

Growth and survival of aerial roots of hemiepiphytes in a lower montane tropical moist forest in Panama

SANDRA PATIÑO*§, GREGORY S. GILBERT†§¹, GERHARD ZOTZ‡§²
and MELVIN T. TYREE #§

* *Institute of Ecology and Resource Management, The University of Edinburgh, Darwin Building, Mayfield Road, Edinburgh EH9 3JU, Scotland, UK*

† *Department of Environmental Science, Policy, and Management, 151 Hilgard Hall #3110, University of California, Berkeley, CA 94720, USA*

‡ *University of Vermont, Department of Botany, Burlington VT 05405, USA*

Northeastern Forest Experiment Station, USDA Forest Service, 705 Spear St., P.O. Box 968, Burlington, VT 05402, USA

§ *Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama*

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ABSTRACT. Hemiepiphytic plants grow for part of their life as true epiphytes, then become terrestrial through the production of aerial roots that grow from the canopy to the ground. Long-term measurement of growth, dieback and mortality of aerial roots of hemiepiphytic plants in a lower montane moist tropical forest in western Panama was used to elucidate life-history strategies of hemiepiphytes from two families. The fates of 156 aerial roots of five species of Clusiaceae and Araceae were followed for 10 mo. Some roots were cut to experimentally study the effect of injury on resprouting and survival. Aerial roots of Araceae grew more than twice as fast as those of Clusiaceae but had a much greater mortality rate. Roots of both families grew much faster during the wet than dry season. Even for the fastest growing roots, growth and survival models suggest that only 18% of Araceae roots were likely to survive long enough to reach the ground from a branch 10 m high, whereas 87% of roots of Clusiaceae were likely to do so. This suggests that only those Araceae hemiepiphytes that produce a large number of aerial roots or are located close to the ground are likely to reach the soil.

KEY WORDS: Clusiaceae, Araceae, aerial roots, dieback, Panama

¹ To whom correspondence should be addressed at: University of California, Dept. ESPM, 151 Hilgard Hall #3110, Berkeley, CA 94720, USA. E-mail: ggilbert@nature.berkeley.edu.

² Present address: Lehrstuhl für Botanik II, Universität Würzburg, Mittlerer Dallenbergweg 64, 97082 Würzburg, Germany.

INTRODUCTION

Aerial roots of hemiepiphytic plants are a conspicuous component of wet tropical forests. Hemiepiphytes include both epiphytic and terrestrial stages in their life cycles (see reviews in Croat 1988, Putz & Holbrook 1989, Williams-Linera & Lawton 1995). Primary hemiepiphytes germinate and grow as epiphytes in the tree canopy and later produce aerial roots that descend freely to the ground and connect with the soil. Some species also produce roots tightly appressed to the tree trunk. Primary hemiepiphytes include representatives from 23 dicotyledonous families, including Moraceae, Clusiaceae and Araliaceae. These plants benefit from early growth in a higher light environment than is available on the forest floor. Secondary hemiepiphytes, including the monocotyledonous families Araceae and Cyclanthaceae and one dicot family (Marcgraviaceae) (Williams-Linera & Lawton 1995) begin life on the ground and then grow along tree trunks to become established in the canopy. This group may lose the original connection to the soil, growing as an epiphyte, and later reconnect to the soil through the production of aerial roots. Epiphytic growth may provide an advantage for access to light and sometimes to nutrients (Nadkarni 1984, Putz & Holbrook 1989), but it also decreases water availability and can reduce nutrient availability (Ball *et al.* 1991). Accordingly, although hemiepiphytes are found in a wide range of habitats, they are most abundant in tropical lower and mid-montane environments where forests often are misted by orographic clouds (Gentry 1988).

Primary hemiepiphytes alleviate water stress by making connections to the ground (often 20 m or more below) through the production of aerial roots, which grow downward from the canopy until contacting soil. Such a connection may be crucial to the life-cycle of the plant; for example, hemiepiphytic figs will not reproduce until they are rooted in the soil (Putz *et al.* 1995). Despite the apparent importance of aerial roots, little is known about their ecology – fundamental aspects such as mortality, growth, and respiration in roots have yet to be measured even in better studied hemiepiphytes like strangler figs (Holbrook & Putz 1996). We do know, however, that aerial roots of strangler hemiepiphytes such as *Ficus* and *Clusia* initiate secondary growth upon reaching the ground, producing tension wood that makes them contract (Zimmerman & Hitchcock 1935). Eventually, these woody aerial roots serve as a supportive trunk for the strangler. Herbaceous Araceae, on the other hand, are not capable of this self-support. For support, Araceae in the genera *Monstera*, *Anthurium* and *Philodendron* produce adventitious roots (clinging as well as feeder roots) in each segment, with feeder roots growing down toward the soil (Ray 1992).

