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Habitat shifts and morphological variation of *Pseudevernia furfuracea* along a topographical gradient

Jouko Rikkinen

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The distribution and phenotypic variation of *Pseudevernia furfuracea* was studied in a deep, densely forested kettle hole in central Finland. This epiphytic lichen responded to environmental variation by habitat shifts and ecomorphological changes. It shifted from vertical to horizontal substrate types along the descending slopes of the kettle hole and exhibited concurrent differences in thallus morphology between sites. The habitat shift mainly reflected a reduction in the levels of photosynthetically active radiation along the slopes. Changes in thallus structure were more specifically related to evaporation regimes and inherent difficulties in maintaining positive net photosynthesis in permanently humid habitats. Systems for external water conduction and storage were described from robust *Pseudevernia furfuracea* thalli. Water conduction was partly controlled by hygroscopical modifications in the dimensions of capillary channels. By linking the morphological variation of the lichen to its multidimensional distribution in the kettle hole and then relating the results to patterns in forest dynamics information on complex processes which influence the structure of epiphytic vegetation in boreal forests may be achieved.

Key words: Lichens, *Pseudevernia furfuracea*, thallus morphology, water relations, habitat shifts.

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Introduction

While investigating relations between land forms, microclimates and vascular plant vegetation in an esker area in central Finland, I noticed many apparent correlations between local topography and the distributions of cryptogamic epiphytes (cf. Rikkinen 1989). Eventually these casual observations led to extensive field work focusing on the abiotic and biotic control of epiphytic vegetation on the Kalmari-Saarijärvi esker chain and in one large kettle hole, in particular. The results of these investigations will be published in a series of case studies focusing on different aspects of epiphyte ecology.

The aim of this paper is to describe and explain patterns in the distribution and morphological var-

iation of *Pseudevernia furfuracea* (L.) Zopf in the deep, densely forested kettle hole of Kivvieru. In this large depression the foliose macrolichen exhibited a bimodal distribution as a function of topographic altitude, slope aspect and phorophyte species. This distribution was accompanied by marked differences in thallus morphology between sites. *P. furfuracea* was most abundant on the trunks of *Pinus sylvestris* on the upper south-facing slope of Kivvieru, but it was also common on the lower branches of *Picea abies* on the central and lower sections of the north-facing slope. Several other foliose and fruticose epiphytes had similar distributions and also many of them exhibited consistent differences in thallus morphology between sites.

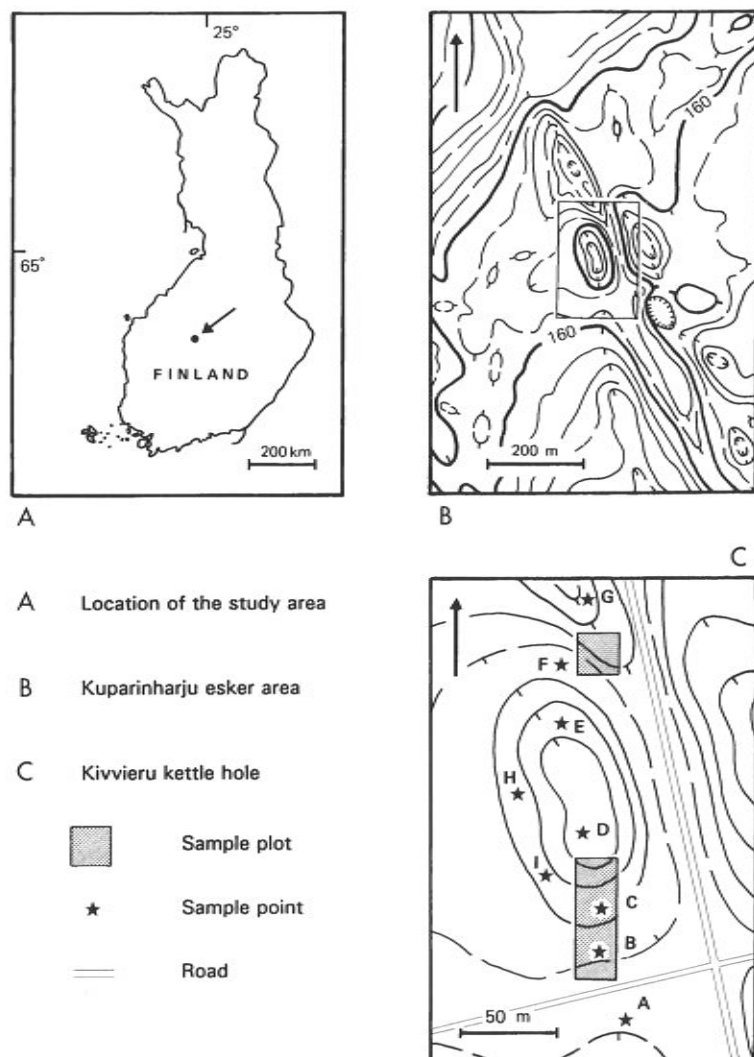


Figure 1. General features of the study area.

Pseudevernia furfuracea (L.) Zopf is widely distributed in Europe and North Africa. It is also known from Pakistan and disjunct populations occur on some high mountains in the Tropics. The species is notorious for its plasticity—good examples of the whole extent of this variation were already published by Bitter (1901, Figs. 42–54) and Zopf (1903, Tafeln II–V). The wide morphological variation of *P. furfuracea* has focused interest on its taxonomy during the years. Furthermore, the lichen occurs with three combinations of medul-

lary substances and contrasting opinions have been expressed on how to treat these chemotypes taxonomically. The two principal chemotypes differ in containing either olivetoric acid or physodic acid in the medulla. In addition at least some specimens contain both acids. Nowadays these chemotypes are generally treated as chemical strains without formal taxonomic status. It is also agreed that all European *Pseudevernia* populations intergrade continuously with respect to thallus morphology (Bitter 1901; Zopf 1903; Rave 1908; Hale

1956, 1968; Culberson 1965; Hawksworth & Chapman 1971; Culberson et al. 1977; Halvorsen & Bendiksen 1982).

The study area

The study area is located in the commune of Saarijärvi in central Finland, about 16 km NW of the town by that name (approx. 62°47'N 25°03'E). The location and principal land forms of the study area together with the location of sampling sites is given in Figure 1. With respect to climate the study area is situated in the transition zone between Suomenselkä divide and northern Lakes Finland. For more climatological details, see Rikkinen (1989). With respect to atmospheric pollution Saarijärvi represents a rural background area, where the deposition of most pollutants is low.

The principal land form in the study area is an esker which runs in a NW-SE direction. The formation comprises the glaciofluvial hill of Kuparinharju and a steep ridge extending from it towards the south-east (Fig. 1B). Further variety to the topography is added by a number of kettle holes. Two such depressions are located side by side immediately south of Kuparinharju hill. The western depression, named Kivvieru, is of particular interest here (Fig. 1C). The difference in altitude between the summit of Kuparinharju and the bottom of Kivvieru is 29 m. At its steepest part the south-facing slope of the kettle hole drops 22 m over a horizontal distance of 50 meters.

The thermal conditions of Kivvieru were monitored by the author over the period 3 May - 31 August in 1986. Steep gradients involving illumination, temperature and moisture were found to exist from the edge of the kettle hole to the bottom, with pronounced differences between slopes of different exposure and inclination. One example of this was provided by diurnal mean temperatures, which showed that during the 1986 growing season the effective temperature sum for the bottom of Kivvieru was only ca 70% of that recorded for the upper south-facing slope (Fig. 2). The two sites were located only 150 meters apart, but the difference in their effective temperature sums was equivalent to the macroclimatic difference gener-

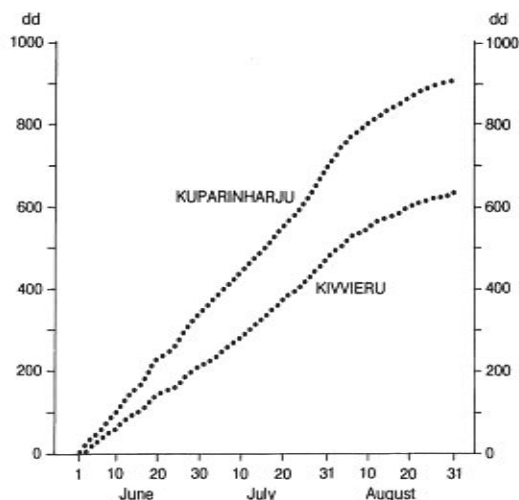


Figure 2. Accumulation of the effective temperature sum (degree days) on the summit of the Kuparinharju esker and in the bottom of Kivvieru kettle hole during the period 1 June - 31 August, 1986 (from Rikkinen 1989).

ally associated with a distance interval of almost 800 km in a north-south direction in Finland (Rikkinen 1989).

Vegetation on the southern rim of Kivvieru consists of a moderately dry *Vaccinium* type (VT) heath forest, which gives way to a fresh *Myrtillus* type (MT) heath forest on the upper north-facing slope. *Pinus sylvestris* is the dominant tree species down to the central north-facing slope, where it is gradually replaced by *Picea abies* (Figs. 1C & 3A). The lower half of the north-facing slope supports a dense spruce forest. Near the base of the slope the fresh heath forest grades into a thin peat spruce mire (KgK), which at the very bottom of the kettle hole is characterized by a swamp effect. The northern end of the kettle hole bottom supports a wet spruce forest, which grades into a narrow zone of fresh heath forest at the base of the south-facing slope. This is soon replaced by a moderately dry heath forest on the lower slope, where pine again replaces spruce as the dominant tree species. The upper south-facing slope supports a dry *Calluna* type (CT) heath forest, which also prevails on the south-facing sample plot (Figs. 1C & 3A).

