Symposia Biologica Hungarica

35

PROCEEDINGS OF THE IAB CONFERENCE OF BRYOECOLOGY

(Part B)

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35

Akadémiai Kiadó, Budapest

PROCEEDINGS OF THE IAB CONFERENCE OF BRYOECOLOGY

Edited by

T. PÓCS, T. SIMON, Z. TUBA, J. PODANI

(Symposia Biologica Hungarica 35)

The ecology of bryophytes has been an area of increasingly intensive studies in the past decade which led to a considerable accumulation of knowledge on the structural and functional adaptation of these plants to the environment. It was many years ago that the International Association of Bryologists decided to organize a conference that is entirely devoted to bryoecology. This volume contains the proceedings of the first world congress of bryoecology, held in Budapest and Vácrátót, on August 5–10, 1985.

A total of 78 papers reporting on original research work comprises the contents. The contributors are noted experts of their rapidly developing specific research areas. The subject matter of papers covers a wide variety of topics, ranging from the ecological aspects of bryophyte biochemistry to the application of mosses as bioindicators. The book falls into six major sections, each corresponding to a main session of the symposium. These are: 1. Physiological ecology, 2. Reproduction and dispersal ecology, 3. Community ecology, 4. Population ecology, 5. Bryophytes in ecosystems, and 6. Bryophytes as bioindicators.

Presenting a review on the "state of art", the book will be an indispensable source of information for all bryologists. It also deserves the attention of those dealing with general ecology, plant genetics and biochemistry, biogeography and environmental science.

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Convener: R. Wyatt (Athens, Georgia, USA)

Symposia Biologica Hungarica 35 (1987)

PEROXIDASE VARIATION IN MARCHANTIA POLYMORPHA: A PRELIMINARY REPORT

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Peroxidase variation was detected in four populations of Marchantia polymorpha subjected to horizontal starch gel electrophoresis. Differences were found both within and between samples from Europe and Japan.

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Marchantia polymorpha L. has attracted the attention of investigators since the time of Linnaeus, who recognized informally a number of "Cryptophorms". These have been studied subsequently by Nees and others interested in morphology, citology and genetics (Bischler 1984, 1986). In recent years this ubiquitous plant also has been used as a model organism for investigating gamma radiation (Sarosiek & Wożakowska-Natkaniec 1967, 1968) and chemical pollution (Briggs 1972, Sarosiek et al. 1972). Its flavonoids (Markham & Porter 1974, Campbell et al. 1979) and terpenoids (Asakawa et al. 1979, 1984) have been investigated, and M. polymorpha is the only liverwort from which chloroplast DNA has been isolated (Ohyama et al. 1982) for the purpose of physical mapping (Ohyama et al. 1983).

Enzymatic studies on M. polymorpha began almost 20 years ago (Maravolo et al. 1967) but have not aroused wide interest until now. The purpose of this study is to demonstrate that electrophoretically detectable genetic variation occurs in M. polymorpha and to suggest studies that might make use of such genetic markers.

MATERIALS AND METHODS

Horizontal starch gel electrophoresis was done on four populations of M. polymorpha from widely separated regions: Japan, France, Czechoslovakia, and Poland. M. polymorpha is dioecious, female (a) and male (b) thalli were analyzed separately.

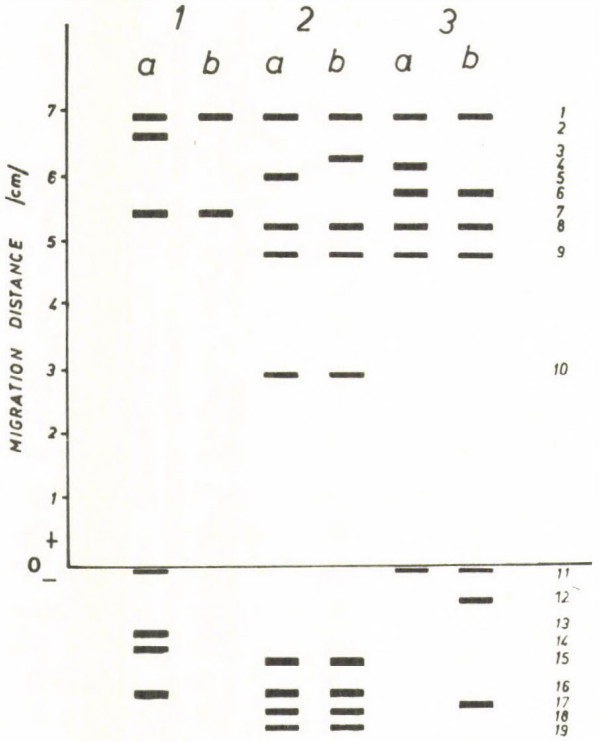

Fig. 1. Band patterns of Marchantia polymorpha peroxidases. Code: 1=sample from Japan, 2= sample from Czechoslovakia, and 3 = sample from France; a = female thallus, b = male thallus.

RESULTS AND DISCUSSION

The sample from France (No. 3) showed an isozyme pattern identical to that of the Polish sample (Fig. 1). Therefore, the latter was omitted from the figure. Differences in phenotypes of the two sexes were not sufficiently reproducible to reflect real differences between the sexes and, probably, result from extensive polymorphism in the species. This should be corroborated by studies of plant material from additional regions. The sample from Czechoslovakia (No. 2) is distinctive, especially in the cathodal part of the zymogram.

From this preliminary study, the peroxidases of M. polymorpha seem very promising and worthy of further investigations.

ACKNOWLEDGEMENTS

We are grateful to Dr. S. W. Greene and R. Wyatt for commenting on the manuscript. Thanks are also due to Dr. C. Suire for collecting and mailing living samples of Marchantia polymorpha from Japan.

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GROWTH FORM VARIATION WITHIN AND BETWEEN POPULATIONS OF CLIMACIUM AMERICANUM BRID

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In the southeastern United States Climacium americanum is known to exhibit a tremendous range of variation in growth form. This study also discovered significant differences between population in eleven microscopic characters. Leaf shape and leaf cell shape were highly correlated in field-collected material, but were only weakly correlated in plants grown in the greenhouse. Leaf cell shapes were correlated with growth forms. Desiccation tolerance differed between populations and was highly indicuble. Morphological and physiological evidence therefore suggests that extensive differentiation exists among populations of C. americanum.

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The Climaciaceae are a small family consisting of a single genus, Climacium, and about three species (fide Index Muscorum). Climacium is characterized by a dendroid habit with a stout subterranean rhizome (the main stem) and erect branches reaching six or more centimeters high. Crum & Anderson (1981) and Horton & Vitt (1976) recognized two species of Climacium in North America. Climacium dendroides (Hedw.) Web. & Mohr has a circumpolar distribution but is replaced in eastern North America by the endemic C. americanum Brid.

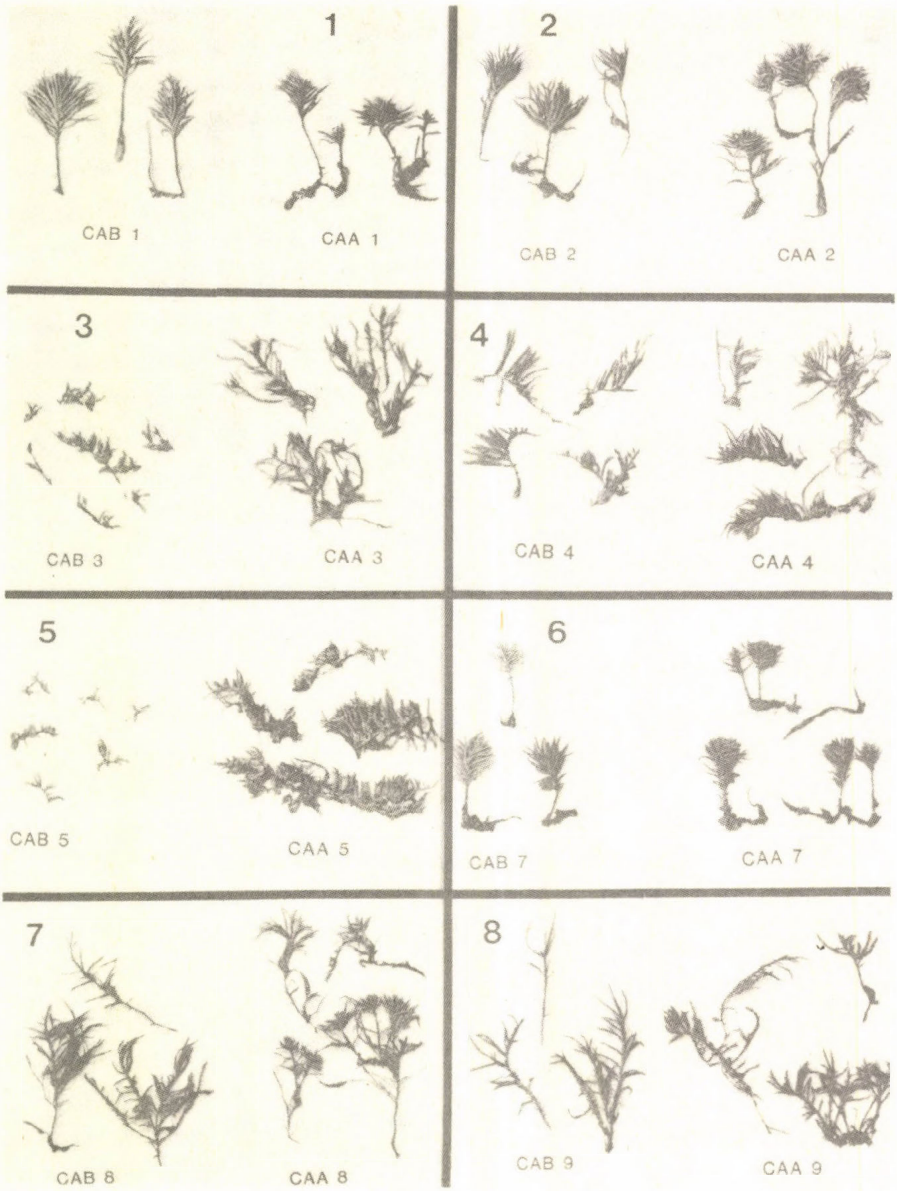
Climacium americanum is common in forested habitats of the southeastern United States, occurring along streams and in river floodplains. Populations of C. americanum are extremely

variable in growth form with most of the variation occurring between, rather than within, clumps. Some populations consist of strongly dendroid plants (Fig. 1), whereas others consist only of more irregularly branched stems (Fig. 15). A wide range of intermediate growth forms occur (Figs 1-15).

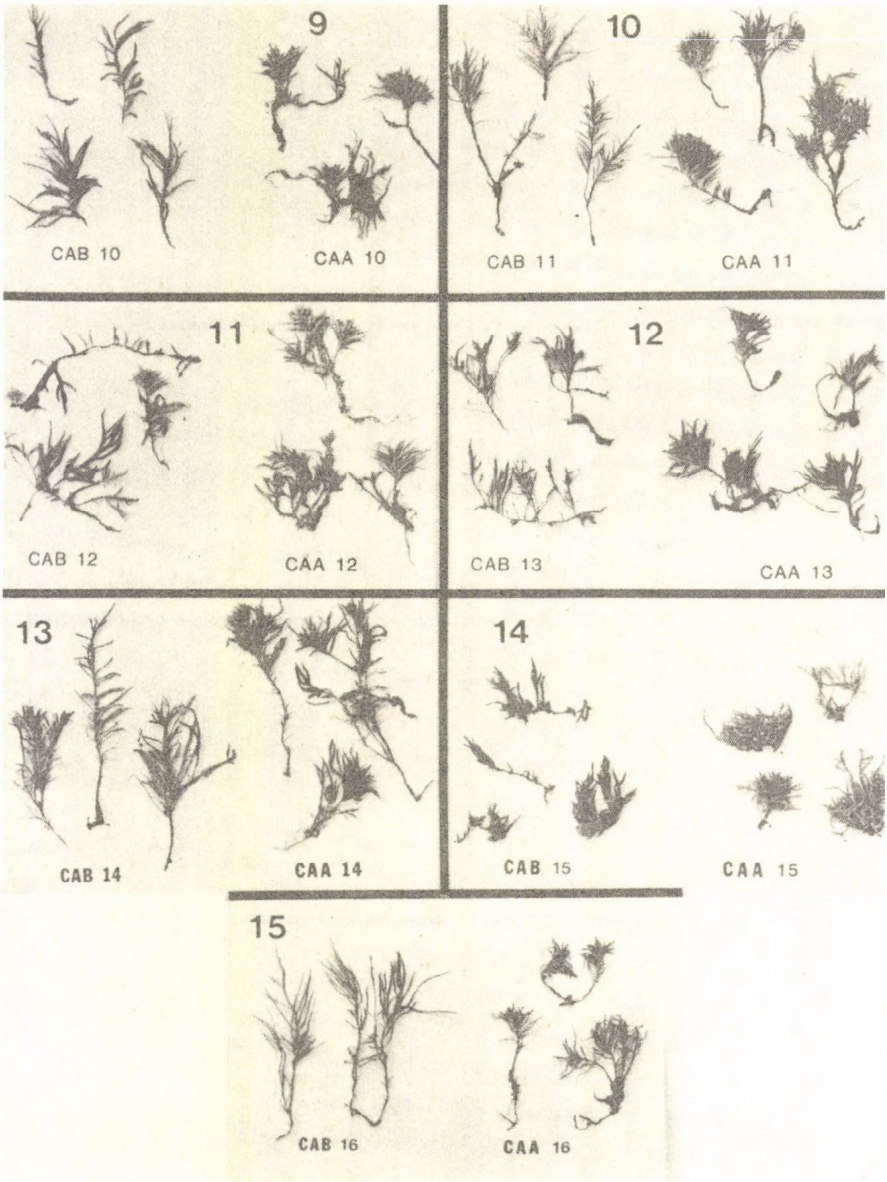
Renauld & Cardot (1890) described C. americanum var. kindbergii, which differed in its shorter, more distant leaves and shorter cells only 1-2 times as long as broad. Grout (1901) made the combination C. kindbergii (Ren. & Card.) Grout, remarking that the species is "distinguished at a glance by its color and habit of growth;..." Crum & Anderson (1981) and Horton & Vitt (1976) interpreted the var. kindbergii as a modification of the var. americanum, induced by submersion in a perennially wet habitat.

MATERIALS AND METHODS

Sixteen clumps of C. americanum were collected in North Carolina, U.S.A. Populations 1-5, 11-14 and 16 originated in Durham Co.; 7-10 were collected in Orange Co.; 15 was collected in Brunswick Co. Vouchers of all populations are deposited in DUKE. One clump subsequently died so analyses are based on fifteen clumps. When single gametophores with a portion of rhizome were separated for growth in individual pots, few survived. Consequently, the original clumps were grown intact with no replication. This presents some problems for statistical analyses of variation, since the within-clump component of morphological variation is probably underestimated relative to between-clump variation. Within-clump variation was estimated by taking measurements on three leaves from each of three gametophores per clump. In subsequent statistical analyses, each of the three gametophores measured per clump was considered a replicate. Measurements were made in October, 1984, utilizing field-grown gametophores, and in May, 1985, utilizing gametophores that had grown in the greenhouse for at least six months. Measurements on field-grown and greenhouse-grown gametophores are designated by CAB 1-15 (C. americanum Before



Figs 1-8. Comparisons of growth forms of Climacium americanum developed by plants grown under field (CAB) and greenhouse (CAA) conditions.



Figs 9-15. Comparisons of growth forms of Climacium americanum developed by plants grown under field (CAB) and greenhouse (CAA) conditions.

1-15) and CAA 1-15 (C. americanum After 1-15), respectively.

The following morphological characters were measured: length and width of branch leaves, length and width of branch leaf upper median cells, length of the largest marginal serration, and length and width of stem leaf cells. From these, the following ratios were computed: length/width of branch leaves, length/width of branch and stem leaf cells, and the ratio of length/width of stem leaf cells to the same ratio for branch leaf cells. The latter measures the degree of differentiation between cells of branch and stem leaves.

Desiccation tolerance was estimated by measuring electrolyte leakage by plants following desiccation treatment . This method was used to assess cellular damage in soybeans by Martineau et al. (1979). Field-collected clumps were split in half and one half was grown submerged in a plastic tub, while the other was grown moist but not submerged in the greenhouse. Five potted clumps fit in a single tub, and the positions of individual pots were shifted weekly when the tub was drained and cleaned. The positions of all non-submerged clumps were also shifted at weekly intervals. CA1, 7, 9, 12, and 16 were included in the desiccation experiment. For measurements of ion leakage, six branch fragments were taken from each of the five submerged and five non-submerged clumps. They were washed first under running tap water and then three times in distilled water to remove exogenous electrolytes. The branches were allowed to air dry for three days before being submerged in deionized water for six hours. The branches were then removed and conductivity of the water was measured. Branch portions were oven-dried and conductivity was computed on a per mg of plant basis.

RESULTS

Greenhouse growth response

There was a consistent difference in mode of growth among the greenhouse populations, Clumps that consisted of strongly dendroid gametophores under field conditions produced new

shoots by growth of the subterranean rhizome (Figs 1-2, 6). The unbranched rhizome turned upward at apparently irregular intervals to produce the dendroid gametophores, and elongation of the rhizome occurred via lateral innovations just below ground level.

Clumps that were irregularly branched under field conditions (CAB 3-5, 8-15) produced few new gametophores by above-ground extension of previously buried rhizomes. The predominant mode of regeneration was by renewed apical growth (e.g., Figs 13, 15).

The three clumps (CA 1, 2, 7) that were markedly dendroid in the field produced only new dendroid growth (Figs 1, 2, 6). Under field conditions CA 3-5 consisted of a horizontal rhizome with short side branches and had the appearance of a typical pleurocarpous, mat-forming moss. After eight months of growth in the greenhouse, one of these populations (CA 3) produced erect, irregularly branched gametophores (Fig. 3). However, two other populations, both collected from the same locality (CA 4, 5) continued to produce only short, erect side branches in the greenhouse (Figs 4, 5).

Clumps that consisted of irregularly branched gametophores under field conditions generally produced growth that was more dendroid in the greenhouse (e.g., Figs 9-12, 15). This was especially dramatic in CA 16 (Fig. 15), where the field-grown plants were usually elongate. Other populations that conformed to the "kindbergii" growth form under field conditions produced new growth that was dendroid to a greater or lesser degree, but none approached the regular pattern of branching found in some forms in nature (Figs 1, 2, 6).

Within- versus between-population variation

The results of a two-way analysis of variance for the eleven microscopic characters showed that there are highly significant population effects for every character. In addition, there are significant treatment effects (field- versus greenhouse-grown) for all but three characters. There is a significant treatment x population interaction for every

character. As discussed above, the ANOVA results should be interpreted with caution, since within-population variation was probably underestimated.

Character correlations

There is a significant correlation between the shape of the leaves and the cells comprising those leaves, and between the shape of cells in the stem leaves and branch leaves (Table 1). Plants tend to have long, narrow dimensions to both leaves and cells, or short, broad dimensions to both.

Character correlations of plants grown in the greenhouse are similar to those of field-collected plants with a few exceptions. Unlike the field-collected plants, there is no correlation between branch leaf shape and branch leaf cell length in plants grown under greenhouse conditions. There is also no correlation between the width of branch and stem leaf cells in greenhouse-grown plants. On the other hand, several new correlations are evident among plants cultivated under uniform conditions. The size of the leaf serrations is positively correlated with both stem cell shape ($p < 0.05$) and branch leaf shape ($P < 0.05$) in the greenhouse-grown plants.

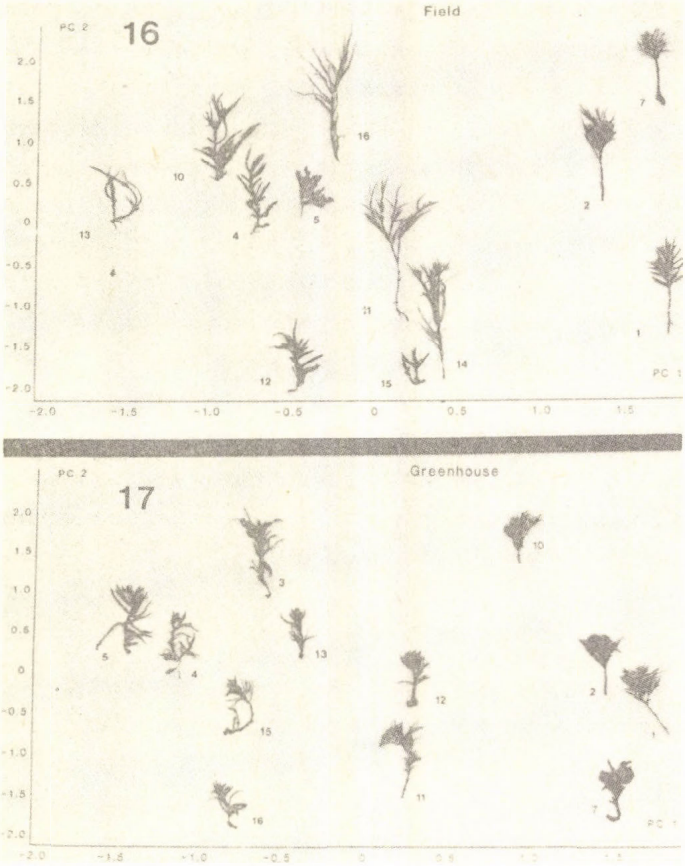
Components of morphological variation such as the position, number, and length of lateral branches, which contribute to the growth form of each population, were not quantified. However, the correlations between microscopic characters and growth form were visualized using principal component analysis. Each population was plotted on a scatter diagram of the first two principal components based on microscopic characters. If populations grouped together because of similar microscopic features also share a similar growth form, this correlation should become evident.

For field-grown plants (CAB 1-15), stem and branch leaf cell shape and stem cell width had high loadings on the first principal component. It is evident that the first principal component groups together the three strongly dendroid populations and separates them from the remaining "kindbergii" populations (Fig. 16). Variation along the second principal

Table 1. Correlation coefficients for morphological characters of Climacium americanum based on field-grown plants.

	(1) BLL	(2) BLW	(3) BCL	(4) BCW	(5) SER	(6) SCL	(7) SCN	(8) LFSH	(9) BCSH	(10) SCSH	(11) CDIF
Branch leaf width (2)	0.42										
Branch leaf cell length (3)	0.26	-0.41									
Branch leaf cell width (4)	0.28	0.24	-0.26								
Serrations (5)	0.19	0.02	0.45	-0.21							
Stem leaf cell length (6)	0.14	-0.35	0.53*	-0.24	0.36						
Stem leaf cell width (7)	0.36	0.37	-0.19	0.74**	-0.19	-0.56*					
Branch leaf shape (leaf length/width) (8)	0.49	-0.56*	0.73**	-0.03	0.20	0.47	-0.02				
Branch leaf cell shape (9)	0.07	-0.39	0.83***	-0.74**	0.41	0.53*	-0.55*	0.52			
Stem leaf cell shape (10)	-0.03	-0.37	0.42	-0.51*	0.31	0.94***	-0.79***	0.33	0.62*		
Cell differentiation (11)	0.15	0.31	0.06	-0.03	0.00	-0.75**	0.54*	-0.09	0.03	-0.73**	

* = < 0.05; ** = < 0.01; *** = < 0.001



Figs 16-17. Principal component analysis of eleven microscopic morphological characters. The positions of populations in relation to the first two principal components are marked by one representative gametophore from each population. Integers next to each gametophore are the population numbers. Fig. 16 is based on field-grown plants, Fig. 17 on greenhouse grown plants.

component does not correlate with plant growth form (Fig. 16).

When the data from greenhouse-grown populations were analyzed, the same characters (cell dimensions) had high loadings on the first principal component. The three dendroid populations are positioned at high values for this component but are not so clearly separated from the remaining populations (Fig. 17). CAA 10, which was positioned much farther to the left in Fig. 16, is positioned closer to CAA 1, 2, and 7 on the basis of greenhouse-grown plants (Fig. 17). This shift in microscopic characters is also reflected in the more dendroid growth of regenerated CAA 10 (Fig. 9). Several other populations that took on a more dendroid appearance under greenhouse conditions are intermediate between the "americanum" and "kindbergii" types along the first principal component based on greenhouse-grown plants (Fig. 17).

Desiccation tolerance

There were clear differences in ion leakage between plants grown submerged versus those grown in moist, but not submerged greenhouse environment. The results of the two-way ANOVA showed that there was a highly significant treatment effect; in fact, most of the variance was contained in that component (Table 2). There was also a significant population effect and a population x treatment interaction. Although the degree of tolerance to desiccation is primarily a result of the previous environment of any particular population, there is also some evidence of genetic differentiation among populations with regard to tolerance. There was no correlation between growth form and innate tolerance; i.e., freely branched forms were not less tolerant of drying than the dendroid forms.

DISCUSSION

The correlation between leaf and cell shape versus growth form is readily evident for field-grown plants as shown in Fig. 16. In addition, there is a clear discontinuity between plants referrable to the vars. americanum and kindbergii.

Table 2. ANOVA table for desiccation tolerance. Main effects are populations (CA 1, 7, 9, 12, 16) and treatments (grown submerged versus terrestrial).

Source	d.f.	SS	MS	F	P
Treatment	1	763.05	763.05	179.10	0.0001
Population	4	153.81	38.45	9.03	0.0001
Treat. x Pop.	4	101.89	25.47	5.98	0.0005
Error	50	213.02	4.26		
Total	59	1231.78	20.88		

However, when plants are grown in a greenhouse, the discontinuity between varieties, in microscopic as well as macroscopic features, is less clear. Nevertheless, even under greenhouse conditions, none of the populations that were irregularly branched in the field became as strongly dendroid as those populations that were originally dendroid. In addition, irregularly branched plants resumed growth in the greenhouse by apical growth of branches whereas dendroid plants grew only via the rhizomatous main stem. One of the three populations (CA 3) that was mat-forming in the field grew larger and highly branched under greenhouse conditions, whereas the other two maintained their prostrate growth form. Although CAB 3 may be an immature expression maintained by frequent disturbance, the other two showed no sign of any change in growth form in the greenhouse.

The picture that emerges from this study is one of extensive differentiation among populations as a resultof both environmental and genetic components. Because of the limitations inherent in the design of these cultivation experiments it is not possible to distinguish environmental versus genetic components of variation. However, the variation among populations

for all of the eleven microscopic characters is so great that the results are highly suggestive of genetic differences between populations.

Desiccation tolerance has been investigated in bryophytes rather extensively (e.g., Hosokawa & Kubota 1957, Lee & Stewart 1971, Bewley 1972, 1979, Dilks & Proctor 1976, Alpert 1982). There have apparently been no previous experiments designed to distinguish inducible versus innate components of variation in desiccation tolerance in a bryophyte. The present results clearly demonstrate the inducible nature of desiccation tolerance in C. americanum and show that this component of variation far outweight innate differences in tolerance among populations. Although some among-population variation was found, there was no clear correlation between the degree or tolerance and growth form, other morphological characters, or habitat. It is, in fact, noteworthy that none of the population differentiation demonstrated by this study can be termed ecotypic in the original sense defined by Turesson (1922).

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TEMPERATURE OPTIMA OF FONTINALIS NOVAE-ANGLIAE: IMPLICATIONS FOR ITS DISTRIBUTION

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The effects of temperature on growth of the moss Fontinalis novae-angliae were determined by laboratory experiments and the annual growth predicted by a computer model. Mosses were grown at laboratory temperatures of 1, 5, 10, 15, and 20 °C. Populations collected in the eastern United States grew significantly faster than populations from the midwestern United States. Lake and stream populations differed little, even in their reponse to flowing versus standing water. A simulation model incorporating these data suggests that F. novae-angliae should be able to spread to a wider geographic area.

INTRODUCTION

In many acidic, rocky, mountain streams in North America, the dominant vegetation is Fontinalis (Glime 1968). Such streams are characterized by low light, low temperatures, low nutrients, and moderate to rapid flow rates. The nearly complete dominance of Fontinalis in these habitats provides a favorable situation in which to evaluate the factors affecting the distribution of Fontinalis, because the effects of competition are minimized.

This study examines the laboratory effects of temperature and flow rates on growth of Fontinalis novae-angliae Sull. from streams in two geographic areas, eastern and midwestern North America, and from one midwestern lake in northern Michigan. These effects form the basis of a predictive

model in which temperature simulations are used to predict the success of the species in different geographic regions.

METHODS

Five populations of F. novae-angliae were sampled: 1, 2) Michigan, Keweenaw Co., Isle Royale National Park, Wallace Creek, 48°2' N, 88°41' W, T65N, R35W, sec 1, elev. 190 m, 22 September 1979 (Toczydlowski 922W4, 922W9); 3) Michigan, Keweenaw Co., Isle Royale National Park, Lake Richie, 48°2' N, 88°41' W, T65N, R35W, sec 1, elev. 190 m, 22 September 1979 (Toczydlowski 922R); 4) New Hampshire, Grafton Co., Fox Pond inlet, near Plymouth, 42°40' N, 71°40' W, 20 October 1979 (Oakland 1020v); 5) New York, Cattaraugus Co., Red House Township, Allegheny State Park, France Brook, 42°30' N, 78°45' W, elev. 610 m, 22 September 1979 (Glime 922AL). Voucher specimens are deposited in MCTC.

Mosses were washed and branch tips were cut to lengths of 2-3 cm. Five moss tips from each population were placed on a Velcro™ strip, and eight strips of each species were placed in each experimental condition.

Five temperatures (1, 5, 10, 15, and 20 °C) and two flow conditions at each temperature ("flow", "pool") were provided by five Living Streams™ (Frigid Units, Inc.). Because all populations growing at 20 °C had become etiolated and chlorotic after week 4, the 20 °C stream was changed to 13 °C during week 5.

The streams were modified to provide ripples of water by using channels made of corrugated fiberglass. Velcro™ strips were suspended into the channels with fishing line, providing free movement to simulate "flow" conditions. "Pool" conditions were created at the end of the basin of the Living Stream™ by separating that end with a wide mesh nylon screen. This permitted the exchange of water without a visible current, ensuring similar water quality and light for both conditions. All water used in the streams came from Cole's Creek, Houghton Co., Michigan (pH ca. 6.5), which was selected because it had

provided a successful culture medium for this species in prior studies (Glime 1982).

Light was provided from above on a 12:12 hr light:dark cycle by 40 watt Duratest™ full spectrum fluorescent tubes, with the number of bulbs adjusted to deliver an intensity of ca. 1000 lux the level of the mosses.

Mosses were measured at the end of weeks 0, 1, 2, 3, 5, 7, 9, 12, and 15. Growth was assessed in terms of incremental increases in length measured to the nearest mm.

RESULTS

Growth of Fontinalis novae-angliae from the two geographic areas differed markedly (Fig. 1). The eastern (New York, New Hampshire) populations achieved a growth rate that was nearly three times that of the midwestern (Isle Royale, Michigan) populations, suggesting that the populations in the east and on Isle Royale might represent two physiological races. On the other hand, growth of the lake population from Isle Royale differed little from the two stream populations (Fig. 1), suggesting that they were the same physiological race.

