

## RESPONSES OF VASCULAR EPIPHYTES TO BRANCH-FALL GAP FORMATION IN *CLUSIA* TREES IN A MONTANE RAIN FOREST

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**ABSTRACT.** The vascular epiphyte community in *Clusia* trees in the elfin forest of the Monteverde Cloud Forest Reserve, Costa Rica, was monitored for one year to evaluate responses to branch-fall gap formation. Plots (10 × 30 cm) were established on inner crown branches of *Clusia* host trees, and artificial branch falls were created over a subset by removing branches 3–5 cm diam. The vascular epiphyte community changed little in response to gap formation, despite a high turnover of individual plants. Branch-fall gap formation did not affect epiphyte density, percent cover, species richness, the Shannon-Weiner diversity index, or Simpson's equitability index for the epiphyte community. Only weakly significant ( $P = 0.15$ ) effects of branch-fall gap formation on the population dynamics of a few species were detected, with gap formation possibly favoring *Blakea chlorantha* and negatively affecting *Burmeistera* spp., *Clusia* sp., and *Grammitis zurquina*. The 12 most common species in the plots did not demonstrate other effects of branch-fall gap formation. Although more extreme changes in exposure, such as those caused by loss of neighboring trees, may affect composition and dynamics of a vascular epiphyte community, we conclude that canopy gaps caused by loss of smaller branches in *Clusia* crowns have little impact.

**Key words:** branch loss, canopy gap, cloud forest, epiphyte, Monteverde

### INTRODUCTION

Epiphyte communities play key roles in the diversity, ecology, and structure of the entire forest. Epiphytes affect nutrient cycles within cloud forests (Nadkarni 1992), and theoretically, another role the epiphyte community may play within the forest community is in influencing deterioration rates of host trees. Epiphytes can be viewed as mechanical parasites in relation to their hosts (Benzing & Seeman 1978). As the biomass of epiphytes on a branch increases, the plants become an increased burden on the host. There is a mechanical limit to each host limb's capacity to support epiphyte biomass. When this limit is reached, the limb will break and fall to the ground. Such limbfalls may create branch-fall gaps, increasing light levels experienced by epiphytes on remaining branches. If canopy openness is correlated with growth rate and/or establishment of vascular epiphytes, then the newly exposed limbs may begin to experience an increase in the mechanical stress caused by supporting larger epiphyte biomass. These newly exposed limbs may experience faster rates of decay caused by increased strain and structural failure. When failure of a host tree limb creates another opening in the canopy, the cycle begins again. The response of the remaining epiphyte community to branch-fall gap formation has the

potential, therefore, of influencing forest turnover rates and forest diversity.

In neotropical montane forests, epiphytes may be more limited by light availability than by water or nutrient availability. The high epiphyte abundance found in neotropical montane rain forests may be related to mist interception (Sugden & Robins 1979). Water that condenses on surfaces as clouds pass through a forest can represent up to 90% of a forest's gross precipitation and can maintain base flow of rivers even during dry spells (Stadtmüller 1987). A pronounced positive relationship exists between epiphyte abundance and exposure to this "horizontal precipitation," causing windward slopes to have more lush epiphyte communities than leeward slopes (Sugden & Robins 1979, Lawton & Dryer 1980, Cavalier & Goldstein 1989). In the Monteverde Cloud Forest Reserve of Costa Rica, horizontal precipitation occurs throughout the year; and epiphyte communities on windward slopes are somewhat, if not completely, buffered from water stress during seasons with low rainfall.

Likewise, these epiphytes experience relatively high nutrient availability. Nutrients may come from cloud deposition, decomposition of canopy organic matter, stemflow (Rieley et al. 1979, Nadkarni 1986, Brown & Bates 1990), deposition of animal feces (Perry 1978), and the activity of nitrogen-fixing bacteria (Bentley & Carpenter 1980). Host trees capitalize on nutrients held by epiphytic bryophytes by producing can-

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opy roots that permeate the bryophytic mat (Nadkarni 1981, 1984). Nadkarni and Matelson (1991) showed that epiphyte litter (primarily bryophytic matter) that falls to the forest floor has a higher nutrient concentration than the litter produced by the tree community. Neither nutrients nor water, therefore, are likely to be the most limiting resources for vascular epiphytes growing out of bryophytic mats exposed to high levels of cloud deposition.

As host trees degrade or are damaged by high winds, limbs fall from the canopy, increasing the light levels for epiphytes that remain in the canopy (Lawton & Dryer 1980). Branch-fall gap formation within the canopy may have a similar influence on epiphytes as treefall gap formation has on the forest understory. Gap-phase regeneration plays a role in shaping the community structure of many tropical forests and in maintaining biodiversity (e.g., White 1979, Hartshorn 1978, 1980, Denslow 1980, 1987, Orians 1983, Levey 1988, Platt & Strong 1989, Schupp & Frost 1989, Whitmore 1989). It is unknown if similar relationships exist within the canopy and its epiphyte community. Young (1995) theorized that gap-edge tree crowns could be a hot spot of resource availability for epiphytes.

