Botanical Journal of the Linnean Society (1989), *100:* 87–96. With 4 figures

Foliicolous lichens: ecological and chorological data*

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Received February 1988, revised and accepted for publication September 1988

SERUSIAUX, E., 1989. **Foliicolous lichens: ecological and chorological data.** Foliicolous lichens are present throughout tropical and subtropical forests but are particularly common in undisturbed rain forests at low elevations. Their presence in south-west Europe and in the Caucasus with 23 species is considered to be a relic of Tertiary times. Ecological groups (in the sense of P. Duvigneaud) are determined, especially for the European taxa. Factorial analysis has been performed on a large collection from Central East Africa which enables the relationships between the foliicolous floras of the different types of forests present in the area (equatorial, mountane, riverine, etc.) to be determined.

ADDITIONAL KEY WORDS:—Central East Africa – Europe – factorial analysis.

CONTENTS

THE FOLIICOLOUS HABIT

Living leaves or leaf-like organs (e.g. cladodes) of vascular plants are available for the support of other autotrophic plants, especially in humid tropical forests. These plants need not, at least theoretically, remove water or nutrients from the leaf on which they grow. As noted by Richards (1984: 1255), "lichens, mosses and foliose hepatics are the most conspicuous epiphyllous plants, but the epiphyllous community is in fact a microcosm–a complete ecosystem in miniature which also includes algae (ndlr: mainly belonging to the Trentepohliaceae), fungi and small animals such as nematodes, mites, insect larvae and rotifers, as well as large (. . .) populations of micro-organisms". The concept of a foliicolous taxon is consequently ecological rather than systematic.

*Paper presented 19 February 1987 at a joint symposium organized by the Linnean Society of London and the British Lichen Society in celebration of the Linnean Society Bicentenary (see *Botanical Journal of the Linnean Society, 96(1)*, 1988).

0024–4074/89/050087 + 10 $03.00/0

The habitat of epiphyllous plants is, by nature, ephemeral; they are necessarily short-lived. Consequently, they have evolved reproductive strategies that involve the rapid production of diaspores and a vigorous ability to colonize new habitats. It is remarkable how quickly foliicolous lichens can produce ascospores or other means of asexual reproduction, within only six to nine months in European species. Foliicolous lichens reproduce either by means of ascospores or by highly specialized vegetative structures (goniocystangia, hyphophores, campylidia; Sérusiaux, 1985, 1986; Vězda, 1979, 1986; Vězda & Poelt, 1987), or by the dispersal of minute granules that form their thalli. Species reproducing by soredia or isidia are exceptional. However, although studied almost exclusively on foliicolous species, complex structures as goniocystangia, hyphophores, and campylidia are not restricted to such species. Indeed, they are widespread amongst corticolous and musicolous species in tropical rain forests, but almost all these taxa remain to be studied and described (Kalb & Vězda, 1987, 1988a).

Bryophilous lichens are not treated as foliicolous species, but bambusicolous species are. My knowledge of species on bamboo culms is restricted to those of Central East Africa (Kahuzi mountains of Zaïre/Kivu) where I have found a few foliicolous species (several *Mazosia* Massal. species, *Opegrapha filicina* Mont.) growing together with normally bark-inhabiting species. I am not aware of any lichen species restricted to bamboo culms.

LIMITATION OF THE STUDY OF FOLIICOLOUS LICHENS

Any analysis of the ecology and chorology of foliicolous lichens is necessarily speculative and can only be provisional at this time. This results from the following circumstances:

1. Available collections and field observations are still very few. The habitats in which foliicolous species grow in great abundance and diversity (undisturbed tropical rain forests at low elevation) remain little explored; such collections as are available are mainly by untrained botanists and in poor condition, especially with respect to delicate structures which are often taxonomically critical.
2. The taxonomy of these groups, as many other tropical crustaceous lichens is likely to progress rapidly. This is demonstrated by the studies of Vězda (Vězda, 1986; Vězda & Farkas, 1988: Vězda & Poelt, 1987; Kalb & Vězda, 1988b).
3. The biology of the specialized organs produced by foliicolous lichens (hyphophores, goniocystangia, campylidia) still requires detailed studies. Indeed their genuine nature has only been elucidated in the last few years.
4. Experimental work on these taxa has never been performed in the field and attempts to grow them in pure culture have not yet been successful.