Only the New Hampshire population showed significantly more growth (Duncan's New Multiple Range test, $p < 0.05$) at its optimum test temperature (10 ^{o}C) than at either adjacent temperature. Nevertheless, the New York population also grew best at 10 ^{o}C, whereas the Isle Royale populations grew best at 15 ^{o}C. All populations showed a sharp drop in growth at 20 ^{o}C.

Both eastern populations had significantly more growth in flowing water than in pool conditions at 10, 15, and 20 ^{o}C, whereas the Isle Royale populations did not differ significantly between the two flow conditions (Fig. 1), except one Wallace Creek population (W9) at 10 and 20 ^{o}C (Fig. 1).

DISCUSSION

Fontinalis species have a relatively low temperature optimum, as low as 5 ^{o}C in some species (Glime, unpublished).

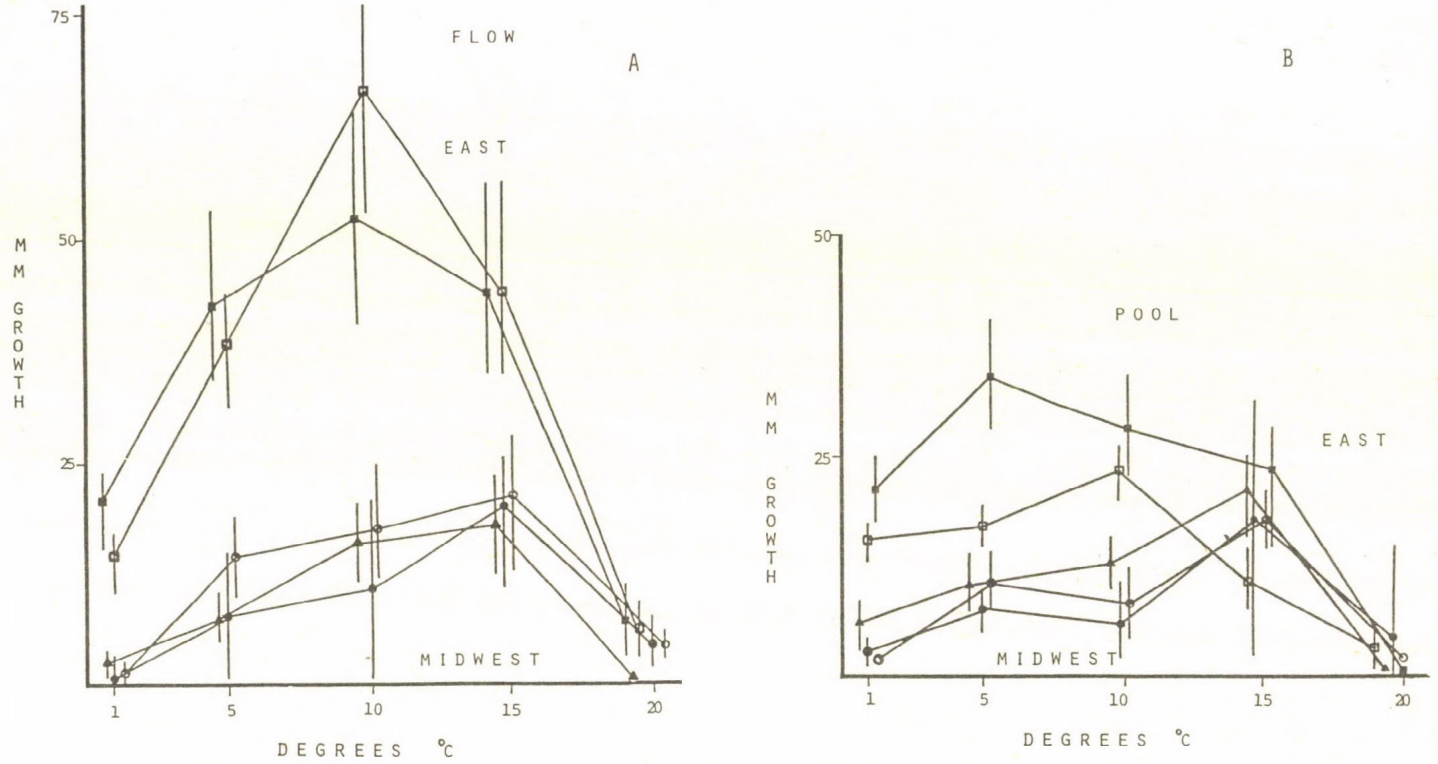

Fig. 1. Comparison of two eastern and three midwestern United States populations of Fontinalis novae-angliae showing the effects of temperature on growth in flowing water (A) and pool (B) conditions. Vertical bars indicate 95% confidence intervals about the means. There were 40 replicates in each condition. Growth was assessed at the end of the 15-week experiment.

Furness & Grime (1982) found the optima of most of the 40 species of bryophytes they tested to be between 15 and 25 °C, whereas 15 °C is the highest optimum for F. novae-angliae in this study. The only bryophyte that Furness and Grime found to exhibit a sharp drop in growth at 20 °C was the streamside collection of the liverwort Chiloscyphus polyanthos.

Temperature optima are dependent upon acclimation of the mosses. Fornwall and Glime (1982) demonstrated a shift to a higher optimum temperature for short-term phytosynthetic activity of Fontinalis duriaei from winter to summer, but the measurement interval was two months. Oechel (1976) measured field temperatures on the five days prior to measurement of photosynthesis in arctic mosses. Based on these temperature data, he concluded that temperature could not explain the observed shifts in photosynthetic temperature optima. Oechel's data suggest that a longer time period than five days is required for the shift. The populations analyzed in this study were completing summer and should therefore be expected to exhibit their maximum acclimation to high temperatures.

This shift to increased productivity at higher temperatures, however, may apply only to short-term photosynthetic activity and not to growth over longer periods of time. Glime (1982) demonstrated that Fontinalis duriaei lost vigor after extended periods or warm temperatures and that populations collected in June grew well at 15-20 °C, whereas populations collected in September ceased growth after 2-3 weeks at 20 °C, as did F. novae-angliae in this study.

Based on the above data and those from five other Fontinalis species (Glime, in prep.), a mathematical model was developed to predict the growth of Fontinalis novae-angliae under differing temperature regimes. The temperature model simulated temperatures that might occur in a warmer or a cooler climate, and the growth of F. novae-angliae was modelled using equations for straight lines fitted to the observed growth rate versus temperature curves. The eastern populations and midwestern populations were modelled separately.

Dilks & Proctor (1975) and Longton (1981) found no correlation between temperature optima and geographic distribution in mosses. Furness & Grime (1982) found that two moss species collected above 300 elevation had the lowest temperature optima of the species they studied, but they also found no convincing evidence of an overall relationship between temperature and distribution of bryophytes. They felt that this lack of correlation could be expected because: 1) The microclimate can be very different from the gross climatic characteristics of a region, 2) Success in the field may depend on factors not related to optimum temperature, such as ability to

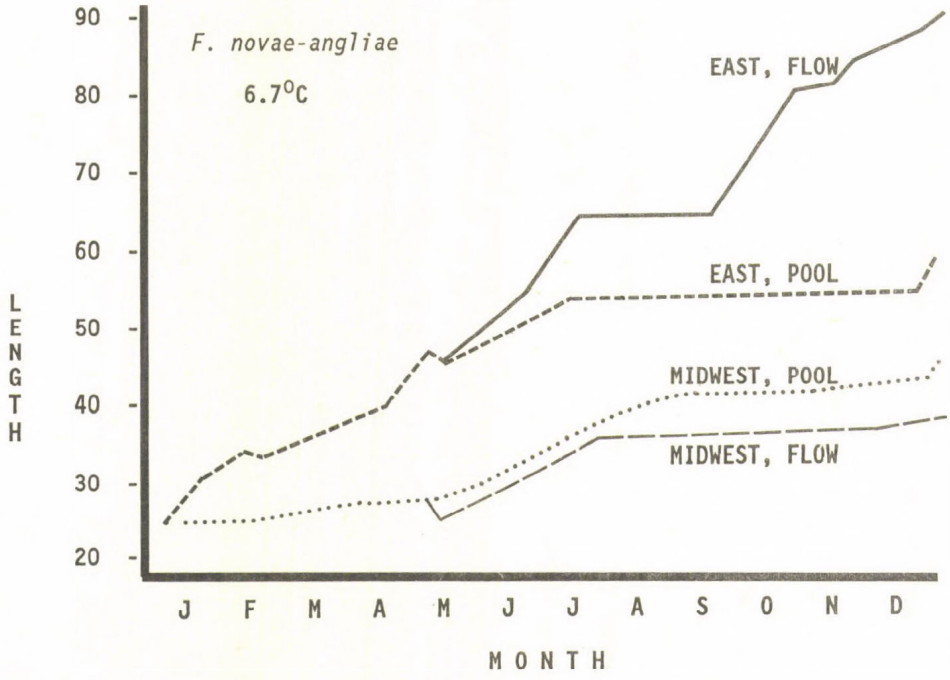

Fig. 2. Model simulation comparing the expected growth in mm of the eastern and midwestern populations of Fontinalis novae-angliae at 6.7 °C mean annual temperature in flowing water and pool conditions. Weekly temperatures are based on temperatures measured in the New Hampshire stream where one population was collected.

grow rapidly at low temperatures (thus conferring a competitive advantage), and 3) Relationships between temperature and growth are dependent upon degree of hydration.

Based on these problems, I felt that an aquatic moss such as Fontinalis novae-angliae should provide a better test of the relationships between temperature and distribution because: 1) Water has less temperature variation, and temperature simulations are therefore more likely to be realistic over a broad geographic range, 2) Few higher plants grow in the streams where Fontinalis occurs, so competition is minimal (Slack & Glime 1985), and 3) Submersed mosses do not have the complicating variable of hydration.

In simulations using water temperatures from Fox Pond inlet (annual mean = 6.7 °C), the model predicted that eastern populations should outperform midwestern populations (Fig. 2).

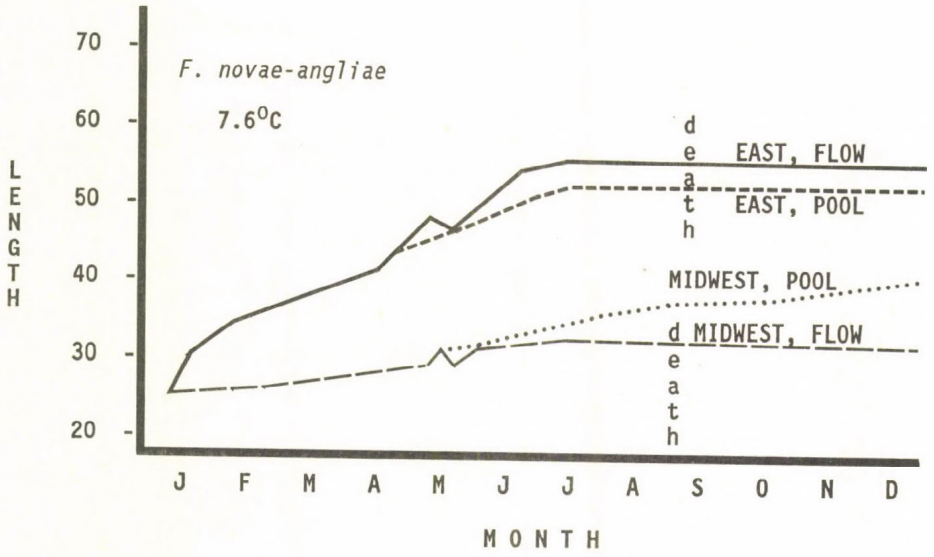

Fig. 3. Model simulation comparing the expected growth in mm of the eastern and midwestern populations of Fontinalis novae-angliae at 7.6 °C mean annual temperature (0.9 °C above mean) in flowing water and pool conditions. Weekly temperatures are based on temperatures measured in the New Hampshire stream where one population was collected.

When the annual mean was raised to 7.6 °C, the model predicted that both the eastern and the midwestern populations in flowing water and the eastern pool population should die due to prolonged heat (Fig. 3). The midwestern pool populations, on the other hand, should die only at an annual mean somewhere between 7.6 and 8.3 °C.

Fontinalis novae-angliae occurs in eastern North America from Florida to Newfoundland. The simulations would suggest that it has sufficient plasticity to expand its distribution, especially in the north. Expansion into the hot tropics is quite unlikely. The midwestern population seems to be stable in lake (pool) conditions, as well as in flowing water, and its occurrence in cold northern lakes is likely.

ACKNOWLEDGMENT

New Hampshire samples were collected by Paul Oakland.

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GENETIC EVIDENCE FOR REPRODUCTIVE ISOLATION BETWEEN TWO EUROPEAN "FORMS" OF CONOCEPHALUM CONICUM

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Two genetically distinct kinds of Conocephalum conicum occur in Europe: the "S-form" and the "L-form". Three enzyme loci (GOT-1, GOT-2, GDH), which are fixed for alleles of different electrophoretic mobility in the two forms, were used as genetic markers in an intensive study of one population from northern Poland. Of 101 colonies that were sampled, only 12 contained both "S-" and "L-forms". None of the III sporophytes sampled from such colonies displayed heterozygosity, as would be expected from cross-fertilization between the two forms. It appears, therefore, that there is complete reproductive isolation between the "S-" and "L-forms" in natural populations.

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Recently, many sources of evidence have demonstrated that the common holarctic liverwort Conocephalum conicum (L.) Dum. is genetically differentiated. Markham et al. (1976) and Porter (1981) discovered that C. conicum actually consists of several flavonoid races, with chemical differences between them as great as usually found between species. Suire & Asakawa (1982) also found significant differences in terpenoid composition between Japanese and French populations. Nevertheless, this variation is usually considered geographic variation within one polymorphic species, because of a lack of major morphological differences associated with these chemical races.

Szweykowski & Krzakowa (1979) reported the occurrence of two forms of C. conicum in Europe, which had different electrophoretic phenotypes for four enzymes. Subsequently, more differences have been found between these two types of plants, including differences in morphology (Szwykowski & Bobowicz 1979). Initially it was unclear whether these electrophoretic variants, termed "S-" and "L-forms", represented separate species or were merely some species case of genetic polymorphism within one species. Szweykowski et al. (1981) found that both types of plants can grow sympatrically, yet they do not produce any recombinant, as we should expect in populations of this dioecious liverwort that frequently reproduces sexually. Absence of recombinants suggests the existence of some kind of barrier to gene flow.

To test this hypothesis, it is important to analyse sporophytes produced in populations where both forms and both sexes grow within "fertilization distance". If reproductive isolation does exist, the hybrid (i.e., heterozygous) sporophytes should not be formed. In this report, I present results of studies performed in one mixed population, where electrophoretic variants of three enzymes were used as markers to detect any interbreeding between the two forms.

MATERIALS AND METHODS

The population chosen for study was located in the valley of Kumielka Creek which flows through high moraine hills in the northern part of Poland near Elbląg. During the last glaciation, this area was covered by a glacier, so that the population is relatively young. The hills are covered now by dense deciduous forest, dominated by Fagus sylvatica. The valley is deep, and habitats close to the stream are humid and protected from direct sunshine. The density of C. conicum colonies is rather low in comparison with populations from the Carpathian Mountains. Colonies can be found in three types of habitats: 1) on banks of the stream close to average water level, 2) on more dry slopes of the second terrace, and

3) around small springs on the slopes with water flowing over the surface of the soil.

The microhabitats occupied by colonies are unstable and plants, especially from habitats of the first type, are frequently flooded. Colonies may become divided and fragments may be transported down the creek, resulting in movement of plants within the population.

Sampling method

In October of 1981 I collected small samples of gametophytic thalli. After two weeks in the refrigerator, plants were placed on peat in the greenhouse, where they started to regenerate. They demonstrated typical spring behaviour, producing young carpocephala on elongate stalks. The capsules contained fully developed, multicellular spores. Using the standard methods of Szweykowski et al. (1981), I determined the electrophoretic phenotype of each plant. Of 59 plants, 41 were of the "S-form" and 18 of the "L-form".

In April of 1982, before the capsules opened, I collected all carpocephala with sporophytes from 101 colonies. Sampling was done from within a circular area 15 cm in diameter (about 700 cm^2). I assumed that this encompassed reasonable "fertilization distance" for this species. Fertilization ranges are probably longer for this flat liverwort, than for some species of mosses, where they were estimated as only a few centimeters (Wyatt 1982), but the range in C. conicum is not larger than within one colony.

Sporophytes were stored for up to seven days in the refrigerator, until the genotypes of sporophytes had been determined. For determination of electrophoretic phenotypes I used the methods described by Szweykowski et al. (1981). Only one capsule was sampled from each carpocephalum.

Enzymatic markers

The "S-" and "L-forms" of C. conicum have different electrophoretic variants for more than half the 33 enzymes studied

by starch gel electrophoresis (Odrzykoski, in prep.). I used three enzyme loci (GOT-1, GOT-2, GDH) as markers in my analyses of mating patterns in C. conicum. They have several favorable properties:

1) They are probably allelic products of homologous genes, fixed as different variants in each form. Very rare variants of GOT-1 and GOT-2 exist in a few populations of the "S-form", but do not occur in the population used for this study. Genetic basis of these differences were not checked directly, but similar mobility differences in three other enzymes (EST-1, ACO, LAP-1) segregate independently in simple Mendelian ratios in crosses involving "L-form" plants with different phenotype (Odrzykoski, in prep.).

2) Differences in mobilities of the variants are stable in different stages of gametophyte development such as during intensive vegetative growth, during production of gametangia in both sexes, and during the resting period in winter. Furthermore, different parts of gametophytes have the same phenotype, as would be expected of plants with the same genotype. Plants collected from pure colonies expressed the same phenotype in female gametophytes, stalks, carpocephala, sporophytes, spores inside the capsule, and multicellular young gametophytes grown from these spores.

3) Extraction and analysis are easy and can be performed from crude extracts, obtained by simple maceration of small fragments of gametophytes or sporophytes. Even the small (1-2 mm) sporophytes provide sufficient material for electrophoretic analysis.

As a source of enzymes, I used sporophytes together with their capsules and spores. This technical simplification does not infleuce the results, because together with the sporophyte, we are analyzing the products of a meiotic division of spore mother cells, which in the case of a heterozygous sporophyte would be a simple mixture of spores possessing both parental enzymes. Using this procedure we avoid the time-consuming and technically difficult separation of sporophytes from capsules.

Expected electrophoretic phenotypes for hybrid sporophytes are presented in Fig. 1. I assumed that hybrid sporophytes should express both parental genes (codominance). This is similar to the situation found in most intraspecific heterozygotes of in F_1 interpsecific hybrids (see e.g., Tanksley & Orton 1983). Suppression of one of the parental genomes is rare. I assumed also that apogamy does not occur and that all sporophytes are diploid and formed by the fusion of haploid gametes.

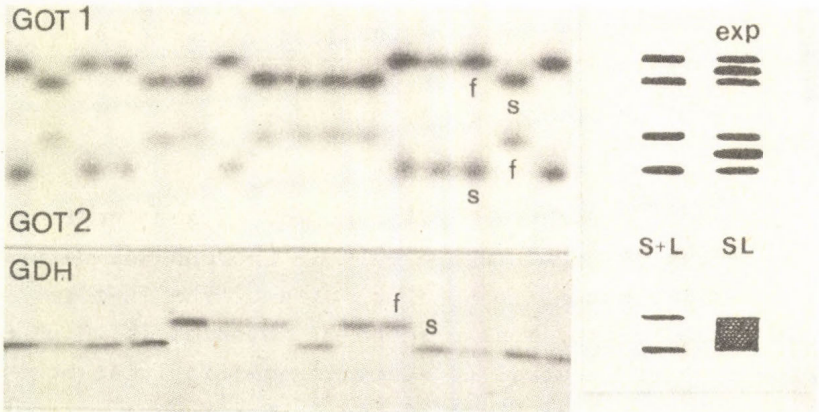

Fig. 1. Sporophyte electrophoretic phenotypes from a mixed colony of "S-" and "L-forms" of Conocephalum conicum. Each of three enzymes (GOT-1, GOT-2, GDH) have two electrophoretic variants: fast (f) and slow (s). The gametophytic genotype of the "S-form" GOT-1^s, GOT-2^f, GDH^f and for the "L-form" GOT-1^f, GOT-2^s and GDH^s. A mixture of extracts shows a simple sum of all variants (S+L), and the expected phenotype of heterozygous sporophytes (exp. SL) is deduced from the behavior of homologous enzymes (Gottlieb 1981). Additional isoenzymes should be formed as a result of the dimeric (GOT) or multimeric (GDH) structure of the active enzyme molecule (Harris & Hopkinson 1976).

Table 1. Number of sporophytes found in pure and mixed colonies of Conocephalum conicum and the mean number of carpocephala collected per colony (= number of sporophytes studied).

Type of colony	N_{col}	N_{sp}	$\%_{sp}$	mean	s.e.
pure "S-form"	56	451	62	7.3	0.9
pure "L-form"	33	166	23	4.9	0.8
mixed	12	111	15	9.3	1.7
total	101	728	100		

RESULTS AND DISCUSSION

Of over 700 sporophytes, 62% occurred in samples from pure colonies of the "S-form" (where only SS sporophytes were found) and 23% occurred in pure colonies of the "L-form" (only LL sporophytes). I also found 12 colonies in which SS or LL sporophytes occurred together, suggesting that both female and male plants of the "S-" and "L-form" were present within "fertilization distance". Of 128 sporophytes, 15% cause such mixed colonies (Table 1). Sporophytes of the "SL genotype", which would be expected from cross-fertilization between the "S-" and "L-forms" did not occur in any colonies (Table 2). The lack of any hybrid sporophytes is simply explained by assuming the presence of genetic isolation that prevents formation of heterozygotes or that leads to their early elimination. The existence of such reproductive isolation was proposed earlier by Szweykowski et al. (1981) as an explanation for the lack of any recombinant gametophytes in mixed populations. We have not found any recombinants in our extensive samples of plants from nearly 300 populations in Central and Western Europe (Odrzykoski, in prep.). The existence of reproductive isolation between the two "forms" is therefore not only a local phenomenon, but probably occurs throughout the range of C. conicum. Such isolation is not un-

Table 2. Numbers of sporophytes with different electrophoretic phenotypes found in twelve mixed colonies of Conocephalum conicum.

Colony Number	Electrophoretic phenotype		
	SS	SL	LL
40	4	0	2
47	2	0	8
49	1	0	1
65	8	0	5
70	1	0	7
71	21	0	1
76	5	0	1
77	2	0	12
88	2	0	13
89	1	0	1
100	3	0	2
105	1	0	7
Totals	51	0	59

expected. Odrzykoski (in prep.) has shown that the "S-" and the "L-forms" are very different genetically as shown by the large values for genetic distance calculated on the basis of allozymic differences. These distances are as large as are usually found between well-defined species of flowering plants (Gottlied 1977, Crawford 1983). The accumulation of so many allelic differences probably required at least a few million years of isolation.

A second hypothesis to explain the lack of recombinant gametophytes was proposed by Szweykowski et al. (1981). They suggested the selective recombination of all recombinants; however, the lack of heterozygous sporophytes casts doubt on the validity of their explanation.

The discovery of complete reproductive isolation suggests that the two "forms" are probably two independent biological species which are morphologically similar (i.e., sibling species). Classical morphological analysis of herbarium specimens has overlooked the differences between these plants.Because

many key characters studied in the field or in herbarium specimens seem to intergrade, it may be very difficult to find morphological markers for the forms. Some differences, however, can be found between plants grown in cultivation (Szweykowski & Bobowicz 1979). Such plants are easily assigned to "S-" or "L-forms" without recourse to electrophoretic analysis.

The existence of such hidden genetic differentiation (sibling species) has rarely been found in bryophytes and flowering plants (see e.g., Grant 1971, Zieliński 1985), possibly because of technical problems connected with their detection. This is especially difficult for thallose liverworts, which are organisms with relatively simple morphology and high phenotypic plasticity. They have more commonly been discovered within well-studied animal groups (e.g., Rosen 1978).

The relative rarity of mixed colonies in populations of C. conicum suggests that the "S-" and "L-forms" to occur as unspecific colonies. Estimation of the frequency of mixed colony formation based on counts of female plants with sporophytes, however, may underestimate their actual frequency. From other studies based on counts of sterile gametophytes (Odrzykoski, in prep.), it is known that these are more frequently formed when frequencies of the two forms are similar and colonies are very dense. In such dense populations, where stable colonies grow for many years and intensively propagate vegetatively, mixed colonies form when one form overgrows previously isolated pure colonists of the other form.

The spatial distributions of pure colonies in the population studied formed a mosaic without any noticeable clustering (Fig. 2). Nevertheless, it is possible that this mosaic distribution follows an underlying mosaic pattern of habitat differences. In culture the "S-" and "L-forms" exhibit differences on tolerance to homogeneous cultivation medium (slightly acidic peat), with "S-forms" being less tolerant but surviving better under desiccation stress. "S-forms" also tend to produce smaller, narrower thalli and more compact colonies, which may protect plants from immediate desiccation. "S-forms"

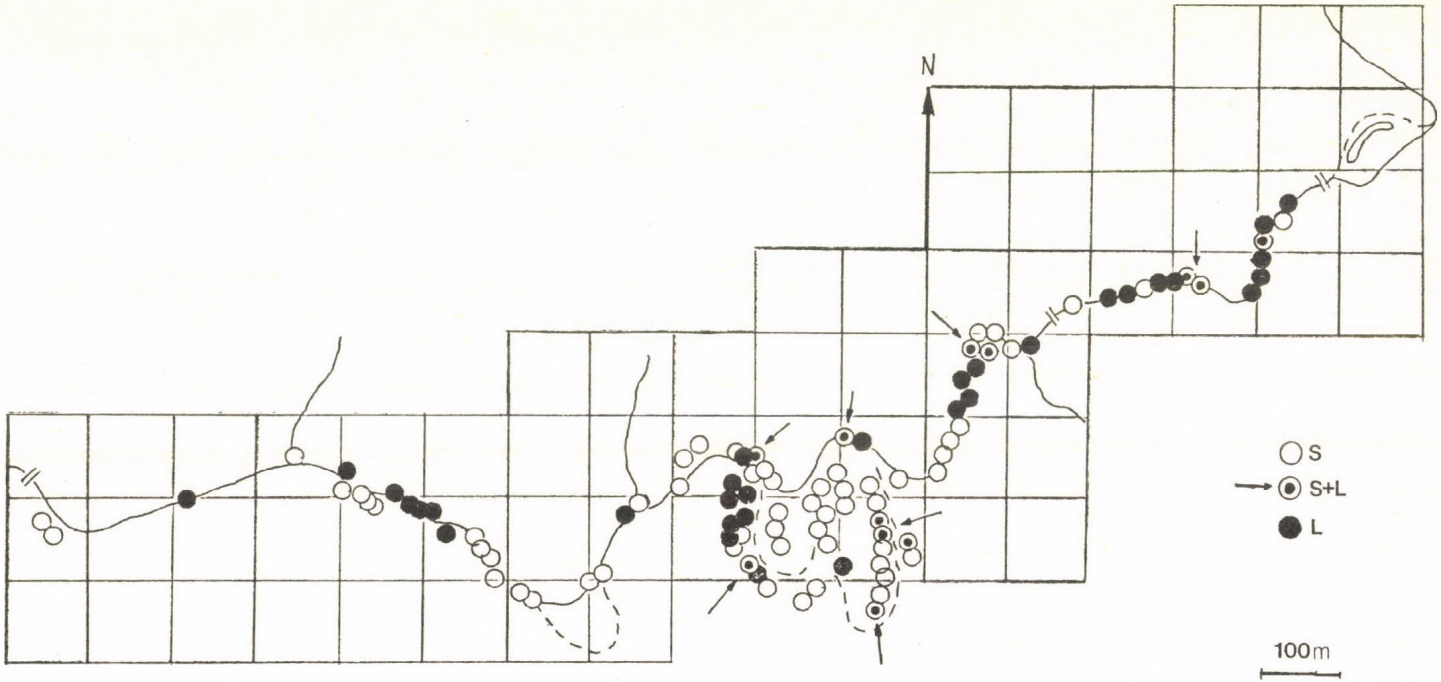

Fig. 2. Spatial distribution of pure and mixed colonies of Conocephalum conicum in the population studied.

have been collected only from the lowlands of Poland, which are characterized by lower precipitation and a more continental climate than in the mountains, where both species occur sympatrically. It is therefore likely that both species may show habitat preferences.

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ELECTROPHORETICALLY DETECTABLE GENETIC VARIATION IN PLAGIOMNIUM CILIARE: A PRELIMINARY REPORT

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Horizontal starch gel electrophoresis was used to measure variability of 14 enzyme loci from 13 natural populations of the dioecious moss Plagiomnium ciliare. Overall levels of genetic polymorphism were extremely high. Using a 1% frequency criterion, 71% of the loci surveyed were polymorphic, a value typically observed only in highly outcrossed plants such as pines. Even using the more stringent 5% frequency criterion, polymorphism in P. ciliare was 36%, a reasonably high value for diploid flowering plants. Genetic distances between populations ranged from 0.0003 to 0.2004, and intensive sampling revealed heterogeneity even within small (5 x 5 cm) clumps. Gene diversity was much greater for populations from primary forests in the Appalachian Mountains (0.11 ± 0.01; mean ± standard error) than for those from secondary forests in the Piedmont (0.04 ± 0.02) of the southeastern United States.

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The traditional view of the genetic structure of bryophyte populations is that mosses and liverworts are genetically depauperate organisms that underwent adaptive radiation long ago and now play only a modest role in nature. The view that bryophytes evolve more slowly than flowering plants and that they have remained relatively unchanged for millions of years has been expressed by many authors (Gemmell 1950, Steere 1954, Anderson 1963, 1980, Schuster 1966, Crum 1972). Such thinking

is based on the fact that most bryophytes are functionally haploid and the genotype is therefore subjected directly to natural selection. Also significant are the widespread occurrence of asexual reproduction and the presumably high levels of self-fertilization in bryophyte populations. Slow rates of evolution are assumed because fossil bryophytes usually closely resemble extant taxa. Some workers, noting the great wealth of biochemical, physiological, and ecological variation in the group have suggested that genetic variation in bryophyte populations may be greater than supposed. Among others, Khanna (1964), Longton (1976), Giannasi (1978), Smith (1978), and Wyatt (1982) have supported this view.

There have been surprisingly few studies of bryophytes that have attempted a direct assessment of levels of genetic variability in natural populations by the technique most commonly used in similar studies of other plants and animals: electrophoresis of proteins. Wyatt (1985) explained some of the limitations of this approach, noting that it is somewhat problematical to what extent the enzymes studied by electrophoresis are representative of the entire genome. Nevertheless, electrophoreric analyses of bryophyte populations suggest that levels of genetic variation are greater than expected under the traditional view. This has been shown for all mosses studied to date (Cummins & Wyatt 1981, Daniels 1982, Vries et al. 1983) and for most liverworts (Krzakowa 1977, Krzakowa & Szweykowski 1977b, 1979, Szweykowski & Krzakowa 1979, Szweykowski et al. 1981b).

As part of a larger study of the evolution of haploid-autodiploid species pairs in the Mniaceae, we assessed levels of genetic variability in natural populations of the dioecious moss Plagiomnium ciliare (C. Mill.) Kop. The gametophytes of this species are haploid (n=6) and occur in colonies consisting of plagiotropic sterile shoots and erect fertile shoots 0.5-2 cm tall. An endemic North American species, P. ciliare occurs abundantly in mesic woods in the eastern United States and adjacent Canada, with its center of distribution in the Appalachian Mountains (Koponen 1971).