Light availability may have a positive or negative effect on individual plant performance. Several studies that measured the vertical light profiles through forest canopies found the majority of incoming solar radiation being absorbed or reflected within the first 5 m of the canopy, which allows only a small fraction to reach the forest floor (e.g., Read 1977, ter Steege & Cornelissen 1989). As canopy gaps are formed, the epiphyte community within a particular crown will experience, therefore, an increase in diffuse light, if not in direct light levels. An increase in light could stimulate an increase in the growth of plants. Alternatively, higher amounts of incoming short-wave radiation will increase a given leaf's temperature, thus increasing the evaporative demand placed on that particular plant. Although cloud forests are unlikely to experience large-scale water stress, the epiphyte community may not be immune to localized water stresses introduced by exposure to light and wind.

Within elfin woods (a dwarfed type of cloud forest), wind stress has a pronounced effect on the structure of canopy trees. In such areas, constant gale force winds may be responsible for stunting the growth of canopy trees (Lawton & Dryer 1980, Lawton 1982), rather than a lack of nutrients. Plausibly, the epiphyte community may be influenced directly by such winds (Ramsey et al. 1987). Aside from mechanical stress, windspeed influences evaporation rates via ef-

fects on boundary layers (Jones 1992). With windspeeds tending to increase with height in the canopy (Read 1977, Lawton 1982, Fetcher et al. 1985), formation of branch-fall gaps may alter the localized windspeed experienced by an individual epiphyte by altering exposure to direct wind.

The purpose of this study was to elucidate the effects of artificially created branch-fall gaps on short-term (one-year) changes in vascular epiphyte community structure and dynamics. We studied the epiphyte community in *Clusia* trees of the Monteverde Cloud Forest Reserve. The frequency of branch-falls in the Reserve's windward-exposed cloud forest is high because of mechanical stress associated with northeasterly trade winds (Lawton & Dryer 1980, Lawton & Putz 1988). We studied the effects of loss of branches 3–5 cm in diam. Loss of such branches is common during degradation of the *Clusia* canopy (R. Lawton, pers. comm.).

#### STUDY SITE

The study was conducted within the Monteverde Cloud Forest Reserve (10°12'N, 84°42'W; ca. 1500 m), along the upper windward slopes and ridge crests of Brillante Gap of the Cordillera de Tilaran, Costa Rica. For a detailed description of the study area, refer to Lawton (1982, 1984, 1990), Lawton and Dryer (1980), and Lawton and Putz (1988). The forest is classified as an elfin wood because of the short stature of canopy trees (Lawton & Dryer 1980).

#### MATERIALS AND METHODS

To study effects of branch-fall gap formation on the dynamics of the epiphyte community of *Clusia* trees, we established monitoring plots on branches, removed branches above a subset of these plots, and compared changes in the vascular epiphyte community in control plots to those in plots exposed to new gaps. Changes in species composition, epiphyte density, cover, species richness, evenness, and diversity were quantified over the year following branch pruning. Effects of gap formation on mortality and recruitment in the vascular epiphyte community were quantified, as were population changes, mortality, and recruitment for the 12 most common species in the plots.

#### Study Species

*Clusia* sp. (Clusiaceae) or diamond leaf, a morphologically distinct but as yet undescribed species, was selected based on its abundance and structural strength. Host trees were identified

within a 2.6 ha region along and directly below the ridge on the windward slopes of the elfin forest. The topography within the sampled area had an elevation range of approximately 50 m. Plots were located on branches accessible with standard climbing equipment (e.g., webbing, carabiners, and a climbing harness) within the same inner crown region of each host. For this study, crown region is defined as the area beyond 1 m from the trunk and up to  $\frac{2}{3}$  the length of the branch within the host tree crown (corresponding to zones 4 and 5 within host canopies as categorized by Johansson 1974).

Permanent rectangular plots (total area 0.03 m<sup>2</sup>) were established on branches (12–44 cm diam.) with a 10 cm (perpendicular to branch axis) by 30 cm (parallel to branch axis) boundary. This small plot area was selected because larger plots become too heterogeneous because of changing host branch characteristics (Heitz & Heitz-Seifert 1995). Plots were permanently marked with nails and flagging. A total of 24 plots were established within 12 host trees. With all plots established ( $N = 24$ ), nine were selected at random to be manipulated by cutting 1–2 branches (3–5 cm diam.) above each plot, simulating the formation of a branch-fall gap. Initial sampling and branch cutting was performed from early June 1994 through August 1994, and resampling occurred one year later.

