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# Recovery and succession of epiphytes in upper Amazonian fallows

With Jan H. D. Wolf and Joost F. Duivenvoorden (Published in Journal of Tropical Ecology 22: 705-717, 2006)



Distribution and succession of vascular epiphytes in Colombian Amazonia

## Abstract

The species richness, number of plants, biomass, and species composition of holo- and hemi-epiphytes were recorded in fifty-six 0.04-ha plots, distributed over forest fallows of 2–30 y old and mature forests in lowland Amazonia (Amacayacu National Park, Colombia). A total of 9190 epiphytic plants representing 162 species were recorded on 4277 phorophytes. Seventy species were classified as holo-epiphyte and 85 as hemi-epiphyte. Aroids were most diverse (58 species) and represented 76% of the total recorded biomass. Anemochory was more dominant among holo-epiphytes and zoochory among hemi-epiphytes. The species richness, density and biomass of both holo and hemi-epiphytes increased significantly from young fallows to old fallows and mature forests. Hemi-epiphytes had greater density and biomass than holo-epiphytes. In canonical ordination, forest age did not relate to the species composition of holo-epiphytes. However, for hemi-epiphytes, the age effect was significant, suggesting that species turnover takes place in the ageing fallows.

**Key Words**: Araceae, canopy, Colombia, dispersal, diversity, hemiepiphytes, holo-epiphytes, tropical rain forest, secondary forest

### INTRODUCTION

EPIPHYTIC PLANTS ARE A CONSPICUOUS COMPONENT of mature tropical rain forest (Gentry and Dodson 1987ab). In Amazonia, epiphytes seem to contribute more to the total plant diversity than previously thought (Benavides et al. 2005; Köster et al. 2005). Little is known, however, about epiphyte proliferation in disturbed forests.

During forest succession, epiphyte species may respond to changes in the environmental conditions, associated with the changing structure of the forest (Barthlott et al. 2001; Cascante-Marín 2006; Merwin et al. 2003; Wolf 2005). For example, it has been shown that during forest succession drought tolerant epiphyte species are replaced by species that appear to be better adapted to a more humid microclimate (Barthlott et al. 2001; Wolf and Flamenco 2006).

Slow invasions of epiphytes may also influence the succesional development of epiphyte communities. In tree plantations fewer epiphytes were found compared with the surrounding forest (Catling et al. 1986; Madison 1979; Merwin et al. 2003). Old cyclically clear-cut oak coppices in southern Mexico supported fewer epiphytes compared with oak forests of similar structure that were never clear-cut, providing evidence for dispersal limitation (Wolf 2005). Within forests, the clumped growth of seedlings around mother plants and field experiments also point at dispersal limitation, at least for wind-dispersed epiphytes (Ackerman et al. 1996; Cascante-Marín 2006; Van Dunné 2001). Wind-dispersed orchids, bromeliads, and ferns may find establishment problematical under frequent downpours in the perhumid Amazonian forest (Wolf and Flamenco-S. 2003). Several studies in upper Amazonia report a preponderance of hemi-epiphytic aroids (Benavides et al. 2005; Leimbeck and Balslev 2001), which are dispersed by animals.

This study aimed to explore successional patterns for holo- and hemiepiphytes in fallows of 2 to 30 y old and mature forests, in a wet Amazonian area. Holo-epiphytes by definition (Benzing 1987) do not root in the soil, and their settlement in the fallows is largely dependent on dispersal. We assume that the increasing branch area in the expanding canopies in developing fallows yields a growing supply of fresh substrate allowing a more or less continuous arrival of new holo-epiphyte species. We hypothesise that because of this condition the patterns in holo-epiphyte composition are largely independent of the degree of fallow development. In contrast, most hemi-epiphytes depend both on the soil for rooting and trunks for settlement and anchoring. For these epiphytes, therefore, we hypothesise that the availability of substrate increasingly limits the establishment and growth in aging fallows, leading to species replacement as the prevailing successional pattern in the fallows.

