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ECOLOGY OF FOLIICOLOUS LICHENS AT THE "BOTARRAMA" TRAIL (COSTA RICA), A NEOTROPICAL RAIN FOREST SITE. PART II. PATTERNS OF DIVERSITY AND AREA COVER, AND THEIR DEPENDENCE ON MICROCLIMATE AND PHOROPHYTE SPECIES*

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Abstract. Thirteen environmental variables, including phorophyte characters and microclimatic factors, were studied on 321 phorophyte individuals belonging to 39 species, in order to establish their influence on foliicolous lichen colonization in a tropical rain forest. Species richness and area cover of foliicolous lichens are multiply correlated with environmental variables, and leaf longevity, presence of hairs or glands, surface fine structure, surface continuity, sample size, and relative air humidity are the most important variables explaining their variation. Species richness and area cover show a logarithmic-linear relationship, i.e., species richness first increases and then decreases with increasing area cover. The 39 phorophyte species differ markedly in species richness and area cover. Those supporting rich foliicolous lichen cover include palms, Araceae, Lauraceae, Meliaceae, and Moraceae, while ferns, Costaceae, Clusiaceae, Melastomataceae, and Myrsinaceae shelter a poor foliicolous lichen flora. High species richness and area cover are correlated with long-lived leaves of the thin leathery dicotyledoneous or palm type, while poor foliicolous lichen colonization is found on phorophytes with short-lived leaves, hairs or glands, or a fine surface structure consisting of large, papillose cells. Intraspecific β-diversity within a given phorophyte species is significantly higher than β-diversity between adjacent individuals belonging to different species, indicating that spatial relationships are more important than phorophyte species in the creation of similar foliicolous lichen floras. The low interspecific β-diversity between different species suggests a low degree of phorophyte preferences among foliicolous lichens. Phorophyte species within the understorey are less similar to each other in their foliicolous lichen species composition than those within light gaps, while on the other hand light gap microsites are less similar to each other in overall species composition than understorey microsites. Obviously, the colonization of phorophytes by foliicolous lichens in the understorey follows more deterministic patterns, while in light gaps it is more stochastic. Species-sample curves show a logarithmic pattern, their inclination and degree of saturation depending on the minimum species richness of the photophytes included. High cumulative species richness is more quickly reached when phorophyte species with high species richness are selected. *Accepted 20 December 1997.*

Key words: Costa Rica, deterministic processes, diversity patterns, alpha-diversity, beta-diversity, gamma-diversity, foliicolous lichens, microclimatic factors, phorophyte characters, stochastic processes.

INTRODUCTION

The high diversity, in particularly the species richness, of tropical rain forests has attracted scientists ever since European naturalists began to explore these vast habitats centuries ago (Wilson 1988, Whitmore 1990). However, it was not until a few decades ago that the mechanisms underlying the maintenance of that high diversity began to be studied in detail (Connell & Orias 1964, Terborgh 1973, Pielou 1975, Ricklefs 1977, Whittaker 1977, Connell 1978, Huston 1979, Bourgeron 1983, Kubitzki 1985, Stocker *et al.* 1985, Linsenmair 1990). High diversity on a small scale is particularly obvious in foliicolous lichens: 40 % of the 550 world-wide known species can be found at a single site (Lücking 1998a), and more than 80 on a single palm leaf (Lücking in

* Part I: Biotropica, in press.

prep.). Lücking (1995a) documented the biodiversity of foliicolous lichens in Costa Rica and discussed possible mechanisms that could account for the high diversity at different scales.

A great deal of information on the mechanisms underlying high diversity on the small scale level can be derived from the analysis of within-site diversity patterns. For this purpose, three parameters covering different aspects of diversity are available: α, β, and γ-diversity (Mac Arthur 1965; Whittaker 1972, 1977). Originally, these parameters were defined within a narrow context related to community ecology but may also be used in general terms. Thus, α-diversity, in its original sense, is the diversity within a given community. It can be measured as species richness ("richness diversity"), or additionally the frequency of each species is taken into account ("heterogeneity diversity"; Lloyd & Ghelardi 1964, Peer 1974, Pielou 1975). In a broad sense, the concept of α-diversity applies to any given entity, particularly the single sample, regardless of whether it represents part of a community or covers several communities at a time. Accordingly, rhe cumulative diversity of adjacent communities is defined as γ-diversity ("landscape diversity"), while in general terms it is the cumulative diversity of any particular set of samples. Thus, α and γ-diversity are relative parameters: given a set of samples, their cumulative diversity is to be considered as γ-diversity with regard to the single sample, but as α-diversity with regard to a higher entity of which the set of samples is part.

In its original definition, β-diversity means the variation in species composition between distinct communities or along an environmental gradient (MacArthur 1965; Whittaker 1972, 1977; Gauch 1982). However, β-diversity can also be regarded as variation in species composition between any given entities or samples: considering different communities, β-diversity is a measure of the variation caused by the environmental variables governing species composition within these communities, while in the case of samples belonging to a single community β-diversity is a measure of the degree of stochasticity governing the distribution of species within parts or patches of a homogeneous environment. Since stochasricity is an important factor explaining the high diversity in tropical environments (Linsenmair 1990), the analysis of within-community β-diversity can be particularly interesting.

The three parameters are correlated with each other: the higher the α and β-diversity, the higher the γ-diversity. Thus, similar γ-diversity might be achieved by either high α and low β-diversity or by low α and high β-diversity. Because the mechanisms governing α or β-diversity are different, the analysis of patterns of α and β-diversity can reveal much information on the causes of high β-diversity at a given scale. Relationships between α, β, and γ-diversity are also reflected in species-sample curves, which in tropical environments with high diversity usually show high inclination and retarded saturation (Ashton 1964, Vareschi 1980, Gradstein *et al.* 1996).

The present paper forms the second part of a series dealing with the ecology of foliicolous lichens in a Neotropical rain forest (Lücking 1998a-c). In the first part, a list of 217 species found at the "Botarrama" trail is presented and their ecogeographical preferences are evaluated. In this second part, patterns of α, β, and γ-diversity of foliicolous lichens are analyzed with regard to different environmental variables, including microclimatic factors and phorophyte characters. For this purpose, 39 different phorophyte species distributed among 321 phorophyte individuals were selected, and 13 environmental variables were measured on each individual and then related to the foliicolous lichen flora found on each of the selected phorophytes.

MATERIAL AND METHODS

The study was carried out between March 1991 and July 1992 at the "Botarrama" trail, a premontane rain forest in the Braulio Carrillo National Park, Costa Rica. The site is described in detail in the first part of this series (Lücking 1998a). For the ecological investigations, 39 phorophyte species were selected (Table 1), with 341 individuals situated along a 750 m long transect laid through the trail. Only phorophytes of the forest understorey or natural light gaps were considered, up to a height of 2.5 m; the canopy was treated in a separate study (Lücking 1995b). Of the initially selected individuals, 20 had to be omitted due to branch litter, flooding or death, a remarkably low rate of loss given the high probability of branch litter in these forests (Hartshorn 1991). According to their position, the remaining 321 individuals were assigned to 14 microsites of three different microsite types (Fig. 1): (1) shady understorey (six microsites with a total of 167 individuals), (2) light gaps (six microsites with a total of 97 individuals), and (3) creek sites (two microsites with a total of 57 individuals).

For each phorophyte individual either the single shoot (in all pteridophytes and monocots) or a re-

TABLE 1. List of phorophyte species selected for the ecological investigations, arranged according to major systematic groups and, within the groups, alphabetically. For each species the number of individuals included in the study is indicated. For additional information on the phorophyte species see Part III (Lücking 1998b).

Pteridophyta	
Ctenitis subincisa (Willd.) Ching (Tectariaceae)	9
Diplazium ceratolepis (H. Christ) L. D. Gómez (Athyriaceae)	8
Diplazium lindbergii (Mett.) H. Christ (Athyriaceae)	8
Salpichlaena volubilis (Kaulf.) J. D. Sm. (Blechnaceae)	14
Thelypteris gigantea (Mett.) Tryon (Tectariaceae)	8
Spermatophyta: Monocotyledoneae	
Arecaceae (palms)	
Calyptrogyne condensata (Bailey) Wessels Boer	12
Chamaedorea tepejilote Liebm.	10
Cryosophila warscewiczii (H. Wendl.) Burret	11
Geonoma cuneata H. Wendl. ex Spruce	10
Iriartea deltoidea Ruiz & Pav.	6
Prestoea decurrens (H. Wendl. ex Burret) H. E. Moore	8
Welfia georgii H. Wendl. ex Burret	5
Araceae (aroids)	
Anthurium bakeri Hook f.	7
Dieffenbachia longispatha Engl. ex Krause	11
Monstera tenuis C. Koch	5
Philodendron verrucosum Mathieu	6
Rhodospatha wendlandii Schott ex Engl.	15
Spathiphyllum friedrichsthalii Schott	7
Zingiberales and others	
Costus curvibracteatus Maas (Costaceae)	7
Costus laevis Ruiz & Pav. (Costaceae)	6
Costus malorticanus H. Wendl. (Costaceae)	7
Cyclanthus bipartitus Poit. (Cyclanthaceae)	8
Heliconia sp. (Heliconiaceae)	8
Renealmia concinna Standl. (Zingiberaceae)	7
Spermatophyta: Dicotyledoneae	
Ardisia auriculata Donn. Sm. (Myrsinaceae)	9
Besleria notabilis Morton (Gesneriaceae)	9
Columnea consanguinea Hanst. (Gesneriaceae)	4
Faramea suerrensis (J. D. Sm.) J. D. Sm. (Rubiaceae)	6
Guarea grandifolia DC. (Meliaceae)	6
Guarea kunthiana A. Juss. (Meliaceae)	7
Guatteria aeruginosa Standl. (Annonaceae)	6
Miconia hamelii Almeda (Melastomataceae)	8
Miconia sp. (Melastomataceae)	9
Naucleopsis naga Pittier (Moraceae)	4
Ocotea atirrensis Mez & J. D. Sm. (Lauraceae)	16
Piper glabrescens (Miq.) C. DC. in DC. (Piperaceae)	13
Pourouma minor Benoist (Cecropiaceae)	8
Schlegelia sulfurea Diels (Bignoniaceae)	7
Vismia billbergiana Beurl. (Clusiaceae)	6

presentative branch (in all dicots except for unbranched individuals of *Ardisia auriculata* and *Besleria notabilis*), always with the whole leaf sequence included, was marked for the determination of environmental variables and the subsequent sampling of the foliicolous lichen flora after a period of twelve months. Thirteen environmental variables were considered: six specific and three individual phorophyte characters, and four microclimatic factors. For each phorophyte species the following six specific characters were determined:

Coarse surface structure. Defined as the surface structure created by the leaf venation (prominence, density, and direction), and determined by means of surface photographs, using a NIKON F 501 with SOLIGOR 90 mm macro lens at a scale of 1:1 in longitudinal and transversal direction with respect to the principal leaf or leaflet axis.