Hemispherical photographs were taken above each plot to quantify effects of branch pruning on canopy openness and at the base (closest to trunk) of each plot. We used a 35 mm Pentax ME Super and an 8 mm Sigma Fisheye lens with Kodak T-max professional black and white film (100 ASA). The camera was housed in a gimble mount, so that the camera was suspended and always level with the horizontal axis. The pictures were scanned with a handheld scanner, and percent canopy openness was characterized using SolarCalc for Macintosh (Chazdon & Field 1987). Hemispherical photographs were taken after each manipulation to quantify the increase in canopy openness; and they were taken immediately post-manipulation for control plots within host trees that had both plot treatments. Thus, it was possible to ensure that the light levels for a control plot did not change because of branch pruning above another plot within the same host tree. Pictures were taken again one year later for all plots to determine how openness changed during the year.

All vascular epiphytes within a plot were given coordinates within the plot for re-identification purposes. Only vascular epiphytes with a stem diam.  $> 0.25$  cm were tagged, since smaller individuals proved too fragile for tagging. We defined an individual as a shoot not physically

connected to another shoot. Epiphytes were lightly tugged to determine if they were individuals. Coordinates of individuals found without tags during the second census were compared to coordinates of individuals not tagged the previous year. Duplicate coordinates of the same species were assumed to be the same individual; therefore, estimates of turnover rates may be slightly conservative. Individuals with at least one true leaf (i.e., more than just cotyledons) were identified to the lowest possible taxonomic category. All voucher specimens were identified by W. Haber of the Missouri Botanical Garden (for a published species list of the area, see Haber 1991). Each plot and vascular epiphyte was drawn to scale; the drawings were transferred to acetate sheets; and a LiCor Model 3100 Area Meter (LiCOR, Inc., Lincoln, NE, USA) was used to estimate total percent cover by vascular epiphytes.

### Statistics and Analyses

In dealing with non-normal distributions, we used non-parametric Wilcoxon signed-ranks tests to determine if branch pruning increased canopy openness above manipulated plots. The same analysis was used to ascertain if exposure levels (canopy openness) changed over the duration of one year within control and/or manipulated plots.

Because most changes in community and population-level parameters were expected to be subtle, with initial community composition strongly influencing population changes and community composition the second year, we used Analysis of Covariance (ANCOVA) to assess the effect of branch pruning on most parameters. These analyses factored out effects of initial composition to reveal differences in changes between control and manipulated plots. The main exception to this approach was the analysis of changes in overall community composition. To determine if branch falls caused greater changes in community composition over a year in manipulated plots than in control plots, we calculated similarity indices (similarity between initial community composition and that of one year later) for each plot (after Bray & Curtis 1957). Indices for control and manipulated plots were then compared with a Mann-Whitney  $U$ -test.

For assessing effects of branch-fall gap formation on changes in various parameters, we used the following covariates in ANCOVAs. The total number of individuals within a given plot during the second year should largely depend on the initial number of individuals within that plot; and thus we analyzed the effect of gap

formation on second-year vascular epiphyte density using initial density as a covariate. Similarly, effects of branch falls on final vascular epiphyte cover, species richness (number of species per plot), and species diversity (Shannon-Weiner index) were analyzed using initial cover, richness, and diversity as covariates, respectively. Effects of branch cutting on changes in species evenness (Simpson's equitability index) were analyzed for treatment effects using a Wilcoxon signed-ranks test, as the homogeneity of slopes assumption required for ANCOVA was violated (Dunn & Clark 1987, Hand & Taylor 1987). Because the number of plants initially present in plots limited the number that could die, effects of branch-fall gap formation on mortality (number of plants that died per plot) was analyzed by ANCOVA, using initial number of plants present as a covariate. Recruitment was analyzed for treatment effects by a Mann-Whitney *U*-test.

For those species with a total population (in all plots combined) of  $N \geq 8$  in one of the two years (the 12 most abundant species), we analyzed effects of branch-fall gap formation on mortality, recruitment, and density. Effects on density were analyzed with ANCOVAs, using initial density as a covariate. Population mortality and recruitment of individual species were analyzed in the same manner as for community dynamics. Only individuals with at least one true leaf were included in these analyses, as plants possessing only cotyledons could not be identified accurately. Only plots with a given species present in one or both years were used in the analyses to avoid numerous zeros in the dataset.

## RESULTS

The study provided data on the effects of branch pruning on canopy openness, community composition and structure, and population changes in the most common species.

