Do Growth and Survival of Aerial Roots Limit the Vertical Distribution of Hemiepiphytic Aroids?[1]

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ABSTRACT

We tested the hypothesis that growth and survival of aerial roots impose a limit on the height at which a primary hemiepiphyte can become successfully established within tree crowns and evaluate the implications for the vertical distribution of hemiepiphytes in the forest canopy. Density and spatial distribution, and growth and survival of aerial roots were studied in two common species of hemiepiphytic Araceae, *Philodendron radiatum* and *Anthurium clavigerum*, in a lowland tropical moist forest in Panama between March and October 2001. Additionally, root growth and survival were studied both in normal, unmanipulated, and experimentally cut roots to investigate the effect of damage on root resprouting and survival. Survival analysis revealed much greater survival of aerial roots of *A. clavigerum* than *P. radiatum*. In contrast, growth rates in the latter were on average about three times higher when compared to *A. clavigerum*. In both species, experimental cutting of the root invariably led initially to the development of dieback symptoms; however, plants responded to root damage by producing resprouts. A risk model for the two species suggests that only the fastest-growing roots of *P. radiatum* are likely to survive long enough to reach the soil from a host branch 6.8 m high, which equals the mean height of occurrence observed for the epiphytic stage of this species at our study site. In contrast, slow-growing appressed aerial roots of *A. clavigerum* may never be able to establish a connection with the soil from similar heights in the canopy before roots die. Consistent with our hypothesis, *A. clavigerum* is found much lower in the forest (it rarely exceeds *ca* 5 m).

RESUMEN

Probamos la hipótesis que el crecimiento y la sobrevivencia de raíces aéreas imponen un límite en la altura en que una hemiepífita primaria puede establecerse con éxito dentro de la copa de los árboles, y evaluamos las implicaciones para la distribución vertical de hemiepífitas en el dosel del bosque. La densidad y la distribución espacial y el crecimiento y la sobrevivencia de raíces aéreas fueron estudiados en dos especies comunes de hemiepífitas de la familia Araceae, *Philodendron radiatum* e *Anthurium clavigerum*, en un bosque húmedo tropical en Panamá entre Marzo y Octubre del 2001. Adicionalmente, el crecimiento y sobrevivencia de las raíces se estudió en raíces normales sin manipular y raíces cortadas experimentalmente para investigar el efecto de daño en la punta de crecimiento y sobrevivencia de raíces. El análisis de sobrevivencia reveló que hay una mayor sobrevivencia en las raíces aéreas de *A. clavigerum* que en *P. radiatum*. En contraste, las tasas de crecimiento en esta última fueron en promedio casi tres veces más altas comparado con *A. clavigerum*. En ambas especies, el corte experimental de la raíz invariablemente conllevó al principio al desarrollo de síntomas de "dieback", sin embargo las plantas respondieron al daño de la raíz, produciendo nuevas puntas de crecimiento. Un modelo de riesgo para las dos especies sugiere que solamente las raíces de crecimiento rápido de *P. radiatum* probablemente sobrevivan un tiempo suficientemente para alcanzar el suelo desde una rama hospedadora a 6.8 m de altura, la cual iguala la altura promedia de ocurrencia observada, para la etapa epífitica de esta especie en nuestro área de estudio. En contraste, debido al crecimiento lento de las raíces aéreas de *A. clavigerum*, probablemente esta nunca sea capaz de establecer una conección con el suelo desde alturas similares en el dosel antes de que las raíces mueran. Consistente con nuestra hipótesis, *A. clavigerum* se encuentra a una altura menor dentro del bosque (raramente suele ocurrir arriba de *ca* 5 m).

HEMIEPIPHYTES FORM A CONSPICUOUS COMPONENT OF TROPICAL FORESTS and their role in forest structure and dynamics is increasingly acknowledged by ecologists. The life cycle of an hemiepiphyte encompasses both an epiphytic and a terrestrial stage. Primary hemiepiphytes germinate in the canopy and later in their life establish a connection with the

