LICHEN FEEDERS AND LICHENICOLOUS FUNGI: DO THEY AFFECT DISPERSAL AND DIVERSITY IN TROPICAL FOLIICOLOUS LICHEN COMMUNITIES?

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Abstract. Frequency and taxonomic composition of lichen feeders and lichenicolous fungi in the phyllosphere were studied in the tropical rainforest at La Selva Biological Station, Costa Rica. Leaf-dwelling invertebrates included Annelida, Gastropoda, Acari, Diplura, Collembola, Psocoptera, Lepidoptera and Hymenoptera (Formicidae). Gastropoda and Psocoptera were the most important lichen feeders, and life cycles of Psocoptera seemed to be linked to individual lichen communities on single leaves. Lichenicolous fungi were most abundant on lichens with a high overall area cover. Feeding traces of Gastropoda did not correlate with lichen frequency parameters, while Psocoptera preferred lichens with large individual thallus size. Experiments failed to show germination of lichen diaspores or thallus parts after passing the digestion tract of lichen feeders. In addition, lichen feeders were rare in terms of individual numbers and / or showed restricted mobility. Thus, the assumption that leaf-dwelling lichen feeders significantly promote dispersal of foliicolous lichens could not be confirmed. However, partly in accordance with the Huston-Connell model, damage and death of individual lichen thalli due to lichen feeders and lichenicolous fungi might promote diversity in foliicolous lichen communities. *Accepted 26 November 1999.*

Key words: Acari, Annelida, Collembola, Costa Rica, diversity, foliicolous lichens, Gastropoda, La Selva, Lepidoptera, lichen feeders, lichenicolous fungi, phyllosphere, Psocoptera, rainforest.

INTRODUCTION

A striking feature of tropical rainforests is the growth of tiny epiphytes in the 'phyllosphere', the surface of living leaves of vascular plants (Richards 1964, Vareschi 1980, Whitmore 1990). Tropical phyllosphere communities are dominated by lichens and bryophytes, accompanied by bacteria, non-lichenized fungi and algae (Santesson 1952, Pócs 1978, Richards 1984, Sérusiaux 1989, Lücking 1995a, A. Lücking 1997, Freiberg 1998). They are also home to a variety of animals, ranging from protozoa, gastropods, tardigrads and mites to diverse insects (Callaghan 1992, A. Lücking & Lücking 1998).

Taxonomical and ecological knowledge on foliicolous lichens and bryophytes is rapidly increasing (Farkas & Pócs 1997, Farkas & Sipman 1997, A. Lücking 1997, Gradstein & Lücking 1997, Lücking et al. 2000a). However, except for nitrogen fixing cyanobacteria and their relation to foliicolous bryophytes (Harrelson 1969, Edmisten 1970, Bentley & Carpenter 1984, Freiberg 1998), interactions between phyllosphere organisms, including attack of foliicolous lichens by lichenicolous fungi and lichen-feeding invertebrates, have rarely been studied.

Lichenicolous fungi are a well-documented phenomenon (Hawksworth 1979, 1981; Triebel 1989; Rambold & Triebel 1992; Diederich 1996; Matzer 1996). They either belong to primarily non-lichenized fungi (e.g., *Lichenopeltella*) or are secondarily delichenized, as in *Arthonia*, *Opegrapha*, and *Gyalideopsis* (Fig. 1). Lichenicolous fungi mostly take advantage of the host phycobiont, acting as commensals or eventually damaging the lichen while developing own reproductive structures. Up to the present, 85 species have been found on the 700 species of foliicolous lichens known worldwide (Hawksworth 1979, 1981; Samuels 1988; Matzer 1996; Lücking et al. 2000b).

Although lichens are believed to be little attacked by "herbivores", numerous invertebrates feed on them, in particular Gastropoda, Acari, and insects of the orders Collembola, Psocoptera, and Lepidoptera (Peake & James 1967, Laundon 1971, Gerson 1973, Seyd & Seaward 1984, Rambold 1985, Seaward 1988, Prinzing 1999). Lichen-feeding Gastropoda form distinct associations on rock surfaces (Pfleiderer & Winkler 1992, Fröberg 1993). Lichens also

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provide shelter or mimetic protection for animals (Seaward 1988, Prinzing & Wirtz 1997). Whether lichen-feeding invertebrates promote diaspore dispersal via epi-, endo- or synzoochory is subject to discussion (Bailey 1976, McCarthy & Healy 1978, Seaward 1988). However, they have been shown to influence lichen morphogenesis (Prinzing 1999) and affect the structure of lichen communities (Laundon 1971).

Lepidoptera larvae (Lycanidae) are known to feed on foliicolous bryophytes (Callaghan 1992), and Seaward (1988) suggested a role of foliicolous lichens in repelling leaf herbivores in tropical forest canopies, but so far these lichens have not been studied with respect to lichen-feeding invertebrates. While gathering collections of leaves covered with epiphylls, we ob-

served that invertebrates feed on foliicolous lichens and even destroy complete floras on individual leaves. Since reproductive structures such as apothecia, campylidia or hyphophores are frequently affected, we established two working hypotheses for the potential role of invertebrates in foliicolous lichen communities: (1) Lichen-feeding invertebrates promote foliicolous lichen dispersal. This would require preference for reproductive structures, high abundance and mobility of the dispersal agents, and germinability of diaspores after external or internal transport. (2) Lichen-feeding invertebrates promote diversity in foliicolous lichen communities by acting as intermediate disturbances and limiting the population density of dominant foliicolous lichens, thus preventing them from outcompeting other species.
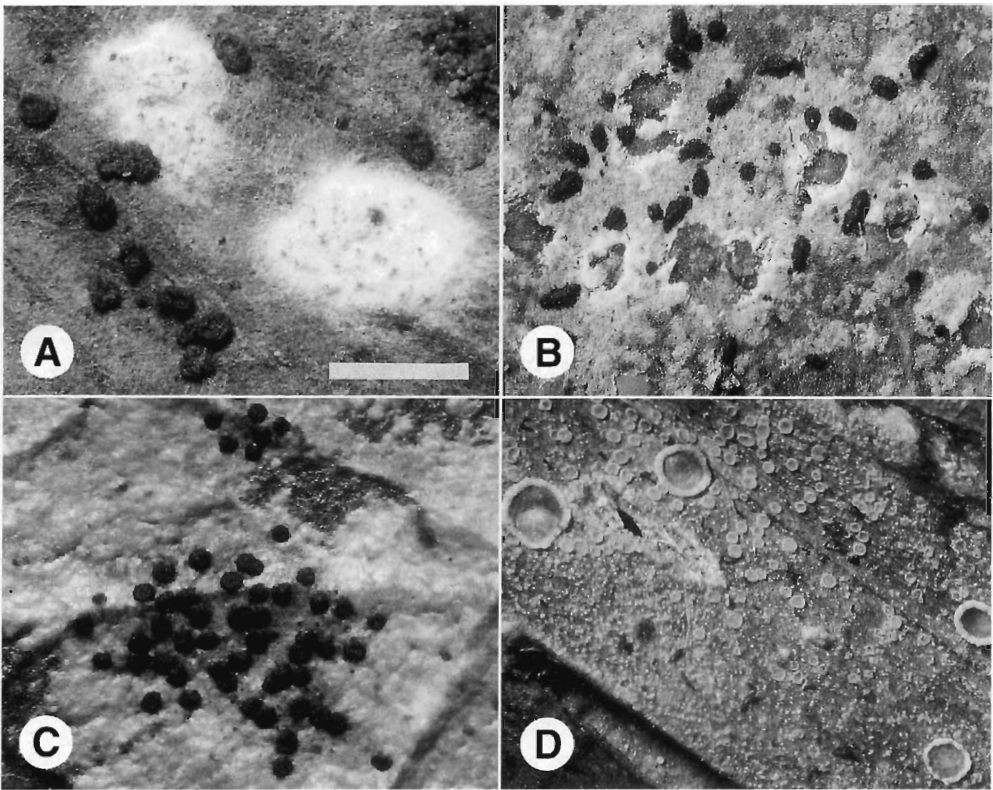

FIG. 1. Lichenicolous fungi on foliicolous lichens. A – *Arthonia cryptotheciae* (small dark ascocarps) on *Cryptothecia candida* (large white ascocarps). B – *Opegrapha matzeri* (black elongate ascocarps) on *Amazonomyces sprucei* (white thallus). C – *Lichenopeltella epiphylla* (black disc-shaped ascocarps) on *Porina mirabilis* (light thallus). D – *Gyalideopsis epithallina* (small ascocarps) on *G. vulgaris* (large ascocarps). Scale in A, C = 1 mm, in B, D = 1.5 mm.