# METHODS

STUDY AREA. – This study was conducted in the Colombian Amazon forest in Amacayacu National Park ( $3^{\circ}$  S and  $69^{\circ}$ - $70^{\circ}$  W; Fig. 4.1) from September 2004 to January 2005. The average annual temperature is ca. 26 °C and relative humidity *c*. 86%. The area receives an average annual precipitation of *c*. 3200 mm, with a less humid period between June and September (Rudas and Prieto 2005; based on climatological records at Leticia airport from 1968-1990). The physiography of the area is slightly undulating corresponding to a dissected sedimentary plain at elevations between 80 and 200 m above sea level (Rudas and Prieto 2005).



**Figure 4.1.** The location of the plots in Amacayacu National Park, Colombian Amazonia. The names refer to the indigenous communities in which territory the plots were made (sites).

The epiphyte sampling was conducted in secondary forests and mature forests (which did not show any sign of human intervention) in *Tikuna* territory of three indigenous communities: Mocagua, Palmeras and San Martín de Amacayacu. Current settlements were established approximately 70 years ago. Nowadays they are surrounded by a mosaic of vegetation patches in different stages of succession as a consequence of the short rotation cycles of the managed forests (Van der Hammen 1992). In the secondary forests, we observed selective extraction of plant products, including rare tree fellings, but no clear-cutting of large areas within the fallows. We also observed occasional weeding around valuable plant species in addition to hunting. Secondary vegetation patches had an approximate size of 0.5-4 ha and were mostly square in shape. The vegetation of the old-growth forest in Amacayacu National Park has been described by Rudas and Prieto (2005).

FLORISTIC SURVEY.-A total of 56 plots was distributed along a chronosequence of fallows and mature forests. The approximate age of the fallows was obtained from interviews with local residents and subsequently corroborated by field observations on the height of Cecropia trees and forest structure. The fallows were assigned to one of four forest age categories (2-8, 9-17, 18-22 and 23-30 y after abandonment). Mature forests were treated as a fifth age category. Plots were square and were 0.04 ha in size, following Gradstein et al. (2003). Plots of the same age category were located more than 300 m apart. Plot coordinates were obtained using GPS (Fig. 4.1). In each plot, the structure of the forest was determined in a 10 x 10 m subplot by estimating the height and measuring the DBH (diameter at 130 cm) of all woody plants. The openness of the canopy was estimated by means of a densiometer at 130 cm height in the centre of each plot (Espherical Densiometer type Robert E. Lemmon, Forest Densiometers, Bartlesville, OK, USA, Model C). Canopy openness was calculated as the mean of four measures in each cardinal direction. Tree stem volume was calculated on the basis of tree height and DBH, assuming a cylindrical bole shape.

Individual vascular epiphytes were recorded when they were attached to trees (including palms and tree ferns) or lianas that rooted within the 0.04ha plots. We defined epiphytes as plants that spend most of their life cycle attached to other plants. Following Benzing (1987), we defined holoepiphytes as those plants that normally spend their entire life cycle perched on trees or lianas and hemi-epiphytes as those plants that spend only part of their life cycle perched on trees or lianas. Primary hemi-epiphytes begin their life cycle as epiphytes and eventually become connected to the ground. Secondary hemi-epiphytes begin as seedlings rooted in the soil but subsequently become detached from the ground. In some species, the boundary between an herbaceous liana and a secondary hemi-epiphyte was not clear (Moffett 2000). Examples were *Manekia sydowii* Trel. (Piperaceae), *Dichorisandra hexandra* (Aubl.) Standl. (Commelinaceae), and *Salpichlaena* cf. *hookeriana* (Kuntze) Alston (Blechnaceae), which were included as hemi-epiphytes. Occasionally, when shoots from one or more individuals from a single species occurred very near to each other, we were not able to distinguish shoots from individual plants. We counted such shoot clusters as one individual (Sanford 1968). Individuals occurring in crowns were examined with the help of binoculars. The DBH of phorophytes was measured (for phorophyte trees smaller than 1.3 m, the stem diameter was recorded at half the height of the tree). Vouchers (AMB 1300-2100) of all species were deposited at the herbarium of the Universidad de Antioquia (HUA).

