surviving plants varied between habitats and species, from 1.0 to 17.1 percent (Fig. 2). The logistic regression of the survival probability after two years indicated a significant effect of the forest successional stage ($P < 0.001$; Table 2) and the fit of the model to the data was high (Hosmer & Lemeshow test; $P = 0.99$). The odds ratio estimates indicated that seedling in the early- and late-successional forest had a 3.2 and 1.5 times greater survival compared to the mature forest, respectively (Table 2). Survival probabilities among species were not significantly different.

The survival curves of the four bromeliad species in the three forest habitats showed a steady decrease in the number of surviving seedlings during the first year (Fig. 3). The seedling survival probabilities of each species among forest types were consistently significantly lower in the mature forest and higher in the successional forest habitats, except for *Tillandsia* (Fig. 3). The cumulative survival probabilities per species after the second year ranged from $S = 0.018$ to 0.032 in the early succession, $S = 0.009$ to

0.019 in the late succession, and $S = 0.003$ to 0.027 in the mature forest.

SEEDLING DEVELOPMENT.—Seedling growth, expressed as plant size and number of leaves, was significantly influenced by habitat and species (Table 3; Fig. 4). *Werauhia* and *Catopsis* seedlings were significantly larger in the younger vegetation than in the older forest habitats (Fig. 4A). The size of *Guzmania* and *Tillandsia* was not affected by the habitat. Similarly, with the exception of *Werauhia*, seedlings of the studied bromeliads developed more leaves in the younger forest habitat (Fig. 4B).

Differences among species were greatest in the early- successional habitat (Fig. 4). In that habitat, seedlings of *Werauhia* attained the largest size but developed significantly fewer leaves. Second largest were *Catopsis* and *Guzmania*, and the latter species produced significantly more leaves per rosette. In older forest habitats, *Werauhia* and *Guzmania* had larger seedlings than *Catopsis* and *Tillandsia*. The number of leaves did not differ among species in late successional and mature forest, except for *Werauhia*, which produced fewer leaves in the latter habitat.

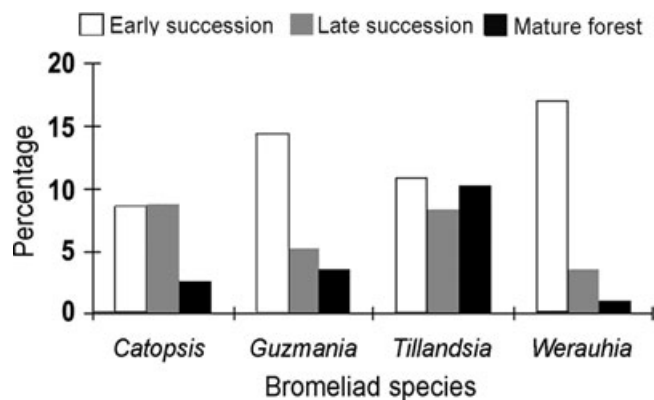


FIGURE 2. Percent survival of epiphytic bromeliad seedlings after 24 mo from germination in three successional premontane forests in Costa Rica.

TABLE 2. Parameter estimates of the logistic regression model for survival of 24-mo-old seedlings of epiphytic bromeliads in successional premontane forests in Costa Rica.

Parameter	Estimate (SE)	Wald's χ^2 ^a	P-value	Odds ratio ^b	95% CI
Intercept	-2.563 (0.065)	1567	< 0.001		
Habitat					
Early succession	0.645 (0.078)	67.7	< 0.001	3.23	2.37, 4.39
Late succession	-0.119 (0.093)	1.65	0.20	1.50	1.06, 2.13
Mature forest	0				

^aThe Wald's χ^2 test evaluates the null hypothesis about the parameter estimate ($\beta = 0$).

^bOdds ratio estimates compare the parameter category against the reference category.

DISCUSSION

The composition of plant communities is the combined result of species-specific competitive interactions, seed availability, and dispersal. The importance of each factor in the establishment of epiphytic communities has been under debate. Our experimental work on the establishment of bromeliad seedlings in various forest types indicates that seed availability and dispersal, and not the species, physiology or morphology, have the strongest effect on the assembly of the studied bromeliad community.