MATERIALS AND METHODS

We sampled a total of 13 populations from throughout the range of Plagiomnium ciliare in the southeastern United States (Fig. 1). These populations were located in several different physiographic provinces. At each site we collected 5 x 5 cm

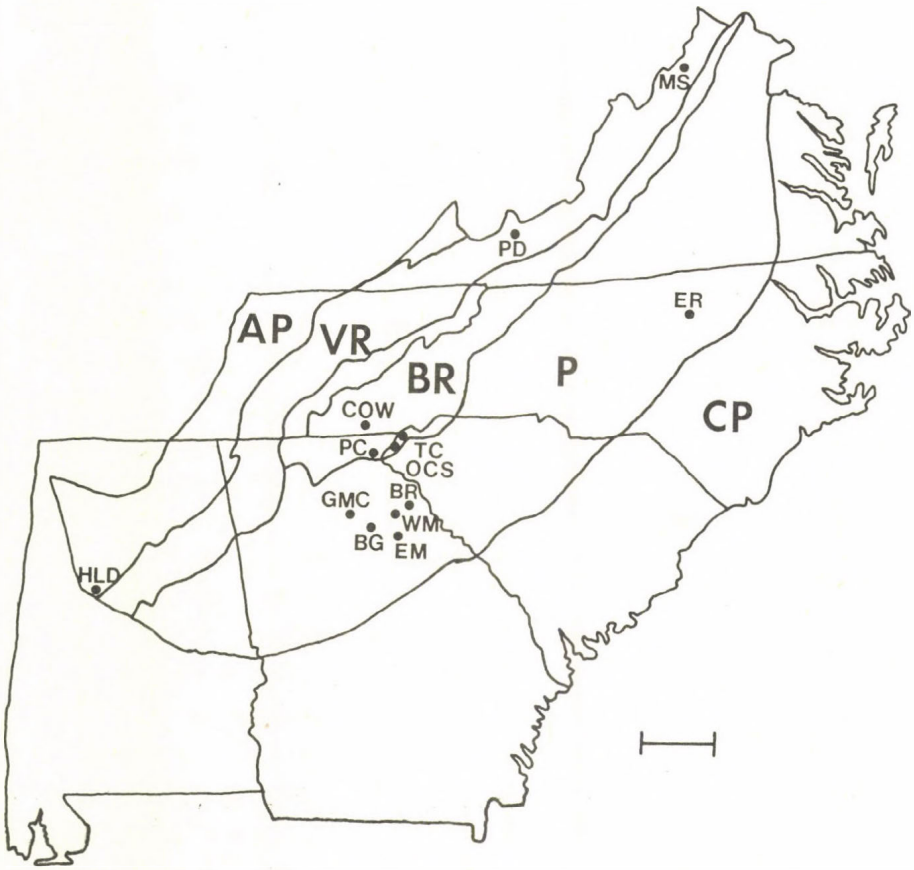

Fig. 1. Locations of the 13 populations of Plagiomnium ciliare sampled in the southeastern United States. Abbreviations for populations (indicated by dots) are given in Table 2. Abbreviations for physiographic provinces are: AP, Appalachian Plateaus; VR, Valley and Ridge; BR, Blue Ridge; P, Piedmont; and CP, Coastal Plain. Scale at lower right indicates 100 km.

clumps from within discrete colonies, placing these samples into small plastic pots. Usually, we collected along a stream until we had sampled a total of 36 clumps or until we had covered a distance of approximately 1 km. Samples were returned to the lab, and a single shoot from each pot was selected for electrophoresis. Thereafter, pots were maintained in a greenhouse. After four months, a single shoot was again chosen from each pot and subjected to electrophoresis. Aside from occasional variation between shoots within clumps (which is reported below), there was no evidence that electrophoretic patterns of any enzymes changed as a result of growing conditions. In this regard, plants from the Botanical Garden (BG) population, which were monomorphic at nearly all loci, were most useful. Plants from this population also were used as "standards" for comparing enzyme mobilities.

To test for the possibility of microscale genetic variation, we sampled the 36 5 x 5 cm clumps from the Morning Star (MS) populations intensively. We removed five erect shoots from each clump, one from the center and one from each corner of the square pots, and subjected these to electrophoresis. We then tabulated the percentage of clumps within which two or more phenotypes occurred.

Electrophoretic procedures were similar to those described by Odrzykoski & Gottlieb (1984). Single shoots were homogenized in 50-100 ml of extraction buffer (0.1 M Tris HCl, pH 7.5, containing 10mM KCl, 10 mM $MgCl_2 \cdot 6\ H_2O$, 1 mM EDTA (Na_2 Salt), 0.1% Triton X-100, and (added just before extraction) 42 mM 2-mercaptoethanol). The extract was then filtered through a small strip of Miracloth onto 4 x 8 mm Beckman paper wicks. All steps of homogenization were done over crushed ice.

Saturated wicks were placed into a vertical slot (the origin) cut across a 10% starch gel, and enzymes were separated in one of three buffer systems. Buffer M, which resolved MDH, TPI, and PGM (for enzyme codes, see footnote in Table 1), consisted of 40 mM citric acid, titrated to pH 6.1 with N-(3-aminopropyl) morpholine. The gel buffer was prepared by diluting 36 ml of electrode buffer with 964 ml of water.

These three enzymes also can be separated using buffer H (43 mM sodium citrate · 2 H_2O, titrated to pH 7.0 with citric acid). The gel buffer for this system consisted of 5 mM DL-histidine HCl titrated to pH 7.0 with NaOH. This buffer gave similar phenotypes to buffer M, but yielded slightly better resolution of PGM. Buffer S was used to separate GOT, ALD, EST, PGI, and PEP. The electrode buffer for this system was 190 mM boric acid and 40 mM LiOH · H_2O, pH 8.3. The gel buffer was a mixture of 50 mM Tris, 6 mM citric acid, pH 8.3, and 10% of the electrode buffer. After mixing, the final pH of the gel buffer dropped to 8.2.

Electrophoresis was performed in a refrigerated chamber at 4°C. Gels were run for 4 hr in buffers M and H at a constant amperage of 35 mA and for 5 hr in buffer S at a constant amperage of 45 mA. By this time in buffers M and H, the bromophenol blue marker had migrated 90 mm. In buffer S, the brown "borate front" had migrated 80 mm. After separation, enzymes were visualized using standard colorimetric methods of staining (Shaw & Prasad 1970, Harris & Hopkinson 1976) with slight modifications. Except for EST, which was stained in liquid assay, all enzymes were stained for 1-3 hr using the agar-overlay method. Staining was carried out in an incubator at a temperature of 37-40°C.

RESULTS

Of the 14 enzymes screened electrophoretically, only 3 (GOT-1, ALD, and PGI-1) were strictly monomorphic (Table 1). Using a 1% frequency criterion, 71% of the loci surveyed were polymorphic. Even using the more stringent 5% frequency criterion, polymorphism in P. ciliare was 36%. The mean number of alleles per polymorphic locus was 2.82± 0.34 (mean ± standard error). Calculations of gene diversity (sensu Nei 1972) for these 13 populations ranged from 0.01 to 0.14, averaging 0.08 ± 0.01. Generally, gene diversity was greater for populations from the Appalachian Mountains (0.11 ± 0.01) than for those from the Piedmont (0.04 ± 0.02) Physiographic

Table 1. Allele frequencies for 14 enzyme loci sampled in 13 populations of Plagiomnium ciliare in the southeastern United States. Abbreviations for populations are given in Table 2.

Locus[1]	Allele	Population												
		BG	GMC	WM	EM	BR	ER	COW	PC	OCS	TC	PD	MS	HLD
GOT-1	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
ALD	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PGI-1	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
EST-1	a	1.00	0.87	1.00	1.00	1.00	1.00	0.94	1.00	1.00	1.00	1.00	1.00	0.92
	b		0.13											
	c													0.08
	null							0.06						
MDH-1	a	1.00	1.00	1.00	0.92	1.00	0.94	0.06	0.45	0.36	0.40	0.03	0.97	1.00
	b				0.08		0.06	0.86	0.55	0.64	0.60	0.97	0.03	
	c							0.08						
MDH-2	a	1.00	1.00	1.00	0.81	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00
	b				0.19								0.06	
PGM-1	a	0.93	0.31	0.07		1.00	0.39	0.75	0.32	1.00	0.80	0.81	0.42	0.29
	b	0.07	0.69	0.93	1.00		0.61	0.25	0.68		0.20	0.19	0.55	0.71
	c												0.03	
PGM-2	a	1.00	0.94	0.90	1.00	1.00	1.00	0.19	0.91	0.44	0.57	0.61	0.61	0.92
	b		0.06	0.10				0.73	0.09	0.56	0.43	0.17	0.35	0.08
	c											0.22	0.04	
	d							0.08						
TPI-1	a	1.00	1.00	1.00	1.00	1.00	0.83	0.78	1.00	0.86	0.70	1.00	0.94	1.00
	b						0.17	0.22		0.11	0.30			
	c									0.03			0.06	
TPI-2	a	1.00	1.00	1.00	1.00	1.00	0.92	0.97	1.00	1.00	1.00	0.94	0.97	1.00
	b						0.08	0.03					0.03	
	c											0.06		
ME-1	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.45	0.19	1.00	0.11	0.25	0.62
	b								0.55	0.81		0.89	0.75	0.38
PEP-1	a	1.00	0.85	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.93	1.00	1.00	0.96
	b		0.15											0.04
	c										0.07			
PEP-2	a	1.00	0.81	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00	0.97	0.83
	b		0.19								0.03		0.03	0.17
PEP-3	a	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00
	b							0.03						

[1] Code for enzymes: GOT, glutamate oxalacetate transaminase; ALD, aldolase; PGI, phosphoglucoisomerase; EST, esterase; MDH, malate dehydrogenase; PGM, phosphoglucomutase; TPI, triose phosphate isomerase; ME, malic enzyme; PEP, peptidase.

Table 2. Sample sizes (N), gene diversities (H_e), and standard errors (se) for 14 enzyme loci surveyed in 13 populations of Plagiomnium ciliare from the southeastern United States. The first six populations are from the Piedmont.

Population		N	H_e ± se
BG	Botanical Garden, Athens, GA	72	0.01 ± 0.01
GMC	Goldmine Creek, Braselton, GA	32	0.10 ± 0.04
WM	Watson's Mill State Park, GA	29	0.02 ± 0.02
EM	Echol's Mill, Lexington, GA	26	0.03 ± 0.02
BR	Broad River, Elberton, GA	15	0.00 ± 0.00
ER	Eno River, Durham, NC	36	0.07 ± 0.04
COW	Coweeta Hydrologic Lab, NC	36	0.13 ± 0.04
PC	Panther Creek, Toccoa, GA	22	0.10 ± 0.05
OCS	Oconee Station Cove, SC	36	0.11 ± 0.05
TC	Tamassee Creek, Walhalla, SC	30	0.14 ± 0.05
PD	Pond Drain, Mt. Lake, VA	36	0.09 ± 0.04
MS	Morning Star, Basye, VA	36	0.13 ± 0.10
HLD	Holt Lock and Dam, Holt, AL	24	0.11 ± 0.04
Total		430	
Grand mean			0.08 ± 0.01

Province of the southeastern United States (Table 2).

Genetic distances between pairs of populations ranged from 0.0003 between Botanical Garden and Broad River to 0.2004 between Echol's Mill and Pond Drain (Table 3). Generally, populations from the Piedmont showed relatively less differentitation among themselves than did populations from the Appalachian Mountains. Beyond this tendency for Piedmont populations to form a discrete cluster with high genetic identities, there were no obvious correlations between geographical distances between populations and their genetic distances.

Table 3. Nei's (1972) genetic distances (below the diagonal) and genetic identities (above the diagonal) between 13 populations of Plagiomnium ciliare in the southeastern United States. Abbreviations for populations are given in Table 2. Geographical locations of the populations are shown in Fig. 1.

	Population												
	BG	GMC	WM	EM	BR	ER	COW	PC	OCS	TC	PD	MS	HLD
BG	***	0.9661	0.9456	0.9339	0.9997	0.9759	0.8865	0.9264	0.8949	0.9516	0.8607	0.9285	0.9560
GMC	0.0345	***	0.9905	0.9839	0.9595	0.9903	0.8684	0.9457	0.8503	0.9287	0.8313	0.9400	0.9865
WM	0.0559	0.0095	***	0.9958	0.9369	0.9890	0.8632	0.9500	0.8360	0.9166	0.8227	0.9412	0.9834
EM	0.0684	0.0162	0.0042	***	0.9244	0.9833	0.8511	0.9492	0.8213	0.9057	0.8184	0.9301	0.9767
BR	0.0003	0.0413	0.0652	0.0786	***	0.9703	0.8851	0.9203	0.8961	0.9511	0.8599	0.9234	0.9493
ER	0.0244	0.0097	0.0111	0.0168	0.0302	***	0.8851	0.9537	0.8677	0.9469	0.8490	0.9420	0.9816
COW	0.1205	0.1411	0.1471	0.1612	0.1221	0.1220	***	0.9127	0.9383	0.9806	0.9177	0.8728	0.8626
PC	0.0764	0.0558	0.0513	0.0521	0.0831	0.0474	0.0913	***	0.9377	0.9391	0.9518	0.9664	0.9703
OCS	0.1110	0.1622	0.1791	0.1969	0.1097	0.1419	0.0637	0.0643	***	0.9389	0.9775	0.9393	0.8892
TC	0.0496	0.0740	0.0871	0.0990	0.0509	0.0546	0.0628	0.0196	0.0630	***	0.9129	0.9083	0.9181
PD	0.1500	0.1848	0.1952	0.2004	0.1509	0.1637	0.0859	0.0494	0.0228	0.0911	***	0.9129	0.8742
MS	0.0742	0.0619	0.0606	0.0725	0.0797	0.0597	0.1360	0.0342	0.0626	0.0962	0.0911	***	0.9774
HLD	0.0450	0.0136	0.0167	0.0236	0.0520	0.0186	0.1478	0.0301	0.1174	0.0854	0.1344	0.0229	***

Intensive sampling within the 36 5 x 5 cm clumps of Plagiomnium ciliare from the Morning Star population detected 5 clumps that were genetically heterogeneous. Furthermore, 3 of these 5 clumps showed variability at more than two enzyme loci.

DISCUSSION

Our results agree with previous electrophoretic surveys of bryophyte populations, which have reported more gneetic variation than is predicted by the traditional model. Wyatt (1982, 1985) and Szweykowski (1982) reviewed this research, which included both mosses and liverworts. There is presently some doubt, however, whether one of the most thoroughly studied series of bryophyte populations actually conforms to this generalization. Originally, it appeared that 21 Polish populations of the thallose liverwort Conocephalum conicum consisted of three multienzyme phenotypes (Krzakowa 1977). Two of these corresponded to minor variants of a "large" race and the third to a "small" race (Szweykowski & Krzakowa 1979). Addition of two more loci to the original sample of four still showed the same restricted pattern of variation. Furthermore, it was shown that the two races often grew intermixed, yet no crossing occurred between them (Szweykowski et al. 1981a). Besides differing electrophoretically, the races differed in ventral scale morphology, growth rate, and flavonoid profiles (Odrzykoski et al. 1981). Plants from Japan and North America were electrophoretically distinct from the European races (Odrzykoski et al. 1981) and it appears that each of these races should be regarded as separate species if consistent morphological markers can be found.

It appears, then that Conocephalum conicum, which is generally regarded as a morphologically uniform species throughout its wide distribution in temperate areas of the Northern Hemisphere, is genetically and biochemically quite diverse. Plants from different continents are widely divergent in flavonoid profiles, and this is further demonstrated by the large values for genetic distance between these races. Variability within

the races is low, and genetic similarity is high even between widely geographically separated populations of a given race. There is no evidence whatsoever of any tendency toward microscale differentiation within populations.

In contrast to C. conicum, genetic polymorphism in populations of Plagiomnium ciliare is higher than expected for a haploid organism. Percentage of loci polymorphic, mean number of alleles per locus, and gene diversity are on the high side of average for diploid seed plants (Levin 1975, Hamrick et al. 1979). In fact, levels of polymorphism using a 1% frequency criterion approach the extremely high values typical of wind-pollinated, highly outcrossed plants such as pines (Guries & Ledig 1982).

Also in distinct contrast to C. conicum, intensive sampling of clumps showed microscale genetic differentiation. Similarly, Cummins & Wyatt (1981) found genetic variation within small patches of the moss Atrichum angustatum. Given the limited range of gene flow in most bryophytes, such differentation is to be expected (Wyatt 1977, 1982, 1985, Wyatt & Anderson 1984).

Genetic distances between the 13 populations of P. ciliare in the southeastern United States are generally within the range observed for conspecific populations of diploid plants (e.g., 0.0954 for Clarkia species tabulated by Ayala 1975). This again contrasts with C. conicum. the populations of which are remarkably uniform regardless of their geographical origin. The populations of P. ciliare from the Piedmont were more similar to each other than were the populations from the Appalachian Mountains. This may be explained by the fact that our Piedmont samples came almost entirely from Georgia, while the Appalachian Mountain populations were sampled from five states and were spread over a much wider geographical area.

It is noteworthy that gene diversity was significantly lower for Piedmont populations than those from the Appalachian Mountains. In the Appalachian Mountains, P. ciliare occurs in primary forest consisting of a highly diverse mixture of hardwood trees. Most of our sampling sites were in forests

that had been minimally, if at all, disturbed. Populations in the Piedmont, however, occur mainly along streams in second-growth oak-hickory-pine forests. Most of these areas were cleared in the 1800's for cultivation of crops and have had only about 100 years in which to recover. Therefore, although the present abundance of P. ciliare in Piedmont forests appears similar to that in the Appalachian Mountains, the genetic diversity of Piedmont populations is strikingly reduced. This impoverishment of genetic stocks may have occurred because of the bottlenecks in population size to which Piedmont populations were subjected. To test this prediction, we sampled Piedmont populations of P. ciliare from two sites that historical records suggested had never been cleared or heavily logged: Gold Mine Creek in the University of Georgia Arboretum and Eno River State Park in North Carolina. These sites showed gene diversities much higher than other Piedmont sites. In fact, their values were more similar to those for sites from undisturbed forests in the Appalachian Mountains.

We have, therefore, two sharply contrasting pictures of genetic population structure within bryophyte species: (1) the "Conocephalum model", in which there are low levels of variation within "races" (which probably represent separate biological species), weak interpopulations differentiation, and no microscale heterogeneity, and (2) the "Plagiomnium model", in which there are high levels of genetic variation, strong interpopulation differentiation, and microscale genetic heterogeneity. Rather than viewing either model as *the model for all bryophytes*, we should perhaps stand back and ask if bryophytes might not be as diverse in terms of genetic population structure as are angiosperms or various groups of animals. Perhaps the two models represent endpoints of a continuum. We might then ask whether the patterns of variation are related to particular features of the biology of the species concerned.

Hamrick et al. (1979) concluded that species of seed plants with wide geographical ranges, high fecundities, predominantly outcrossed progeny, wind pollination, long generation times, and which came from mature, stable communities possessed more

genetic variation than did species with other sets of life history characteristics. At present, the body of data for relating life history traits to genetic variation in bryophytes is too meager to allow any generalizations to be made. Conocephalum conicum is a long-lived, dioecious thallose liverwort of streambanks in well-developed forests. Plagiomnium ciliare, like C. conicum, is dioecious, probably long-lived, and occurs in mature forests. Neither species possesses specialized means for asexual reproduction, and both produce sporophytes regularly. The reason for the great disparity in genetic population structure between these two species is unknown. We have estimates of genetic variability for only a very few species of bryophytes. We are even more deficient in basic information regarding survivorship and fecundity schedules for natural populations of these organisms (Wyatt 1982). Closer study of the population biology of C. conicum and P. ciliare may reveal the resons for their differences in population structure.

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Session 5

BRYOPHYTES IN ECOSYSTEMS

Convener: R.E. Longton
(Reading)

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OBSERVATIONS ON THE BRYOFLORA OF AUSTRALIAN RAINFORESTS

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Little detailed knowledge of the species diversity or function of the bryophytes in rainforests in Australia, particularly of the tropical and subtropical areas, is available. Much of the vegetation of Australia was dominated by warm temperate and subtropical rainforests prior to its separation from Gondwanaland. Cooling and rying of the Australian continent, together with the appearance of New Guinea, led to retreat of the warm subtropical and expansion of the cooler temperate rainforests at the time of expansion of Eucalyptus forests. Dramatic climatic changes and fire in the last 2 million years forced the retreat of rainforests to isolated pockets on the east coast and tablelands north to New Guinea. The colonisation of Australia by Europeans and subsequent logging has resulted in destruction of the major proportion of this in the last 200 years. The complexity of rainforests in this continent is reflected in their classification into many structural types (Webb 1978).

There are distinct differences in brophyte diversity and distribution in different rainforest types. Some preliminary investigations show that hepatics predominate in the lowland vine forests whereas mosses occur in greatest profusion in wet, higher altitude or valley forests. Species distribution within the forests, e.g., at soil level or on fallen logs, on tree trunks or as canopy species is discussed. Some comparisons between North Queensland and New Guinea, Australian and New Zealand rainforests bryoflora are made.

INTRODUCTION

Although rainforests in Australia occupy a tiny proportion (estimated at 0.3%) of the continent, they are ecosystems of great biological diversity, perhaps supporting about half the total terrestrial flora. In New Zealand and New Guinea, much younger land surfaces in terms of geology, rainforests occupy a much larger proportion of the land area (Fig. 1).

A revolution in our thinking about the importance of rainforest is taking place here as fears grow that it will soon be lost as an ecosystem, even before we know what plants are there, unless quick action is taken. In spite of much reserach in Australia in the last decade, many of the trees, e.g., about 15% of the taxa in North Queensland, are still unnamed and knowledge of mosses, lichens, fungi, and even invertebrates and small vertebrates is very poor. Over the last 200

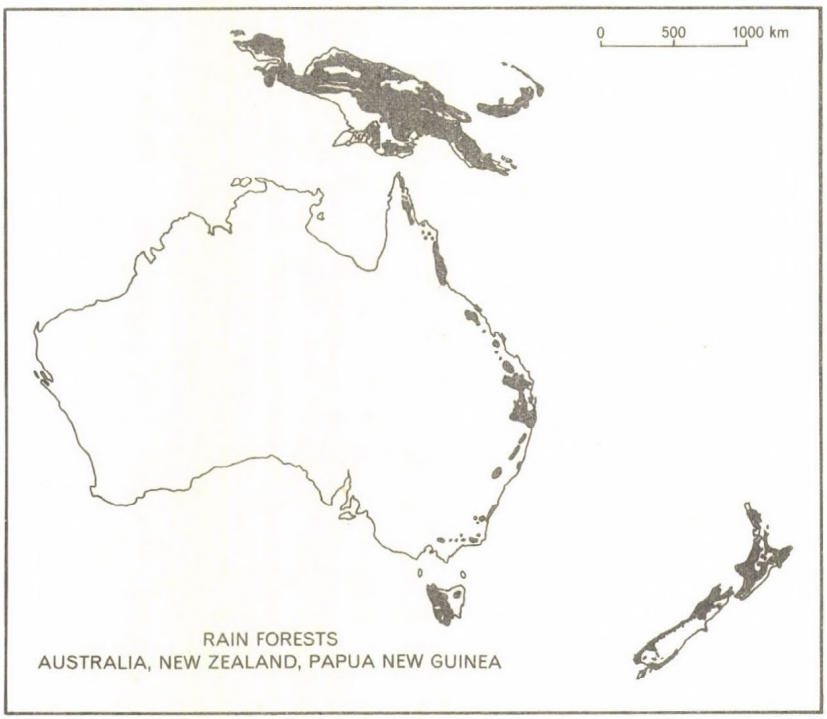

Fig. 1.

years about three quarters of the rainforest in Australia has been destroyed by clearing and the 'Big Scrub' in northern New South Wales - one of the largest stands of lowland subtropical rainforest in the world - has virtually disappeared. Only now when the great value of rainforest has beenrecognised are serious measures to conserve the remaining fragments being made. Similar problems occur in New Guinea and New Zealand as land is cleared for agriculture, etc. Until recently it was considered that the majority of organisms in the tropical and subtropical rainforests in Australia were relatively recent invaders from the Indo-Malaysian region. New palaeobotanical evidence on vegetation history, particularly of Gondwanaland, strongly suggests that rainforest was the dominant vegetation over Australia for much of the Tertiary, declining under drier conditions at the end of the Tertiary.

DEFINING RAINFOREST

The concept of rainforest in the Australasian region, particularly Australia, has been undergoing a marked revision as a result of recent research and the employment of new approaches such as numerical analyses of structure and floristic composition (Webb et al. 1984). Definitions differ in the Northern and Southern Hemispheres and between tropical and temperate latitudes. In New Guinea, for example, montane forests containing gymnosperms such as Dacrydium, Podocarpus and Phyllocladus are not necessarily regarded as rainforests, nor are the monsoonal semideciduous vine forests of northern Australia. We have taken a rather broad view, and have used the terms tropical, subtropical and temperate rainforests.

Our discussion will concentrate most on mosses in Australia, the situation known best to us, but reference to New Guinea and New Zealand will be made. Most recent classifications consider rainforests as typically having a closed canopy (70% light intercepted by the canopy; Webb 1978, Specht 1981), with an environment at ground level more constant, sheltered by wind, cooler and more humid, and with a lower light intensity

than other forests. Other criteria of importance are life forms present (epiphytes, lianes, palm-like plants, absence of annual herbs, presence of buttressed roots, etc.) and many layered stratification (tall trees sometimes with emergents, smaller trees, shrubs but no ground herbs). Angiosperm diversity is high in the tropical areas and low in the cooler rainforests.

The present distribution of rainforests (Fig. 1) indicates the discontinuity of their occurrence in Australia, from coastal lowlands to highlands along the eastern region, rarely extending further than 150 km inland (Hitchcock 1977). In New Guinea, rainforest (closed forest) occurs in lowland areas and extends from the foothills to treeline. At high altitudes conifers are an important element (Richards 1979), while in Australia and New Guinea some conifers, e.g., Agathis and Araucaria are emergents. In New Zealand and New Guinea, Nothofagus and Podocarpus forests are important. In mountainous areas Podocarpus is confined to the lowlands, while Nothofagus extends up to the treeline. The types of rainforest present in the Australasian region are quite diverse in species composition and physiognomy.

In comparison of rainforest sites in New Zealand, southeastern Australia, and New Guinea, Webb (1978) concluded that in New Zealand, rainforests are warm or cool temperate, with a marginally cool subtropical type in the area north of Auckland. The degree of affinity of these New Zealand forests with tropical rainforests is low. The cool temperate rainforests of New Zealand and Australia are comparable, and New Zealand's warm temperate rainforests are closer to Australia's high altitude forests.

At high elevations in tropical areas of New Guinea and North Queensland, the occurrence of frost and the small range of mean monthly temperature produces a climate more similar to cool subantarctic than any northern temperate climate (Richards 1979), thus explaining the larger representation of southern than northern temperate floras in the tropical mountains. These montane forests of the tropics show similarities to the

rainforest of New Zealand and southern Chile (Troll 1960).

Webb & Tracey (1981) classified rainforests in Australia into four main floristic elements that are geographically and ecologically discontinuous - hot/dry in the north; hot/moist in the northeast; warm/moist and cool/moist in the southeast. Within these they recognise a larger number of different categories (Webb et al. 1984). Williams et al. (1984) delimited four main structural types of rainforest in New South Wales, 1) subtropical (STRE), 2) warm-temperate (WTRF), 3) cool-temperate (CTRF), and 4) dry rainforest (DRF). Other categories have also been recognised (cf. Tracey 1982): tropical rainforest (TRF) in northern Queensland, littoral rainforest (LRF) representing coastal communities, gallery (riverine) rainforest, palm rainforest, and vine thickets. Jarman & Brown (1983) have given a detailed analysis of cool temperate rainforest in Tasmania based on floristic composition, regeneration processes and phytogeography. Except in Tasmania and parts of Victoria analogues of the New Zealand Podocarpus - Dacrydium - Nothofagus temperate forests do not occur. The tropical lowland forests in north Queensland and New Guinea are poor in epiphytes of all kinds including bryophytes, while the montane forests are often rich in all forms of epiphytes.

Rainforest is mostly absent from Western Australia in spite of favourable climatic conditions at present, but fossil evidence of Nothofagus suggests that warm-temperate rainforest may have occurred in northern Australia in the past.

BRYOPHYTES IN RAINFORESTS

Within rainforests a large diversity of microhabitats and microclimates suitable for bryophytes is available. Inside the forest gradients of light and humidity determine the number and type of species present. The growth forms and complexity of the bryophyte communities within the forest are dependent on the forest structure, especially the height and spacing of trees. Pócs (1982) and Richards (1984) provide the most recent summaries of tropical rainforest bryoecology. All the growth forms of tropical rainforest bryophytes (Richards 1984) can be

found in the various rainforest types in Australasia. Pócs (1982) demonstrated a positive correlation between biomass of epiphytes, including bryophytes, and surplus rainfall in rainforest climates in Africa. The capacity of the bryophytes within rainforests to absorb minute quantities of nutrients from rainwater, exudates from forest leaves, excrement of insect larvae and to release these as leachates over time gives bryophytes a vital role in the maintenance of the forest. The bryophyte covering makes these rainforests important catchments, reducing the detrimental effects of torrential rains, keeping the environment moist during dry periods and regulating release to water courses. Bryophytes contribute to humus accumulation increasing the nutrient reserves in the soil through release of organic and inorganic substances during decay.

BRYOPHYTES OF AUSTRALASIAN RAINFORESTS

Although those involved in research on rainforests in the region are fully aware of the presence of bryophytes, attention has been concentrated on the vascular plant species. Research on the role of bryophytes in rainforests in Australia is scant, even in New Zealand where the study of bryophytes has a long and continuous history.

Scott (1971) suggests that the importance and role of bryophytes in the New Zealand rainforests is probably greater than in realised. Some methods suitable for field studies are described by Scott (1969) who points out the physical difficulties of studying higher level epiphytes, and of estimating recycling time of logs which may take hundreds of years to decay. The relationship of epiphyte to phorophyte has recently been studied for some tree fern species in the North Island of New Zealand by Beever (1984), who was able to demonstrate distinct preferences for some epiphytic species (Beever, Fig. 1). Scott (1971) notes that Orthorrhynchium elegans and Ephemeropsis trentepohlioides may occur in restricted habitats such as on specific phorophytes in some regions but may occupy more varied habitats in other areas. Some bryophytes may be

important in pruning upper or dead branches by weight of sodden mantles, e.g., Chandonanthus, Dicnemon and Leptostomum.