A non-destructive sampling method was used to estimate epiphyte dry weight biomass of all epiphyte species (Wolf and Konings 2002). Dry weight was estimated on the basis of counts of leaves, fronds or rosettes, depending on the growth form of the species. For hemi-epiphyte species, stem length was used to estimate weights. At least ten leaves or stem sections of *c*. 10 cm in length were sampled and weighted (0.02 g precision), after having been dried at 65° C until constant weight. Subsequently, dry weights were calculated from the average of these values for each species.

NUMERICAL ANALYSES.—Linear regression was used to analyse the response of epiphyte properties to the age of the fallows, excluding the mature forests for which no age was established. To test for differences in plot species richness between holo-epiphyes and hemi-epiphytes, we used analysis of covariance (ANCOVA) with the age of the fallows as covariate. The relation between both the number of individuals and biomass with the

age of the fallow was distinctly non-linear for holo- or hemi-epiphytes, the reason for which here ANCOVA was not attempted.

To test for differences in forest and epiphyte properties between forest age categories or sites, we used analysis of variance (ANOVA) and subsequent Tukey-Kramer's Honestly Significance Difference (HSD) post-hoc multiple comparisons. To improve additivity and homoscedasticity the response variables were log or square root transformed, if needed. To test the degree of association between dispersal syndrome and epiphyte type (holo- or hemi-epiphyte), we used contingency table analysis.

The response of holo- and hemi-epiphytes to environmental variables was further explored using indirect (Detrended Correspondence Analysis, DCA) and direct (Canonical Correspondence Analysis, CCA and Redundancy Analysis, RDA) multivariate gradient analysis. In these, epiphyte species biomass values were log transformed. In CCA, the independent variables were site (a nominal variable in four classes corresponding to each of the three indigenous settlement areas and the area of mature forest), forest age (an ordinal variable of increasing age ranging from 1-5, with the ranks corresponding to the forest age categories), four quantitative variables of forest structure recorded in the 0.01 ha subplot (log-transformed stem basal area, average tree height, log-transformed densities of trees with DBH < 10 cm and DBH  $\geq$  10 cm) and spatial variables. For the latter we used the nine terms of the third-degree polynomial of the latitude and longitude coordinates in decimal degrees, following Borcard et al. (1992) and Legendre and Legendre (1998). In a preliminary CCA with epiphyte species biomass, significant spatial variables were detected using forward selection in CANOCO (P < 0.05). In the final CCA, only these spatial terms were used. The variable inflation factors of the variables remained below 31. Unless otherwise indicated, canonical axes together and the first ordination axis of all CCA were significant in Monte Carlo permutation tests under reduced model (199 permutations). If needed, plot scores along CCA axes were tested for difference against fallow age categories in ANOVA. For the numerical analyses we used JMP (version 3.2.2) and CANOCO (version 4.0; ter Braak and Smilauer 1998).

#### RESULTS

FOREST STRUCTURE.—Not surprisingly, values for tree height, tree volume, and tree basal area in young fallows were lower than in old fallows and mature forest (Table 4.1). There were no significant differences in tree density and canopy openness between the forest age categories (Table 4.1). Forest structural variables did not differ significantly between the sites (ANOVA, P > 0.05; sites defined as in the CCA analysis below).

