COMPOSITION AND DISTRIBUTION OF THE VASCULAR EPIPHYTE FLORA OF AN ECUADORIAN MONTANE RAIN FOREST

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ABSTRACT. In a 175 m² sample plot of montane rain forest at 2,900 m elevation in southern Ecuador. a total of 33 families, 138 species and 3,454 stands of vascular epiphytes was found. Orchidaceae, Bromeliaceae, and Hymenophyllaceae were the most important families in terms of species richness, cover, and density. Epiphytic individuals of species that are normally terrestrial contributed greatly to the diversity. Most species had a narrow vertical distribution that in some cases was related to substrate preferences. Compared to lowland forests, the epiphytes in the montane forest had: higher density; a more even vertical distribution of abundance and diversity; and less pronounced dependence on humus accumulations.

Composición y distribución de las epífitas vasculares en un bosque montaño al sur de Ecuador.

RESUMEN. En una parcela de 175 m² en un bosque húmedo montaño a 2,900 m.s.n.m. en el sur del Ecuador se encontraron en total 33 familias, 138 especies, y 3,454 individuos des epifitas vasculares. Las familias más importantes en cuanto al número de especies, cobertura, y densidad fueron Orchidaceae, Bromeliaceae, Hymenophyllaceae, Dryopteridaceae, Polypodiaceae, y Ericaceae. Individuos epifiticos de especies que normalmente son terrestres, contribuyeron con mucho a la diversidad. La mayoria de las especies presentaron una distribuci6n vertical estrecha que, en algunos casos, estuvo relacionada con las preferencias de sustrato. En comparación con los bosques de las tierras bajas, las epífitas de los bosques montanos tienen una mayor densidad, su distribuci6n vertical de diversidad y abundancia fue mas pareja, y su dependencia en acumulaciones de humus fue menos pronunciada.

INTRODUCTION

Mid-elevation neotropical montane rain forests support the most abundant and species rich vascular epiphytic vegetation in the world (Madison, 1977; Gentry & Dodson, 1987). Several studies at altitudes between 500 m and 3,300 m support this claim (Grubb *et aI.,* 1963; Sugden & Robins, 1979; Cleef *et ai.,* 1984; Catling & Lefkovitch, 1989). According to these studies, maximum diversity values ranged from 24 to 91 species in sample plots of varying sizes at 1,700 m to 2,350 m. Maximum values for cover and density were found at similar altitudes.

Vascular epiphytes have specific vertical distribution patterns, and these patterns probably reflect different tolerances to light and humidity conditions (e.g., Schimper, 1888; Pittendrigh, 1948; Grubb & Whitmore, 1966; Johansson, 1974; ter Steege & Cornelissen, 1989). In lowland forests, the most abundant and species rich vascular epiphytic flora has been found on humus accumulations in forks or on large branches of the lower canopy (Johansson, 1974; ter Steege & Cornelissen, 1989). The ability of such humus deposits to buffer fluctuations in the humidity available to epiphytes, and their role as sources of mineral nutrients has been emphasized by Benzing (1987,1989).

The purpose of this study was to quantitatively describe the composition and distribution of the vascular epiphytic flora of a montane rain forest in Ecuador, with special reference to vertical distribution and substrate preferences.

STUDY SITE

The study plot was located 15 km south of Loja in southern Ecuador at 2,900 m, ca. 4 km east of Nudo de Cajanuma (79°lO'W, 04°05'S). The plot (hereafter referred to as the Cajanuma plot) was located in undisturbed forest on a SW facing slope with 15% inclination, just north of the "Centro de Informacion" of "Parque Nacional Podocarpus."

Annual precipitation in the area is 2,000-4,000 mm, with a relatively dry period from July through September and a relatively wet period from February through April (Apolo, 1984). Easterly winds prevail, and since the study site is located on a leeward slope 300 m below the mountain ridge, it is probably subject to a slight rain-shadow effect. Precipitation thus falls at the lower end of the quoted range, but the frequent occurrence of fog, for which no quantitative measures are available, may be more important for the epiphytic vegetation (Grubb & Whitmore,

FIGURE 1. Height zones drawn schematically. Zone $1 = 0.25$ to 3 m above the forest floor. Zone $2 =$ the trunk from 3 m above the forest floor to the first major branches. Zone $3 =$ large branches. Zone $4 =$ mediumsized and thin branches. Zone $5 =$ twigs. Note that not all trees have a zone 2 and that all sizes of branches can occur in zone 1.

1966). Mean annual temperature at the study site is ca. **11°C** (Christensen, 1989).