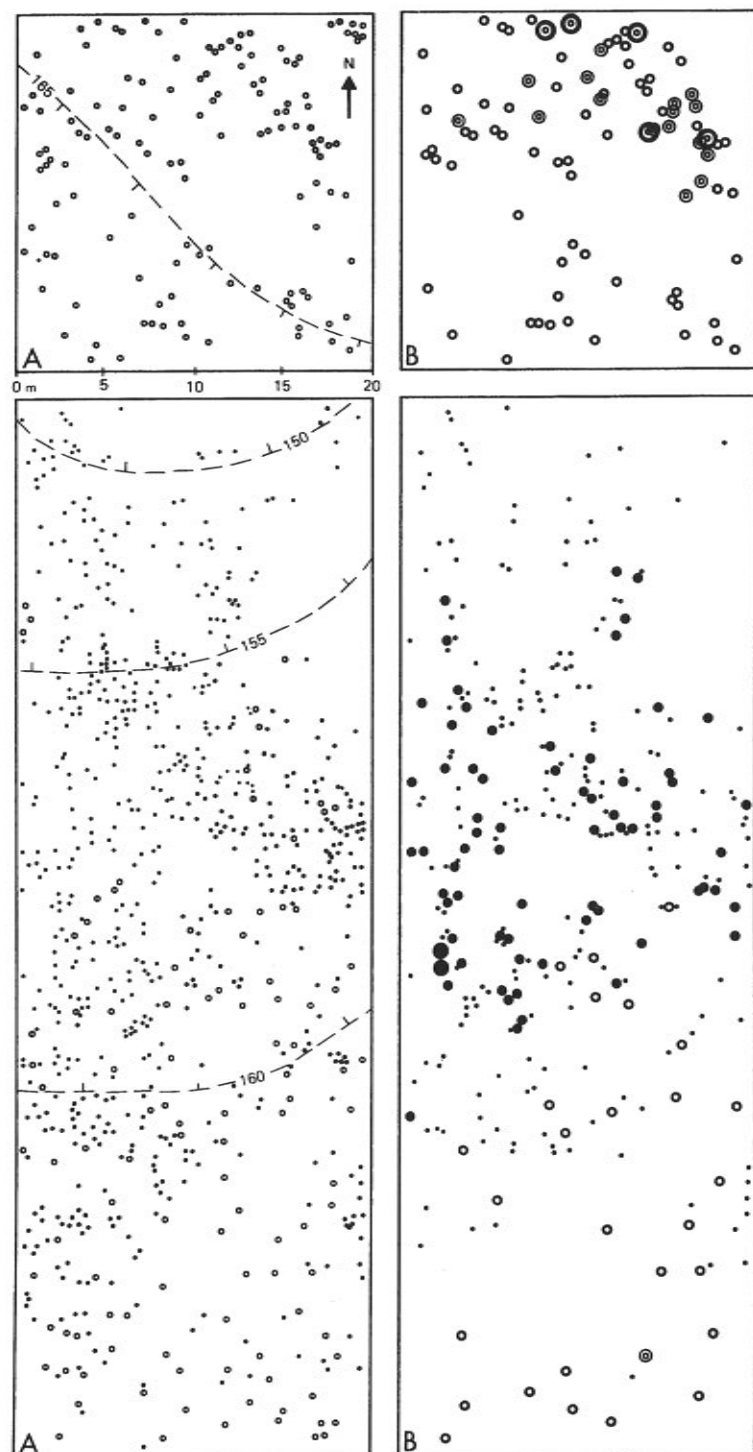


Figure 3. Forest sample plots in Kivieru. (For location of the plots, see Fig. 1C). A. Distribution of *Pinus sylvestris* (circles) and *Picea abies* (dots) on the sample plots. — B. Occurrences of *Pseudevernia furfuracea* on lower pine trunks (circles) and lower spruce branches (dots). Symbol size indicates the abundance of *Pseudevernia* thalli on the phorophytes (estimated cover: small symbols < 0.1%; medium symbols 0.1–0.9%; large symbols 1–3%).

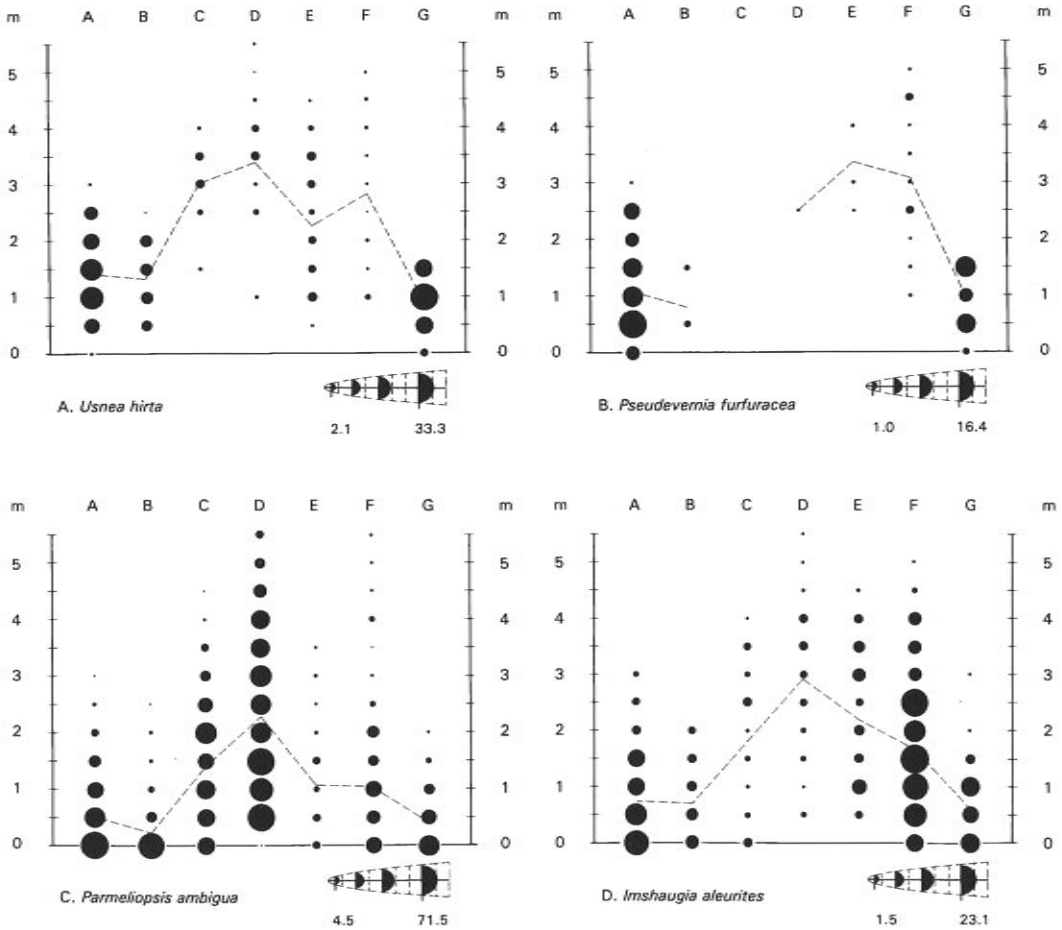


Figure 4. A–D: Vertical distribution of selected macrolichens on seven large pines (A–G) along a south-north oriented transect across Kivvieru. For the location of sample trees, see Fig. 1C. The circles represent the average local frequencies of epiphytes on eight 100 cm² sample plots on each 50 cm height segment of the trunks. Note that the scale of the circles varies between epiphyte species.

Pines are generally taller on the upper north- and east-facing slopes and on the lower south-facing slope than on the upper south-facing slope and at the bottom of Kivvieru, respectively (Fig. 3A). Some of this variation is due to differences in forestry practices, but more of it can be attributed to topographically induced variations in illumination conditions, soil moisture and nutrient availability. Pines on the north-facing slope are characterized by tall branchless boles, while pines on the south-facing slope generally support branches much closer to the ground. At the bottom of Kivvieru, in

the shade of large spruces, pines tend to support very restricted crowns.

The spruce forest on the lower north-facing slope of Kivvieru has a multi-layered and heterogeneous structure (Fig. 3A). The average height and circumference of spruce trunks generally increases with diminishing altitude, with the largest trees being located at the bottom of the kettle hole. The appearance of low spruces changes along the descending slope. The central slope supports thickets of vigorous spruce saplings, while the spruce stands on the lower slope are characterized

by a relatively high mortality among standing trees. Low spruces in the latter location are mainly old, suppressed individuals, which continue to exist in the shade of higher trees. Intense competition for light and frequent snow-damage has led to decreased vitality amongst these low spruces.

Studies in Kivvieru revealed major differences in the structure of epiphytic assemblages between different parts of the depression. Most epiphytic lichens were unevenly distributed along the slopes. Also the vertical distributions of pine trunk epiphytes varied markedly along the topographical gradient. Examples of this can be seen in Fig. 4, which shows the distribution of four common macrolichens on large pine trunks along a south-north transect across Kivvieru (sample points A–G in Fig. 1C). The broken lines indicate changes in positional values along the topographical gradient (weighted average technique). In addition to shifts in vertical distribution, many epiphytes exhibited clear changes in substrate preference along the slopes of Kivvieru.

Material and methods

The distribution of *Pseudevernia furfuracea* in Kivvieru was studied on two sample plots, set up on the north- and south-facing slope of the kettle hole, respectively (Fig. 1C). The species composition of epiphyte assemblages was determined for all trees and shrubs higher than 30 cm on the sample plots (Fig. 3A). The trees were examined up to the height of two meters and the occurrences of epiphytes on tree boles and branches were recorded separately. In addition, the vertical distribution of macroepiphytes on 18 pine trunks was studied in more detail. These trees were located on nine sample points forming a south-north gradient across Kivvieru (A–I in Fig. 1C).

In order to study the thallus morphology a total of two hundred *P. furfuracea* thalli were collected from pine trunks on the upper south-facing slope and from spruce branches on the lower north-facing slope, respectively. The morphological characteristics of these thalli were examined under a dissecting microscope, a compound microscope and an incident light microscope. Additional observa-

tions were made by scanning electron microscopy. One representative lobe from the central section of each thallus was chosen for determination of dry weight, wet weight, water holding capacity and medullary chemistry (chlorine spot test).

