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Ecology of Foliicolous Lichens at the "Botarrama" Trail (Costa Rica), a Neotropical Rain Forest. III. Phorophyte Ranges and Patterns of Phorophyte Preferences

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With 12 Figures

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Summary

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Phorophyte ranges and patterns of phorophyte preferences in foliicolous lichens were studied by clustering of individual phorophytes on the basis of their lichen species composition. Foliicolous lichens exhibit broad phorophyte ranges and low specifity. Phorophytes of the same species only cluster together as long as their leaf characters are sufficiently different from each other, but the number of discriminating foliicolous lichens is low. A distinct grouping effect of phorophytes with similar foliicolous lichen diversity indicates that phorophyte preferences are quantitative rather than qualitative, resulting in different diversity stages rather than different species composition. These diversity stages can be interpreted as different stages of succession. Species composition is strongly affected by microclimatic conditions, in particular relative light intensity. Two large groups of foliicolous lichen species can be found discriminating between shady understory and light gap phorophytes, with *Arthoniaceae*, *Opegraphaceae* and *Trichotheliaceae* being typical for shady understory phorophytes, and *Gomphillaceae* and *Ectolechiaceae* dominant on light gap phorophytes.

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Anhand von Clusteranalysen individueller Phorophyten auf der Basis ihrer foliikolen Flechtenflora wurden Phorophytpräferenzen foliikoler Flechten untersucht. Diese zeigten ein breites Phorophytenspektrum und nur geringe Präferenzen zugunsten einzelner Phorphytenarten. Phorophyten der gleichen Art gruppieren sich nur bei sehr unterschiedlichen Blattmerkmalen, wobei die Anzahl der zwischen den Gruppen diskriminierenden Flechtenarten vergleichsweise gering bleibt. Die hingegen deutliche Gruppierung von Phorophyten mit vergleichbarer Flechtendiversität läßt auf das Vorhandensein eher quantitativer als qualitativer Phorophytpräferenzen schließen, die sich in unterschiedlichen Diversitätsstadien, aber nur beschränkt in unterschiedlicher Artenzusammensetzung äußern. Die unterschiedlichen Diversitätsstadien können als Sukzessionsstadien interpretiert werden. Auf der anderen Seite wird die Artenzusammensetzung foliikoler Flechten stark durch die mikroklimatischen Bedingungen beeinflußt, besonders durch die relative Lichtstärke, wobei zwei artenreiche Gruppen foliikoler Flechten zwischen Unterholz und Lichtlücken diskriminieren. Hierbei sind die *Arthoniaceae*, *Opegraphaceae* und *Trichotheliaceae* typisch für das Unterholz und die *Gomphillaceae* und *Ectolechiaceae* charakteristisch für Lichtlücken.

1. Introduction

A striking feature of wet tropical forests is the abundance and diversity of epiphytes (Richards 1952, Vareschi 1980, Kress 1986, Benzing 1990, Whitmore 1990). A number of studies have addressed the question as to whether epiphytes are phorophyte specific and if their abundance and diversity depend on the composition of available phorophytes (Benzing 1990, Oldeman 1990, Wolf 1993). Such correlations would be an important aspect when discussing sustainable management of tropical rain forests with regard to their diversity maintenance.

True epiphytes are free of direct physiological relationships with their phorophytes (Benzing 1986, 1990), and hence phorophyte specifity would be expected to be less marked than in parasites. However, phorophyte preferences have been demonstrated in corticolous epiphytes, including lichens, which might be due to morphological and chemical bark characteristics (Barkman 1958, Benzing 1990, Wolf 1993, Hietz & Wolf 1996). Corticolous lichens such as the widespread and diverse tropical families *Pyrenulaceae, Thelotremataceae* and *Graphidaceae,* live within the peripheral bark tissue and might depend on morpho-chemical features of the phorophyte bark (Sipman & Harris 1989, Sipman 1996). Negative phorophyte preferences are found with regard to phorophytes which regularly shead their bark, e.g. members of the families *Myrtaceae* and *Combretaceae,* or which have special relationships with ants, such as *Mimosaceae* or *Cecropiaceae,* and hence prevent epiphyte colonization.

Phorophyte preferences in epiphytes include a qualitative and a quantitative aspect. Firstly, certain epiphytes might show preferences towards certain phorophyte species, i.e. different phorophyte species would have different epiphyte assemblies but might exhibit similar diversities

(qualitative aspect). Secondly, different phorophyte species might support various degrees of epiphyte diversity but those epiphyte species occurring on a low diversity phorophyte would also be part of the epiphyte flora found on a high-diversity phorophyte (quantitative aspect).

Phorophyte preferences are probably less marked in tropical regions than in temperate zones, due to the high diversity of available phorophytes on the small scale: while the average number of tree species in a temperate forest does not exceed 5–10 species per ha, it amounts to 100–300 or more species per ha in tropical forests (WHITMORE 1990, VALENCIA & al. 1994). This implies low individual numbers of potential phorophyte species, and hence, epiphytes with marked phorophyte preferences would be in a disadvantage. Furthermore, high phorophyte diversity mitigates the ecomorphological differences between phorophyte species and produces a continuum of phorophyte characters rather than distinct types, making the establishment of phorophyte preferences difficult. When studying such preferences, it is therefore necessary to include a sufficiently high number of different phorophyte species instead of selecting a few particular types because otherwise the resulting patterns appear more distinct than they actually are (WOLF 1993). In fact, hitherto studies on phorophyte preferences in foliicolous lichens were based on few phorophyte species only (NOWAK & WINKLER 1975, BARILLAS & al. 1993, CONRAN 1997), and hence their results cannot be generalized.

In foliicolous lichens, possible reasons for phorophyte preferences must be assigned to leaf characteristics, such as surface structure and longevity (NOWAK & WINKLER 1975, BARILLAS & al., CONRAND 1997; see also Part II: LÜCKING 1998b). Such preferences, if they exist, should be less distinct than in corticolous lichens, since the direct relationship with the substrate is less marked, due to the fact that the leaf surface must be kept intact for the foliicolous colonizers to survive. The analysis of diversity patterns in the second part of this study (LÜCKING 1998b) indicated that while phorophyte characters have a significant influence on the α-diversity of foliicolous lichens, interspecific β-diversity between different phorophyte species is less affected and lower than intraspecific β-diversity. In other words, there is a distinct quantitative aspect of phorophyte preferences in foliicolous lichens while the qualitative aspect is probably low and only detectable by subtle methods such as the clustering of individual phorophytes on the basis of their foliicolous lichen species composition (see CONRAN 1997). Such clustering approaches have been applied in the present paper in order to evaluate differences in species composition on different phorophytes and to investigate whether these differences are due to phorophyte characters or merely depend on microclimatic fators.

2. Materials and Methods

The study area is described in detail in Part I (LÜCKING 1998a). For the evaluation of the foliicolous lichen flora, 321 phorophytes belonging to 39 species (Table 1) were included, and 13 environmental parameters (nine phorophyte characters and four microclimatic factors) were determined for each phorophyte (Table 2; for details see Part II: LÜCKING 1998b). The 39 phorophyte species were selected according to the following criteria. (1) High frequency at the study site; rare species were only considered when having characters of particular interes. (2) Wide geographical distribution and wide altitudinal range, in order to facilitate comparison with other areas. (3) Easy recognition in the vegative state, since understory phorophytes are often juvenile and may not produce the flowers or fruits necessary for their sure determination. (4) High diversity of leaf characters, such as shape, size, surface structure and presence of particular characters. (5) High diversity of life forms, such as herbs, shrubs, trees, hemiepiphytes and epiphytes. (6) High systematic diversity, e.g. pteridophytes, monocots, and dicots. (7) Inclusion of extremes in foliicolous lichen cover, in order to determine the possible reasons why certain phorophyte species carry an extraordinarily rich or poor foliicolous lichen flora.