In this paper we present data on the occurrence of lichen-feeding invertebrates and lichenicolous fungi in the phyllosphere at La Selva Biological Station, Costa Rica. The main goal of the field study was to quantify the abundance of these organisms and their effect on foliicolous lichens, to test our working hypotheses and to provide data as a base for further studies.

STUDY AREA

La Selva Biological Station is situated in the Atlantic lowlands of Costa Rica, Heredia province, north of the Cordillera Central near Puerto Viejo de Sarapiquí (Fig. 2). It is connected by a corridor with Braulio Carrillo National Park. The vegetation consists of tropical lowland rainforest and swamp forest, with an annual precipitation of 4000 mm, but also includes secondary forest and successional plots (McDade *et al.* 1994).

The rainforest at La Selva is characterized by the abundance of the canopy tree *Pentaclethra macroloba* (Mimosaceae). *Euterpe macrospadix*, *Iriartea deltoidea*, *Socratea exorrhiza*, and *Welfia georgii* are common palms of the subcanopy. Light gaps and secondary vegetation are dominated by the Cecropiaceae *Cecropia insignis*, *C. obtusifolia*, and *Pourouma bicolor* as well as *Rollinia microsepala* (Annonaceae). In the understory, the palms *Asterogyne martiana*, *Chamaedorea tepejilote*, and *Geonoma cuneata* abound, together with *Ocotea atirrensis* (Lauraceae), *Naucleopsis naga* (Moraceae), and *Mabea occidentalis* (Euphorbiaceae). The Araceae *Anthurium bakeri*, *Dieffenbachia longispatha*, *Monstera tenuis*, and *Rhodospatha wendlandii* grow as terrestrial herbs or (hemi)epiphytes (Hartshorn & Hammel 1994). These plants are the most important phorophytes for foliicolous lichens.

MATERIAL AND METHODS

To ensure sampling of a rich but reasonably homogeneous foliicolous lichen flora, only phorophytes in the shady understory (diffuse site factor = 0–5 %, see Lücking 1998) with leaves belonging to the mesophyll dicotyledon type (Vareschi 1980, Lücking 1998) were considered, such as *Ocotea atirrensis*, *Naucleopsis naga*, and *Mabea occidentalis*. Phorophytes were selected in primary and old growth secondary forest, along CES, SUR and ARBOLEDA trails (Fig. 2). On each phorophyte, 1–3 leaves with an estimated relative area cover of foliicolous lichens > 10 % were collected during different hours of the day (8:00 h, 14:00 h, 20:00 h),

to ensure sampling of both diurnal and nocturnal invertebrates. Sampling was performed during March-June 1997 (200 leaves) and January 1999 (50 leaves).

The leaves were immediately studied in the station laboratory, using a ZEISS stereomicroscope (8–50x) and a ZEISS microscope (40–1000x). Invertebrates were captured with a sucking device and conserved in 95 % ethanol. As far as possible, insects were determined to order, suborder and family level using pertinent literature (Borror *et al.* 1989). Stomach contents of selected individuals were studied after careful preparation, differentiating between bryophyte parts, hyaline hyphae and spores (assumed to belong mostly to lichens), brown hyphae and spores (assumed to belong mostly to fungi), as well as unicellular and filamentous algae (mostly Chlorococcaceae or Trentepohliaceae). Germination tests were made on stomach contents of individuals not preserved in alcohol and excrements from the leaf surface, using LB medium (Lilly & Barnett 1951). Excrements were rehydrated in demineralized water. *Dimerella siquirrensis* and *Calopadia foliicola* served as positive controls, with apothecia of freshly collected specimens fixed to a petri dish containing the agar on top.

Foliicolous lichen thalli were determined to species level and classified in two ways: (1) absence / presence of lichenicolous fungi or feeding traces, and (2) individual condition, i.e., sound and fertile vs. sterile (in usually fertile species) vs. necrotic (concluded from decolorations or ascocarp contents). Selected leaf parts were separated and herbarized to conserve representative lichen thalli showing feeding traces. For the nomenclature of the treated taxa, see Farkas & Sipman (1997), Lücking (1999a) and Lücking *et al.* (2000a, b).

The following parameters were measured: (1) abundance (= number of individuals), (2) dominance (= area cover; approximation according to Lücking 1998), and (3) average thallus size (= area cover / number of individuals) for each foliicolous lichen species; (4) abundance of potential lichen feeders; (5) composition of stomach contents in selected invertebrates (semi-quantitative); (6) proportion of foliicolous lichens attacked by lichenicolous fungi or lichen feeders; (7) proportion of foliicolous lichens being sterile or necrotic. Correlation between abundance, dominance or average thallus size of foliicolous lichens, and proportion of thalli attacked by lichenicolous fungi or lichen feeders was established using Pearson's correlation coefficient. Selectivity of lichenicolous fungi or lichen feeders towards certain foli-

icolous lichen species was tested by comparing the observed frequency of affected thalli with the frequency expected from the abundance / dominance values of a species. Similarly, differences in the pro- portion of sterile or necrotic thalli attacked by lichenicolous fungi or lichen feeders were determined by a χ^2-test. All statistical calculations were made with STATISTICA™ 5.0.
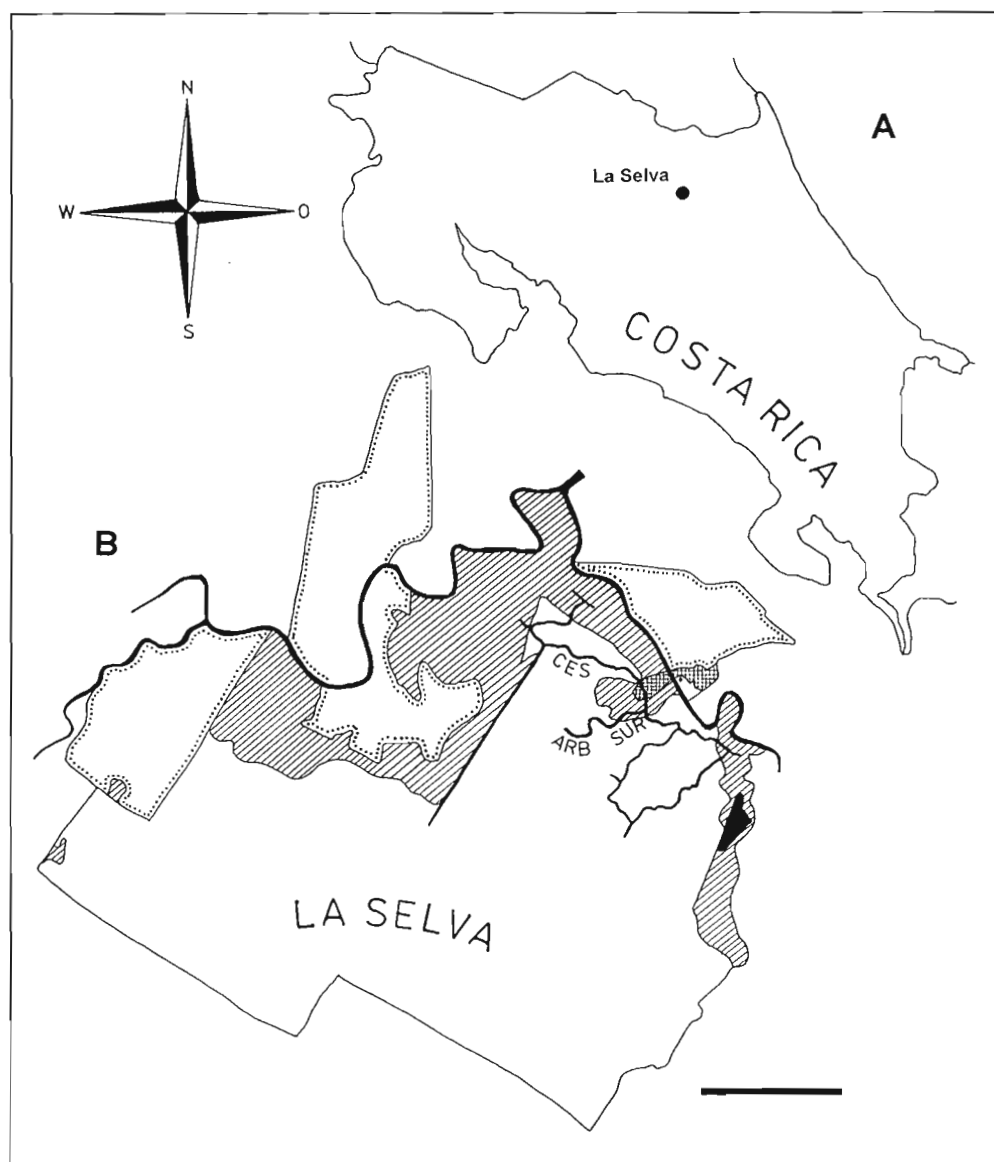

FIG. 2. A – Geographic location of the study area in Costa Rica. B – Map of the study area indicating trails where leaves with foliicolous lichens were sampled (CES, SUR, ARB = ARBOLEDA). White areas = primary forest; hatched areas = closed secondary forest; dotted lines = open pasture; black area = succession plots; cross-hatched area = laboratory and living area. Scale in B = 1 km.