EPIPHYTE IDENTIFICATIONS AND DISPERSAL SYNDROMES.—In a total sampling area of 2.32 ha (56 0.04-ha plots), we recorded 9190 individual epiphytic plants in 162 species and morphospecies, occurring on 4277 phorophytes (Appendix 4.1). Of the species and morphospecies, 22% were not identified beyond genus and 1% not beyond family level. Of the total, 70 species were classified as holo-epiphyte (26% were not identified beyond genus and 4% not beyond family level) and 85 species were classified as hemi-epiphyte (29% were not identified beyond genus and 1% not beyond family level). Only seven of these were classified as primary hemi-epiphytes. Seven species occurred as occasional epiphytes and these were excluded from further analyses. Holo- and hemi-epiphytes together were distributed in 28 families, 11 of which belonged to pteridophytes. Araceae was by far the most speciose and abundant (Fig. 4.2; Appendix 4.1).

Aroids represented 76% of the total epiphyte biomass of the 356 kg dry weight recorded in all plots together, followed by Cyclanthaceae (9%) and

Dryopteridaceae (8%). The genus Philodendron comprised 57% of the total

epiphyte biomass followed by *Polybotrya* (8.3%) and *Rhodospatha* (7.9%). Five species (*Philodendron ernestii* Engl., *P. fragantissimum* (Hook.) G. Don, *P. asplundii* Croat, *Rhodospatha latifolia* Poeppig Endl., and *Evodianthus funifer* (Poit.) Lindm.) encompassed together 50% of the total of epiphyte biomass (Appendix 4.1).

Zoochoric epiphytes (112 species, 7436 individuals) prevailed over anemochoric species (51 species, 1754 individuals). In terms of number of species, anemochory was more dominant among holo-epiphytes, and zoochory among hemi-epiphytes (contingency table analysis, Pearson Chi-square = 36, P < 0.0001). These same tendencies were found regarding number of individuals (Pearson Chi-square = 1500, P < 0.0001).

EPIPHYTE PATTERNS IN SPECIES RICHNESS, NUMBER OF INDIVIDUALS AND BIOMASS .- The species richness, number of individuals, and biomass of both holo-epiphytes and hemi-epiphytes were positively correlated with fallow age, and clearly showed highest values in the mature forest plots (Table 4.2, Fig. 4.3). The fallow and mature forest plots contained about twice the number of hemi-epiphyte species as holoepiphytes. The average species richness of holo-epiphytes increased from 4 species/0.04 ha in fallows of 5 y to 11 species/0.04 ha in fallows of 30 y old (1.6-fold rise). The relative increment was quite similar in hemi-epiphytes, with species numbers increasing from 10 to 23 species over the same fallow sequence (1.3-fold rise). The slopes of the two regressions (Fig. 4.3A and 4.3D) were not significantly different (test of homogeneity of regression slopes, *F* ratio of interaction term of AGE x epiphyte type = 3.1, *P* = 0.08).

Hemi-epiphytes were far more abundant than holo-epiphytes regarding number of individuals and biomass (Fig. 4.3). On average, five holo-



**Figure 4.2.** Number of epiphyte species of the most diverse families in fallow and mature forest in fifty-six 0.04-ha plots in Amacayacu National Park, Colombian Amazonia. The total number of individuals found in these plots is given in parentheses.

epiphytes were found in fallow plots of 5 y and 35 individuals in fallow plots of 30 y, which represented a 4.6-fold increase. The plot densities of hemi-epiphytes were higher and increased from 60 to 185 over the same chronosequence. However, this rise represented only a 2.1-fold increment. For biomass, the same tendencies were found. Absolute biomass values were low for holo-epiphytes (averaging from 13 to 200 g/0.04 ha in fallows from 5 to 30 y) compared to 1628 to 8387 g/0.04 ha for hemi-epiphytes), but in terms of relative increment the holo-epiphyte biomass increased by a factor of 14.7 in the fallow sequence, while hemi-epiphyte biomass increased only by a factor of 4.1.