According to the definition of Holdridge *et al.* (1971) this forest is a typical montane rain forest. **It** is relatively species-rich and has an irregular, 10-12 m high canopy, with few trees reaching a height of 15 m. Trunks and branches incline at all angles, and gaps created by fallen, still vigorously growing, trees are common. Herbaceous climbers and parasitic shrubs (Loranthaceae) are conspicuous in the canopy. A dense undergrowth (predominantly *Chusquea* (Poaceae) species) occasionally forms a second canopy layer about 3 m above the forest floor. Epiphytic orchids, ferns, and bromeliads, as well as non-vascular epiphytes, abound.

MATERIALS AND METHODS

Field work was conducted from September through November 1989. In a 5 m \times 35 m sample plot, all living trees with a diameter \geq 5 cm (measured 1.3 m above the base) were sampled. In total, 39 trees of varying sizes rooted within the 175 m^2 area were examined. Each tree was divided into five zones following Johansson (1974) (FIGURE 1). Due to the irregular structure of the trees, branches of all sizes were present in zone 1, and some trees did not have all five zones.

For each tree and height zone, the following

information was recorded for each species of vascular epiphyte: number of stands, cover, height above forest floor, and substrate. A stand was defined as a compact group of plants well-separated from conspecifics (Sanford, 1968). Cover was estimated as a projection of the area covered by a stand upon the plane of the surface of the supporting tree limb. Substrates were divided into the following categories: bark (bark surface either completely bare or covered by mosses and lichens with only slight humus accumulation); minor humus deposits (humus deposits less than 5 cm thick); large humus deposits (deposits more than 5 cm thick).

Based on definitions given by Kress (1986), the epiphytes were divided into the following life form categories: 1) True epiphytes (t, species that normally spend their entire life span as epiphytes); 2) primary hemi-epiphytes (ph, species that germinate on trees and later establish root contact with the ground); 3) casual epiphytes (ca, species that can complete their life cycles either as terrestrials or epiphytes); 4) parasites (pa, species with direct vascular contact with living host tree tissue); and 5) accidental epiphytes (ac, species that are normally terrestrial and are found growing epiphytically only as juveniles).

All vascular plants growing epiphytically were sampled, including parasites and immature terrestrials. Only seedlings that were less than 3 cm tall were disregarded. To reduce difficulties in determining whether a particular plant was rooted in the ground or on a tree base, the basal 25 cm of the trees was not surveyed.

Access to the canopy was achieved with a ladder, and specimens which were beyond reach were collected using a long tube with hooks. Inaccessible branches were examined with binoculars. Collected specimens were identified and deposited at AAU (APPENDIX 1). Due to difficulties in determining sterile specimens, the number of species reported should be regarded as minimal. The number of species in the genera An *thurium, Odontoglossum, Oncidium, Pleurothallis,* and *Stelis* are likely to be somewhat underestimated.

Importance value indeces (IVI) (Curtis & Mc-Intosh, 1951) have been~calculated for all species as the sum of the relative density, the relative cover, and the relative frequency (percentage of trees on which an epiphyte species occurred). Family importance values (FlY) (Mori *et aI.,* 1983) have been calculated as the sum of the relative cover, relative density, and relative diversity (percentage of the total species number belonging to a particular family) for all true epiphytes.

Vertical distribution of the 53 species with more than 10 stands (i.e., relative density $\geq 0.29\%$) was analyzed using the computer program TWIN-SPAN (Hill, 1979). Each height zone on an individual tree was considered a separate subplot. The relative cover and the relative density was calculated (percentages of the total) for all species present in the subplot. Half of the sum of the relative cover and relative density values were used in the analysis. The program was run with default cut levels (2, 5, 10, 20, 40).

RESULTS AND DISCUSSION

Composition and Abundance

All epiphytic taxa on the surveyed trees are listed in ApPENDIX 1 with their life form, relative density, relative cover, relative frequency, and IVI. In total, 3,454 stands, with a cover of 46.4 m², and 138 species representing at least 33 families and 57 genera, were found. If accidental epiphytes are excluded, there were 3,379 stands, with a cover of 46.0 m^2 , 104 species , 36 genera , and 15 families. Among the true epiphytes, pteridophytes accounted for 6 families, 9 genera and 33 species; monocotyledons for 3 families, 17 genera, and 57 species; and dicotyledons for 6 families, 11 genera, and 14 species (APPENDIX 1). Unless specified, the term epiphyte will hereafter be used to designate only true epiphytes.