soil by sending roots or shoots to the ground, while secondary hemiepiphytes start as terrestrially established plants that sever all stem connections with the ground after reconnecting to the soil through the production of aerial roots (Putz & Holbrook 1986, Croat 1988, Williams-Linera & Lawton 1995). Primary hemiepiphytes are found in more than 20 plant families (*e.g.*, Moraceae, Clusiaceae, and Araliaceae); the most important families with secondary hemiepiphytes are Araceae, Cyclanthaceae, and Marcgraviaceae (Williams-Linera & Lawton 1995). Our knowledge of the ecology of hemiepiphytes is extremely biased taxonomically. Almost all studies focus on woody hemiepiphytes in the genera *Clusia* and *Ficus* (Putz & Holbrook 1986, 1989; Todzia 1986; Michaloud & Michloud-Pelletier 1987; Ting *et al.* 1987; Clark & Clark 1990; Daniels & Lawton 1991; Putz *et al.* 1995; Holbrook & Putz 1996; Zotz *et al.* 1997; Prósperi *et al.* 2001); studies on other taxa, *e.g.*, Araceae or Araliaceae, are very few (Feild & Dawson 1998, Patiño *et al.* 1999, López-Portillo *et al.* 2000).

Terrestrial and arboreal environments differ profoundly in terms of light, water, and sometimes also nutrient supply (Putz & Holbrook 1986, 1989; Benzing 1990; Williams-Linera & Lawton 1995; Mulkey *et al.* 1996; Zotz & Andrade 2002). Although epiphytic growth in the forest canopy may provide better access to light than in the forest understory, epiphytes must both hold on to their host plants and acquire water from an environment in which it is scarce, relative to the forest floor. In hemiepiphytes, these challenges are met through the development of an adventitious root system including anchor roots for attachment to limbs or trunks of the host and aerial feeder roots that may freely descend to the ground and establish a connection with the soil (Croat 1997). These connections buffer hemiepiphytes from problems of water and nutrient acquisition faced by holoepiphytes (*i.e.,* exclusively epiphytic plants; Williams-Linera & Lawton 1995). In response to a dry environment, hemiepiphytes have developed several morphological and anatomical adaptations (Kapil & Rustagi 1966, Putz & Holbrook 1986). For example, the apices of aerial roots of some species are covered with a gelatinous mucus that is likely to reduce water loss and prevent desiccation of the traveling root (Gill 1969). Other species respond to damage of aerial roots through the production of secondary growing tips (*i.e.,* by resprouting, allowing for continuous growth of the root; Gill 1969, Gill & Tomlinson 1973, Patiño *et al.* 1999).

In spite of the pivotal role that aerial roots play in the life cycle of many hemiepiphytes (Putz *et al.* 1995), patterns of growth and survival of these structures remain largely unexplored. This holds true even for the otherwise well studied strangler figs. Only one study has quantified *in situ* growth and survival of aerial roots in hemiepiphytes in an effort to explain life history strategies in these plants; Patiño *et al.* (1999) compared rates of growth and survival of aerial roots in hemiepiphytes of two families, Clusiaceae and Araceae, in a lower montane tropical moist forest in western Panama. They found significant differences between these families, and reasoned that root-growth strategies may correlate with vertical distribution. Unfortunately, they neither collected data on the actual vertical distribution of their study organisms nor distinguished individual species.

In this paper, we report the results of a survey of two primary hemiepiphyte species (Araceae) in a lowland tropical moist forest in Panama, estimating population densities and their vertical distribution within the forest. Root growth and survival were then studied on a subset of the population both in undamaged and experimentally manipulated, damaged roots. We hypothesized that differences in the rates of growth and survival of aerial roots would constrain the maximum height at which a hemiepiphyte can become successfully established. This idea was tested by developing a risk model that linked our distributional data with the analyses of growth and mortality of aerial roots. As in true epiphytes, mechanisms leading to vertical stratification within the forest may decrease interspecific competition and thus promote the coexistence of these hemiepiphytic species.

MATERIAL AND METHODS

Study site and species.—This study was conducted on Barro Colorado Island (BCI, 9°10′N, 79°51′W), a 1560 ha biological reserve located in Gatun Lake, Republic of Panama. The island is covered with tropical moist forest in several successional stages (Holdridge *et al.* 1971, Croat 1978, Foster & Brokaw 1982). Annual precipitation averages *ca* 2600 mm, with a pronounced dry season during the first months of the year (Windsor 1990, Paton 2001). Based on the beginning and end dates of the Panama Canal watershed dry season as defined by the Meteorological and Hydrological Branch of the Panama Canal Authority (Paton 2001), we defined data from the beginning of the study on 30 March until 26 May as "dry season"

data (rainfall: 26.2 ± 12.5 mm/wk; x ± SE) and those from 27 May until the end of the study on 28 October 2001 as "wet season" data (42.5 ± 3.2 mm/wk).