To eventually connect a hemiepiphytic plant with the soil, aerial roots must endure a hostile, dry environment not normally encountered by terrestrial roots. In many respects aerial roots are anatomically more similar to stems than to roots (Kapil & Rustagi 1966), but some characteristics normal to roots may be important in helping them cope with that environment. For instance,

some species produce copious quantities of gelatinous slime, which may help protect the roots from desiccation (Gill 1969) or possibly help protect roots from fungal infection (Ivey 1994). Such slime production is common even in terrestrial roots; tomatoes excrete as much as 30% of net fixed carbon from their roots (Lynch & Whipps 1991).

Another potential survival adaptation of aerial roots is the production of resprouts, secondary growing tips of branches. Gill (1969) reported that resprouts coming from aerial roots of *Clusia grisebachiana* in Puerto Rico were consistently associated with injury to the growing tip of the root. Gill also reported that *Clusia* aerial roots grew up to 3 m without injuries, whereas aerial roots of most tree species in the area showed injuries and resprout formation every 4–40 cm. Similarly, aerial roots of the terrestrial fig *Ficus benjamina* (Gill & Tomlinson 1973), of red mangroves (*Rhizophora mangle*) (Gill & Tomlinson 1977, Simberloff *et al.* 1978), and of the tropical vine *Vitis* sp. (Zimmerman & Hitchcock 1935) respond to damage by producing resprouts. However, Kapil & Rustagi (1966) suggest that aerial roots in *F. benghalensis* produce lateral roots without injury, and that this phenomenon is related to seasonality.

In this study, we compared representatives of the two major groups of hemiepiphytes in a lower montane moist tropical forest in western Panama to determine how long it takes for aerial roots to reach the soil, what kinds of impediments they encounter *en route*, and whether the two groups differ in strategies for overcoming these obstacles.

Specifically, we compared the rate of growth, mortality, incidence of dieback, and production of resprouts of aerial roots that freely descend to the ground from woody hemiepiphytes in the Clusiaceae and non-woody hemiepiphytes in the Araceae over a period of 10 mo or more. We conducted experiments to determine the effects of damage to the growing tip. Finally, we combined these analyses into a model of risks to aerial roots to elucidate differences in life-history strategies.

METHODS

Site and species

We conducted the study in the Fortuna Natural Reserve (8°43'N, 82°14'W), Center for Scientific Investigations Jorge L. Araúz, Republic of Panama. The forest of this natural reserve is classified as a lower montane rain forest (1300 m above sea level), with mean annual rainfall of *c.* 3900 mm and a dry season from mid December to late April (Cavelier 1992). For this study we defined the wet season to include dates from the start of the study on 25 May through 15 December (mean rainfall $99.1 \pm \text{SD } 83.1 \text{ mm wk}^{-1}$ in 1994) and the dry season from 16 December to the end of the study on 5 April ($28.3 \pm 21.2 \text{ mm wk}^{-1}$) (see Figure 2 later). Detailed descriptions of vegetation, climate, and soils were reported by Cavelier (1992).

Field measurements were taken on 156 hemiepiphyte aerial roots from plants growing 1.6 to 22 m above ground in crotches or branches of 23 different trees. The hemiepiphyte species included *Clusia stenophylla* and *Clusia* sp. (Clusiaceae), and *Philodendron* sp., *Monstera* sp., and *Anthurium* sp. (Araceae). We selected every hanging root within 5 m to the left and to the right of two transects. It was at times difficult to determine what was an individual of a hemiepiphyte, but at least 14 different *Clusia* individuals, and 16 different Araceae individuals were included in the study. Nine trees contained hemiepiphytes from both families. Height of a subset of the parent plants was measured; for Araceae, plants were 1.6–18.1 m above the ground (mean = $8.7 \pm$ SD 6.5, $n = 9$) and for Clusiaceae 1.9–22 m (mean = $10.6 \pm$ SD 6.9, $n = 13$). Transects began at the clearing of the research station and extended 70 and 116 m inside the forest along pre-existing trails, which hemiepiphytes spread along both transects. We arbitrarily assigned roots to one of three treatments: aerial, terrestrial and cut roots. Aerial roots were those hanging in the air without touching the ground, terrestrial roots descended from the trees and were rooted in the ground, and cut roots originally were aerial or terrestrial that we cut at about 1.3 m from the ground. For aerial and cut roots, we placed a ring of tape around the root 5 cm from the tip. We measured roots weekly for 10 mo, recording the diameter just below the tape ring and the distance from the tip to the tape. There were no growth measurements for the terrestrial roots. We recorded survival weekly for 12 mo, and again after 31.5 mo.

Once we had marked all of the roots along the transects, we climbed the trees using single-rope techniques to determine the hemiepiphyte species to which each root corresponded. Voucher specimens are deposited in the herbarium on Barro Colorado Island, Smithsonian Tropical Research Institute, Republic of Panama. In order to relate seasonal pattern of root growth and mortality to rainfall, we also recorded precipitation at the study site using a pluviometer.