In addition, lobe width, medullary thickness and cortical thickness were determined for 20 dry thallus lobes from both locations. This was done after the water holding capacity had first been determined. Ten measurements were made from cross sections through the central part of each thallus lobe. For this purpose free hand sections were obtained with a razor blade. Cortical thickness was measured from the ventral cortex because isidia caused considerable intralobal variation in the structure of dorsal cortices. All thicknesses were measured according to the limits of the cortical matrix. Thus, isidia, protruding tips of cortical hyphae and/or accretions of crystallized substances were not included in the measurements.

To determine water holding capacity each *P. furfuracea* lobe was weighed. The lobes had first been kept in paper bags at room temperature for several weeks and then in a mushroom drier for 48 hours at 30°C. After weighing, the lobes were laid on flat dishes and sprayed with water until surplus water accumulated around them. The lobes were left partly submerged until maximum hydration had been reached. Preliminary tests had shown that the absorption of liquid water by *P. furfuracea* lobes was a rapid process. Maximum hydration was generally achieved within a few minutes, this being consistent with the observations of Vicente and Velasco (1985), who found that dry *Pseudevernia* thalli generally reached saturation within eight minutes from being immersed in distilled water.

Before determining wet weight each hydrated *P. furfuracea* lobe was shaken against a piece of blotting paper. This was done in order to remove free drops of water from thallus surfaces. Thus, the water held by "wet" *Pseudevernia* lobes included most imbibition and capillary water, while some surface water had been lost. As pointed out by Jahns (1984), the method of shaking inevitably introduces a considerable error in the measurement. The quantity of remaining surface water on robust,

abundantly isidious thallus lobes, in particular, was difficult to control with any degree of precision. When saturated, such lobes held large amounts of surface water between isidia and within the ventral concavities. This water was impossible to shake off. On the other hand, removing all the surface water with blotting paper would have eliminated the characteristic external water reserves of the thalli.

Capillary conduction of water along the surfaces of rehydrating *Pseudevernia* thalli was observed under dissecting and incident light microscopes. General trends in hygroscopic thallus movements were also assessed in wetting experiments in which whole thallus lobes and relatively thick cross sections (ca 0.5 mm) from thallus lobes were studied under an incident light microscope.

Results

Phenotypic variation

Mature thalli of *Pseudevernia furfuracea* are usually ascending to subpendulous, mainly attached to their substrate at the base. The dorsiventral lobes are divergently, mainly dichotomously branched and corticated both above and below. Especially the lobes of large thalli have concave lower surfaces which often darken to a purplish black. In Kivviero, mature *P. furfuracea* thalli on the upper slopes were large and robust, and their thick lobes were usually covered by dense layers of isidia and small lobuli (Fig. 5A). Mature thalli in the low-lying parts of the depression were invariably much smaller and their finely branched lobes generally supported only few, widely separated isidia (Fig. 5B).

Site dependent variation in the thallus size of *P. furfuracea* was clearly reflected in the average weights of single thallus lobes. The average dry weight of thallus lobes from the lower north-facing slope was less than 17% of that on the upper south-facing slope (Table 1). Variation in the dry weights was higher on the lower slope, but differences between the sites were quite small. The consistent, site dependent differences in lobe diameter largely reflected differences in medullary thickness (incl. the photobiont layer). Thalli from the upper south-

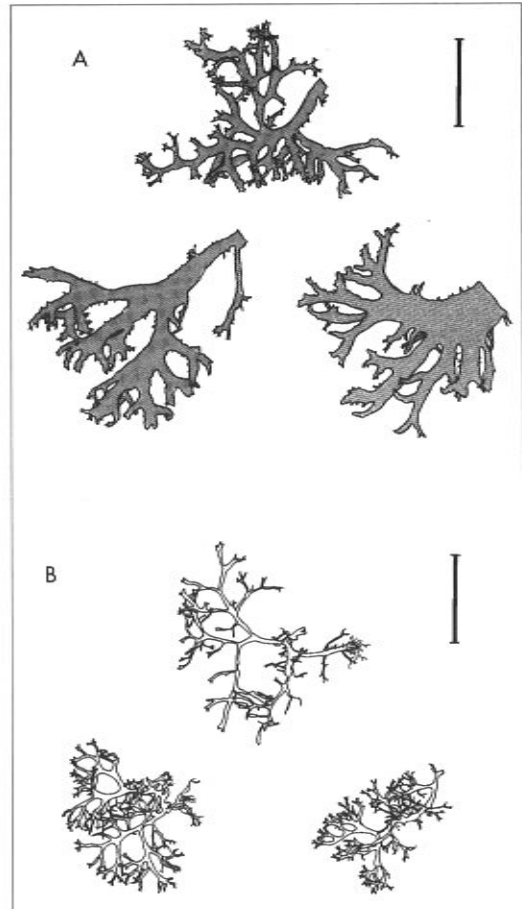


Figure 5. Examples of representative *Pseudevernia furfuracea* thallus lobes from the two contrasting sites in Kivviero. – A. Thallus lobes from the upper south-facing slope. – B. Thallus lobes from the lower north-facing slope. – Bars 2 cm.

facing slope were characterized by having a thick medulla, while medullary tissue accounted for a smaller proportion of the thallus diameter on the lower slope. A highly significant difference was also found in cortical thickness, with thalli from the lower north-facing slope generally having thicker cortices. *Pseudevernia* thalli from the upper slope usually had a relatively dark, ash grey colour, while thalli from the lower slope were pale grey to almost white.

The distribution of the two main chemical

Table 1. Population variability of *Pseudevernia furfuracea* in Kivvieru. All measurements were made from single thallus lobes.

Samples	Medullary reaction C +		Lobe width (mm)	Medullary thickness (μm)	Cortical thickness (μm)	Dry weight (mg)	Wet weight (mg)	Water content (%)
Combined data (n = 200)	36%	Mean	3.35	236.84	16.81	44.36	128.40	177.70
		SD	2.66	76.92	3.39	37.60	113.60	28.95
Upper slope (n = 100)	39%	Mean	5.46	286.32	13.96	76.00	223.51	192.57
		SD	2.28	69.13	1.94	27.91	85.85	24.32
Lower slope (n = 100)	33%	Mean	1.28	187.35	16.97	12.71	33.26	162.73
		SD	0.39	46.51	3.36	6.32	16.73	25.37
		Difference between slopes	4.20	98.97	3.01	63.29	190.25	29.84
		t-Test	25.66	16.80	10.99	22.11	21.75	8.49
		Probability	.0001	.0001	.0001	.0001	.0001	.0001

strains of *P. furfuracea* appeared indifferent to local topography (Table 1). The physodic acid strain (C-) prevailed at both locations, with the percentage frequency of olivetoric acid-containing thalli (C+) being slightly higher on the upper south-facing slope. At this location the percentage of thalli containing olivetoric acid was 39, this being practically equal to the 40% reported for Finland as a whole (Hale 1956).

External conduction of water

A linear correlation existed between the dry weights (x) and wet weights (y) of *P. furfuracea* thallus lobes from Kivvieru ($y = -4.58 + 2.30x$; $r^2 = .985$, $n = 200$). This correlation was highly significant at both sites (upper slope $F = 1819.78$; lower slope $F = 3735.94$). The average water holding capacities of thalli from the upper and lower slopes were ca 190% and 160% of dry weight, respectively. The considerable difference between sites could clearly be addressed to the greater external water holding capacity and greater proportion of medullary tissue in robust thalli from the upper slope.

Robust *P. furfuracea* thalli from the upper slopes had several features which promoted the conduction of water along thallus surfaces. In addition, external capillary spaces stored considerable amounts of surface water and thus formed an

integrated part of the overall water storage of saturated *Pseudevernia* thalli. Water was being conducted along three main routes, i.e., in the ventral concavities of thallus lobes, in the capillary spaces between isidia and in minute crevices between protruding tips of perpendicular cortex hyphae. Together these capillary systems formed a diverse network which rapidly dispersed water along the thallus surface and enabled the transport of water from spaces between the lichen and its substrate to the tips of erect thallus lobes.

The first capillary system operated on the deeply furrowed lower surfaces of *P. furfuracea* lobes. The cross sections of individual thallus lobes varied from flat to nearly tubular, but most mature lobes had convex upper surfaces with reflexed margins and more or less concave ventral surfaces. The lower surfaces of thallus lobes were further roughened by longitudinal furrows, which often gave the ventral grooves a wrinkled appearance (Figs. 6 & 7). The grooved structure of the thallus lobes increased their resistance to bending and almost tubular, erect lobes were often seen in the fruticose central sections of large *Pseudevernia* thalli. Often such erect lobes tended to twist upside down. Under natural conditions such lobes must have collected rainwater efficiently. In any case, water tended to collect in the ventral cavities while the convex upper surfaces of thallus lobes remained relatively dry. The ventral grooves also