RESULTS

Foliicolous lichens. The 250 sampled leaves revealed 5495 individual lichen thalli belonging to 115 species in 35 genera, 14 families and seven orders (Table 1). Abundant taxa were *Porina epiphylla*, *P. limbulata*, *P. mirabilis*, *Sporopodium leprieurii*, and *Microtheliopsis uleana*, while dominant species included *Bapalmuia palmularis*, *B. lineata*, *Dimerella siquirrensis*, *Calopadia foliicola*, and *Calenia triseptata* (Fig. 3, Table 2). The latter species had large thalli up to 400 mm² on average, while those of the small-sized *Aulaxina minuta*, *Microtheliopsis uleana* or *Gyalectidium filicinum* did not exceed 10 mm², even when fully mature (Table 3). Average thallus size of the commonest species, *Porina epiphylla*, equals overall average (52 mm²), while *Bapalmuia palmularis* / *Dimerella siquirrensis* on one hand and *Sporopodium lepri-*

TABLE 1. Genera, families and orders of foliicolous lichens identified on 250 leaves at La Selva Biological Station, Costa Rica, arranged in alphabetical order.

Order	Family	Genus	Number of species
Arthoniales	Arthoniaceae	*Arthonia*	3
		Eremothecella	1
	Opegraphaceae	*Mazosia*	9
Dothideales	Microtheliopsidaceae	*Microtheliopsis*	1
	incertae sedis	*Caprettia*	1
Gyalectales	Gyalectaceae	*Dimerella*	5
Lecanorales	Ectolechiaceae	*Calopadia*	2
		Lasioloma	1
		Sporopodium	2
		Tapellariopsis	1
	Lecanoraceae	*Bacidina*	3
	Pilocarpaceae	*Badimia*	1
		Bapalmuia	2
		Byssolecania	2
		Byssoloma	3
		Fellhanera	4
Ostropales	Asterothyriaceae	*Gyalidea*	1
	Gomphillaceae	*Actinoplaca*	1
		Aulaxina	2
		Calenia	3
		Echinoplaca	5
		Gyalectidium	2
		Gyalideopsis	1
		Tricharia	7
	Thelotremataceae	*Chroodiscus*	2
Pyrenulales	Aspidotheliaceae	*Aspidothelium*	2
	Monoblastiaceae	*Anisomeridium*	1
	Strigulaceae	*Flavobathelium*	1
		Phyllobathelium	2
		Strigula	7
	incertae sedis	*Phylloblastia*	1
		Pocsia	3
Trichotheliales	Trichotheliaceae	*Porina*	24
		Trichothelium	6
Fungi Imperfecti	incertae sedis	*Phyllophiale*	3

eurii / *Microtheliopsis uleana* on the other represent deviating colonization strategies: large thalli combined with low abundance in the first case vs. small thalli combined with high abundance in the latter (Fig. 4).

According to an earlier study (Lücking 1999a), La Selva harbors 280 foliicolous lichen species, of which about 120 are typical for the shady understory, including the genera *Porina*, *Mazosia*, and *Bapalmuia*. Species composition and abundance / dominance of foliicolous lichens on the 250 leaves thus confirm the sampling as representative.

Lichenicolous fungi. Twelve species of lichenicolous fungi were found, among them the hyphomycete *Ampullifera* sp. and the ascomycetes *Gyalideopsis cochlearifera* (Ostropales: Gomphillaceae), *Hemigrapha tenellula* (Dothideales: Microthyriaceae), *Nectriopsis* sp. (Hypocreales: Nectriaceae), *Pyrenidium santessonii*

(Dothideales: Dacampiaceae), *Opegrapha epiporina*, *O. phylloporinae*, *O. porinicola*, *O. sipmanii* (Arthoniales: Opegraphaceae), and *Stigmidium epiphyllum* (Dothideales: Mycophaerellaceae).

Ampullifera sp., *Opegrapha epiporina*, *O. phylloporinae*, *O. porinicola*, and *Stigmidium epiphyllum* are new records for the study area (Lücking 1999a), while the conspicuous *Arthonia cryptotheciae* and *Pyrenidium zamiae* were not detected on the studied leaves. The lichenicolous fungi found on the 250 leaves represent 63 % of the species known from La Selva Biological Station.

Invertebrates. The 468 captured invertebrate individuals represent a variety of taxonomic groups (Figs. 5–6). Most belonged to the insect orders Diplura, Collembola (Entomobryidae, Sminthuridae), Psocoptera (Pseudocaeciliidae, Psocidae), Thysanoptera
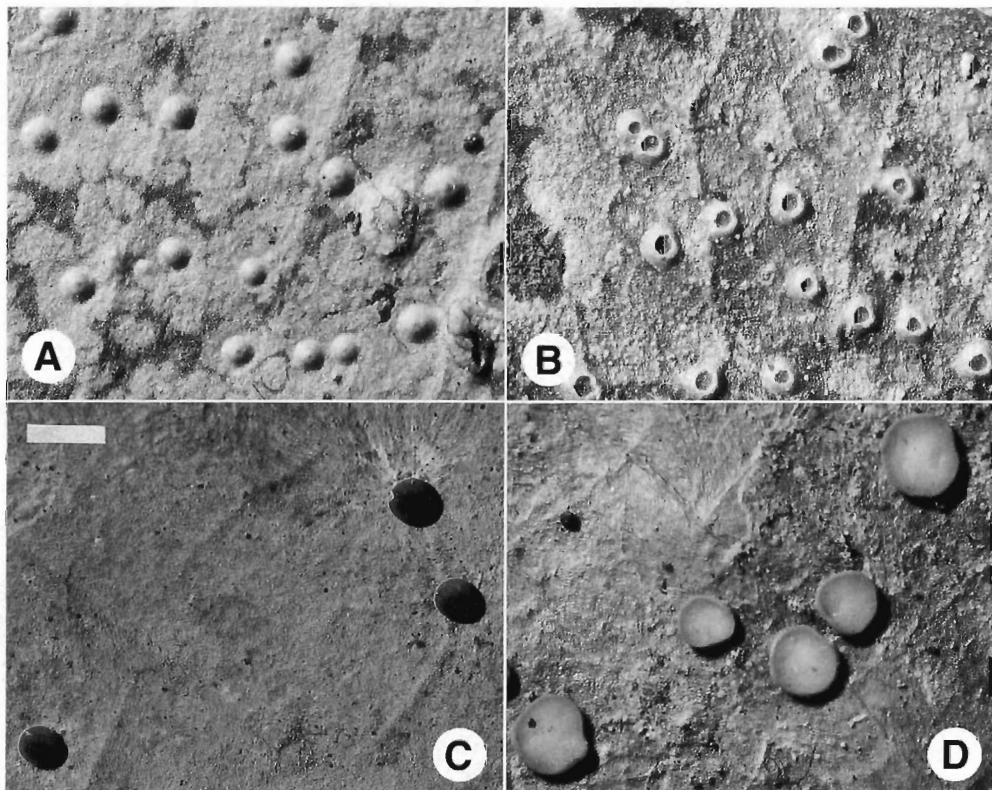

FIG. 3. Dominant foliicolous lichen species that were often attacked by lichenicolous fungi or lichen feeders. A – *Porina epiphylla*. B – *Calenia triseptata*. C – *Bapalmuia palmularis*. D – *Dimerella siquirrensis*. Scale in A, B, D = 0.75 mm, in C = 1 mm.

TABLE 2. Individual numbers and area cover per leaf of selected foliicolous lichens. Average leaf size was 10500 mm².

