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LONGEVITY OF FALLEN EPIPHYTES IN A NEOTROPICAL MONTANE FOREST

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Epiphytes, plants that normally live perched on other plants, encounter different conditions than those that prevail on the forest floor. Canopy habitats, unlike forest floor habitats, are usually described as "rigorous" because tree crowns presumably have more limited storage capacity for available nutrients and water, more sporadic and dilute nutrient inputs, less physical stability, and more patchy "safe sites" for establishment (Ackerman and Montalvo 1990, Benzing 1990). Although the vertical distance between canopy and forest floor may be small, the differences between canopy and forest floor microhabitats can be great. In general, the canopy environment is characterized by more extreme fluctuations in moisture supply and temperature, stronger insolation, higher windspeeds, and more severe and variable vapor pressure deficits (e.g., Chacon and Duval 1963, Chazdon and Fetcher 1984). Other differences may include the invertebrate fauna (e.g.,

Nadkarni and Longino 1990) and microbial activities (Vance and Nadkarni 1989), leading to different rates of decomposition and nutrient release (Nadkarni and Matelson 1991). Some of the structural and physiological features that permit epiphytes to thrive in the canopy are absent or very different from those on the forest floor. In fact, the vast majority of epiphytes are obligate, i.e., occur only in the canopy (Kress 1986). The basis for this exclusivity is not known.

The physical movement of live epiphytes from the canopy to the forest floor is a frequent event in epiphyte communities. Live epiphytes fall to the forest floor because they are dislodged by wind or animals or because branches and trees break and fall (Strong 1977). Some epiphytes with poorly developed root systems (e.g., tank bromeliads), tend to fall as individuals. However, live epiphytes in the form of contiguous mats, connected by interwoven root systems and a layer of crown humus (Jenik 1973), often fall intact, as "clumps." The continued association of individual epiphytes with their original canopy organic material may affect the survival of these individuals. The fate of an epiphyte falling as part of an intact mat, in contrast to falling as an individual, may differ because roots imbedded in mats may be less disturbed than the unprotected roots of individual plants. Also, the sponge-like mats retain considerable amounts of water in the absence of drying conditions, which affects the water status of the plants and conditions for associated pathogens and mutualists.

Anecdotal observations of fallen epiphytes include a range of responses: some epiphytes vanish within weeks, while others persist and even thrive for months to even years (N. M. Nadkarni, T. J. Matelson, and A. Pounds, *personal observation*). Apparently, there are diverse factors that allow or limit the survival of epiphytes after they land on the forest floor. If we could understand why certain epiphytes live or die on the ground, we might better understand the nature of epiphytism, the factors that contribute to the widespread occurrence of epiphytic plants (10% of all vascular plants are epiphytic (Kress 1986)), and the relatively low incidence of facultative epiphytism.

The longevity of fallen epiphytes also has implications for ecosystem-level nutrient cycling. Epiphytes derive all or nearly all of their nutrients from non-terrestrial sources, mainly atmospheric nutrients (Benzing 1990, Nadkarni and Matelson 1991). The nutrients in live epiphytes that fall to the ground will ultimately be mineralized and absorbed by terrestrial vegetation. However, their prolonged survival on the ground would delay mineralization, with consequent effects on storage, cycling, and potential loss of nutrients from the ecosystem.

In this paper, we document the longevity of a variety

of fallen epiphytes relative to: (a) light regime (contact forest understory, hereafter "shade," vs. gap), (b) attachment to fallen branch, (c) physical dimensions of the "clump" (defined here as a contiguous epiphyte mat that falls from the canopy), and (d) the number of epiphytes in the clump.