Fine surface structure. Defined as the surface structure created by the external shape of the epidermal cell walls and leaf cuticle. Determined by means of SEM photographs, using a ZEISS NOVASCAN 30 at a magnification of 500x. Pieces of leaves not covered by epiphylls were collected in the field and conserved in 70% ethanol, later dehydrated in 100% ethanol and critical point dried (BAL-TEC CPD 030), then finally covered with gold-palladium target (BALZERS UNION MED 010).

Surface continuity. Since the influence of leaf shape on foliicolous lichen cover is subtle and difficult to meaningfully correlate with the latter when multiple factors are involved, surface continuity was selected as an alternative variable. Surface continuity was defined as the diameter to which a lichen thallus can grow on a given leaf before reaching the leaf margin or prominent leaf structures which possibly prevent further growth. For example, taxa such as the subcuticular *Strigula nemathora* Mont. have difficulties in passing major leaf veins (Santesson 1952), and this might prevent their growth and reproductive success on a given phorophyte species. Species which do not produce mature fruit bodies until the thallus has reached a certain age and diameter might be unable to successfully colonize finely divided leaves, e.g., those of many pteridophytes. In that way, surface continuity conforms to a simplified variable dependent on both leaf shape and coarse surface structure.

Presence of hairs (on the upper leaf surface).

Presence of glands (on the upper leaf surface).

Presence of drip tip. The ecological importance of drip tips and their influence on epiphyll cover have been controversially discussed (Seybold 1957, Vareschi 1980, Ellenberg 1985). This character was therefore included in the present study. A drip tip was diagnosed when the tip of the leaf (or leaflet in case of compound leaves) was distinctly narrowed and provided with parallel margins over a length of at least 5 mm.

Three further characters were determined for each phorophyte individual:

Height of exposure (of the selected branch). In the forest understory, plants growing close to the ground

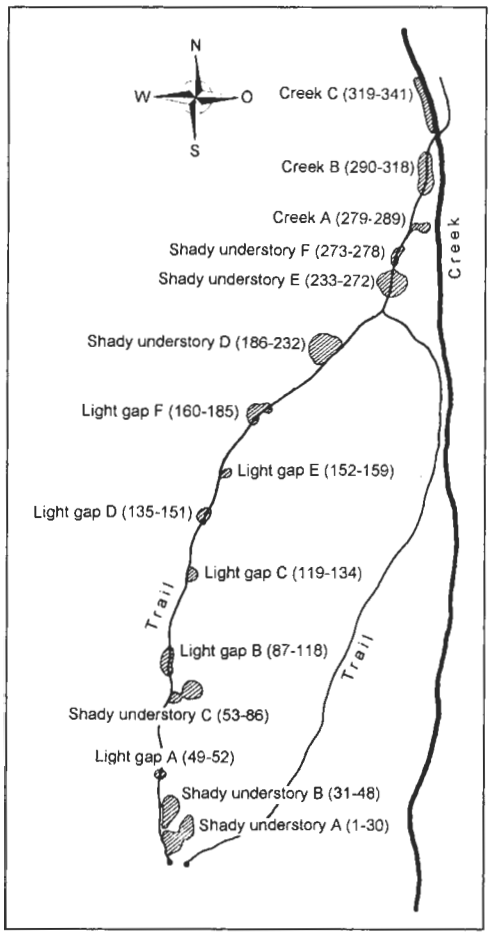

FIG. 1. Map of the transect laid through the "Botarrama" trail, showing position of microsites and numbering of phorophyte individuals.

are affected by splashing rain-water carrying ground detritus, and this might influence the conditions for epiphyll colonization. Therefore this character was included. In the case of horizontal branches, the branch center was selected as the reference point, while in unbranched monocots with vertical orientation, height of exposure was calculated as average of all leaves along the shoot.

Leaf longevity. The age of the oldest leaf on a shoot or selected branch was taken as an estimate for leaf longevity of a given phorophyte individual. Since the observation period did not allow direct measurements of leaf age, the age of the oldest leaf was estimated by measuring the time span between the formation of two subsequent leaves and multiplying with the number of leaves occurring along the shoot or selected branch. In phorophytes where the oldest leaves were regularly shed, this procedure gave a rather reliable estimate of leaf longevity, while in those phorophytes where the oldest leaf remained during the whole observation period, the leaf longevity was underestimated.

Sample size. Contrary to usual phytosociological approaches, it was not possible to apply a constant sample size for each phorophyte individual when sampling the foliicolous lichen flora, since each leaf or branch forms an isolated sample in itself. Therefore, except for phorophytes with very large leaves, the sample size was defined as the area formed by all leaves occurring along the shoot or selected branch. In phorophytes with very large leaves (more than 500 cm^2), particularly palms and *Heliconia* sp., for each leaf four subsamples with a size of 10×10 cm^2 each were selected, close to the petiole and apex and at both sides of the center of the leaf. In the case of large compound leaves (pteridophytes and palms), 50 % of the leaflets, but 20 at most, were selected as subsamples (see also Part I: Lücking 1998a). In that way the sample size varied according to the phorophyte individual, and thus had to be included as an additional variable possibly influencing foliicolous lichen cover.

The reliable measurement of microclimatic factors in nature is difficult, especially in complex ecosystems and when many reference points have to be considered over a prolonged period (Unwin 1980, Greig-Smith 1983). However, in order to characterize communities in a phytosociological context, measurements do not have to be as exact as in the case of physiological processes to be correlated with multiple microclimatic factors. In the present case, the aim was to determine microclimatic differences between phorophyte individuals acting as microsites for foliicolous lichens. Thus, those extremes had to be taken into consideration which are likely to be caused by the location of the individual within the vegetation, and not by single, stochastic events such as temporary light flecks (Chazdon & Fetcher 1984a, b). While such events are of great physiological importance for the plant (Chazdon 1988), they are quite difficult to meaningfully correlate with its presence or the colonization with foliicolous lichens at a given microsite. Hence, the following four microclimatic factors were determined for each phorophyte individual over a period of twelve months:

Relative light intensity. Light intensity was chosen as a universal measure to characterize the light environment of a given phorophyte individual. Relative light intensity was defined as the intensity at a given phorophyte individual, relative to the intensity on a free area outside the forest ("diffuse site factor": Anderson 1964, Steubing 1965, Janetschek 1982). Relative light intensity was measured every four weeks in five repetitions between 10:00 am and 12:00, during diffuse light conditions, i.e., homogeneous cloud cover, using TESTOTHERM Luxmeters 0500 with Silicium photocells. Homogeneous cloud cover is thereby necessary since only in this way the differences caused by the microsite become obvious. To protect against damage, the measuring devices (not the sensors) were held in plastic bags with drying material.

Air temperature and relative air humidity. These variables were measured simultaneously, using a TESTOTHERM testo 600 electronic hygrometer with capacitive sensor (NTC). Like relative light intensity, air temperature and relative humidity were determined every four weeks in five repetitions between 10:00 am and 12:00. Based on previous studies, the measurements were carried out during dry conditions with low cloud cover around midday, expected to yield the lowest values for relative air humidity and the highest values for temperature possible at a given microsite. The measuring device (except for the sensor) was protected in the same way as the luxmeters.

Evaporation. Evaporation was measured using devices similar to Piche evaporimeters but modified in a way that enabled their exposure during prolonged periods. This modification was necessary since evaporation in the understory of tropical rain forests is too low to give reliable data during short-time measure-

ments. To protect the devices from the influence of rainwater, they were positioned in a reverse way and covered by a plastic top of 20 cm in diameter. The usual filter discs (SCHLEICHER & SCHÜLL, no. 2652 green) were positioned at the top of the devices, and continuous evaporation was guaranteed by means of a wool cord connecting the filter disc with the water column (see A. Lücking 1995). The available 100 devices were exposed in a way that groups of 1–6 spatially adjacent phorophyte individuals could be referred to each device.

Two data sets were obtained to characterize and quantify foliicolous lichen colonization. For comparison of α, β, and γ-diversity between phorophytes, the presence / absence of foliicolous lichen species on all 321 individuals was taken into consideration. For the correlation of species richness and area cover with environmental variables, a subset of 139 phorophyte individuals belonging to 16 species was selected (see Part I: Lücking 1998a), and both species richness and area cover of all foliicolous lichens on a given phorophyte individual were calculated, the latter as a percentage relative to the sample size, i.e., all leaves on a given branch. In addition to area cover, the developmental state of each lichen thallus was taken into consideration, assuming the following values: 1 = sterile, 2 = asexual reproductive organs present, 3 = young sexual reproductive organs present, 4 = mature sexual reproductive organs present. This value was multiplied with the area cover of each lichen thallus and yielded a modified value for cumulative area cover, here called developmental state. The three diversity parameters were determined as follows:

Species richness (α-diversity): Number of foliicolous lichen species on a given phorophyte individual.

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Multiple regression was performed with the subset of 139 phorophyte individuals to demonstrate correlations between species richness and area cover and selected environmental parameters, and relationships between various parameters were approximated by non-linear estimation. Species-sample curves were constructed by computer-based random selection of phorophyte individuals, with 10 times repetition and calculation of the arithmetic mean. The resulting curves were smoothed by a Daniell transformation (Blomfield 1976). Phorophyte individuals were selected considering different minima of species richness ($\alpha_{min.}$ = 5, 10, 20, and 30 species) to construct different species-sample curves. All statistic calculations were performed with STATISTICA 5.0, except for the calculation of β-diversity and species-sample curves which were carried out by means of Q-BASIC programs written by the author.