Less than one-third of the large trees and lianas (DBH  $\geq$  10 cm) supported holo-epiphytes (Table 4.2). The phorophyte occupancy by holo-epiphytes increased weakly with fallow age (Pearson correlation coefficient of square root transformed occupancy and fallow age was 0.30, P < 0.05). In mature forests, the phorophyte occupancy by holo-epiphytes rose to 55%. Contrary, hemi-epiphytes were found on the majority of the trees and lianas (DBH  $\geq$  10 cm) in the fallows. Phorophyte occupancy by hemi-epiphytes did not increase with fallow age (Pearson correlation coefficient of square root transformed occupancy and fallow age was 0.27, 0.05 < P < 0.10). The occupancy in mature forests did not differ significantly from that in the fallows (Table 4.2).

Aroids dominated the hemi-epiphytes and were therefore largely responsible for the high starting biomass in young fallows and the rather gradual increase in hemi-epiphyte biomass along with fallow age (Fig. 4.4; the family patterns in numbers of individuals were similar to those in biomass and are therefore not shown). In the non-aroid families, holoepiphytes and hemi-epiphytes hardly differed in the way their biomass increased from young to older fallows. With the exception of Gesneriaceae, Polypodiaceae, and the (rarely found) Cecropiaceae and Blechnaceae, all holo-epiphytic and hemi-epiphytic families were most abundant in the mature forest plots. Begoniaceae were entirely restricted to mature forests (Appendix 4.1).

PATTERNS IN EPIPHYTE COMPOSITION.—For the holo-epiphytes the gradient length along the first two DCA axes in the preliminar DCA analyses was 3.5 (axis 1) and 3.4 (axis 2), indicating that even the plots with most divergent species composition still shared species (Ter Braak 1987). Analysed by CCA, holo-epiphyte species composition was related to sites, as shown by the high canonical coefficients for Mocagua and Palmeras (Table 4.3) and the configuration of the plots in the CCA ordination diagram (Fig. 4.5). On the other hand, holo-epiphyte species composition was not related to the structure and age of the forest (Table 4.3, Fig. 4.5).

The forest age categories did not differ in plot scores along the first and second CCA axes (ANOVA *F* ratio = 1.3, P = 0.28 and *F* ratio = 0.3, P = 0.90 for axis 1 and 2, respectively). When the mature forest plots were removed from the CCA analyses, fallow age categories did not show any relationship with holo-epiphyte species composition.

Hemi-epiphytes species patterns showed shorter gradient lengths than holo-epiphytes (2.4 for axis 1, and 2.2 for axis 2). Because linear response patterns prevail in case of gradient lengths below 3 (Ter Braak 1987), the CCA analyses were also done using RDA. However, all CCA results were highly similar to those of RDA, and only CCA results were further presented. Similarly to the holo-epiphytes, hemi-epiphyte species composition was related to sites but not to forest structure (Table 4. 3, Fig. 4.5). However, the age category did show a significant effect, as shown by the fairly high canonical coefficients (Table 4.3). Repeating the CCA analyses after excluding the mature forest plots and subsequent ANOVA analyses of the fallow plot scores along the first CCA axis against fallow age categories yielded a significant result (F ratio = 12.9, P < 0.0001). Also, applying a partial CCA of these fallow data with age category as single explanatory variable and singling out the effect of all other explanatory variables by entering them as co-variables, yielded a significant first canonical axis (F ratio = 1.6, P = 0.01).



**Figure 4.3**. Relationship between forest age and species richness, number of epiphyte individuals and epiphyte biomass for holo-epiphytes (a–c) and hemi-epiphytes (d–f) in Amacayacu National Park, Colombian Amazonia.



**Figure 4.4.** Biomass of the most abundant and diverse epiphyte families in five forest age classes for holo-epiphytes (left) and hemi-epiphytes (right) in Colombian Amazonia. Shown are plot averages and one standard error bar above and below. See Table 4.1 for number of plots.

**Table 4.1**. Properties of forest structure for the fallows and mature forests studied in Amacayacu National Park, Colombian Amazonia. Mean  $\pm$  SD is shown for *n* plots. In the case of significant differences between forest classes, the small letters denote the results of Tukey–Kramer HSD post-hoc comparison tests (with a significance level of 0.05).