ECOLOGICAL GROUPS

Following Santesson's monograph (1952), four types of foliicolous lichens have been distinguished with reference to their localization on the leaf structure:

1. Supracuticular species that grow over the leaf cuticle.
2. Subcuticular species that grow underneath the cuticle of the leaf, i.e.

between the epidermal cells and the cuticle, as in species of *Strigula* Fr. and *Raciborskiella* Höhnel (Fig. 1).

3. Epiphyllous species growing on the upperside of the leaf, or more accurately the better-lit one.

4. Hypophyllous species growing on the underside of the leaf, or more accurately the less-lit one.

Santesson recognized a further type, which can be designated as 'marginal', for species colonizing the margin of the upperside of the leaf (on which they can otherwise spread over a large surface) where they are lichenized and sterile or reproducing by asexual means, and simultaneously extend to the edge of the underside where they are not lichenized and reproduce sexually (e.g. *Byssoloma subundulatum* (Stirton) Vězda, *Bacidia palmularis* (Müll. Arg.) Zahlbr.).

These rather simple categories might imply that a living leaf provides only a few niches for lichens. Closer examination, however, indicates that there are species which prefer flat and more or less smooth surfaces, species whose thalli are initiated near leaf hairs or veins, and even species which start to grow on leaf wounds or other points of weakness. An example of this latter case is *Strigula nemathora* Mont., a subcuticular species restricted to leaf wounds. This could be due to this providing a point of entry underneath the cuticle, but other foliicolous *Strigula* species are not necessarily restricted to wounds.

Finally, if the ecological niches that foliicolous lichens exploit in a particular locality are examined, the following categories must be added: species restricted to living leaves (obligately foliicolous species), species mainly developed near or

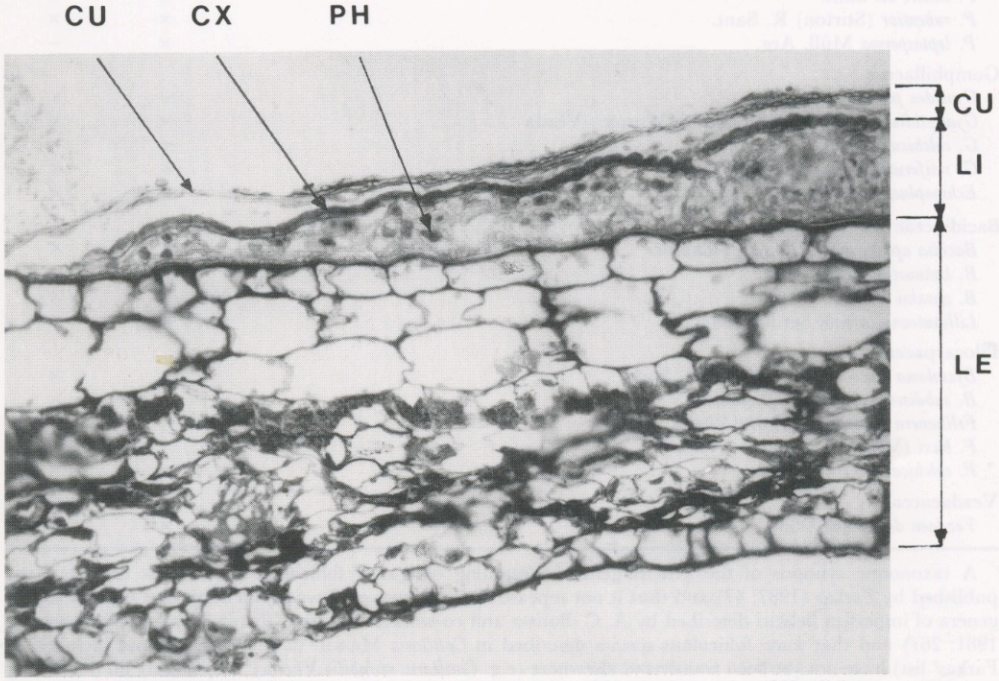

Figure 1. Vertical section through *Strigula smaragdula*. CU = leaf cuticle; CX = lichen cortex; PH = lichen photobiont (algae belonging to the genus *Cephaleuros*); LI = lichen; LE = leaf.

around the nodes, species mainly growing on petioles and twigs, and further species whose presence on leaves is occasional (facultatively foliicolous species) or opportunist (ubiquitous species).