Considerable effort has been put into analyses of Australian rainforest angiosperms particularly in recent years by Bauer (1957), Floyd (1960-1982), Webb (1959, 1978), Webb & Tracey (1981a,b), Webb et al. (1984), and Williams et al. (1984), but bryophytes have not been included. Chapman & King (1983) presented an interesting paper on the bryophytes of a rainforest 25 years after logging, revisiting a site for which species lists, including bryophytes, had been published by Burges & Johnston (1953). Helman (1983) lists bryophytes for one area, Mt Dromedary, in her study of the rainforests on the south coast of New South Wales. Ashton & McCrea (1970) have presented the only detailed analysis of rainforest bryophytes for Australia. They investigated the vertical distribution of epiphytes on trees and shrubs and their ability to withstand desiccation, as well as succession. Butt, trunk, crown and twig communities were examined. The rate and extent of development of each species was found to be affected by microclimate. In the crown succession of species from prostrate or small upright to large cushion mosses, e.g., Leptostomum inclinans, occurred only on the upper surfaces of branches. Instability of cushion mosses with age opened up new habitats as they fell. Furrowing of bark with age also provided new niches. Ability to withstand desiccation graded from highly tolerant crown species to least tolerant on the butt. Desiccation at 17% RH discriminated between species. Length of exposure was important between 3-12 hrs while little further damage occurred after that. Resistance to desiccation is an important feature of the ecology of epiphytes which are often, therefore, sensitive indicators of microclimate.

Stone (1982) and Hicks in Hattori (1984) and in Yamada (1984) have recently added new species of bryophytes for the rainforests of northern Queensland but there are many taxa in herbaria, some probably new species, awaiting study and many still uncollected. Stone has illustrated this well in her many publications.

No ecological data have been available on New Guinea rainforest bryophytes until recently but work by Koponen, Norris and Piippo is currently recording information of value. Some mosses of wet forests in Australia are listed in Scott & Stone (1976). We have summarised the families and genera of mosses commonly present in the rainforests of the Australasian region in Table 1 together with their ecological preferences and general distribution in the area.

A total of 29 families of mosses are listed in Table 1. Out of the total of 91 genera, 70 occur in Australia, 53 in New Guinea and 41 in New Zealand. Of the 53 in New Guinea, 20 do not occur in Australia. Some taxa in, for example, the Polytrichaceae and in genera Dawsonia, Ditrichum, Bryum and Campylopus often occur in disturbed sites. Some small families and genera are often represented by a few or only a single species, e.g., Buxbaumia, Echinodium, Ephemerum, Erpodium, Calyptrochaeta. Some families, e.g., Sematophyllaceae and Hypnaceae are poorly understood and may be more widely represented than indicated at present. In New South Wales 30% of the moss families (Ramsay 1984) and many of the genera present there occur almost exclusively in rainforests. In tropical rainforests 28 genera not found in other types of rainforest occur (Table 1). Seven genera are confined to cool temperate rainforest. The seven genera found in all the major rainforest types are: Macromitrium, Racopilum, Hymenodon, Pyrrhobryum, Rhizogonium, Sematophyllum, Thuidium. Hepatics are not included in Table 1, but the major hepatic genera in New Guinea rainforests are listed below, based on Streimann collections and data from Piippo and Grolle (pers. comm.):

Acrolejeunea, Acroscyphella, Anastrophyllum, Andrewsianthus, Aneura, Anthoceros, Archilejeunea, Asterella, Balantiopsis, Bazzania, Caudalejeunea, Cheilolejeunea, Diplophyllum, Drepanolejeunea, Dumortia, Folioceros, Frullania, Gottschelia, Gymnomitrion, Heteroscyphus, Isotachis, Jackiella, Jungermannia, Kurzia, Lejeunea, Lepidolejeunea, Lepidozia, Lopholejeunea, Lophocolea, Marsupella, Marchantia, Mastigolejeunea, Mastigophora,

Metahytrobiella, Plagiochila, Plagiochilion, Pleurozia, Porella, Pseudolepicolea, Ptychanthus, Radula, Reboulia, Riccardia, Riccia, Scapania, Schistochila, Spruceanthus, Teleranea, Thysananthus, Weisnerella.

Of these 51 genera the largest proportion occur in lowland rainforests and fewest in montane forests.

General observations on bryophytes in rainforests of Australia suggest that species richness varies between rainforests in the region. Lowland tropical vine forests are poor in epiphytic bryophytes, particularly mosses, having more hepatics. Montane and cool temperate forests have greater bryophyte diversity where the climate is cooler. The mass of epiphytic bryophytes increases with altitude. Quantifiable data or lists are not yet available to support these observations.

MACROMITRIUM AND AUSTRALASIAN RAINFORESTS

Studies on the genus Macromitrium in Australasia (Vitt & Ramsay 1985) provide information on the relationship between distribution of this moss and its habitat for Australia and New Zealand. New Guinean species have not yet been analysed. At present, species of Macromitrium are mostly confined to rainforest habitats scattered along the eastern and northern coast of the Australian continent where rainforests occur in small, remnant patches, "the patches resembling an archipelago of refugia" (Webb & Tracey 1981). Represented among these remnant patches are several different types of rainforest that vary considerably in the species composition, physiognomy, and geographic distribution.

The greatest Macromitrium species diversity is found in the lower elevation ravine rainforests where six of the species occur most frequently. Four of the endemic Australian (or Australian - New Caledonian) species occur most frequently in Nothofagus moorei dominated, higher elevation, rainforests. The montane tropical rainforests are sites for three endemic species, all of these with restricted distributions, M. peraristatum, M. dielsii, and M. funiforme.

Table 1. Families and genera commonly present in Australasian rainforests. Regions: A = Australia, Z = New Zealand, N = New Guinea. Rainforest types (3 general types used): TR = Tropical, CT = Temperate, ST = Subtropical. Ecological preferences: S = mostly on shrubs, palms or tree ferns, T = butt or lower tree trunk, C = upper tree trunk, branch or canopy species, L = fallen logs, G = ground, including earth banks, R = rocks and stones including near streams and waterfalls, E = epiphylls.

FAMILY	GENERA	REGION[1]	RAINFOREST TYPE[2]	ECOLOGICAL PREFERENCES[3]
BARTRAMIACEAE	Breutelia	A,Z,	CT,ST	R
	Philonotis	A,Z,N	CT,ST	
BRACHYTHECIACEAE	Rhynchostegium	N	TR	T,L
BRYACEAE	Brachymenium	N	TR	L
	Bryum	A,Z,N	CT,ST,TR	G,L
	Rhodobryum	N	TR	G,L
BUXBAUMIACEAE	Buxbaumia	A,Z	CT,ST	L,R
CALOMNIACEAE	Calomnion	N,Z	CT	S
CALYMPERACEAE	Arthrocormus	N	TR	T
	Calymperes	A,N	TR	T
	Exodictyon	N	TR	C
	Leucophanes	N	TR	C
	Mitthyridium	A,N	TR	C
	Syrrhopodon	A,N	TR	C
	Octoblepharum	N	TR	T,L
CRYPHAEACEAE	Cryphaea	A,Z	ST	T
CRYTOPODACEAE	Bescherellia	A,N	ST	T
DALTONIACEAE	Daltonia	A,Z	CT	S
DAWSONIACEAE	Dawsonia	A,Z,N	CT,ST,TR	G
DICNEMONACEAE	Dicnemon	A,Z	CT	C,L
	Eucamptodon	A,Z	ST	C,L
DICRANACEAE	Campylopus	A,Z,N	CT,ST,TR	G,R
	Dicranoloma	A,Z,N	CT,ST,TR	T,L
	Leucobryum	A,Z,N	CT,ST,TR	T,L
DIPHYSCIACEAE	Diphyscium	A	ST	G
DITRICHACEAE	Ditrichum	A,N	CT	G
ECHINODIACEAE	Echinodium	A,N	CT	G

→

Table 1. (continued)

FAMILY	GENERA	REGION[1]	RAINFOREST TYPE[2]	ECOLOGICAL PREFERENCES[3]
ENTODONTACEAE	Entodon	A,N	TR	T
EPHEMERACEAE	Ephemerum	A,N	CT	C
PHYLLOGONIACEAE	Calyptrochaeta	A	CT	R
POLYTRICHACEAE	Atrichum	A,Z	CT	G
	Dendroligotrichum	A	CT	G
	Pogonatum	A,N	CT,ST	G
	Polytrichadelphus	A,Z	CT	G
	Polytrichum	A,Z	CT,ST	G
PTEROBRYACEAE	Calyptothecium	N	TR	T
	Euptychium	A	TR	T
	Garovaglia	A,N	ST,TR	T
	Muellerobryum	A	ST,TR	T
	Pterobryella	N	TR	T
	Symphysodon	N	TR	C,T
	Trachyloma	A	ST	T
PTYCHOMNIACEAE	Glyphothecium	A,Z	CT	
	Ptychomnion	A,Z	CT	L,G
RACOPILACEAE	Racopilum	A,Z,N	CT,ST,TR	G,L
RHIZOGONIACEAE	Goniobryum	A	CT	G,L
	Hymenodon	A,Z,N	CT,ST,TR	L,T
	Mesochaete	A	CT	G
	Pyrrhobryum	A,Z,N	CT,ST,TR	L,T
	Rhizogonium	A,Z,N	CT,ST,TR	G,L
SEMATOPHYLLACEAE	Sematophyllum	A,Z,N	CT,ST,TR	L,T
	Taxithelium	N	TR	L,T
	Trichosteleum	N	TR	L,T
	Warburgiella	A	ST,TR	L,T
	Wijkia	A,Z	CT,ST	L,T
SPIRIDENTACEAE	Spiridens	N	TR	ST
THUIDIACEAE	Pelekium	N	TR	L,T
	Thuidium	A,Z,N	CT,ST,TR	L,T

Table 1. (continued)

FAMILY	GENERA	REGION[1]	RAINFOREST TYPE[2]	ECOLOGICAL PREFERENCES[3]
ERPODIACEAE	Erpodium	A	ST	T
FABRONIACEAE	Fabronia	A	CT	T
FISSIDENTACEAE	Fissidens	A,Z,N	CT,ST,TR	G
HOOKERIACEAE	Achrophyllum	A	CT	G,R
	Chaetomitrium	N	TR	G,R
	Distichophyllum	A	CT	G,R
HYPNACEAE	Ctenidium	N	ST,TR	T,L
	Hypnum	A	CT,ST	T,L
HYPNODENDRACEAE	Braithwaitea	A	ST	T
	Hypnodendron	A,Z,N	CT,ST,TR	G,L,R
LEMBOPHYLLACEAE	Camptochaete	A,Z,N	CT,ST	T,L,R
	Lembophyllum	A,Z	CT	T,L
LEPTOSTOMATACEAE	Leptostomum	A,Z	CT	C
METEORIACEAE	Aerobryidium	A,N	TR	C
	Aerobryopsis	A,N	TR	C
	Floribundaria	A,N	TR	C
	Meteoriopsis	A,N	TR	C
	Meterorium	A,N	CT,ST,TR,	C,T
	Papillaria	A,Z,N	CT,ST,TR	C,T
	Pinnatella	A,N	TR	C
MITTENIACEAE	Mittenia	A	CT	G
MNIACEAE	Mnium	N	TR	G
	Orthomnium	A,N	ST,TR	G
	Plagiomnium	Z,N	CT,TR	G
NECKERACEAE	Homaliodendron	N	TR	T
	Neckeropsis	N	TR	T
	Himantocladium	N	TR	T
	Neckera	A,Z	CT	T
ORTHOTRICHACEAE	Macrocoma	A,Z	CT	C
	Macromitrium	A,Z,N	CT,ST,TR	C,L
	Orthotrichum	A,Z	CT	C
	Schlotheimia	A,Z,N	ST	C,L
	Zygodon	A,Z	CT	C

While Macromitrium species occur more commonly as epiphytes on certain tree species (e.g., Nothofagus, Ceratopetalum, Araucaria, Doryphora, Eucryphia, and Casuarina) there seems no specificity between epiphyte and phorophyte.

Species groups (Vitt & Ramsay 1985) are not confined to individual rainforest types, rather, species of each group occur in two to several of the habitat types. Sister species are often ecologically or geographically separated. Four of the six taxa most frequent in Nothofagus dominated habitats (M. exsertum, M. leratii, M. microstomum, and M. stoneae) are the plesiotypic sister groups of more derived species or sister groups.

Macromitrium occurs infrequently in gallery forests as a trunk epiphyte. Along the sea coast, on both rocks and tree trunks, Macromitrium is sometimes an abundant member of the littoral rainforest communities. Only in Tasmania are habitats for Macromitrium similar to those in New Zealand, with Dacrydium-Podocarpus-Nothofagus temperate rainforest present in both areas. Thus, in Australia, Macromitrium is mostly restricted to rainforest habitats and has evolved along with the rainforests in response to climatic changes (Vitt & Ramsay 1985). This suggests that an understanding of the palaeogeography of the area is essential for any understanding of the distribution of bryophytes within the Australasian rainforests.

CONCLUSIONS

Longton (1984) provides ample evidence in support of the concept that bryophytes have a substantial and distinctive influence on the functioning of ecosystems where they are abundant. Bryophytes may have a greater input in nutrient cycling, soil temperature, moisture regimes, and provision of microhabitats for other organisms than is generally recognised in ecosystem studies. A true assessment of their role cannot be made until detailed studies are carried out.

In the Australasian region all types of studies on rainforest bryophytes are urgently needed while there are still

rainforests to study. Research on bryophytes is most likely to receive support if interdependence of the total rainforest environment and its bryoflora can be demonstrated.

Richards (1984) made a plea for studies on African bryophytes. We would add another plea to that of Scott (1982) for studies on the role of bryophytes in rainforests of the Australasian region, indeed all rainforests, as habitats under threat of extinction.

Areas for investigation should include:

1. Identification of taxa present. Collectors should record more specific ecological data on herbarium labels.
2. Studies on distribution of species in relation to types of rainforest, and within each rainforest type.
3. Analysis of phytogeographical relationships of species present.
4. Studies on the ecological contribution of bryophytes to the rainforest biomass, water carrying capacity, nutrient levels, and recycling capacity.
5. Analysis of substrate specificity and likely changes in the bryoflora if forests are damaged.
6. Determination of the extent of interdependence of microflora and microfauna on presence of bryophytes including any specificity of these as hosts or for protection.
7. Determination of the extent to which bryophytes are ecological and biogeographical indicators of rainforest.
8. Studies on reproductive biology and dispersal mechanisms to determine requirements for survival of the bryophyte community.

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HUMAN INFLUENCE ON THE MOSSFLORA OF TROPICAL RAINFOREST IN PAPUA NEW GUINEA

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The Koponen and Norris collection of bryophytes made in 1981 from the Huon Peninsula of Papua New Guinea is large enought (18,000 numbers) to allow generalization as to the habitat preferences of many tropical rainforest mosses. We have examined the distribution of forty-three species of New Guinea mosses as to comparative frequency in disturbed and undisturbed habitats. Some of these (14 species) are restricted to undisturbed habitats; others (16) appear about equally in both habitats; and some (13) are preferentially distributed in disturbed areas. Terrestrial and epiphytic species dominate the list of mosses from primeval habitats, while weedy plants of open sites characterize the flora of disturbed habitats.

The results suggest that many mosses can find suitable niches in tropical areas unless the destruction of the habitat is complete, but others are eliminated by current patterns of land use.

MATERIAL AND METHODS

In 1981 two of us (Koponen & Norris) made an expedition to Huon Peninsula in Papua New Guinea (Koponen & Norris 1983a). We collected about 18,000 bryophyte specimens, for taxonomic study, mainly on the Huon Peninsula. We tried to collect all species present at each collection site and carefully noted the habitats and substrates of the plants. Very few of the species were identified in the field so the collections were

rather indiscriminate. This is advantageous in the present connection, because common species were collected in large enough numbers to indicate the outlines of their ecology. Certain species were collected from thirty to fifty different sites and on a wide variety of substrates. Identification of the specimens with subsequent publication continues (Frahm et al. 1985, Koponen & Norris 1983b, 1984a, 1984, 1985a,b, Norris & Koponen 1985). This report is based on 43 species from 10 families. These species are represented with sufficient frequency to allow ecological generalisations.

The collecting sites (142) were crudely divided into two groups on the basis of amount of human disturbance. Of these habitat groups primeval forest are closed forests without, or with little human influence (e.g., hunting). Disturbed forests have been cut either for lumber or firewood. Habitats described as scrub may represent primeval high elevation associations, and as it is uncertain how far man has influenced their formation, only few of them are taken into account here. Savannahs and grasslands are open, and predominantly or totally maintained by man by burning. Some of the specimens were collected also in gardens, on the roofs of huts and in other man-made habitats. Altogether we have 128 collecting sites which can be classified according to human influence: 57 of them primeval and 71 disturbed.

The 43 species under consideration were divided into groups according to their presence or absence in primeval or disturbed habitats. No statistical methods were used and borderline cases were arbitrarily assigned.

Collections were made in 16 different localities (Koponen & Norris 1983a), each with a wide altitudinal range. Each of these collection localities include many separate collection sites (same geographic locality but with different ecological parameters). Species can be tabulated according to the number of localities in which each is found, and they can be tabulated based upon their elevational range as shown on the Huon Peninsula. Thus, each species has a certain number of sites on which it potentially could have been found. That number will

usually be less than the 57 primeval and 71 disturbed sites included in the Koponen & Norris collection.

For example, Macrothamnium hylocomoides (see Table 1) was found on only 10 of the 16 collection localities, and its altitudinal range was 1,600-3,500 m. This geographical and altitudinal restriction leaves only 29 disturbed and 48 primeval sites on which we consider it potentially capable of occurring. Its occurrence on 10 of the 29 disturbed sites which could potentially support it gives a 35% occurrence value. Its occurrence on 37 of 48 potential sites in the primeval forest gives a value of 77%. The difference between the percentages is (-42%) with the negative signature indicating a disproportionate occurrence on primeval sites.

RESULTS

The species were placed in three groups according to effect of disturbance: (1) decreasing species, (2) persisting species, and (3) increasing species.

1. Decreasing species

The group of decreasing species can be divided into three or four subgroups according to the most usual substrate of the plant. Exclusively or mainly epiphytic are Meteorium buchananii, Trachypus bicolor, T. humilis, Aerobryopsis wallichii, Papillaria fuscescens, and Thuidium contortulum. Campylopus clemensiae and Leptocladiella flagellaris may also grow on living trees but most often they are found growing on rotten wood. The species collected mainly on forest soil include Dawsonia grandis, D. papuana, and Rhodobryum giganteum. Macrothamnium hylocomioides, Thuidium cymbifolium and T. glaucinum seem to be rather indiscriminate as regards their substrate.

One can assume that all the above species demand the very humid micro-climate of the primeval forest. Naturally there could be many other limiting factors in disturbed habitats: competition with faster growing, light-demanding species, too intense sunlight, too high temperatures, etc. Accurate tests

Table 1. Decreasing species (14)

	distribution (collecting localities)	altitudinal range	disturbed sites: potent. occurr.	disturbed sites: actual occurr.	disturbed sites: occurr. value	primeval sites: potent occurr.	primeval sites: actual occurr.	primeval sites: occurr. value	occurrence value difference	substrate
Macrothamnium hylocomioides	10	1600 - 3600 m	29	10	35%	48	37	77%	-42%	diverse
Trachypus humilis	2	2000 - 2600 m	9	1	11%	10	5	50%	-39%	epiphytic
" bicolor	7	2100 - 3500 m	19	2	11%	38	18	47%	-36%	"
Rhodobryum giganteum	8	1500 - 3000 m	36	4	11%	41	18	44%	-33%	epigeic
Leptocladiella flagellaris	6	1800 - 3000 m	15	3	20%	33	17	52%	-32%	mainly epixylic
Papillaria fuscescens	5	1200 - 2400 m	25	3	12%	26	11	42%	-30%	" epiphytic
Campylopus clemensiae	5	1200 - 3300 m	17	3	18%	29	12	41%	-23%	" epixylic
Dawsonia papuana	7	1900 - 3100 m	9	2	22%	35	14	40%	-18%	epigeic
" grandis	5	1450 - 2900 m	10	1	10%	32	9	28%	-18%	"
Thuidium cymbifolium	10	350 - 3570 m	43	19	44%	52	30	58%	-14%	diverse
" glaucinum	8	300 - 2500 m	36	7	19%	34	11	32%	-13%	"
Meteorium buchananii	12	400 - 3200 m	55	33	60%	53	38	72%	- 12%	epiphytic
Aerobryopsis wallichii	9	400 - 1500 m	22	13	59%	30	21	70%	-11%	mainly epiphytic
Thuidium contortulum	7	1200 - 2850 m	40	7	18%	39	11	28%	-10%	" "

are needed to evaluate which factors are involved in each case.

2. Persisting species

The largest group of species are those which are found in undisturbed forests but persist also in habitats altered by human activities. Bryum apiculatum and Plagiomnium integrum are included in this group although, according to the figures, they seem to decrease quite remarkably when the habitats are altered. However, Bryum apiculatum was found in primeval forests on open places such as on stones by creeks and Plagiomnium integrum was especially abundant in some second growth forests. Our figures indicate that Leptostomum intermedium increases under human influence, but it is an epiphyte of outer tree crowns which area extremely difficult to reach. We, therefore, believe that the percentage recorded for in primeval forests is smaller than in reality.

Five species are consistently or primarily epiphytic: Floribundaria floribunda, F. pseudofloribunda, Leptostomum intermedium, Meteoriopsis squarrosa and Thuidium sparsifolium. On a variety of substrates (rotten wood, boulders, soil, on living trees, etc.) grow Campylopus comosus, Meteoriopsis reclinata, Pelekium velatum and Plagiomnium integrum. Nearly restricted to soil and boulders are Bryum apiculatum, B. capillare, B. clavatum, B. perdecurrens, B. russulum, Duthiella flaccida and Thuidium plumulosum.

There is a clear difference between this and the group of decreasing species in regard to the ecology of the terrestrial species. The reason for their survival might be that in primeval forest they grow in open microhabitats. The effect of forest disturbance is less devastating for them than for more shade-demanding species.

3. Increasing species

Almost half of the third group - species which seem to benefit from human activities - grow mainly in quite open places even in otherwise undisturbed habitats, Brachymenium nepalense,

Table 2. Persisting species (16)

	distribution (collecting localities)	altitudinal range	disturbed sites: potent. occurr.	disturbed sites: actual occurr.	disturbed sites: occurr. value	primeval sites: potent occurr.	primeval sites: actual occurr.	primeval sites: occurr. value	occurrence value difference	substrate
Bryum apiculatum	5	to 1500 m	16	7	44%	6	5	83%	-39%	epilithic, epiphytic
Plagiomnium integrum	11	1000 - 3000 m	56	23	41%	54	32	60%	-19%	diverse
Bryum russulum	5	1900 - 2200 m	16	4	25%	15	5	33%	- 8%	mainly epigeic
Pelekium velatum	8	to 1450 m	18	9	50%	7	4	57%	- 7%	diverse
Floribundaria floribunda	12	120 - 3250 m	55	32	58%	52	33	64%	- 6%	mainly epiphytic
Thuidium plumulosum	7	100 - 1700 m	18	7	39%	9	4	44%	- 5%	" "
Meteoriopsis squarrosa	4	1500 - 2400 m	9	3	33%	19	7	37%	- 4%	epiphytic
Campylosus comosus	6	1800 - 3300 m	29	8	28%	39	12	31%	- 3%	diverse
Duthiella flaccida	8	300 - 2500 m	41	12	29%	30	8	27%	+ 2%	epilithic
Bryum perdecurrens	5	1500 - 3500 m	29	4	14%	34	3	9%	+ 5%	epilithic, epigeic
Floribundaria pseudofloribunda	7	120 - 1800 m	23	11	48%	12	5	42%	+ 6%	mainly epiphytic
Thuidium sparsifolium	4	1500 - 2800 m	18	4	22%	23	3	13%	+ 9%	epiphytic
Bryum capillare	4	600 - 2600 m	29	6	21%	18	2	11%	+10%	mainly epilithic
Meteoriopsis reclinata	7	400 - 2400 m	33	7	21%	28	3	11%	+10%	diverse
Bryum clavatum	9	700 - 3300 m	51	15	29%	51	9	18%	+11%	epilithic, epigeic
Leptostomum intermedium	5	2000 - 3500 m	16	9	56%	31	11	36%	+20%	epiphytic

Table 3. Increasing species (13)

	distribution (collecting localities)	altitudinal range	disturbed sites: potent. occurr.	disturbed sites: actual occurr.	disturbed sites: occurr. value	primeval sites: potent occurr.	primeval sites: actual occurr.	primeval sites: occurr. value	occurrence value difference	substrate
Barbella cubensis	4	1000 - 1800 m	19	5	26%	11	1	9%	+17%	epiphytic
Campylopus exasperatus	6	1700 - 3400 m	26	9	35%	34	5	15%	+20%	epigeic
Aerobryum speciosum	3	1800 - 2400 m	4	3	75%	10	5	50%	+25%	epiphytic
Brachymenium nepalense	9	700 - 3600 m	49	15	31%	48	3	6%	+25%	"
Campylopus umbellatus	8	1300 - 3600 m	43	13	30%	49	2	4%	+26%	epigeic
Pelekium bifarium	6	100 - 1000 m	9	6	67%	5	2	40%	+27%	diverse
Bryum argenteum	5	1750 - 3350 m	25	7	28%	-	-	-	+28%	"
" microerythrocarpum	6	1700 - 3500 m	21	7	33%	-	-	-	+33%	epigeic
Elmeriobryum philippinense	5	1200 - 3570 m	30	12	40%	30	1	3%	+37%	diverse
Orthomnion elimbatum	9	350 - 3300 m	40	20	50%	47	6	13%	+37%	mainly epiphytic
Bryum billardieri	6	2000 - 3500 m	29	20	69%	39	12	31%	+38%	diverse
Campylopus crispifolius	7	1500 - 3300 m	27	17	63%	43	10	23%	+40%	epixylic, epiphytic
Rhodobryum aubertii	4	350 - 2350 m	16	9	56%	18	2	11%	+45%	diverse

Bryum billardieri, Campylopus exasperatus, C. umbellatus, Elmeriobryum philippinense and Orthomnion elimbatum. Others were never collected in undisturbed habitats, e.g., Bryum argenteum, and B. microerythrocarpum. They can probably be classified as weeds. The rest of the group is quite homogeneous, including mainly or consistently epiphytic species such as Aerobryum speciousum, Barbella cubensis and Campylopus crispifolius as well as those growing on diverse substrates, e. g., Pelekium bifarium and Rhodobryum aubertii.

DISCUSSION

In this admittedly incomplete sampling of the ecology of some New Guinea mosses which are tolerant of or actually increased by disturbance. Similar observations have been made on man-made plantations (Pócs 1982). Bryophytes can live in physically very small microhabitats, and they are even hypothesized to persist in such sites despite extreme changes of the macroclimate (e.g., Schuster 1979). Arctic taxa are usually cited as examples of such relictual species, but such patterns may also be shown in tropical floras.

Many of the species which show increased abundance in disturbed areas are widespread, often weedy, taxa. As a result the size of the flora in disturbed areas may not be reduced as compared with primeval sites. It is obvious that evaluation of the effects of disturbance should be done on a species-by-species basis. Mere counting of the species in an area may even show an increased floristic diversity to result from disturbance.

The present data are quite preliminary, and the results may be different when all our material has been identified. It seems evident, however, that at least a part of the tropical forest bryoflora survives under prevailing patterns of human disturbance. If the present pattern of slash and burn agriculture in New Guinea were to be exchanged for large-scale cultivation of monocultures, more drastic impacts upon the bryophyte vegetation can be anticipated. Similarly, the present

selective cutting within the forest for local needs may be replaced by large scale clear-cutting for limber exports. More drastic changes in the bryophyte vegetation would, then, surely occur.

Even with current land-use patterns, some species are drastically reduced, or even extirpated. This parallels Richard's (1984) statement that some species rarely, if ever, occur outside of the primary forests.

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ALTITUDINAL BRYOPHYTE ZONATION IN THE ANDES OF COLOMBIA: A PRELIMINARY REPORT

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Preliminary results of an analysis of bryophyte distribution in the forests and treeless belts of the tropical Andes of Colombia are presented. Field work was carried out along seven altitudinal transects, ranging from about 300 m to 4500 m altitude. Relevés taken at 200 m elevational intervals were inventoried and percentage cover was estimated for the bryophyte species. Zonation diagrams are being prepared showing the presence and percentage cover of terrestrial and epiphytic bryophyte species along the transects. An attempt has been made to determine the altitudinal bryophyte zonation in the Colombian Andes based on cluster analysis of relevé similarity values.

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This paper deals with the altitudinal zonation of Colombian bryophytes and form part of an intergrated ecosystem analysis carried out in the Andes of Colombia (ECOANDES-project; van der Hammen et al. 1983, in press). For the analysis, relevés were made along altitudinal gradients at about 200 m intervals in which total cover of both terrestrial and epiphytic bryophytes were estimated. Detailed information onmethodology is given in van der Hammen et al. (1983) and as far as the bryophytes concerned, in van Reenen & Gradstein (1983).

Field work on seven transects has been carried out so far, viz. on the northern slope of the Sierra Nevada de Santa Marta, Río Buritaca area (BUR-NORTH), on the west and east slopes of

the Central Cordillera, Sierra Nevada de Santa Isabel area (TPN-WEST and TPN-EAST), in the eastern Cordillera, Páramo de Sumapaz area (SUM-WEST and SUM-EAST) and in the western Cordillera, Páramo de Tátamá area (TAT-WEST and TAT-EAST). Results of this zonation study, which will be dealt with elsewhere in full (van Reenen, in prep.) are briefly summarized here.

In his paper on the BRYOTROP-Peru transect (this session of the conference), Dr. Frahm showed that the total cover of epiphytic bryophytes increases considerably from the lowland forest to the high-andean forest. This agrees with our studies in which it was observed that not only the epiphytic but also the terrestrial cover increases in relation to altitude. Moreover, it appeared that along the altitudinal gradient bryophyte cover may change rather abruptly, thus indicating boundaries of bryophyte zones.

In an earlier paper on altitudinal bryophyte zonation in Colombia (van Reenen & Gradstein 1983), five bryophyte zones along BUR-NORTH could be described which are characterized as follows (Fig. 1):

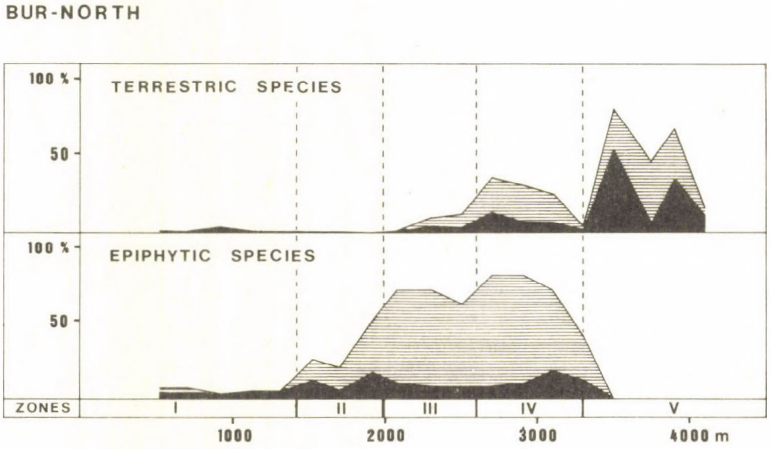

Fig. 1. Bryophyte zonation along the BUR-NORTH transect. Total percentage cover diagrams are given for the terrestrial species and epiphytic species. In black the mosses, in shade the liverworts.