Forest age category	п	Mean tree height (DBH $\ge$ 10 cm) in plots (m)	Basal area (m² per 0.01 ha)	Stem volume (m <sup>3</sup> per 0.01 ha)	Tree density (DBH < 10 cm) in 0.01 ha	Tree density (DBH ≥ 10 cm) in 0.01 ha	Total tree density in 0.01 ha	Canopy openness (%)
2-8 y	12	$8.7 \pm 2.2^{a}$	$0.18 \pm 0.06^{ab}$	$1.4 \pm 0.8^{a}$	$64.3 \pm 32.3$	$7.2 \pm 2.9^{ab}$	71.6 ± 33.2	$8.7 \pm 6.9$
9 <b>-</b> 16 y	12	$11.6 \pm 4.3^{ab}$	$0.15 \pm 0.09^{a}$	$1.5 \pm 1.0^{\mathrm{a}}$	$55.9 \pm 34.9$	$5.2 \pm 4.0^{a}$	$61.3 \pm 34.8$	$6.0 \pm 3.6$
17-22 y	13	$13.9 \pm 3.3^{b}$	$0.37 \pm 0.23^{b}$	$5.4 \pm 4.4^{b}$	$59.5 \pm 20.3$	$8.9 \pm 5.8^{b}$	$68.4\pm22.5$	$7.8 \pm 2.4$
23-30 y	11	$15.3 \pm 4.0^{\mathrm{b}}$	$0.37 \pm 0.23^{b}$	$5.8 \pm 4.4^{\mathrm{b}}$	$63.6\pm20.6$	$7.2 \pm 2.4^{ab}$	$71.0 \pm 21.3$	$7.1 \pm 3.5$
Mature forest	8	15.6 ± 3.1 <sup>b</sup>	$0.28 \pm 0.13^{ab}$	$5.7 \pm 4.7^{b}$	69.6 ± 29.9	$5.6 \pm 1.4^{\mathrm{ab}}$	75.8 ± 29.9	$3.7 \pm 1.5$
ANOVA F		7.6***	5.3***	9.5***	0.6	2.7*	0.72	2.1

\* =  $0.01 \le P < 0.05$ ; \*\*\* = P < 0.001.

**Table 4.2**. Properties of epiphyte structure for the fallows and mature forests studied in Amacayacu National Park, Colombian Amazonia. Mean  $\pm$  SD is shown for *n* 0.04-ha plots. In the case of significant differences between forest classes, the small letters denote the results of Tukey–Kramer HSD post-hoc comparison tests (with a significance level of 0.05). \*\*\* = P < 0.001.