### Effects of Branch Pruning on Canopy Openness

Branch pruning significantly increased canopy openness above plots (Wilcoxon signed-ranks test,  $z = 2.7$ ,  $P = 0.008$ ; FIGURE 1). This change, however, was insufficient to increase exposure levels above those of control plots, which experienced a range of canopy openness (Mann-Whitney *U*,  $U = 47.5$ ,  $P = 0.23$ ). Community differences between control and manipulated plots, therefore, cannot be interpreted as differences between high light and low light environments. Changes in the communities are interpreted as dynamic responses to branch-fall gap formation and are contrasted with changes in

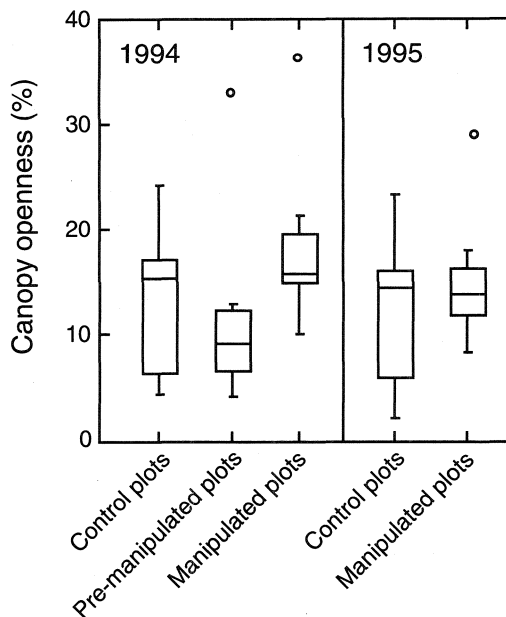


FIGURE 1. Canopy openness above epiphyte plots before branch pruning, immediately after branch pruning, and one year later. Median values, ranges, and interquartile ranges are shown. Circles represent outliers (data outside the interquartile range by a distance  $> 1.5$  times the interquartile range).

control, relatively unchanged environments. Mean canopy openness above manipulated plots increased from 11.4% (one standard deviation  $\pm 8.6$ ; hereafter  $\pm$ ) to 18.0% ( $\pm 7.7$ ) because of limb removal. Canopy openness decreased slightly but significantly over the year of study for both control and manipulated plots (Wilcoxon signed-ranks test,  $z = -2.6$ ,  $P = 0.009$ , and  $z = -2.7$ ,  $P = 0.008$ , respectively). The mean openness of control plots decreased 1.4% (from  $12.9 \pm 6.6\%$  to  $11.5 \pm 6.3\%$ ); and the mean openness of manipulated plots decreased 3.1% (from  $18.0 \pm 7.7\%$  to  $14.9 \pm 6.1\%$ ).

### Community Composition and Structure

The vascular epiphyte community sampled had a few abundant species and many rare species (FIGURE 2). A total of 35 species were found. Despite random selection of plot treatments, the initial (1994) species composition within manipulated plots differed significantly from the species composition of initial control plots (Kolmogorov-Smirnov two-sample test,  $P = 0.006$ ). Similarity of the same plots from one year to the next was not influenced significantly by the formation of branch-fall gaps (Mann-Whitney *U*,  $U = 60.5$ ,  $P = 0.67$ ). After one year,