Zone I: In this zone a very low cover of both epiphytic and terrestrial bryophytes is evident and species characteristic of the entire neotropical lowland region may be found here.

Zone II: The epiphytic cover increases whereas the terrestrial cover remains unchanged. Small creeping liverworts, pendent and dendroid mosses are striking in this zone.

Zone III: A high epiphytic cover and an increasing cover of terrestrial bryophytes are notable. Pendent liverworts, at the cost of the mosses, are predominantly responsible for this high cover.

Zone IV: Both epiphytic and terrestrial bryophytes reach peak values. In this zone, substrate preference seems to diminish. Species which mostly occur as epiphytes grow here also on soil, while the converse is also true.

Zone V: In this zone we are dealing with the open páramo. The percentage cover of the terrestrial species increases considerably while epiphytic cover, in the absence of trees and shrubs, is lacking.

A dendrogram technique generating clusters of samples of various degrees of similarity was used to determine the changes in species presence (= species turn-over) with altitude. It appeared that the altitudinal zones based on species turn-over are rather similar to those determined from the percentage cover (van Reenen & Gradstein 1983).

Bryophyte cover values are presumably determined by climatic conditions (cf. Richards 1984, Frahm in this session), and high air humidity and rainfall are often regarded as the most important factors. As local climatological data are mostly not available in the tropics, a number of pluviometers and thermo-hygrometers were installed along the transects for at least one year. The sites of this apparatus are close to the relevés, and render much information on annual, monthly and daily precipitation, intensity of rainfall and daily variation of temperature and air humidity. However, as the measurements are not yet available, only data on precipitation released

from the nearest weather stations are used here.

In BUR-NORTH, the mean annual rainfall is up to 4500 mm (van der Hammen in press). Orographic precipitation caused by northeastern tradewinds is partly responsible for this. But also convective precipitation is common here, and in the tropics is regarded as the most important type of precipitation (Ayoade 1983). It is strongly diurnal in character and occurs in the warmer hours of the day when intense solar radiation heats the land surface resulting in a vertical motion of an ascending mass of air forming, after condensation, cumulus and cumuluomnibus clouds. Mostly these clouds are developed at specific altitudes resulting in so-called "condensation-zones" (Cleef 1981). Apparently zone IV corresponds with such a "condensation zone" and hygrographic measurements made during field work indicate that a constantly high air humidity of almost 100% RH during 24 hours is one of the factors characterizing this zone.

As the identification of bryophyte collections of the other six ECOANDES-transects is not yet completed, zonation presented here is based on total bryophyte percentage cover only. The similarity of the zonations based on species presence or on total percentage cover along the BUR-NORTH transect, however, leads to the assumption that the diagrams presented here may be fairly adequate to characterize the altitudinal bryophyte zonation along the transects.

The total percentage cover diagram of SUM-EAST strikingly resembles that of BUR-NORTH (Fig. 2). Also the climatological conditions along the two transects are comparable. At SUM-EAST moist air masses coming in from the Amazon basin cause orographic precipitation, and the mean annual rainfall in the city of Villavicencio, located at 423 m above sea level and about 20 km north of SUM-EAST, is 4100 mm (Müller 1982).

The total percentage cover diagram of SUM-WEST is quite different (Fig. 3). Though a division into five zones can be made, there is a strong shift in zone boundaries as compared with Figs 1-2. Zone I is very long whereas zones III and IV are relatively short, with their boundaries about 600 m higher.

SUM-EAST

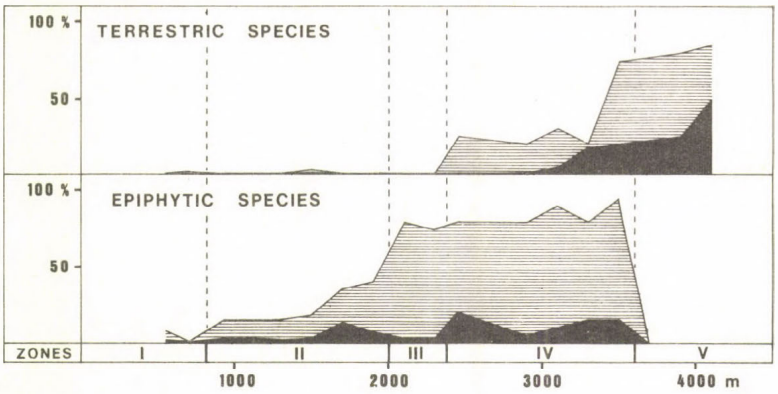

Fig. 2. Bryophyte zonation along the SUM-EAST transect.

SUM-WEST

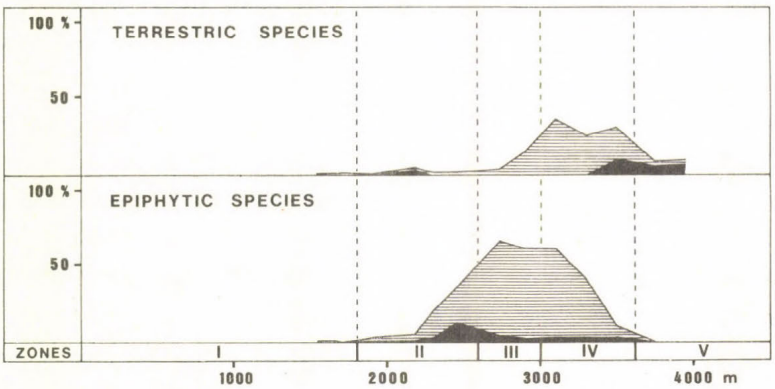

Fig. 3. Bryophyte zonation along the SUM-WEST transect.

Most probably this difference is due to the fact that the leeward SUM-WEST slope receives less precipitation due to the rain shadow effect. This is demonstrated by the presence of Cactaceae at lower altitudes. Only in zone IV, the "condensation zone", is the bryophyte cover value high. The different altitudes at which zone boundaries are found on the east and west sides of the Eastern Cordillera, as well as on the Central and Western Cordilleras (transects TPN-EAST, TPN-WEST, TAT-EAST and TAT-WEST), are also demonstrated in Fig. 4. Like BUR-NORTH and SUM-EAST, the western sides of the Western and

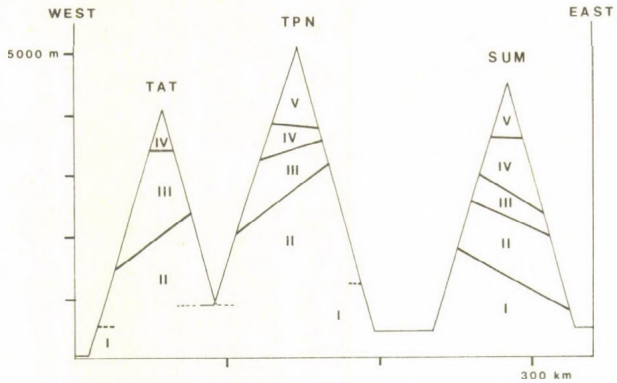

Fig. 4. Cross-section through the three Colombian Cordilleras in the areas of the transect studies, showing the strong differences in zone boundaries between east and west slopes.

Central Cordillera, TAT-WEST and TPN-WEST, are also influenced by orographic precipitation, here caused by moist air currents coming from the Pacific. These result in mean rainfall of 7000 mm, and locally even to 10,000 mm in TAT-WEST (Weischet 1969, Müller 1982). Due to the relatively low altitude of the Western Cordillera, these moist air currents may also reach the western slopes of the much higher Central Cordillera, where the mean annual rainfall is about 3500 mm (van der Hammen, in press). Short zones I/II and long zones III/IV are found along these western exposed slopes. The associated eastern exposed slopes, TAT-EAST and TPN-EAST, lie in the rain shadow and as might be expected the total cover percentage diagrams are in proportion, with long zones I/II and relatively shorter zones III/IV.

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WHICH FACTORS CONTROL THE GROWTH OF EPIPHYTIC BRYOPHYTES IN TROPICAL RAINFORESTS?

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In tropical rainforests, the epiphytic bryophyte vegetation changes considerably from lowland forests with poor bryophyte vegetation to "mossy-forests" at higher elevations. This effect has been explained by differences in light intensity, precipitation, temperature or humidity. However, none of these hypotheses is completely satisfying. For this reason, the problem was studied during the BRYOTROP-Peru expedition along a transect from the Amazon lowland to the alpine forest boundary. Along this transect, from 200 to 3200 m altitude, the phytomass of epiphytic bryophytes, light intensity on epiphyte habitats, temperature and relative humidity were determined. The phytomass of epiphytic bryophytes increased from the lowland to the forest boundary and this was correlated with the increases in light intensity and air humidity, but no casuality between these factors could be assumed. Measurements of photosynthesis under laboratory conditions with different combinations of temperature and light intensity, simulating lowland and mountain-forests conditions, revealed that a combination of high temperature and low light intensity, as occurs in tropical lowland forests, does not allow sufficient net photosynthesis. This shows that the altitudinal distribution of epiphytic bryophytes is controlled by physiological factors.

1. INTRODUCTION

One of the most surprising phenomena in the ecology of tropical rain forest bryophytes is the contrast between the epiphytic brophyte vegetation of tropical lowland rain forests and that of mountain forests. In spite of presumably optimal ecological conditions such as high temperature and humidity, the epiphytic bryophyte vegetation in lowland rain forests is very poor, and even poorer than in some dry forests, although it increases with elevation. The low abundance of epiphytic bryophytes is combined with a low number of species, as has been stated by several authors from Spruce (1908) to Richards (1984). This effect has been the subject of various hypotheses. Ule (1907) stated that the epiphytic bryophyte vegetation in the Amazon lowland is less developed than in the Andes. He supposed that the constant temperatures, lack of strong winds and heavy rainfalls in the lowlands might be the reasons. Giesenhagen (1910) considered the high humidity in the mountain forests of Java as the cause for the high number of epiphytic bryophytes there. Seifriz (1924) proposed the same, perhaps in combination with the light factor. He interpreted the occurrence of different life forms and species of bryophytes as resulting from variation in wind velocity and thus in rates of evaporation. Richards (1957) explains this effect by the cooler climate and the constant humidity at higher elevations. Higher air humidity and precipitation are the reasons given by Vareschi (1980) for the presence of epiphytes in general. Also Pócs (1982) believes that increasing precipitation and the compensation of dry periods by fog is responsible for the increase in bryophyte vegetation. Ellenberg (1975) supposes that the low air humidity in lowland rainforests on the east slope of the Andes might be the cause of the rareness of epiphytes there. Besides climatic factors, light intensity is also an essential factor for the development of epiphytic bryophytes (Richards 1957). The last contribution to this discussion has been made by Richards (1984), who mentions the influence of temperature on assimilation rate. Differences in

light, temperature, precipitation, wind and humidity or combinations of these factors are thus mentioned as responsible for the different development of epiphytic bryophyte vegetation in rainforests. However, none of these theories seems to give a sufficient explanation. The theory of the light factor is insufficient, because there are also no epiphytes in sunny places in tropical lowland rainforests, as along road sides or clearings. The theory of precipitation seems to be insufficient, because we can show a better developed epiphytic vegetation in vegetation types with less precipitation than in the tropical lowland forest. The theory of temperature is insufficient, because there are certain vegetation types in the tropical lowland, such as the campina of the Amazon lowland, which show a rich epiphyte vegetation under more or less the same temperatures as in the high, dense rain forests.

Thus, "the reason why the number of species in lowland forests is less than in tropical montane or temperate forests must be a matter of speculation" (Richards 1984). To clarify this problem, studies were undertaken during the BRYOTROP-Peru Expedition 1982, to elucidate the factors responsible for the different epiphytic bryomass at different elevations of the tropical rain forests.

2. METHODS

Along a transect from 200 to 3200 m altitude on the east slope of the Andes of northeastern Peru, measurements of the phytomass of epiphytic bryophytes ("bryomass"), of light intensity, temperature and air humidity were undertaken at 200 m intervals. The "bryomass" was determined in grams of dry weight per 0.5 m^2 on the trunks of trees between 0.5 and 1.5 m high. Light intensity was measured in epiphyte habitats with a luxmeter and calculated as percent of the light intensity in the open. Temperature and relative humidity were measured with an electronic psychrometer between 6 a.m. and 9 p.m. at 1-2 hours intervals.

In addition, measurements of the CO_2 gas exchange were performed under laboratory conditions with different combinations of temperature and light intensity. Photosynthesis was measured with URAS 2a infrared gas analyser (Hartmann & Braun, Frankfurt/M.), with which the CO_2 uptake or release of the plants is measured with reference to the CO_2 content of air in an open system. For the test, bryophyte specimens collected in Colombia in October 1984 in a montane rain forest at 2300 m elevation were used. These 150 cm^2 specimens of Neckera sp., Heterophyllium affine, Porotrichum sp. and Metzgeria sp. were treated with a fungicide to avoid errors due to fungal respiration. The mosses were removed from their substrates, soaked in nutrient solution, and stored moist in climatic chambers within plastic boxes connected to the URAS. They were kept and measured during several days under conditions of a lowland rain forest (300 Lux/30 °C) and a montane forest (1500 Lux/10 °C), and a light/dark phase of 12 hours. Supplementary measurements were made with 1500 Lux/30 °C and 300 Lux/10 °C.

3. RESULTS

3.1 Determination of the epiphytic bryomass

Dry weight of the epiphytic bryophytes per 0.5 m^2 is shown in Fig. 1. The weight increases from 5-6 g at 200-900 m to 70 g at 3200 m. These measurements give a first impression of the altitudinal change in epiphytic bryophytes, and show a weight ten times higher at the forest line as compared with the lowland forest.

3.2 Measurements of light intensity

The measurements of light intensity show a strong correlation with the bryomass (Fig. 1). The light intensity in epiphyte habitats of the lowland forest is 1% of full daylight (corresponding with data published by Richards 1957) and increases to 44% at 3200 m. The increase in light intensity is probably due to the decrease of the height of the trees, which

is 40-50 m at 200 m and 8-10 m at the forest line. This is suggested by the fact that light intensity is higher in a low forest at 1900 m as compared with the plots at 1700 and 2100 m, where the trees were taller. Although the measurements are varying from plot to plot, there is a strong correlation between light intensity and epiphytic phytomass.

3.3 Measurements of temperature and air humidity

In Figs 2-5, the daily curves of temperature and air humidity are shown for 300, 900, 1300 and 2700 m elevation. A comparison of these curves shows that the air humidity increases with elevation and has a definite decrease at noon. These data reveal that at low altitudes uptake of water vapour

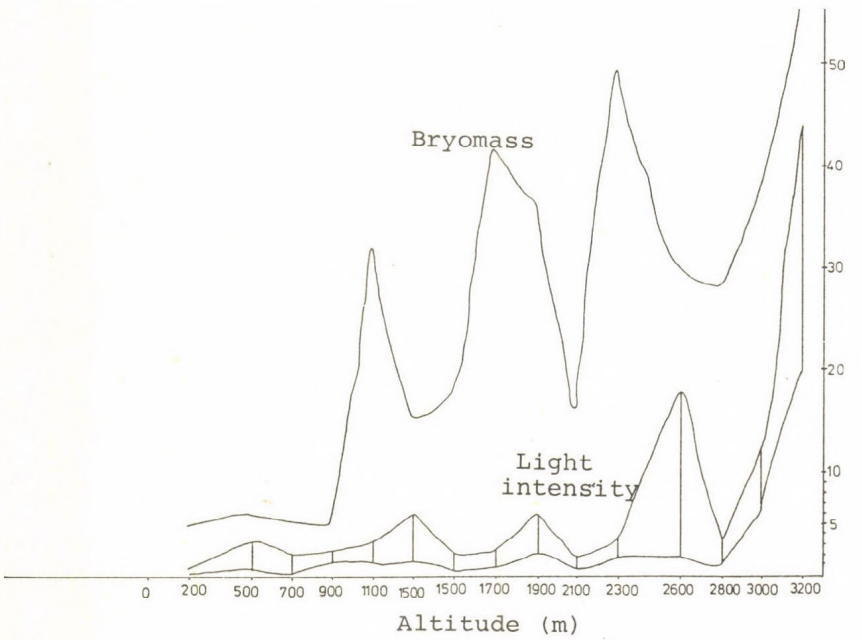

Fig. 1. Altitudinal variation in phytomass of epiphytic bryophytes on stem surfaces (g dry weight/o.5 m^2) and light intensity (minimum and maximum values) at the stem surface as percentage of the daylight.

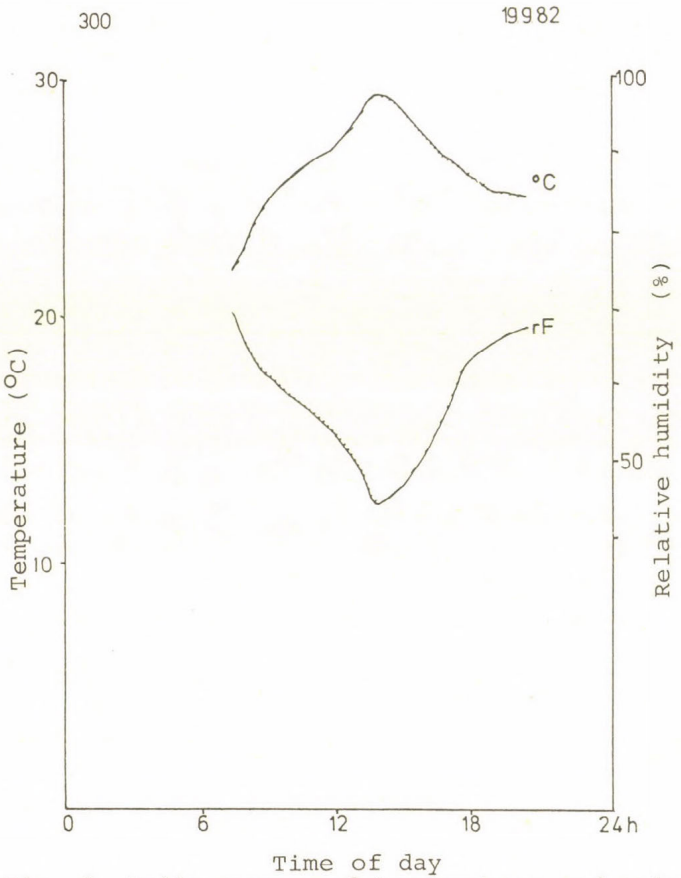

Fig. 2. Daily curves of temperature and relative humidity in epiphytic habitats at 300 m altitude along the BRYOTROP-Peru-Transect.

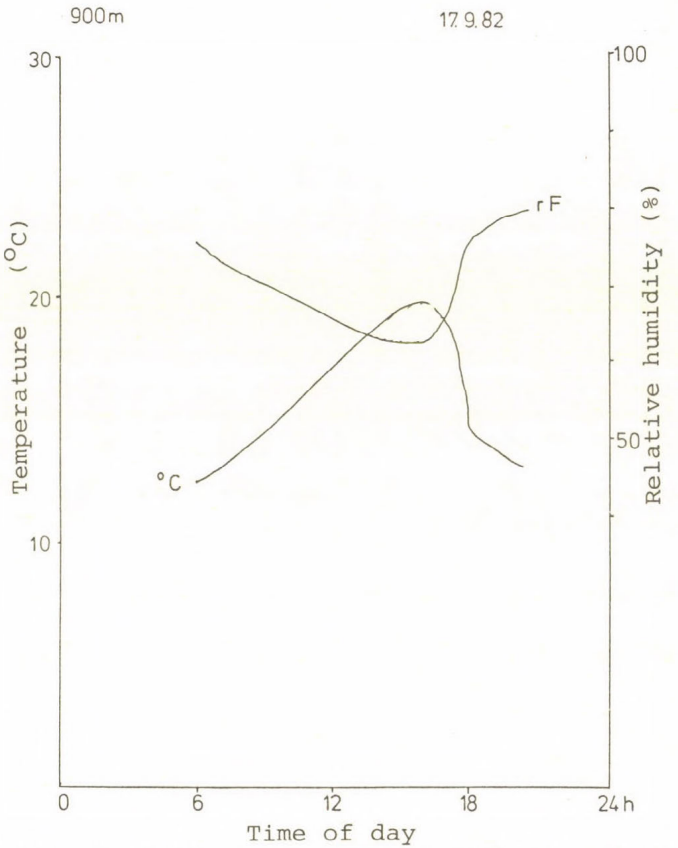

Fig. 3. Daily curves of temperature and relative humidity in epiphytic habitats at 900 m alt. along the BRYOTROP-Peru-Transect.

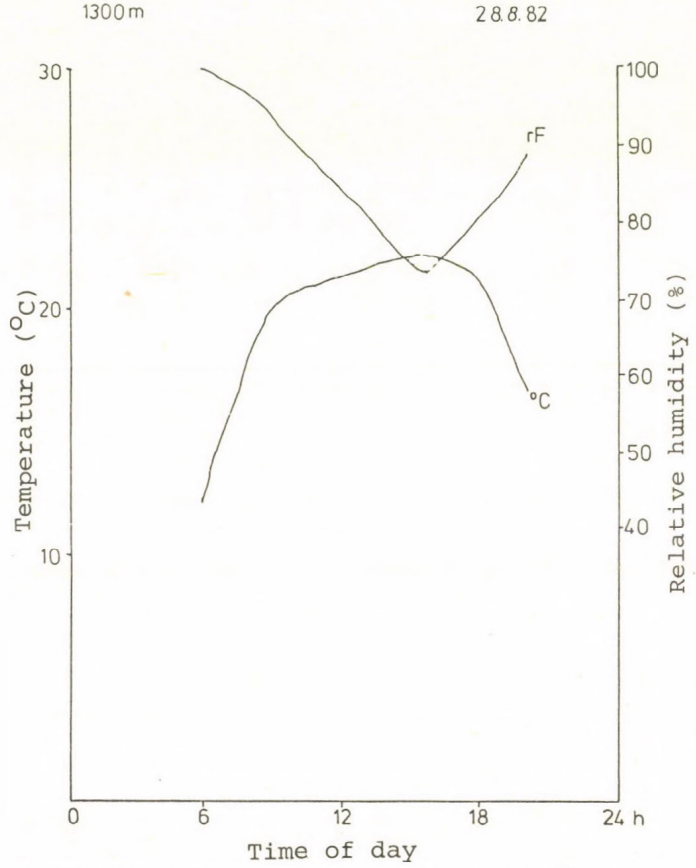

Fig. 4. Daily curves of temperature and relative humidity in epiphytic habitats at 1300 m alt. along the BRYOTROP-Peru-Transect.

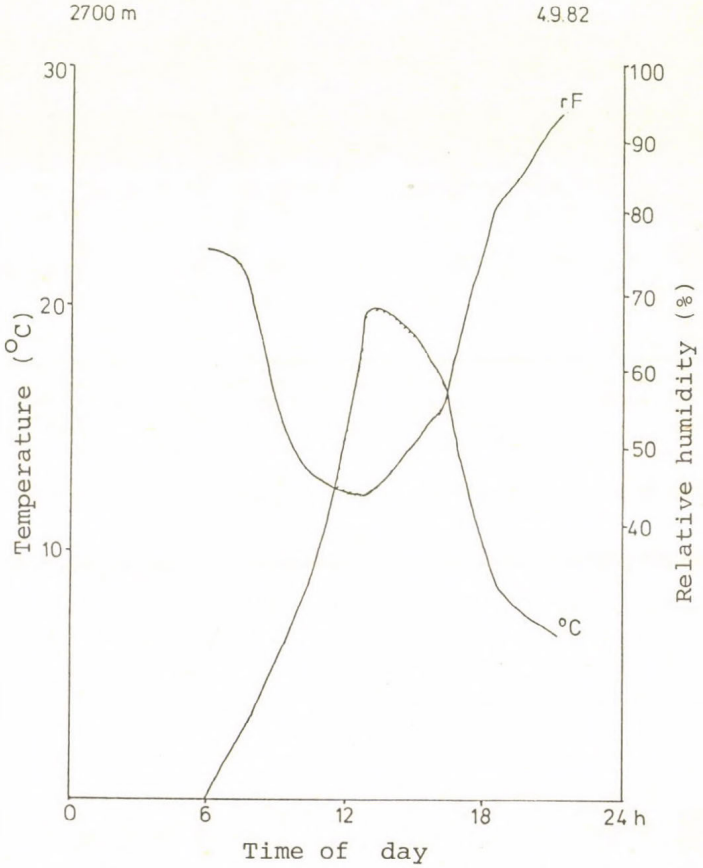

Fig. 5. Daily curves of temperature and relative humidity in epiphytic habitats at 2700 m alt. along the BRYOTROP-Peru-Transect.

at relative humidity less than 70% (hatched part of the curves) is more or less impossible during the day, but does occur at higher elevations. Similar measurements have been published by Ellenberg (1975) for the eastern slope of the Andes. From these curves it becomes apparent that the bryophytes can dry up for a longer daily period with less than 70% relative humidity in the lowland forest, whereas they remain turgid nearly the whole day at higher elevations.

3.4 Measurements of gas exchange

Although correlations could be found in the field between the epiphytic bryomass and light, as well as temperaure and relative humidity, these factors give no perfect explanation. Especially the fact that epiphytic bryophytes are lacking in lowland rain forests in open sites with sufficient light, and an air humidity low for a certain period per day but far from a lethal level, suggests that other factors or combinations of factors are responsible. Recently, Richards (1984) has published another theory, combining the factors temperature and light intensity: "The lack of tolerance of high temperatures might be because of high rates of respiration and because bryophytes are unable to maintain sufficiently high values of net assimilation at high temperatures and relatively low light intensity. Studies of photosynthesis, respiration and net assimilation rates in lowland and montane forest bryophytes might be of great interest in this connection."

Therefore, measurements of the assimilation rate under different combinations of temperature and light intensity have been performed under laboratory conditions. Under montane rain forest conditions (10 °C/1500 Lux), the plants showed a normal diurnal change between positive net assimilation and respiration, the rates depending on the species (Figs 6-8). Under lowland conditions (30 °C/300 Lux), all these montane mosses showed only negative net assimilation as respiration exceeded gross photosynthesis even during the light period. The only hepatic studied was damaged, apparently by the high temperature (Fig. 7), which it could not tolerate in the wet state. How-

ever, plants exposed to high temperatures and high light intensity (30 °C/1500 Lux, as realized in "heath forests" in tropical lowlands), showed positive net assimilation during the day at a rate considerably higher than the respiration during the night and thus showed overall a positive carbon balance.

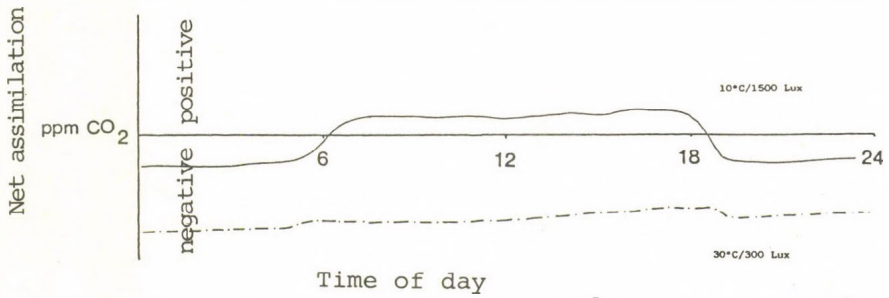

Fig. 6. Net assimilation rate (mg CO_2/g^{-1} dry weight/hr^{-1}) in Neckeropsis sp. at 10 °C/1500 lux and 30 °C/300 Lux, with darkness from 18.00 h to 06.00 h.

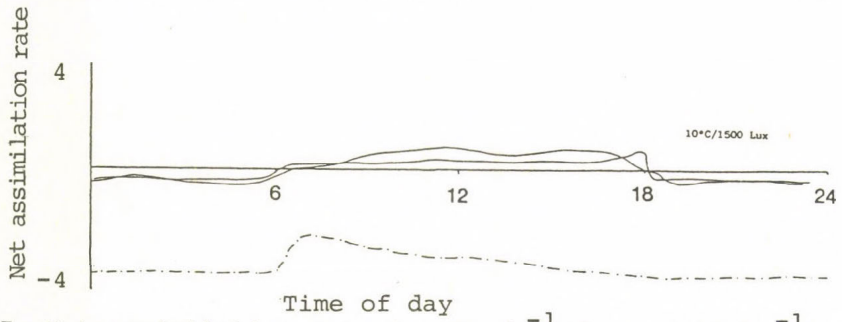

Fig. 7. Net assimilation rate (mg CO_2/g^{-1} dry weight/hr^{-1}) of Metzgeria sp. under different combinations of temperature and light intensity with darkness from 18.00 h to 06.00 h.

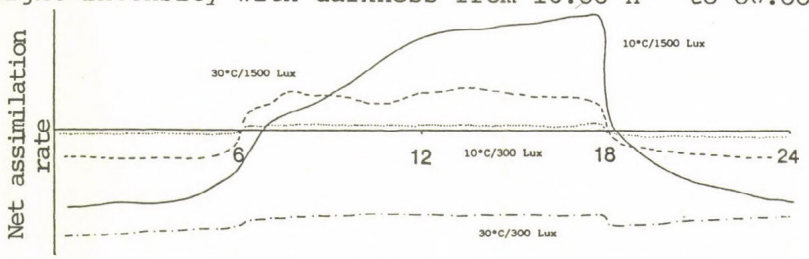

Fig. 8. Net assimilation rate (mg CO_2/g^{-1} dry weight/hr^{-1}) of Heterophyllium affine under different combinations of temperature and light intensity with darkness from 18.00 h to 06.00 h.

A control test with low temperature and low light intensity (10 °C/300 Lux) revealed again a low net assimilation rate. This shows that photosynthesis is inhibited not only by low light intensity, but by the combination of low light intensity and high temperatures.

These tests using bryophytes from montane forest demonstrate that these species cannot descend to lower elevations for physiological reasons and that the increasing bryomass with higher altitudes is a result of a high net photosynthesis caused by light intensity combined with low temperatures, Thus, the tropical lowland rain forest, which seems to be a very fertile habitat, is limited for epiphytic bryophytes, being tolerated by only a few specialists, predominantly flat crusty hepatics. It would be interesting to know whether these hepatics have special adaptations or physiological strategies, which allow them to tolerate these conditions.

ACKNOWLEDGEMENTS

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THE LIMESTONE MOSS FLORA OF MALAYA

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Limestone habitats in Malaya support a moss flora of about 73 species in 40 genera and 18 families, representing 15.2% of the species, 33.2% of the genera and 52.9% of the families from a total of 481 species, 124 genera and 34 families recorded from Malaya. Species of Pottiaceae, Meteoriaceae, Neckeraceae, Thuidiaceae and Hypnaceae predominate the limestone flora. Some limestone mosses are found elsewhere in Malaya only at considerably higher altitudes. Some limestone mosses only fruit when they occur on non-limestone habitats at higher altitudes.

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The limestone landscape in Malaya is dominated by tower-like, craggy limestone formations with sheer rock walls. As a result of erosion and weathering of calcareous rock, the limestone hills are typically steep, and jagged summits jut prominently out of the surrounding landscape (Figs 1-2). The hills occur as isolated crags throughout most of the northern half of Malaya. According to Paton (1961), simple sub-aerial denudation, modified in certain cases by marine erosion, has probably caused the formation of the spectacular karst-tower hills. Erosion has also caused the formation of solution caves in many of the hills. Archaeological evidence shows that these caves were used as human dwellings in prehistoric times. Apart from the archaeological aspect, the caves have been given prominence by the Hindus who used them as temples of worship. The

Fig. 1. Bukit Takun limestone hill, Selangor.