RESULTS

Phorophyte characters. The principal types of coarse surface structure are parallel and net venation (Fig. 2A-B), typical of palms and most dicots (Table 2). Leaves with a smooth surface are found in the aroid *Dieffenbachia longispatha* and the dicot *Guarea kunthiana* (Fig. 2C), while *Thelypteris gigantea* and *Miconia* spp. have perpendicularly crossed veins (Fig. 2D). In most phorophyte species, the fine surface structure appears isodiametric to ± prosenchymatic (Table 2), the size of the protruding epidermal cells being about 10 mm (Fig. 3A-B). *Guatteria aeruginosa* exhibits a rather smooth surface (Fig. 3C), while in *Philodendron verrucosum*, *Costus* spp., and *Heliconia* sp. it consists of rather large, papillose cells about 30 mm in diam. (Fig. 3D). In a few species, the protruding cells are narrow and elongate, creating a grooved appearance as in the palm *Iriartea deltoidea* (Fig. 3E), or the cuticle itself is ornamented, such as in *Rhodospatha wendlandii* and *Guarea grandifolia* (Fig. 3F); in both cases the structural dimensions are in the region of 1–3 mm. Surface continuity

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RESULTS

Phorophyte characters. The principal types of coarse surface structure are parallel and net venation (Fig. 2A-B), typical of palms and most dicots (Table 2). Leaves with a smooth surface are found in the aroid *Dieffenbachia longispatha* and the dicot *Guarea kunthiana* (Fig. 2C), while *Thelypteris gigantea* and *Miconia* spp. have perpendicularly crossed veins (Fig. 2D). In most phorophyte species, the fine surface structure appears isodiametric to ± prosenchymatic (Table 2), the size of the protruding epidermal cells being about 10 mm (Fig. 3A-B). *Guatteria aeruginosa* exhibits a rather smooth surface (Fig. 3C), while in *Philodendron verrucosum*, *Costus* spp., and *Heliconia* sp. it consists of rather large, papillose cells about 30 mm in diam. (Fig. 3D). In a few species, the protruding cells are narrow and elongate, creating a grooved appearance as in the palm *Iriartea deltoidea* (Fig. 3E), or the cuticle itself is ornamented, such as in *Rhodospatha wendlandii* and *Guarea grandifolia* (Fig. 3F); in both cases the structural dimensions are in the region of 1–3 mm. Surface continuity

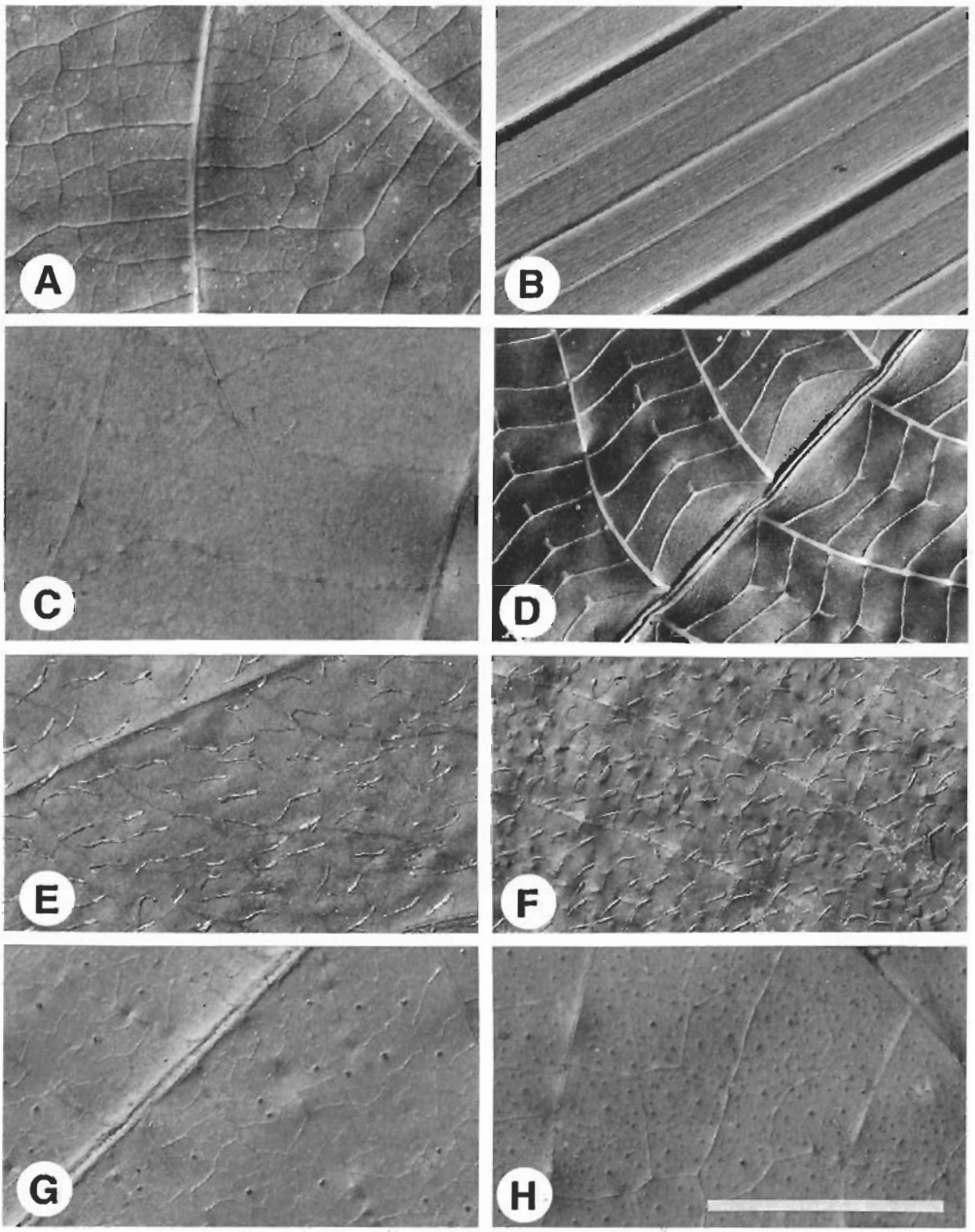

FIG. 2. Coarse leaf surface structure of different phorophyte species. A – *Ocotea atirrensis*. B – *Geonoma cuneata*. C – *Guarea kunthiana*. D – *Thelypteris gigantea*. E – *Besleria notabilis* (upper surface hairs). F – *Miconia hamelii* (upper surface hairs). G – *Ardisia auriculata* (glands). H – *Vismia billbergiana* (upper surface glands). Scale: 1 mm.

varies between 3 and 220 mm (Table 2), values of less than 20 mm being found in phorophyte species with narrow or finely divided leaves, such as *Ctenitis subincisa* and *Cryosophila warscewiczii*, or with very prominent veins, like *Thelypteris gigantea* and *Chamaedorea tepejilote*.

Hairs on the upper leaf surface are found in *Costus curvibracteatus*, *C. malortieanus*, and *Miconia*

TABLE 2. Distribution of characters among the phorophyte species (arrangement as in Table 1). For surface continuity, height of exposure, leaf longevity, and sample size, the ranges within the species are given, and, in addition, the average in the case of leaf longevity. Statements in brackets indicate that hairs are only present on young leaves, and that a drip tip is only moderately developed. Abbrevations: Prosen. = prosenchymatic, ornam. = ornamented, isodiam. = isodiametric.

Taxa	Coarse surface structure	Fine surface structure	Surface continuity [cm]	Presence of hairs or glands	Presence of marked drip tip	Height of exposure [cm]	Leaf longevity [months]	Sample area [dm^2]
Ctenitis	smooth	prosen.	3- 6	(hairs)	–	40-100	8- 43 / 18	9- 32
Diplazium c.	smooth	prosen.	25- 34	–	(+)	30- 80	15- 27 / 21	19- 65
Diplazium l.	smooth	smooth	8- 11	–	–	70-120	5- 45 / 19	7- 23
Salpichlaena	smooth	grooved	12- 15	–	(+)	50-250	6- 48 / 29	6- 36
Thelypteris	crossed	prosen.	9- 13	–	+	40- 70	5- 53 / 28	15- 50
Calyptrogyne	parallel	prosen.	13- 16	–	(+)	130-180	16- 68 / 43	40- 99
Chamaedorea	parallel	grooved	6- 9	–	+	140-220	10- 23 / 16	20- 47
Cryosophila	parallel	prosen.	12- 15	–	+	130-160	20- 63 / 33	49- 91
Geonoma	parallel	prosen.	14- 18	–	(+)	100-170	18- 46 / 30	24- 81
Iriartea	parallel	grooved	140-220	–	–	50-250	40-107 / 73	18- 48
Prestoea	parallel	grooved	13- 16	–	+	70-220	18- 50 / 35	19- 36
Welfia	parallel	grooved	14- 17	–	+	140-230	26- 76 / 42	62-117
Anthurium	net	ornam.	15- 22	–	(+)	100-210	30- 70 / 46	6- 15
Dieffenbachia	smooth	smooth	85-125	–	(+)	40-110	15- 70 / 32	20- 58
Monstera	parallel	prosen.	15- 55	–	–	100-250	23-101 / 51	10- 25
Philodendron	parallel	papillose	75-150	–	+	30-240	10- 31 / 20	14- 69
Rhodospatha	parallel	ornam.	58- 67	–	(+)	100-180	16- 45 / 29	28- 64
Spathiphyllum	parallel	large	95-120	–	(+)	60-140	11- 45 / 28	53-116
Costus c.	parallel	prosen.	44- 54	hairs	(+)	50-150	8- 25 / 14	7- 14
Costus l.	smooth	papillose	45- 52	–	(+)	110-160	16- 39 / 29	7- 25
Costus m.	smooth	papillose	43- 69	hairs	(+)	40-110	9- 21 / 15	2- 13
Cyclanthus	crossed	smooth	33- 58	–	(+)	30-150	25- 81 / 45	9- 24
Heliconia	parallel	papillose	80-120	–	(+)	130-170	20- 40 / 28	10- 45
Renealmia	smooth	isodiam.	25- 32	–	(+)	40-110	16- 52 / 35	5- 8
Ardisia	net	isodiam.	55- 75	glands	(+)	80-140	12- 22 / 16	17- 47
Besleria	smooth	isodiam.	58- 65	(hairs)	(+)	50-130	15- 30 / 21	8- 15
Columnea	smooth	prosen.	28- 37	–	(+)	40-180	11- 17 / 15	6- 12
Faramea	net	prosen.	22- 34	–	+	80-160	14- 56 / 31	3- 8
Guarea g.	net	ornam.	52- 58	–	+	50-210	34- 78 / 46	34-106
Guarea k.	smooth	smooth	56- 78	–	(+)	140-220	17- 43 / 30	19- 94
Guatteria	net	smooth	42- 52	(hairs)	+	130-180	18- 49 / 31	18- 37
Miconia h.	crossed	prosen.	28- 35	hairs	(+)	140-180	12- 21 / 17	5- 9
Miconia sp.	crossed	isodiam.	52- 67	–	+	80-210	16- 76 / 38	16- 28
Naucleopsis	net	prosen.	44- 58	–	+	40-190	26- 85 / 67	14- 31
Ocotea	net	isodiam.	48- 65	–	+	90-210	17-137 / 63	13- 33
Piper	net	isodiam.	28- 36	–	(+)	30-170	12- 38 / 28	2- 9
Pourouma	crossed	smooth	52- 85	–	+	130-180	13- 37 / 20	17- 39
Schlegelia	net	smooth	32- 38	–	+	90-160	16- 60 / 39	3- 8
Vismia	net	isodiam.	28- 45	glands	+	120-180	12- 28 / 17	1- 5

hamelii (Fig. 2E-F), as well as in young leaves of *Ctenitis subincisa*, *Besleria notabilis*, and *Guatteria aeruginosa* (Table 2). Their size and density does not vary significantly between species. *Ardisia auriculata* and *Vismia billbergiana* have glands on the upper leaf surface (Fig. 2G-H), originating from the mesophyll and accompanied by specialized hairs (Fig. 3G-H). Drip tips are found in species of all systematic groups (Table 2) but are absent, for example, in *Ctenitis subincisa*, *Iriartea deltoidea*, and *Monstera tenuis*.