For establishing the phorophyte range of a foliicolous lichen species, four parameters were determined. The theoretical (1) maximum and (2) minimum phorophyte range were derived from the number of phorophytes colonized by a given lichen species. The phorophyte species were thereby arranged according to their frequency, i.e. the number of phorophytes included in this study, beginning with *Ocotea atirrensis* (16) and followed by *Salpichlaena volubilis* with 14, *Piper glabrescens* (13), and so on (see Part II: LÜCKING 1998b). The theoretical minimum range is the number of phorophyte species whose number of phorophytes together equals or exceeds the number of phorophytes colonized by the lichen species. For example, a lichen species found on 39 phorophytes would occur, in the case of absolute specifity, on at least three different phorophyte species, since the first three phorophyte species summarize 43 phorophytes which exceed 39. The theoretical maximum range corresponds to the number of phorophytes colonized by the lichen species but cannot be higher than 39. (3) The expected phorophyte range was also derived from the abdundance of a lichen species. For example, if a lichen species is randomly distributed among different phorophyte species and found on a total of 39 phorophytes, according to a probability distribution the most probable number of phorophyte species to which these phorophytes belong is not 39 but 23. Calculated over all possible lichen frequencies (1–321), the expected phorophyte range follows a logarithmic pattern. These three paramets were compared to (4) the actually observed phorophyte range in a lichen species.

Pairs of phorophytes, a and b, were compared with regard to their foliicolous lichen species composition using the coefficient of community as defined by SØRENSEN 1948: $S_{a,b} = 2 \times n_{a+b}/(n_a + n_b)$, where S = coefficient of community (taking values between 0 and 1), n_{a+b} = number of foliicolous lichen species in common between the two phorophytes, and n_a, n_b = number of foliicolous lichen species occurring on each phorophyte, a and b. This coefficient is stable with regard to different degrees of α-diversity between the phorophytes to be compared, focusing more on the qualitative aspect of foliicolous lichen species composition (GOODALL 1978). By comparison with "spatial" reproductions of the Sørensen matrices by means of multi-

Table 1

Selected phorophyte species, their habit and ecogeography as far as known. For nomenclature see Part II (LÜCKING 1998b). After STANDLEY 1937-1938, HARLING 1958, SMITH 1965, WESSELS BOER 1968, BURGER 1971-1977, GENTRY 1973, HOLDRIGDE & POVEDA 1975, STOLZE 1976, MAAS 1977, ZAMORA 1989, BURGER & VON DER WERFF 1990, SCHEMSKE 1991, VANDERMEER 1991, WAGNER & GÓMEZ 1991, HODEL 1992, KAHN & al. 1992, BURGER & TAYLOR 1993, and specimens deposited in the National Herbarium of Costa Rica (CR) and the Herbarium of the Escuela de Biología, Universidad de Costa Rica (USJ). Abbreviations: CA = Central America, SA = South America, WI = West Indies, s = southern, nw = northwestern.

Species and systematic affinity	Life and growth form	Altitudinal range	Distribution
Pteridophyta			
Ctenitis subincisa (*Tectariaceae*)	terrestrial herb	lowl. to upper mont.	CA, SA, WI
Diplazium ceratolepis (*Athyriaceae*)	terrestrial herb	premont. to lower mont.	CA
Diplazium lindbergii (*Athyriaceae*)	terrestrial herb	premont. to lower mont.	CA
Salpichlaena volubilis (*Blechnaceae*)	hemiepiphytic climber	lowl. to mont.	CA, SA
Thelypteris gigantea (*Tectariaceae*)	terrestrial herb	lowl. to lower mont.	CA
Spermatophyta: Monocotyledoneae: Arecaceae			
Calyptrogyne condensata	large herb or small tree	lowl. to premont.	s CA
Chamaedorea tepejilote	small tree	lowl. to lower mont.	CA
Cryosophila warscewiczii	small tree	lowl. to premont.	s CA
Geonoma cuneata	large herb or small tree	lowl. to premont.	s CA
Iriartea deltoidea	medium sized tree	lowl. to lower mont.	s CA, SA
Prestoea decurrens	small tree	lowl. to lower mont.	s CA
Welfia georgii	medium sized tree	lowl. to premont.	CA, SA
Spermatophyta: Monocotyledoneae: Araceae			
Anthurium bakeri	epiphyte	lowl. to premont.	Costa Rica
Dieffenbachia longispatha	large herb	lowl. to premont.	CA
Monstera tenuis	hemiepiphytic climber	lowl. to lower mont.	CA
Philodendron verrucosum	hemiepiphyte	premon. to lower mont.	s CA
Rhodospatha wendlandii	hemiepiphytic climber	lowl. to lower mont.	Costa Rica
Spathiphyllum friedrichsthalii	large herb	lowl. to premont.	CA, nw SA
Spermatophyta: Monocotyledoneae: Others			
Costus curvibracteatus (*Costaceae*)	large herb	lowl. to premont.	CA
Costus laevis (*Costaceae*)	large herb	lowl. to lower mont.	CA
Costus malortieanus (*Costaceae*)	large herb	lowl. to premont.	Costa Rica
Cyclanthus bipartitus (*Cyclanthaceae*)	large herb	lowl. to lower mont.	CA, SA, WI
Heliconia sp. (*Heliconiaceae*)	large herb	—	—
Renealmia concinna (*Zingiberaceae*)	large herb	lowl. to premont.	s CA, nw SA
Spermatophyta: Dicotyledoneae			
Ardisia auriculata (*Myrsinaceae*)	shrub or small tree	lowl. to premont.	Costa Rica
Besleria notabilis (*Gesneriaceae*)	shrub	premont. to lower mont.	s CA
Columnea consanguinea (*Gesneriac.*)	epiphytic shrub	premont. to lower mont.	Costa Rica
Faramea suerrensis (*Rubiaceae*)	shrub or small tree	lowl. to premont.	Costa Rica
Guarea grandifolia (*Meliaceae*)	medium sized tree	lowl. to premont.	CA
Guarea kunthiana (*Meliaceae*)	medium sized tree	lowl. to mont.	CA, SA
Guatteria aeruginosa (*Annonaceae*)	medium sized tree	lowl. to premont.	s CA
Miconia hamelii (*Melastomataceae*)	shrub or small tree	premont. to lower mont.	CA
Miconia sp. (*Melastomataceae*)	shrub or small tree	—	—
Naucleopsis naga (*Moraceae*)	medium sized tree	lowl. to premont.	s CA
Ocotea atirrensis (*Lauraceae*)	small tree	lowl. to lower mont.	s CA
Piper glabrescens (*Piperaceae*)	shrub	lowl. to lower mont.	s CA, SA
Pourouma minor (*Cecropiaceae*)	medium sized tree	lowl. to premont.	s CA, nw SA
Schlegelia sulfurea (*Bignoniaceae*)	epiphytic shrub	lowl. to premont.	CA, SA
Vismia billbergiana (*Clusiaceae*)	small tree	lowl. to premont.	CA

Table 2

Distribution of characters among the investigated phorophyte species (see Part II: LÜCKING 1998b). In the case of surface continuity, height of exposure, leaf longevity, and sample area, the ranges over all phorophytes within the species are given, and, in addition, the average in case of leaf longevity. Statements in brackets indicate that hairs are only present on young leaves, or that a drip tip is only moderately developed.