Fig. 2. Bukit Serdam limestone hill, Pahang.

caves have recently been found to be important for the production of the Malayan national fruit, the durian (Durio zibethinus). The durian flower is only pollinated by bats of the species Eonycteris spelea which roost principally in limestone caves. A recent decrease in the annual production of durian fruit was found to have been caused by wholesale quarrying of limestone hills for road construction, which destroyed the roosting places of the bats. Thus, the preservation of the limestone hills became a national issue and a mass signature campaign in 1981 forced the government to close down a large limestone quarry.

The total area of limestone in Malaya is about 260 km^2 (estimate based on Scrivenor 1931, in Burkill 1935), a small area when compared to the total area of Malaya which is 131,588 km^2. The mean elevation of the limestone is 244 m and the highest limestone hill is only 713 m, while non-limestone hills commonly attain altitudes of 1000 m, the highest reaching 2187 m. Their age is estimated to be between Ordovician and Triassic. Malayan limestones are very pure with about 2.5% insoluble residue. Hutchinson (1968) notes that 81% of samples he had studied consisted of $CaCO_3$ and dolomite ($CaMg(CO_3)_2$). The limestone soils in Malaya are not rich in aluminium.

Figure 4 shows the distribution of the main limestone outcrops. These outcrops are mainly found in the northern half of the country, especially in the states of Kedah and Perlis, in Kinta Valley, near Kuala Lumpur, in southwest Kelantan and northwest Pahang. The Langkawi group of islands are mostly made up of limestone.

The vegetation over limestone in Malaya is unique and many studies on the flora have been carried out (Henderson 1939, Corner 1960, Chin 1977). According to Chin (1977), the limestone habitat can be divided into various subdivisions based on the geology, topography, and physiognomy of the vegetation and the floristic composition of the hill. The same subdivisions are used here for purposes of classifying the habitats of the limestone moss flora. All the mosses mentioned in this

Fig. 3. Map of Peninsular Malaysia (Malaya) showing all the states.

study were collected growing on the limestone, epiphytes not being considered. Apart from collections made by the author on limestone hills, which are deposited in KLU, specimens from KLU, SING and UKMB which were clearly labelled as originating from limestone habitats were also studied.

The limestone habitat in Malaya is subdivided into the following groups:

1. Base of hills

The base of the hills is covered by a mixture of soil derived both from limestone and other rocks. Wherever water drips from overhanging hills and the area is partly shaded by higher plants, bryophytes are seen growing luxuriantly. Gymnostomiella vernicosa, Calymperes dozyanum, Hyophila involuta, and Barbula involuta, Philonotis hastata are the common species found in this habitat.

2. Talus slopes

The accumulation of boulders, organic matter and debris from the hill creates a habitat on the slopes which has a tall and closed vegetation. The mosses found here are mainly of pleurocarpous habit, e.g., Ectropothecium zollingeri, Vesicularia montagnei, Rhynchostegium celebicum and Barbula louisiadum.

3. Gullies and vallies

These sheltered spots are ideal for bryophytes as they easily trap water and are somewhat shady. The shallow layer of soil and organic debris at the ground support many mosses such as Fissidens crassinervis, Gymnostomum recurvirostrum, Rhodobryum aubertii, Hypopterygium aristatum, Pelekium bifarium, and a number of species of Isopterygium and Ectropothecium.

4. Cliffs and vertical slopes

The mosses that are to be found in this habitat belong mainly to the families of Thuidiaceae, Meteoriaceae and Neckeraceae and have a creeping habit. They are mostly found growing on the summit and the creep down on the cliffs. However, soil pockets on the walls also have mosses growing on them.

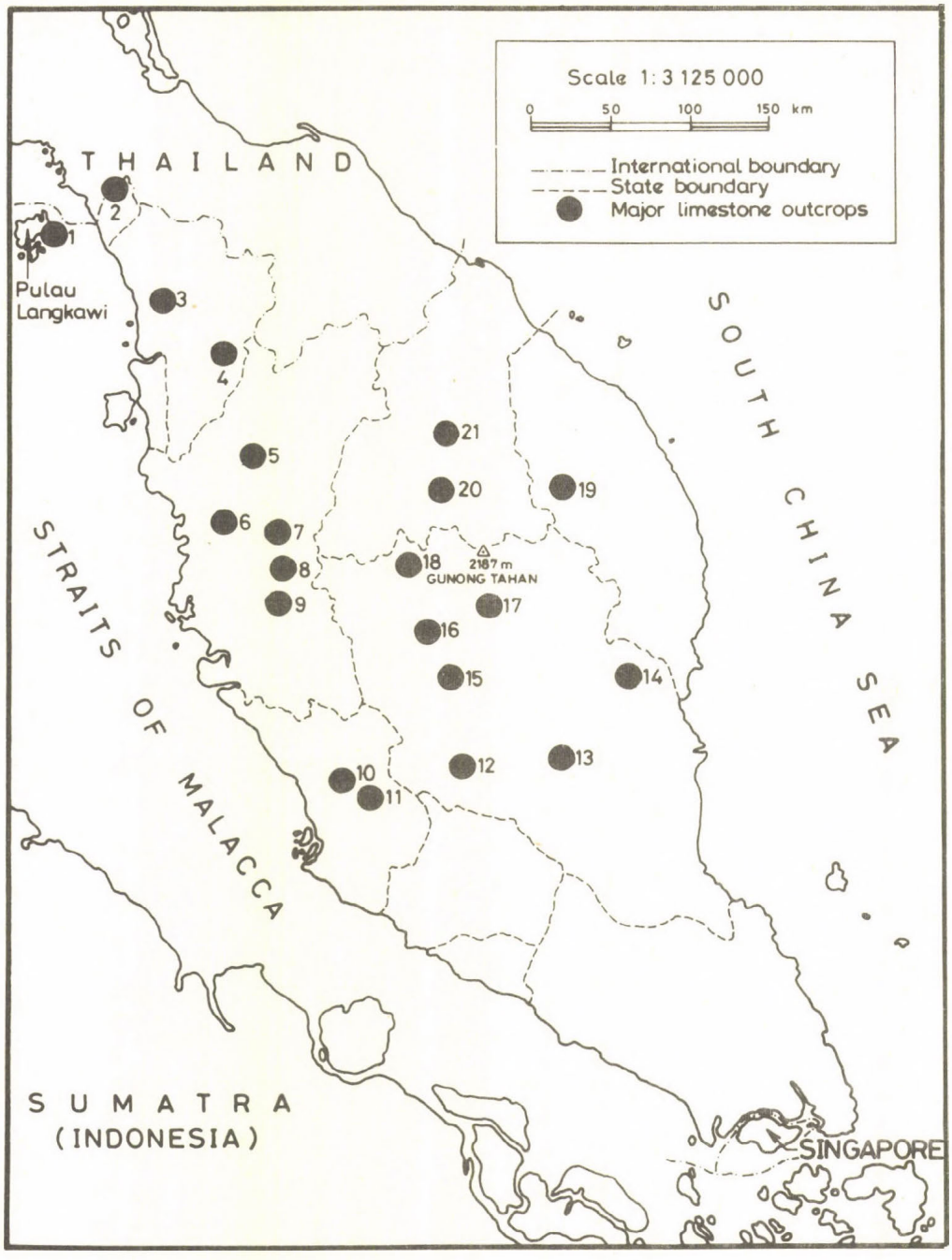

Fig. 4. Map of Peninsular Malaysia showing the main limestone outcrops.

5. Summits

The ground vegetation here is quite rich in bryophytes, especially in sheltered sites with considerable soil cover. Members of the Hypnaceae, Neckeraceae, Meteoriaceae and Pterobryaceae are to be found here. In more exposed areas, Calympores taitense, Bryum coronatum, Pinnatella ambigua and Neckeropsis lepineana are common.

6. Coastal limestone

This is mainly found in the eastern part of the Langkawi Islands. The limestone here is near sea-level and exposed to extreme influences of wind and the sun. Chionoloma latifolium is endemic to this habitat while Bryum coronatum can be found on coral just above the high water mark off the shore. Fissidens ceylonensis is often found on soil pockets on the coastal limestone.

7. Disturbed areas

These are limestone on which disturbances had occurred either by natural means (fire, etc.) or activities of man (agriculture, quarrying, etc.). The earliest colonisers of these disturbed areas are Bryum coronatum, Hyophila involuta and Barbula indica.

In order to study the degree of affinity of the mosses to the limestone habitat, an arbitrary classification has been formulated. The criteria of whether a moss is an 'exclusive', 'preferent', 'indifferent' or 'casual' is based on the percentage of the number of times a particular species was collected on limestone compared to the total number of known collections for the species throughout Malaya. To confirm the calcicolous nature of the species another criterion was used. Table 1 shows the number of collections made for a particular species from limestone hills in various states of Malaya. The presence of a particular species in several of the limestone localities which are separated by appreciable distances confirm its affinity to limestone habitats.

Table 1. Numbers of collections of moss species from five groups of limestone hills in different states of Malaya.

SPECIES	Limestone Hills (Hill Numbers Correspond to Hills on Map 2)				
	Perlis, Kedah (Hills No.1-4)	Perak (Hills No.5-9)	Selangor (Hills No.10-11)	Pahang (Hills No.12-18)	Trengganu, Kelantan (Hills No.19-20)
1. Fissidens hollianus			2		2
2. F. mangaravensis				2	
3. F. crassinervis				1	
4. F. subangustus					1
5. Wilsoniella decipiens			1		
6. Dicranella coarctata			1		
7. Leucophanes candidum			2	2	1
8. Octoblepharum albidum					2
9. Calymperes taitense				8	
10. C. dozyanum		1			
11. Syrrho odon albovaginatus			1		
12. Gymnostomiella vernicosa		1	5		
13. Gymnostomum recurvirostrum		2	1	4	2
14. Chionoloma latifolium	5				
15. Hyophila involuta	3	1	5	2	1
16. Barbula louisiadum	1				
17. B. indica	1	2	2	1	1
18. B. javanica		1		2	
19. Weissia edentula	1				

20.	Trichostomum sarawakense		1			
21.	Bryum coronatum	3	4	5	2	3
22.	Rhodobryum aubertii	1	2	1	7	1
23.	Philonotis hastata		1	2	1	
24.	Macromitrum subtile				2	
25.	M. cuspidatum				1	2
26.	M. orthostichum					
27.	M. semipellucidum				1	
28.	Duthiella wallichii				2	1
29.	Garovaglia elegans			1		
30.	G. plicata				1	
31.	G. powellii			1		
32.	Meteorium miquelianum			1	1	
33.	Aerobryopsis wallichii		1	1	2	1
34.	Floribundaria floribunda			2	2	1
35.	Aerobryidium crispifolium				1	2
36.	A. filamentosum			1		
37.	P. kuehliana			1	2	
38.	P. ambigua	1			7	2
39.	P. alopecuroides				2	3
40.	P. anacamptolepis			1		
41.	P. microptera			5	3	
42.	Neckeropsis lepineana		2	3	3	5
43.	N. gracilenta			1	2	
44.	N. andamana	1				

Table 1. (continued)

SPECIES	Limestone Hills (Hill Numbers Correspond to Hills On Map 2)				
	Perlis, Kedah (Hills No.1-4)	Perak (Hills No.5-9)	Selangor (Hills No.10-11)	Pahang (Hills No.12-18)	Trengganu, Kelantan (Hills No.19-20)
45. Homaliodendron exiguum				3	1
46. H. microdendron			2		
47. Himantocladium plumula				5	
48. Hypopterygium aristatum				2	
49. Chaetomitrium orthorrhynchum				2	
50. Pursellia phyllogonioides	1				
51. Claopodium prionophyllum				1	
52. Pelekium velatum		3	5	7	1
53. P. bifarium		1	4	3	5
54. Thuidium plumulosum				1	
55. Rhynchostegium celebicum				2	
56. R. javanicum				2	2
57. Ectropothecium singapurense			1		1
58. E. incubans			1		1
59. E. zollingeri				1	
60. E. dealbatum					1
61. E. perminutum				1	
62. Trachythecium calcicolum				3	
63. Ectropotheciella distichophylla					
64. E. decrescens				4	1
65. Vesicularia miquelii				5	

Table 1. (continued)

SPECIES	Limestone Hills (Hill Numbers Correspond to Hills On Map 2)				
	Perlis, Kedah (Hills No.1-4)	Perak (Hills No.5-9)	Selangor (Hills No.10-11)	Pahang (Hills No.12-18)	Trengganu, Kelantan (Hills No.19-20)
66. V. reticulata				2	
67. V. montagnei			3	2	
68. V. dubyana			2		
69. Isopterygium laxissimum			1		
70. I. minutirameum			3		1
71. I. albescens			2		
72. I. bancanum			4	3	
73. Pogonatum junghuhnianum			2		

The limestone moss flora of Malaya could be roughly divided into four categories on the basis of their affinity to the limestone habitat. They are:

1. Exclusives. These are species which are restricted to limestone and not found in other habitats. Examples are Chionoloma latifolium, Trichostomum sarawakense, Duthiella wallichii, and Gymnostomiella vernicosa.
2. Preferents. Species which occur mainly on limestone (50 to 75% of the time) but are also found on non-limestone habitats. Examples are Calymperes taitense, Hyophila involuta, Rhodobryum aubertii, Neckeropsis lepineana and Pelekium velatum.
3. Indifferents. Species with no particular preference for either limestone or non-limestone habitats. Examples are Macromitrium orthostichum, Ectropothecium perminutum and Vesicularia montagnei.
4. Casuals. Non-limestone mosses which are occasionally collected on limestone. Examples are Meteorium miguelianum and Ectropothecium dealbatum.

Table 2 shows the percentage of limestone mosses found in Malaya. The species of mosses from the families Pottiaceae, Meteoriaceae, Thuidiaceae and Hypnaceae seem to predominate in the limestone moss flora. Sematophyllaceae with a total of 97 species is not represented at all on the limestone habitat. This is probably explained by the fact that most of the species of this family are found at altitudes above 1000 m, whereas the highest limestone hill is only 713 m. Another reason could be that most of the species in this family are epiphytes. The same reasons also apply to the scarcity of Dicranaceae and Hookeriaceae on limestone. Since Sphagnum avoids calcium, its absence on the limestone is understandable. The comparatively dry nature of the limestone hills probably excludes members of the Leucobryaceae which occur mostly in constantly moist areas. European calcicolous vascular plants are aluminium sensitive and since Malayan limestones are deficient in aluminium, it is possible that this factor might play a role in determining the presence or absence of species of mosses on limestone.

Table 2. Number and percentage of species of mosses collected from limestone habitats as compared to total number of mosses reported from Malaya.

Family	Total Number of species reported for Malaya	Number of species collected on limestone	Percentage found on limestone
Sphagnaceae	5	0	0
Polytrichaceae	7	1	14
Diphysciaceae	3	0	0
Fissidentaceae	17	4	23.5
Ditrichaceae	2	0	0
Dicranaceae	34	2	5.8
Leucobryaceae	27	2	7.4
Calymperaceae	69	3	4.3
Pottiaceae	13	9	69.2
Funariaceae	1	0	0
Bryaceae	19	2	10.5
Mniaceae	4	0	0
Phyllodrepaniaceae	1	0	0
Rhizogoniaceae	4	0	0
Hypnodendraceae	5	0	0
Bartramiaceae	6	1	16
Erpodiaceae	1	0	0
Orthotrichaceae	16	4	25
Racopilaceae	3	0	0
Trachypodaceae	2	1	50
Pterobryaceae	14	3	21.4
Meteoriaceae	15	5	33.3
Phyllogoniaceae	1	1	100
Neckeraceae	22	11	50
Ephemeropsaceae	1	0	0
Daltoniaceae	5	0	0
Hookeriaceae	32	2	6.25
Thuidiaceae	9	4	44.4
Brachytheciaceae	2	2	100
Entodontaceae	3	0	0
Plagiotheciaceae	2	0	0
Sematophyllaceae	97	0	0
Hypnaceae	40	16	40
Total	482	73	15.1

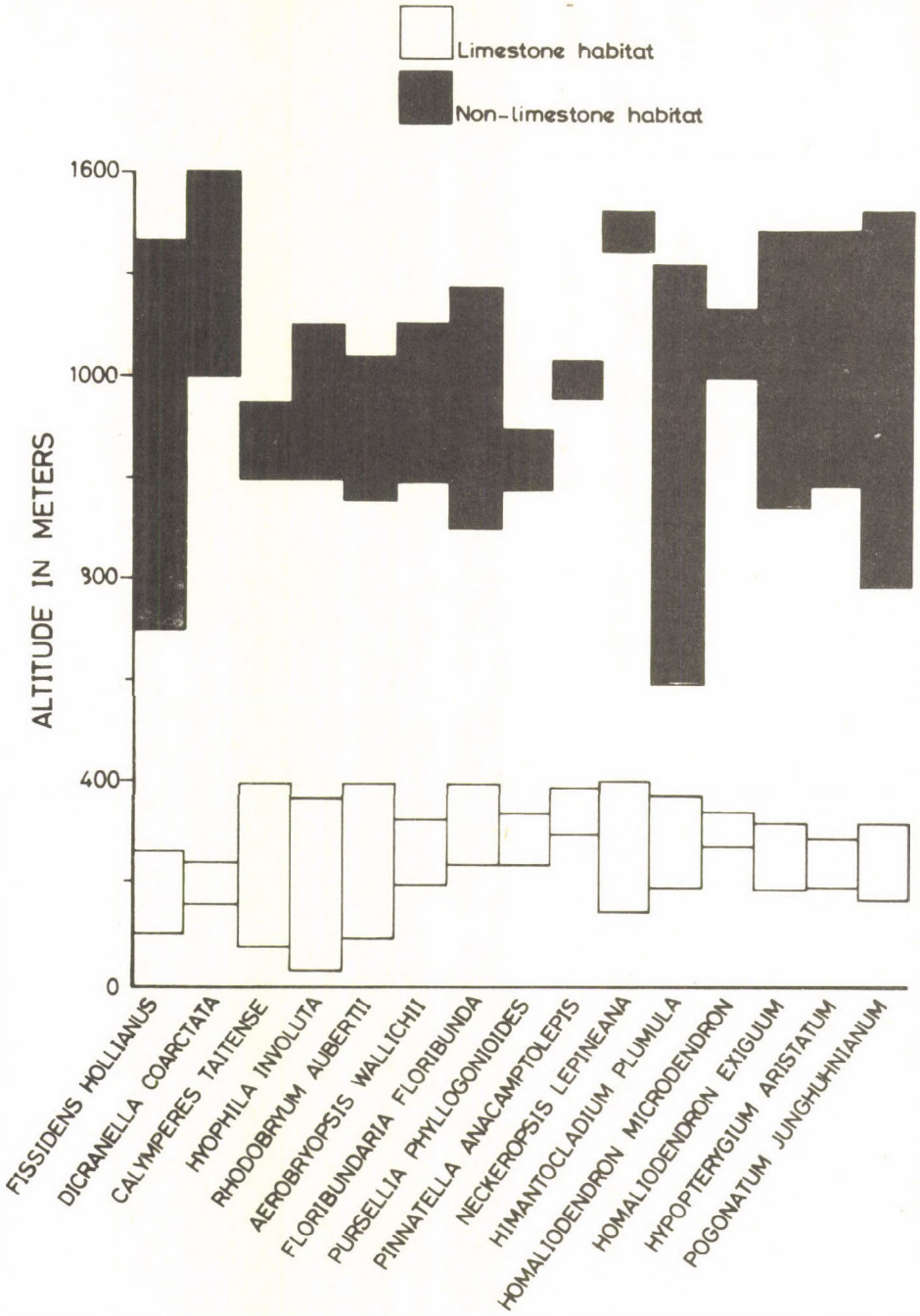

Fig. 5. Graph showing altitudinal distribution of some Malayan limestone mosses on non-limestone habitats.

Figure 5 shows the altitudinal range of a number of mosses on limestone and on non-limestone habitats. It is notable that some mosses occurring on limestone are found elsewhere in Malaya only at significantly higher elevations. A similar observation was made by Chin (1977) for vascular plants. The physiological basis for this phenomenon needs further study. Another interesting phenomenon is that the mosses rarely or never produce sporophytes on limestone. However, when these limestone mosses grow on non-limestone habitats at higher altitudes, sporophytes are commonly produced. Examples of limestone mosses which produce sporophytes only at higher altitudes are Hyophila involuta, Rhodobryum aubertii, and Fissidens hollianus, etc. This is another aspect on which further studies need to be carried out.

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THE ROLE OF BRYOPHYTES IN A CHALK GRASSLAND ECOSYSTEM

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In grasslands bryophytes are often neglected, but as in some other ecosystems they can play an ecologically important role. There are several published examples concerning the influence of bryophytes on germination and establishment of seedlings. The impact of this phenomenon depends mainly on cover and biomass of the bryophytes. In this paper cover and biomass in several Dutch chalk grasslands are discussed. These grasslands differ, among other factors, in aspect and management. Biomass of the bryophytes increases from south- to north-facing slopes, and also increases in the sequence abandoned grasslands → grasslands burnt once a year → grasslands mowed in autumn → grasslands grazed by sheep. Results of a decomposition experiment with bryophytes are shown and attention is paid to the possible role of bryophytes in the nutrient cycle. In nutrient-poor chalk grasslands bryophytes can be of importance in this respect.

INTRODUCTION

Bryophytes form an often neglected part of the vegetation, except in communities where they are dominant, e.g., bogs and arctic systems. Here, much attention has been paid to the role of bryophytes in the nutrient cycle, to their production, biomass and decomposition and to their consumption by animals (Longton 1984). For ecosystems in which bryophytes play a less conspicuous role, much less is known about their impact on

the other compartments of the system.

In our research we are trying to elucidate the role bryophytes play in grasslands. Special attention is being given to the influence of the bryophyte layer on germination and establishment of seedlings, on microclimate, and as emphasized in this paper, on the nutrient cycle.

The research is being carried out in chalk grasslands in the South of Limburg (The Netherlands). These grasslands (belonging to the Mesobromion) are very rich in species, in phanerogams as well as in bryophytes (Willems 1980, During & Willems 1985). Chalk grasslands are severely threatened in Western Europe. Formerly they were mostly grazed, but most of them are now abandoned resulting in a strong increase in species diversity. In the Netherlands their survival has been almost restricted to nature reserves. Within these reserves a management of grazing has sometimes been reintroduced or the grasslands are mown or burned once a year.

In these grasslands several short-lived species occur for which regular regeneration from seeds is essential. As bryophytes and seedlings occupy the same space, and germination and establishment of seedlings is often determined by microclimatic triggers, bryophytes could be important for the regeneration of these short-lived species. The presence of a bryophyte layer could thus result in habitat differentiation, one of the factors contributing to the high species diversity of these grasslands (Grubb 1977, Grubb et al. 1982, Keizer et al. 1985).

The presence of a bryophyte layer reduces seed germination of several species in chalk grasslands (Keizer et al. 1985) and in several other ecosystems (Johnson & Thomas 1978, Mallik et al. 1984, Perttula 1941). On the other hand bryophytes enhance the survival of seedlings (Johnson & Thomas 1978, Keizer et al. 1985, Pavone & Reader 1985). The impact of these phenomena depends mainly on bryophyte cover. We have investigated first, bryophyte cover and biomass on several slopes to see whether the effects on germination and establishment could be sufficient to have a significant effect on, for example,

species diversity. Secondly, we have tried to relate bryomass on the slopes to aspect and management. Third, the bryomass data together with the preliminary results of a decomposition experiment give information about the role of the bryophytes in the nutrient cycle of these ecosystems.

METHODS

The chalk grasslands are situated in the South of the Netherlands (Fig. 1). One slope, 'Melaten', is close to the Dutch border in Western Germany, near Aken. Most of the grasslands are owned and managed by the Government Department of Agriculture and Fisheries. Management, aspects and other site factors are summarized in Table 1.

Table 1. Biomass and cover of the bryophytes in several chalk grasslands in South-Limburg in spring, 1985. n = no. of samples

	management	aspect	date day/month	biomass (ton/ha)	cover bryophytes (%)	n
Bemelerberg	abandoned	SW	2-4	0.01 ± 0.01	3.2 ± 6.9	16
Kunderberg	burning	S	6-3	0.04 ± 0.04	12.3 ± 10.1	16
Vrakelberg	mowing	SE	6-3	0.09 ± 0.09	12.8 ± 10.6	30
Berghofweide	grazing	S	26-3	0.12 ± 0.11	8.4 ± 6.8	16
Melaten	grazing	S	3-5	0.19 ± 0.14	26.4 ± 23.4	16
Wylrer Akkers	burning	NW	4-2	0.23 ± 0.27	41.2 ± 31.8	16
Gerendal I	mowing	NW	3-5	0.36 ± 0.26	44.6 ± 26.2	16
Gerendal II	mowing	NW	8-3	0.46 ± 0.49	51.6 ± 25.4	16
Wylrer Akkers	mowing	NW	7-3	0.68 ± 0.48	41.3 ± 21.5	16
Gerendal II	grazing	W	8-3	0.68 ± 0.45	39.8 ± 22.9	10

During the period February - April 1985, 10, 16 or 30 randomly chosen 20 x 30 cm relevés were made within a plot of about half a hectare at each site. Total cover of phanerogams

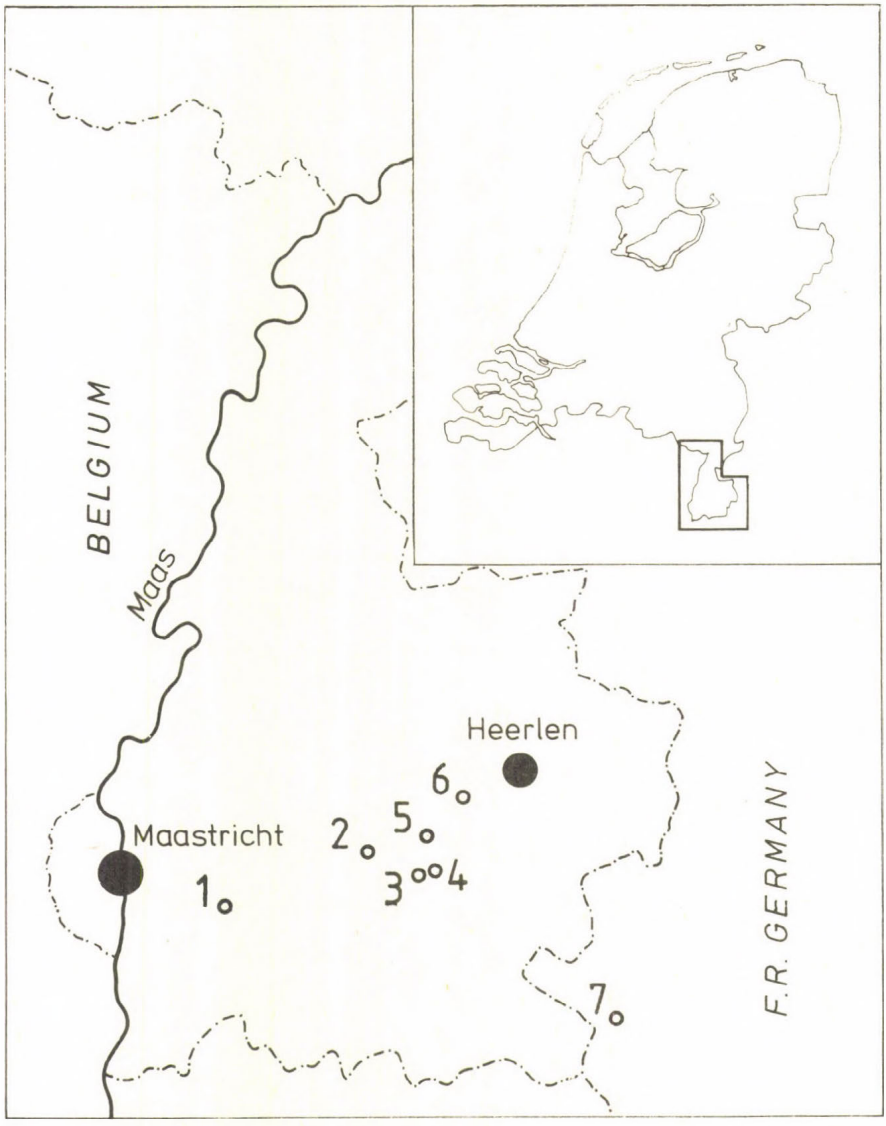

Fig. 1. Distribution of the chalk grasslands. 1. Bemelerberg; 2. Gerendal I and II; 3. Wylrel Akkers; 4. Berghofweide, 5. Vrakelberg; 6. Kunderberg; 7. Melaten.

and percentage cover of each bryophyte species were estimated in each relevé. From a central area of 10 x 10 cm all bryophytes were removed and cleaned by removing soil particles, etc. Afterwards, they were rinsed briefly in water. Air-dry weight of the total bryophyte layer was determined after drying for 48 h. at 70 °C. On some slopes fluctuations in bryomass have been followed during almost one year by the same method.

Rate of decay of the bryophytes was measured by means of litter bags (polyethylene bags 10 x 10 cm with mesh width of 0.3 mm). In March 1984, a mixture of Calliergonella cuspidata and Pseudoscleropodium purum was collected on the Wylrer Akkers, and air-dried at room temperature. Half of the moss was killed by heating at 180 °C for 30 minutes. Afterwards, the killed bryophytes were air-dried again at room temperature. One hundred litter bags containing 1.0 gram of moss, 50 air dry and 50 killed, were spread out on 5. 4. 1984 on the soil surface of the Wylrer Akkers below a mostly thin carpet of bryophytes. Nitrogen, phosphorous and potassium content was determined for ten additional replicates of the two types of material, using an autoanalyzer. Five times within one year, samples of 10 litter bags of both types were removed, the remaining moss was weighed after drying for at least 48 hours at 70 °C, and N, P and K content estimated as before. It was necessary to rinse the samples with water to remove small soil particles, etc. Unfortunately, K is easily washed out by water (including rain), so it was not possible to get very accurate data for the K-content.

RESULTS

The bryomass on several slopes in spring, 1985, is shown in Table 1. Bryomass is primarily determined by aspect: north-facing slopes have higher bryomass than south-facing slopes. Regardless of aspect, there is an increase in bryomass in the sequence abandoned → burned → mowed → grazed slopes. Only a few bryophyte species, mainly pleurocarpous species, reach high cover, e.g., Calliergonella cuspidata, Eurhynchium hians, E. striatum, Brachythecium rutabulum, Campylium chrysophyllum,

Ctenidium molluscum and Pseudoscleropodium purum, but also Fissidens cristatus and F. taxifolius. Many acrocarpous species are sometimes present but, with the exception of Weisia controversa and W. longifolia on some slopes, their cover is mostly negligible.