Height of exposure ranges between 30 and 250 cm (Table 2). Phorophyte individuals belonging to *Diplazium ceratolepis*, *Thelypteris gigantea*, or *Costus malortieanus*, among others, mostly grow to less than 100 cm. Estimated leaf longevity varies from (5-) 12 to 48 (-137) months (Table 2). Short-lived leaves (less than 24 months) are found in the ferns *Ctenitis subincisa* and *Diplazium ceratolepis*, in the palm *Chamaedorea tepejilote*, in *Costus curvibracteatus*, and *C. malortieanus*, and in the dicots *Ardisia auriculata*, *Besleria notabilis*, *Columnea consanguinea*, *Miconia hamelii*, and *Vismia billbergiana*. Depending on leaf size and number of leaves per shoot or branch, the sample size of a given phorophyte individual varies between 1 and 117 dm^2 (Table 2). The lowest values (less than 10 dm^2) are due to small-leaved species with few leaves per shoot or branch, such as *Faramea suerrensis*, *Schlegelia sulfurea*, or *Vismia billbergiana*, while most palms and aroids show very high sample sizes averaging 50–100 dm^2.

Microclimatic factors. Outside the forest, absolute light intensity amounted to 35,000–70,000 lux in diffuse light, reaching up to 115,000 lux in direct insolation and less than 10,000 lux before rainfall. In the forest interior, absolute light intensity varied between 360 and 16,400 lux in diffuse light. Accordingly, relative light intensity oscillated between 0.7 and 30.8 %, with 1–4 (–10) % on an average at understory microsites and (1–) 4–15 (–30) % at light gap microsites (Table 3). Phorophyte individuals at the margins of light gaps showed values comparable with those at understory microsites. Daily maximum air temperature varied between 23.7 and 24.9°C on average according to the microsite, with minima of 21.1–22.9°C and maxima of 25.4–28.0°C depending on the weather conditions (Table 3). The lowest values were found along the creek and the highest in light gap microsites.

Starting from nearly 100 % at dawn, day minimum relative air humidity could sink as low as 69 % during dry conditions but usually remained above 85 %, with an average of 90 %. The minima found at understory and light gap microsites do not differ markedly, on an average amounting to 86–91 % at light gap and 90–93 % at understory microsites (Table 3). Near the creek, relative air humidity rarely dropped below 90 %, with the daily minima oscillating around 94 %. Accordingly, daily evaporation amounted to 0.14–0.37 (–0.50) mm at understory and (0.12–) 0.30–0.70 mm at light gap microsites, while along the creek it was 0.09–0.33 mm (Table 3).

Two light gap microsites, nos. 3 and 5, showed lower air temperature, higher relative air humidity, and lower evaporation compared to the other light gap microsites, and might be classified as humid light gaps. One understory microsite, no. 6, which was located near the creek microsites, showed lower air temperature, higher relative air humidity, and lower evaporation than the other understory microsites.

The four microclimatic factors are significantly correlated (Table 4). There is a high redundancy between air temperature and relative air humidity and between relative air humidity and evaporation. The punctual measurements of relative air humidity, as carried out here, are thus sufficiently well supported by the long-term measurements of evaporation. On the other hand, the high redundancy indicates relative light intensity and relative air humidity, in contrast to evaporation measured at each phorophyte individual, as those microclimatic factors which carry most of the information.

Within a given phorophyte species, the individuals are rather evenly distributed over different microclimatic conditions (Fig. 4A-B), and significant preferences of a given species for certain conditions are not obvious (Kruskal-Wallis H-test: $P = 0.3347$, for relative light intensity, and $P = 0.9618$, for relative air humidity).

Multiple correlation of species richness and area cover with environmental variables. Of the three parameters representing different aspects of foliicolous lichen colonization, species richness, area cover, and developmental state, the last two are perfectly redundant ($r = 0.996$, $P < 0.001$). This means that developmental state gives no further information beyond area cover, and for all further calculations, only species richness and area cover are taken into consideration.

Multiple correlation of species richness with 10 environmental variables is highly significant at r =

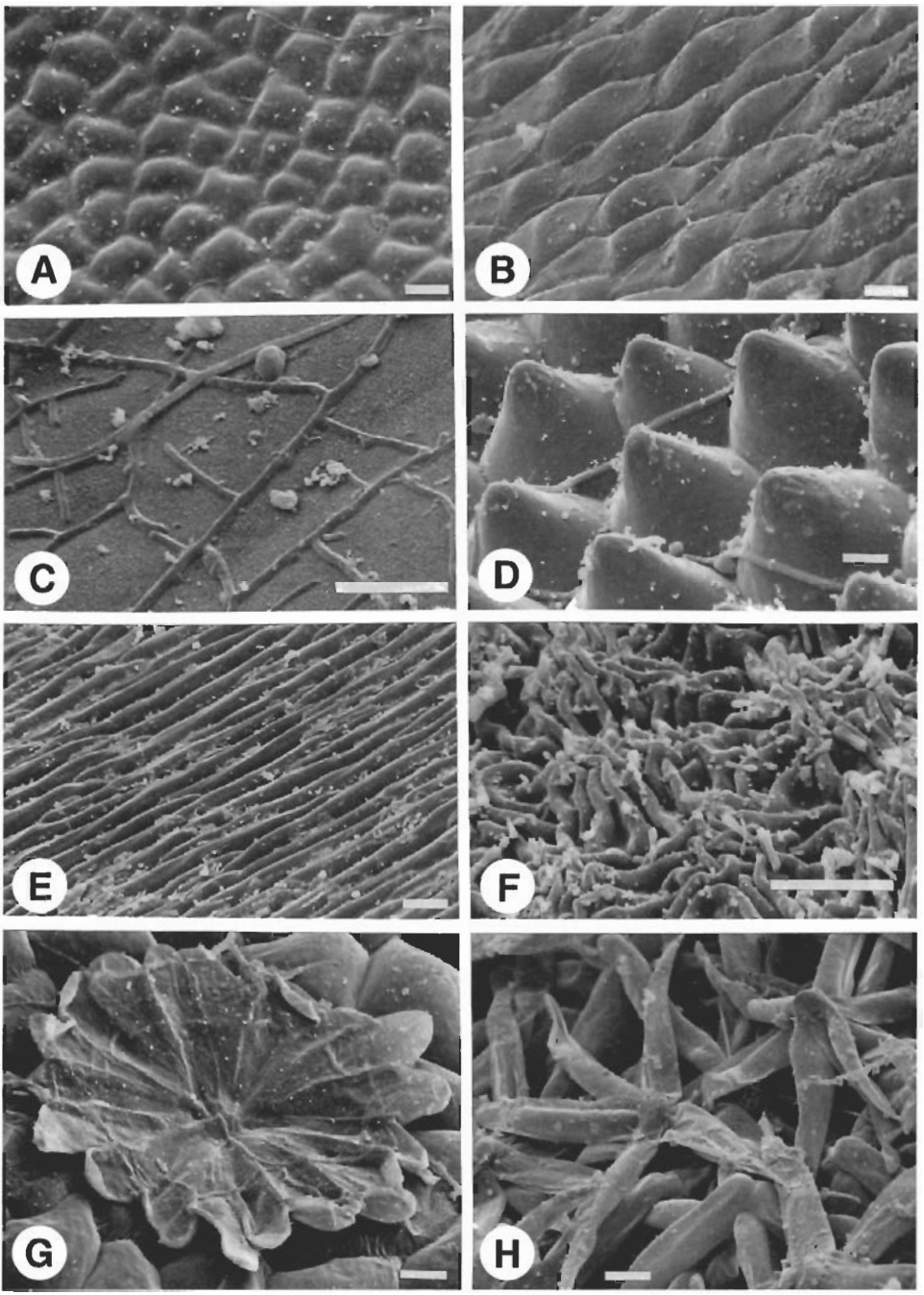

FIG. 3. Fine leaf surface structure of different phorophyte species. A – *Vismia billbergiana*. B – *Geonoma cuneata*. C – *Guatteria aeruginosa*. D – *Philodendron verrucosum*. E – *Iriartea deltoidea*. F – *Guarea grandifolia*. G – *Ardisia auriculata* (lower surface glandular hairs). H – *Vismia billbergiana* (lower surface glandular hairs). Note the fungal hyphae in C and D. Scale: 10 µm.

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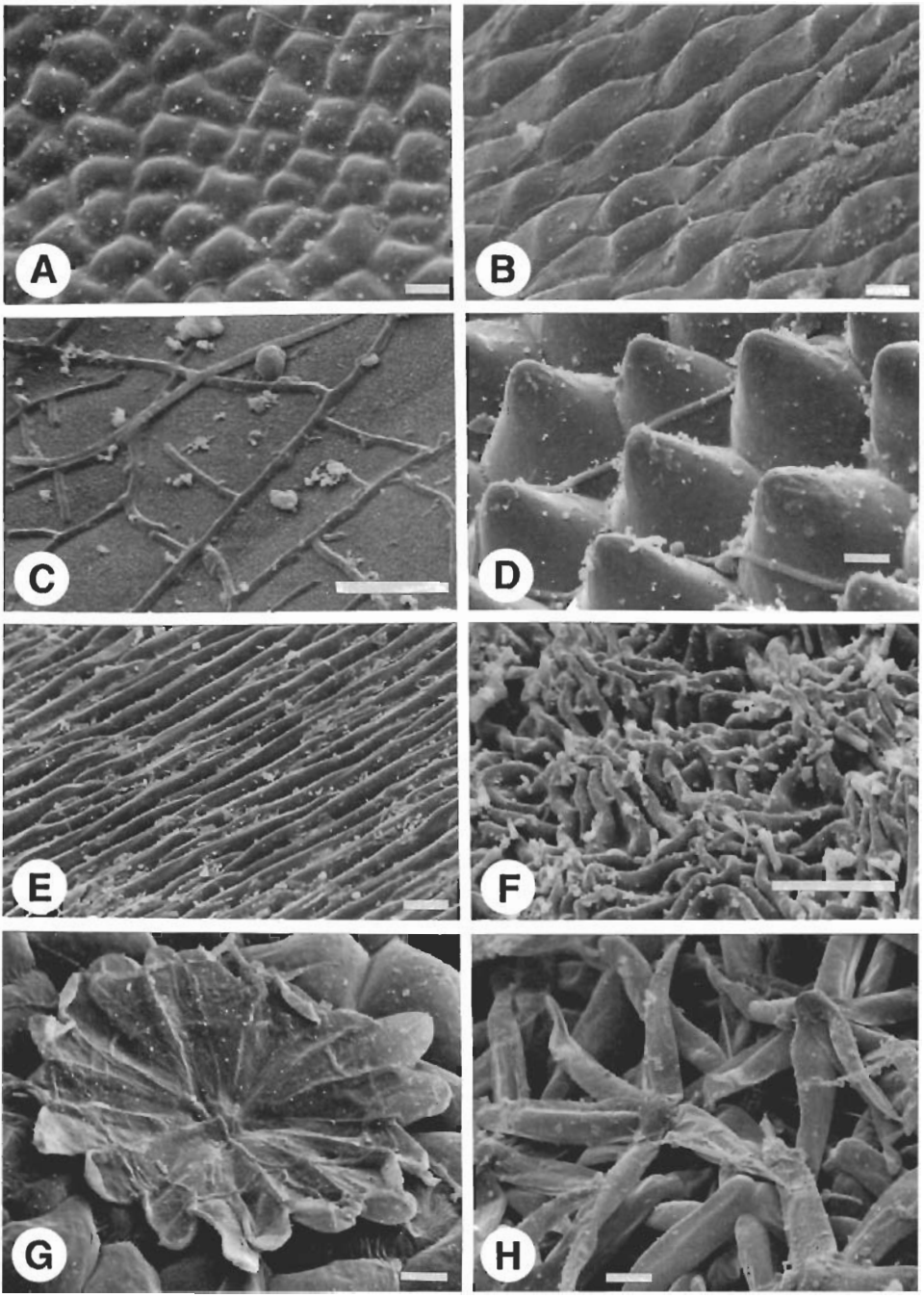