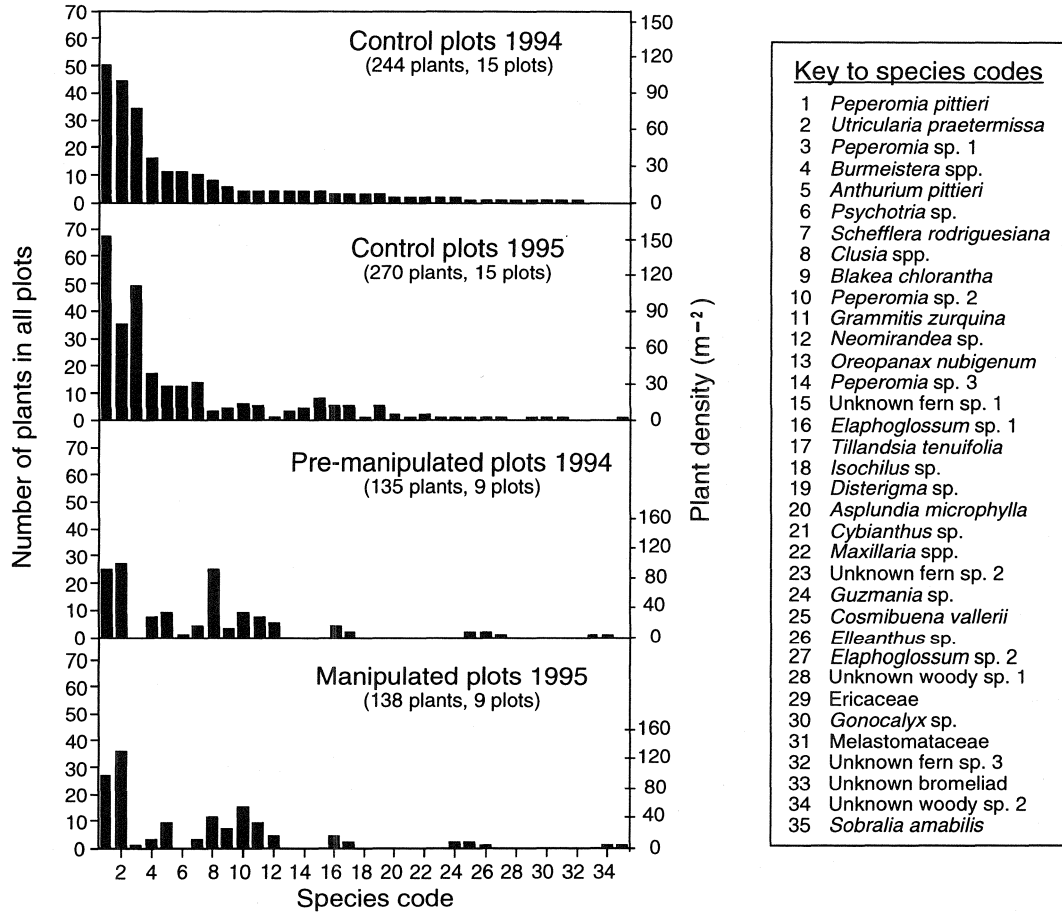


FIGURE 2. Species of vascular epiphytes encountered in plots. Densities in manipulated and control plots are shown for the two years of the study.

mean similarity for control plots was 77.9% ( $\pm 14.4$ ) and 74.4% ( $\pm 29.9$ ) for manipulated plots.

Neither density nor percent cover of vascular epiphytes was influenced by branch-fall gap formation. Mean number of individuals with true leaves (one or more leaves other than cotyledons) in control plots was 16.3 ( $\pm 6.2$ ) in 1994 and 17.9 ( $\pm 10.2$ ) in 1995. The number in manipulated plots, 15.1 ( $\pm 5.6$ ) in 1994 and 15.3 ( $\pm 11.3$ ) in 1995, did not change in response to branch pruning (ANCOVA,  $df = 21$ ,  $F = 0.146$ ,  $P = 0.71$ ). For ANCOVA results, treatment  $df = 1$ , and only error  $df$  (deviations from a common slope) are presented. Mean estimated vascular epiphyte cover for control plots was 22.3% ( $\pm 11.1$ ) in 1994 and 27.6% ( $\pm 16.3$ ) in 1995, while manipulated plots had a mean estimated cover of 17.6% ( $\pm 8.9$ ) in 1994 and 23.7% ( $\pm 14.8$ ) in 1995. Estimated vascular epiphyte

cover was not influenced by branch pruning (ANCOVA,  $df = 21$ ,  $F = 0.119$ ,  $P = 0.73$ ).

Species richness, diversity, and evenness were used to monitor changes in the complexity of the vascular epiphyte community structure. Species richness in control plots did not change ( $6.1 \pm 2.4$  in 1994 and  $6.1 \pm 2.2$  in 1995); however, within manipulated plots, mean species richness decreased from 5.9 ( $\pm 1.5$ ) species per plot to 5.1 ( $\pm 2.3$ ) species per plot. This effect of branch-fall gap formation on species richness was only weakly significant (ANCOVA,  $df = 21$ ,  $F = 2.328$ ,  $P = 0.14$ ). The mean diversity (Shannon-Weaver index) within control plots was 0.64 ( $\pm 0.23$ ) in 1994 and 0.60 ( $\pm 0.23$ ) in 1995.

Manipulated plots had a mean diversity of 0.68 ( $\pm 0.12$ ) and 0.54 ( $\pm 0.23$ ), for the 2 years, respectively. Diversity may have declined with the formation of branch-fall gaps, but the effect was only weakly significant (ANCOVA,  $df =$

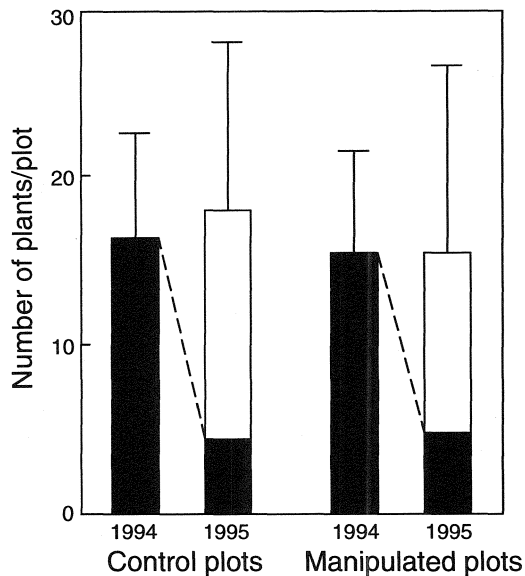


FIGURE 3. Turnover of plants with at least one true leaf from 1994 to 1995. Black bars represent plants with true leaves present in plots in 1994. Dashed lines indicate their mortality between censuses. White bars represent new plants with true leaves in 1995. Means and SD of total number of plants per plot are shown.