Fig. 2 shows the decline in dry weight and the loss of N, P and K during the first year of the decomposition experiment. As expected, the decay of the killed bryophytes is much greater than of the air-dried bryophytes, which formed many new shoots in the litter bags. However, even here there has been a decline in weight of over 20% in one year. The loss of weight

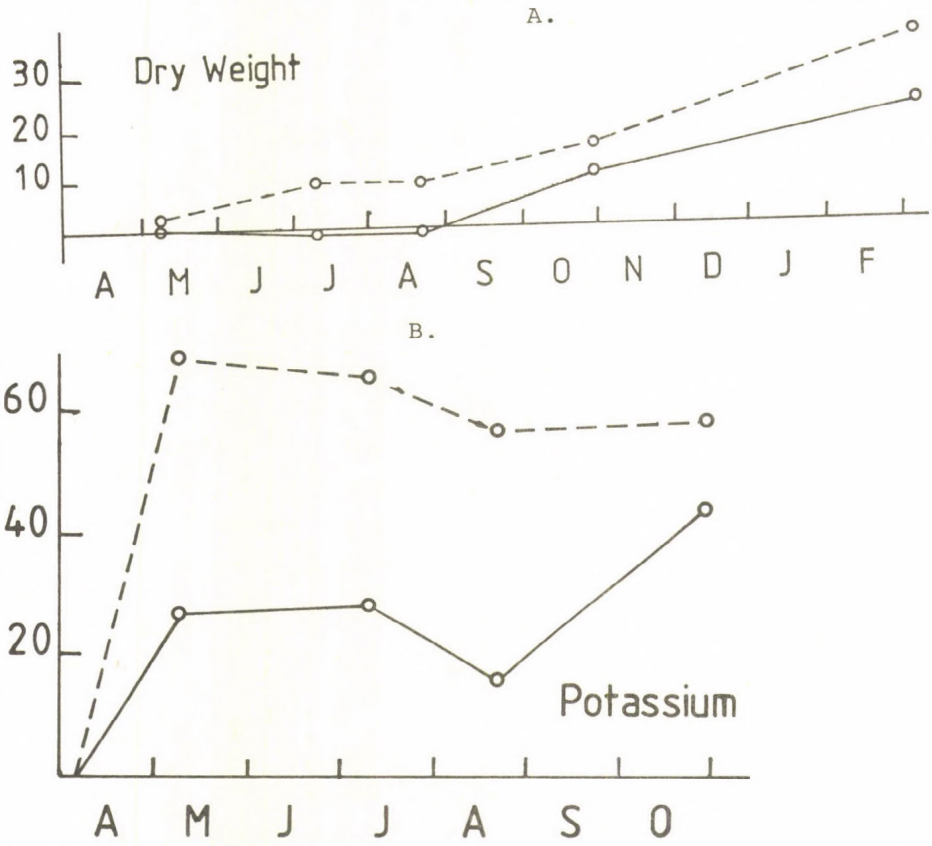

Fig. 2. Percentage decrease in (A): dry weight and (B) potassium in litter bags with dead (- - -) or air dried (——) shoots of Calliergonella cuspidata and Pseudoscleropodium purum in a north-facing grassland during the first year, starting 5.4.1984.

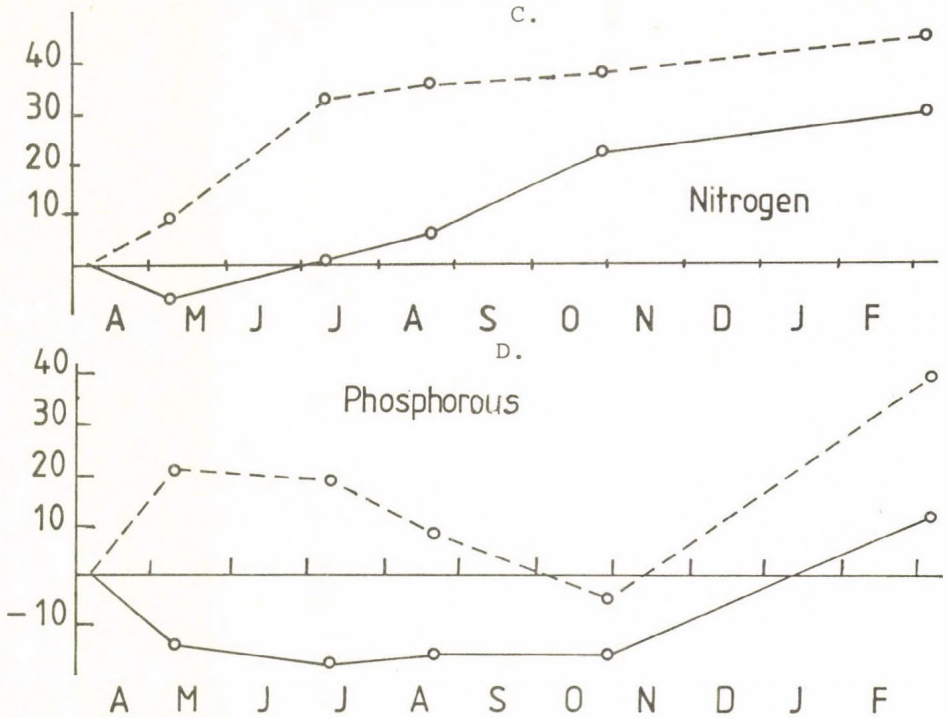

Fig. 2. (continued). Percentage decrease in (C) nitrogen and (D) phosphorous in litter bags with dead (- - -) or air-dries (——) shoots of C. cuspidata and P. purum in a north facing grassland during the first year, starting 5.4.1984.

was highest for K but, as stated before, the methods used made it very difficult to get a clear picture of the real loss of K from the killed bryophytes. Ca. 30% of the nitrogene disappeared after half a year.

DISCUSSION

The differences in bryomass between south- and north-facing slopes are easily interpreted as a result of the more extreme microclimate of the former. It is surprising that on south-, as well as on north-facing slopes increase of the bryomass is in the sequence no management → burning → mowing → grazing with sheep.

The absence of bryophytes from the abandoned chalk grasslands in Table 1, and many similar sites, is the result of the very high cover of tall grasses together with the accumulation of huge amounts of litter. Only a few species, e.g., Brachythecium rutabulum, are able to grow here, and then in small quantities (Furness & Grime 1982, During & Willems 1985). On burned slopes the bryophytes are severely damaged every winter resulting in low bryomass throughout the year (the sampling on the burned slopes (Table 1) was shortly before burning).

Preliminary observations suggest that bryomass is very constant during the year on grazed slopes while on mown slopes there are strong fluctuations: on south-facing slopes the bryomass seems to decrease after mowing while on the north-facing slopes the reverse is true. We suggest that on south slopes bryophytes decrease due to the sudden intense light input combined with decreasing air humidity. In contrast, on the north-facing slopes, with mostly a higher biomass of phanerogams in summer, light reduction below the phanerogams prevents growing of the bryophytes in summer so they can profit from the mowing. Soil and air humidity are mostly much higher on north- than on south-facing slopes, especially in autumn.

The slope Gerendal-II is divided into a grazed and a mown part. The grazing started in 1979: before that management was as on the other part, mowing in autumn. The bryophyte layer was similar on both slopes (H. J. During, personal observation). The bryomass is now greater in the grazed part (Table 1). Also, species composition on the grazed area has much changed in the last five years (During & Spooren, in prep). Ctenidium molluscum and acrocarpous species such as Pottia spp. and Ephemerum serratum have increased. On the other hand, Plagiomnium undulatum has decreased. So the changed phanerogam structure is already reflected in the bryophytes. We can conclude that there is wide variation in bryomass and moss cover on these chalk grasslands. As cover can be as high as 50% in spring (Table 1), the impact on germination and establishment of seedlings may be severe. Interestingly, high cover and bryomass may be expected on grazed slopes, i.e., the slopes with, in general, the lowest cover of phanerogams. These slopes often

have open spots due to trampling, etc. So, while the possibilities for germination of species vulnerable to reduced Red/Far Red ratios or light transmission are reduced by the presence of bryophytes other biotic factors enhance possibilities for seed germination. However, in some grazed British chalk grasslands, bryomass can be very low, due to the very compact and closed phanerogam turf, resulting from a long, intense grazing history (Shimwell 1971, pers. observation).

It is tempting to suggest that the bryomass and its nutrient content play an important role in the nutrient cycle of the ecosystem. On the Dutch chalk grasslands R. Bobbink (in prep.) showed that input of N to the system stimulates growth of the phanerogams strongly while P in most cases did not. N content of the bryophytes in the litter bags was on average 1.13%. Loss of N from the litter bags during the growing season was ca. 20% in the air-dried samples (Fig. 2). If we assume a bryomass of 0.5 ton/hectare, the release of N from bryophytes during the growing season of the phanerogams will be 1.1 kg/ha. Comparing these and growth-analysis data in these grasslands (R. Bobbink, in prep.), we may assume that the contribution of the bryophytes to the N-uptake from the system of the phanerogams will be 10% at most. However, it can be more important locally as biomass can be as high as 2-3 ton per hectare in some patches of bryophytes. Perhaps superficially rooting seedlings can profit from this source of nutrients. This aspect will be subjected to further research.

The results of our research show that bryomass in Dutch chalk grasslands is small: it seldom exceeds 20% of the peak phanerogam standing crop which generally reaches ca. 4 ton/ha. From other published data about grasslands we may assume that the bryomass will not normally exceed this 20%. Exceptions can be found in Hillier et al. (1984) and Fliervoet (1984) who recorded bryomass as high as 30-40% of total aboveground biomass in summer.

Bryophytes could play a role in other aspects of the nutrient cycle. Their most-pronounced growth-period is in the winter (Al-Mufti et al. 1977) and their nutrient uptake might be important in preventing leaching of nutrients from the sys-

tem, especially as nutrient input increases as a result of 'acid rain'. This input of nutrients will not be used by the phanerogams during the winter and is, without bryophytes, lost from the ecosystem. Bryophytes can retain these nutrients because of their capacity for uptake by the whole plant. The result may thus be an increased amount of nutrients within the ecosystem. We have not yet tried to quantify this.

Although bryophytes form only a small part of the total vegetation, we have to keep in mind that chalk grasslands are very nutrient-poor communities. Even a small extra flux of nutrients could be important for growth or regeneration of the phanerogams. During recent years this has been demonstrated dramatically by the N-input from air pollution resulting in increased dominance of the tall grass Brachypodium pinnatum (Bobbink & Willems 1984).

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DISTRIBUTION OF BRYOPHYTES ON SUBANTARCTIC MACQUARIE ISLAND

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Bryophytes are a significant component of all vegetation types on subantarctic Macquarie Island. A pilot study using a computer database program has shown that useful information on distribution of bryophytes can readily be assembled from notes on herbarium labels.

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On subantarctic Macquarie Island (54°30' S, 158°55' E), bryophytes are a significant component of all vegetation types. Macquarie is a small island, approximately 34 x 4 km, made up of an undulating plateau, 200-400 m above sea level, surrounded by cliffs and steep coastal slopes. Coastal flats and terraces surround about 50% of the coast. The climate is uniformly cool (mean annual temperature 4.7 °C, Jacka et al. 1984), wet (mean annual precipitation 893 mm) and windy (mean wind speed 8.3 m/sec, Löffler 1983).

The 45 species of vascular plants, approximately 117 species of bryophytes and approximately 100 species of lichens (Seppelt et al. 1984, Seppelt 1984a,b) form a number of vegetation types, recognisable by their dominant vascular plant species.

As part of a study of the role of bryophytes in each vegetation type, and the distribution of bryophyte species amongst them, we have begun an examination of information associated with herbarium collections we have made since 1979. We present

here the results of a pilot study, using a computer program, based on 1,000 bryophyte collections.

For each collection, as much of the following information as available has been entered into the database:

> genus; species; family; collection date; locality; the following site details: altitude, substrate, vegetation type, associated species, "niche notes" (e.g., beside waterfall, on rock in creek...).

Not all information was immediately available for all specimens. For instance, not all specimens have been fully identified: where queries remained as to the specific name, the record has either been omitted from the following summary or entered by genus name only. Altitude was not always recorded, but where a grid reference to the topographical map has been recorded, altitude can be determined. At this stage, however, only specimens for which altitude has been recorded have been included in the summary tables. The tables summarise qualitative information only - numbers of specimens in each category are not indicated. Although the data in the pilot study are limited, it is clear that the system can provide certain kinds of useful information.

Table 1 shows that species such as Amblystegium serpens, Macromitrium longirostre, Pottia heimii and Ulota phyllantha have been collected only at lower altitudes, which on Macquarie Island ensompass coastal flats, rocky outcrops on beaches, sea stacks, beach terraces and lower coastal slopes. In Table 2, these species are seen to have been collected in tall tussock grassland (common on lower coastal slopes), on sea stacks and on rocky substrates. Other species, such as Ditrichum strictum, Pogonatum alpinum, Psilopilum australe and Racomitrium lanuginosum occur only at higher altitudes, in fellfield and herbfield vegetation types and on rocky substrates. About half the area of the undulating plateau of the island supports fellfield vegetation. In the herbfield or short tussock grassland areas of the plateau, small rocky outcrops are common, and it is from these that Ditrichum, Po-

Table 1. Distribution of selected species by altitude from pilot study.

Altitude range (m)	1- 50	51-100	101-150	151-200	201-250	251-300	301-350	over 350
Amblystegium serpens	+	+						
Andreaea spp.				+		+	+	+
Bartramia papillata	+	+					+	+
Blindia magellanica		+		+				
Brachythecium				+		+		
Breutelia elongata		+						
Breutelia pendula		+			+			
Bryum argenteum				+				
Calyptrochaeta apiculata	+							
Campylopus spp.						+		+
Conostomum pentastichum						+		+
Dicranella cardotii		+	+		+			
Dicranoloma billardieri						+		+
Dicranoweisia antarctica							+	+
Ditrichum punctulatum			+			+	+	
Ditrichum strictum							+	+
Drepanocladus		+				+		
Fossombronia		+						
Frullania rostrata		+				+		
Funaria sp.					+			
Grimmia apocarpa		+	+					
Jamesoniella colorata		+						
Lepidolaena			+			+		
Lepidozia spp.			+					
Lophocolea bidentata		+						
Lophocolea bispinosa			+					
Macromitrium longirostre	+		+					
Metzgeria sp.		+						+
Muelleriella crassifolia	+	+	+	+				
Plagiochila spp.			+	+				+
Pogonatum alpinum						+		
Polytrichum juniperinum			+					
Pottia heimii	+	+						
Psilopilum australe							+	
Ptychomnion aciculare		+				+		
Racomitrium crispulum							+	+
Racomitrium lanuginosum						+	+	+
Rhacocarpus purpurascens						+		+
Rhizogonium mnioides		+			+			
Riccardia aequicellularis			+		+			
Riccardia colensoi		+						
Sphagnum falcatulum					+			
Tayloria octoblepharis	+							
Thuidium furfurosum		+		+		+		
Tortula spp.		+						
Ulota phyllantha		+						

Table 2. Distribution of selected species amongst vegetation types, by association with dominant vascular plants and by substrata from pilot study.

	Vegetation type				Dominant vascular species			Sub-strate	
	Tall tussock grassland	Herbfield	Fellfield	Mire	Pleurophyllum	"short grass"	Azorella	Beach stack	Rock
Achrophyllum dentatum	+								
Amblystegium serpens	+							+	+
Andreaea	+		+						+
nitida			+						+
sp. (orange)			+						
Aulacomnium palustre				+					+
Bartramia papillata	+		+				+	+	+
Blindia			+						+
Brachythecium rutabulum	+	+		+	+				
Breutelia	+	+	+		+	+			
elongata		+				+			
pendula		+		+		+			+
Bryum				+		+	+		
billardieri		+		+		+			
dichotomum		+							
laevigatum			+	+					+
Calyptrochaeta apiculata	+							+	+
Campylopus introflexus	+	+				+			+
Cephaloziella				+					
Ceratodon purpureus		+							
Chandonanthus squarrosus		+	+						
Cheilothela chilensis				+					
Clasmatocolea rotata		+		+	+				
Conostomum pentastichum		+	+	+					+
Cryptochila		+	+	+					
Dicranella cardotii		+		+	+				
Dicranoloma		+	+			+	+		
billardieri		+							+
Dicranoweisia antarctica	+								+
Ditrichum			+						+
brevirostre						+			
punctulatum		+							
strictum			+						
Drepanocladus aduncus		+		+	+				+

Table 2. (continued)

Drepanocladus uncinatus										+
Fissidens rigidulus										+
Funaria		+								
Grimmia apocarpa										+
Hypnum cupressiforme		+		+	+					
Isotachis intortifolia				+						
Jamesoniella colorata		+	+	+		+				+
Jungermannia inundata		+				+				
Jungermannia		+		+	+					
Lembophyllum divulsum					+					
Lepidolaena allophylla		+	+							
Lepidozia		+	+	+	+		+			+
Lophocolea	+	+		+	+	+		+		+
bispinosa	+									
bidentata		+				+				
pallida				+	+					
Macromitrium longirostre								+		+
Marchantia berteroana				+						
Megaceros		+		+	+					
Metzgeria	+	+			+					+
Muelleriella crassifolia	+							+		+
Philonotis scabrifolia	+	+								
Plagiochila	+	+	+		+	+	+			
Pogonatum alpinum		+	+			+	+			+
Pohlia sp.		+		+						
Polytrichum juniperinum		+								
Pottia heimii	+									+
Psilopilum australe		+								+
Ptychomnion aciculare		+			+					
Racomitrium crispulum	+		+		+		+			+
Racomitrium lanuginosum		+	+				+			+
Rhacocarpus purpurascens			+							
Rhizogonium mnioides	+	+								
Riccardia aequicellularis		+	+	+						
Riccardia cochleata			+	+	+					
Riccardia colensoi		+			+					
Sematophyllum		+	+				+			
Sphagnum falcatulum		+		+	+					
Tayloria octoblepharis	+	+					+			
Thuidium furfurosum		+	+		+		+			+
Tortula rubra	+			+						
Tridontium tasmanicum										+
Ulota phyllantha										+

* "short grass" includes *Agrostis magellanica*, *Festuca contracta*, *Luzula crinita*.

gonatum, Psilopilum and Racomitrium have frequently been collected.

Those taxa which are recorded over a wide altitudinal range may (1) occur in a vegetation type(s) with a wide altitudinal range (e.g., Ptychomnion aciculare in herbfield, Thuidium furfurosum in herbfield and fellfield), (2) occur on a specific substrate relatively independently of the surrounding vegetation (e.g., Bartramia papillata on rock) or (3) include a number of species which have, between them, a wide altitudinal and habitat tolerance (e.g., Plagiochila spp.).

The vegetation type listed in Table 2 as "herbfield" is far from homogeneous, including, on drier sites, short tussock grassland dominated by Luzula crinita and Agrostis magellanica and, on wetter sites, a wet herbfield dominated by Pleurophyllum hookeri (Seppelt et al. 1984). This distinction can be seen interestingly in the distribution of some of the bryophytes: Brachythecium rutabulum and Clasmatocolea rotata have been collected from mire as well as herbfield, suggesting a tolerance of very moist conditions. Table 2 shows them to be associated with Pleurophyllum hookeri but not Agrostis/Luzula. Pogonatum alpinum and Campylopus introflexus have been collected from fellfield as well as herbfield, and on rock substrate, suggesting a good tolerance for well-drained sites. These two species are associated with Agrostis/Luzula but not Pleurophyllum in Table 2.

This pilot study, although based on only a small proportion of the collections that have been made, has shown that useful information of a variety of types can be obtained by collating collection notes from herbarium material in this way. Considerably more information will be available and more reliable interpretations will be possible when the information from the approximately 7,000 specimens now available is included in the database.

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THE EFFECT OF FOREST AMELIORATION ON THE UNDERSTOREY BIOMASS, SPECIES RICHNESS AND DIVERSITY OF SOUTHERN BOREAL FINNISH MIRES

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The effect of forest amelioration (drainage, drainage + fertilization) on understorey biomass, species richness (S) and Shannon - diversity (H') was studied on peatlands in southern Finland. The field and ground layers were analyzed separately and combined. Three ombro-oligotrophic site types were used as case studies.

Concerning the ground layer, biomass decreased but both S and H' usually increased after drainage and especially after fertilization. In this case, the relative changes of S and H' were significantly positively correlated. With the field layer, biomass usually increased, H' decreased, and S increased in most cases. Dwarf shrubs and/or cottongrass increased in dominance after forest amelioration, causing a decrease in H', and hence a nonsignificant correlation between relative changes of S and H'. Combined understorey behaved more like the field layer regarding changes in biomass, owing to the greater influence of the increase in field layer biomass.

INTRODUCTION

Finland is one of the world's richest countries in peatland resources. Kivinen & Pakarinen (1981) estimated the peatland area of the world to be c. 420 million hectares, of which a little more than 10 million hectares are located in Finland. Of this, c. 9.34 million hectares were classified as "forestry land" in the 6th National Forest Inventory (Paavilainen 1982).

Forest amelioration (e.g., drainage, fertilization) is intensive on Finnish peatlands. It began in the 19th century and was at its maximum in the 1960s when approximately 300,000 hectares were drained annually. At the turn of this decade, the total area drained for forestry purposes stood at 5.3 million hectares and the aim is to drain c. 6.5 million hectares by the 1990s (Heikurainen 1982).

Because of the great economic profit of peatland afforestation, the conditions for forest growth as well as the growth, biomass and production of, in particular, the stem wood have been intensively studied in Finland. With the exception of Sarasto's study (1964), it was not until the 1980s that the other components of peatland forest ecosystems and especially their reaction to forest amelioration, were studied (e.g., Paavilainen 1980, Vasander 1982, Silvola et al. 1985 and their references).

In this paper I have analyzed the changes in biomass, species richness and Shannon - diversity in the understorey caused by drainage and fertilization in southern boreal ombro-oligotrophic peatland sites. In particular, the relationship between changes in biomass and diversity is considered, to determine whether changes in biomass lead to a change in species diversity as proposed, for example, by Bakelaar & Odum (1978). Field and ground layers are analyzed separately and combined.

MATERIAL AND METHODS

The study material consists of three different data sets.

1) Kosonen (1976, 1981) studied one virgin and five drained or drained/fertilized ombrotrophic dwarf shrub pine bog (IR) sites (for Finnish mire site types, see e.g., Ruuhijärvi 1983) from Vilppula, southern Finland. The drained sites were in the second or third (final) stage of drainage succession (Heikurainen & Pakarinen 1982).

2) Ouni (1977) studied a virgin and two drained oligotrophic sedge fen (SD) sites in Lyly, southern Finland. One was drained 10 years previously and was in its first stage of drainage succession. The other was drained 40 years previously and was in its second stage. The latter site had been fertilized twice with NPK-fertilizer.
3) Vasander (1981, 1982) studied virgin, drained and drained/fertilized hummock and hollow pine bog (KeR, ITR) in Lammi, southern Finland. The drainage was made 13 years and the NPK-fertilization 9 years previous to data collection. The sites were still in their first or second stage of drainage succession. The sites were separated into different plant communities which were here handled separately. The data were used by Vasander (1984) when analyzing the diversity changes of those plant communities. In this paper, the tree layer is excluded.

Together, the material consists of 19 cases where virgin sites or communities are compared with the ameliorated ones. In all three studies, the material was gathered during late summer - early autumn by a harvesting method described in Vasander (1982). The diversity of different sites and communities is expressed as species richness (S) and by means of the Shannon H' values: $H' = -\sum p_i \ln p_i$, where p_i is the proportion of the total biomass contributed by species i. Biomass, species richness and Shannon-diversity are expressed separately for the field and ground layers and also for the combined values to give the "whole understorey". The nomenclature follows Koponen et al. (1977) for mosses and hepatics and Hämet-Ahti et al. (1984) for vascular plants.

RESULTS

Biomass, species richness and diversity of the virgin site types

The above-ground biomass of the field layer varies between 44 g/m^2 (No. 5 in Table 1) and 282 g/m^2 (Nos 1, 9 in Table 1).

Table 1. Above-ground biomass (B, g/m^2), species richness (S) and Shannon-diversity (H') of the virgin site types and plant communities. Finnish abbreviations of the site types: KeR = hummock and hollow pine bog (Vasander 1982), SN = sedge fen (Ouni 1977), ITR = dwarf shrub pine bog with cottongrass (Vasander 1981), IR = dwarf shrub pine bog (Kosonen 1976, 1981).

	Field layer			Ground layer			Whole understorey			
Site type	B	S	H'	B	S	H'	B	S	H'	No.
KeR, high hummocks	281.6	7	1.339	185.8	9	1.185	467.4	16	1.950	(1)
" low hummocks	179.1	7	1.632	239.3	8	1.526	418.4	15	2.254	(2)
" upper hollows	118.8	8	1.606	271.3	6	1.505	390.1	14	2.150	(3)
" moist hollows	91.3	6	1.060	311.3	6	0.704	402.6	12	1.321	(4)
" wet hollows	43.9	5	1.237	453.0	3	0.779	496.9	8	1.126	(5)
" whole site	213.1	9	1.506	233.7	13	1.764	446.8	22	2.333	(6)
SN	151.4	6	1.569	432.0	3	0.454	583.4	9	1.316	(7)
ITR	237.9	11	1.520	69.2	9	1.092	307.1	20	1.957	(8)
IR	282.2	11	1.300	82.9	7	1.428	365.1	18	1.865	(9)

The biomass in the former site type was formed by five species with a H' value of 1.237. Scheuchzeria palustris (33.3%), Vaccinium oxycoccos (30.1%) and Carex limosa (28.9%) formed the bulk of the biomass. As Empetrum nigrum, Vaccinium uliginosum and Ledum palustre formed 85.3% of the biomass the H' value (1.3) was lower on IR* (11 species) than on high hummocks of KeR (1.339, 7 species) where the three most prominent species (Empetrum nigrum, Calluna vulgaris, Eriophorum vaginatum) formed 88.2% of the biomass. The H' value was the lowest (1.06) for moist hollows of KeR, where Eriophorum vaginatum alone formed 63.3% of the biomass.

Due to the dominance of dwarf shrubs and cottongrass, the relationship between S and H' was low (r = 0.256, n = 9). This was the case also with the relationship between the biomass and H' (r = 0.233). However, as there were many species associated with those site types where biomass was high, there was a significant correlation between S and biomass (r = 0.724*) **.

The biomass of the ground layer varies from 69 g/m^2 (No. 8 in Table 1). Sphagnum angustifolium (47.0%) and Pleurozium schreberi (41.9%) formed the bulk of the biomass on the former site. On the latter site the biomass was formed only by three species (Sphagnum balticum 68.3%, S. majus 25.6%, S. tenellum 6.1%), with H' of 0.779.

There was a negative relationship between ground layer biomass and S (r = -0.661*) as also between ground layer biomass and S (r = -0.582). Concerning the composition of the biomass of the ground layer, S and H' described well the same phenomenon (r = 0.757*). High biomass was associated with low diversity.

When the field and ground layers were combined, the range of biomass diminished. The difference between the minimum (307

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* For Finnish abbreviations of the site types, see Table 1.

** Asterisks (*, **, ***) refer to statistical significance of $p<0.05$, $p<0.01$ and $p<0.001$, respectively.

g/m^2, ITR) and maximum (497 g/m^2, wet hollows in KeR) was 190 g/m^2, i.e., 38.2% of the maximum value. This figure is 84.4% for the field layer and 84.8% for the ground layer. The relationship between biomass and S was negative (r = -0.633*) as was the relationship between biomass and the H' value (r = -0,471). There was a significant correlation between S and H' value (r = 0.807**).

Effect of forest amelioration on biomass, species richness and diversity

The biomass of the field layer increased in most cases after drainage and especially after drainage and fertilization (Table 2, Figs 1-2). On drained sites, the increase was the greatest on oligotrophic sedge fen (3.2-fold). This was largely due to the biomass "explosion" of Betula nana. Its biomass was 37 g/m^2 (24.5%) on the virgin fen and 336 g/m^2 (69.9%) on the drained fen. On drained hummocks of the ombrotrophic bog, dwarf shrubs increased in biomass after drainage and this led to a decrease in H' value. In moist hollows drainage caused a decrease in the biomass of Eriophorum vaginatum (58 g/m^2, 81.3% $\longrightarrow$ 22 g/m^2, 48.6%). In the case of the drained IR, the biomass decreased in two cases out of three (Nos 9, 11 in Table 2). This was caused by a decline in Empetrum nigrum.

The effect of fertilization on the field layer was to compound the infleuce of drainage. The increase in biomass, caused mostly by dwarf shrubs and cottongrass, generally decreased the H' value. As new species were able to colonize the sites and old ones able to remain and thrive, S mostly increased (Table 2). As biomass increase was mostly by dominants, there was a negative relationship between the change of field layer biomass and H' value (r = -0.535*, n = 19). Also, the relationship between the changes in S and H' was negative (r = -0.274). The changes in biomass and S were positively correlated (r = 0.694***).

The biomass of the ground layer usually decreased sharply after drainage and especially after fertilization. On drained sites the decrease was highest on high hummocks of KeR (No. 1

Table 2. Relative values of biomass (B), species richness (S) and Shannon-diversity (H') of drained (D) and fertilized (DF) site types and plant communities compared to virgin ones (having value 1). Abbreviations of the site types as in Table 1. Figures in brackets after IR-sites denote years since drainage (D) and fertilization (F). Figures in brackets on the right side of the Table are the same as in Figures 1-2. Sources: 1-6: Vasander (1982), 8: Vasander (1981), 9-13: Kosonen (1976). - = no data.