Materials and Methods

Study area. Fieldwork was conducted from 12 May 1989 to 1 March 1991 in the Monteverde Cloud Forest Reserve (MVCFR), a lower montane moist forest in Costa Rica (10°18' N, 84°48' W). The study area (elevation: 1480 m) was in Leeward Cloud Forest (Lawton and Dryer 1980). The annual gross precipitation is ≈ 2000 mm, but actual wet deposition is much higher because of frequent wind-driven mist and fog (Lawton and Dryer 1980). During the dry-windy season (November–April) much of the area intercepts clouds borne on the strong northeast trade winds, resulting in a particularly species-rich cloud forest with complex structure (Hartshorn 1983).

The Monteverde epiphyte flora is extremely diverse and abundant (Nadkarni 1984, 1986). Branch surfaces in the crown interior of nearly all mature trees support epiphytes (bryophytes, herbs, woody shrubs, and hemi-epiphytes) in interwoven root-humus mats up to 25 cm thick. Epiphyte dry mass falls from the canopy throughout the year at a mean rate of $50 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Nadkarni and Matelson 1992). Epiphytes fall in a variety of forms, from individual plant parts to large mats that cover whole branches. The mean standing crop of fallen epiphytic material on the ground is $35 \text{ g} \cdot \text{m}^{-2}$ (Nadkarni and Matelson 1992).

Methods. A 2-ha study area was established within the 20-ha Research Area of the MVCFR. It encompassed a variety of slopes (0% to 20%) and areas of closed canopy and gaps. Mean tree diameter at breast height (dbh) for trees > 10 cm dbh was 65.5 cm; mean tree density was 154 individuals/ha.

In May 1989 we collected 49 newly fallen epiphyte clumps from the forest floor within the study plot. Each clump consisted of live and robust-appearing vascular and non-vascular epiphytes with associated dead organic matter and roots intact. All clumps had fallen within the previous two weeks (T. J. Matelson and N. M. Nadkarni, *personal observation*). Each sample clump was placed on the ground in one of four 10×10 m plots within 50 m of where they had originally fallen. The plots encompassed the variability of the study area with respect to canopy cover; two of the plots, which contained 33 of the 49 clumps, were in gaps with little or no understory cover. The other two plots, which contained 16 of the clumps, were in the shaded understory. Most of the clumps (41 of the 49) were found unattached to branches, but those that were attached

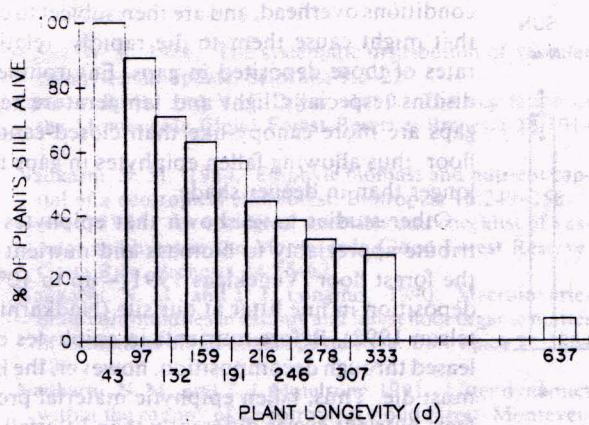


FIG. 1. Longevity of a cohort of individual epiphytes after falling to the forest floor. Longevity is defined as time between day 1 and the last sampling day a plant was recorded alive after placement on the forest floor. $N = 223$ plants (including non-vascular plants).

were left that way. A drawing was made of each clump, and individual plants were identified to one of the following plant categories: Piperaceae ($N = 15$ plants), Araceae (12), Orchidaceae (26), Bromeliaceae (31), Ericaceae (24), other angiosperms (26), Pteridophyta (40), and non-vascular plants (49). Non-vascular plants, mainly mosses and liverworts, were not monitored individually, but were considered a single entity on a clump. The clumps ranged in size from 90 cm³ to 36 000 cm³ (mean = 2880 cm³), and the number of individual plants per clump (we could not distinguish between ramets and genets) ranged between 2 and 9 plants (mean = 4.5 plants).