The two focal species, *Philodendrum radiatum* Schott and *Anthurium clavigerum* Poepp. & Endl., are both large, thick-stemmed (5–12 cm) hemiepiphytes. They are common on BCI, with the former generally occurring higher in the forest (Croat 1978; C. Meyer, pers. obs.). Seeds of both species usually germinate on trees, juvenile plants being wholly epiphytic (Croat 1978, 1997). Aerial feeder roots, which eventually establish a connection with the ground, are cable-like and freely dangling in the former, flat and tightly appressed to the host tree trunk in the latter. Although influential reviews on hemiepiphytism (Putz & Holbrook 1986, Williams-Linera & Lawton 1995) do not mention the occurrence of primary hemiepiphytism in the Araceae (*cf.* Croat 1997), both species clearly belong to this plant group.

Philodendron radiatum ranges from Mexico to South America. In Panama, this species appears to be restricted to the Atlantic slope, where it is known from tropical moist forests in the Canal Zone and Bocas del Toro and from premontane wet forests in Colón (Croat 1978). *Anthurium clavigerum* ranges from Costa Rica to Peru and Brazil. In Panama, it is known to occur in various forest types on both the Atlantic and Pacific slopes (Croat 1978).

Data collection.—To assess the overall abundance of the two hemiepiphyte species, we conducted a population survey along nine of the existing trails traversing sections of both secondary and old-growth forest on BCI. We recorded the number of individuals of each species occurring 6 m to the left and 6 m to the right of a section of *ca* 630 m per trail, the total area surveyed being *ca* 7 ha. The length of the longest leaf including the petiole (LL_{max}) and height of attachment of the stem apex on the host tree were estimated from the ground for each individual plant, with the aid of binoculars whenever necessary, to determine size structure and vertical distribution of the two hemiepiphyte populations. Leaf length, which was a good proxy for total plant dry weight (DW_P, in g) in both species (*P. radiatum*: $\log(DW_P) = -5.85 + 4.07*\log(LL_{max})$, $R^2 = 0.89$, $P < 0.001$, $N = 17$; *A. clavigerum*: $\log(DW_P) = -4.00 + 3.00*\log(LL_{max})$, $R^2 = 0.96$, $P < 0.001$, $N = 12$), was estimated to the nearest 10 cm, height of attachment to the nearest 20 cm in the lower 3 m, and

to the nearest 50 cm higher up. For *P. radiatum*, we noted the number of terrestrial roots per plant. Depending on whether a root connection with the soil was established or not, we could readily distinguish between epiphytic-phase individuals and those rooted in soil. A similar distinction was frequently not possible for *A. clavigerum*, because many roots could not be unambiguously assigned to individual plants. Therefore, we refrained from analyzing epiphytic/soil rooted individuals separately in this species. For a section of 100 m per transect, we counted the number of potential host trees (*i.e.*, trees or shrubs ≥5 cm diameter at breast height [DBH]; neither species was observed to grow on smaller trees).

For each hemiepiphyte species, we used a subset of the individuals occurring in each transect (*P. radiatum*: 110 plants on 85 host trees; *A. clavigerum*: 85 individuals on 83 host trees) to determine the growth rate of aerial roots and to monitor root survival. We assigned roots to one of three treatments: (1) aerial roots: roots hanging in the air with no firm connection to the ground (*P. radiatum*: $N = 32$; *A. clavigerum*: $N = 27$); (2) terrestrial roots: those rooted in soil (*P. radiatum*: $N = 132$; *A. clavigerum*: $N = 86$); and (3) cut roots: roots that were originally terrestrial and were cut *ca* 1.5 m above the ground (*P. radiatum*: $N = 86$; *A. clavigerum*: $N = 52$). Root tips of aerial and cut roots were marked at the beginning of the study with a tape ring that was placed 5 cm behind the tip. Root growth was determined by repeatedly measuring the distance from tape to root tip. Measurements were taken at approximately weekly intervals during the first two months of the study and once per month thereafter. Survival of roots (= presence of at least one active growing tip) in all three treatments was monitored at approximately biweekly intervals over a period of 212 days from late March until the end of October 2001.