Foliicolous lichen species	Individuals / leaf	Foliicolous lichen species	Area cover / leaf [mm²]
Porina epiphylla	2.5	*Bapalmuia palmularis*	137
Porina limbulata	1.1	*Porina epiphylla*	131
Sporopodium leprieurii	1.0	*Dimerella siquirrensis*	104
Microtheliopsis uleana	0.9	*Bapalmuia lineata*	58
Porina mirabilis	0.8	*Calopadia foliicola*	46
Gyalectidium filicinum	0.7	*Calopadia* sp.	40
Strigula phyllogena	0.7	*Calenia triseptata*	35
Trichothelium epiphyllum	0.6	*Sporopodium leprieurii*	33
Anisomeridium foliicola	0.6	*Mazosia rotula*	28
Bapalmuia lineata	0.5	*Phyllobathelium epiphyllum*	26

(Phlaeotripidae), Hemiptera, Lepidoptera and Hymenoptera (Formicidae). Acari were also abundant, while Gastropoda and Annelida were rare (Table 4).

Except for Formicidae, Rotatoria, and Tardigrada (the latter two inhabiting the leaf lobules of hepatics and disregarded in this study), the most frequent inhabitants of the phyllosphere were Psocoptera and

TABLE 3. Average thallus size of selected foliicolous lichens. Overall average thallus size was 52 mm².

Foliicolous lichen species	Average thallus size	Individuals measured
Phyllobathelium thaxteri	589	4
Bapalmuia palmularis	402	85
Byssolecania variabilis	314	5
Dimerella siquirrensis	273	96
Calopadia sp.	253	39
Calopadia foliicola	210	56
Tricharia heterella	188	6
Calopadia phyllogena	157	4
Sporopodium antonianum	154	14
Calenia triseptata	146	62
Porina epiphylla	53	621
Tricharia vainoi	8	44
Gyalectidium filicinum	8	168
Phyllophiale alba	7	71
Microtheliopsis uleana	7	234
Aulaxina minuta	6	59
Porina tetramera	6	15
Echinoplaca verrucifera	5	9
Trichothelium minus	4	10
Aulaxina intermedia	3	5
Bacidina apiahica	2	4

Collembola. Collembola were mostly represented by rather large, pale Entomobryidae, which moved quickly on the leaf surfaces. The identified Psocoptera, chiefly belonging to the Pseudocaeciliidae, formed aggregations of up to 15 animals (Fig. 6B, Table 4). The eggs (10–20) were usually deposited on the lower side of the leaf (rarely on the upper side; Fig. 6A) and often covered by a silken web that served as protection for the hatched larvae. As far as observed, the larvae stayed together on the leaf until the last (sixth) instar or even the adult (winged) stage. Feeding behavior was similar in most aggregations: the larvae are usually nocturnal, passing the day on the lower side of the leaf and feeding at night on the upper side.

TABLE 4. Abundance of potentially lichen-feeding invertebrates on 250 leaves at La Selva Biological Station, Costa Rica.

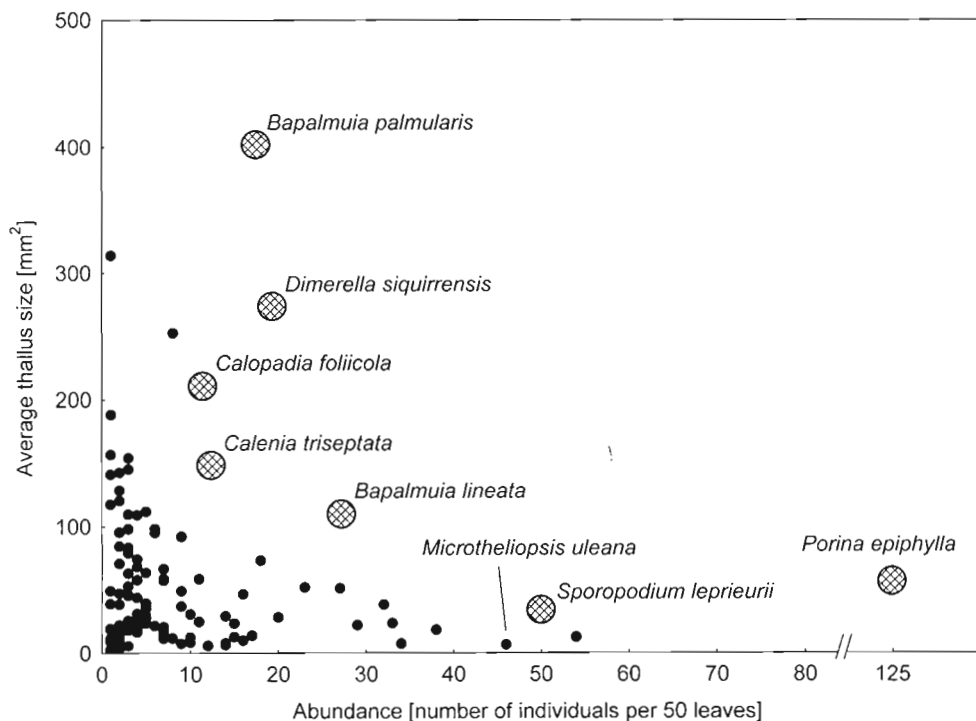| Systematic group	Individuals per 100 leaves
Annelida (annelids)	3
Gastropoda (snails)	4
Acari (mites)	33
Diplura (diplurans)	13
Collembola (springtails)	25
Psocoptera (psocids, barklice), individuals	65
[Psocoptera, nests or aggregations]	[11]
Thysanoptera (thrips)	4
Coleoptera (beetles)	6
Lepidoptera: (moths, larvae)	30
Hymenoptera: Formicidae (ants)	24

FIG. 4. Relationship of abundance and average thallus size in foliicolous lichens. Large gray dots indicate dominant species in terms of overall area cover.

Lichen-feeding. Annelida, Gastropoda, Psocoptera and Lepidoptera were observed feeding on foliicolous lichens (Figs. 5–6). Gastropoda produced characteristic traces (Fig. 7), while Annelida, Psocoptera, and Lepidoptera destroyed the lichen thalli. Stomach contents attributable to lichen thalli (hyaline hyphae and spores, algae) indicate that Gastropoda, Collembola, Psocoptera, and Lepidoptera are important lichen feeders (Table 5). In Annelida, Acari, and Formicidae, mostly amorphic contents or residues not attributable to algae, fungi or lichens were detected. Lepidoptera larvae seemed to prefer either bryophytes or lichens, since in no case were residues of both found in the same individual.

TABLE 5. Stomach contents, attributed to fungi, lichens and bryophytes, of potentially lichen-feeding invertebrates. [+++] = abundant, [++] = scattered, [+] = rare, [–] = not present.

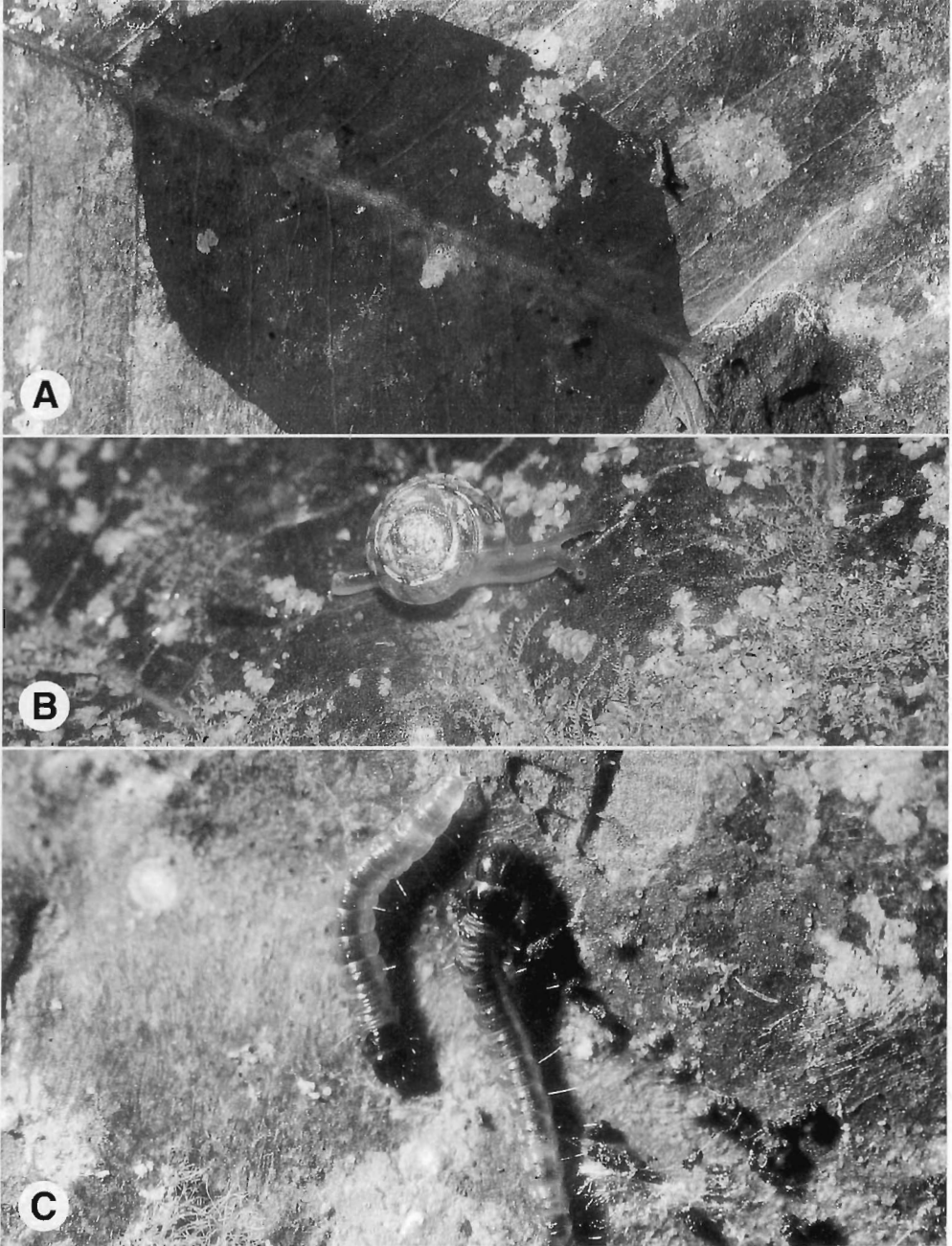| Systematic group	Bryo-phytes	Hyaline hyphae	Hyaline spores	Brown hyphae	Brown spores	Unicell. algae	Filament. algae
Annelida	–	–	–	–	–	+	–
Gastropoda	–	+	+	++	++	++	+
Acari	–	–	–	–	–	–	–
Collembola	–	+	+	++	++	+	++
Psocoptera	–	+	+	++	++	+	+++
Lepidoptera	+++	+	–	–	+	+	+++
Formicidae	–	–	–	–	–	–	–