	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 [dm²]
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

Table 3

Composition of phorophytes for nine different clustering designs, in terms of phorophyte species, leaf types, microclimatic conditions, and foliicolous lichen diversity.

Design	Phorophyte species	Microclimatic conditons	Diversity
I = Phorophytes A	6 species, 2 different leaf types	shady understory (1-4 % light, 89-95 % humidity)	high diversity (26-65 species)
II = Phorophytes B	6 species, 6 different leaf types	shady understory (1-4 % light, 89-95 % humidity)	high diversity (26-65 species)
III = Phorophytes C	10 species, 10 different leaf types	shady understory (1-4 % light, 89-95 % humidity)	no selection
IV = Microclimate A	no selection	shady understory vs. light gaps (1-2 % vs. 6-13 % light, 90-95 % vs. 84-88 % humidity)	high diversity (26-65 species)
V = Microclimate B	9 species, 5 different leaf types	different light intensity (1-2 % vs. 6-13 %) intermediate humidity (87-92 %)	no selection
VI = Microclimate C	9 species, 5 different leaf types	different humidity (84-88 % vs. 90-95 % humidity) intermediate light intensity (2-6 %)	no selection
VII = Mixed	10 species 5 different leaf types	shady understory vs. light gaps (1-2 % vs. 6-13 % light, 90-95 % vs. 84-88 % humidity)	high diversity (26-65 species)
VIII = Diversity A	no selection	shady understory (1-4 % light, 89-95 % humidity)	two groups (5-10 vs. 31-40 species)
IX = Diversity B	no selection	shady understory (1-4 % light, 89-95 % humidity)	successive increase (1-59 species)

dimensional scaling, three different clustering algorithms, i.e. complete linkage, weighted pairgroup average, and Ward's method, were tested. All gave rather similar results with regard to the clustering designs, and Ward's method was selected for the dendrograms presented here since the clusters appear more distinct than those derived from the other algorithms.

In order to demonstrate how clustering of individual phorophytes is affected by phorophyte characters, microclimatic factors and foliicolous lichen diversity, nine clustering designs were applied, each one selecting particular phorophytes out of the total of 321 (Table 3). Designs I–III include different compositions of phorophyte species and leaf typus while the microclimatic conditions are held ± homogeneous. In design IV, two distinct microsites (shady understory and light gaps) are compared, and in designs V and VI, the effects of light intensity and humidity are considered separately. Design VII include phorophyte species and microclimatic conditions at the same time, using phorophyte species in which phorophytes occurred either under shady understory or under light gap conditions. Finally, in designs VIII and IX, phorophytes with different foliicolous lichen diversity are compared.

Distribution of phorophyte species, microclimatic conditions and foliicolous lichen diversity among the resulting clusters was analyzed by means of a Chi-square

test. Foliicolous lichen species discriminating between the clusters were identified with a modified Median test, based on the relative frequency of the foliicolous lichens within each cluster. All statistical calculations were made using the program package STATISTICA 5.0, except for the calculation of the coefficient of community of Sørensen which was made with a Q-BASIC program written by the author.

3. Results

The observed phorophyte range, i.e. the number of phorophyte species colonized by a given foliicolous lichen species, comes close to the expected range as calculated from the frequency of the lichens (Fig. 1). Most lichens (82 %), deviate by 30 % or less from the expected range, while 18 taxa (10 %) deviate by more than 40 % (Fig. 2). The most distinct deviations, mostly towards a restricted phorophyte range, are found in species with intermediate frequency (occurring on 20–70 phorophytes). Among these, the abdundance of subcuticularly growing species of the genus *Strigula*, viz. *S. nemathora, S. antillarum, S. nigrocarpa, S. concreta*, and *S. subtilissima*, is particularly remarkable (Table 4). Further species with strong deviations form the expected phorophyte range are *Eremothecella calamicola, Porina rubescens, Asterothyrium microsporum, Gyalideopsis minutissima, Echinoplaca melanotrix, Tricharia helminthospora, Paratricharia paradoxa* and *Byssoloma multipunctata*.

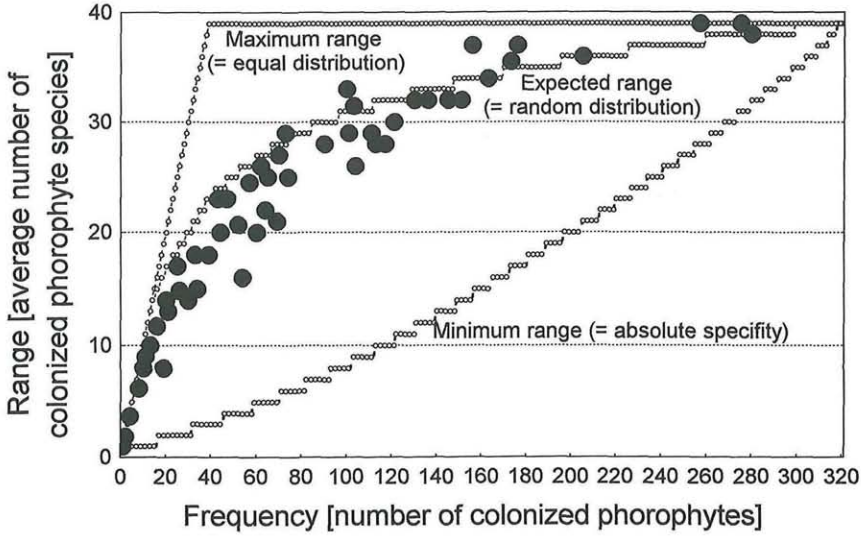

Fig. 1. Expected and observed phorophyte ranges of foliicolous lichen species, plotted against their frequency. The black points indicate the observed phorophyte range for each foliicolous lichen species (in the case of species with identical frequency values, the arithmetic mean is given).

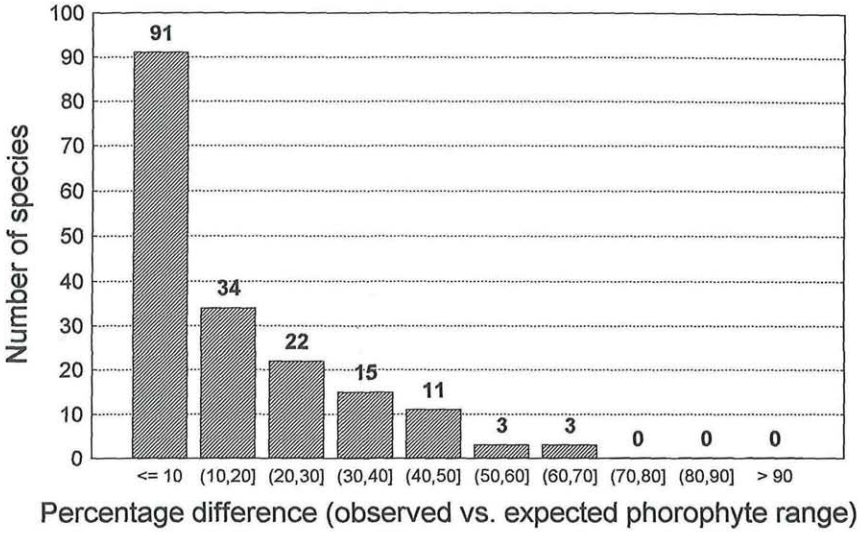

Fig. 2. Number of foliicolous lichen species deviating at different degrees from their expected phorophyte range.