SEED GERMINATION.—The germination probability was greater in mature forest than in late-successional forest but did not differ from that in early-successional forest. We do not have a clear explanation for these differences. Although moisture availability is important for seed germination (Bewley & Black 1994), we believe that at all sites moisture was not a limiting factor because germination occurred

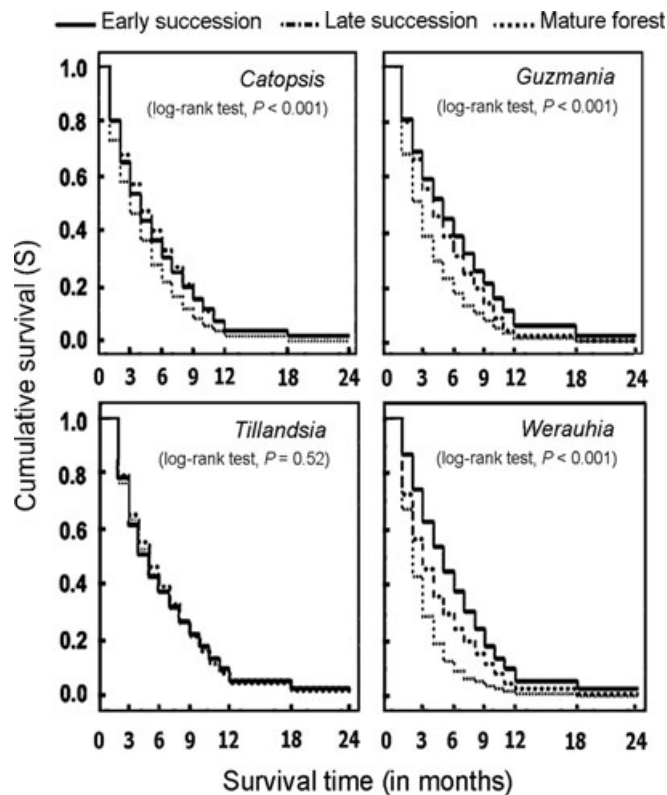


FIGURE 3. Kaplan–Meier survival functions of epiphytic bromeliad seedlings for a period of 24 mo after germination in successional premontane forests in Costa Rica. Statistic values for the comparisons among habitats for each species are indicated.

at the onset of the rainy season. However, we found a positive effect of bryophyte and lichen presence on germination. It has been suggested that lichens and bryophytes facilitate establishment of epiphytes because they retain humidity and nutrients longer than bare bark (Nadkarni 2000). Bryophyte and lichen covers were more developed in the mature forest.

A previous study showed that under natural conditions the seedling density of all studied bromeliad species varied greatly between the successional forest habitats (Cascante Marín *et al.* 2006a). Most species had lower densities in the mature forest compared to secondary forests. In secondary forests, *Guzmania* and *Catopsis* were more abundant than any of the other species. This study shows that these differences among habitats and species may not be explained by differences in germination probability.

SURVIVAL AND SEEDLING DEVELOPMENT.—The early-successional forest canopy was the most favorable habitat for seedling establishment of epiphytic bromeliads, whereas the mature forest was the least favorable (Table 2; Fig. 4). The changes in the number of surviving seedlings from one census to the next were usually associated with the disappearance of the seedlings. Whether this was the result of biotic (*e.g.*, herbivory) or mechanical agents (*e.g.*, wind dislodgement) could not be determined. Some authors have

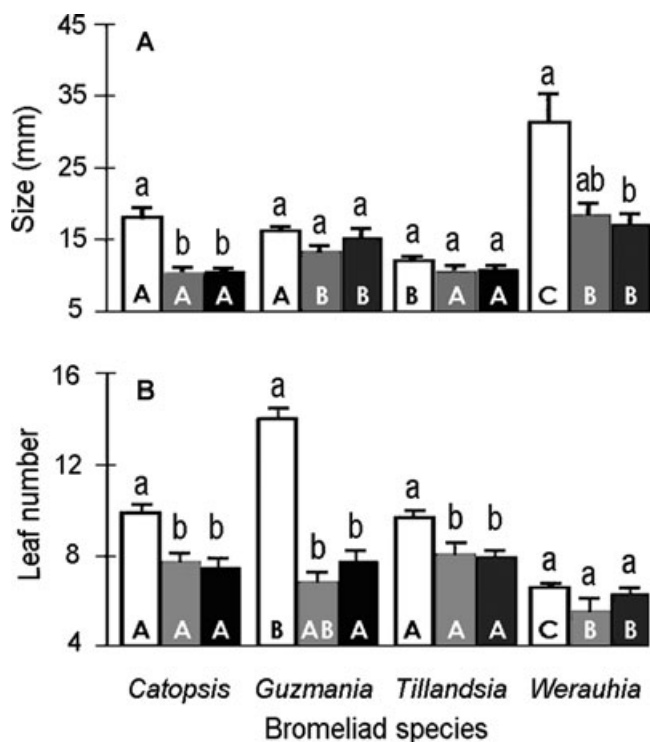


FIGURE 4. The mean (± 1 SE) of (A) plant size and (B) number of leaves of four bromeliads 24 mo post germination in three forest types: early-succession (white columns), late-succession (gray column), and mature forest (black columns). Small letters above columns show differences among habitat for each species and capital letters show differences among species within each habitat after Contrast Analyses.