Data analysis.—All statistical tests were performed using NCSS 2001 (Number Cruncher Statistical Systems, Kaysville, Utah). Before using parametric tests, data were tested for normality and homoscedasticity, applying standard transformations if necessary. Nonparametric tests were used whenever these assumptions were not met even after transformation.

We compared the survival of roots between the two species within and among treatments using survival time analysis (Lee 1992, Klein & Moeschberger 1997). The same approach was also used to compare the elapsed time to production of the first

resprout in response to dieback. Survival analysis is the study of the elapsed time between an initiating event (*e.g.*, start of treatment) and a terminal event (*e.g.,* death or resprout production). Data are usually a mixture of complete (terminal event occurred) and censored (terminal event has not occurred) observations. For these analyses, we considered a root as dead when it had completely died off. Survival probabilities were calculated using the nonparametric Kaplan–Meier product-limit estimator. We used log-rank χ^2-tests to test for differences in the survival curves, and thus the hazard rates, between the two species and among the three different treatments. Probability levels for these tests were computed using a randomization procedure as outlined by Edgington (1987); the reported *P*-values are based on 10,000 Monte Carlo samples.

To evaluate whether slow growth or high mortality of aerial roots can limit the height of long-term establishment in the two focal species of aroids, we generated model survival curves by fitting a Weibull probability distribution (Lee 1992) to the survival data. Additionally, for a hypothetical plant growing at a height of 6.8 m (the average height of epiphytic *P. radiatum*) above the ground, we calculated how long it would take for aerial feeding roots to reach the soil. For both undamaged aerial roots and those that resprouted after cutting or dieback, we calculated a mean daily growth rate per root tip for each intercensus interval. Mann–Whitney *U*-tests were performed separately for aerial roots and resprouts to test for differences in growth rates between the dry and the rainy season and to compare growth rates between species. Least squares linear regression was used to assess relationships between variables. Unless stated otherwise, numerical results reported throughout the text are means ± 1 standard error (SE).

RESULTS

POPULATION SURVEY.—Population densities of *P. radiatum* and *A. clavigerum* in the total area surveyed were, respectively, 20 and 17 individuals/ha (*P. radiatum*: 142 individuals on 91 host trees; *A. clavigerum*: 116 individuals on 81 host trees). The proportion of potential host trees that was actually colonized by at least one individual of either species was 1.6 and 0.9 percent, respectively. The size-class distribution for *P. radiatum* was left-skewed with a high proportion of large individuals, while in *A. clavigerum* individuals were spread more evenly among size classes (Fig. 1a). Overall, 13.7 percent
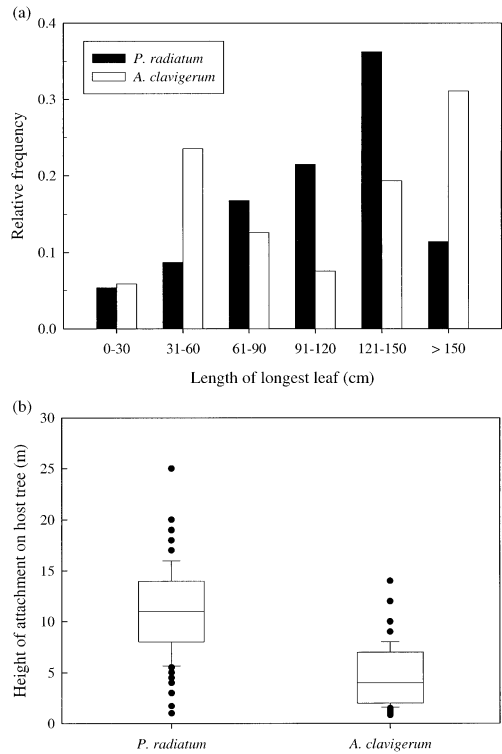

FIGURE 1.   (a) Size-class distribution of the two focal hemiepiphyte populations surveyed on BCI. Plant size was estimated using the length of the longest leaf (including the petiole). (b) Box plots indicating height of attachment on the host tree of 142 individuals of *Philodendron radiatum* and 116 individuals of *Anthurium clavigerum* found in the survey. Given are medians (solid lines), 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers) and outliers (black dots).