30

FIG. 5. Lichen-feeding invertebrates in the phyllosphere. A – Annelid embedded in a layer of mucilage, the digested material visible as dark mass in the lower right corner. B – Snail (Gastropoda). C – Larvae of a still unidentified moth (Lepidoptera).
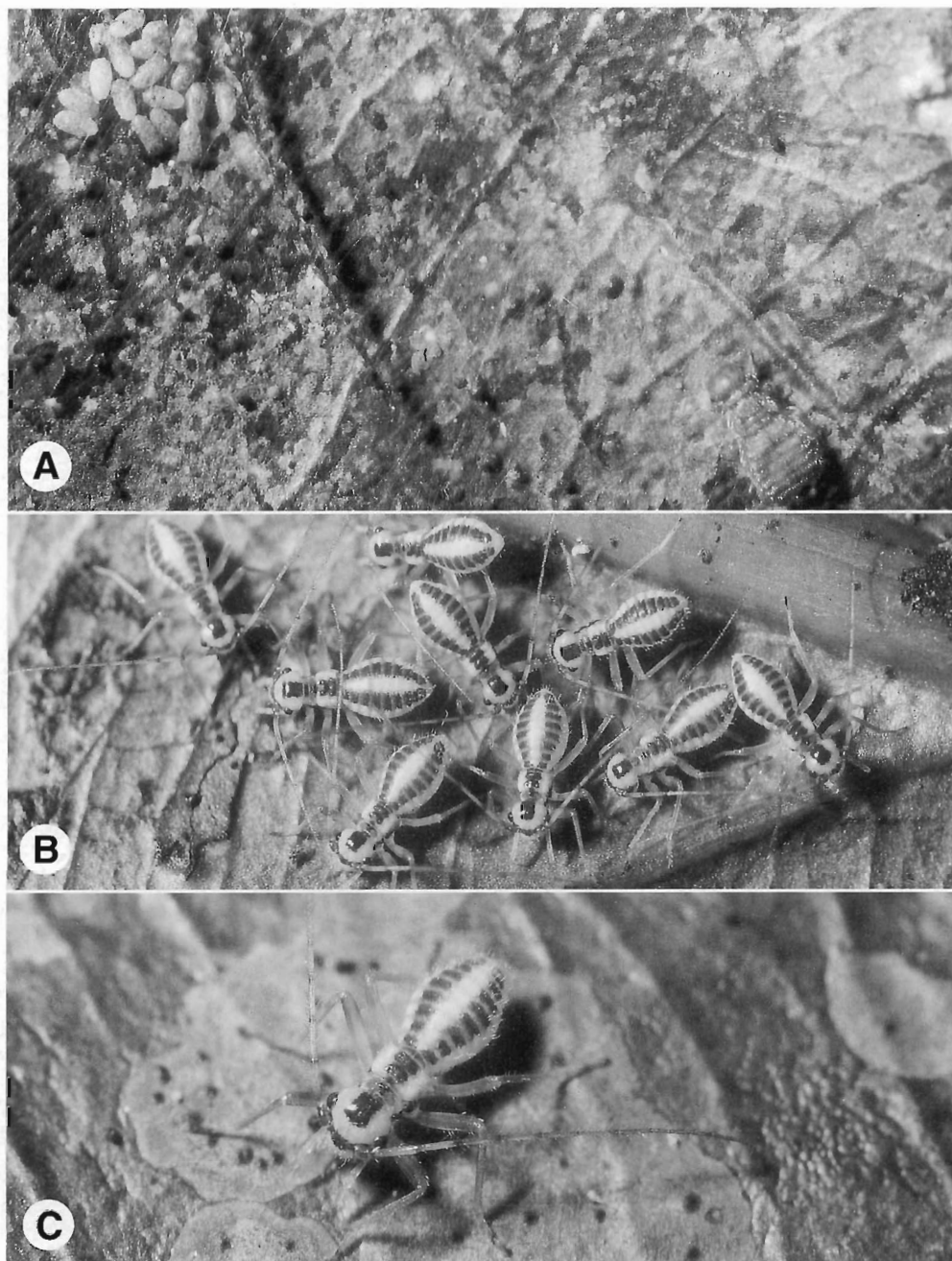
FIG. 6. Lichen-feeding invertebrates in the phyllosphere. A – Psocid (Psocoptera: Pseudocaeciliidae) nest with eggs (upper left corner) and adult female (lower right corner). B – Aggregation of psocids on the lower side of a leaf. C – Psocid feeding on a thallus of the foliicolous lichen *Microtheliopsis uleana*.
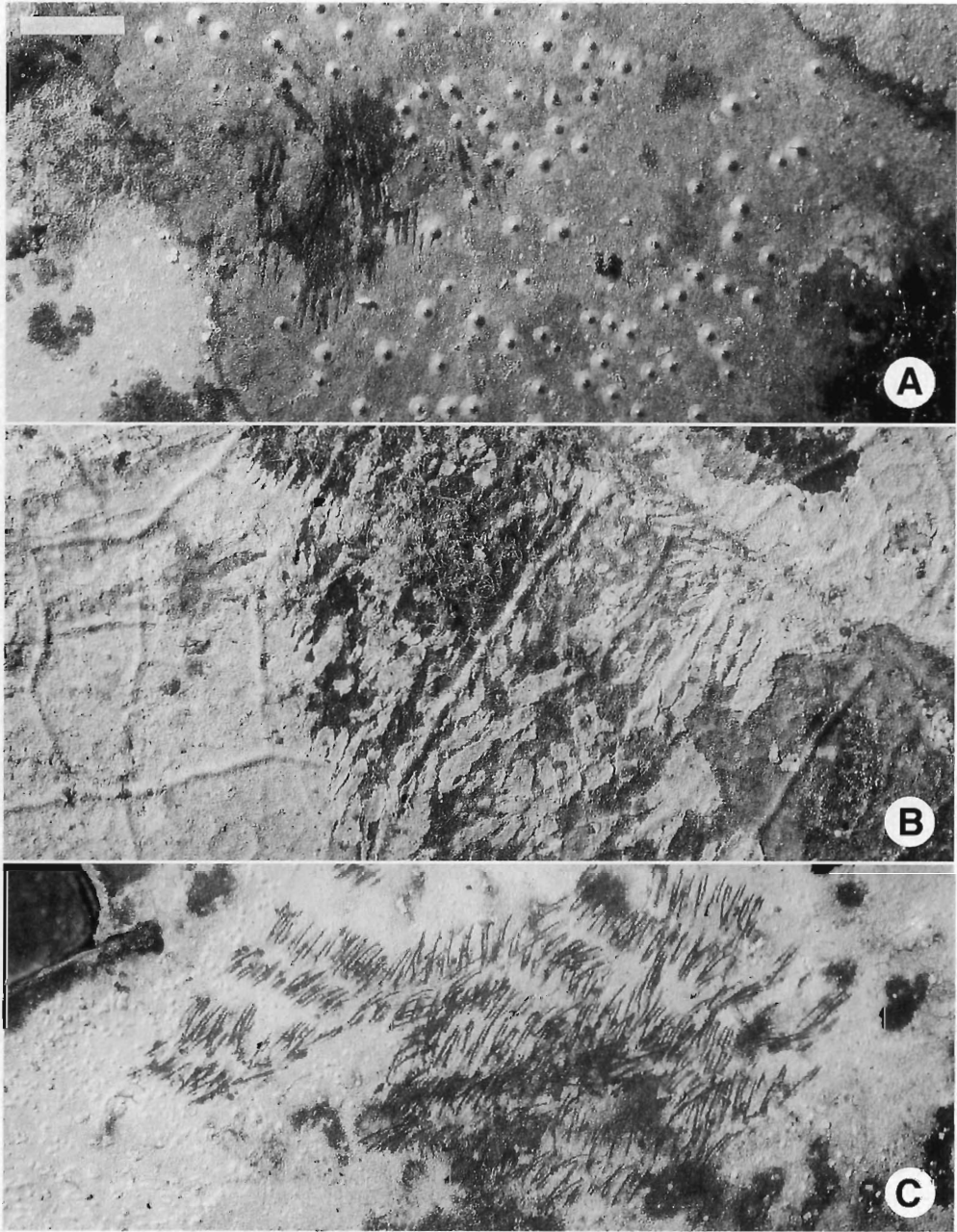
FIG. 7. Feeding traces of snails (Gastropoda) on foliicolous lichens. A – *Strigula obducta*, a pyrenocarpous lichen with trentepohlioid phycobiont. B – *Bapalmuia palmularis*, a discocarpous lichen with chlorococcoid phycobiont and containing the secondary substance 4,5-dichlornorlichexanthone. C – *Sporopodium* sp., an undescribed discocarpous lichen with chlorococcoid phycobiont and complex secondary chemistry, containing usnic acid and thiophanic acid as majors and isousnic acid, arthothelin and 4,5-dichlornorlichexanthone as minors (H. T. Lumbsch, pers. comm. 1998). Scale = 1 mm.