The Orchidaceae vastly surpassed all other

TABLE 1. The families of true epiphytes listed in decreasing order of Family Importance Value (FIV, calculated as the sum of relative cover, relative density, and relative diversity).

| | Rel. cover (%) | Rel. density (%) | Rel. diver- sity (%) | FIV |
|---------------------|----------------------|------------------------|-------------------------------|--------|
| Orchidaceae | 24.43 | 52.44 | 45.71 | 122.59 |
| Bromeliaceae | 25.47 | 9.56 | 5.71 | 40.74 |
| Hymenophyllaceae | 15.15 | 3.28 | 6.67 | 25.10 |
| Polypodiaceae | 3.19 | 7.66 | 11.43 | 22.29 |
| Dryopteridaceae | 6.94 | 7.55 | 7.62 | 22.10 |
| Ericaceae | 11.04 | 3.05 | 6.67 | 20.75 |
| Vittariaceae | 0.86 | 7.93 | 0.95 | 9.75 |
| Araceae | 4.95 | 0.74 | 2.86 | 8.55 |
| Aspleniaceae | 0.98 | 5.47 | 0.95 | 7.41 |
| Loranthaceae | 5.26 | 0.09 | 1.90 | 7.25 |
| Piperaceae | 0.89 | 1.04 | 2.86 | 4.78 |
| Lycopodiaceae | 0.13 | 0.12 | 3.81 | 4.06 |
| Clusiaceae | 0.17 | 0.77 | 0.95 | 1.89 |
| Araliaceae | 0.44 | 0.24 | 0.95 | 1.63 |
| Solanaceae | 0.10 | 0.06 | 0.95 | 1.11 |

families in FlV (TABLE 1). It was followed by Bromeliaceae, Hymenophyllaceae, Polypodiaceae, Dryopteridaceae, and Ericaceae.

Within the Orchidaceae the subtribe Pleurothallidinae, represented by the genera, *Lepanthes* (6spp.), *Masdevallia* (3 spp.), *Pleurothallis* (7 spp.), *Stelis* (8 spp.), and *Trichosalpinx* (2 spp.), accounted for 26 species. Among the ferns, the most important genera were *Elaphoglossum* (9 spp.), *Grammitis* (8 spp.), and *Hymenophyllum* (6 spp.). No other genus was represented by more than four species.

Total epiphyte species diversity in neotropical montane forest plots ranges between 9 and 181 (Grubb *et al.,* 1963; Sugden & Robins, 1979; Gentry & Dodson, 1987; Catling & Lefkovitch, 1989). The total of 104 species found in the present study falls within this range, but at altitudes similar to the Cajanuma plot, 68 species (Catling & Lefkovitch, 1989; 2,225 m) and 15 species (Sugden & Robins, 1979; $3,070$ m) have been recorded. Compared to these figures, the diversity at Cajanuma is very high. However, as noted by Gentry and Dodson (1987), the epiphytic flora is influenced by complex interactions of moisture and altitudinal effects. This, and the fact that the diversity figures were registered in plots of varying sizes, makes meaningful comparisons difficult.

One difference between neotropical epiphytic floras at high and low altitudes is the preponderance of Pleurothallidinae (Orchidaceae) species at high altitudes (ter Steege & Cornelissen, 1989). At Cajanuma, the Pleurothallidinae accounted for 19% of the total species diversity and

FIGURE 2. Examples of vertical distributions of individual species. Vertical axes show height above forest floor. Horizontal axes show percentages of the number of stands (number of individuals in parentheses).

38% of the density. The genus *Stelis* alone accounted for 28% of the density.

Although quantitative comparisons of density are hampered by difficulties in defining stands in an objective manner, it is evident that the density of 1,973 stands per 100 m2 in the Cajanuma plot is high. At altitudes similar to the Cajanuma plot, Sugden and Robins (1979) documented a density of 123 and 143 stands in two 100 m2 plots. However, the effect of altitude was difficult to separate from climatic effects. One hundred square meter plots at more humid sites at lower altitudes contained up to 4,632 epiphyte stands.

Vertical Distribution

The TWINSPAN analysis identified three major groups of subplots, which reflected vertical differences in the composition of the epiphyte vegetation. These results are summarized as follows:

Section 1 (division level 1, eigenvalue: 0.66): Tree bases (zone 1) were characterized by small ferns (e.g., *Asplenium cuspidatum, Elaphoglossum* cf. *lloense, Hymenophyllum fucoides* and *Vittaria remota),* the large bromeliad *Guzmania gloriosa, Stelis* sp. 1 and other orchids, and various accidental epiphytes (e.g., *Myrsine* sp.).

Section 2 (division level 3, eigenvalue: 0.42): Trunks and major branches (zones 2 and 3) were inhabited by numerous orchid species and ferns of more xerophytic appearance than those from zone 1. *Tillandsia* spp. and *Vriesea* sp. were also common.