Data analysis

The survival of roots between Araceae and Clusiaceae within treatments was compared using survival data analysis. Survival analysis is designed specifically to compare times to the occurrence of a given event, such as death, among populations of individuals (Lee 1992). Survival analysis specifically accounts for three problems usually associated with analysis of survival times: skewed distributions of survival times, loss of individuals from the study prior to the end of the study for factors external to the study, and survival of the individual past the end of the study. The latter two are types of censoring, or truncation. We tested for differences in survival times between families using the log-rank χ^2 -test of homogeneity between groups of the Kaplan–Meier product-limit survival analyses (Lee 1992) of JMP 3.1 (SAS Institute Inc., Cary, NC). A root was considered alive if the original root or any of its resprouts remained alive. For the analysis we labelled survival times as truncated if the host tree fell over

before the end of the study or if the end of the study was reached before the root died. For aerial roots of Araceae, we also fitted a Weibull generalization of the exponential distribution to the survival curve to predict expected survival times of non-manipulated roots. The Weibull model has the advantage over the exponential distribution in not assuming a constant failure rate over time, and has widespread applications in survival (hazard) analyses (Weibull 1951). Mortality rates of *Clusia* were too low to fit a Weibull model, so we calculated a per-day mortality rate using the compound-interest model given by Campbell & Madden (1990), and modelled survival assuming a constant mortality rate through time.

We used χ^2 analysis to compare seasonal patterns of mortality, dieback and resprouting to seasonal patterns of rainfall. Specifically, comparing the number of deaths, diebacks, or resprouts observed in the wet and dry seasons to the expected number of each of those events, given that the wet season comprised 65% of the study period.

To determine whether roots produced resprouts in response to the loss of the growing tip (through cutting or dieback), we compared the time to production of the first resprout after cutting or dieback of a root tip of aerial roots, using the survival-analysis approach. In survival analyses, statistics can also be calculated based on time to 'failure' – time from the inclusion of an individual into the study until the occurrence of the event of interest (often death or symptom expression). In our study, a root tip 'failed' when it produced its first resprout after cutting or when dieback symptoms appeared. For roots that suffered no damage, the time to first resprout was calculated from the first day of inclusion in the study. Survival time was truncated when the entire root tip died or the end of the study was reached before resprouting occurred. We compared resprout frequencies using the Kaplan–Meier analysis described above (Lee 1992).

To determine the rate of growth of aerial roots, the mean growth per day was calculated for each intercensus interval (*c.* 1 wk) for each growing tip (root or resprout). For each tip we then calculated the mean growth rate for both the wet and dry seasons. Each of these within-growing-tip means served as the experimental unit for further analyses. We tested for differences between families (within season) and between dry and wet seasons (within family) using t-tests for populations with unequal variances. Data were analysed independently for aerial roots, for aerial roots after touching the ground, and for resprouts.

RESULTS

Survival

Roots of Clusiaceae had much greater survival (retaining at least one active growing tip) than those of Araceae (Figure 1). For Clusiaceae, 94% ($n = 17$) of aerial roots survived until the end of the study (up to 314 d) whereas only

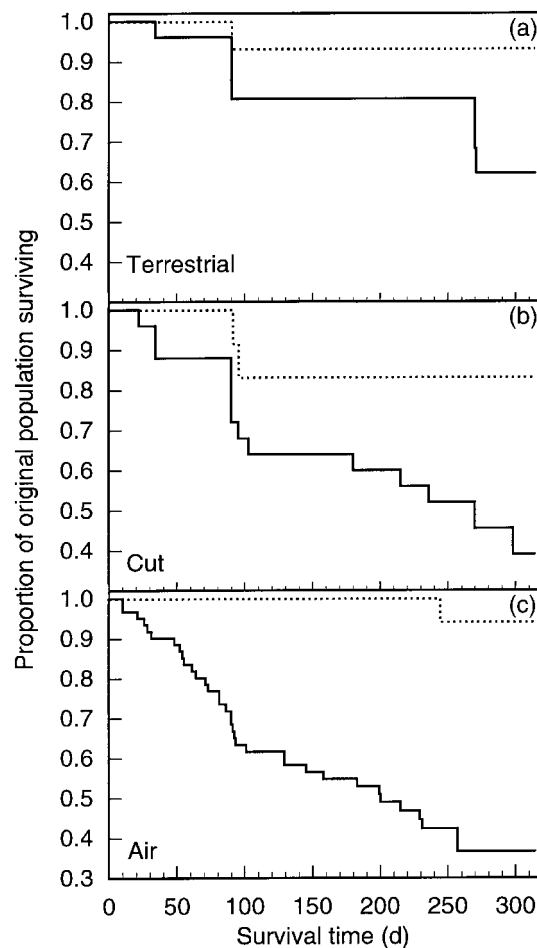


Figure 1. Product-limit (Kaplan–Meier) survival estimates for roots of Araceae (solid line) and Clusiaceae (dotted line) hemiepiphytes, under three treatments: (a) terrestrial – those reaching the ground, (b) cut roots (aerial and terrestrial), and (c) aerial roots (not to ground).