TABLE 6. Frequency of parasite attack and feeding damage in foliicolous lichen thalli. Psocoptera potentially include indifferential feeding traces of other invertebrates (Collembola, Lepidoptera), although the latter are comparatively less abundant.

Group	Percentage of affected foliicolous lichen thalli	
	(relative to all individuals)	(relative to total area cover)
Lichenicolous fungi	6.0 %	9.1 %
Gastropoda	4.4 %	10.9 %
Psocoptera	2.2 %	8.7 %
Total	12.6 %	28.7 %

Reproductive structures were often attacked by lichen feeders, but intact ascospores, conidia or vegetative diaspores were rarely identified in the stomach contents, indicating that these structures are rapidly digested. Germination experiments were unsuccessful not only for both stomach contents and rehydrated excrements, but also for most of the positive controls, making the results of these tests ambiguous.

Correlation between foliicolous lichen frequency, lichen feeders and lichenicolous fungi. About 12 % of the foliicolous lichen individuals were attacked by lichen feeders or lichenicolous fungi, the latter with a higher proportion (Table 6). The attacked thalli amount to almost 30 % of total area cover, which means that large thalli are more frequently attacked than small ones. This effect is particularly pronounced in Psocoptera (Table 6).

Lichenicolous fungi were found on 21 of the 115 foliicolous lichen species. Frequently attacked hosts were *Porina epiphylla, Bapalmuia lineata, Calenia triseptata,* and *Flavobathelium epiphyllum* (Table 7). Most lichens were attacked by a single species of lichenicolous fungus, except for *Calenia triseptata* (2), *Gyalectidium filicinum* (2), and *Porina epiphylla* (7). The distribution of attacked lichen thalli among species differed significantly from that expected based on their abundance ($\chi^2 = 297$) and dominance values ($\chi^2 = 214$, $P < 0.001$). Thus, frequently attacked hosts do not simply reflect host frequency; instead, the lichenicolous fungi are selective in favor of abundant and dominant lichens. Selectivity (proportion of affected thalli vs. overall frequency) was highest for *Flavobathelium epiphyllum* (factor 7.4 for abundance / 3.6 for dominance values), followed by *Calenia triseptata* (6.9 / 4.2), *Bapalmuia lineata* (4.9 / 4.1), and *Porina epiphylla* (3.8 / 2.9).

The most abundant lichenicolous fungus was *Hemigrapha tenellula,* whereas *Pyrenidium santessonii* dominated with regard to area cover of the attacked lichens (Table 7). Most lichenicolous fungi were restricted to one or two hosts, but *Nectriopsis* sp. and *Gyalideopsis cochlearifera* were found on up to six. While *Nectriopsis* sp. is possibly a collective taxon, the broad host range of *Gyalideopsis cochlearifera* in the family Gomphillaceae (*Actinoplaca strigulacea, Calenia graphidea, C. phyllogena, C. triseptata, Gyalecti-*

TABLE 7. Species composition of foliicolous lichens attacked by lichenicolous fungi, and abundance of lichenicolous fungi in terms of attacked individuals and area cover. Proportion indicates area cover and number of thalli relative to the total of attacked individuals.

Foliicolous lichens	Proportion (individuals)	Proportion (area cover)	Lichenicolous fungi	Proportion (individuals)	Proportion (area cover)
Porina epiphylla	42.4 %	32.5 %	*Hemigrapha tenellula*	25.8 %	17.5 %
Bapalmuia lineata	12.1 %	20.7 %	*Pyrenidium santessonii*	13.6 %	27.5 %
Calenia triseptata	7.6 %	12.9 %	*Gyalideopsis cochlearifera*	10.6 %	5.8 %
Flavobathelium epiphyllum	6.1 %	5.1 %	*Opegrapha sipmanii*	10.6 %	5.0 %
Actinoplaca strigulacea	3.0 %	4.0 %	*Nectriopsis* sp.	9.1 %	11.6 %
Phyllobathelium firmum	3.0 %	2.6 %	*Ampullifera* sp.	9.1 %	7.7 %
Bapalmuia palmularis	1.5 %	6.8 %	*Opegrapha phylloporinae*	4.5 %	5.6 %
Byssolecania hymenocarpa	1.5 %	3.6 %	*Stigmidium epiphyllum*	3.0 %	9.7 %
Porina atropunctata	1.5 %	2.7 %	*Opegrapha epiporina*	1.5 %	1.8 %
Sporopodium lepricurii	1.5 %	2.3 %	*Opegrapha porinicola*	1.5 %	0.4 %
others (11 species)	19.8 %	6.8 %	others (2 species)	4.5 %	4.3 %

TABLE 8. Feeding spectrum of Gastropoda and Psocoptera, as inferred from feeding traces on foliicolous lichen thalli. Proportion indicates number of individuals and their area cover relative to all thalli affected by the respective invertebrate group.

Gastropoda	Proportion (individuals)	Proportion (area cover)	Psocoptera	Proportion (individuals)	Proportion (area cover)
Porina epiphylla	16.7 %	10.1 %	*Dimerella siquirrensis*	37.5 %	50.3 %
Bapalmuia palmularis	12.5 %	45.1 %	*Dimerella isidiifera*	20.8 %	11.7 %
Sporopodium leprieurii	12.5 %	6.0 %	*Calopadia foliicola*	8.3 %	8.2 %
Calenia triseptata	6.3 %	8.5 %	*Phyllobathelium thaxteri*	4.4 %	11.8 %
Echinoplaca pellicula	4.2 %	6.6 %	*Bapalmuia palmularis*	4.4 %	11.8 %
Badimia dimidiata	4.1 %	5.0 %	*Trichothelium epiphyllum*	4.3 %	1.9 %
Bapalmuia lineata	3.9 %	4.4 %	*Echinoplaca leucotrichoides*	4.2 %	1.6 %
Porina octomera	3.6 %	3.4 %	*Bacidina defecta*	4.1 %	1.6 %
Calopadia foliicola	2.1 %	2.8 %	*Gyalideopsis vulgaris*	4.1 %	0.5 %
others (14 species)	33.1 %	9.6 %	others (2 species)	8.2 %	0.6 %
with trentepohlioid algae	41.7 %	17.9 %	with trentepohlioid algae	70.8 %	76.1 %
with chlorococcoid algae	58.3 %	82.1 %	with chlorococcoid algae	29.2 %	23.9 %

dium filicinum), is well-known (Lücking & Sérusiaux 1998). *Hemigrapha tenellula* and the four *Opegrapha* species were, with a few exceptions, restricted to *Porina epiphylla*, while *Pyrenidium santessonii* was confined to *Bapalmuia lineata*.