Forest age category	п	Holo-epiphytes				
		species	density of	biomass	occupancy for	
		richness	individuals	(kg)	DBH ≥ 10 cm (%)	
2-8 у	12	$5.2 \pm 4.2^{a}$	$10.3 \pm 10.1^{a}$	$0.05 \pm 0.07^{a}$	$13.8 \pm 15.4^{a}$	
9-16 y	12	$5.3 \pm 4.1^{a}$	$12.3 \pm 10.6^{a}$	$0.06 \pm 0.07^{a}$	$22.0 \pm 27.9^{a}$	
17-22 у	13	$8.2\pm5.0^{ab}$	$18.8 \pm 15.2^{a}$	$0.16 \pm 0.23^{ab}$	$15.7 \pm 13.5^{a}$	
23-30 y	11	$11.3 \pm 4.1^{bc}$	$37.1 \pm 16.5^{b}$	$0.19 \pm 0.14^{\mathrm{b}}$	$31.0 \pm 19.2^{ab}$	
Mature forest	8	$15.4 \pm 4.2^{bc}$	61.6 ± 23.9 <sup>b</sup>	$0.42 \pm 0.34^{b}$	55.3 ± 17.4 <sup>b</sup>	
ANOVA F		9.4***	14.7***	6.9***	6.2***	
Forest age	п	<i>Hemi-epiphytes</i>				
category		species	density of s individuals	biomass	occupancy for	
		richness		(kg)	DBH ≥ 10 cm (%)	
2-8 у	12	$10.9 \pm 6.4^{a}$	$66.6 \pm 51.1^{a}$	$2.2 \pm 1.9^{a}$	$49.5 \pm 44.1$	
9-16 y	12	$11.8 \pm 6.7^{ab}$	$77.5 \pm 62.6^{a}$	$3.0 \pm 2.9^{ab}$	$78.0 \pm 89.2$	
17-22 y	13	$18.8 \pm 7.1^{\mathrm{abc}}$	$121.0 \pm 54.3^{a}$	$5.3 \pm 2.7$ ab	$57.7 \pm 23.1$	
23-30 y	11	$21.5 \pm 5.3^{bc}$	$182.7 \pm 81.2^{a}$	$8.4 \pm 4.0^{\mathrm{b}}$	83.3 ± 32.7	
Mature forest	8	$29.3 \pm 5.0^{\circ}$	$305.4 \pm 69.4^{b}$	15.4 ± 3.9°	$100.0 \pm 28.3$	
ANOVA F		14.2***	17.6***	21.5***	2.5	

	Holo-epiphytes	3	Hemi-epiphytes		
	Axis 1	Axis 2	Axis 1	Axis 2	
Mocagua	-0.92	-0.10	0.06	-0.03	
Palmeras	-0.70	-0.49	0.38	-0.14	
San Martín	-0.19	-0.01	0.21	-0.07	
Mature forest	-	-	-	-	
Age forest	-0.02	-0.49	-0.28	-0.09	
ln basal area	0.06	-0.01	-0.01	-0.03	
Height trees	0.00	0.44	0.13	-0.01	
ln small trees	0.03	-0.13	-0.03	0.07	
ln large trees	-0.21	-0.09	-0.02	0.06	
x	-0.37	-0.23	0.05	0.32	
у	-0.17	0.35	0.02	0.14	
y <sup>2</sup>	0.05	0.22	-	-	
У <sup>3</sup>	-	-	-0.01	0.06	

**Table 4.3.** Canonical coefficients of the variables used (see text) in the CCA of holoepiphytes and hemi-epiphytes, based on fifty-six 0.04-ha plots in Colombian Amazonia.



**Figure 4.5**. CCA ordination diagrams based on holo-epiphyte and hemi-epiphyte species biomass in 56 0.04-ha plots. For holo-epiphytes the eigenvalues of CCA axis 1 and 2 were 0.32 and 0.26, respectively (total inertia was 5.8, sum of all canonical eigenvalues was 1.7). For hemi-epiphytes the eigenvalues of CCA axis 1 and 2 were 0.24 and 0.18, respectively (total inertia was 2.9, sum of all canonical eigenvalues was 0.92). Left: plots labeled according to forest age category. Right: plots labeled according to site.

# DISCUSSION

SPECIES RICHNESS, NUMBER EPIPHYTE RECOVERY IN OF INDIVIDUALS, AND BIOMASS.-The species richness, number of individuals and biomass of both holo- and hemi-epiphytes increased significantly from young fallows to old fallows and mature forests. These results correspond to the widely documented dependence of epiphyte proliferation on tree size (Burns and Dawson 2005; Wolf 2005; Zimmerman and Olmsted 1992; Zotz and Vollrath 2003). In general, older forests have larger trunk and branch surface areas that represent more habitat partitioning and more available space for seed interception, colonisation and biomass development (Tewari et al. 1985; Zotz and Andrade 2002). While most epiphyte families showed the highest levels of species richness and abundance in mature forests, some families, in particular Polypodiaceae and Gesneriaceae, showed a preference for fallows. Species of the Gesneriaceae, such as Codonanthe calcarata and C. crassifolia are wellknown for being recorded in association with ant gardens in successional forests (Kleinfeldt 1978).