suggested that dislodgement is the main cause of seedling mortality in epiphytic bromeliads (Bennett 1986, Castro-Hernández *et al.* 1999). Although epiphytic bromeliad roots possess morphological adaptations to facilitate attachment to the substrate (Benzing 2000), it is likely that in early seedling stages the root system is still insufficient for this purpose. The reasons for the higher survivorship of bromeliads in the early- and late-successional forest compared to mature forest are not clear. One possible mechanism is that in the more open younger forests the bromeliads develop an anchoring root system more rapidly. In mature forests, seedling mortality may be higher also due to the larger abundance and diversity of herbivores and arboreal mammals, such as capuchin monkeys, coatis, and porcupines. Their use of trunks and limbs as transit routes could dislodge seeds and seedlings (*sensu* Perry 1978b). Additionally, the taller canopies in mature forests are more exposed to winds, which may also dislodge seeds and seedlings. The gluing that we did probably led to an overestimation of survivorship compared to natural conditions, under which seeds and seedlings do not have that advantage.

Apart from showing a higher survivorship, seedlings in the younger vegetation developed faster. The lower stature of the younger vegetation with its scattered trees and small crowns possibly

TABLE 3. Results of the univariate ANOVAs on the parameters of seedling development (24 mo after germination) of epiphytic bromeliads in successional premontane forests in Costa Rica.

Effect	Seedling size				Number of leaves			
	df	MS	F-ratio	P	df	MS	F-ratio	P
Intercept	1	208.9	6100	< 0.001	1	1276	10,048	< 0.001
Habitat (Hab)	2	0.41	12.0	< 0.001	2	6.88	54.2	< 0.001
Species (Sp)	3	0.44	12.7	< 0.001	3	1.64	12.9	< 0.001
Hab \times Sp	6	0.05	1.49	0.18	6	1.33	10.5	< 0.001
Error	319	0.03			319	0.13		

creates more favorable light conditions for seedling growth. Other studies have shown that seedling establishment may be positively influenced by canopy openness (Winkler *et al.* 2005, Toledo-Aceves & Wolf, in press). Similarly, Fischer and Araujo (1995) suggested that the more shaded conditions under the closed canopy cause the rarity of epiphytic bromeliads in dense canopy forests compared to riparian forests in Brazil. This observation concurs with the frequently reported higher abundance of tillandsioid epiphytic bromeliads in secondary forest habitats (Dunn 2000, Barthlott *et al.* 2001, Cascante Marín *et al.* 2006a). Therefore, we conclude that establishment success of epiphytic bromeliads is significantly influenced by forest successional stage.

NICHE SPECIFICITY VERSUS DISPERSAL LIMITATION DURING COMMUNITY ASSEMBLY.—It has been hypothesized that morphological and physiological traits of epiphytic bromeliads strongly influence establishment (*e.g.*, Pittendrigh 1948, Benzing & Renfrow 1971, Martin 1994, Hietz 1997, Griffiths & Maxwell 1999). Our data suggest that such supposedly eco-physiological adaptations (*e.g.*, metabolic pathway, C₃ vs. CAM) in epiphytic bromeliads do not accurately predict their establishment success and the future community composition. We expected a higher establishment of species adapted to high light exposure and water stress conditions (*i.e.*, CAM species with thicker leaves covered by trichomes) in the younger successional stage because of the greater light and lower humidity typical of these areas. However, our data show that all the studied bromeliads performed better in the younger forest compared to older forest stages. For example, our *Werauhia* species with putative adaptations to mesic conditions, established poorly in the shaded mature forest while establishment was higher in the younger vegetation. In contrast, desiccation-adapted *Tillandsia* showed very similar establishment success among the studied successional forests.