of all available host trees were palms, and while *P. radiatum* was frequently observed on larger palms (mostly *Attalea butyracea*), there was no significant association with this particular host tree type (log likelihood ratio *G*-test, $G = 0.33$, df = 1, $P = 0.57$). Host trees of both species were significantly larger (*P. radiatum* 52 ± 7 cm DBH; *A. clavigerum* 25 ± 3 cm DBH) than uncolonized trees (*P. radiatum* and *A. clavigerum*: 13 ± 0.4 cm DBH; Mann–Whitney *U*-test, $P < 0.001$). This preference was, however, much more pronounced in *P. radiatum* than in *A. clavigerum* ($Z = -3.10$, $P = 0.002$). Both species differed significantly with respect to their vertical distribution in the forest. Mean height of attachment on the host tree was 10.9 ± 0.3 m for *P. radiatum* and 4.5 ± 0.3 m for *A. clavigerum* ($Z = -11.27$, $P < 0.001$; Fig. 1b). In *P. radiatum*, when epiphytic and soil-rooted
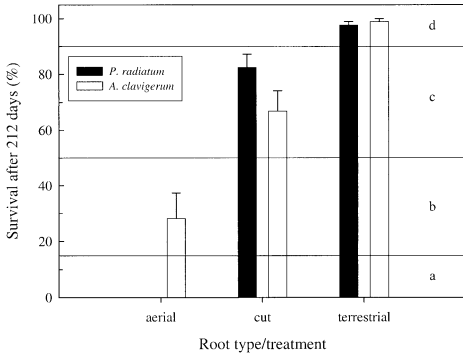
FIGURE 2. Root survival as a function of plant species and treatment. Given are percentages of roots surviving until the end of the study period (212 d). Horizontal line intervals dividing letters a–d indicate significant differences between species and among treatments based on log-rank χ^2-tests.

individuals could be distinguished, epiphytic individuals grew at mean heights of 6.8 ± 0.5 m (N = 34), whereas hemiepiphytic plants grew at significantly greater heights (11.8 ± 0.4 m, N = 101, $Z = -6.06$, $P < 0.001$). There was a significant, positive relationship between height of occurrence on the host tree and plant size (LL_{max}) for both species (*P. radiatum*: $R^2 = 0.22$, $F_{1, 73} = 21.04$, $P < 0.001$; *A. clavigerum*: $R^2 = 0.56$, $F_{1, 52} = 64.97$, $P < 0.001$).

SURVIVAL ANALYSIS.—Survival of aerial roots as inferred from Kaplan–Meier survival analysis was generally greater for *A. clavigerum* than for *P. radiatum* (Fig. 2). There was no apparent seasonality in root mortality for either species (χ^2-test, $P > 0.5$ for both species). While in the latter species none of the marked aerial roots survived until the end of the study period (*i.e.*, up to 212 d), survival of aerial roots in *A. clavigerum* was 28.1 percent (log-rank test, $\chi^2 = 8.93$, df = 1, $P = 0.005$). For cut roots, survival estimates were 82.5 percent and 66.8 percent for *P. radiatum* and *A. clavigerum*, re-

spectively. These differences in survival times were, however, not significant (log-rank test, $\chi^2 = 2.74$, df = 1, $P = 0.1$). Survival of feeder roots was greater when they became firmly rooted in soil (*A. clavigerum*: 97.7%; *P. radiatum*: 98.9%) but did not differ between species (log-rank test, $\chi^2 = 0.42$, df = 1, $P = 0.31$).

In both aroids, there was an overall significant effect of treatment on root survival (*A. clavigerum*: log-rank test, $\chi^2 = 79.66$, df = 2, $P = 0.001$, *P. radiatum*: $\chi^2 = 250.75$, df = 2, $P < 0.001$). Pairwise comparison of survival curves revealed highly significant differences among aerial, cut, and terrestrial roots (log-rank test, $P < 0.001$ for all comparisons; Fig. 2).

Although severed roots invariably desiccated at the cut, a large proportion of them developed resprouts (*i.e.*, a lateral growing tip, adjacent to the cut, effectively resuming root growth; Table 1). In unmanipulated aerial roots, resprouting was observed less frequently and occurred only after dieback of the root tip. Resprout production differed significantly between the two species only for damaged roots.

ROOT GROWTH.—Undamaged aerial roots of *P. radiatum* grew much faster than those of *A. clavigerum* (Fig. 3; Mann–Whitney U-test, $Z = -10.31$, $P < 0.001$). Only for *A. clavigerum* was there a significant effect of season on root growth. In this species, aerial roots grew twice as fast in the rainy (12.5 ± 1.3 mm/d, N = 38) than in the dry season (6.3 ± 0.7 mm/d, N = 67; $Z = 3.87$, $P < 0.001$). The average growth rate over an entire year was calculated as a weighted average, considering that the rainy season lasts about twice as long as the dry season. The difference in average growth rates between *P. radiatum* (29.6 ± 1.3 mm/d) and *A. clavigerum* (9.6 ± 0.6 mm/d) was more than threefold.