A first approach to the ecological groups (as defined by Duvigneaud, 1946) of foliicolous lichens can be made by the combination of their 'topographical' position on the leaf and their ecological amplitude (Fig. 2). Examples of this approach are provided by the species growing in deep gorges in south-west and central France. My studies of these areas in 1985 and 1986 led to the discovery of 18 species (Table 1). The application of the scheme is possible here because only one host was involved (*Buxus sempervirens* L.), which (1) permits the elimination of any possible specificity of a peculiar taxon to its host, and (2) because the biotopes with foliicolous lichens are well circumscribed (i.e. the bottoms of deep ravines, with a constantly high humidity, and little disturbed by human activities) also permit variations due to mesoecological factors to be excluded.

TABLE 1. The foliicolous lichen species collected in France (Sérusiaux, unpublished data) and in the Caucasus (Vězda, 1983)

	France	Caucasus
Strigulaceae		
Raciborskiella minor Vězda	×	×
Strigula smaragdula Fr. : Fr.	×	×
[= *S. elegans* (Fée) Müll. Arg.]		
S. nitidula Mont.	×	×
Trichotheliaceae		
Porina colchica Vězda	–	×
P. hoehneliana (Jaap) R. Sant.	×	×
P. oxneri R. Sant.	×	×
P. rubentior (Stirton) R. Sant.	×	×
P. leptosperma Müll. Arg.	×	–
Gomphillaceae		
Gyalidea phyllophila Vězda	–	×
Gyalectidium caucasicum (Elenkin & Woron.) Vězda	–	×
G. colchicum Vězda	–	×
G. setiferum Sérus. & Vězda ined.	×	×
Echinoplaca epiphylla Fée	–	×
Bacidiaceae		
Bacidia apiahica (Müll. Arg.) Zahlbr.	×	×
B. kakouettae Sérus. ined.	×	–
B. vasakii Vězda	×	×
Lilliputeana curvata Sérus. ined.	×	–
Pilocarpaceae		
Byssoloma leucoblepharum (Nyl.) R. Sant.	×	×
B. subdiscordans (Nyl.) P. James	×	×
Fellhanera bouteillei (Desm.) Vězda	×	×
F. buxi (Vězda & Vivant) Vězda	×	×
F. colchica (Vězda) Vězda	×	×
Vezdaeaceae		
Vezdaea dawsoniae Döbb.	×	×

A taxonomic synopsis of the lichens genera containing obligately foliicolous species has recently been published by Farkas (1987: 47) and thus is not repeated here. However, I would mention that none of the 37 genera of imperfect lichens described by A. C. Batista and co-workers are cited (list in Vobis & Hawksworth, 1981: 267) and that some foliicolous species described in *Catillaria* Massal. (a generic name not included in Farkas' list) have not yet been transferred elsewhere (e.g. *Catillaria mirabilis* Vězda); they clearly do not belong to *Catillaria* or any of the genera cited by Farkas. Moreover, a foliicolous species of *Roccellinastrum* Follm. (Lecideaceae) described from Chile (Henssen, Vobis & Renner, 1982) is omitted.