Table 4

Foliicolous lichen species in which the observed phorophyte range deviates by more than 40 % from that expected on the basis of their frequency. Only species which occurred on at least three phorophytes are considered.

Foliicolous lichen species	Frequency (number of phorophytes)	Number of phorophyte species		Percentage difference
		Expected range	Observed range	
Porina rubescens	3	3	1	67 %
Byssoloma multipunctata	3	3	1	67 %
Gyalideopsis minutissima	8	8	3	63 %
Mazosia paupercula	7	7	3	57 %
Strigula nemathora	35	22	10	55 %
Paratricharia paradoxa	22	17	8	53 %
Echinoplaca melanotrix	19	16	8	50 %
Asterothyrium microsporum	14	14	7	50 %
Mazosia dispersa	12	12	6	50 %
Strigula subtilissima	6	6	3	50 %
Porina nitidula	6	6	3	50 %
Calopadia foliicola	6	6	3	50 %
Strigula antillarum	22	17	9	47 %
Eremothecella calamicola	9	9	5	44 %
Tricharia helminthospora	14	14	8	43 %
Strigula concreta	54	26	15	42 %
Strigula nigrocarpa	12	12	7	42 %

The first clustering design (I = Phorophytes A), considering six phorophyte species belonging to two distinct leaf types (dicot vs. palm), does not show a distinct grouping of phorophyte species (Fig. 3). The two leaf types are almost equally distributed among the two main groups A and B (Chi-square text: $\chi^2 = 0.003$, $p = 0.96$ for palm leaves; $\chi^2 = 0.002$, $p = 0.97$ for dicot leaves). More distinctive groups appear when six different leaf types instead of two are considered (design II = Phorophytes B): Except for the palm *Iriartea deltoidea*, the phorophyte species cluster well together (Fig. 4). *Ocotea atirrensis* is only found in group A (Chi-square text: $\chi^2 = 8.20$, $p < 0.05$), while *Rhodospatha wendlandii* is confined to group B (Chi-square test: $\chi^2 = 12.2$, $p = 0.001$). Also, the fern *Salpichlaena volubilis* and the palm *Calyptrogyne condensata* are more frequent in group A but without statistical significance (Chi-square test: $\chi^2 = 0.30$, $p = 0.585$, and $\chi^2 = 1.80$, $p = 0.18$, respectively). However, in both groups the two species form either pure or mixed subgroups consisting of two to five phorophytes. *Ocotea atirrensis* also forms two pure subgroups of three and four phorophytes, and in group B, a pure subgroup of six phorophytes of *Rhodospatha wendlandii* is found. This is particularly remarkable as in all cases the phorophytes of a given species are spatially distant from each other.

When comparing the phorophytes of *Ocotea atirrensis* in group A with those of *Rhodospatha wendlandii* in group B, the following foliicolous lichen species appear to be discriminant between both phorophyte species: *Arthonia aciniformis, Strigula nemathora, S. smaragdula, S. concreta, S. viridis, Porina leptospermoides, Aspidothelium fugiens, Phyllobathelium anomalum, Dimerella dilucida, D. flavicans, Fellhanera emarginata, Byssoloma minutissimum, B. leucoblepharum* and *Sporopodium leprieurii* for *Ocotea atirrensis*, and *Mazosia rotula, M. melaniophthalma*, as well as *Microtheliopsis uleana*, for *Rhodospatha wendlandii*. In addition, species richness is significantly higher in *Ocotea atirrensis* (KRUSKAL-WALLIS H-test: $H = 6.98$, $p < 0.05$). A comparison of the six phorophytes of *Ocotea atirrensis* in group B with the sister subgroup formed by the palms *Calyptrogyne condensata* and *Iriartea deltoidea* gives the following discriminant species: *Strigula nemathora, S. concreta, Phyllobathelium anomalum, Calenia thelotremella* and *Dimerella siquirrensis* for *Ocotea atirrensis*, and *Eremothecella calamicola, Opegrapha filicina, Porina fulvella, Trichothelium minutum, T. echinocarpum, Aulaxina intermedia, Calenia phyllogena, Paratricharia paradoxa, Tricharia helmithospora, T. hyalina, T. heterella, T. couepiae, Byssoloma absoconditum, B. wettsteinii, Fellhanera verrucifera* and *Gyalideopsis minutissima* for the palms.

When phorophyte species with particular leaf characteristics affecting foliicolous lichen colonization, such as hairs, glands, a papillose surface fine structure, low surface continuity, or short leaf longevity (see Part II: LÜCKING 1998b), are compared with phorophytes in which such features

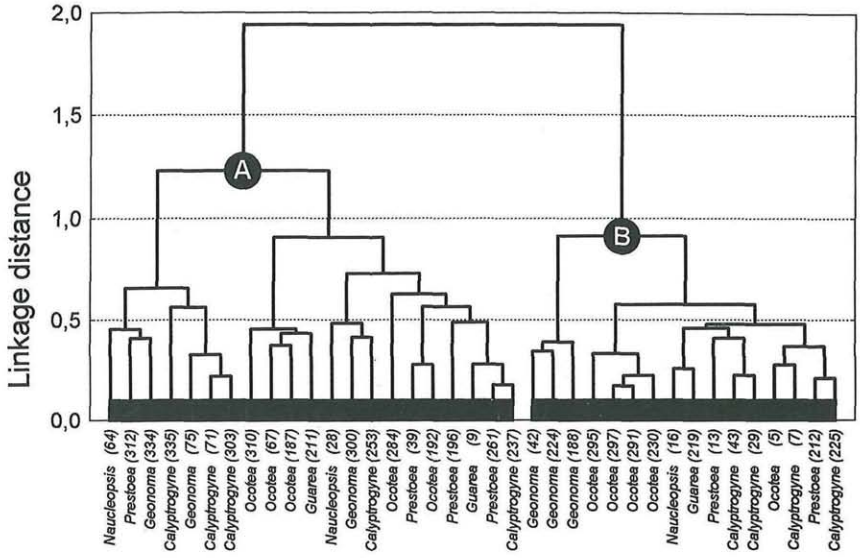

Fig. 3. Cluster dendrogram for six different phorophyte species and two different leaf types, i.e. dicot vs. palm type (design I in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text.

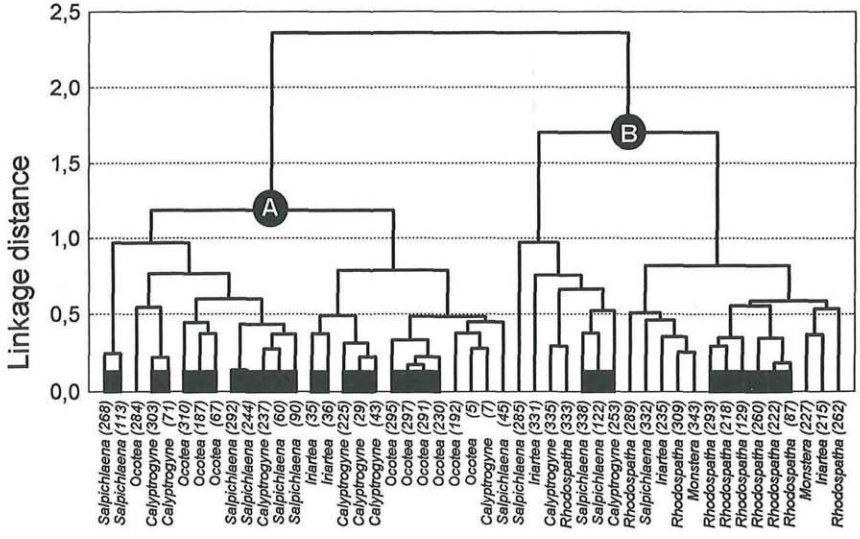

Fig. 4. Cluster dendrogram for six different phorophyte species and six different leaf types (design II in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text.