Section 3 (division level 3, eigenvalue: 0.42): Minor branches and twigs (zones 4 and 5) supported fewer species, chiefly bromeliads. Except for *Grammitis* sp. 1, ferns were absent. Relatively few orchid species occurred here, and they were not always present (e.g., *Maxillaria alpestris, Maxillaria* sp. 5, *Stelis* spp. 3 and 4, and Orchidaceae sp. 5). The vertical distribution of individual species was not revealed by this coarse division into sections. With a few exceptions, species had narrow vertical distributions (FIGURE 2).

Due to the heterogeneous structure of the trees, some of the subplots were small (e.g., a single branch) and contained very few epiphyte species, with high relative abundances. Such subplots had diverging species compositions and were disregarded in the interpretation of the results.

Floristic gradients resembling those demonstrated in the present study have been reported previously (Johansson, 1974; ter Steege & Cornelissen, 1989). However, I found the greatest diversity and abundance on the tree bases rather than on large branches in the canopy, as reported by these authors (FIGURE 3). The light regimes in a montane forest were studied by Grubb and Whitmore (1967), who found that light penetration was not the most important reason for the abundance of epiphytes found near the ground. The canopy at Cajanuma is low and irregular and gaps are common. Light penetration may thus contribute to the high abundance and diversity in the lowest tree section.

Substrate

In all three vertical sections, more than half of the epiphyte stands were found on bark (FIGURE 4). Plants growing in minor humus deposits were mainly found in sections I and 2, and plants from large humus deposits were most common in section 2.

Twenty-nine species had at least half of their

FIGURE 3. Numbers of epiphytic species (horizontal axis) found in the three tree sections.

stands on bark, and the following species had more than 90% of their stands on bark: *Fernandezia subbiflora, Maxillaria* sp. 5, *Pleurothallis* sp. 5, *Stelis* sp. 7, and Orchidaceae sp. 5. Three fern species *(Asplenium cuspidatum, Grammitis subtilis.* and *Vittaria remota),* accidental epiphytes (e.g., *Myrsine* sp.), casual epiphytes (e.g., *Semiramisia speciosa, Disterigma pentandrum,* and *Ceratostema* cf. *lanceolatum),* and hemiepiphytes (e.g., *Anthurium* sp. 1 and *Clusia* sp.) are most common on minor humus deposits. Finally, two species *(Elaphoglossum* sp. 5 and *Hymenophyl/um multialatum)* had ca. half of their stands on large humus deposits.

These substrate preferences may relate to differences in the amount of humus accumulated in the sections where the species occurred. **In** most cases, the common occurrence on bark was probably the result of most of the available tree surface not being covered by humus deposits. Minor humus deposits were mainly found as debris trapped by interwoven bryophytes and small scrambling ferns. Patches of humus accumulated in this way covered considerable areas on the lower parts of the trees. Most of the species that were most common on this substrate category have life forms that are characterized by a dependency on soil. Large humus deposits provide the plants growing in them with an ample and stable source of water and nutrients (Benzing, 1987). Such deposits were mainly found around the bases oflarge specimens of *Maxillaria* sp. 1, *Tillandsia* cf. *wurdackii, Tillandsia tetrantha,* or *Elaphoglossum* sp. 6. which were most common in section 2.

The above mentioned patterns are similar to those found in lowland forests by Johansson (1974) in Liberia and ter Steege and Cornelissen (1989) in Guyana. However, those authors reported greatest epiphytic diversity and density

FIGURE 4. Numbers of stands (horizontal axis) of all species (including accidental epiphytes) found rooted in the three substratum classes in the three tree sections.

on humus accumulations on large canopy branches. **In** the Cajanuma plot, the epiphytes appeared more independent of humus deposits. Although most large deposits were found in section 2, most epiphytes occurred on bare bark even in that section. Climatic differences between montane and lowland regions (Grubb & Whitmore, 1966) provide a possible explanation for the relative independence of epiphytes from humus found in the present study. The waterstoring properties of humus deposits may be less important in a wet montane climate where fog occurs frequently.

CONCLUSIONS

Conditions in wet montane forests are more favorable to epiphytes than in lowland regions. But even in the montane forest studied here, which had high epiphytic diversity and density, the majority of the epiphyte species had narrow vertical distributions. The distribution of some species may be affected by a preference for a certain type of substrate. A prime advantage of being rooted in humus deposits is access to a relatively stable. water supply (Benzing, 1987). At Cajanuma, very few species appeared to depend on such deposits.

Vascular epiphytes constitute a significant part of rain forest floras and they play an important role in elemental cycling (Nadkarni, 1984; Gentry & Dodson, 1987). Studies of rain forests should therefore always include studies of the epiphytes. This applies especially to montane rain forests, which are extremely rich in epiphytes.

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APPENDIX 1. List of taxa found on the surveyed trees. Abundance values and life form abbreviations are defined in the text. All vouchers are deposited at AAU. Collection numbers are in parentheses.

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