We also expected a positive association between seedling establishment success and the species presence and abundance in the studied secondary and mature forests. In a previous study, we reported that in young- and late-successional forest stages *Guzmania* and *Catopsis* were the most common species with high recruitment levels, and that they were replaced by *Tillandsia* in the mature forest, although with low recruitment, whereas *Werauhia* was absent from the studied forests (Cascante Marín *et al.* 2006a). The data from the present study do not really concur with the observed

patterns of species presence and abundance. Our results indicated that the higher establishment success of *Guzmania* and *Catopsis* in the younger forest matched their high population abundance. Nevertheless, we found that *Tillandsia* showed no differences in establishment between young vegetation and mature forest. In view of the almost complete absence of *Werauhia* in the studied forests, its high establishment success in the younger vegetation is remarkable. A possible explanation for the observed differences between the ability to establish and the population densities of the studied epiphytic bromeliads is that seeds are not dispersed to every suitable place for germination and establishment. The wind-borne seeds of epiphytic bromeliads exhibit relatively short-distance dispersal ranges and they mainly land in the vicinity of the mother plants (García-Franco & Rico-Gray 1998). A small fraction may travel long distances but it is possible that the number of incoming propagules is not enough to overcome the initial high mortality rates during establishment. In addition, the presence and spatial distribution of populations as potential seed sources may affect the composition of epiphytic communities on a regional scale (Wolf 2005). Seed-trapping experiments in the studied forests indicated that inside the mature forest the probability of catching seeds was very low, even for bromeliad species located < 700 m away, while the influx of *Werauhia* seeds into the study site was extremely low (Cascante Marín 2006).

In conclusion, the composition of the studied epiphytic bromeliad communities in our studied successional forests is not the exclusive result of species-specific competitive abilities during the early phases in establishment. Community composition is best understood when dispersal and seed availability are taken into account. A low seed influx into the studied successional forest habitats explains the absence or low abundance of some species. In the mature forest, however, it is difficult to maintain that not enough time has passed for all species to be able to establish. Here, the general low abundance of epiphytic bromeliads may be caused by the shaded conditions in that habitat, which hamper development. Additional differences in generation time (*i.e.*, the time from germination to seed production) among species might also explain the observed differences in abundance and recruitment rates. *Guzmania* exhibited a higher growth rate, seed production, and reproductive turnover compared to *Tillandsia*, which can explain its higher abundance and recruitment rates in secondary forests (Cascante Marín *et al.* 2006b). For conservation purposes, the recovery of epiphytes in successional or degraded habitats can be improved by increasing the numbers of seeds available for germination and further seedling establishment, thus eliminating the constraints to seed dispersal in natural conditions. One method to attain this is to spare large trees with a considerable diversity of epiphytes during logging, as proposed by Wolf (2005). Another is to repopulate trees with seedlings (Toledo-Aceves & Wolf, in press).

ACKNOWLEDGMENTS

We thank the staff of the Ecolodge San Luis and Research Station (UGA) for their logistic support. A. Fuentes and C. Lobo provided

invaluable help during the field experiments. E. Enslow collaborated during the seed planting in the field and R. Solano kindly provided extra climbing gear. This is a project funded by WOTRO, The Netherlands (Grant W85-334), in collaboration with the National Museum of Costa Rica. We acknowledge the valuable comments and suggestions from three anonymous reviewers.