are absent (Design III = Phorophytes C), the resulting clusters are also rather distinctive (Fig. 5). Phorophyte species with unspecialized leaf types, i.e. the dicot *Ocotea atirrensis* and the palm *Calyptrogyne condensata,* are confined to group B (Chi-square test: $\chi^2 = 15.5$, $p < 0.001$, and $\chi^2 = 11.8$, $p < 0.001$, respectively). *Ocotea atirrensis* forms a pure subgroup of six phorophytes and *Calyptrogyne condensata* one of three phorophytes. Group A, the sister group of group B, is dominated by the fern *Thelypteris gigantea* (Chi-square test: $\chi^2 = 34.0$, $p < 0.001$) which also forms a pure subgroup of five phorophytes. In groups C and D, the phorophytes with characters which negatively affect foliicololus lichen diversity are concentrated: the dicot *Miconia hamelii* with hairy leaves (Chi-square text: $\chi^2 = 10.4$, $p < 0.05$), the fern *Ctenitis subincisa* with finely divided, partly hairy leaves (Chi-square test: $\chi^2 = 6.70$, $p < 0.05$), and, though not significant, the monocot *Costus malortieanus* with hairy leaves and papillose fine surface structure (Chi-square test: $\chi^2 = 2.40$, $p = 0.12$) in group C, and the dicots *Ardisia auriculata* and *Vismia billbergiana,* with glands on the leaf surface, in group D (Chi-square test combined: $\chi^2 = 20.8$, $p < 0.001$). The two phorophyte species *Dieffenbachia longispatha* and *Heliconia* sp. are scattered among all groups, with no apparent clustering pattern.

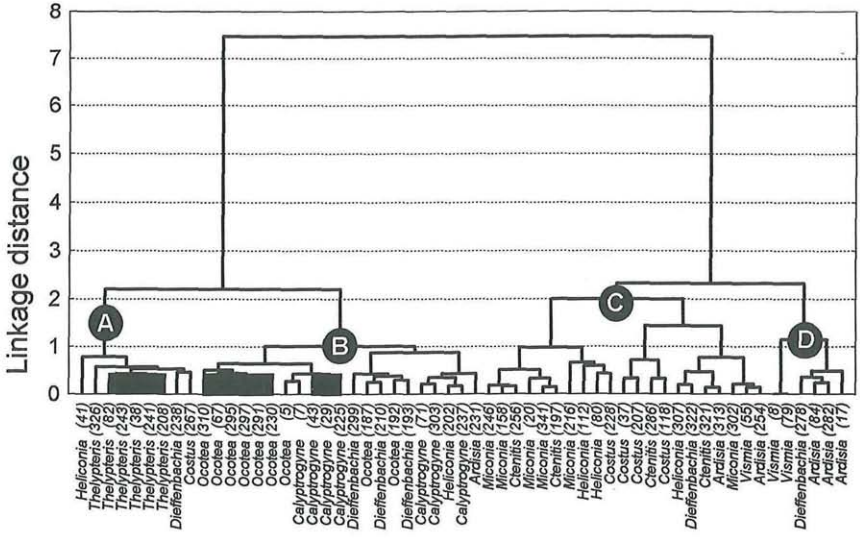

Fig. 5. Cluster dendrogram for ten different phorophyte species and ten different leaf types with characters affecting foliicolous lichen diversity (design III in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text.

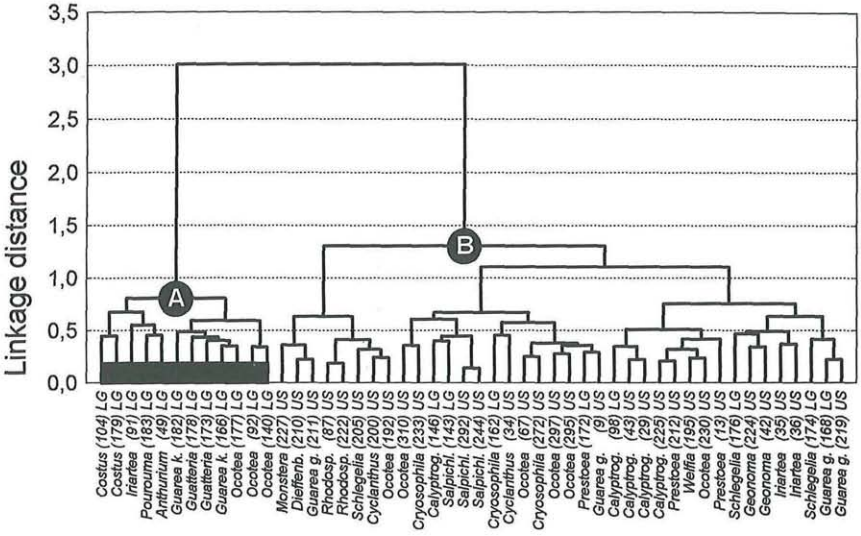

Fig. 6. Cluster dendrogram for two differnt microsite types, i.e. shady understory vs. light gaps (design IV in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text. US = shady understory phorophyte, LG = light gap phorophyte.

A comparison of the pure subgroups of *Ocotea atirrensis* in group B and *Thelypteris gigantea* in group A gives no discriminant foliicolous lichen species for the latter but 20 discriminant species for *Ocotea atirrensis*. In addition, species richness is significantly higher in *Ocotea atirrensis* as compared to *Thelypteris gigantea* (Kruskal-Wallis H-Test: H = 8.34, $p < 0.05$).

The comparison of shady understory and light gap phorophytes gives a rather clear separation, with group A consisting of twelve light gap phorophytes (Chi-square test: $\chi^2 = 14.2$, $p < 0.001$) and group B including the remaining eight light gap phorophytes and all shady understory phorophytes (Fig. 6). Interestingly, half of the light gap phorophytes merged with the shady understory phorophytes are palm species, while only one light gap palm is found in group A. A large number of foliicolous lichen species discriminate between the light gap phorophytes in group A and the shady understory phorophytes in group B (Table 5). Among group A, the families *Gomphillaceae* and *Ectolechiaeceae* are dominant, and species of the genera *Aulaxina, Calenia, Echinoplaca, Tricharia, Gyalideopsis* and *Calopadia* abound, while group B is mainly characterized by the families *Arthoniaceae, Opegraphaceae* and *Trichotheliaceae,* in particular the genera *Arthonia, Mazosia, Porina, Trichothelium* and *Dimerella.*

Table 5

Foliicolous lichen species which discriminate between group A (light gap phorophytes) and group B (shady understory phorophytes) in the clustering design IV (= microclimate A; see Fig. 6).