In both species, growth rates for resprouts produced after injury were significantly higher than for

TABLE 1. *Differences in resprout production among species and between aerial control and experimentally cut roots (df = 1). Sample size is given in parentheses.*

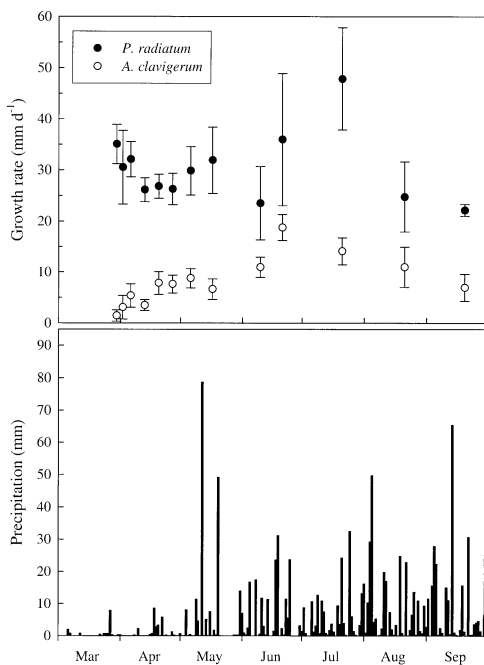| Percent resprouts Treatment	Species		χ^2	P
	Philodendro radiatum	*Anthurium clavigerum*		
Aerial	7.7 (27)	36.9 (22)	0.7	0.41
Cut	87.7 (64)	50.5 (42)	14.36	<0.001
χ^2	19.3	1.39		
P	<0.001	0.24		

FIGURE 3. Mean daily growth rate (±SE) per sampling interval for on average 15 and 8 aerial roots of *Philodendron radiatum* and *Anthurium clavigerum*, respectively (top), and distribution of rainfall events (bottom) during the study period.
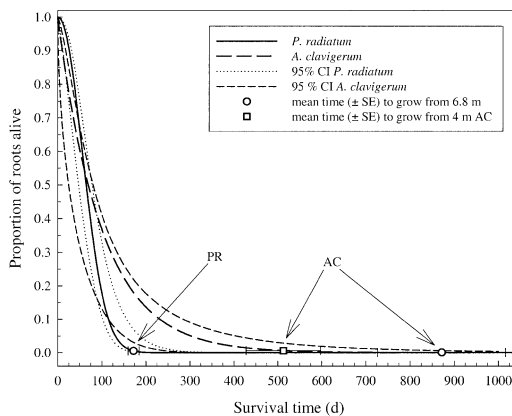

FIGURE 4. Risk model for aerial roots of *Philodendron radiatum* and *Anthurium clavigerum*. Survival curves were obtained by fitting a Weibull probability distribution to the survival data. Also given is the time needed for an aerial root to reach the ground from a 6.8 m height (*i.e.* the mean height of occurrence of epiphytic *P. radiatum*; calculated based on the mean of the 50% fastest growing roots in the population). Additionally, for *A. clavigerum*, the time needed to reach the ground from 4 m, which approximates the mean height of occurrence for this species, is indicated; PR: *P. radiatum*, AC: *A. clavigerum*, CI: confidence interval.

intact aerial roots (*P. radiatum*: $Z = 4.12$, $P < 0.001$; *A. clavigerum*: $Z = 3.59$, $P < 0.001$). As for undamaged aerial roots, resprouts grew substantially faster in *P. radiatum* (39.4 ± 2.1 mm/d, $N = 95$) than in *A. clavigerum* (15.0 ± 1.6 mm/d, $N = 40$; $Z = -6.39$, $P < 0.001$).

For both species, growth rates of aerial roots were independent of plant size as estimated by the length of the longest leaf (*P. radiatum*: $R^2 < 0.01$, $F_{1, 25} = 0.004$, $P = 0.95$; *A. clavigerum*: $R^2 = 0.11$, $F_{1, 15} = 1.88$, $P = 0.19$). In *P. radiatum*, however, root growth was significantly correlated with the number of terrestrial roots: plants that had already established several root connections with the soil exhibited faster growth of aerial roots than those with fewer terrestrial roots (growth rate = $1.5 + 2.7$*number of terrestrial roots; $R^2 = 0.22$, $F_{1, 19} = 5.37$, $P = 0.03$).