37% ($n = 61$) of the Araceae aerial roots survived (log-rank $\chi^2 = 14.4$, $df = 1$, $P \leq 0.0001$). For cut roots, Clusiaceae had significantly greater survival (83%, $n = 12$) than Araceae (39%, $n = 25$) (log-rank $\chi^2 = 4.9$, $df = 1$, $P \leq 0.03$). Among terrestrial roots there was no statistically significant difference in survival between the two families, although the trend is the same as for cut and aerial roots (Clusiaceae = 93%, $n = 15$; Araceae = 62%, $n = 26$; $\chi^2 = 2.2$, $df = 1$, $P \leq 0.14$).

We then compared root survival among the aerial, cut, and terrestrial roots, separately for each family (Table 1). For Araceae there was an overall significant effect of treatment, and pairwise comparison of survival curves indicated that survival of terrestrial roots was significantly greater than that of aerial roots ($P \leq 0.005$). However, there was no significant difference between cut

Table 1. Percentage of roots surviving until end of study (314 d), and log-rank χ^2 -test (df = 2) for within-family difference among Kaplan–Meier survival curves.

Family	Percent survival (n) of roots			χ^2	P
	Aerial	Cut	Terrestrial		
Araceae	37 (61)	39 (25)	62 (26)	7.92	0.02
Clusiaceae	94 (17)	83 (12)	93 (15)	1.14	0.57

and aerial roots ($P \leq 0.43$) or cut and terrestrial roots ($P \leq 0.06$). For Clusiaceae, survival was high for all three treatments ($\geq 83\%$), with no significant differences among them. There was no apparent seasonality for root mortality for either family (χ^2 -test $P > 0.1$ for all comparisons) (Figure 2).

In January 1997 (954 d from the start of the experiment), we revisited the site and found 88% (aerial), 75% (cut), and 93% (terrestrial) of Clusiaceae

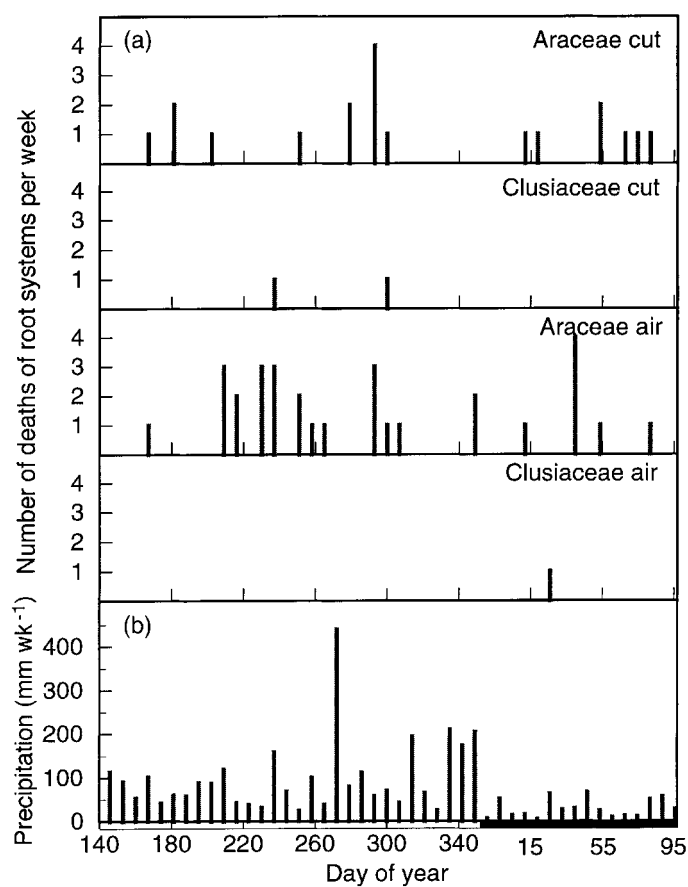


Figure 2. Date of death of cut or non-cut (air) aerial roots for two families of hemiepiphytes (a), and weekly precipitation measure in the laboratory clearing (b). Open and closed boxes at the bottom indicate wet and dry seasons respectively.

Table 2. Percentage of roots of Araceae and Clusiaceae showing dieback symptoms (aerial and cut roots only) and log-rank χ^2 -tests (df = 1).

Family	Treatment	% dieback (n)	χ^2	P
Araceae	Aerial	21 (61)	4.54	0.03
	Cut	44 (25)		
Clusiaceae	Aerial	35 (17)	0.35	0.55
	Cut	25 (12)		

roots still alive (all but four of the 38 live roots were rooted in the soil). By contrast, only 16% (aerial), 12% (cut), and 46% (terrestrial) of roots of Araceae remained alive (all but one of 25 live roots were rooted in the soil).