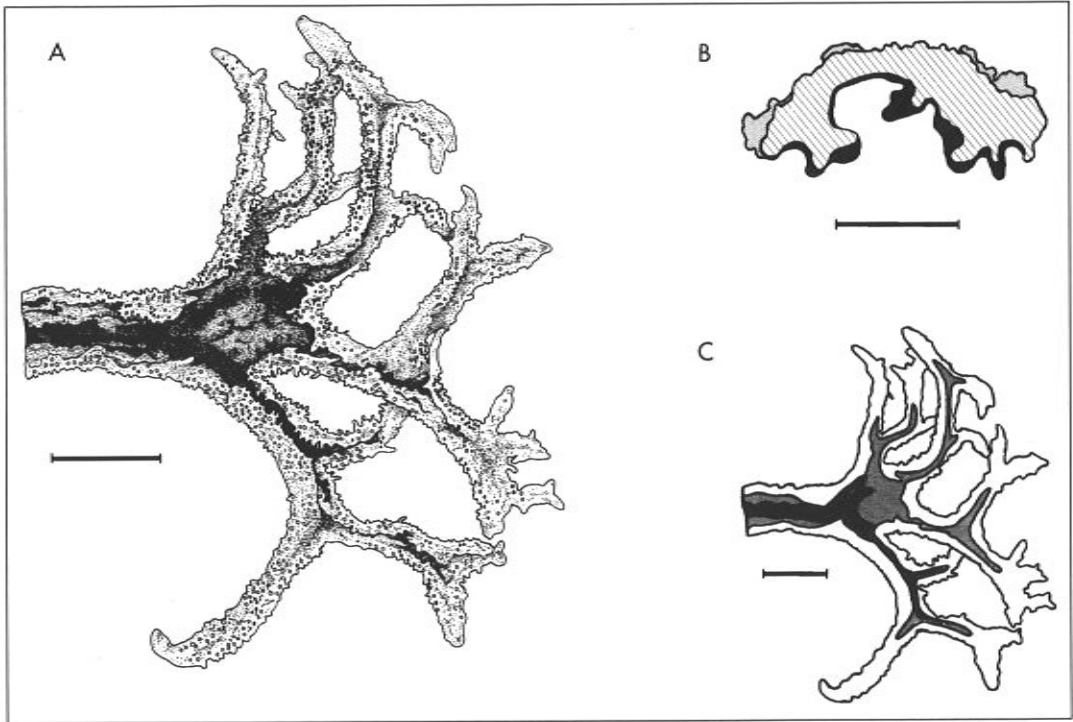


Figure 6. Robust *Pseudevernia furfuracea* lobe from the upper south-facing slope of Kivvieru. – A. Habit, showing the ventral groove and reflexed, densely isidate thallus margins. Scale bar 3 mm. – B. Cross-section from the base of the lobe, showing the deeply furrowed ventral concavity. Scale bar 1 mm. – C. Capillary conduction along the ventral concavity when drops of water are applied onto the base of the dry thallus lobe (first drop: dark shading; second drop: light shading). Bars 3 mm.

acted to conduct water along the lobes. This phenomenon was confirmed in numerous wetting experiments where drops of water were applied onto dry lobe surfaces (Fig. 6C).

The second external capillary system was formed by isidia which often covered much of the upper surfaces of robust *P. furfuracea* thalli (Figs. 6 & 7). Large amounts of water were collected, held and conducted in the capillary spaces between individual thallus appendages. The convex tops of isidia had positive water potentials and tended to remain dry even when much water was held between the isidia. Capillary spaces between isidia were relatively large, usually being in the range of 5–30 μm across. Such channels could disperse a drop of water over a lobe surface in a matter of seconds. Despite the swelling of individual isidia during hydration isidium layers could also

store large quantities of water. The varying shape and irregular surface topography of isidia may have been important in this context.

The third external capillary system of *P. furfuracea* was provided by the rough microtopography of mature cortex surfaces (Fig. 8). The thallus surface was roughened by the tips of perpendicular cortex hyphae protruding from the extracellular matrix. The hyphal tips were separated by minute crevices, with the hyphal tips of the dorsal cortex often protruding somewhat higher than those of the ventral cortex. The roughness of cortex surfaces was further increased by massive accretions of crystallized lichen compounds. The accretions could be removed by warm acetone and were thought to mainly consist of atranorin, the main cortical lichen substance in *P. furfuracea*.

In ventral cortices the crystallized accretions

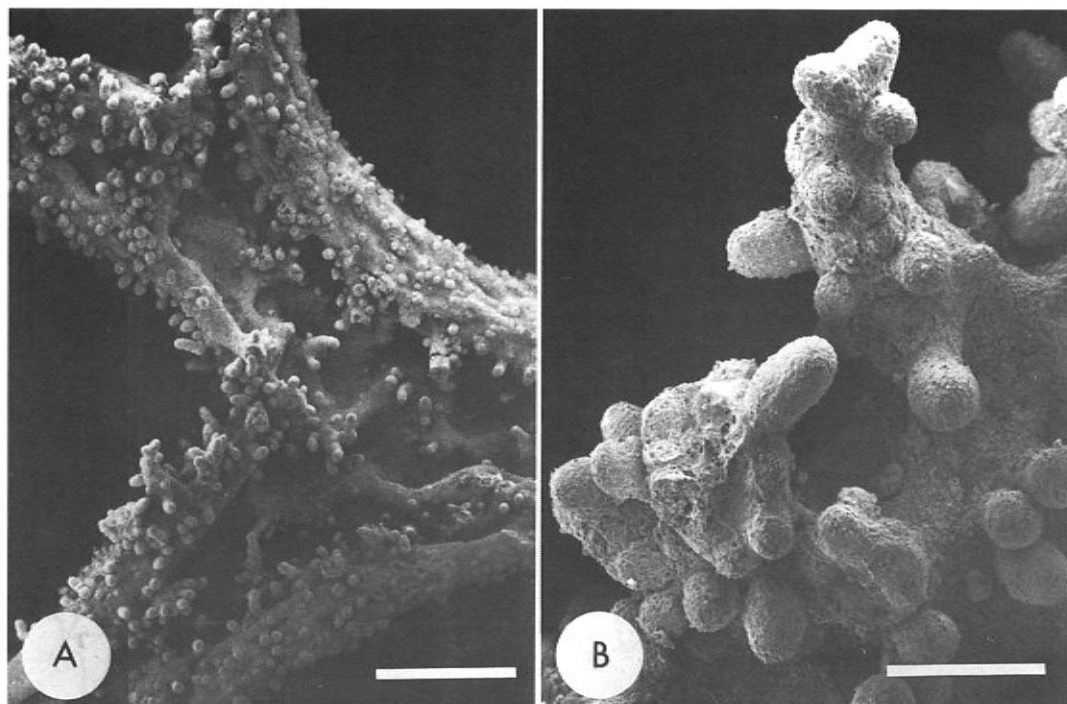


Figure 7. SEM micrographs of a robust *Pseudevernia furfuracea* lobe from the upper south-facing slope of Kivvieru. – A. Capillary conducting systems formed by the furrowed ventral concavity and isidium layer, respectively. Scale bar 1 mm. – B. Detail of isidia and lobuli on the reflexed thallus margin. Scars left by detached isidia connect the photobiont layer with the atmosphere. Bar 200 μ m.

were often relatively restricted in extent and their close association with hyphal tips could be clearly seen. Often the dark extracellular matrix of the cortex gave a striking contrast to the highly reflective accretions (Rikkinen 1995, Figs. 4–6). The secretions of several hyphae combined to form irregular lumps separated by deep crevices. On mature thallus lobes the accretions often formed a more or less continuous, rough layer on the cortex surface (Fig. 8D). Near the tips of young thallus lobes this roughness was hidden under a smooth epicortex (Fig. 9). The development from a smooth, continuous epicortex to a rough surface topography typical of old *Pseudevernia* thalli seemed to involve transitional stages where the epicortex first achieved a pored structure (Figs. 8A & 8B) and finally deteriorated (Figs. 8C & 8D).

Especially on the ventral surfaces of *Pseudevernia* lobes rapid superficial conduction of water oc-

curred, much in the same way as among papillae on moss leaves. The interhyphal cavities generally had a radius of only 1–3 μ m and could thus develop very low water potentials. The height of capillary rise in such systems can be several metres, and thus interhyphal conduction insured an efficient dispersion of water along cortex surfaces.

The specific effect of epicortical accretions on capillary conduction remained somewhat dubious. Many lichen substances are hydrophobic and accretions of such compounds could potentially prevent liquid water from freely penetrating the thallus. However, the epicortical accretions of *P. furfuracea* did not seem to inhibit the superficial conduction of water. Water penetrated the accretions with ease and fluctuations in the water contents of cortex surfaces gave a visual impression similar to that commonly associated to water movements in wet icy snow or sludge. By no means was water