RISK MODEL.—Assuming average growth rates, the projected times for aerial roots to reach the soil for plants established at a height of 6.8 m (the average height of epiphytic *P. radiatum*) were 303 ± 121 (95% confidence interval, CI) days in *P. radiatum* compared to 2764 ± 1790 days in the case of *A.*

clavigerum. Hence, roots are invariably expected to die before reaching the ground. Using only the 50 percent fastest roots for the same calculation yielded 172 ± 28 and 872 ± 401 days, respectively. The survival model suggests that only in *P. radiatum* is root growth fast enough to allow at least a small proportion (*ca* 0.5%) of aerial roots to survive long enough to reach the soil. In contrast, despite their much greater survival probability, slow growth in *A. clavigerum* will not allow aerial roots to reach the soil from 6.8 m high during the life expectancy of a root (Fig. 4). Our risk model allowed, however, for successful establishment of rooted individuals of *A. clavigerum* at *ca* 4 m height (*i.e.,* the average height of attachment in that species; Fig. 1b).

DISCUSSION

To date, information on population density, population structure, or other demographic variables is very limited for any hemiepiphyte (Williams-Linera & Lawton 1995), even for rather well studied woody taxa such as strangler figs (Todzia 1986, Michaloud & Michaloud-Pelletier 1987, Putz & Holbrook 1989, Daniels & Lawton 1991). To our knowledge, the present study is the first to provide

such information for hemiepiphytic aroids from a lowland tropical forest. Remarkably, in the forest on Barro Colorado Island, the two species of herbaceous aroids of this study are much more abundant than any co-occurring woody hemiepiphyte. We report densities of 20 and 17 individuals/ha, respectively, while Todzia (1986) never found more than 4 individuals/ha for the 20 woody species she studied in the old-growth forest on BCI.

Similar to previous observations on other hemiepiphytes (Leighton & Leighton 1983, Williams-Linera & Lawton 1995), both species preferentially occurred on larger trees. We expected palms to be frequent host trees because many species of dispersing animals (*e.g.*, bats; Morrison 1978) use them as feeding roosts, or because humus accumulations in leaf bases provide suitable sites for germination and establishment (Putz & Holbrook 1989, Williams-Linera & Lawton 1995); however, although *P. radiatum* was frequently observed growing in the leaf axils of large palms, there was no statistically significant preference for this kind of host tree.

The two species of this study differed significantly in their vertical distribution. Differences in the spatial distribution of (hemi)epiphytes can be caused by a number of factors, *e.g.,* differences in the behavior of dispersal agents (Todzia 1986), differential germination requirements and survival of seedlings (Putz & Holbrook 1986, Todzia 1986, Laman 1993), or differences in ecophysiological traits of adult plants (Griffiths & Smith 1983, Hietz & Briones 1998, Stuntz & Zotz 2001). Our study suggests yet another possible mechanism behind vertical stratification: interspecific differences in the distance that can be bridged by the aerial roots of primary hemiepiphytes. Judging from the outcome of the risk model, only aerial roots of *P. radiatum* should be capable of reaching the ground from a branch in the canopy *ca* 7 m high and hence be able to ensure long-term establishment of the entire plant (Fig. 4). In contrast, much slower growth should not allow *A. clavigerum* to reach the soil from a similar height.

Any analysis of the vertical distribution of species with a climbing growth habit is complicated by possible vertical movements during ontogeny. Plants may move from unsuitable sites to locations with more favorable microenvironmental conditions by the displacement of the apical shoot meristem and the senescence of the trailing stem (Ray 1992). This also creates the possibility to exploit quite different spatial niches during early and later stages of ontogeny. The significant differences in

the height of epiphytic and soil-rooted individuals of *P. radiatum*, along with the positive correlation of plant size and height of attachment in both species, suggest such a shift in height from moist understory to less shaded growing sites. Since the establishment and maintenance of a firm root connection with the soil seems essential for maturation and thus ultimately for the reproduction of hemiepiphytes (*cf.* Putz *et al.* 1995), root growth and survival potentially limit these vertical movements. Thus, irrespective of whether the proposed mechanism prevents epiphytic plants from becoming soil-rooted or it restricts vertical movements of an already soil-rooted plant, the vertical distribution of a given species would inevitably be influenced by its root-growth strategy. Although the significant interspecific differences in the vertical distribution in the forest and the results of our risk model are consistent with our hypothesis, other factors are likely to influence the vertical distribution of primary hemiepiphytes as well, possibly long before root growth comes into play (*e.g.*, germination requirements). Clearly, whether or not root-growth strategies actually limit vertical distributions of primary hemiepiphytes under natural conditions or whether they only constitute a theoretical limitation can only be determined experimentally.