Group A (light gap phorophytes)	Group B (shady understory phorophytes)
Cryptothecia candida	*Arthonia leptosperma*
Strigula antillarum	*Arthonia aciniformis*
Strigula smaragdula	*Eremothecella calamicola*
Strigula nitidula	*Mazosia rotula*
Aspidothelium fugiens	*Mazosia melanophthalma*
Musaespora kalbii	*Strigula maculata*
Aulaxina intermedia	*Strigula phyllogena*
Aulaxina quadrangula	*Strigula platypoda*
Aulaxina dictyospora	*Porina andreana*
Aulaxina opegraphina	*Porina atropunctata*
Calenia triseptata	*Porina epiphylla*
Calenia depressa	*Porina subepiphylla*
Calenia thelotremella	*Porina lucida*
Calenia lueckingii	*Porina limbulata*
Calenia rolandiana	*Porina leptospermoides*
Actinoplaca strigulacea	*Porina leptosperma*
Echinoplaca pellicula	*Porina fusca*
Echinoplaca leucotrichoides	*Trichothelium minus*
Echinoplaca verrucifera	*Trichothelium epiphyllum*
Echinoplaca epiphylla	*Phylloblastia amazonica*
Echinoplaca fusconitida	*Anisomeridium foliicola*
Echinoplaca marginata	*Microtheliopsis uleana*
Tricharia lancicarpa	*Dimerella dilucida*
Tricharia urceolata	*Dimerella siquirrensis*
Tricharia albostrigosa	*Byssoloma absconditum*
Gyalideopsis montana	*Badimia dimidiata*
Gyalideopsis verruculosa	
Gyalideopsis rubescens	
Gyalideopsis epithallina	
Bacidina apiahica	
Fellhanera bouteillei	
Fellhanera semecarpi	
Byssoloma subdiscordans	
Tapellaria epiphylla	
Calopadia foliicola	
Calopadia puiggarii	
Calopadia fusca	
Sporopodium citrinum	
Sporopodium phyllocharis	
Loflammia flammea	
Lasioloma arachnoideum	

A rather similar pattern is found when considering only phorophytes with high relative light intensity in comparison to those with low relative light intensity while holding relative air humidity within a narrow range. Again, most phorophytes with high relative light intensity are clustered together in a peripheral group A (Chi-square test: $\chi^2 = 17.6$, $p < 0.001$), while the remainder are scattered among the phorophytes with low relative light intensity in group B (Fig. 7). On the other hand, when discriminating

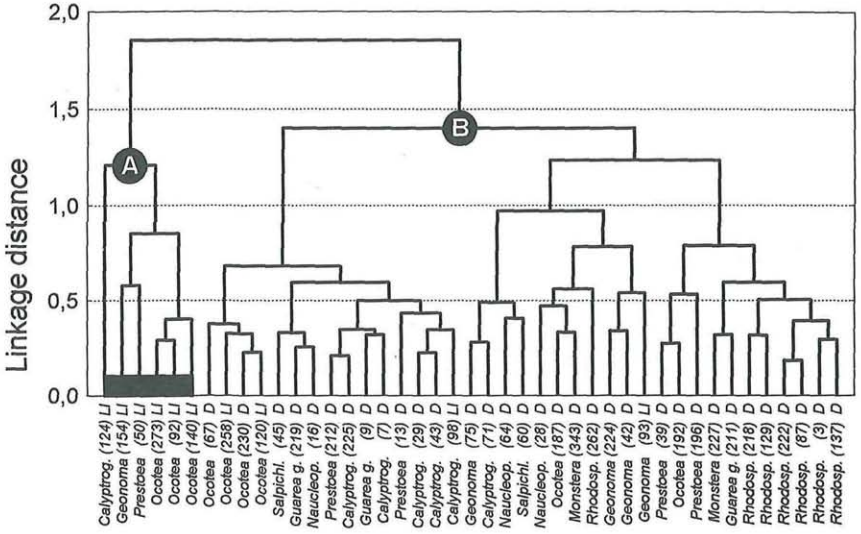

Fig. 7. Cluster dendrogram for nine different phorophyte species with five different leaf types and different categories of relative light intensity (design V in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text. D = low relative light intensity, LI = high relative light intensity.

between phorophytes with different relative air humidity and at the same time a narrow range of relative light intensity, those phorophytes with low relative air humidity are not found in a peripheral group but cluster together in a more central group B (Fig. 8), and the clustering effect is less distinct (Chi-square test: $\chi^2 = 9.08$, $p < 0.05$).

Regarding phorophyte species in which either shady understory or light gap phorophytes occur, then the clustering pattern is very similar to that found in the more general comparison of shady understory and light gap phorophytes above. Again, there is a peripheral group A with light gap phorophytes only (Chi-square test: $\chi^2 = 18.8$, $p < 0.001$), and scattered light gap phorophytes are also found in groups C and D, while group B consists of understory phorophytes only (Fig. 9). In *Ocotea atirrensis, Guarea kunthinana, Chamaedorea tepejilote, Pourouma minor,* and *Anthurium bakeri,* the corresponding phorophytes basically cluster together according to their microclimatic conditions and irrespective of the phorophyte species. In *Prestoea decurrens,* one light gap phorophyte is found in the peripheral group A while the other appears in a group together with an shady understory phorophyte of the same species. In four phorophyte species, viz. *Salpichlaena volubilis, Geonoma cuneata, Calyptrogyne condensata,* and *Schlegelia sulfurea,* all light gap phorophytes are merged with the shady

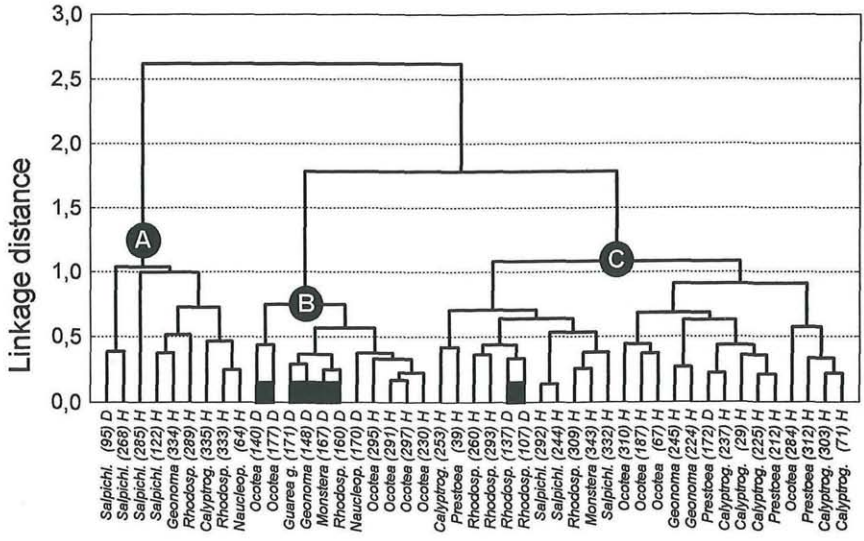

Fig. 8. Cluster dendrogram for nine different phorophyte species with five different leaf types and different categories of relative air humidity (design VI in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text. H = high relative air humidity, D = low relative air humidity.

understory phorophyte in group B and in five of seven cases cluster together with shady understory phorophytes of the same species.

The comparison of phorophytes with different foliicolous lichen diversity results in a separation of phorophytes with low (5–10 species) and high diversity (31–40 species; Chi-square text: $\chi^2 = 37.6$, $p < 0.001$): all low diversity phorophytes cluster together in a separate group (Fig. 10). When phorophytes with successively increasing diversity (1–59 species) are considered, then three groups with different ranges of foliicolous lichen diversity are apparent (Fig. 11): group A, with 1–19(–22) foliicolous lichen species per phorophyte; group B, with (13–)20–35 species; and group C, with (29–)34–59 species. The degree of overlap between the three groups is very low (Kruskal-Wallis H-test: $H = 39.7$, $p < 0.001$; see Fig. 12). Within group A, a separation of three subgroups with the following diversity ranges is also apparent: 1–3 species, 4–10 species, and 11–19(–22) species. No such subgroups can be found in groups B and C. Foliicolous lichen species with a ± constant appearance in the subgroup with 1–3 species, are *Porina mirabilis* and *Gyalectidium filicinum,* while in addition to these taxa, *Strigula phyllogena, S. platypoda, Porina epiphylla, P. rufula, Pocsia septemseptata, Phylloblastia amazonica, Gyalideopsis vulgaris, Tricharia vainioi, Dimerella dilucida, D. epiphylla* and *Sporopodium leprieurii,* appear rather constantly in the subgroup with 4–10 species.