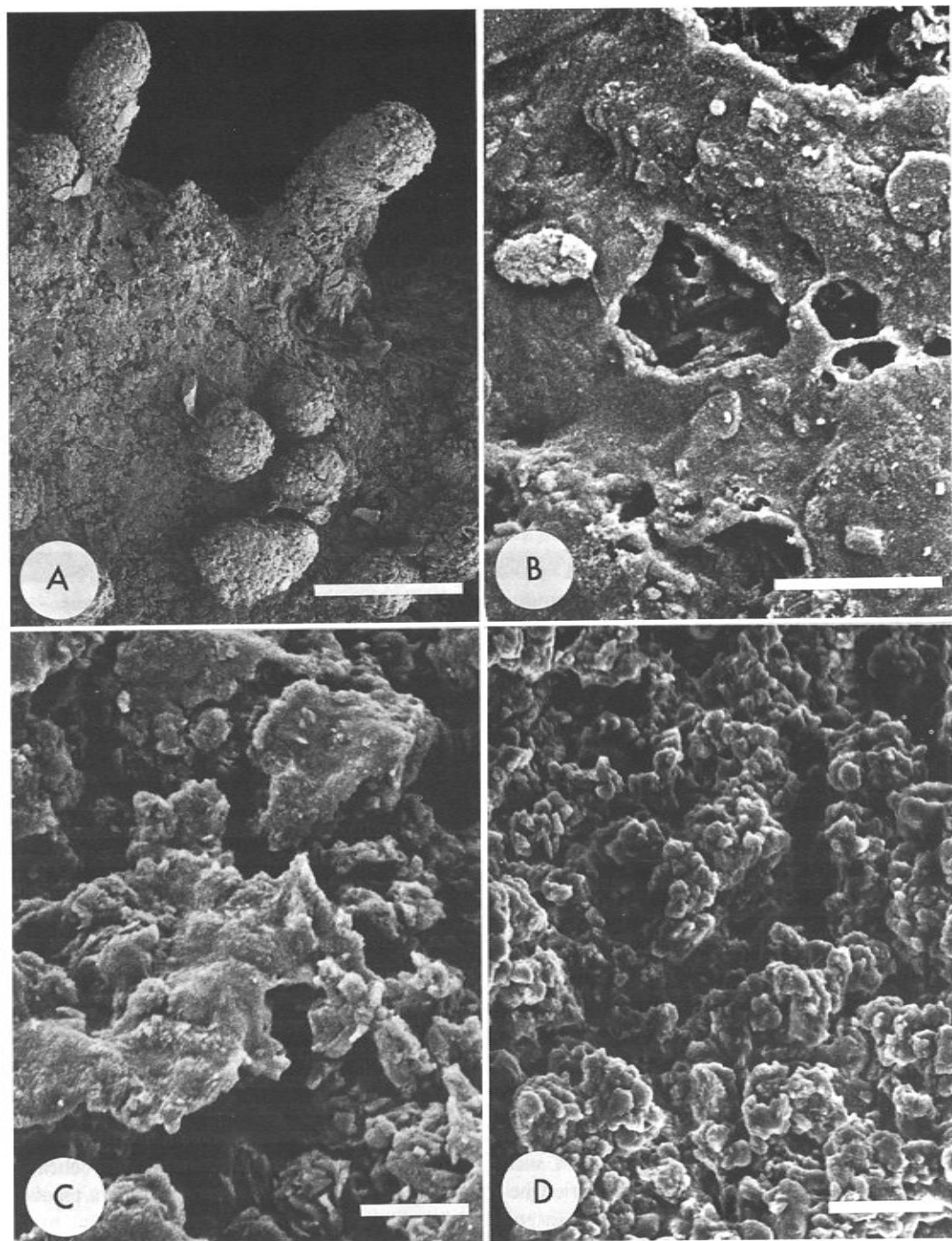


Figure 8. SEM micrographs of rough cortex structures in ageing lobe sections of *Pseudevernia furfuracea*. – A. Pored epicortex on the upper surface of a thallus lobe. Scale bar 100 μm . – B. Detail of epicortical pores. Scale bar 5 μm . – C. Remnants of a pored epicortex on the upper surface of a mature thallus lobe. Scale bar 5 μm . – D. Non-epicorticate surface structure typical of mature thalli. Minute crevices between tips of cortical hyphae form a diverse network of capillary channels on the thallus surface. Bar 5 μm .

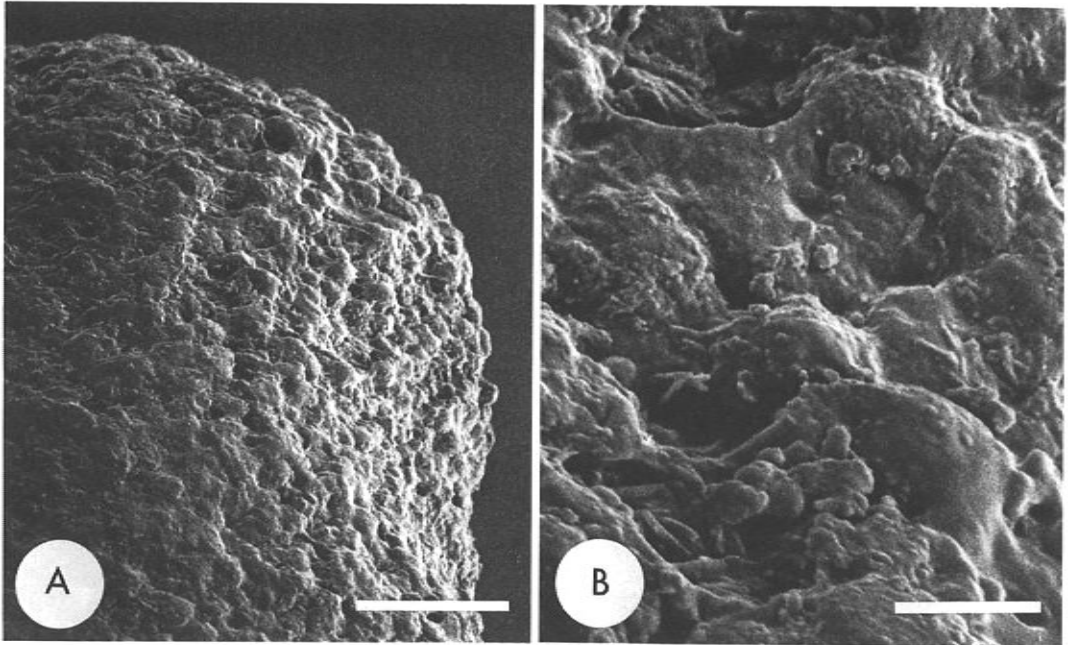


Figure 9. SEM micrographs of smooth surface structures in young lobe sections of *Pseudevernia furfuracea*. – A. Nonpored epicortex covering the tip of a thallus lobe. Scale bar 25 μm . – B. Detail of epicortical surface. Bar 5 μm .

left standing as droplets on the surface of crystallized accretions—a situation, which may often be observed on the hydrophobic surfaces of leprose lichens (e.g. many *Lepraria* species) or lichen soralia.

Hygroscopic thallus movements

Wetting experiments revealed that *P. furfuracea* thalli often exhibited hygroscopic movements during rehydration. Such movements were clearly related to differences in the water uptake and swelling capacities of different thallus layers. The movements were particularly striking in robust, reflexed thallus lobes from the upper south-facing slope of Kivvieru. This was due to the relative structural complexity and large volume of such lobes. The magnitude of movements varied between samples, but general trends were consistent. These are visualised in Fig. 10, which shows changes in the cross-sectional dimensions of six *Pseudevernia* lobes during rehydration. Fig. 11

shows three main phases (A–C) in the wetting and drying cycles of typical thallus lobes. The shadowed areas show the estimated distribution of water on and within a thallus during different phases of the hydration cycle.

When water was first applied onto the upper surface of dry *Pseudevernia* lobes the previously described capillary systems insured a rapid dispersion of water along the cortex surface. Some water was immediately absorbed by the hyphal walls and extracellular matrix. The subsequent swelling of the dense, strongly agglutinated cortex forced the reflexed margins of the thallus lobe to curve inward (Figs. 10 & 11). The rapid increase in lobe curvature changed the dimensions of the ventral groove: the mouth of the concavity became more narrow and especially in small, strongly concave thallus lobes the groove often achieved a tubular shape. Quite frequently the reflexed thallus margins fitted each other with some precision and the thallus lobe formed a semi-closed tube (Fig. 10 & 11B). This, in turn, had a considerable effect on

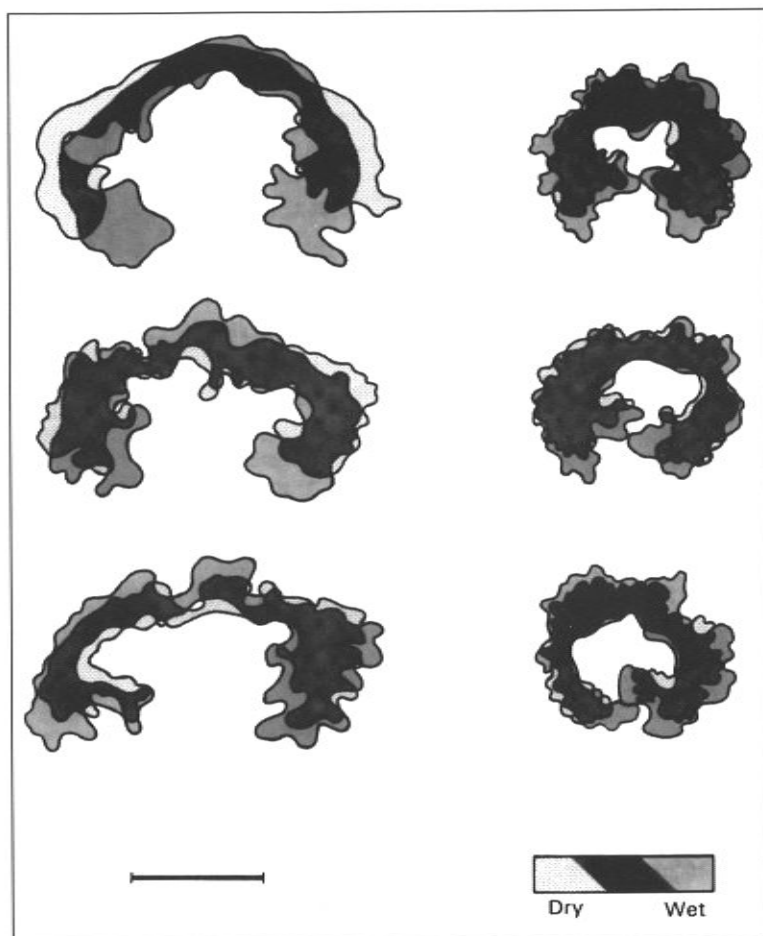


Figure 10. Changes in the cross-sectional dimensions of *Pseudevernia furfuracea* lobes during the first moments of resaturation. Bar 1 mm.

water conduction. The water potential of any concavity depends on its dimensions, i.e., the maximum tension of a groove is inversely proportional to its radius. In a half cylindrical groove the maximum capillary tension can be at most half of that in a closed capillary with similar dimensions. In wide *Pseudevernia* lobes the changes in the dimensions of ventral cavities were less pronounced, and they rarely achieved tubular shapes (Fig. 10). However, individual furrows in ventral cortices could sometimes behave in a similar manner as the entire concavities of smaller lobes. Especially deep furrows under the reflexed margins of wide thallus lobes often exhibited pronounced changes in dimensions.

All the above phenomena took place within a

few seconds after water was first applied onto a dry lobe surface. As the outer surface of a swelling *P. furfuracea* lobe became more convex, its water potential increased and excess surface water tended to flow into the ventral groove. As the entrance of the groove simultaneously narrowed the capillary tension of the concavity was increased, and a "pulse" of water advanced along the groove. This phenomenon helped to conduct water from the basal sections of erect thallus lobes towards the tips of apical branches (Fig. 11B).