21,  $F = 2.325$ ,  $P = 0.14$ ). Because the homogeneity of slopes assumption was not met for evenness ( $P = 0.013$ ), we used Wilcoxon signed-ranks tests to evaluate changes in evenness. Neither the control plots, nor the manipulated plots showed a significant change from one year to the next ( $P = 0.33$  and  $P = 0.95$ , respectively). Mean evenness in control plots was  $0.29 (\pm 0.14)$  and  $0.27 (\pm 0.16)$  for the 2 years, respectively. Mean evenness in manipulated plots was similar ( $0.33 \pm 0.28$  and  $0.34 \pm 0.32$ , respectively).

Analysis of the dynamics of the vascular epiphyte community revealed a fairly stable density but a large turnover of individuals during the year of study. Branch-fall gaps did not influence mortality (ANCOVA,  $df = 21$ ,  $F = 0.077$ ,  $P = 0.78$ ) or the number of new vascular epiphyte individuals that appeared in the second census (Mann-Whitney  $U = 82$ ;  $P = 0.39$ ). Mean number of new individuals in control plots was  $17.1 (\pm 11.0)$  with 23% possessing only cotyledons. Manipulated plots had a mean of  $13.9 (\pm 11.4)$  new individuals (21% with cotyledons only). Despite the high number of new individuals within plots, the total number of plants with true leaves changed little over the year (from  $16.3 \pm 6.2$  to  $17.9 \pm 10.2$ , FIGURE 3).

Of the initial number in control plots, a mean of

$4.5 (\pm 2.8)$  individuals survived; a mean of  $13.5 (\pm 11.2)$  individuals with one or more primary leaves were recruited; and a mean of  $11.8 (\pm 7.0)$  individuals died. Thus, within control plots, 72% of the initial individuals with true leaves died, and 75% of the individuals with true leaves during the second year were newly recruited. Manipulated plots averaged  $4.8 (\pm 2.9)$  survivors (31%),  $10.7 (\pm 6.0)$  deaths (69%), and  $10.6 (\pm 10.7)$  new recruits (69% of second-year individuals). The result was a fairly stable density of individuals with true leaves between years ( $15.4 \pm 6.0$  in 1994 and  $15.3 \pm 11.3$  in 1995).

#### Population Changes in the Most Common Species

Among the 12 most abundant species encountered (FIGURE 2), densities of *Blakea chlorantha* Almeda (Melastomataceae) in plots exhibited a weakly significant increase (ANCOVA,  $df = 4$ ,  $F = 3.785$ ,  $P = 0.07$ ), while densities of *Burmeistera* spp. (Campanulaceae) exhibited a weakly significant decrease (ANCOVA,  $df = 9$ ,  $F = 2.227$ ,  $P = 0.15$ ) in response to branch pruning. Densities of the ten other species tested did not change significantly in response to branch-fall gap formation (ANCOVA,  $P > 0.3$ ).

Recruitment and mortality of the 12 most abundant species were also evaluated for treatment effects. The homogeneity of slopes assumption was not met for *Grammitis zurquina* (Copel) F. Seym. (Grammitidaceae) ( $P < 0.001$ ) which was, therefore, evaluated using a Mann-Whitney  $U$ -test. Mortality of *G. zurquina* showed a weakly significant increase ( $U = 0.50$ ,  $P = 0.10$ ) with the formation of branch-fall gaps. No significant treatment effect was found on the mortality of any other species (ANCOVA,  $P > 0.4$ ; for all species). Recruitment of *Burmeistera* spp. was reduced (ANCOVA,  $df = 8$ ,  $F = 5.514$ ,  $P = 0.05$ ), while *Clusia* recruitment may have decreased (ANCOVA,  $df = 7$ ,  $F = 3.236$ ,  $P = 0.12$ ) in response to branch-fall gaps. All other species tested ( $N = 10$ ) showed no treatment effect on recruitment (ANCOVA,  $P > 0.18$ ).

Because the high death rate in control plots (72% per year) could have been caused by the germination of numerous, ephemeral seedlings that never truly became established in the community, we analyzed the size distribution of plants that died. For the eight most abundant species in the plots, we classed individuals by size, based on appropriate descriptors of size for each species (FIGURE 4). These species represented 69% of the vascular epiphytes in control plots. No individual of *Peperomia pittieri* C. DC. (Piperaceae), *Utricularia praetermissa* P.