Each of the 223 plants was examined with minimal handling at near-monthly intervals during the first year (43, 97, 132, 159, 191, 216, 246, 278, 307, 333 d after placement) and again near the end of the second year (day 637). One person monitored the clumps for the entire study. Some of the leaf litter that accumulated on clumps was unavoidably disturbed at each inventory in order to assess plant status. Each plant was scored as live or dead at each inventory. Plant death was indicated by browning, loss of leaves, fragmentation, and shrivelling of stems or rhizomes.

Longevity was defined as the time (in days) between day 1 and the last sampling day a plant was recorded alive after placement on the forest floor. For purposes of analyses, longevity was defined as the time interval a plant was seen alive, with time interval being an integer from 1 to 12, representing the day of placement and the 11 subsequent censuses. Thus, longevity from 1 to 10 reflected monthly mortality during the first year, a longevity of 11 reflected total second year mortality,

and a longevity of 12 indicated that a plant remained alive at the end of the study. Clump longevity (as opposed to longevity of individual plants) was defined as the average longevity of all plants within a clump. Analyses are complicated by two levels of spatial association, within clumps and within plots, which are addressed in the results. Individual plant longevity, which was not normally distributed, was analyzed with non-parametric tests. Clump longevity, which was normally distributed, was analyzed with parametric ANOVA and regression. Statistical procedures were carried out with SYSTAT (SYSTAT 1984).

Results

By the end of the first year only 27% of the plants remained alive, and by the end of the study (21 mo), only 7% had survived (Fig. 1). The branches to which clumps had been originally attached were intact, but had deteriorated. Of the cases in which the clumps were unattached to branches, some clumps had disappeared, while for others, lumps of dead organic matter knit together with remains of the root mat were detectable on the forest floor.

All plant categories exhibited similar rates of mortality. Discounting spatial association, there were no significant differences in longevity among the eight plant categories (Kruskal-Wallis test, $P < .07$). Plant categories were dispersed across clumps and plots, making it less likely that a spatial association would obscure a real plant category difference in longevity.

In contrast, there was a significant plot effect on longevity (Kruskal-Wallis test, $P < .001$). The two gap plots had higher mean ranks than the two shade plots. Clump longevity showed similar strong plot effects (Fig. 2, ANOVA, $F_{3,45} = 5.09$, $P < .004$). Shade plots had lower longevity than gap plots (SYSTAT a posteriori "Hypothesis" procedure, linear contrast of two shade plots and two gap plots, $F_{1,45} = 14.14$, $P < .001$).

There was no effect of epiphyte attachment to branches on clump longevity (t test, $P < .35$), and no significant regressions of clump longevity on clump volume ($r^2 = 0.04$, $P < .19$) or number of plants per clump ($r^2 = 0.01$, $P < .64$).

Discussion

A variety of factors might cause live epiphytes to die after falling to the ground. First, epiphytes may die due to diminished photosynthesis caused by environmental differences between canopy and forest floor—especially light and moisture regimes and air movement. Water and nutrient inputs may differ because fallen epiphytes receive primarily throughfall, which is deposited in larger drops than in mist or fog; throughfall chemistry is often altered by contact with the canopy (Vitousek and Sanford 1986, Veneklaas and Van Ek

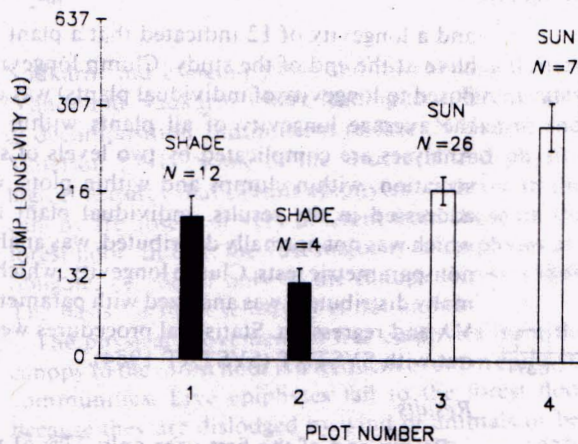


FIG. 2. Plot effects on longevity of epiphyte clumps. Means \pm 1 SE are shown. Clump longevity (as opposed to longevity of individual plants) was defined as the average longevity of all plants within a clump. N = number of clumps.