Soon the *Pseudevernia* lobe became fully hydrated. Usually within 30 seconds the strong curvatures of the thallus lobe began to ease and the ventral concavity was opened (Fig. 12C). This opening was presumably caused by the gradual

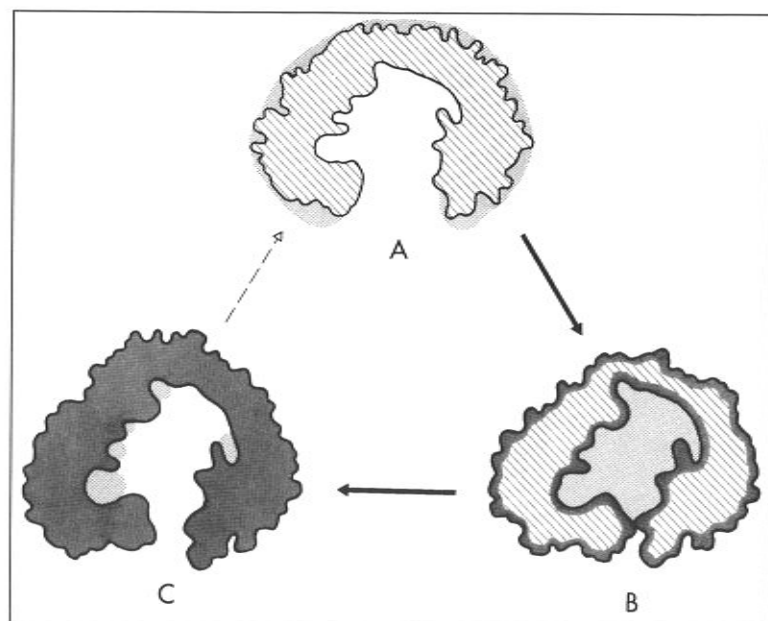


Figure 11. Three phases (A–C) in the hydration cycle of *Pseudevernia furfuracea* as seen in the cross-section of a thallus lobe. The shading indicates the approximate distribution of water on and within the thallus. Changes in the dimensions of the lobe were sketched during the rehydration of a dry thallus sample from the upper south-facing slope of Kivvieru.

swelling of internal tissues which forced the lobe margins to curve outward. Also the swelling of the ventral cortex was involved, but it alone was probably not sufficient to open the groove, as it should have opened the concavity much faster. Thus, due to its relatively large volume, the upper cortex seemed to resist the tension caused by the wrinkled lower cortex, but it yielded when the swelling medulla approached its maximum volume.

The ventral grooves of fully hydrated *P. furfuracea* lobes were often slightly more narrow than those of air-dry lobes (Fig. 11C). However, considerable variation existed between individual lobes, and in some cases the entrances of concavities were more open when the lobes were saturated. This interlobal variation was probably related to differences in lobe structure, especially in the amounts of medullary tissue. Towards the end of the wetting phase the ventral cavities of *Pseudevernia* lobes were invariably more open than during the first moments of resaturation. This allowed the grooves to store maximal amounts of water, but also made them more vulnerable to changes in the water potentials of their surroundings.

Discussion

Habitat shifts as an example of illumination control

The importance of topographical factors in controlling epiphyte distributions is well known from wide geographical scales. The literature includes many accounts of changes in cryptogamic vegetation along altitudinal gradients and numerous studies have dealt with the altitudinal zonation of bryophytes and lichens (e.g. Koponen 1988; Frahm & Gradstein 1991; Wolf 1993). The altitudinal zonation of cryptogamic epiphytes correlates with climatic parameters, such as temperature and precipitation. Still, relatively few attempts have been made to elucidate the relative importance of specific climatic factors in controlling the altitudinal distribution of cryptogamic epiphytes.

Many cryptogamic epiphytes exhibit shifts in substrate preferences in accordance with macroclimatic conditions and also some habitat shifts along microclimatic gradients have been described (e.g. Barkman 1958). The height and aspect preferences of epiphytes may vary between areas and some

lichens and bryophytes are known to shift from epiphytic habitats to rocks with increasing altitude or latitude, or to soil in the maritime limits of their distribution. In eastern Fennoscandia the shift of epiphytic bryophytes from trees to rocks has been related to a general increase in continentality (Pippo 1982). Saturation deficit resulting from decreased atmospheric humidity has been used to explain qualitatively similar phenomena in North America (Slack 1976).

Topographically induced variation in moisture availability is clearly reflected in the vascular plant vegetation of esker areas. For example, favourable moisture conditions explain the occurrences of oceanic vegetation types in many deep kettle holes (e.g. Rajakorpi 1984, 1987; Rikkinen 1989; Tikkanen & Heikkilä 1991). Evapotranspiration from the lush vegetation, in turn, acts to maintain a relatively high atmospheric humidity at such sites. This is a crucial factor in explaining the overall abundance of cryptogamic epiphytes in Kivvieru. Some specific patterns in epiphyte distributions, like the common occurrence of terrestrial bryophytes and lichens (e.g. *Cetraria islandica*, *Pleurozium schreberi*) as epiphytes in the low-lying parts of Kivvieru, were also closely related to high humidity.

However, the habitat shifts of *P. furfuracea* and other photophilic lichens seemed to more reflect differences in illumination conditions between sites. These habitat shifts did not reflect mere differences in substrate availability. There were plenty of pines in the low-lying parts of the kettle hole, but their lower trunks were always devoid of photophilic lichens. Instead, the observed phenomenon corresponded to inherent differences in the irradiation climates of vertical and moderately inclined substrate types, respectively.

The orientation of a surface has a major effect on the amount of solar radiation it receives, but also inclination affects the amount of incident radiation. During sunny days and in open habitats, when a major proportion of the global radiation flux arrives in the form of direct radiation, vertical south-facing surfaces will generally receive more radiation than a horizontal plane. Conversely, an increase in the inclination of a north-facing surface

will invariably decrease the amount of radiation received. During cloudy days and in shaded habitats diffuse radiation is the most important radiation component and horizontal or moderately inclined surfaces tend to receive more global radiation than vertical surfaces. With no direct radiation even a south-facing vertical surface will receive at most half of the global radiation obtained by a free horizontal surface (Table 2).

The distribution of solar radiation as described above is sufficient to explain the shift of photophilic lichens from pine trunks to spruce branches along the descending slopes of Kivvieru. On the upper slope, where direct and reflected radiation are major radiation components, vertical tree trunks receive large amounts of solar radiation and represent a highly suitable habitat for photophilic epiphytes. Conversely, in the low-lying parts of the depression, these being effectively overshadowed by the densely forested upper slopes, indirect radiation is the most important radiation component. As direct radiation is blocked out, the total amount of light is limited. On vertical tree trunks the photophytes themselves block out a major proportion of the diffuse radiation flux and even south-facing trunk surfaces become light-limited habitats for photophilic lichens.

In the low-lying parts of Kivvieru spruce branches represent a relatively favourable habitat type, as even in densely forested situations they receive diffuse radiation from a relatively large proportion of the sky dome. The upper surfaces of moderately inclined (40–50°), south-facing spruce branches may provide a particularly favourable habitat, as they receive relatively large amounts of global radiation during autumn and spring, when moisture conditions are most favourable for lichen growth. This pattern may, of course, be distorted by local variations in canopy structure. The penetration of solar radiation into forest canopies is a complex phenomenon controlled by the spectral properties and distributions of various canopy elements, together with the angle of solar elevation. For example, in the low-lying parts of Kivvieru the relative amounts of spruces and deciduous trees were clearly important in determining radiation conditions in epiphytic habitats.

Table 2. Variation in solar radiation incident upon variously oriented and inclined surfaces in Luonetjärvi, central Finland. The distribution of diffuse radiation is assumed isotropic and reflected radiation is not included. Derived from Tammelin and Hyvönen (1989).

A. Seasonal variation in the amounts (kWh/m²) of direct radiation (S), diffuse radiation (D) and global radiation (G) on variously oriented and inclined surfaces in Luonetjärvi

Inclination	Orientation	June			December			Monthly average		
		S	D	G	S	D	G	S	D	G
0°	South	106.85	63.43	170.28	0.65	2.10	2.74	42.15	31.88	74.03
45°	South	107.61	54.14	161.76	0.45	1.79	2.21	57.30	27.22	84.51
90°	South	56.08	31.72	87.79	0.53	1.05	1.58	41.52	15.94	57.46
0°	North	106.85	63.43	170.28	0.65	2.10	2.74	42.14	31.88	74.03
45°	North	47.84	54.14	101.99	0.00	1.79	1.79	10.53	27.22	37.75
90°	North	17.45	31.72	49.17	0.00	1.05	1.05	3.58	15.94	19.53

B. Estimated relative intensities of solar radiation for different orientations in Luonetjärvi (relative intensity is radiation on a vertical surface / radiation on a horizontal plane, assuming an elevation of 5° for the horizon)

Radiation intensity	NW	N	NE	E	SE	S	SW	W
Direct radiation	0.32	0.04	0.32	0.64	0.81	0.98	0.81	0.64
Global radiation	0.42	0.27	0.42	0.58	0.67	0.77	0.67	0.58

Relations between thallus structure and evaporation

The morphological variation of *P. furfuracea* in Kivvieru was interpreted as an expression of phenotypic plasticity. Many epiphytic lichens are known to exist as morphologically distinct sun and shade forms, which may have different relationships of net assimilation rate to temperature, irradiance and thallus water content. In most cases such forms have been seen as expressions of phenotypic plasticity rather than genetically differentiated variants (Kershaw 1985).

While the habitat shift of *P. furfuracea* was directly related to the availability of photosynthetically active radiation, the morphological variation seemed to reflect changes in irradiation in a more complex manner. Several types of evidence suggest that the morphological variation was more closely connected to differences in evaporation rates than to insufficient levels of photosynthetically active radiation *per se*. Photosynthesis in

most lichens becomes saturated at relatively low flux densities. Furthermore, in the range of photosynthetically active radiation, reductions in the amount of direct radiation along the descending slope of Kivvieru must have been partially offset by the enhanced blue component of diffuse radiation (Fitter & Hay 1987; Stoutjesdijk & Barkman 1992).