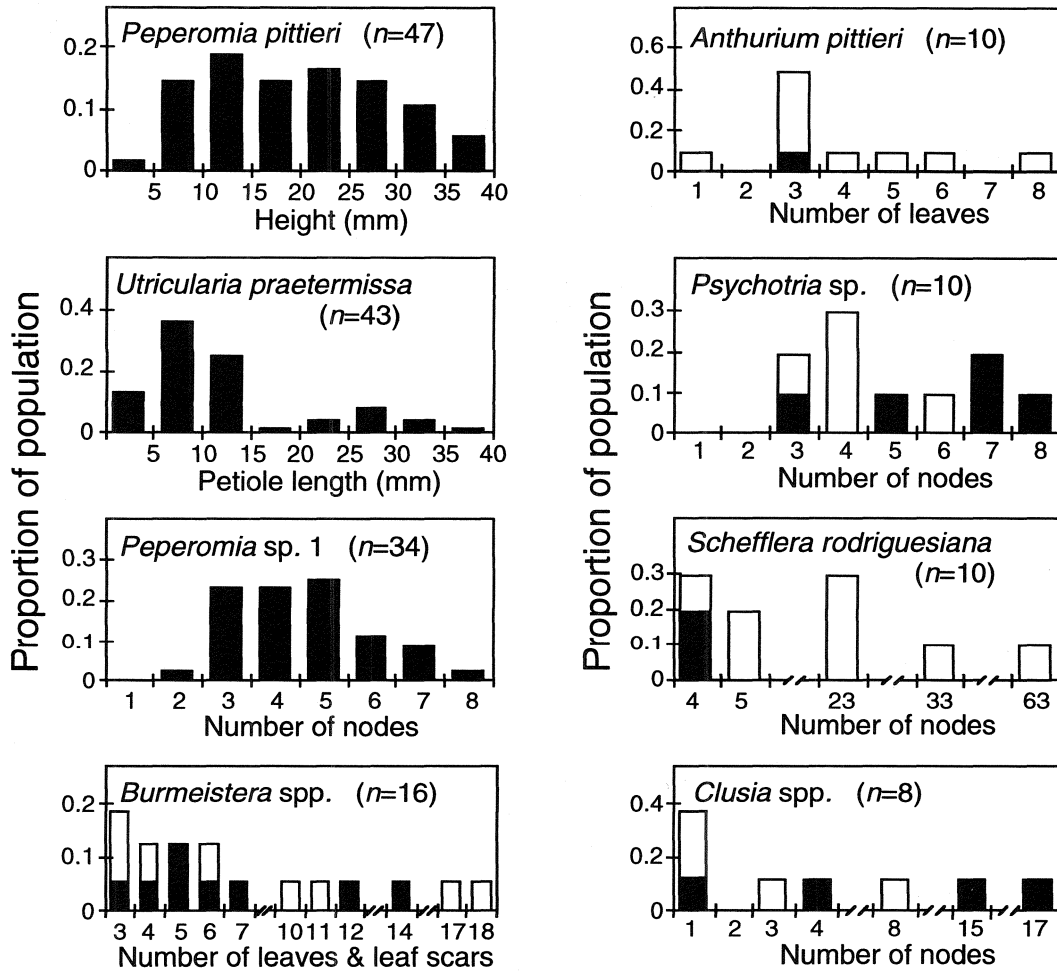


FIGURE 4. Size-class distributions of the eight most common species in control plots, showing their fates over one year. Black bars represent individuals that died; white bars represent individuals that survived.

Taylor (Lentibulariaceae), or *Peperomia* sp. 1 (51% of total epiphyte population) survived a year in control plots. The other species examined showed variable degrees of vulnerability in relation to size. Among plants that had produced at least one true leaf, we observed no general relation between size and probability of death.

#### DISCUSSION

The vascular epiphyte community studied in the Monteverde Cloud Forest Reserve is complex and highly diverse. Within the prescribed outer crown area of *Clusia* sp. (zones 4 and 5, after Johansson 1974), we found 35 species of vascular epiphytes. In other regions of the host crowns, we observed vascular epiphyte species not reported in this paper. Our study, therefore,

does not provide a comprehensive species list for this luxuriant epiphyte community.

In contrast to its resistance to short-term changes in species composition, the vascular epiphyte community within the inner crowns of *Clusia* sp. experienced a surprisingly high rate of turnover of individuals. Of the average 16 individuals per control plot, four survived, 12 died, and 13 were recruited, resulting in a fairly stable density. The three most prevalent species (*Peperomia pittieri*, *Utricularia praetermissa*, and *Peperomia* sp. 1) initially comprised 51% of the community and had no survivors. This accounted for 68% of the turnover of individuals with true leaves. Despite this high turnover rate, population sizes and community composition remained fairly stable during the study.