Dieback

Often, the growing tips of aerial and cut roots died back several centimetres, drying up or rotting away, symptoms classified as dieback. Terrestrial roots could not be observed for assessment. The cause of the dieback was not obvious; pathological studies are planned. In many cases, dieback of the root tip did not lead to the death of the entire root but to the production of resprouts that continued growing. Aerial roots of Araceae and Clusiaceae were equally susceptible to root dieback ($\chi^2 = 1.41$, $P \leq 0.24$) (Table 2). However, only in Araceae did cutting roots lead to a significant increase in dieback – more than double that of control aerial roots (Table 2). Appearance of dieback was not significantly different among seasons (Figure 3; χ^2 -test, $P > 0.2$ for both families).

Resprouts

We hypothesized that roots that lose their growing tips to cutting or dieback will resprout (produce a second growing tip) more often than non-damaged roots. There was no statistically significant induction of resprouting after damage, though there was a tendency toward more resprouts after damage for both families (Araceae, log-rank $\chi^2 = 2.83$, $df = 1$, $P \leq 0.09$; Clusiaceae, log-rank $\chi^2 = 3.56$, $df = 1$, $P \leq 0.06$). Indeed, 73% of damaged Araceae roots produced resprouts compared to only 48% of undamaged aerial roots; for Clusiaceae, 93% (cut or dieback roots) and 78% (undamaged roots) produced resprouts.

A number of roots with no obvious damage produced resprouts. Araceae roots that produced resprouts but remained healthy throughout the study grew significantly slower (mean = 4.6 ± 10.1 mm d⁻¹, $n = 9$) than healthy roots that grew to the ground without producing resprouts (23.3 ± 21.1 mm d⁻¹, $n = 11$) ($t = 2.60$, $df = 15$, $P \leq 0.02$). This may indicate that the resprouting roots suffered from some non-symptomatic or presymptomatic problem, possibly the same one that led to dieback in other roots.

There was no effect of seasonality on resprout production for non-cut aerial roots for either family (Figure 4; χ^2 -test, $P > 0.1$ for both). There was significantly more resprout production in the wet than dry season for cut roots of

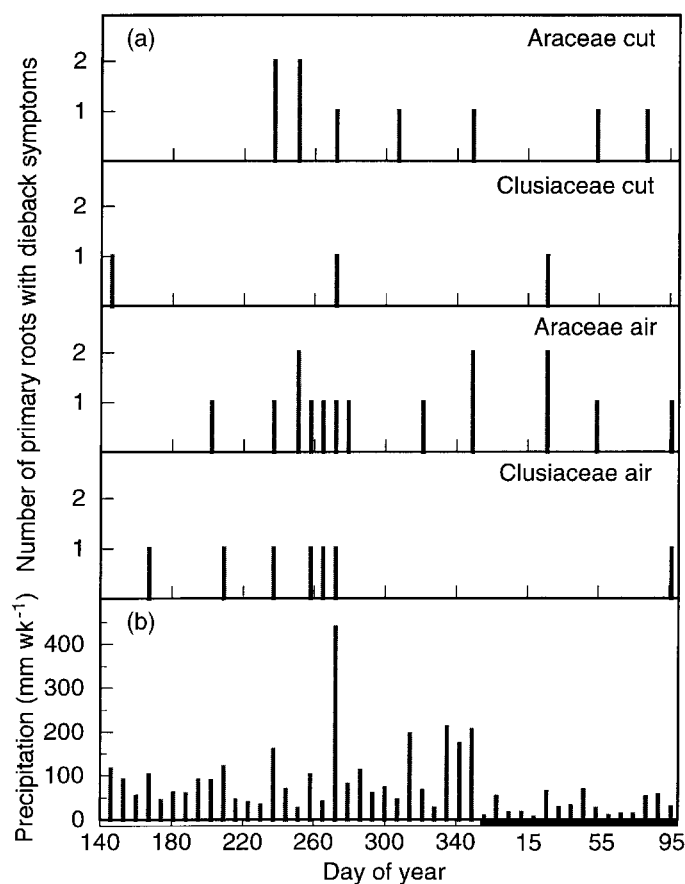


Figure 3. First occurrence of dieback symptoms on primary roots only for cut or non-cut (air) aerial roots (a) for two families of hemiepiphytes (b) precipitation as in Figure 2).

both families (Araceae, $\chi^2 = 8.7$, $df = 1$, $P \leq 0.01$; Clusiaceae, $\chi^2 = 11.9$, $df = 1$, $P \leq 0.01$). However, roots were cut early in the wet season; this is more likely a reflection of the tendency of roots to resprout after damage rather than a true effect of seasonality.