The humid and cool microclimate of Kivvieru was favourable for many poikilohydric organisms as it generally promoted high levels of thallus hydration. However, in robust macrolichens, like *P. furfuracea*, this situation was complicated by the intricate relationships that exist between levels of thallus hydration, photosynthesis and respiration. Net assimilation rates in lichens generally decline at supraoptimal water contents and wet event duration has major influences on rates of carbon dioxide exchange. In extreme cases a combination of excessive moisture and limited light may lead to situations where the amount of carbon stored by lichen photobionts is insufficient to balance the

respiration of the fungal biont. A prolonged supra-optimal water content may also hinder CO₂ exchange within lichen thalli.

The structural features of lichens, on the other hand, affect their desiccation rates. Water loss is generally promoted by fine, filamentous branching, whereas robust thallus structures tend to slow down evaporation. Thus, also the two morphotypes of *P. furfuracea* were likely to experience evaporation quite differently. Many structural attributes in the robust morphotype promoted boundary layer resistance. Large amounts of water could also be collected and held within external capillary systems. Thus, the lichens could experience periods of favourable thallus hydration even under direct solar radiation, this being rich in desiccating infra-red wavelengths. However, at the bottom of Kivvieu such thalli would have stayed hydrated for excessive lengths of time. As a result, they would have faced high respiration losses, even at times when thalli on the upper slopes were inactive due to low hydration. This may have become detrimental, even though the relatively low temperatures in the kettle hole would have acted to lower respiration rates and thus partly compensate for the negative effects of excessive moisture and limited light.

The cool and humid conditions in Kivvieu could be expected to favour morphological traits that promote water loss. In the case of *P. furfuracea*, with its specialized systems for external water conduction and storage, only a highly reduced thallus structure insured regular periods of dehydration. Indeed, consistent increases in the surface-to-volume ratios of *Pseudevernia* thalli along the descending slope acted to promote their susceptibility to evaporation. In finely branched thalli the internal CO₂ pathways were also kept as short as possible. This may have given finely branched lichens an ability to maintain positive net assimilation rates at higher water contents than was possible for their more robust counterparts on the upper slopes.

Thus, as a whole, the fragile thallus morphology of *P. furfuracea* in the low-lying parts of Kivvieu seemed to reflect high carbon losses due to excessive periods of thallus hydration. High thal-

lus hydration was being promoted by low temperatures, high atmospheric humidity, calm wind conditions and the lack of desiccating direct radiation. Without unusually high carbon losses due to respiration, the diffuse sky radiation, as such, would probably have been sufficient for the development of more robust *Pseudevernia* thalli in the kettle hole.

The mechanisms for external water transport in *P. furfuracea* were complex and of obvious importance in the water relations of the lichen. The hygroscopically controlled capillary systems seemed to represent one central attribute, which enabled the lichen to achieve a large size in optimal habitats. In fact, few epiphytic lichens in the study area were able to achieve comparable thallus volumes. However, the anatomically controlled "capillary pump" could only benefit the lichen in relatively dry environments. In the low-lying parts of Kivvieu this morphological adaptation would have acted against the lichen by helping to keep it too moist. It was not surprising that all morphological changes in *P. furfuracea* along the descending slope tended to reduce its capillary pump capabilities.

Specialized methods for water conduction and storage were not needed in the humid conditions of Kivvieu. Instead, hydration by condensation may have been an important method of water uptake. The finely branched *Pseudevernia* thalli were characterized by minimal heat storage terms and high surface-to-volume ratios and usually projected well outside the laminar boundary layers of their substrates. At night the net radiant emission of such thalli could often lead to energy deficits and overcooling. Under such conditions fine thallus appendages undoubtedly served as condensation points for water vapour in the surrounding air.

Role of cortical perforations

Although the cortex of *P. furfuracea* is only 10–20 µm thick, its thick-walled and heavily agglutinated hyphae form a coherent and more or less continuous outer cover of the thalli. Several studies have indicated that cortical openings may play important roles in gas exchange. Hygroscopical phe-

nomena may, in turn, be involved in regulating such processes.

The ventral cortex of *P. furfuracea* has been described to be perforated by two types of pores, defined as aeration pores or pseudocyphellae and cyphellae-like pores by Legaz et al. (1985). The rims of pseudocyphellae are evidently formed by tips of fungal hyphae perpendicular to the thallus surface, while cyphellae-like pores are surrounded by protruding rims of hyphae running parallel to the thallus surface. Legaz and her co-workers detected both types of pores from Spanish *Pseudevernia* specimens. They also provided SEM photographs of the surface views of both types of pores (Legaz et al. 1985, Figs. 4–6).

I was unable to find either type of pores from the ventral cortices of *P. furfuracea* thalli from Kivvieru. Pore-like structures were always present and frequently abundant on the lower surfaces of *Pseudevernia* lobes, but they were invariably filled with the tips of fungal hyphae strongly conglutinated within an extracellular matrix. The hyphae within the pore-like structures may have originated in the medulla as they frequently lacked the crust of cortical compounds typical of normal cortex hyphae. Thus, the pores appeared as dark, naked patches on an otherwise crystallized cortex, with the cell lumina of perpendicular hyphae being clearly visible from above (cf. Rikkinen 1995, Fig. 4). These closed pores could well have had the potential of developing into open pseudocyphellae through the disintegration of their extracellular matrices. According to Beltman (1978) the cortical disintegration which eventually leads to the formation of pseudocyphellae in parmelioid lichens begins near the outer surface of the cortex and gradually progresses inward. Conversely, Hale (1981) suggested that this process would begin just above the photobiont layer and proceed outward. In any case, the actual mechanism which triggers the formation of pseudocyphellae in lichens is not known.

While no open pseudocyphellae or cyphellae-like pores were found in *Pseudevernia furfuracea* thalli from Kivvieru, other cortical openings were frequently observed. Fine cracks were common on thallus surfaces. They had presumably been

caused by the physical bending of dry thallus lobes and seemed to provide a major route into the medulla. Numerous scars left by detached isidia were even more important in this respect (cf. Fig. 7). For the purpose of gas exchange these two types of openings offered a more feasible route into the photobiont layer than the closed pores of the ventral cortex. During rehydration some types of cortical openings could also represent routes for water into the medulla. However, recent studies on taxonomically diverse macrolichens have indicated that water does not generally fill the intercellular spaces of hydrated lichen thalli, but is mainly confined to fungal hyphae and to the apoplast. Thus, the medullary layers of heteromerous lichens remain largely gas-filled even in an oversaturated state and do not usually function as water reservoirs (Honegger & Peter 1994).

While no mass flow of water could have occurred through the closed ventral pores of *P. furfuracea*, these structures may still have represented preferential sites of water absorption. As water is mainly conducted within the cell walls of fungal hyphae and as the closed pores seemed to contain tips of medullary hyphae, the pores may well have acted to conduct water into the medulla. The conspicuous lack of crystallized substances on many pore surfaces may, in turn, have been related to water permeability. During rehydration hyphae within the ventral pores would generally start to absorb water simultaneously with the overall contraction of ventral concavities. During the final stages of rehydration the gradual opening of ventral grooves could, in turn, promote water absorption by decreasing the water potentials of the cavities (cf. Figs. 11B & C).

Despite many efforts to directly observe water absorption through ventral pores their exact role in thallus rehydration remained unclear. However, there is little reason to believe that the closed pores could have provided a preferential route for gas exchange. For example, the occurrence of aeration pores in the ventral cortex would have suggested that while considerable quantities of water could be temporarily stored within the ventral concavities of *Pseudevernia* lobes, these structures would not be suitable for prolonged water storage, as wa-

ter in the grooves would have seriously hindered CO₂ diffusion.

Vicente and Velasco (1986) suggested that *P. furfuracea* would possess a system of volume preservation, which helps the lichen to control its volume loss during desiccation. The authors based this hypothesis on the assumption that if both surface area and fresh weight of a lichen thallus decreased linearly in parallel to water loss, also the area of cortical openings would similarly decrease. The shrinking of pseudocyphellae and cyphellae-like pores would lead to an increase in cortical resistance to water vapour efflux which, in turn, would help the lichen to preserve its medullary volume.

The drying process of saturated *P. furfuracea* thalli can be divided into several phases, rather similar to those described by Jahns (1984) for *Parmelia saxatilis*. This becomes evident if one compares the drying curve of *P. furfuracea* to that of *P. saxatilis* (cf. Vicente & Velasco 1986, Fig. 4C and Jahns 1984, Fig. 4, respectively). First the drying lichen rapidly loses its surface water. When all external water has been lost the lichen begins to lose water from its tissues. Intrathalline water conduction is likely to keep the cortex turgid as long as there are significant amounts of water within the medulla. During the final phase of desiccation the rate of evaporation is again accelerated, presumably because the shrinking of fungal hyphae acts to increase the evaporating surface. For example, the shrinking of cortical hyphae may widen cortical openings. Jahns (1984) found that in *Parmelia saxatilis* micropores opening between cortical hyphae were responsible for a rapid decline in thallus water content during the final phase of desiccation. In *P. furfuracea* larger cortical openings may operate in a similar manner. This phenomenon may help to minimize the time during which the lichen is in a "wilted" state where respiration exceeds photosynthesis.

Major differences were seen in the isidium layers of *P. furfuracea*, with mature thalli from the upper south-facing slope of Kivvieu having much more isidia than comparable thalli from the lower north-facing slope. As previously described, the capillary spaces within dense isidium layers have

important functions in water conduction and storage. However, the convex tops of isidia tend to remain dry even when water is being held within the capillary spaces between isidia. Inside isidia the photobiont layer penetrates the cortex and at the tips of the appendages only a few cortical hyphae may separate algal cells from the atmosphere. Furthermore, the breaking off of isidia frequently brings medullary tissue into direct contact with the atmosphere. Thus, the isidia of *P. furfuracea* may play a significant role in gas exchange, especially during times when the external water storage of the lichen is full.