LITERATURE CITED

- ACKERMAN, J. D., A. SABAT, AND J. K. ZIMMERMAN. 1996. Seedling establishment in an epiphytic orchid: An experimental study of seed limitation. *Oecologia* 106: 192–198.
- BARTHLOTT, W., V. SCHMIT-NEUERBURG, J. NIEDER, AND S. ENGWALD. 2001. Diversity and abundance of vascular epiphytes: A comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. *Plant Ecol.* 152: 145–156.
- BENNETT, B. C. 1986. Patchiness, diversity, and abundance relationships of vascular epiphytes. *Selbyana* 9: 70–75.
- BENNETT, B. C. 2000. Ethnobotany of Bromeliaceae. In D. H. Benzing (Ed.). *Bromeliaceae: Profile of an adaptive radiation*, pp. 587–608. Cambridge University Press, Cambridge, UK.
- BENZING, D. H. 1981. Bark surfaces and the origin and maintenance of diversity among angiosperm epiphytes: A hypothesis. *Selbyana* 5: 248–255.
- BENZING, D. H. 2000. *Bromeliaceae: Profile of an adaptive radiation*. Cambridge University Press, Cambridge, UK.
- BENZING, D. H., AND A. RENFROW. 1971. The significance of photosynthetic efficiency to habitat preference and phylogeny among Tillandsioid bromeliads. *Bot. Gaz.* 132: 19–30.
- BEWLEY, J. D., AND M. BLACK. 1994. *Seeds: Physiology of development and germination*, 2nd edition, Plenum Press, New York, New York.
- BROWN, S., AND A. E. LUGO. 1990. Tropical secondary forests. *J. Trop. Ecol.* 6: 1–32.
- CARDELÚS, C., AND J. E. WATKINS JR. 1998. Epiphytic fern diversity and stratification on trunks of *Hyeronima alchorneoides* (Euphorbiaceae) at La Selva Biological Station, Costa Rica. *Selbyana* 19: 270.
- CASCANTE MARÍN, A. 2006. Establishment, reproduction and genetics of epiphytic bromeliad communities during premontane forest succession in Costa Rica. PhD Dissertation. Universiteit van Amsterdam, The Netherlands.
- CASCANTE MARÍN, A., J. H. D. WOLF, J. G. B. OOSTERMEIJER, J. C. M. DEN NIJS, O. SANAHUJA, AND A. DURÁN-APUY. 2006a. Epiphytic bromeliad communities in secondary and mature forest in a tropical premontane area. *Basic Appl. Ecol.* 7: 520–532.
- CASCANTE MARÍN, A., M. DE JONG, E. BORG, J. G. B. OOSTERMEIJER, J. H. D. WOLF, AND J. C. M. DEN NIJS. 2006b. Reproductive strategies and colonization ability of two sympatric epiphytic bromeliads in a tropical premontane area. *Int. J. Plant Sci.* 167: 1187–1195.
- CASTRO-HERNÁNDEZ, J. C., J. H. D. WOLF, J. G. GARCÍA-FRANCO, AND M. GONZÁLEZ-ESPINOZA. 1999. The influence of humidity, nutrients and light on the establishment of the epiphytic bromeliad *Tillandsia guatemalensis* in the highlands of Chiapas, Mexico. *Rev. Biol. Trop.* 47: 763–773.
- DUNN, R. R. 2000. Bromeliad communities in isolated trees and three successional stages of an Andean Cloud Forest in Ecuador. *Selbyana* 21: 137–143.
- FAO. 1993. Summary of the final report of forest resources assessment 1990 for the Tropical World. Paper prepared for the 11th Committee on Forestry (COFO) Meeting. Food and Agriculture Organization for the United Nations, Rome, Italy.
- FISCHER, E. A., AND A. C. ARAUJO. 1995. Spatial organization of a bromeliad community in the Atlantic rainforest, south-eastern Brazil. *J. Trop. Ecol.* 11: 559–567.