Rate of growth

Rate of growth in the wet season was more than double that in the dry season for both families (Araceae, $t = 2.18$, $df = 114$, $P \leq 0.03$; Clusiaceae, $t = 2.89$, $df = 82$, $P \leq 0.005$) (Figure 5). Roots of Araceae grew nearly twice as fast as those of Clusiaceae (Figure 5), but the difference was significant only in the wet season (wet season, $t = 2.26$, $df = 129$, $P \leq 0.03$; dry season, $t = 1.13$, $df = 57$, $P \leq 0.26$).

The growing tip of resprouts had the same rate of growth as the growing tip of healthy original roots. For Araceae roots in the wet season (the only group with a large enough sample size for analysis), there was no significant difference between the rate of growth of original aerial roots that grew to reach the

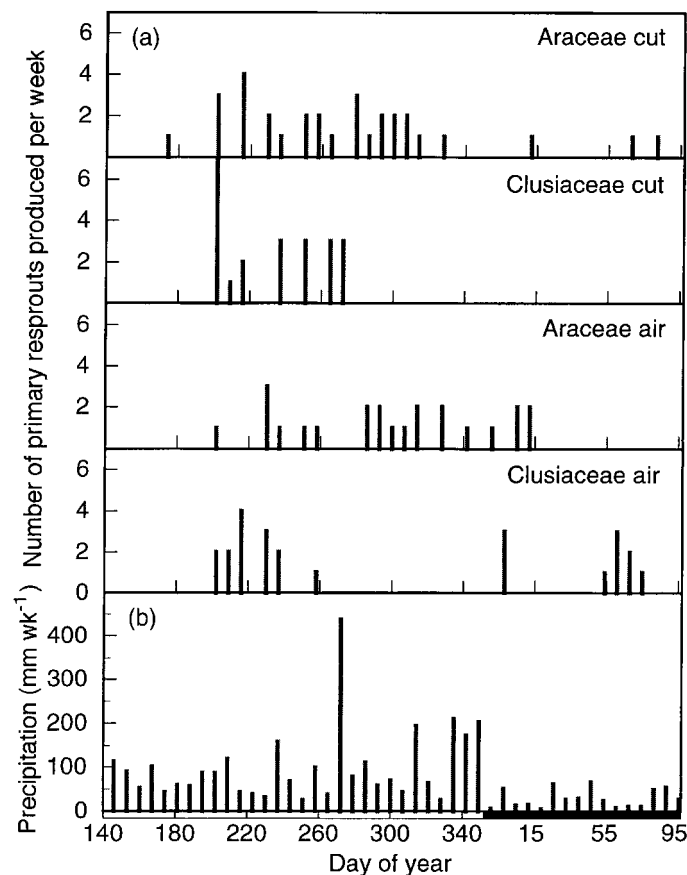


Figure 4. Production of resprouts from primary roots for cut or non-cut (air) aerial roots (a) for two families of hemiepiphytes (b) precipitation as in Figure 2).

soil without resprouting (as mentioned previously, mean = 23 ± 3 21.1 mm d^{-1} , $n = 11$) and resprouts that grew to reach the soil without producing additional resprouts (mean = $20.3 \pm 21.3 \text{ mm d}^{-1}$, $n = 7$) ($t = 0.29$, $df = 16$, $P \leq 0.77$).

The cut root tips showed no biologically significant growth for either family (not significantly different from zero; Araceae, $t = 0.43$, $df = 25$, $P \leq 0.66$; Clusiaceae, $t = 1.28$, $df = 11$, $P \leq 0.23$).

For growing tips (of original roots or resprouts) that grew first in the air and then reached the soil, we performed paired t-tests to compare the rates of growth in the air with growth rates across the surface of the soil. There was no significant difference in growth rates for either Araceae or Clusiaceae in the wet season (the only groups with large enough sample sizes) (Araceae, $t = 1.49$, $df = 9$, $P \leq 0.17$; Clusiaceae, $t = 0.05$, $df = 6$, $P \leq 0.96$).

Risk model

We fitted a Weibull model to the survival data for aerial roots of Araceae. For Clusiaceae, there was insufficient mortality to reliably fit a survival model,

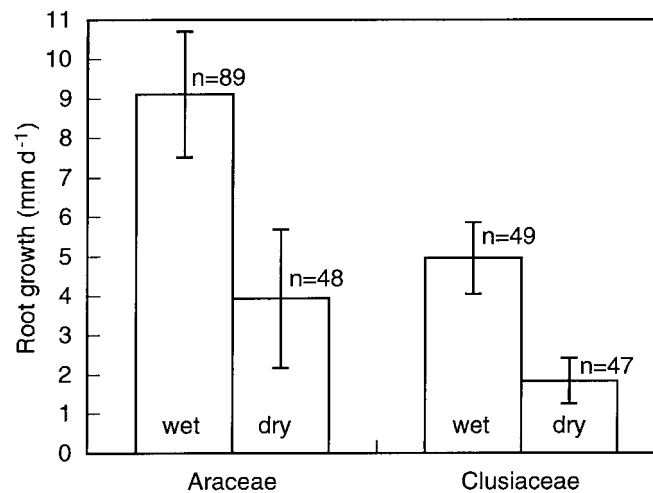


Figure 5. Mean growth rate for growing tips of all roots and resprouts of non-cut aerial roots of hemiepiphytes in the wet and dry seasons (as defined in Figure 2). Bars indicated \pm SE of the mean. Seasonal differences within families are significant ($P = 0.03$), as described in the text.