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TABLE 3. Variation of microclimatic factors at each phorophyte according to their location at different microsites. In the case of relative light intensity and evaporation, spatial variation at each microsite is given, while air temperature and relative air humidity represent temporal variation vs average values.

Microsite and No. of phorophyte	Relative light intensity [%]	Day max. air temperature: low/average/high [°C]	Day min. relative air humidity: low/average [%]	Evaporation [mm/d]
Understory 1 (1-30)	0.7- 3.5	22.3 / 24.3 / 26.1	70 / 90	0.19-0.37
Understory 2 (31-48)	1.2- 4.7	22.6 / 24.6 / 26.6	69 / 90	0.35-0.50
Understory 3 (53-86)	1.0- 4.5	22.9 / 24.6 / 26.2	74 / 91	0.07-0.36
Understory 4 (186-232)	0.9- 4.6	21.9 / 24.3 / 26.2	73 / 91	0.14-0.36
Understory 5 (233-272)	1.5- 7.1	22.0 / 24.3 / 26.7	72 / 91	0.15-0.32
Understory 6 (273-278)	3.0-10.3	21.7 / 24.1 / 25.7	84 / 93	0.15-0.22
Light gap 1 (49-52)	1.5-20.6	22.9 / 24.9 / 28.0	69 / 87	0.43-0.45
Light gap 2 (87-118)	1.6- 9.9	22.6 / 24.7 / 26.5	74 / 88	0.16-0.53
Light gap 3 (119-134)	1.0-10.4	22.6 / 24.5 / 26.2	76 / 91	0.12-0.22
Light gap 4 (135-151)	2.2-14.1	22.5 / 24.7 / 26.8	75 / 87	0.30-0.42
Light gap 5 (152-159)	4.3-30.8	22.2 / 24.7 / 27.2	82 / 90	0.18-0.21
Light gap 6 (160-185)	1.8-11.9	22.3 / 24.8 / 27.4	69 / 86	0.19-0.70
Creek 1 (279-318)	1.0- 5.0	21.1 / 23.8 / 25.8	88 / 94	0.09-0.33
Creek 2 (319-341)	1.0- 4.6	21.8 / 23.7 / 25.4	89 / 94	0.12-0.17

0.84 ($P < 0.001$): 71 % of the variation in species richness can be explained by these variables. Significant β-values were found for presence of hairs, presence of drip tip, height of exposure, leaf longevity, sample size, and relative air humidity (Table 5). Species richness is positively correlated with presence of drip tip, height of exposure, leaf longevity, and sample size, and negatively with presence of hairs and relative air humidity. Leaf longevity, sample size, and relative air humidity show highest β-values (0.38, –0.33, and 0.26, respectively) and appear to be the most important variables controlling species richness. Accordingly, multiple correlation with these three parameters alone amounts to r = 0.78 ($P < 0.001$), i.e., 62 % of the variation in species richness are explained by leaf longevity, sample size, and relative air humidity. Species richness seems not to be correlated with coarse and fine surface structure, surface continuity, and relative light intensity.

Area cover also shows a highly significant multiple correlation with the same variables, although less marked than species richness (r = 0.63, $P < 0.001$; explained variation: 39 %). Significant β-values are due to fine surface structure, surface continuity, presence of hairs, leaf longevity, sample size, relative light intensity, and relative air humidity (Table 5). Relative area cover is positively correlated with fine surface structure, surface continuity and leaf longevity, and negatively correlated with presence of hairs,

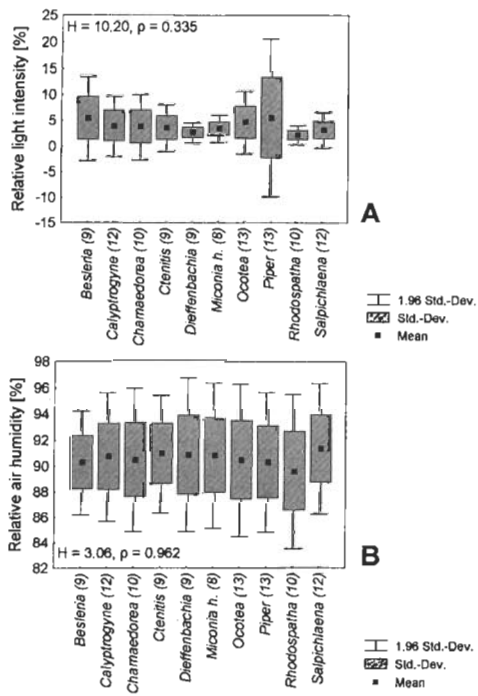

FIG. 4. Distribution of phorophytes of ten selected species (out of the subset of 139 phorophytes) within different microclimatic conditions, based on a Kruskal-Wallis H-test. (A) Relative light intensity. (B) Relative air humidity.

TABLE 4. Pearson's correlations between the four microclimatic factors, based on the set of the 321 phorophyte individuals.

	Relative light intensity	Temperature	Relative air humidity	Evaporation
Relative light intensity	–	r = 0.38 ($P < 0.001$)	r = 0.30 ($P < 0.05$)	r = 0.25 ($P < 0.5$)
Temperature	–	–	r = 0.81 ($P < 0.001$)	r = 0.53 ($P < 0.001$)
Relative air humidity	–	–	–	r = 0.64 ($P < 0.001$)

sample size, relative light intensity, and relative air humidity. Multiple correlation with the three parameters showing highest β-values, i.e., surface continuity (0.34), fine surface structure (0.28), and leaf longevity (0.25), amounts to r = 0.52 ($P < 0.001$), which means that only 27 % of the variation in relative area cover is explained by these three parameters. Relative area cover is not correlated with coarse surface structure, presence of drip tip, and height of exposure.

Besides the fact that variation in area cover is less explained by the environmental variables than species richness, there are also marked differences in the correlation patterns. While area cover is positively correlated with fine surface structure and surface continuity, species richness instead follows height of exposure. A striking difference is found in the positive correlation of species richness with sample size and the negative correlation of area cover with the same parameter: the larger the sample size of a given phorophyte individual, the higher the species richness, but the lower the area cover relative to the sample size. On the other hand, both parameters correspond in their positive correlation with leaf longevity and their negative correlation with relative air humidity.

Patterns of diversity within phorophyte species. Average foliicolous lichen α-diversity within a given phorophyte species varies between 4.3 in *Diplazium ceratolepis* and 40.3 in *Guarea grandifolia* (Fig. 5). Phorophytes with high average α-diversity include the dicots *Ocotea atirrensis* and *Naucleopsis naga*, the palms *Welfia georgii*, *Iriartea deltoidea*, and *Calyptrogyne condensata*, and the aroid *Monstera tenuis*. Very

TABLE 5. Multiple regression of species richness and area cover of foliicolous lichens with ten different environmental variables, based on the subset of 139 phorophytes taken for quantitative evaluations. The phorophyte character "presence of glands" was not presented in this subset, and of the microclimatic factors, two representative ones were selected. Significant β-values ($P < 0.05$) are highlighted.

Environmental variable	Species richness (r = 0.84)			Area cover (r = 0.63)		
	β-value	part. corr.	P-level	β-value	part. corr.	P-level
Coarse surface structure	–0.11	–0.15	0.088	–0.05	–0.05	0.563
Fine surface structure	0.07	0.09	0.304	0.28	0.25	0.004*
Surface continuity	0.00	0.00	0.975	0.34	0.33	0.000***
Presence of hairs	–0.12	–0.18	0.038*	–0.19	–0.21	0.019*
Presence of drip tip	0.13	0.19	0.027*	–0.14	–0.14	0.111
Height of exposure	0.24	0.35	0.000***	0.05	0.06	0.518
Longevity	0.38	0.51	0.000***	0.25	0.27	0.003*
Sample size	0.26	0.38	0.000***	–0.21	–0.22	0.011*
Relative light intensity	–0.04	–0.06	0.465	–0.14	–0.18	0.046*
Relative air humidity	–0.33	0.48	0.000***	–0.24	–0.27	0.002*

low average species richness is found in *Costus malortieanus*, *Vismia billbergiana*, *Ctenitis subincisa*, *Ardisia auriculata*, *Miconia hamelii*, and *Thelypteris gigantea*. Accordingly, the α-diversity on single individuals is as high as 65 species in *Ocotea atirrensis* and as low as 1 in various other phorophytes. Intraspecific variation of α-diversity is remarkably high, ranging, for example, from 2 to 56 in *Salpichlaena volubilis* or from 1 to 52 in *Calyptrogyne condensata*.

Cumulative species richness, or γ-diversity, on a given phorophyte species is highest in *Ocotea atirrensis*, with 130 foliicolous lichen species (Fig. 5), followed by *Calyptrogyne condensata*, *Iriartea deltoidea*, *Salpichlaena volubilis*, and *Guarea grandifolia*, and lowest in *Diplazium ceratolepis* (16 species), *Costus malortieanus*, *Columnea consanguinea*, *Vismia billbergiana*, and *Thelypteris gigantea*. In general, low a and γ-diversity values are found in phorophytes with hairs or glands on the leaf surface, a papillose fine structure, low surface continuity, low height of exposure, short-lived leaves, and small sample size, while high α and γ-diversity are associated with phorophytes lacking particular features, except for a grooved or ornamented fine structure, and belonging to the "normal" dicotyledoneous or the palm leaf type (compare Fig. 5 and Table 2).