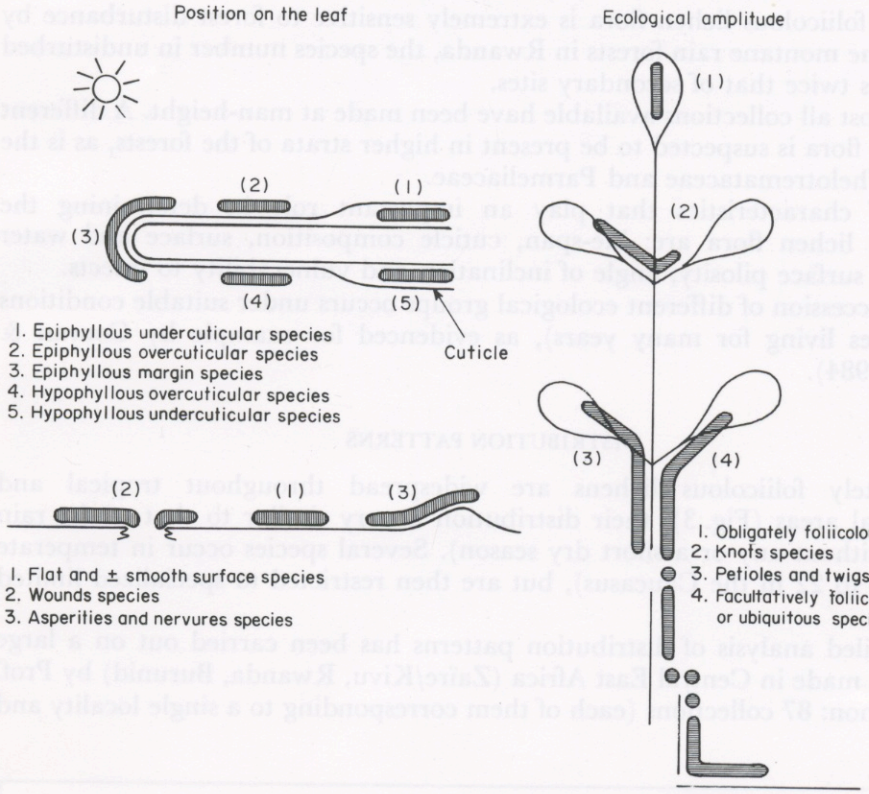

Figure 2. An approach to the ecological groups of foliicolous lichens.

Fellhanera bouteillei (Desm.) Vězda is common in these biotopes but, although known elsewhere as a corticolous or saxicolous species, here it is restricted to the box leaves. Its thallus is entirely composed of minute soredia. On young leaves, the first thalli appear along the main vein or against any relief, and from where spread over the leaf surface. *Fellhanera bouteillei* is thus an obligately foliicolous species preferring the relief niche.

Byssoloma leucoblepharum (Nyl.) R. Sant. is not uncommon in south-west France where, in deep ravines, it can be found on *Quercus* bark, on *Corylus* branches and twigs, and on *Buxus* twigs, petioles and leaves. It is a ubiquitous species here, able to colonize the flat and smooth leaf surface.

Porina hoehneliana (Jaap) R. Sant. is typically a twig species of *Buxus* where it is frequently associated with *P. oxneri* R. Sant. From its main colonies on the twigs it can follow the growth of the twigs, and spread to the petioles and so to the leaves which are invaded from their bases.

Bacidia vasakii Vězda has a thallus of densely packed coralloid goniocysts. It typically first appears along the leaf veins, and especially on the knots where goniocysts accumulate, and forms thick thalli. There is no doubt that this species is preferential to *Buxus* knots.

A complete survey of the ecological groups of foliicolous lichens in tropical areas would need to consider mesoecological factors, such as humidity, rain and/or fog variation, light, etc., as well as host leaf characteristics. I do not have enough data to comment on these aspects in depth, but it is evident that:

1. The foliicolous lichen flora is extremely sensitive to forest disturbance by man. In the montane rain forests in Rwanda, the species number in undisturbed localities is twice that of secondary sites.

2. Almost all collections available have been made at man-height. A different foliicolous flora is suspected to be present in higher strata of the forests, as is the case for Thelotremataceae and Parmeliaceae.

3. Leaf characteristics that play an important role in determining the foliicolous lichen flora are: life-span, cuticle composition, surface and water potential, surface pilosity, angle of inclination and vulnerability to insects.

4. A succession of different ecological groups occurs under suitable conditions (e.g. leaves living for many years), as evidenced for example by Conran & Rogers (1984).