- FREIBERG, M. 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. *Biotropica* 28: 345–355.
- GARCIA-FRANCO, J. C., AND V. RICO-GRAY. 1998. Experiments on seed dispersal and deposition patterns of epiphytes—the case of *Tillandsia deppeana* Steudel (Bromeliaceae). *Phytologia* 65: 73–78.
- GENTRY, A. H., AND C. H. DODSON. 1987. Diversity and biogeography of Neotropical vascular epiphytes. *Ann. Mo. Bot. Gard.* 74: 205–233.
- GRIFFITHS, H., AND J. A. C. SMITH. 1983. Photosynthetic pathways in the Bromeliaceae of Trinidad: Relations between life-forms, habitat preference and the occurrence of CAM. *Oecologia* 60: 176–184.
- GRIFFITHS, H., AND K. MAXWELL. 1999. In memory of C. S. Pittendrigh: Does exposure in forest canopies relate to photoprotective strategies in epiphytic bromeliads? *Funct. Ecol.* 13: 15–23.
- HABER, W. A. 2000. Plants and vegetation. In N. M. Nadkarni, and N. T. Wheelwright (Eds.). *Monteverde: Ecology and conservation of a tropical cloud forest*, pp. 39–69. Oxford Press, New York, New York.
- HIETZ, P. 1997. Population dynamics of epiphytes in a Mexican humid montane forest. *J. Ecol.* 85: 767–775.
- HIETZ, P., AND O. BRIONES. 1998. Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. *Oecologia* 114: 305–316.
- HOSMER, D. W., AND S. LEMESHOW. 2000. *Applied logistic regression*, 2nd edition, Wiley, New York, New York.
- HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. *Monographs in population biology* No32. Princeton University Press, Princeton, New Jersey.
- HUBBELL, S. P., R. B. FOSTER, S. T. O'BRIEN, K. E. HARMS, R. CONDIT, B. WECHSLER, S. J. WRIGHT, AND S. LOO DE LAO. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283: 554–557.
- HURT, G. C., AND S. W. PACALA. 1995. The consequences of recruitment limitation: Reconciling chance, history, and competitive differences between plants. *J. Theor. Biol.* 176: 1–12.
- KLEIN, J. P., AND M. L. MOESCHBERGER. 1997. *Survival analysis: Techniques for censored and truncated data*. Springer-Verlag, New York, New York.
- KRÖMER, T., AND S. R. GRADSTEIN. 2003. Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. *Selbyana* 24: 190–195.
- MARTIN, C. E. 1994. Physiological ecology of the Bromeliaceae. *Bot. Rev.* 60: 1–82.
- MEDINA, E. 1974. Dark CO₂ fixation, habitat preference and evolution within the Bromeliaceae. *Evolution* 28: 677–686.
- MEDINA, E., AND J. H. THROUGHTON. 1974. Dark CO₂ fixation and carbon isotope ratio in Bromeliaceae. *Plant Sci. Lett.* 2: 357–362.
- MERWIN, M. C., S. A. RENTMEESTER, AND N. M. NADKARNI. 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. *Biotropica* 35: 37–47.
- NADKARNI, N. M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica* 32: 358–363.
- PERRY, D. R. 1978a. A method of access into the crowns of emergent and canopy trees. *Biotropica* 10: 155–157.
- PERRY, D. R. 1978b. Factors influencing arboreal epiphytic phytosociology in Central America. *Biotropica* 10: 235–237.
- PITTENDRIGH, C. S. 1948. The bromeliad–*Anopheles* malaria complex in Trinidad. I. The bromeliad flora. *Evolution* 2: 58–89.
- SAS INSTITUTE INC. 2001. *The SAS system for Windows*, version 8.02. SAS Institute Inc., Cary, North Carolina.
- SMITH, L. B., AND R. J. DOWNS. 1977. *Tillandsioideae (Bromeliaceae)*. *Flora Neotropica Monograph* 14, Part 2. Hafner Press, New York, New York.
- STATSOFT, INC. 2000. *STATISTICA for Windows: Computer program manual*. StatSoft Inc., Tulsa, Oklahoma.
- SVENNING, J. C. 2001. Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rain forest (Maquipicuna, Ecuador). *J. Trop. Ecol.* 17: 97–113.
- TER STEEGE, H. J., AND H. C. CORNELISSEN. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica* 21: 331–339.
- TOFTS, R., AND J. SILVERTOWN. 2002. Community assembly from the local species pool: An experimental study using congeneric species pairs. *J. Ecol.* 90: 385–393.
- TOLEDO-ACEVES, R., AND J. H. D. WOLF. 2008. Germination and establishment of *Tillandsia eizii* (Bromeliaceae) in the canopy of an oak forest in Chiapas, Mexico. *Biotropica* doi: 10.1111/j.1744-7429.2007.00344.x.
- TURNBULL, L. A., M. J. CRAWLEY, AND M. REES. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88: 225–238.
- VAN DUNNÉ, H. J. F. 2001. Establishment and development of epiphytes in secondary Neotropical forests. PhD Dissertation. Universiteit van Amsterdam, The Netherlands.
- VAN LEERDAM, A. R., J. ZAGT, AND E. J. VENEKLAAS. 1990. The distribution of epiphyte growth-forms in the canopy of a Colombian cloud-forest. *Vegetatio* 87: 59–71.
- WINKLER, M., K. HÜLBER, AND P. HIETZ. 2005. Effect of canopy position on germination and seedling survival of epiphytic bromeliads in a Mexican humid montane forest. *Ann. Bot.* 95: 1039–1047.
- WOLF, J. H. D. 1994. Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* 112: 15–28.
- WOLF, J. H. D. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *For. Ecol. Manage.* 212: 376–393.
- WOLF, J. H. D., AND C. J. F. KONINGS. 2001. Toward the sustainable harvesting of epiphytic bromeliads: A pilot study from the highlands of Chiapas, Mexico. *Biol. Conserv.* 101: 23–31.
- YEATON, R. I., AND D. E. GLADSTONE. 1982. The pattern of colonization of epiphytes on Calabash trees (*Crescentia alata* HBK) in Guanacaste Province, Costa Rica. *Biotropica* 11: 137–140.
- ZAR, J. H. 1999. *Biostatistical analysis*, 4th edition, Prentice-Hall Inc., New Jersey.
- ZOTZ, G., AND B. VOLLRATH. 2002. Substrate preferences of epiphytic bromeliads: An experimental approach. *Acta Oecologica* 23: 99–102.