so we assumed that the observed mortality rate (5.9%) in the first year would remain constant in each successive year. We then took the mean growth rate for roots that grew to the soil without dying back or resprouting (the fastest growing roots in the populations) and calculated the time needed for a root to reach the soil from a branch 10 m above the ground (Figure 6). A fast-growing Araceae root should reach the ground in 1.2 y (452 d), whereas fast-growing *Clusia* roots would take 2.2 y (815 d) provided they are not damaged along the way. However, the much greater survival rates among *Clusia* suggest that 87% of roots should survive long enough to reach the soil; only 18% of Araceae roots are likely to survive the needed time.

DISCUSSION

The much greater mortality rates of aerial roots of Araceae than Clusiaceae hemiepiphytes may reflect different life-history strategies for coping with a heterogeneous environment. The species of Araceae in this study can cope with a locally unfavourable environment by 'migrating' – that is, climbing to more favourable positions in the canopy with older stem parts dying off as the growing part moves into new, more favourable microhabitat (Ray 1992). By contrast, *Clusia* does not climb so it must cope with different microclimatic conditions through physiological plasticity. Many species in this genus show a flexible use of the CAM pathway of photosynthesis (Zotz & Winter 1993); this helps ensure growth and survival, particularly during the vulnerable epiphytic stage. Aerial roots of both families are equally susceptible to pathological dieback, suggesting that the woodiness of the roots of Clusiaceae do not necessarily protect it from damaging attacks. We suggest that the greater mortality in

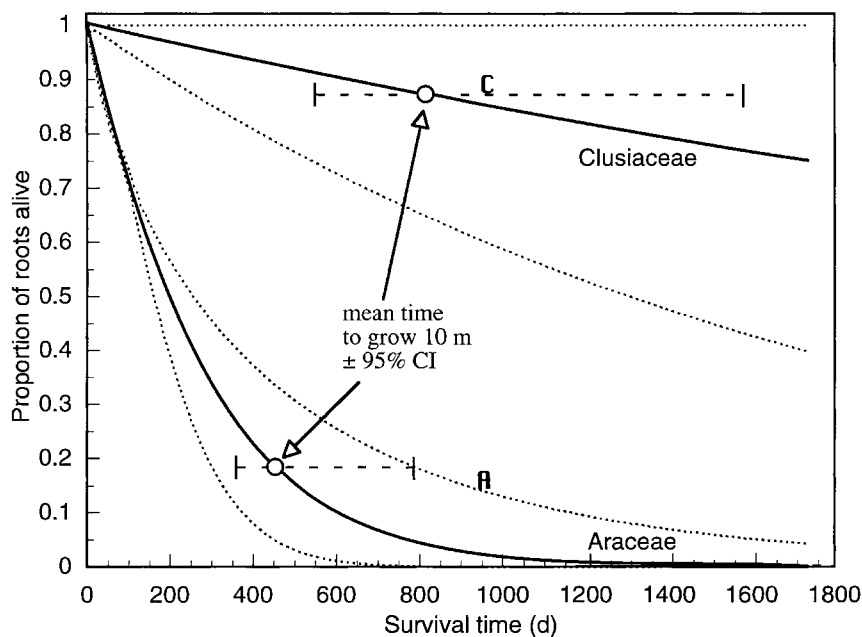


Figure 6. Model survival curves for Araceae and Clusiaceae aerial roots. Solid curves indicate the predicted value from a Weibull model of the survival data (Araceae) or for constant 5.88% annual mortality (Clusiaceae) (dotted curves are upper and lower 95% confidence intervals). Also indicated is the time needed for a root to reach the soil from a branch 10 m high (based on the mean of the fastest growing roots in the population, which were the aerial roots that grew without making resprouts or dying back). We then expected 18% of undamaged Araceae and 87% of undamaged Clusiaceae to survive long enough to reach the soil. Bold capital letters indicate the actual proportion of aerial roots of Clusiaceae (**C**) and Araceae (**A**) surviving to 954 d from the start of the experiment.

aerial roots in Araceae may be related to senescing of older stem parts that did not find adequate water sources or an appropriate light regime while growing portions of the same plant effectively migrate into a new microsite and produce new aerial roots.