This homeostasis in population sizes may be

more likely to occur in clonal populations than in populations of short-lived species reproducing from seeds. In general, *Peperomia* species are suspected to be clonal, because they are often found spatially clustered (Heitz & Heitz-Seifert 1995). Species that are perennial in addition to having a clonal growth strategy often complicate interpretations of community dynamics, since individual genets are difficult to follow over time. Anecdotal evidence, however, suggests that *P. pittieri* may be short lived; individuals are rarely taller than 3 cm, have thin leaves, and only show a limited amount of root branching. Furthermore, we found no evidence of persistent root stocks or rhizomes. *Utricularia praetermissa*, described by Taylor (1989) as possessing stolons, is another possible clonal species. As with *P. pittieri*, however, we never found *U. praetermissa* individuals connected to another module. This suggests that, if these two species do propagate clonally, their ramets are only connected for a short time (i.e., less than a year).

Many epiphyte species have high juvenile mortality rates (Benzing 1981a, Larson 1992, Zotz 1995). This suggests that, in general, the most critical stage for an epiphyte may be during establishment. Various researchers have suggested that the composition of epiphyte communities is largely governed by mechanisms of seed dispersal and seedling establishment (Zimmerman & Olmsted 1992), by the quantity of propagules produced by each species (Yeaton & Gladstone 1982), and by disturbance (Benzing 1981b). Thus, persistence and distribution of an epiphyte species may be a function of producing a large number of seedlings, such that only a few individuals may find themselves in locations that favor survival over one year. Such a strategy would be evident in high mortality rates in smaller size categories. We could not quantify mortality rates among the youngest plants of each species (those possessing cotyledons only). Among plants that had produced at least one true leaf, however, we found no general trend of decreasing mortality with increasing size.

The loss of branches 3–5 cm in diam. from *Clusia* crowns did not elicit strong biological responses from the epiphyte community. Only weakly significant reductions in diversity and population changes in some of the component species were observed. This is surprising, since a complex dynamic system is generally thought to have a smaller dampening effect and thus to be more likely to experience rapid community change after a disturbance.

When a limiting resource is added to a community, a reduction often occurs in species diversity and an increase in biomass (Goldberg & Miller 1990). Species richness per plot which

showed a weakly significant ( $P = 0.14$ ) decrease with the formation of branch-fall gaps was paralleled with a weakly significant ( $P = 0.14$ ) reduction in diversity indices. We did not measure epiphyte biomass, but percent cover of vascular epiphytes and density of vascular epiphytes were unaffected by branch-fall gap formation. Changes in percent cover and epiphyte density may not reflect changes in productivity. In other studies, a considerable amount of carbon gained by epiphytes was allocated to reproductive effort (Benzing & Davidson 1979, Zotz 1995). Studies quantifying reproductive effort in relation to exposure may detect higher productivity (via higher reproductive effort) in more exposed individuals. The lack of change in epiphyte density and cover in response to branch-fall gap formation, however, suggests that the creation of canopy gaps of the size studied did not elicit a response from the vascular epiphyte community that increased the biomass load on host limbs.

Only a few weakly significant relationships regarding individual species were revealed. All population level results are presented as plausible interactions that should be tested further; because at an alpha level of 0.15, one would predict 1.8 Type I errors to have occurred in the number of population analyses performed. Populations of *Blakea chlorantha* density may increase in response to branch-fall gap formation, while those of *Burmeistera* spp. may decrease. The response of *Burmeistera* spp. is consistent with its distribution; it tends to occur on larger branches, deep in the canopy, on host trees in relatively sheltered sites (Rosenberger 1996). Since epiphyte life histories are largely unknown, it is risky to contend that the slight reductions in species richness and diversity in manipulated plots are explained by these generally weak species responses to an initial increase in canopy openness. The observed population changes, however, indicate species that may be sensitive to changes in exposure.

Overall, we conclude that the loss of branches 3–5 cm in diam., a common phenomenon during degradation of the canopy of *Clusia* sp., is unlikely to cause responses in the remaining epiphyte community that contribute to further degradation of the crown. Such branch falls may shift community composition and diversity but do not result in obvious increases in epiphyte density and size. Loss of branches of the size studied resulted in only modest increases in canopy openness. The epiphyte community may respond more strongly to larger increases in openness, such as those that occur when neighboring trees fall. Young (1995) has suggested that tree-fall gaps produce epiphyte "hot spots" in host trees encircling gap edges, perhaps through an



increased reproductive effort, changes in biomass, or in differential survival and recruitment of individual species. From this study, however, it appears that the loss of minor branches does not elicit a response in the epiphyte community on remaining branches that would lead to further crown degradation.

#### ACKNOWLEDGMENTS

We thank R.O. Lawton for suggestions and support, W.A. Haber for identifying voucher specimens, and F.E. Rosenberger for designing and constructing the gimble camera mount. We thank F.E. Putz, W.S. Judd, and A.E. Rosenberger for comments on the study design and manuscript. Finally, we are indebted to F.G. Chamberlain, the Monteverde Cloud Forest Reserve, and the Tropical Science Center for permission to conduct this research in the Reserve. This study was partially supported by a National Science Foundation grant to K. Williams (DEB 9357080).

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