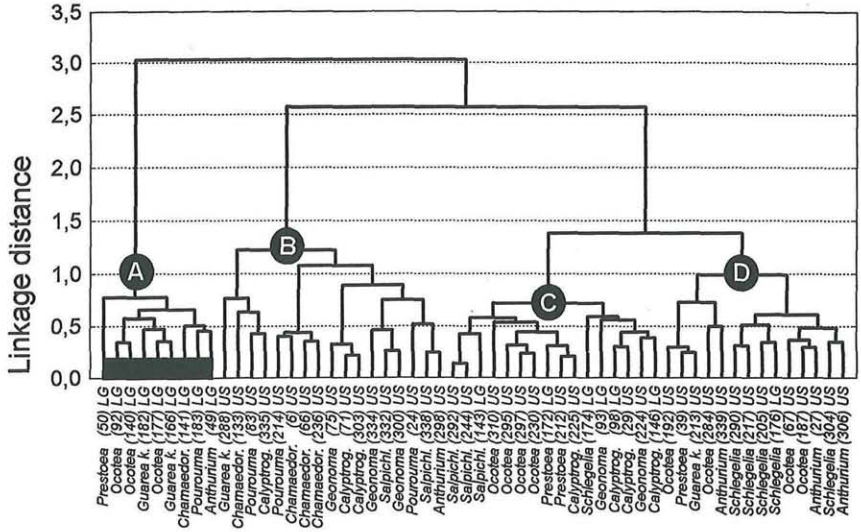

Fig. 9. Cluster dendrogram for ten different phorophyte species with five different leaf types in combination with two different microsite types, i.e. shady understory vs. light gaps (design VII in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text. US = shady understory phorophytes, LG = light gap phorophytes.

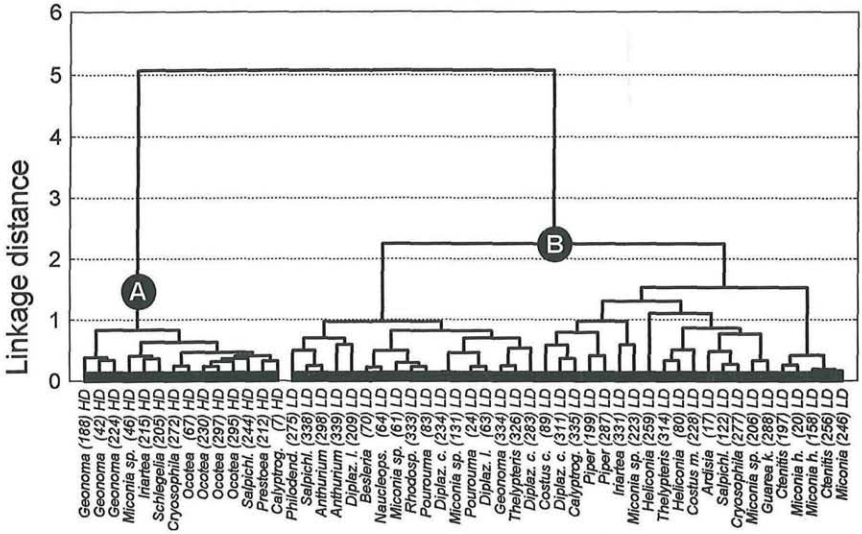

Fig. 10. Clusterdendrogram for two different categories of foliicolous lichen diversity (design VIII in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text. LD = low diversity phorophytes, HD = High diversity phorophytes.

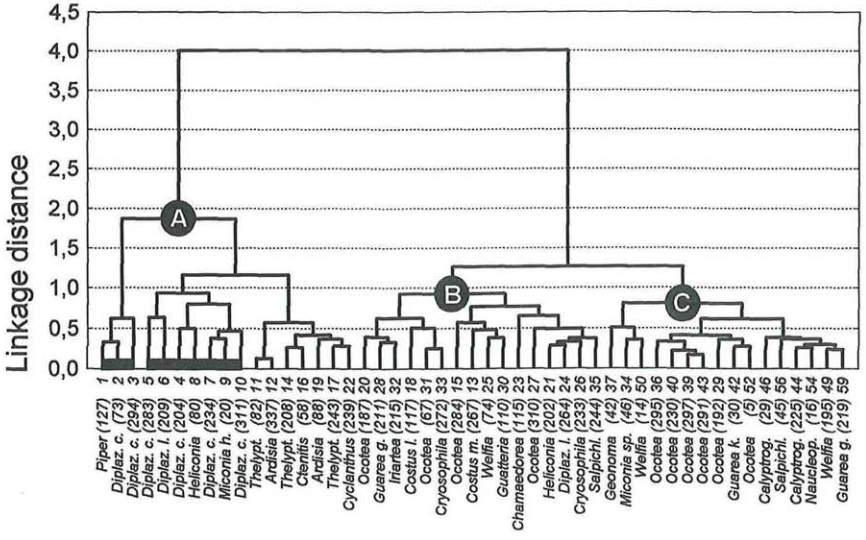

Fig. 11. Cluster dendrogram for phorophytes with continuously increasing foliicolous lichen diversity (design IX in Table 3). Dendrogram based on Sørensen's (1948) coefficient of community and Ward's clustering algorithm. For further explanation see text. The figures behind the phorophytes indicate the numer of foliicolous lichen species present on each phorophyte.

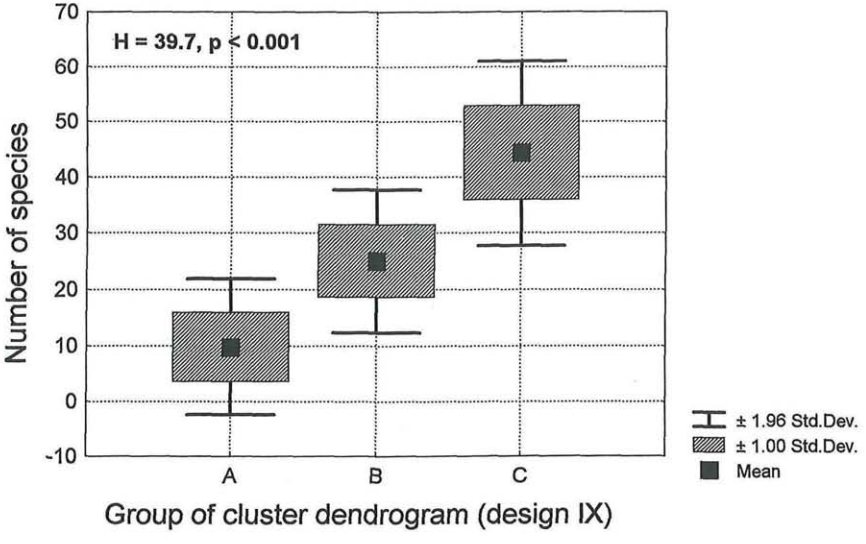

Fig. 12. Box and whisker diagram (Kruskal-Wallis H-test) showing the degree of overlap in foliicolous lichen diversity between the groups defined in the cluster dendrogram of Fig. 11.