Aerial roots of Araceae grow quickly, at 9 mm d^{-1} in the wet season (and more than 20 mm d^{-1} for non-damaged, non-sprouting roots). These rates compare favourably with field measurements of the similarly fast-growing Amazonian apogeotropic roots which grow as much as 19 mm d^{-1} (Sanford 1987), and with *Philodendron* (Araceae) aerial roots growing *c.* 20 mm d^{-1} (Went 1895). In the greenhouse, Araceae roots showed growth rates of 1.3 to 26.8 mm d^{-1} (Linsbauer 1907). The faster root growth in Araceae compared to Clusiaceae is compatible with the different root-growth strategies outlined earlier; Araceae roots must grow quickly to reach the soil before the older portion of the stem becomes senescent. Once roots reach the soil, continued survival of the root (and presumably of the stem section) is much greater than survival of roots still in the air, probably because of increased access to water (Putz & Holbrook 1989). Our results support the suggestion by Williams-Linera & Lawton (1995) that there should be a selection for those hemiepiphyte individuals that most efficiently establish an umbilical connection to the soil.

Roots grew faster in the wet than dry season, suggesting that water stress may limit the growth of aerial roots. Resprouts grew as quickly as the original roots, indicating that resprouting is an efficient mechanism for recovering from damage to the growing tip of a root. This agrees with Linsbauer (1907), who also showed that resprouts of Araceae roots grew as quickly as the original roots. Damage to the growing tip may come from insect attack, infection by microbial pathogens, damage from vertebrate herbivores, or damage from winds and falling branches. Although there was no statistically significant effect of damage on root resprout production, the trend toward resprouting associated with damage to the root tip is consistent with frequent reports of damage-induced lateral root production in aerial roots (Gill 1969; Gill & Tomlinson 1973, 1977; Simberloff *et al.* 1978, Zimmerman & Hitchcock 1935). We did not find a seasonal effect on the production of lateral roots in the absence of injuries, as reported by Kapil & Rustagi (1966). Resprout production in the absence of root injury was associated with greatly reduced growth rates in the original roots, suggesting an otherwise non-symptomatic dysfunction in the growing tip that may be associated with resprout production.

Additional research is needed on other stimuli that may induce resprouts or lateral root formation. It is curious that upon reaching the soil, aerial roots often grew across the soil surface without penetrating the soil or producing lateral roots. Some roots wound across the soil surface for weeks before penetrating the soil. Whether particular soil moisture conditions or other environmental cues are necessary for roots to penetrate is unknown.

Intact roots of both families are equally susceptible to dieback, but cutting roots of Araceae doubled the rate of dieback, whereas in Clusiaceae there was no change in dieback incidence. Removing the root tip of Araceae also removes the slime that covers the root tips; Clusiaceae has no such slime coating. Ivey (1994) showed strong antifungal activity in slime from aerial roots of *Piper* and unidentified roots that probably were from Araceae. Root slime from Araceae roots at the La Selva Biological Station in Costa Rica contained abundant fungal spores, but the spores were not germinated, suggesting antifungal activity in the slime (G. S. Gilbert, *pers. obs.*) One function of the slime may be to protect the growing root tip from fungal infection, as the tip is the site of pathogenic infections in most roots (Mehrotra 1970).

In addition to providing a protective function against fungal attack, slime on Araceae root tips may help provide water to roots by absorbing moisture from the air. Mucilage could extend the moisture-absorbing period available to the root by increasing water-storage capabilities (soaking up water quickly but drying out slowly). Indeed, Darwin (1876) observed that young roots of *Ficus repens* excrete a clear fluid with 'the remarkable property of not soon drying' – that is, remaining fluid for at least 128 d under hot, dry conditions. This clear fluid may have multiple functions, including adhesion, disease defence, hydration, or even increasing the absorptive surface area of an aerial root by prolonging survival of the root hair.

The zone of elongation in aerial roots of both families is much shorter than the 10 to 16 cm reported for prop roots of *Rhizophora mangle* (Gill & Tomlinson 1971). No growth was observed between the tape mark placed 5 cm from the growing tip (see Methods) and another mark 5 cm farther back for any of the roots included in this study (data not shown).

According to the risk model, Araceae hemiepiphytes (compared to *Clusia*) should produce more roots and/or live closer to the ground for aerial roots to have a reasonable success in reaching the ground. Araceae produce more roots than *Clusia* owing largely to their climbing growth habit. It would be interesting to measure vertical stratification in survival or reproductive rates in hemiepiphytes of different root-growth strategies. Also, it might be enlightening to compare the relative energetic costs of producing one or few roots without slime (but perhaps with other costly defences as is the case with Clusiaceae) and producing many slimy, short-lived roots (as for Araceae). The frequency of resprouting, the apparent resiliency to damage, woodiness, and the longevity of roots of Clusiaceae suggest a substantial investment in individual aerial roots compared to the nearly 'disposable' herbaceous roots of Araceae.

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