Feeding traces of Gastropoda were detected in 238 lichen thalli belonging to 23 species. Among the affected lichens, *Bapalmuia palmularis* strongly dominated in terms of area cover, while the attacked lichen individuals were more evenly distributed among species (Table 8). Psocoptera showed a similar pattern: their feeding traces were found in 11 foliicolous lichen species. Most heavily attacked were *Dimerella siquirrensis* and *D. isidiifera*, together representing more than half of the affected lichen thalli (Table 8). In both groups, the observed feeding spectrum differed significantly from chance distribution based on foliicolous lichen abundance and dominance. This difference was lower for Gastropoda (χ^2 = 487 for abundance and χ^2 = 257 for dominance values, $P < 0.001$) than for Psocoptera (χ^2 = 1935 and χ^2 = 494, $P < 0.001$), indicating that feeding preferences are highly selective in the latter. Degree of selectivity in Psocoptera was greatest for *Dimerella isidiifera* (factor 38 for abundance and 11.3 for dominance values) and *D. siquirrensis* (22 / 5.6). In Gastropoda, it was highest for *Echinoplaca pellicula* (15 / 8.7), *Porina octomera* (15 / 7.7), *Badimia dimidiata* (9.1 / 5.1), and *Bapalmuia palmularis* (8.3 / 3.8), while for *Porina epiphylla*,

the frequency of affected thalli did not differ significantly from abundance and dominance values.

Nests or aggregations of Psocoptera were confined to leaves with a high area cover of *Dimerella* species (between 23.1 % and 94.2 % relative to overall lichen cover). The affected leaves made up half (28 out of 55) of all such leaves, which indicates a strong preference by Psocoptera for leaves that are predominantly colonized by large-sized *Dimerella* (χ^2 = 90.5, $P < 0.001$). *Bapalmuia palmularis*, *Calopadia foliicola*, and *Echinoplaca* spp. were shared by various lichen feeders. Gastropoda did not feed on *Dimerella*, while Psocoptera avoided *Porina*. In addition, Gastropoda frequently fed on lichens with a chlorococcoid phycobiont, whereas Psocoptera preferred those with a trentepohlioid phycobiont (χ^2 = 41.0 for abundance and χ^2 = 186 for dominance values, $P < 0.001$).

A significant correlation of low magnitude was found between the occurrence of lichenicolous fungi and area cover of the affected foliicolous lichen species: dominant species were more frequently attacked (Table 9). A similar tendency was observed in Psocoptera, which also showed a strong correlation with foliicolous lichen species having large average thallus size. Gastropoda did not show any significant correlations, and none of the three organism groups correlated with foliicolous lichen abundance (Table 9).

Significant differences (χ^2 = 76.4, $P < 0.001$) were found in foliicolous lichen thalli when lichenicolous

TABLE 9. Correlation between frequency of parasite attack and feeding damage and different parameters of abundance (no. of individuals, area cover, average thallus size) in foliicolous lichens on 250 leaves at La Selva Biological Station, Costa Rica. *** = highly significant ($P < 0.001$); ** = significant ($P < 0.05$); * = tendency ($P < 0.10$).

Group	No. of individuals	Area cover	Thallus size
Lichenicolous fungi	0.12	0.24**	0.04
Gastropoda	− 0.05	0.10	0.07
Psocoptera	− 0.04	0.18*	0.54***

fungi or feeding traces were absent or present (Fig. 8). Thalli attacked by lichenicolous fungi or lichen feeders were more often necrotic, and sterile thalli occurred in species that usually form reproductive structures, indicating that lichenicolous fungi supress the formation of ascomata or conidiomata of the host lichen.

DISCUSSION

Invertebrates are abundant in the phyllosphere of tropical rainforests and form an integral part of epiphyll communities, such as Rotatoria and Tardigrada living in the leaf lobules of hepatics (Gerson 1982). Psocoptera and Lepidoptera found here seem to spend a large part of their life cycle on leaves, and larval development in the former is linked to the presence of certain foliicolous lichen species providing the appropriate feeding substrate.

In temperate lichen communities, Gastropoda, Acari, and Psocoptera are the most important lichen feeders (Seaward 1988, Prinzing 1999). This is also true of tropical foliicolous lichen associations, although Acari could not be shown to feed on lichens here. If they do, the absence of stomach contents attributable to lichen thalli might be explained by rapid decomposition of hyphae and algal cells. This might also be the case in leaf-dwelling Annelida, which could be observed feeding on lichens but, except for a few algal cells, no particles pertaining to lichens were found in the stomach contents. A few arboreal Annelida (Oligochaeta), feeding on debris, have been reported from the tropics (Barnes 1974). Nematoda frequently associate with lichens (Seaward 1988) and are known to feed on hyphae, algal cells and lichens, either by piercing or ingesting particles (Perry & Wright 1998). Leaf-dwelling ants seem not to feed on lichens but are probably predatory on invertebrates, possibly in some kind of association with the phorophyte (Beattie 1985, Davidson & McKey 1993).

Gastropoda were much less frequent than Psocoptera, but lichen thalli affected by their characteristic feeding traces were more abundant. This may indicate that, while Psocoptera concentrate on single thalli at a time, Gastropoda are more extensive in their feeding behavior grazing on different, adjacent lichens when active. This is known from Gastropoda associated with saxicolous lichens (Pfleiderer & Winkler 1992, Fröberg 1993). Leaf-dwelling Gastropoda may also shelter in other places when inactive so that possibly only a proportion of actually larger populations was captured.

Lichens are generally little attacked by "herbivores", which is attributed to a supposedly protective secondary chemistry. Certain lichen compounds, such as fumarprotocetraric, stictic and vulpinic acid, repel lichen feeders or retard larval growth (Lawrey 1980, Rambold 1985, Emmerich et al. 1993, Fröberg 1993, Giez et al. 1994). Lichen compounds are even sequestered by lichen feeders, e.g., larvae of the Arctiidae, and potentially used for their own protection (Richardson & Young 1977, Hesbacher et al. 1995). Compared with corticolous and saxicolous crustose lichens, the chemistry of foliicolous lichens is poorly developed. Secondary substances have been found in a few genera and species only (Elix et al. 1992, Lücking et al. 1994, Elix et al. 1995). The chemistry of foliicolous taxa, e.g., Badimia and Fellhanera, is rather simple, containing mostly usnic acid, isousnic acid and zeorin (Lücking et al. 1994), while Sporopodium shows more complex patterns (Elix et al. 1992, 1995). Meaningful correlations between the observed feeding preferences of invertebrates and secondary chemistry of foliicolous lichens cannot be drawn from the data. It might be noted, however, that taxa known to contain secondary compounds, such as Bapalmuia (Kalb et al. 2000) and Sporopodium, were not avoided by lichen feeders (see Fig. 7B-C), and the same was true of species with a high content of calcium oxalate

crystals, e.g., *Porina epiphylla*, *Calenia triseptata*, and *Echinoplaca pellicula* (see Santesson 1952, Lücking 1997, Lücking & Vezda 1998).

Lichenicolous fungi are found over a broad range of host lichens, regardless of the presence or absence of secondary substances. In this study, the foliicolous lichens affected by lichenicolous fungi represented 37 % of the genera, 57 % of the families and 71 % of the orders. Many lichenicolous fungi are not absolutely specific to their hosts but found over a range of related species within a genus, family or order (Hawksworth 1979, 1981; Triebel 1989; Rambold & Triebel 1992; Diederich 1996; Matzer 1996). However, there seems to be a relation between host range and abundance of potential hosts: the commoner the hosts, the narrower the host range. Lichenicolous fungi on abundant hosts are often concentrated on single species, such as *Arthonia pseudopegraphina* on *Mazosia rubropunctata* (Matzer 1996, Cáceres 1999) or, as in the present study, *Pyrenidium santessonii* on *Bapalmuia lineata*. The opposite strategy is found in *Gyalideopsis cochlearifera*, which occurs on a number of rare to moderately common species in several genera (Lücking & Sérusiaux 1998).

In the present study, the most important parameter influencing selectivity of lichen feeders and lichenicolous fungi was dominance and size of potential host lichens. The most affected lichens, i.e., *Porina epiphylla*, *Bapalmuia palmularis*, *B. lineata*, *Dimerella siquirrensis* and, *Calenia triseptata*, were the commonest species in terms of individual numbers and area cover. The degree of selectivity, although highly significant in all cases, was lower in lichenicolous fungi compared with lichen feeders and, among the latter, higher in Psocoptera than in Gastropoda.