DISTRIBUTION PATTERNS

Obligately foliicolous lichens are widespread throughout tropical and subtropical areas (Fig. 3); their distribution is very similar to that of the rain forests (without any or a short dry season). Several species occur in temperate areas (up to 22 in the Caucasus), but are then restricted to specialized limited habitats.

A detailed analysis of distribution patterns has been carried out on a large collection made in Central East Africa (Zaïre/Kivu, Rwanda, Burunid) by Prof. J. Lambinon: 87 collections (each of them corresponding to a single locality and

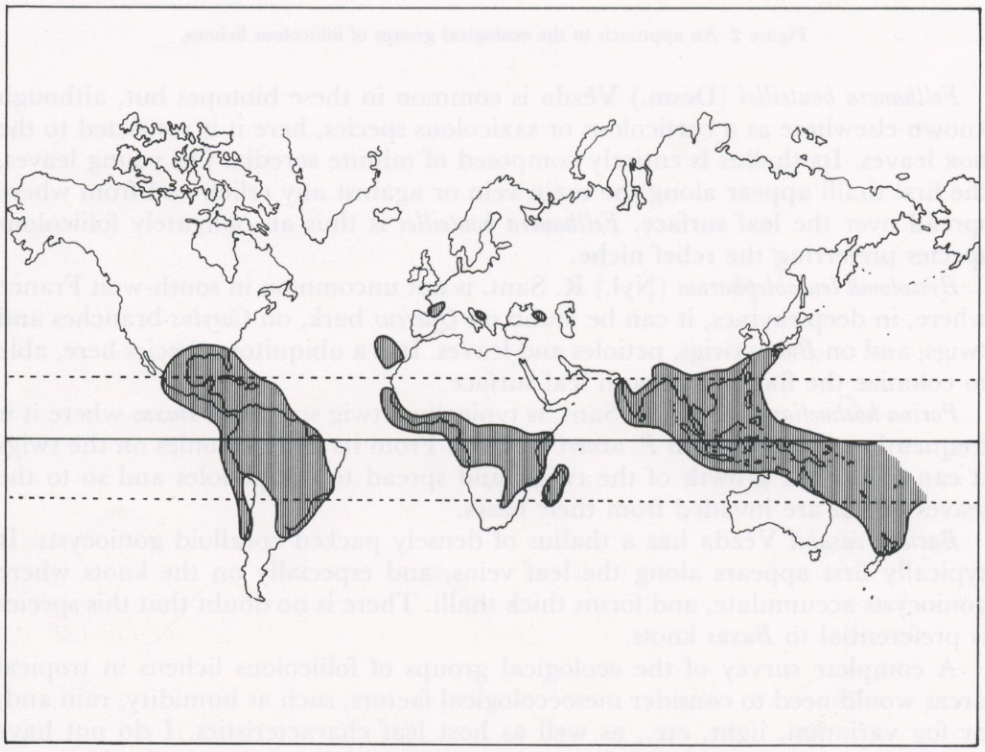

Figure 3. World distribution of obligately foliicolous lichen species.

TABLE 2. Phytogeographical spectrum of the lichen foliicolous flora of Zaïre/Kivu, Rwanda and Burundi

	% of the total species number
Subcosmopolitan (widespread throughout tropical and oceanic areas)	10.0
Pantropical	43.3
Africa and South America	7.7
East Africa and South-East Asia (*sensu lato*)	1.1
Africa	8.0
Endemic	22.2
Unassigned	0.7

to a single species of phorophyte), out of which 102 foliicolous species were identified. The phytogeographical spectrum of this flora is shown in Table 2.

Although I have not seen enough collections from other parts of the world, preliminary observations for south-east Asia and tropical America tend to be similar, almost half of the species present being pantropical. This indicates that they are very old species, well-established before the break-up of Pangea (180 Myr BP), or that they have sufficient dispersal capacity to enable them to colonize suitable habitats all over the tropics. It is also remarkable that exclusively African species (including species endemic to the studied area) account for more than 30% of the species; this same observation has been made in each continent analysed. The number of endemic species now recognized is probably over-estimated by the discovery of new species that will eventually be recorded elsewhere, but is nevertheless significant.