In addition to the high intraspecific α-diversity variation, there is a high variation in the composition of foliicolous lichen species on different phorophyte individuals of a given species, as is obvious from the intraspecific β-diversity which oscillates between 0.36 and 0.79 (Fig. 5). High β-diversity is found in *Heliconia* sp. (0.79) and *Diplazium ceratolepis*, while *Ctenitis subincisa* (0.36) exhibits a rather low value. There is a tendency towards higher intraspecific β-diversity in phorophytes with lower average α-diversity, but a significant correlation is not apparent ($r = -0.30$, $P > 0.5$). Also, intraspecific β-diversity is not correlated with intraspecific variation of α-diversity. While, for example, individuals of *Calyptrogyne condensata* show comparatively low β-diversity in spite of their high variation in α-diversity, the reverse pattern is found in *Ardisia auriculata*, where higher intraspecific β-diversity goes along with lower variation in α-diversity between single phorophyte individuals.

Average intraspecific β-diversity, calculated as the mean of all 39 phorophyte species, amounts to 0.62.

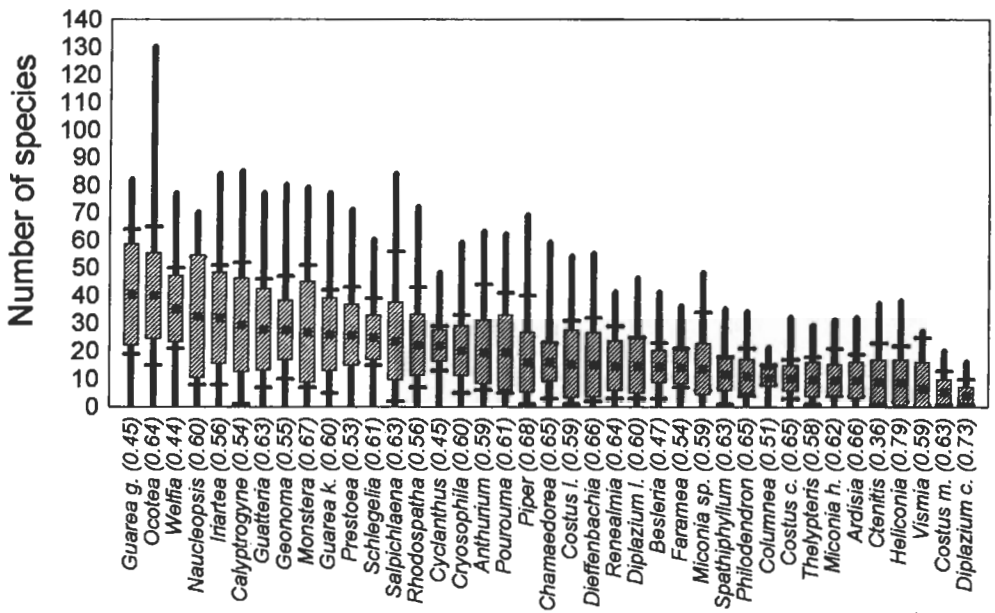

FIG. 5. Diversity patterns in different phorophyte species. Black points: average α-diversity; hatched boxes: standard deviation of α-diversity; black horizontal bars: absolute range of α-diversity (min./ max.); black vertical bar: γ-diversity; in brackets behind phorophyte species: average interspecific β-diversity.

Accordingly, the proportion of average α-diversity *vs* γ-diversity results in a mean of 33.5 ± 6.9 % over all phorophyte species. This means that a single individual on average supports only one third of the foliicolous lichen species potentially growing on the phorophyte species. This could be explained by the different microclimatic conditions under which the single individuals of each species grew. Indeed, considering only phorophyte individuals within a narrow range of relative light intensity (1–4 %) and relative air humidity (89–95 %), average α-diversity is hardly affected (19.4 *vs* 18.8) while average γ-diversity distinctly decreases (41.6 *vs* 55.4). In this case, the ratio between average α and γ-diversity amounts to 45.9 ± 9.0 % over all phorophyte species, which is significantly higher than before (t-test: $P < 0.001$). However, this ratio is still less than 50 %, that is even when microclimatic factors are more homogeneous, the intraspecific β-diversity remains high.

Considering the cumulative foliicolous lichen species richness or γ-diversity over all individuals of a given phorophyte species, the average interspecific β-diversity, i.e., the dissimilarity in foliicolous lichen species composition between any given pair of phorophyte species, amounts to 0.45. This value is significantly lower than the average intraspecific β-diversity (Mann-Whitney U-test: $P < 0.001$), indicating that the foliicolous lichens on different phorophyte species are more similar to each other than to those on different individuals of the same species. With 130 species, *Ocotea atirrensis* supports more than 70 % of the foliicolous lichen species richness found on all phorophyte species. In the remaining species, the percentage of foliicolous lichens in common with *Ocotea atirrensis* increases with decreasing γ-diversity ($r = 0.79$, $P < 0.001$). The lower the γ-diversity in a given phorophyte species, the more similar, except for the different species richness, is its foliicolous lichen flora to that of *Ocotea atirrensis*. Hence, phorophytes with low γ-diversity do not contribute to overall site diversity. The highest dissimilarities compared to Ocotea atirrensis are found in *Iriartea deltoidea*, and *Monstera tenuis*, but even here the similarity amounts to 75 %. In general, there are no marked differences in foliicolous lichen species composition between phorophyte species, and nearly the whole diversity is found on the three phorophytes *Ocotea*

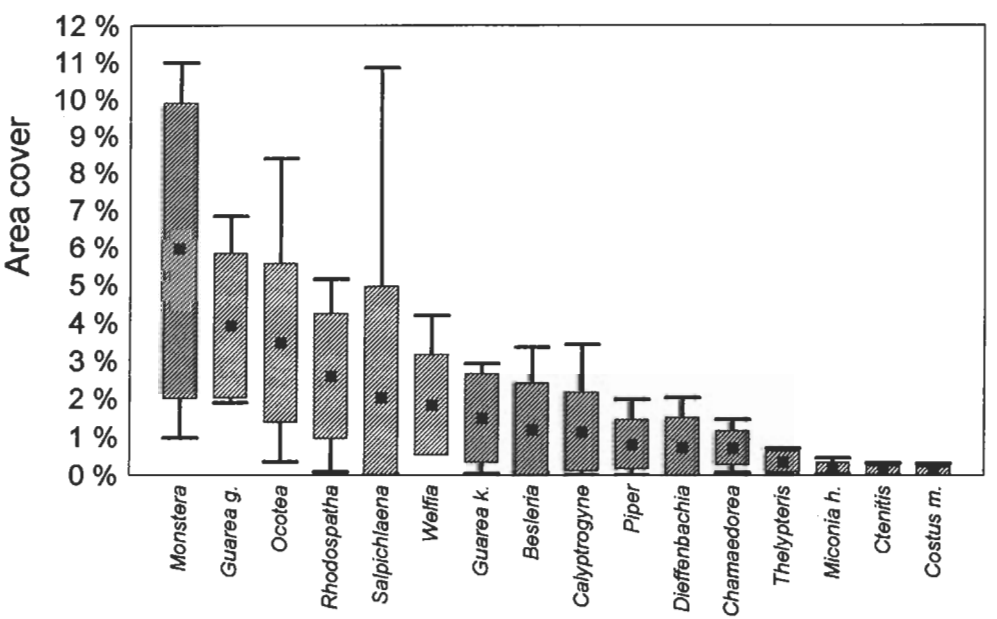

FIG. 6. Area cover in different phorophyte species (out of the subset of 139 phorophytes). Black points: average area cover; hatched boxes: standard deviation of area cover; black vertical bars: absolute range of area cover.

TABLE 6. Average dissimilarity or β-diversity between adjacent phorophytes within ten selected microsites belonging to the three different microsite types. The mixture ratio is calculated as the number of phorophyte species vs the number of individuals per site.

Microsite and No. of phorophyte	Number of phorophytes	Number of combinations	Mixture ratio	Average β-diversity
Understory 1 (1-30)	29	406	86 %	0.38
Understory 3 (53-86)	32	496	88 %	0.42
Understory 4 (186-232)	43	903	77 %	0.43
Understory 5 (233-272)	38	703	71 %	0.39
Average understory	142	–	–	0.41
Light gap 2 (87-118)	28	378	86 %	0.36
Light gap 3 (119-134)	15	105	100 %	0.21
Light gap 4 (135-151)	17	136	82 %	0.39
Light gap 6 (160-185)	25	300	72 %	0.35
Average light gaps	85	–	–	0.33
Creek 1 (279-318)	40	780	60 %	0.30
Creek 2 (319-341)	16	120	93 %	0.32
Average creek	56	–	–	0.31

atirrensis, *Iriartea deltoidea*, and *Monstera tenuis*. These species represent the three basic leaf types with high diversity: "normal" dicots, palms, and aroids.

Patterns of area cover within phorophyte species. The 16 phorophyte species selected for quantitative evaluation of the foliicolous lichen flora differ markedly in area cover (Fig. 6). Average values, calculated over the whole set of leaves along a given shoot, including the youngest, uncolonized ones, reach 2–6 % in the most densely colonized phorophyte species and hardly exceed 10 %, with the highest values on single individuals being due to *Monstera tenuis* (11.0 %), *Salpichlaena volubilis* (10.9 %), and *Ocotea atirrensis* (8.4 %). Again, *Salpichlaena volubilis* shows a very high variation, ranging from nearly 0 to almost 11 %. Compared with species richness, area cover is comparatively high in the aroids *Monstera tenuis* and *Rhodospatha wendlandii* but relatively low in the palms *Welfia georgii* and *Calyptrogyne condensata*. In fact, species richness and area cover do not correlate in a linear way but show a complex relationship which is best approximated by a logarithmic-linear estimation ($r = 0.71$, $P < 0.001$; Fig. 7). As long as area cover is low, species richness and area cover are positively correlated. With increasing area cover, species richness approaches saturation and then slightly decreases.

Patterns of β-diversity within and between microsites. Of the 14 microsites, 10 exhibit a minimum number of 15 phorophyte individuals each and are suitable for cross-comparison of β-diversity. Within a given microsite, average β-diversity, i.e., the mean of all possible phorophyte individual pair-combinations, varies between 0.21 and 0.43 (Table 6). These values are significantly lower than the average intraspecific β-diversity 0.62 (see above; Mann-Whitney U-test: $P < 0.001$), in spite of the high mixture ratios of phorophyte species at each microsite, which lie between 60 and 100 %. Thus, independent of the phorophyte species, spatially adjacent individuals are more similar in their foliicolous lichen flora than distant individuals belonging to the same species. The values at understory microsites are significantly higher than those found at light gap microsites (Kruskal-Wallis H-test: $P < 0.05$). This means that at light gap microsites, spatially adjacent phorophytes are more similar in their foliicolous lichen flora than at understory microsites.