1990). At our study site, throughfall tends to be enriched in NH_4^+ and K^+ , and depleted in NO_3^- compared to bulk deposition at the same site (K. Clark and N. Nadkarni, unpublished data). Extremes of temperature, substrate moisture content, and wetting/drying cycles are greater in the canopy than on the forest floor (T. J. Matelson, S. Bohlmann, and N. M. Nadkarni, unpublished data). The most striking microenvironmental difference is the lack of extremely dry periods on the forest floor during the dry and windy-misty seasons, which creates a more constantly wet environment for fallen epiphytes than for canopy counterparts, where such "dry-downs" occur.

Second, biotic factors may distinguish the canopy from the forest floor, including differences in pathogens, herbivores, and symbionts. Overall density of invertebrates is lower in the Monteverde canopy than on the forest floor, and certain taxa are virtually absent in the canopy (Nadkarni and Longino 1990).

Third, accumulation of leaf litter on top of fallen epiphytes may encourage their death on the forest floor. Leaf litter accumulation blocks insolation, changes the moisture regime, and may influence herbivores and pathogens. Rates of litter accumulation differ between canopy and forest floor, due to higher wind in the canopy and the non-contiguous surface area of canopy substrates (Nadkarni and Matelson 1991).

Although little is known about the spatial distribution of fallen epiphytes, much fallen epiphytic material is deposited in gaps, as it "rides down" large branch- and treefalls (Nadkarni and Matelson 1992). Epiphytes also fall in a continual manner in smaller amounts, reaching the forest floor on smaller branches or as individual epiphytes. The latter encounter closed-canopy

conditions overhead, and are then subject to conditions that might cause them to die rapidly, relative to the rates of those deposited in gaps. Environmental conditions (especially light and temperature regimes) in gaps are more canopy-like than closed-canopy forest floor, thus allowing fallen epiphytes in gaps to survive longer than in deeper shade.

Other studies have shown that epiphytes can contribute appreciably to biomass and nutrient inputs to the forest floor (Veneklaas 1991)—up to 10% of total deposition in fine litter at our site (Nadkarni and Matelson 1992). Before nutrients in epiphytes can be released through decomposition, however, the live plants must die. Thus, fallen epiphytic material probably affects nutrient cycles differently than litterfall from terrestrially rooted plants, whose nutrients can be mineralized faster because that material is already dead (Vitousek and Sanford 1986). For fallen live epiphytes, then, there is a potential lag time in nutrient release via mineralization. In forests with well-developed canopy communities, epiphytes can profoundly affect both the amounts of nutrient storage and the timing of nutrient release.

This study has shown that the rate of nutrient release from epiphyte biomass varies with microhabitat. Further investigations should pursue the spatial and temporal distribution of fallen epiphytes at the species level in relation to microhabitat characteristics in order to determine both the role of epiphytes at an ecosystem level as well as for insights into mechanisms that foster epiphytism.

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Epiphyte plants are normally low growing plants—herbaceous, different conditions than those found on the forest floor. Canopy and forest floor habitats are usually described as "open" because they receive presumably unlimited storage capacity for available nutrients and water from sporadic and dilute downward inputs, less soil, less habitat, and more patchy "rain trees" for water. (Auerman and Montelvo 1990, Strong 1977) Although the vertical distance between canopy and forest floor micro-habitats can be great, within the canopy environment is characterized by more extreme fluctuations in humidity, light, and temperature, stronger insolation, high windspeeds, and more severe and variable vapor pressure deficits (e.g., Chazdon and Duval 1988, Chazdon and Fetcher 1981). These differences may include the invertebrate fauna and