A few distribution patterns are more unusual and might be explained by plate tectonics: *Vezdaea dawsoniae* Döbb. is now known from New-Guinea, the Caucasus, south-west France and Cuba, all localities which were on the northern side of the Tethys sea in the lower Cretaceous. *Bacidia olivaceorufa* Vainio, known from south-east Asia (Indonesia, Philippines, New Guinea), has a vicariant in south Europe (south-west France, Caucasus) in *B. colchica* Vězda; again these localities were on the northern edge of the Tethys sea.

Except for the most common species (e.g. *Fellhanera bouteillei*), the foliicolous lichen flora of southern Europe is most probably a relic of more humid Tertiary times. This is supported by the localization in deep gorges, disjunct distributions (south-west France and the Caucasus), the extraordinary scarcity of some species (in south-west France, despite very careful searching in suitable habitats, species such as *Gyalectidium setiferum* and *Bacidia kakouettae* were found on a few *Buxus* bushes in only one locality).

In the collection from Central East Africa mentioned above, a relevé (bryophytes and algae not included) was made on each collection, using an abundance index (numbered from 1 to 4). These relevés represent the data matrix on which factorial analysis was performed by the 'analyse factorielle des correspondances' ('reciprocal averaging') method introduced in France in 1965 by B. Cordier (Dagnelie, 1975: 222; Hill & Gauch, 1980). This powerful method projects all collections and all recognized taxa into the same space in which each collection is encompassed by the taxa present in it, and each taxon by the

collections where it is present. Two axes can then be chosen to convey as much information as possible.

Nine different types of forests were examined:

A, Zaïre/Kivu, Irangi: undisturbed equatorial rain forest (850 m).
B, Zaïre/Kivu, Kahuzi-Biega: undisturbed montane rain forest (2250–2560 m).
C-a, Rwanda, Rugege: ± disturbed montane rain forest (1900–2500 m).
C-b, Rwanda, Rugera: disturbed montane rain forest (± 2400 m).
C-c, Burundi, Bururi: ± disturbed montane rain forest (2100–2200 m).
C-d, Burundi, Siguvyaye: montane forest in deep ravine (1750 m).
D-a, Rwanda, Butare: plantations (1700 m).
D-b, Burundi, "Gouffre des Allemands": forest in deep ravine (1750 m).
D-c, Rwanda and Burundi: forest along rivers and thickets in savannas (1200–1500 m).

The first result of the analysis was the recognition of chorological types within the studied area (Table 3).

From this analysis, it is clear that foliicolous lichen species have strict distribution patterns, albeit ubiquitous species reach 20%, the equatorial rain forest at mid-elevation has 23% of the species of the area on its own, and there is a sharp difference between the flora of the high montane forest and that of lower elevations (41.6% of the species are absent over 1800 m, whereas 17.7% appear only over that elevation).

Interesting results are also obtained by performing the analysis with collections from the same forest type. In Fig. 4, obtained from montane forests C-a and C-b, the horizontal axis can be interpreted as an elevation gradient (from left to right). The 21 collections made around 1800–1900 m elevation are very similar to each other although 19 different species of host trees are involved. This demonstrates that leaf characteristics are not important for this foliicolous lichen community, which is dominated by species of *Echinoplaca* Fée and *Tricharia* Fée. Collections from higher elevations are more heterogeneous, but have nevertheless typical species (*Strigula* Fr. and *Asterothyrium* Müll. Arg.) that appear over 2300 m.