Comparing the cumulative foliicolous lichen species composition on all phorophyte individuals at each microsite, the average β-diversity between understory microsites amounts to 0.25, significantly lower than between light gap microsites with 0.34 (Mann-Whitney U-test: $P < 0.001$). While individuals in light gap microsites are more similar to each other than those in understory microsites, understory microsites are more similar to each other in their cumulative foliicolous lichen flora than light gap microsites.

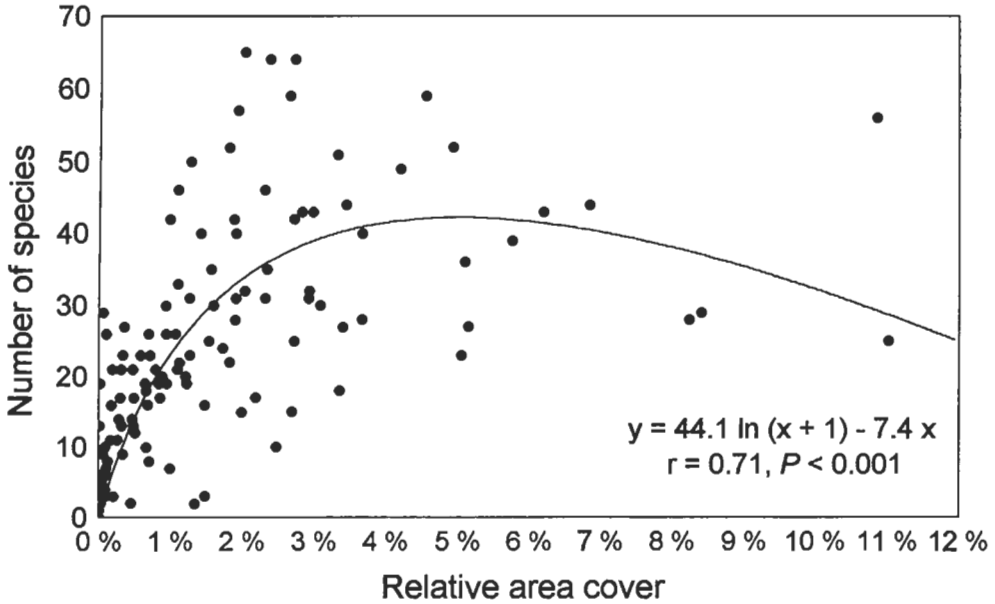

FIG. 7. Logarithmic-linear relationship between species richness and area cover of foliicolous lichens, calculated on the base of the subset of 139 phorophytes.

Species-sample curves. The species-sample curves follow a logarithmic pattern, without distinct saturation (Fig. 8), and can be approximated by two different non-linear models: (1) a logarithmic estimation and (2) a limit value estimation. The logarithmic estimation takes the general equation $y = a + b \times \log_{10}(x) + c \times x$, while the limit value estimation follows the equation $y = a \times [1-1 / (x + 1)^{1/b}]$; in both equations y = cumulative species richness and x = number of included phorophyte individuals. Both estimations give rather good approximations in all cases, i.e., $\alpha_{min.}$ = 5, 10, 20, and 30 species, with r = 0.99 or higher (Table 7). For $x \rightarrow \infty$, the limit value estimation converges against a figure which theoretically gives an estimate for the cumulative species richness of foliicolous lichens to be finally reached. However, the estimates for this figure in the four cases are quite heterogeneous and not meaningful, except for $\alpha_{min.}$ = 30 which yields a more or less useful value with a = 351 species (Table 7). If values for cumulative species richness are predicted on the base of 321, 1000, and 10000 phorophyte individuals, the logarithmic estimation is closer to the actual figures for 321 individuals and gives an exact value in the case of $\alpha_{min.}$ = 10 (Table 8). However, when higher numbers of individuals are considered, the limit value estimation gives more conservative, homogeneous estimations, while the logarithmic estimation diverges widely (Table 8).

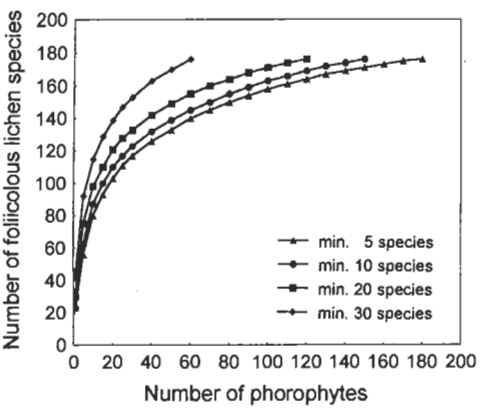

FIG. 8. Species-sample curves based on different sets of phorophytes with different minimum α-diversity (5, 10, 20, and 30 species).

TABLE 7. Parameter estimates for non-linear estimation of species-sample curves and their dependence on the minimum α-diversity of included phorophytes.

Minimum α-diversity	Logarithmic approximation $y = a + b \times \log(x) + c \times x$				Limit value approximation $y = a \times [1 - 1/(x + 1)^{1/b}]$		
	a	b	c	r	a	b	r
5 species	16.7	66.0	0.075	0.9983	690043	20277	0.9995
10 species	19.5	68.1	0.064	0.9992	2331	63.8	0.9997
20 species	28.3	70.2	0.023	0.9996	510	11.3	0.9999
30 species	41.2	73.8	0.706	0.9998	351	6.0	0.9993

DISCUSSION

Environmental variables. The estimates of leaf longevity agree rather well with other studies. Generally, leaf longevity in tropical rain forests averages 12–36 months (Odum 1970, Bentley 1979, Coley 1988, Richards 1988). Some phorophyre species, particularly palms and the rain forest cycad *Zamia skinneri*, may retain their leaves much longer, up to 7–12 years in extreme cases (Winkler 1967, Kiew 1982, Rogers & Barnes 1986, Clark *et al.* 1992, Coley *et al.* 1993, E. Freiberg 1994). It is assumed that older leaves no longer contribute substantially to photosynthesis but take over functions such as storing nutrients or excretions (Chabot & Hicks 1982, Kiew 1982), in that way compensating for the probable detrimental effect of light interception by epiphylls in the shady understory (Waterman & McKey 1989, Coley *et al.* 1993).

Depending on the structure of the forest, relative light intensity is generally estimated to (0.5–) 1–3 (–5) % in the understory and (5–)10–30 % in light gaps (Richards 1964, Chazdon & Fetcher 1984b, Oberbauer *et al.* 1988, M. Freiberg 1996). Similar proportions are found when radiation energy or photon flux density are considered (Chazdon & Fetcher 1984a, b; Kira & Yoda 1989). The high variation in light gap microsites is due their variation in size, exposition, and height of the surrounding vegetation (Chazdon & Fetcher 1984b). Generally, relative light intensity in the understory corresponds to the amount of canopy opening (Anderson 1964, Whitmore 1990, Wolf 1993).

Relative air humidity in the forest interior varies between 90 and 100 % but may eventually decrease to 60–70 % (Bourgeron 1983, Lauer 1989, M. Freiberg 1996). Microsites along creeks are considered as constantly humid (Marino & Salazar-Allen 1991). However, the generalization that light gaps are less humid than the understory could only partly be verified. Depending on their structure, light gaps may also be constantly humid (E. Freiberg 1994) and provide very particular conditions for epiphyll growth.

The measured evaporation rates appear negligibly low when compared to the precipitation, which amounted to 21 mm/d, i.e., 80 times higher than daily evaporation (see Part I: Lücking 1998a). How-

TABLE 8. Predicted values for overall foliicolous lichen diversity using non-linear estimation of species-sample curves and different numbers of phorophytes (321 / 1000 / 10000).

Minimum α-diversity	Logarithmic approximation $y = a + b \times \log(x) + c \times x$ Number of phorophytes			Limit value approximation $y = a \times [1 - 1/(x + 1)^{1/b}]$ Number of phorophytes		
	321	1000	10000	321	1000	10000
5 species	206	290	1033	196	235	313
10 species	179	233	581	202	239	313
20 species	170	209	342	204	233	284
30 species	239	395	2059	217	240	275

ever, most of the precipitation falls within a few hours, and leaves covered with epiphylls are able to retain only 0.01–0.05 g/cm^2 water at a time (A. Lücking 1995). This means that only 0.1–0.5 mm of the daily precipitation can in fact be used, and thus, particularly in light gaps, evaporation rates are possibly high enough to cause water stress in poikilohydric organisms.

Patterns of diversity and area cover of foliicolous lichens. Hairs or glands on the upper leaf surface do significantly influence species richness and area cover, confirming the early studies of Busse (1905) and Fitting (1910). Apart from their ecomorphological importance, hairs are considered an unspecific defense against herbivores and parasites (Steadman & Shaik 1988, Allen *et al.* 1991). However, hairs do not simply prevent foliicolous lichens from growth but rather work indirectly by influencing air and water currents on the leaf surface, thus rendering the successful establishment of diaspores more difficult (Burrage 1969, Allen *et al.* 1991). In addition, invertebrates as possible vectors of diaspores might be deterred (Southwood 1986).

The secretion of etheric oils through bark or leaf surfaces is often given as a cause of either positive or negative phorophyte preferences in epiphytes (Benzing 1983, Galloway 1992). That there is no straightforward correlation between glandular secretion and colonization with epiphylls is illustrated by the observation that in the present case both phorophyte species with glands are hardly overgrown by foliicolous lichens, while leaves of the Rutacean genus *Citrus*, which also have secretive glands, usually show luxuriant epiphyll cover (Lücking 1992). The assumption in the case of *Ardisia auriculata* and *Vismia billbergiana* that the secretion might have negative influence on foliicolous lichen growth is supported by the observation that individuals of *Vismis billbergiana* located in light gaps showed distinctly higher species richness than those found in the understory. According to Engler (1960), the formation of secretive glands in the Clusiaceae is reduced at higher light intensities. This, and the supposedly faster evaporation of the etheric oils, would reduce any detrimental effect on foliicolous lichen growth. Whether such an effect exists remains to be studied, although secondary substances are known to prevent fungal growth in some cases (Cherret 1989).

Since in the phorophytes with hairs or glands, those with longer-lived leaves had a better developed foliicolous lichen flora, it is assumed that the influence of hairs and glands is relative in retarding foliicolous lichen colonization rather than preventing it completely. At a given age, leaves of *Costus malortieanus*, *Miconia hamelii*, *Ardisia auriculata*, or *Vismia billbergiana*, show a foliicolous lichen flora comparable to that found on much younger leaves of, for example, *Ocotea atirrensis*.