Lichenicolous fungi were more frequent on foliicolous lichen species with high dominance values. This might be interpreted as a feedback mechanism that maximizes the probability of finding appropriate host thalli while minimizing the risk of wiping out the host population. The same regulative mechanisms are found in herbivores and parasites associated with
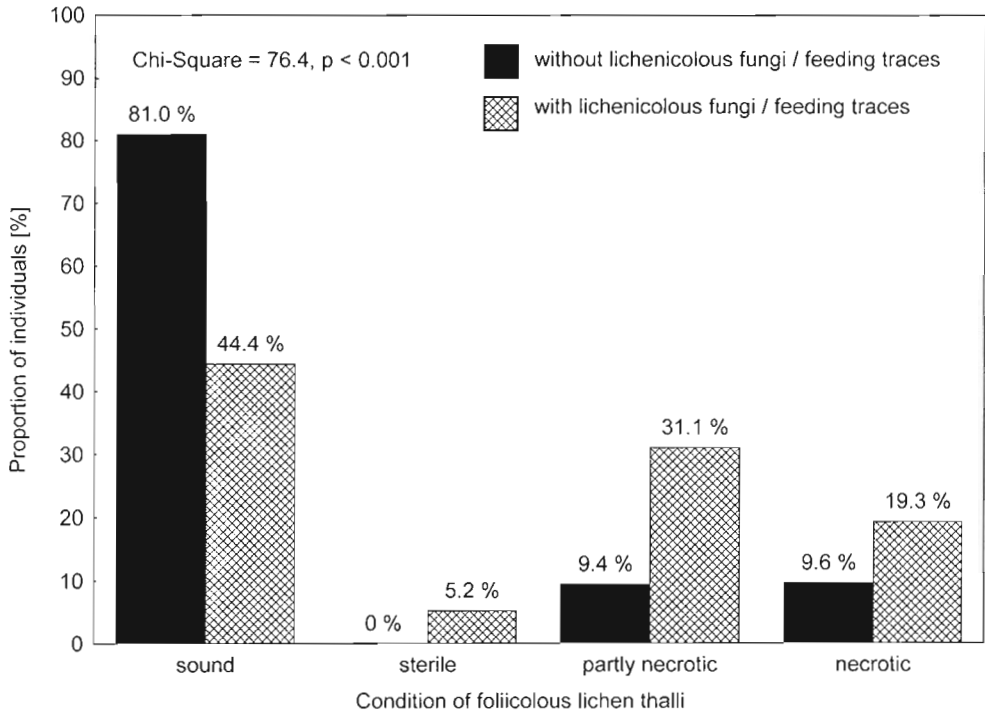

FIG. 8. Condition of foliicolous lichen thalli in relation to absence or presence of lichenicolous fungi or feeding traces. Black columns = thalli lacking lichenicolous fungi and feeding traces. Hatched columns = thalli with lichenicolous fungi or feeding traces.

vascular plants (Pirozynski & Hawksworth 1988, Waterman & McKey 1989, Jermy 1993, Marquis & Braker 1994, Putman 1994, Folgarait *et al.* 1995).

Psocoptera fed mostly on lichens with large thallus size, probably due to the fact that the larvae spend a large part of their life cycle on a single leaf and depend on the presence of sufficient feeding substrate. Their strong preference for *Dimerella* (and *Phyllobathelium*) might actually reflect a preference for the lichen phycobiont (filamentous *Trentepohlia*), fragments of which are frequently found in the stomach contents of these animals. In fact, besides *Porina imitatrix* and its relatives (with calcium oxalate-bearing thalli!), *Dimerella* and *Phyllobathelium* are the only abundant and large-sized foliicolous lichens whose phycobiont is a genuine *Trentepohlia* (Lücking 1999b). Similar feeding preferences of Psocoptera were observed in temperate lichen communities (Broadhead 1958). The question arises how Psocoptera, when depositing their eggs, detect leaves with a high proportion of these lichens in favorable growth condition. Do they use chemical traits of the fungal component or do they recognize the phycobiont?

The less biased feeding range of Gastropoda compared with Psocoptera, and absence of correlations with lichen abundance and dominance, might be due to non-selective grazing on adjacent lichen thalli of different systematic affinity and size. However, although lichens with a trentepohlioid phycobiont are more common in the rainforest understory (Lücking 1999a, b), Gastropoda fed more often on lichens with chlorococcoid phycobionts and, in addition, on species with a high content of calcium oxalate crystals (*Porina epiphylla, Calenia triseptata, Echinoplaca pellicula*) or secondary compounds (*Sporopodium leprieurii, Badimia dimidiata*). Such lichens are unimportant in the diet of Psocoptera, probably because their mouth parts and digestion tract are less effective for grazing rigid structures compared with the specialized gastropod radula (Pfleiderer & Winkler 1992). These deviations might indicate niche differentiation between both invertebrate groups.

Viability of fungal spores after passing the digestion tract of invertebrates and vertebrates has been demonstrated in a number of studies (McInveen & Cole 1976, Redell *et al.* 1997). Due to the ambiguous results, we are not able to assess the viability of digested lichen diaspores in the present case. However, the low abundance of diaspores in the stomach contents, and the rapid digestion of intact structures in, for example, Annelida and Acari, do not support the assumption that diaspores are selectively transported and able to germinate after passing the digestion system. Gastropoda and Psocoptera, as the most important lichen feeders, are rare or only moderately abundant, and their mobility is restricted compared with diaspore dispersers of vascular plants (Howe & Smallwood 1982, Howe 1990). In addition, both groups, even when combined, have a selective feeding spectrum. Based on these findings, the hypothesis that leaf-dwelling invertebrates, via endozoochory, are significant dispersal agents of foliicolous lichens is not supported. Although they may contribute to dispersal in individual cases, for the foliicolous lichen flora as a whole rainwater is certainly much more effective. This is shown by the formation of specialized reproductive organs and the often vertically clustered distribution of individuals (Lücking 1995b, Sérusiaux 1995).

The only invertebrates with a mobility and abundance that would allow effective diaspore dispersal are ants, considered a keystone group in tropical rainforests (Carroll & Janzen 1973, Beattie 1985, Hölldobler & Wilson 1990, Davidson & McKey 1993). In fact, foliicolous lichens produce reproductive organs that might be attractive to ants in that the diaspores are displayed externally in gelatinous, translucent drops, e.g., hyphophores in the Gomphillaceae or tubulate pycnidia in *Dimerella flava*. External transport of foliicolous lichen diaspores by ants via epi- or synzoochory could not be demonstrated in this study, but such observations are quite difficult and require more sophisticated methods.

Lücking (1995a) suggested that foliicolous lichen diversity is positively affected by the dynamics of leaf renewal, which follow the Huston-Connell model of intermediate disturbances interacting with individual growth rates (Connell 1978; Connell & Lowman 1989; Huston 1979, 1994). It assumes that succession reaches a diversity maximum, after which diversity decreases as dominant species start to outcompete others. The reaching of a low-diversity climax stage is delayed by mechanisms that prevent competitive species from becoming dominant and hence maintain diversity at high-level equilibrium. This mechanism is comparable to gap dynamics affecting tree communities, where intermediate disturbances are attributed to periodic events such as storms or landslides (Hubbell & Foster 1986, Denslow 1987, Kessler 1999), and also to the death of individual trees (Hubbell *et al.* 1999). In the sense of the latter, damage and death of individual foliicolous lichen thalli

due to attack by lichenicolous fungi and lichen-feeding invertebrates might also promote diversity in accordance with the Huston-Connell model. Strictly, this applies for stochastic disturbances that are not selective for certain lichen species, e.g., in the present case the grazing of Gastropoda on the most abundant and dominant species, *Porina epiphylla*.

The high selectivity of lichenicolous fungi, Gastropoda and Psocoptera in most other cases does not quite agree with the Huston-Connell model, although it equally enhances diversity since the affected foliicolous lichens are large-sized species with a high area cover, presumably the most competitive ones. By feeding on reproductive structures without effectively dispersing the diaspores, lichen-feeding invertebrates might even be compared with seed predators that strongly affect population dynamics and hence diversity (Crawley 1992). Thus, like herbivores and parasites for vascular plants (Pacala & Crawley 1992, Schulze & Mooney 1995), lichenicolous fungi and lichen feeders do not only affect the structure of lichen communities but might have a positive effect on their diversity, although long-term experiments are needed to confirm this hypothesis.

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