The total analysis, as well as analyses between each forest type, enables the following relationships between the foliicolous lichen flora of those forests to be recognized: (1) the equatorial forest is isolated and has a characteristic foliicolous

TABLE 3. Chorological patterns of foliicolous lichens in Zaïre/Kivu, Rwanda and Burundi (see text for details)

Forest types	% of species present
A-B-C-D	19.7
A-B-C	6.2
A-B	1.0
A	22.9
B-C-D	12.5
B-C	2.1
B	4.2
C	11.4
D (+ C-d)	12.5
A-D (+ C-d)	6.2

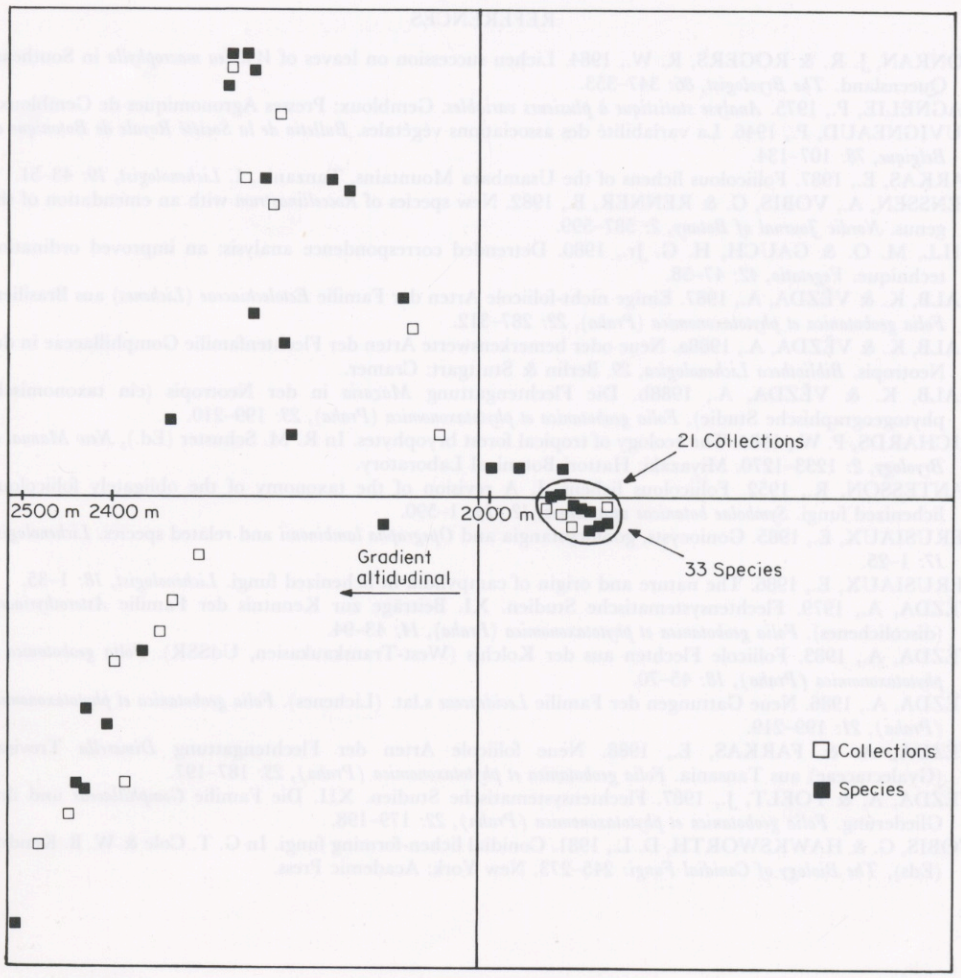

Figure 4. Reciprocal averaging analysis of the foliicolous lichen flora of montane forests in Rwanda (see text for details).

lichen flora; (2) montane forest show a sharp differentiation between high elevations (2300–2500 m) and lower ones (1800–2000 m), but are otherwise very similar; and (3) riverside forests and thickets in savannas are closely related, but several sites present a flora similar to that of the montane forests (site D-b falls within the variation of the highest level of montane forests, whereas site C-d is comparable to the lowest one).

ACKNOWLEDGEMENTS

This paper is based on a talk at the Symposium entitled "Horizons in Lichenology" organized by the Linnean Society of London and the British Lichen Society in London on February 19th, 1987. The financial support of both Societies is gratefully acknowledged. I also wish to thank Prof D. L. Hawksworth and Prof J. Lambinon for assistance in preparing the manuscript.

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