In mature *Pseudevernia* lobes a large percentage of all photobiont cells are located in the isidium layer. Thus, also a considerable proportion of the metabolic activity is likely to take place there, where favourable illumination and moisture conditions are combined with efficient gas exchange. This agrees well with the views of Jahns (1984, 1988) who has emphasized the importance of isidia in increasing the surface areas of lichens along with their more commonly appreciated role in dispersal (see also Ott & Sancho 1993). The mechanism which initiates the formation of isidia in lichens is not known. It has been suggested that an initiating increase in photobiont productivity could sometimes be triggered by a local increase in irradiance within a light-limited photobiont layer (Rikkinen 1995).

One curious observation in Kivvieu was the existence of an epicortex in *P. furfuracea*. The Parmeliaceae has been divided into three broad groups according to epicortical characteristics, i.e., taxa lacking an epicortex, this group including only the genus *Pseudevernia*, those with a pored epicortex and those with a nonpored epicortex (Elix 1993). However, all three surface types were observed in *Pseudevernia* lobes from Kivvieu (Figs. 8 & 9). In fact, a developmental series seemed to exist from young thallus sections with smooth, continuous epicortices via pored epicortices to mature thallus sections without a continuous epicortex.

The epicortex has been interpreted as an extra layer of protection against evaporation. However, as the epicortex could also resist gas exchange it

must be punctured by perforations of some sort and a vast majority of epicorticate macrolichens either have a pored epicortex or they are pseudocyphellate, i.e., both the epicortex and the cortex are punctured by pseudocyphellae. The epicortex also forms an extensive network of light scattering air cavities just above the cortex hyphae. Thus, even a pored epicortex may have a significant impact on light permeability and help to protect drying lichens against the detrimental effects of UV-B radiation (Rikkinen 1995).

Relations to forest dynamics

On the scale of individual *Pseudevernia furfuracea* thalli the ability to achieve a fragile thallus morphology was clearly advantageous, as it enabled lichens to exist in the low-lying parts of Kivvieru. However, on the population level the situation is more complex. One could argue that for real evidence of adaptation it is not sufficient to show that colonization of lower spruce branches had occurred in the low-lying parts of the kettle hole, but it would also be necessary to demonstrate that this population was capable of maintaining itself or otherwise promoting the existence of the lichen in the area.

One may question the ability of fragile *P. furfuracea* thalli in maintaining their population size over long periods of time. This is because their reproductive capabilities are severely reduced. In Kivvieru the finely branched morphotype was never found fertile and it seemed to produce only limited amounts of isidia. Were these isidia sufficient for the effective colonization of thin spruce branches or was the population of finely branched *Pseudevernia* thalli dependent on diaspore rain from the upper slopes and/or from the upper canopy, especially the lower crown branches of large pines, where the robust and more abundantly isidious morphotype prevailed? A somewhat similar system of interactions between moisture dependent thallus morphology and dispersal ecology has been described from wood and stone inhabiting populations of *Parmelia saxatilis* (Jahns & Fritzel 1982; Jahns 1984).

The possible relation between neighbouring, phenotypically different *Pseudevernia* populations

growing at different heights on different phorophyte species opens interesting views into the population dynamics of epiphytic lichens during forest stand development. Changes in irradiation and moisture conditions along the descending slopes of Kivvieru resemble changes in physical conditions generally experienced within conifer forests during stand development. Thus, the bimodal distribution and phenotypic variation of *P. furfuracea* may reflect some general patterns in its relations to stand structure and age (cf. McCune 1993). In fact, one could suspect that most fragile *Pseudevernia* thalli in the lower strata of closed forests may represent reproductively insignificant by-products of dispersal activity within higher canopies.

According to this hypothesis, local populations of *P. furfuracea* in shaded forest understories would mainly reflect the density dependent nature of lichen dispersal, i.e., when diaspore input from the canopy is large enough, isolated lichens tend to be established even in the most suboptimal of habitats. If conditions within forests remain stable, such peripheral populations will have little significance for the further success of the species. However, if conditions within the understory were to change, e.g. through the opening of a canopy gap, the peripheral thalli would be well established and ready to exploit the new, more favourable conditions. Thus, fragile *Pseudevernia* thalli within the lower strata of closed forests may in many respects resemble suppressed conifer saplings in the forest understory.

The above reasoning underlines problems in epiphyte studies which concentrate on single habitat classes, like the basal trunks of one phorophyte species. Colonization between habitat classes may often have major effects on the structures of epiphytic assemblages. Indeed, as many boreal epiphytes have wide ecological amplitudes such local scale effects may often be central in determining the species compositions of epiphytic communities. Thus, any attempt to understand the dynamics of a specific community type would always require a careful evaluation of interhabitat dispersal and colonization effects. This statement may be a truism, but so far it has often been ignored in studies of epiphytic vegetation.

Conclusions

The purpose of this study is to analyse the role of environmental variation in explaining local patterns in the distribution and morphology of *Pseudevernia furfuracea*. This photophilic macrolichen responded to its environment both through habitat shifts and ecomorphological adaptations. In Kivviero the microclimatic effects of both slope aspect and relief were reflected in the structure of epiphytic vegetation. For the present purpose the effects of both variables could justly be combined into one complex gradient across the kettle hole.

In Kivviero many patterns in epiphyte distributions were closely related to atmospheric humidity or substrate availability. However, the observed shift of *P. furfuracea* and other photophilic lichens from vertical pine trunks to moderately inclined spruce branches was mainly connected to the uneven distribution of solar irradiation. In the low-lying part of the depression, this being effectively overshadowed by the upper slopes, indirect radiation was the most important radiation component. As direct radiation was largely blocked out, the amount of photosynthetically active light was limited. On vertical tree trunks the phorophytes themselves blocked out a large proportion of diffuse sky radiation and even south-facing pine trunks became to represent light-limited habitats for photophilic lichens. In the low-lying parts of Kivviero moderately inclined spruce branches represented a more favourable habitat type, as even in densely forested situations they tended to receive diffuse radiation from a relatively large proportion of the sky dome.

The morphotypes of *P. furfuracea* were seen as expressions of phenotypic plasticity with morphological variation being achieved and maintained by direct responses to the physical environment. Often these responses did not reflect the effects of any single environmental factor, but rather the combination of several influences. For example, the occurrence of fragile *Pseudevernia* thalli in the low-lying parts of Kivviero was not related to insufficient levels of photosynthetically active radiation *per se*, but rather to differences in evaporation re-

gimes and inherent difficulties in achieving positive net photosynthesis in permanently humid habitats.

Due to their different structures the two morphotypes of *Pseudevernia* experienced the effects of solar radiation, air temperature and wind on evaporation differently. The robust morphotype was well suited for dry upper slope positions. However, at the bottom of Kivviero such thalli would have faced high respiration losses, even at times when thalli on the upper slopes were inactive due to low hydration. In the low-lying parts of the kettle hole only a highly reduced thallus structure insured regular periods of dehydration. The fragile thallus structure also kept internal CO₂ pathways as short as possible.

External capillary channels played an important role in the conduction and storage of water in robust *P. furfuracea* thalli. Water was being conducted along three routes on thallus surfaces, i.e., in the ventral cavities of thallus lobes, in capillary spaces between isidia and in minute crevices between protruding tips of perpendicular cortex hyphae. Together these formed a diverse network which rapidly dispersed water along the thallus surface and enabled the translocation of water from large capillary spaces between the lichen and its substrate towards the tips of erect thallus lobes. This process was promoted by hygroscopical thallus movements.

Closed pseudocypheae-like pores in the ventral cortex of *P. furfuracea* were suspected to represent preferential sites for water absorption. As water is mainly conducted within the cell walls of fungal hyphae and the ventral pores seemed to contain tips of medullary hyphae, the pores may have provided a preferential route for water into the medulla or directly into the photobiont layer. The lack of crystallized substances on pore surfaces may have been related to water permeability. During rehydration the absorption of water through ventral pores would have occurred simultaneously with the overall contraction of ventral concavities. Together these phenomena may have acted to "pump" water into the medulla. During the final stages of rehydration the gradual opening of ventral concavities could, in turn, promote water absorption by decreasing the water potentials of ventral concavi-

ties. The anatomically controlled water storage of *P. furfuracea* could only be beneficial in relatively dry environments. In the humid low-lying parts of the kettle hole it would have acted against the lichen by keeping it too moist.

By linking the morphological variation of *P. furfuracea* to its multidimensional distribution in Kivvieru and then relating these patterns to forest dynamics, one achieved some novel information of processes, which may influence the structure of epiphytic communities in boreal forests. The results emphasized that colonization between habitat classes may often have major impacts on the structure of epiphytic vegetation.

Epiphytic lichens have special properties and requirements partly because of their early histories in restricted environments. Each species has a history of restriction to a limited habitat and so at least some of its structural and functional attributes are likely to reflect adaptations to the environmental conditions of this early habitat. There is reason to believe that the morphological attributes of *P. furfuracea* reflect a history of previous confinement to a southern distribution area and of adaptive responses to a warm, relatively dry climate. After the Pleistocene glaciation the lichen has migrated to central Finland, but it has remained largely confined to relatively open, warm and dry microhabitats. This, in turn, has acted to reinforce its early adaptations.

The capability to develop a reduced thallus morphology, without specialized capillary pump adaptations, enables *P. furfuracea* to extend its range into the humid low-lying parts of Kivvieru. This ability to "hide" structural adaptations may also have helped the species to colonize cool and humid, suboptimal parts of its present range. For example, Olga Hilmo (1990) mentioned that robust *P. furfuracea* thalli were uncommon in an moist spruce forest in central Norway. In this oceanic environment the species was evidently only represented by fragile, practically non-isidiate thalli.

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