4. Discussion

The results indicate that phorophyte specifity in foliicolous lichens is comparatively low, and the phorophyte range of most of the species comes close to the range expected from their respective frequency. Among the few species with low phorophyte range, two groups dominate: species of the genus *Strigula,* frequent on dicot leaves, and some species of various affinities which are more common on palm type leaves: *Eremothecella calamicola, Opegrapha filicina, Porina fulvella, Trichothelium minutum, T. echinocarpum, Aulaxina intermedia, Calenia phyllogena, Paratricharia paradoxa, Tricharia helminthospora, T. hyalina, T. heterella, T. couepiae, Byssoloma absconditum, B. wettsteinii, Fellhanera verrucifera* and *Gyalideopsis minutissima.* The high frequency of *Strigula* species on dicot leaves has also been observed by other workers (SANTESSON 1952, NOWAK & WINKLER 1970, 1975, BARILLAS & al. 1993) and is probably due to their subcuticular growth. Observations indicate that these species often grow along leaf wounds which apparently enhance their intrusion beneath the leaf cuticle, and such wounds are more common in dicot than in palm leaves.

The low degree of phorophyte specifity is also demonstrated by the low number of discriminant foliicolous lichen species in the different clustering designs. Regarding phorophyte characters, the highest number of discriminant species is found in respect to palm leaves, and these are to a large extent the species which, in addition to those of the genus *Strigula,* show a restricted phorophyte range. However, inspite of the few discriminant lichen species, in certain cases the phorophyte species cluster together in distinctive groups, particularly when having distinctive character combinations. There might be two reasons for this: (1) subtle differences in the assembly of lichen species between phorophyte species, and (2) a comparatively constant lichen species composition within a given phorophyte species, for example in *Rhodospatha wendlandii.*

Apart from qualitative differences in species composition, clusters of phorophytes that are formed by a single species are also separated by different foliicolous lichen diversity, as in the case of *Ocotea atirrensis* and *Thelypteris gigantea.* This is especially so when characters that affect foliicolous lichen diversity are considered, such as leaves with hairs, glands, a papillose fine surface structure, or short longevity (see Part II: LÜCKING 1998b). The clustering of phorophytes with low diversity against those with high diversity in design VIII can only be explained by the fact that low diversity always leads to similar species composition, since the use of the coefficient of community of SØRENSEN 1948, in contrary to other measures such as Euklidean distance, would cluster phorophytes with low diversity only in cases of similar species assembly (GOODALL 1978). In Part II of this series (LÜCKING 1998b), it has already been demonstrated that not

only individual phorophytes but also phorophyte species as a whole with low foliicolous lichen diversity are rather similar to each other in their species composition.

The low phorophyte specifity demonstrated here partly contradicts previous results (NOWAK & WINKLER 1975, BARILLAS & al. 1993, CONRAN 1997). It has to be considered, however, that the studied localities have their particular conditions and history which makes the generalizations difficult. The investigations were based less than ten phorophyte species or carried out in low diversity areas with respect to the occurence of foliicolous lichens. CONRAN 1997 even compares phorophytes from two different localities and makes no reference to the effect of different diversity levels between phorophyte species. From these investigations it might be concluded, however, that phorophyte preferences in foliicolous lichens are more distinct in low diversity areas and if only few phorophyte species are included, whereas in high diversity areas with a high number of potential phorophytes, phorophyte preferences are reduced to quantitative differences between phorophytes species.

That phorophyte specifity is mostly expressed by different patterns of diversity is also known from vascular epiphytes (BENZING 1983). However, in corticolous vascular and non-vascular epiphytes, qualitative phorophyte preferences are generally more distinct than indicated here for foliicolous lichens (BEEVER 1984, CORNELISSEN & TER STEEGE 1989, BENZING 1990, WOLF 1993).

The clustering of phorophytes with low diversity suggests that the different diversity stages represent subsequent stages of succession. This is also indicated by clustering design IX in which continuous diversity stages cluster into five groups which could represent five subsequent successional stages. The first stage would then have *Gyalectidium filicinum* and *Porina mirabilis* as characteristic species and typical early colonizers. In the second stage, with 4–10 species, further taxa appear as early colonizers, i.e. *Strigula phyllogena*, *S. platypoda*, *Porina epiphylla*, *P. rufula*, *Pocsia septemseptata*, *Phylloblastia amazonica*, *Gyalideopsis vulgaris*, *Tricharia vainioi*, *Dimerella dilucida*, *D. epiphylla* and *Sporopodium leprieurii*. This pattern was confirmed by direct studies on foliicolous lichen succession (Part V: LÜCKING, in prep.). The clustering of phorophytes into these and further stages, with c. 10–20, 20–35, and 35–60 species, indicates repeated changes in species composition probably due to the age of the leaf and the time different lichen species need for successful colonization. The kind of succession reflected here is not a typical succession with pioneer species providing the base for the subsequent settlement of other species, i.e. the classical Clementian model (HORN 1981, NOBEL & SLATER 1981) , but rather follows the tolerance model as defined by NOBEL & SLATER 1981 (see also BEGON & al. 1991).

Microclimatic factors are obviously more important for species composition than phorophyte characters. This has also been observed in foliicolous bryophytes (MARINO & SALAZAR-ALLEN 1991). By direct comparison there seems to exist a slightly hierarchical structure: microclimate factors are responsable for the grouping of individual phorophytes in the first place, while phorophyte characters appear to affect the clustering patterns in the second place only. Palm leaves largely escape from this pattern, probably because they are large and create a special microclimate which favours the growth of both light gap and understory species on the same phorophyte. In this way, palms could be considered as supporting microclimatically "extrazonal" foliicolous lichen vegetation.

The assumption that microclimate affect foliicolous lichen species composition more than phorophyte characters is also underlined by the much higher amount of species which discriminate between the shady understory and light gaps, compared to those which distinguish between different phorophyte types, and by the systematic homogeneity of these lichens (see also Part IV: LÜCKING 1998c). Relative light intensity seems to be more important than relative air humidity with regard to the qualitative aspect of foliicolous lichen species composition, while relative air humidity affects the quantitative aspect, i.e. species diversity. In the same way, microclimatic factors account principally for differences in foliicolous lichen species composition whereas phorophyte characters influence species diversity (see Part II: LÜCKING 1998b).

5. Conclusions

In high diversity areas, in particular tropical lowland rain forests, phorophyte preferences in foliicolous lichens are low and quantitative rather than qualitative, i.e. different phorophyte species support foliicolous lichen diversity but only to a small degree different species composition. Phorophytes with a distinctive foliicolous lichen flora are basically found among palms. The different stages of diversity found on different phorophytes indicate subsequent stages of succession towards a diversity maximum which then might slightly diverge in species composition. The early, species-poor stages are similar in all phorophytes and include typical early colonizers. This type of succession follows the so-called tolerance model.

Qualitative differences with regard to species composition of foliicolous lichens are mainly due to microclimatic factors, particularly relative light intensity, with a high number of species discriminating between the shady understory and light gaps of the forest. These species can be assigned to distinct systematics affinities.

In conclusion, it is postulated that the diversity of microsites with different microclimate, provoked for example by strong gap dynamics, is

more important for the overall diversity and species composition of foliicolous lichens at a given site than the diversity of phorophyte species. This also implies that a change of phorophyte species over time by anthropogenic influence or paleofloristical evolution, for example, might not have markedly affected the foliicolous lichen flora as long as the structure and dynamics of the rain forest remained about the same.

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