The influence of other surface structures on foliicolous lichen colonization is difficult to evaluate. Coarse surface structure does not notably affect species richness or area cover, in contrast to fine surface. In experiments with artificial substrata, Winkler (1967) demonstrated differences in the growth of epiphyllous bryophytes on different surfaces, while Coley *et al.* (1993), using manipulated leaves, failed to show such an effect in foliicolous lichens. Lichenized and non-lichenized fungi, as well as bryophytes, adhere to the leaf surface by a mucilage layer (Modenesi *et al.* 1986, Nicholson & Epstein 1991), without damaging the leaf surface. Since the mucilage fills the space between the leaf surface and the lichen thallus, a leaf surface which requires production of large amounts of mucilage, such as the large, papillose epidermal cells in *Philodendron verrucosum* or *Heliconia* sp., is disadvantageous, especially as a large amount of water has to be stored outside the lichen thallus to ensure continuous adherence. Lichens growing on phorophytes with papillose fine surface structure are in fact easily detached by mechanical forces, especially under dry conditions. Phorophytes with a grooved or ornamented structure, such as the fern *Salpichlaena volubilis*, the palm *Iriartea deltoidea*, or the dicot *Guarea grandifolia*, seem to be particularly suitable for foliicolous lichen colonization since they do not only require a thinner mucilage layer but also facilitate the growth of fungal hyphae possibly acting as "rhizoids" in the depressions between the epidermal cells or cuticular folds.

Low surface continuity as created by divided leaves and prominent veins obviously prevents continuous growth of lichen thalli and hence decreases area cover. Diversity is not affected, probably because the negative effect on the growth of individual lichen thalli is compensated for by the independent colonization of spatially isolated parts on the leaf by different species.

The presence of a drip tip is much discussed with regard to both its ecomorphological importance and its effect on epiphyll cover. Stahl (1893) and Dean & Smith (1978) observed that the surface of leaves

provided with distinct drip tips dried more rapidly after wetting, and Vareschi (1980) demonstrated the frequent occurrence of leaves with drip tips in seasonal rain forests, adapted to the very different conditions of the rainy and the dry season. Seybold (1957) and Ellenberg (1985) failed to demonstrate any such function, and the latter considers the drip tip to be a consequence of the leaf development of tropical woody plants, without any function in the mature leaf. Accordingly, while Jungner (1891) and Dean & Smith (1978) found less colonization by epiphylls on leaves with drip tips, Busse (1905) and Fitting (1910) did not notice any such correlation.

Althought there is little doubt about the existence of an ecomorphological effect of drip tips, the lack of influence on foliicolous lichen cover is confirmed here, since high species richness and area cover are found in leaves both with and without drip tips. Still, there is a subtle tendency towards lower area cover but higher diversity in leaves with drip tips, which might be explained if drip tips do really accelerate desiccation of the leaf surface. Rapid change between wetting and drying would increase the mechanical forces on lichen thalli and hence facilitate their detachment from the leaf, while simultaneously favoring the establishment of new diaspores (A. Lücking & Lücking 1995). In that way it would reduce the continuous growth of already established lichen thalli and increase the possibilities for other species to colonize the leaf. To prove such an effect, experiments with artificial leaf surfaces (Monge-Nájera & Blanco 1995) are required.

Leaf longevity is the most important character affecting foliicolous lichen colonization (Allan 1928). Young trees in the forest understory, such as *Ocotea atirrensis* and *Guarea grandifolia*, often have long-lived leaves (Hartshorn 1991) and are particularly suitable for epiphyll growth (Sipman 1991). In phorophytes with low species richness, the highest diversity occurred on individuals with longer-lived leaves. Short-lived leaves, i.e., those not exceeding 24 months in age, require particular adaptations to be successfully colonized by foliicolous lichens, such as specialized diaspores and rapid reproduction (A. Lücking & Lücking 1995). Further, the likelihood of foliicolous lichen colonization increases with leaf age since surface characteristics change, either induced by the onrogeny of the leaf itself or by the growth of microorganisms. Coley *et al.* (1993) observed slower growth of epiphylls on phorophytes with long-lived leaves, supposedly due to the presence of particular defense mechanisms, but such a correlation could not be verified here.

Foliicolous lichen colonization seems to be negatively affected by increasing relative air humidity, and both species richness and area cover are particularly low when relative air humidity and relative light intensity are high, i.e., in humid light gaps. This can partly be explained by physiological shortcomings, since lichens seem to need a regular change between humid and drier conditions, i.e., drying and rehydrating, to perform their basic metabolism (Sipman & Harris 1989). On the other hand, it has been shown that epiphyllous bryophytes known to be strong competitors, like *Cyclolejeunea* and *Odontolejeunea* spp., grow particularly well under conditions of high relative air humidity and high relative light intensity (A. Lücking 1995) and probably outcompete foliicolous lichens at these microsites.

Although species richness and area cover of foliicolous lichens are distinctly higher at "low" relative air humidity (around 80 % daily minimum), both parameters behave slightly differently with respect to relative light intensity. This is explained by the fact that relative light intensity governs species composition (Lücking 1998c). Values of 5–10 % relative light intensity correspond to the transition between understory and light gap microsites, where two different foliicolous lichen communities overlap, and hence species richness slightly increases, while area cover is not significantly affected. The relationship between species richness and area cover shows that the former first increases and then decreases along with the latter. This phenomenon, which has also been found in epiphyllous bryophytes (A. Lücking 1995), is generally known from plant communities and is explained by the assumption that high area cover goes along with the dominance of strong competitors which outcompete other species, reducing diversity (Huston 1979).

The strong correlation of species richness and area cover with a few environmenral variables is particularly astonishing when considering that the selected variables represent only a fraction of all factors possibly influencing epiphyll cover. Some have been excluded because of their highly stochastic nature, and orhers remain to be studied, such as the physico-chemical nature of the leaf cuticle (Linskens 1952, Holloway 1971) and the leaching of substances from the leaf (Tukey 1966, 1971; Witkamp 1970; Golley 1983; Rogers & Barnes 1986), which might affect the establishment of diaspores (Gregory &

Stedman 1953, Gregory 1971, Ingold 1971, Allen *et al.* 1991, Juniper 1991). Also, the interactions between foliicolous organisms certainly influence epiphyllous communities but they have not yet been studied in any detail.

Although important for plant distribution patterns, nutrient supply has not been considered here, because on atmospheric surfaces, such as leaves, this factor depends mostly on external inputs like detritus, leaf litter, and rainfall (Tukey 1966, Witkamp 1970, Golley *et al.* 1975, Jordan *et al.* 1979, Vareschi 1980), which follow stochastic, unpredictable patterns at the scale of the individual leaf or phorophyte. It can also be assumed that, due to the high input of organic matter in the forest understory (Jordan & Herrera 1981, Nadkarni & Matelson 1992), nutrient supply is not a limiting factor for the distribution of epiphylls at the level of phorophyte individuals (Golley *et al.* 1975, Rogers & Barnes 1986). Diaspore dispersal depends not only on the nature of the diaspores and their vectors (Gregory & Stedman 1953, Ingold 1971, Bailey 1976, Sipman & Harris 1989, Allen *et al.* 1991), but also on the availability of parental thalli. It is of a highly stochastic nature and a principal cause of high β-diversity between samples with supposedly homogeneous environmental conditions, the "noise" in ecological data (Kinkel 1991, Wolf 1993d).

The low interspecific β-diversity between phorophyte species compared with the high intraspecific β-diversity indicates that, while phorophyte characters affect α and γ-diversity, they hardly have any influence on species composition of foliicolous lichens. Marked phorophyre preferences are not obvious, and different phorophyte species do not contribute substantially to overall site diversity. In particular, there is no specialization of foliicolous lichens towards a given species in phorophytes with low α and γ-diversity, but there is a slight tendency for specialization in high-diversity phorophytes. Obviously, the overall diversity of a site is hardly affected by the diversity of phorophytes, as long as phorophytes supporting high α and γ-diversity are present. This might explain the high diversity of foliicolous lichens and epiphylls found in plantations of *Citrus* trees, a phorophyte supporting high α-diversity (Lücking 1992).

Patterns of β-diversity within and between microsites could be explained by the dynamic structure of tropical rain forests: the understory forms a continuum while light gaps are spatially isolated and stochastically distributed within the forest (Hartshorn 1978, 1980). In the understory, diaspore dispersal and distribution of foliicolous lichens is continuous in space and time, leading to a dynamic equilibrium corresponding to later successional stages, and hence following more deterministic patterns. Eventually, this leads to the levelling of spatially distant but comparable understory microsites towards a similar foliicolous lichen flora, and the establishment of subtle, predictable differences between adjacent phorophytes belonging to different species. On the other hand, the discontinuous colonization of light gaps, with a dynamic equilibrium close to early successional stages, provides a high degree of stochasticity between spatially distant microsites but low differentiation between adjacent phorophytes of a given light gap.

Achieving reliable estimates of overall site diversity from species-sample curves is rather difficult, even when the latter are closely approximated by mathematical equations. The reason for this is that species-sample curves initially follow a certain pattern but later on may change to another, unknown pattern. Since equations are based on the first, known part of the curve, while estimations extrapolate the unknown second part, the degree of predictability for overall site diversity is low. In the present case, the limit value approach gives more reliable estimates than the logarithmic approach for higher numbers of phorophyte individuals, and the closest estimate for overall site diversity of foliicolous lichens in the forest interior at the study site might be between 200 and 250 species. To these, about 25–30 species restricted to the forest canopy have to be added (Lücking 1995b), resulting in a rough estimate of 225–280 species in total, of which 217 have already been found (see Part I: Lücking 1998a).

CONCLUSIONS

The variation in species richness and area cover, as the principal parameters of foliicolous lichen colonization, is well explained by a few environmental variables, particularly phorophyte characters, even if the number of factors possibly influencing epiphyll cover is high. The principal factors governing species richness and area cover are fine surface structure, surface continuity, and leaf longevity, as well as relative air humidity. Species richness is particularly high on phorophytes having long-lived leaves with grooved or ornamented fine surface structure and high sur-

face continuity, as well as at microsites with "low" relative air humidity (around 80 % daily minimum).

Species richness and area cover show slightly different patterns with regard to environmental variables. They are positively correlated when area cover is low, but negatively when area cover is high. This is due to competition phenomena, assuming that high area cover is caused by highly competitive species forming large thalli, which outcompete other species and hence decrease species richness.

Phorophyte characters distinctly affect α and γ-diversity of foliicolous lichens on different phorophyte species, while their influence on interspecific β-diversity is small. Hence, there is a low degree of phorophyte preferences within foliicolous lichens, and patterns of specialization upon certain phorophyte species are not apparent.

The distribution of foliicolous lichens in the understory follows more deterministic patterns, allowing for the establishment of subtle phorophyte preferences, while in light gaps it is more stochastic. Thus, as long as providing comparable conditions, spatially distant understory microsites within a homogeneous site are rather similar to each other in their foliicolous lichen flora, while light gap microsites show differences.

Although these results are based upon investigations in a limited area of tropical rain forest in Costa Rica, the rather wide geographical distribution of foliicolous lichen species and the low degree of phorophyte preferences indicate that the conclusions drawn from these studies might be valid for tropical rain forests in general, but this remains to be tested.

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