The two species of this study showed pronounced differences in root growth and survival. In *P. radiatum*, fast root growth was associated with high mortality rates while the reverse pattern (low growth rates and comparatively low mortality) was found in *A. clavigerum*. The low mortality in aerial roots of *A. clavigerum* may, at least in part, reflect structural and functional differences in the development of the adventitious root system. *Anthurium clavigerum* features aerial roots, which at the same time serve as feeding roots that descend along the trunk of the host tree and allow for water and mineral uptake (*i.e.*, they do not descend freely to the ground as in *P. radiatum*). These feeding roots may be capable of sufficient water and nutrient uptake to ensure prolonged survival of the root, whereas in *P. radiatum* dangling aerial roots are constantly exposed to dry conditions and consequently more prone to desiccation. Once firmly established in the soil, root mortality is strikingly reduced compared to aerial roots in both species, a finding likely attributable to improved water and/or nutrient acquisition for the plant (Putz & Holbrook 1989). The same effect was also noted by Patiño *et al.* (1999) for aroids in a lower montane tropical moist forest. The results of both studies suggest considerable selection pressure for an individual hemie-

piphyte to establish a connection with the soil as fast as possible.

The mean growth rates of aerial roots found in *P. radiatum* (30 mm/d) and *A. clavigerum* (10 mm/d) were in the range of those found in earlier studies. Went (1895) reported *ca* 20 mm/day for *Philodendron melanochrysum* in the lowlands of Java, and Patiño *et al.* (1999) documented mean growth rates of 23 mm/day for a variety of aroids (*Philodendron* spp., *Monstera* spp., and *Anthurium* spp.) from a lower montane forest in Panama. Patiño *et al.* (1999) also showed that growth rates of aerial roots in the rainy season exceeded those in the dry season two-fold. Given the much lower annual rainfall at our lowland site (2600 vs. 3900 mm at the montane site), we had anticipated lower growth rates and also a strong seasonality in root growth, but only the seasonal differences in growth rates in *A. clavigerum* met these expectations. Mortality showed no seasonality in either species, similar to observations by Patiño *et al.* (1999) for aroids in a lower montane forest.

All hemiepiphytic aroids studied so far (including *P. radiatum*) showed positive root pressure (Fisher *et al.* 1997, López-Portillo *et al.* 2000), allowing for water transport from the grounded roots to the growing aerial roots. This may promote the higher rates of aerial root growth observed in plants that had more grounded feeding roots.

In both of our study species, the growing tip of resprouts attained significantly higher growth rates than originally non-cut aerial roots. We are unable to offer a satisfactory explanation for this unexpected finding. Similar to Patiño *et al.* (1999), we expected manipulated roots to produce more resprouts than undamaged ones since cutting of the root should result in the loss of apical dominance and subsequent development of suppressed buds (Cline 1997). This expectation was only met in *P. radiatum*. Damage-induced resprout production of aerial roots is thought to be an effective survival adaptation and has been observed in a range of hemiepiphyte taxa (various Araceae: Patiño *et al.* 1999; *Clusia*: Gill 1969, Patiño *et al.* 1999; *Ficus*: Gill & Tomlinson 1973). Roots of *A. clavigerum*, which are appressed to the trunk of the host tree, may be less prone to damage by, *e.g.*, falling branches than the dangling aerial roots of *P. radiatum*. This may result in a lower tendency of resprouting in *A. clavigerum* after root damage.

In conclusion, our study lends support to the idea that differences in root-growth strategies, *i.e.*, in growth and survival of aerial roots, influence the vertical distribution of primary hemiepiphytes. Future experimental work should try to assess if differences in germination requirements and ecophysiological properties could serve as alternative or complementary explanations.

ACKNOWLEDGMENTS

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