Holo-epiphytes were almost absent in the youngest fallows, whereas hemiepiphytes, which were mostly represented by aroids, were already substantially present shortly after abandonment. As holo-epiphytes in young fallows must enter from outside the fallows, the slow immigration process often recorded for many epiphytes (Nadkarni 2000; Merwin et al. 2003; Wolf 2005), may largely explain their near-absence in incipient fallows. In particular shade-tolerant species arrive late in the succession (Barthlott et al. 2001; Wolf and Flamenco-S. 2006). For hemi-epiphytes, we suggest that, in addition to immigration, individuals may establish from viable vegetative fragments, or perhaps even from seeds, that have survived the slash-and-burn practices of the pre-fallow stage. Most hemiepiphytes in the current study begin their life-cycle rooted in the soil and

Chapter 4

the relatively fertile condition of the soils in young fallows may have contributed to their fast initial growth.

Whilst the density and biomass of hemi-epiphytes in incipient fallows were higher than those of holo-epiphytes, in aging fallows the holo-epiphytes showed a slightly faster increase in density and biomass. Presumably, the within-fallow expansion rate of the epiphyte population in terms of number of individuals and biomass is relatively independent of the influx of seeds from outside the fallow, a reportedly slow process (see references above). Once a holo-epiphyte is established in the fallow, its high production of wind-dispersed seeds may contribute to its rapid expansion within the fallow. In time, this process may be facilitated by the exponentially expanding branch surface area in aging fallows. Contrary, hemi-epiphytes produce relatively few seeds. In addition, most hemiepiphytes depend on germination in the soil and bark surface area along tree trunks or lianas for attachment and support. Soil surface and stem density hardly increase in aging fallows. Furthermore, stems become rapidly covered by hemi-epiphytes, as shown by the high occupancy values (Table 4.2). This may limit the within-fallow expansion of hemiepiphytes.

EPIPHYTE SPECIES TURNOVER IN TIME.—The eigenvalues of the principal CCA axes were rather low. The first CCA axes explained only a tiny fraction of the variation in the epiphyte species patterns. Congruent with other epiphyte studies it seems that random processes predominated the structuring of the epiphyte assemblages (Wolf 1994). Also, the small plot size probably limited the explanatory power of the CCA.

Fallows are colonized by epiphytes with propagules arriving from nearby locations, leading to configurations of species assemblages which reflect the local species pools. The latter is shown by the effect of the spatial coordinates and the sites on the holo- en hemi-epiphyte species composition (Table 4.3; Fig. 4.5).

The lack of an age effect on the patterns of holo-epiphyte species composition in the fallows corresponded to our expectation that through time holo-epiphyte species have a more or less equal chance to settle and grow in the expanding crown areas of the fallows. During the development of the holo-epiphyte community in any fallow the incoming species would essentially represent a random draw from the surrounding fallows and mature forests. Because the species tend to accumulate in aging fallows (Fig. 4.3), eventually this process should make older fallows more similar to each other in holo-epiphyte species composition. However, evidence for this was not found in the CCA, probably because the effect of the randomly incoming species still prevailed and masked any trend in time (regarding species composition). Also, the lack of an age effect on holo-epiphyte species composition might be partially due to the low density of species and individuals in the plots, prohibiting the detection of changing species composition in time because of the small sample size.

The age effect was clearer for the hemi-epiphytes, suggesting that species turnover takes places in the aging fallows. In view of the increasing density and biomass of hemi-epiphytes in developing fallows (Fig. 4.3), the withinplot hemi-epiphyte expansion probably becomes more limited by space (phorophyte density, bark surface area, or soil availability). Monitoring of colonization and growth of hemi-epiphytes in permanent plots in combination with experimental studies (e.g. species removal or artificial elimination of the above-mentioned limitations) is needed to test if the species turnover in time is due to successive replacement of competitively inferior species.

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