	Field layer						Ground layer						Whole understorey						
	D			DF			D			DF			D			DF			
Site type	B	S	H'	B	S	H'	B	S	H'	B	S	H'	B	S	H'	B	S	H'	No.
KeR high hummocks	1.12	1.14	0.69	2.44	1.43	1.03	0.37	1.22	1.50	0.29	1.22	1.27	0.93	1.19	0.81	1.89	1.31	0.79	(1)
" low hummocks	1.12	1.29	0.88	3.64	1.14	0.81	0.41	0.88	0.90	0.30	1.38	1.08	0.73	1.07	0.92	1.80	1.27	0.79	(2)
" upper hollows	-	-	-	4.22	1.13	0.86	-	-	-	0.20	1.67	1.29	-	-	-	1.43	1.36	0.92	(3)
" moist hollows	0.89	1.17	1.22	1.61	1.33	1.00	0.57	0.67	0.73	0.28	2.17	2.20	0.64	0.92	1.04	0.59	1.75	1.61	(4)
" wet hollows	1.23	1.20	0.75	7.79	1.80	0.59	0.97	1.00	0.18	0.21	2.33	1.77	1.00	1.13	0.51	0.88	2.00	1.40	(5)
" whole site	1.07	1.00	0.82	2.36	1.33	1.03	0.50	0.92	1.09	0.27	1.15	1.18	0.93	0.95	0.84	2.23	1.23	0.64	(6)
SN	3.20	1.00	0.75	1.27	1.17	0.87	0.43	2.00	2.56	0.32	1.33	2.29	1.14	1.33	1.31	0.57	1.22	1.44	(7)
ITR	-	-	-	1.09	0.91	0.72	-	-	-	1.17	0.67	0.28	-	-	-	1.10	0.80	0.74	(8)
IR (D 20)	0.45	1.00	1.18	-	-	-	0.69	1.43	1.21	-	-	-	0.51	1.17	1.19	-	-	-	(9)
" (D 20, F 13)	-	-	-	0.18	0.73	1.10	-	-	-	0.57	1.00	0.83	-	-	-	0.27	0.83	1.07	(10)
" (D 51, D 39)	0.74	1.09	1.25	-	-	-	1.12	1.00	1.11	-	-	-	0.83	1.06	1.19	-	-	-	(11)
" (D 65)	1.08	0.91	1.08	-	-	-	0.41	0.71	0.84	-	-	-	0.93	0.83	0.91	-	-	-	(12)
" (D 65, F 9)	-	-	-	1.23	0.91	0.85	-	-	-	0.46	0.57	1.21	-	-	-	1.06	0.78	0.74	(13)

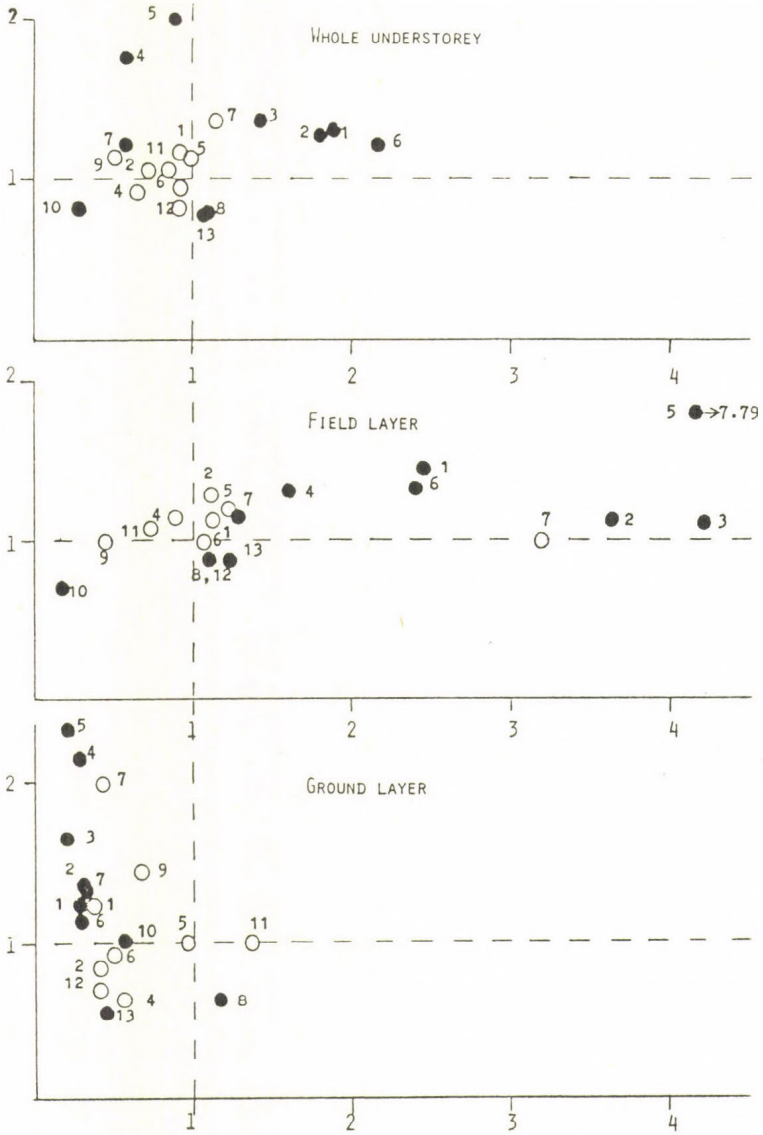

Fig. 1. The relative values of biomass (x-axis) and species richness (y-axis) of drained (o) and fertilized (●) site types and plant communities. The corresponding virgin site marked as one. Numbers correspond to those of Table 2.

in Table 2). The decrease of Sphagnum fuscum biomass was the greatest (125.5 g/m^2, 67.5% -- 28.6 g/m^2, 41.2%) there.

On fertilized sites the biomass of the ground layer was mostly between 20-30% of that on the virgin site. The de-

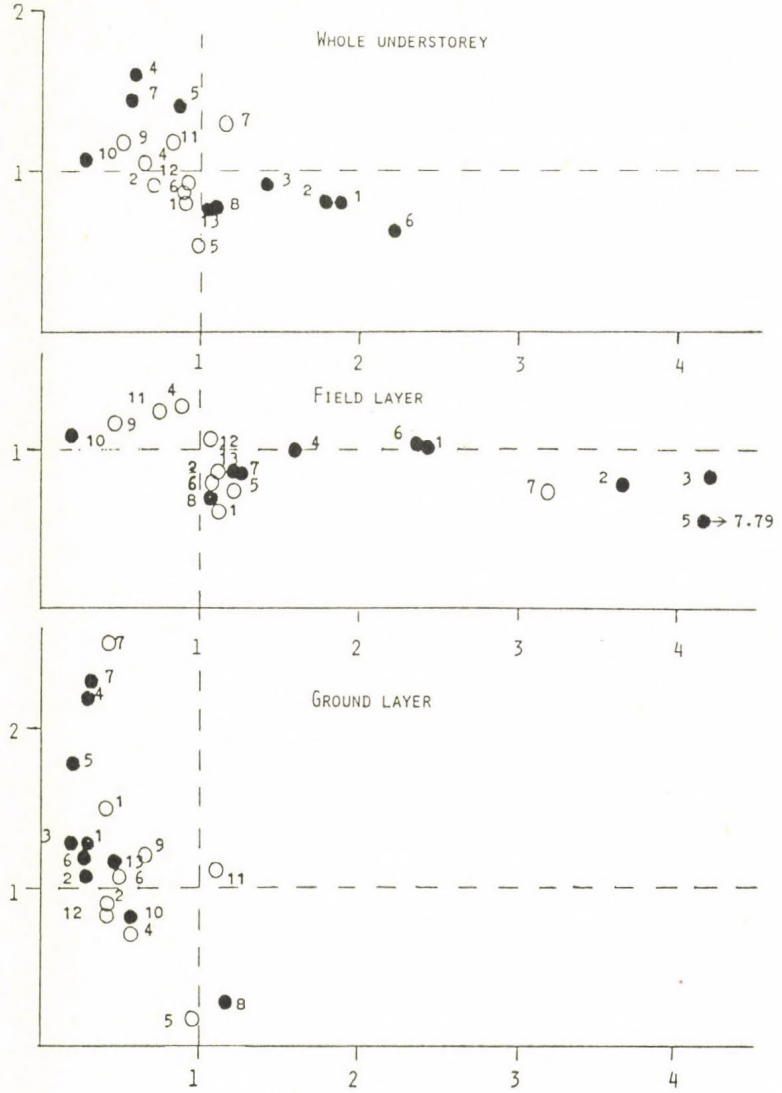

Fig. 2. The relative values of biomass (x-axis) and Shannon-diversity (y-axis) of drained (o) and fertilized (●) site types and plant communities. The corresponding virgin site marked as one. Numbers correspond to those of Table 2.

crease of the biomass was the greatest on upper hollows of KeR (No. 3 in Table 2). Colonization by new species (Pleurozium schreberi - 4.7% of the biomass, Pohlia nutans - 18.2%, Dicranum undulatum - 16.4% and D. polysetum - 0.4%), as well as the

decrase of the earlier dominants (Sphagnum balticum from 36.4% to 0%, S. rubellum from 19.6% to 0% and S. fuscum from 19.2% to 16.2%) caused the simultaneous increase of S and H'.

The relative increase of S was the highest in fertilized wet hollows (No. 5 in Table 2). Sphagnum majus and S. tenellum disappeared, being replaced by S. angustifolium (36.5% of the biomass), Drepanocladus fluitans (28.8%), S. rubellum (5.8%), Pohlia nutans (3.0%), Polytrichum strictum (0.5%) and Mylia anomala (0.1%). On the ameliorated sedge fen sites the trend was similar. Colonization by new species (Polytrichum strictum, Aulacomnium palustre, Pleurozium schreberi, Pohlia nutans), combined with the decrease of the dominant sphagna increased both S and H' while the biomass decreased.

In contrast to the general trend, ground layer biomass increased on fertilized ITR (No. 8 in Table 2). After fertilization the amount of sphagna decreased and that of Pleurozium schreberi increased (19.0 g/m^2, 41.9% on the virgin bog, 74.6 g/m^2, 92.4% on the fertilized bog). The increase in the biomass of Pleurozium schreberi had the same effect on drained IR site (No. 11 in Table 2).

Concerning the ground layer, the changes in biomass were negatively correlated with the changes in both S ($r = -0.477^*$) and H' ($r = -0.577^{**}$). Changes in S and H' were positively correlated ($r = 0.735^{***}$).

To analyse which of the two layers had the most effect on the changes of the whole understorey, the relationships between relative changes of B, S and H' of field and ground layers with the whole understorey were calculated. Using relative changes of biomass, the relationship between field layer and whole understorey gave the r-value of 0.376, while with the ground layer it was negative ($r = -0.280$). Although the correlation coefficients are not significant, they indicate that the changes in the field layer biomass have more effect on the changes of the whole understorey biomass. Changes in S were affected both by field layer ($r = 0.815^{***}$) and ground layer ($r = 0.929^{***}$) while the changes in combined understorey H' value were more affected by ground layer ($r = 0.741^{***}$) than by field layer ($r = 0.144$).

DISCUSSION

After drainage ecological conditions are changed; moisture is decreased and acidity increased, decomposition and the mineralization of bound nutrients are increased due to the increased microbial activity, and shading is increased due to increased tree growth. Fertilization can result in a "salt shock" (e.g., Reinikainen 1981). Fast dissolving and micronutrient mixture fertilizers have been found to be especially detrimental to bryophytes (Jäppinen 1985). All these changes in ecological conditions "stress" true mire plants resulting in the decrease of biomass and production observed.

When the fertility of the site increases a shift in limiting factors probably occurs, from nutrients (root) to light (shoot) (Newman 1973). This shift was evident here because whole understorey biomass was primarily affected by the ground layer in the virgin site and by the field layer on drained sites. The shift described above leads to a diminishment of peatland bryophytes especially Sphagnum species, which function as "perennial stayers" (During 1979) or "non-opportunistic climax species" (Johnson 1977). Where there are sufficient gaps in ground layer communities other species can establish themselves and regenerate (Grubb 1977). Colonists (e.g., Pohlia nutans, Ceratodon purpureus) begin to colonize the site after which forest moss species (e.g., Pleurozium schreberi) appear. This generally increases the diversity of the ground layer but at the same time the biomass is decreased (Figs 1-2). Structural complexity of the ground layer communities is increased, implying more diverse ways of exploiting the environmental resources (Bazzaz 1975). Species packing is an important factor in increasing the diversity during (secondary) succession (e.g, Mellinger & McNaughton 1975). The dominant field layer species (cottongrass, dwarf shrubs) are more competitive than the dominant ground layer species and have thus an advantage in the changed environmental conditions (e.g., Seppälä 1978, Vasander 1982). This will lead to the decrease of both field layer and whole understorey diversity (Table 2, Fig. 2).

Generally, the poorer the site the less there are species able to colonize during secondary succession (Grime 1977). This is especially so when tree and field layers are compared with the gound layer. It must be remembered that the material presented here consists of very or rather poor site types. On more fertile mire site types, where the amount of species and the nutrient status are greater (Reinikainen et al. 1984), the ground layer diversity would probably decrease after drainage.

The differing ability of plant species in different vegetation layers to colonize the site after disturbance is probably why different plant communities are practically independent of one another as far as diversity is concerned (e.g., Whittaker 1972, Slack 1984). This independence also extends to within whole vegetation layers. For example, Oksanen (1983) found prominent differences between diversity of moss and lichen vegetation in xeric Finnish pine forests along climatic gradients.

To conclude: the diversity of the ground layer usually increases in poor mire site types after drainage and especially after fertilization. This increase in α-diversity will, however, usually lead to a decrease in γ-diversity of the region (diversities in the sense of Whittaker 1972). This must be noted, for example, when conservation programs for peatlands are planned.

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THE LEAF-AREA INDEX OF THREE MOSS SPECIES (TORTULA RURALIS, CERATODON PURPUREUS, AND HYPNUM CUPRESSIFORME)

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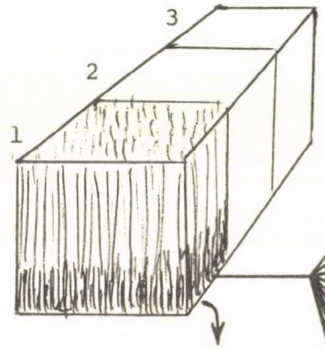
Leaf area index was estimated in cushions of two xerophytic, light demanding species, Tortula ruralis and Ceratodon purpureus, and in mats of one meso-xerophytic, sciophytic species, Hypnum cupressiforme. Five to ten stems were selected from each of several 1 cm^2 sample areas in tufts of the species studied. The numbers of living leaves on these stems were counted, giving totals of 2184 leaves in Tortula, 2827 in Ceratodon and 2811 in Hypnum. Length and breadth were measured on samples of 120 leaves (Tortula), 150 leaves (Ceratodon) and 300 leaves (Hypnum). Data are presented showing mean values and variability for these parameters. Leaf-area indices were estimated as 44 in Tortula, 129 in Ceratodon and 103 in Hypnum.

INTRODUCTION

A fundamental character expressing the adaptation of mosses to light is the leaf-area index, which may be defined as the total area of living leaves within a unit area of the moss tuft. In this paper, leaf area indices are expressed per cm^2. This measure is proportional to light absorption and it affects the process of nutrient cycling. It is likely that the tufts strongly influence the humidity and temperature of the soil by intercepting precipitation. Moss tufts may also be significant from a geological viewpoint: the extensive leaf surfaces remove carbon-dioxide from hydrocarbonated water, thus

Table 1. Samples of Ceratodon tuft.



Number of stems/cm^2= =102

Ten selected stems

No. of leaves counted	No. of leaves measured	Mean leaf area of leaves measured (mm^2)	Leaf area on one stem per mm^2
246	5	0.48	118
195	5	0.53	101
220	4	0.48	106
286	6	0.51	147
346	5	0.47	163
256	4	0.56	144
250	5	0.50	127
175	5	0.49	86
373	5	0.50	189
559	6	0.47	267
2906			1449

$\bar{x}$ = 1449/10 = 144.9 mm^2. Leaf area of an average stem = 144.9 mm^2

Leaf area of the first sample: 144.9 x 102 = 14779.8 mm^2 = 147.8 cm^2

forming a lime cover on the mosses and contributing much to the formation of travertino terraces.

Leaf-area indicaes in mosses appear intuitively to be large, but no quantitative data were previously available. A large leaf area would seem to be an effective adaptation to the high carbon-dioxide concentration close to the ground surface, especially within moss tufts. This is favourable for intensive photosynthesis provided that sufficient light is available.

MATERIAL AND METHODS

In my studies the leaf area of two acrocarpous and one pleurocarpous species was examined. The species were the xerophytic, heliophytic Tortula ruralis and Ceratodon purpureus, and the meso-xerophytic, sciophytic Hypnum cupressiforme. The life strategy of the first two species is colonist, whereas Hypnum is perennial (During 1979, Orbán 1983). These three species are abundant in Hungary. Tortula is a pioneer of dry habitats on basic soils. Hypnum is common on the less calcareous soils of the forest steppe and oakwood zone, while Ceratodon is characteristic of rather dry soils poor in lime and nutrients (Boros 1968).

The method used was very simple. Samples 1 cm^2 in area were selected from typical moss tufts, six being examined in the case of Hypnum and Tortula and three in the case of Ceratodon. The stems in each sample were counted and, for Hypnum, measured to give an estimate of their total length. The leaves were counted on thirty stems from each species, and the area of four to six leaves from each of these stems was estimated. Leaf area indices were then claculated by multiplying mean leaf area per stem by the mean number of stems per cm^2.

Leaf area was estimated using two different formulae. For Ceratodon and Hypnum, leaf width was multiplied by leaf length and the product divided by two. For Tortula, leaf area was measured separately for the base and for the upper part of each leaf, and the values summed. Basal area was given by

Table 2. Summary of measurements

	No. of samples/cm^2	Mean No. of stems/cm^2	Mean No. of leaves per stem	Mean leaf area per stem	Mean LAI/cm^2
T. ruralis	3	29	70	153	44
C. purpureus	6	118	237	110	129
H. cupressiforme	6	33*	93	310	103

* Total length of stems and branches in cm in Hypnum

Table 3. Important counts and measurements

Tortula ruralis

No. of stems per cm^2	No. of leaves per stem	Leaf area on one stem (mm^2)	Mean leaf area for 5 stems (mm^2)	Mean LAI (cm^2)
	62	146		
	57	139		
26	83	138	163.6	42.5
	47	82		
	97	310		
	82	205		
	67	120		
25	64	184	163.2	40.8
	65	157		
	89	149		
	64	121		
	76	164		
23	61	149	155.2	35.8
	97	228		
	73	117		
	62	154		
	76	169		
	66	132		
30	56	100	153.4	46.0
	79	180		
	75	185		
	57	157		
	58	153		
37	58	108	135.7	50.2
	74	162		
	59	97		

Table 3. (continued)

No of. stems per cm^2	No. of leaves per stem	Leaf area on one stem (mm^2)	Mean leaf area for 5 stems (mm^2)	Mean LAI (cm^2)
	85	184		
	68	112		
33	86	158	147.6	48.7
	56	104		
	85	180		
Ceratodon purpureus				
	246	118		
	195	102		
	220	106		
	286	147		
	346	163		
102	256	144	144.9	148
	250	127		
	175	86		
	373	189		
	559	267		
	206	75		
	223	70		
	330	128		
	364	125		
	191	58		
160	212	81	89.7	144
	192	59		
	314	113		
	253	98		
	269	85		
	213	104		
	292	117		
	278	99		
	217	108		
97	212	69	99.4	96
	243	112		
	211	87		
	192	90		
	246	105		
	263	102		

(continued on next page)

Table 3 (continued)

Hypnum cupressiforme				
Mean stem length (cm)	No. of leaves per stem	Leaf area on one stem (mm^2)	Mean leaf area for 5 stems (mm^2)	Mean LAI (cm^2)
	84	196		
	96	175		
33.2	81	210	223	74.0
	101	253		
	65	280		
	91	369		
	93	416		
33.2	97	358	384	127.5
	110	500		
	79	276		
	106	384		
	95	274		
33.2	109	338	332	110.2
	98	364		
	78	299		
	94	364		
	100	433		
33.2	100	354	343	113.8
	152	244		
	89	322		
	108	284		
	118	412		
33.2	99	341	298	98.9
	79	259		
	50	202		
	87	235		
	79	259		
33.2	75	269	284	94.3
	122	402		
	76	256		

multiplication of base width by base length. For the upper part the procedure applied to Ceratodon and Hypnum was used. Based on SEM pictures at a magnification of 5000x, I also attempted to estimate the area of papillae on Tortula leaves.

An example of the calculations for leaf-area index is given in Table 1. For Ceratodon, 359 stems and 7827 leaves were counted in 3 cm^2 of a tuft. Considering just the first 1 cm^2 sample, multiplication of the number of stems (102) by the mean leaf area of the ten measured stems (144.9 mm^2) gave a leaf area index of 147.8.

RESULTS

The results are summarised in Table 2, which shows the numbers of samples, the mean numbers of stems for Ceratodon and Tortula, the mean length of the stems and their branches for Hypnum, the mean numbers of leaves per stem, and the leaf-area indices. More detailed information for each species is given in Table 3. The variation in the data is relatively high in all columns for Ceratodon and Hypnum. In Tortula, the number of stems per sample and estimated leaf area per stem are more variable than the number of leaves per cm^2 or leaf area index.

It may be concluded from these data that moss tufts represent a significant active surface although the leaf-area indices vary between species, being 129 in Ceratodon, 103 in Hypnum and only 44 in Tortula. However, the active surface of Tortula is considerably increased by the papillae which, according to my estimates, may increase leaf surface area by a factor of 30-40.

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ACCEPTABILITY OF MOSSES AS FOOD FOR A HERBIVORE, THE SLUG, ARION HORTENSIS

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Acceptability of mosses as food for a generalist herbivore, the slug Arion hortensis, was investigated by comparing consumption of Atrichum undulatum, Funaria hygrometrica, Mnium hornum and Polytrichum commune with that of flowering plants, Lactuca sativa and Taraxacum officinale. Young leaves of L. sativa were preferred food type. T. officinale was also eaten in substantial amounts, but consumption of moss shoots was negligible, except for F. hygrometrica during summer. Moss shoots extracts in calcium alginate gel or filter paper appeared to be more acceptable than intact shoots. Capsules, and especially developing spores of F. hygrometrica and P. commune were eaten, but in P. commune this occurred only when the capsule walls were broken. Observations on slug behaviour suggested the presence of physical and chemical barriers to consumption of P. commune and M. hornum shoots respectively.

INTRODUCTION

There is a general belief that bryophytes, despite their locally high biomass, are seldom freely consumed by herbivores. Many invertebrates live, oviposit or pupate in bryophyte colonies, but few species, e.g., the tardigrade, Echiniscus testudo (Morgan 1977), have been shown to eat the gametophytes freely. Gerson (1982) considers that many bryophytes possess physical or chemical defences against grazing which few animal species have evolved effective methods of countering.

Longton (1984) noted that sporophytes appear to be more commonly eaten than gametophytes, and commented on the ecological significance of low rates of bryophyte consumption and decomposition, and on their potential in terms of pest control. The latter point has been explored in greater detail by Ando & Matsuno (1984).

Most of the evidence for low rates of grazing is observational. We have thus initiated an experimental study of the acceptability of bryophytes to herbivores, and of the resons for rejection. This paper gives preliminary results on moss consumption by the slug Arion hortensis Férussac. Mosses appear to provide an ideal environment for slugs, being moist and protective, and readily apparent to ground living animals, but there are few observations on their consumption by gastropods. Water snails feed on Octodiceras fontanum, possibly contributing to its scarcity (Gerson 1982). Moss leaf fragments have been found in the excrement of terrestrial molluscs, but they may have been ingested accidentally (Dirzo 1980, Jennings & Barkham 1975), and Boycott (1934) observed that molluscs seldom eat mosses.

MATERIALS AND METHODS

A. hortensis, a small slug reaching 2.5-3.0 cm in length, is abundant in European woodland, gardens and cultivated land. It has been classed as a major agricultural pest (Duthoit 1964, Godan 1983). Eggs are laid in February to April and hatch in early summer, the life span of the adults being 7-12 months. A. hortensis feeds nocturnally, and is likely to encounter mosses as it travels distances up to 90 cm overnight and usually remains near ground level (Godan 1983).

Experimental animals were collected from a garden in Reading and stock cultures of 50-60 individuals were maintained in tanks with drainage holes in the base, and containing gravel overlain by moist paper towel. The tanks were covered with plastic net and kept under diffuse lighting with darkness at night. Food comprised lettuce leaves (Lactuca sativa L.) with chopped carrot root (Daucus carota L.) as a source of vitamins

A and B. Soiled paper towelling was replaced every two to three days. These conditions appeared to be favourable and the density of individuals was below the level promoting decline in longevity and fecundity in A. hortensis (Godan 1983). Stock cultures were established in May for experiments during May and June (summer), and in October for experiments during October and November (autumn). Body weight distributions of the two stocks were similar. Some mortality occurred and numbers were maintained by periodic addition of newly collected individuals.

Consumption of the four mosses Atrichium undulatum (Hedw.) P. Beauv., Funaria hygrometrica Hedw., Mnium hornum Hedw. and Polytrichum commune Hedw. was compared with that of the flowering plants Lactuca sativa and Taraxacum officinale Web. The flowering plants were present in the garden where the slugs were collected and both M. hornum and A. undulatum occurred in adjacent woodland. F. hygrometrica grows in greenhouses and other places where A. hortensis is a pest, but the heathland species, P. commune may seldom be encountered by A. hortensis.

Plants were collected locally, or in the case of Lactuca, purchased, no more than 24 hours before each experiment, except for some sporophyte material. The angiosperms were offered as 1.5 cm diameters disks cut from the innermost (young) and the yellowing outer leaves (senescent). Bryophytes were presented as portions of shoots 1-2 cm long from the shoot apex where the leaves were bright green (young) and from lower down where the leaves were dark green to brown (senescent). Sporophytes with green, but fully expanded capsules were also tested, those of P. commune in autumn experiments having been collected during summer and stored, air-dry at 4 ^{o}C. Capsules were offered intact, or with the walls broken to expose the developing spores. Further comparisons involved extracts prepared by grinding 20 g fresh weight of plant material in 40 ml of deionised water and filtering through muslin. The extracts were offered in 1.5 cm diameter disks of filter paper or in calcium alginate gel. The gel was prepared as described by Whelan (1982a) but the additives of bran and other material that he employed were omitted.

The experimental arenas were carefully washed 9 cm diameter petri dishes with carpets of filter paper soaked in deionised water. Four food items representing one (one-choice test) or two (two-choice test) plant species were placed in each dish, arranged as in Fig. 1. Each food item comprised one angiosperm leaf disk, one or two portions of moss shoot, or comparable amounts of sporophyte material or artificial media. Each test involved 10 replicates with 40 food items. Slugs were drawn from the stock cultures and kept without food for 24 hours before the experiments, in darkness for the final 1-2 hours. One slug was placed in each arena, initially facing midway between two food items (Fig. 1). Experimental material was handled using disposable gloves and blunt forceps. Experiments were initiated in the early afternoon, and ran for 90 minutes under laboratory lighting conditions or for 18 hours with an overnight dark period.

A saturation technique was used to determine consumption. The food items of each species were initially immersed for 10 minutes in separate beakers of deionised water, blotted with paper towel, and weighed. After the experiment each food item was classed as eaten where totally consumed, rasped where partially consumed or uneaten where there was no visible evidence of consumption. The remaining material was reimmersed in deionised water for 10 minutes, blotted and re-weighed, subtraction of final from initial weight giving fresh weight consumption by the ten slugs. The samples were then dry-weighed (80-85 ^{o}C) and dry weight consumption was estimated as the product of fresh weight consumption and the fresh:dry weight ratio. A total of 74 experiments involving 2960 food items was run, and only a representative selection of the results can be presented here.

RESULTS

Consumption in two-choice tests is indicated in Table 1. Young flowering plant leaf, especially of L. sativa, was consistently consumed in significant quantities, and was preferred

to senescent material (experiments 1-3). Where young angiosperm leaf was offered with moss shoots (4-7, 11-14), consumption of the former remained substantial, but moss consumption was negligible. Moss consumption was similarly low when no flowering plant alternative was offered (9-10). In some cases the moss samples showed a slight weight gain, indicated by negative values for consumption in Table 1. These negative values were uniformly less than 6% of the fresh weight, and presumably arose through the samples not being fully hydrated at the initial weighing. Prolonged soaking at this stage might have removed soluble, biologically active compounds. In general, the acceptability of a given species did not vary with season (7, 14), but the results suggested slightly greater consumption of F. hygrometrica in a test against young L.sativa in summer (4) than against this, or other types of material, in autumn (11, 13). Due to uncertainties about levels of hydration it is doubtful whether the results in Table 1 should be regarded as evidence that any moss material was actually eaten, but the figure of 16 mg fresh weight consumption for F. hygrometrica in Experiment 4 is supported by visible evidence that 10% of the food items had been rasped. Consumption in one-choice tests gave broadly similar results (Table 2). There is again a suggestion that F. hygrometrica was consumed in low amounts in summer (16) but not in autumn (23), but this result could have been influenced by the longer exposure time in the summer experiment.

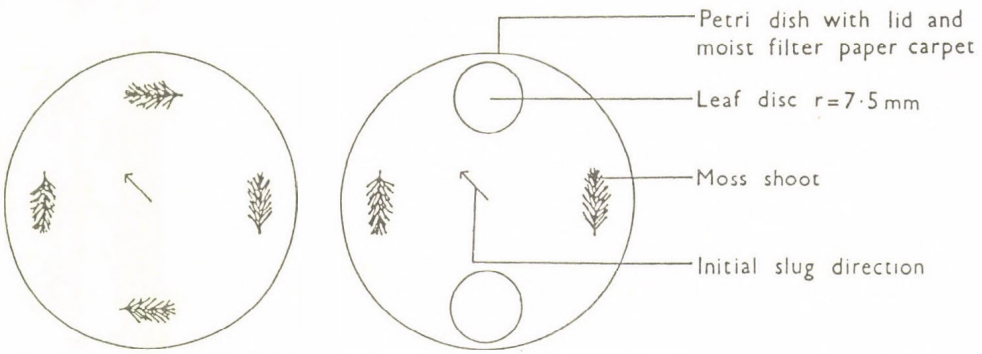

Fig. 1. Design of experimental arenas in one-choice (left) and two-choice (right) tests.

Table 1. Consumption of leaf and shoot material in two-choice tests.

Experiment number	Plant material		Consumption (mg) by 10 slugs Fresh wt	Dry wt	Percentage of food items* Rasped	Eaten
1	L. sativa	Y	170	5.6	60	5
	T. officinale	Y	30	3.0	15	0
2	L. sativa	Y	180	5.9	30	10
	L. sativa	S	130	5.7	35	5
3	T. officinale	Y	50	5.2	45	0
	T. officinale	S	20	3.8	5	0
4	L. sativa	Y	203	8.5	40	10
	F. hygrometrica	Y	16	2.6	0	10
5	L. sativa	Y	183	14.3	75	10
	M. hornum	Y	3	1.0	0	0
6	T. officinale	Y	52	5.2	65	0
	M. hornum	Y	7	2.2	0	0
7	T. officinale	Y	30	3.6	65	0
	P. commune	Y	7	2.0	5	0
8	T. officinale	S	27	2.0	30	0
	P. commune	Y	0	0	0	0
9	M. hornum	Y	3	0.8	0	0
	P. commune	Y	8	2.4	5	0
10	M. hornum	S	2	0.7	0	0
	P. commune	S	0	0	0	0
11	L. sativa	Y	307	26.4	65	15
	F. hygrometrica	Y	-9	-1.6	0	0
12	L. sativa	Y	331	29.8	65	5
	A. undulatum	Y	0	0	0	0
13	T. officinale	Y	104	11.9	75	0
	F. hygrometrica	Y	4	1.3	0	0
14	T. officinale	Y	29	3.5	30	0
	P. commune	Y	0	0	0	0

All experiments were run for 90 minutes, 1-10 in summer and 11-14 in autumn. Y = Young plant material; S = Senescent plant material; * n = 20

Table 2. Consumption of leaf and shoot material in one-choice tests.

Experiment number	Plant material		Consumption (mg) by 10 slugs Fresh wt	Dry wt	Percentage of food items* Rasped	Eaten
15	L. sativa	Y	303	13.9	35.0	10.0
16	F. hygrometrica	Y	37	5.2	0	13.5
17	M. hornum	Y	-12	-3.7	0	0
18	L. sativa	Y	290	16.0	32.5	2.5
19	T. officinale	Y	86	9.6	37.5	0
20	M. hornum	Y	1	0.4	2.5	0
21	P. commune	Y	10	3.5	0	0
22	A. undulatum	Y	10	3.0	0	0
23	F. hygrometrica	Y	5	0.9	5.0	2.5

Experiments 15-17 were run for 18 hours in summer, and 18-23 for 90 minutes in autumn. Y = Young plant material; * n = 40.

Consumption of moss sporophytes is summarised in Table 3. Intact capsules were not eaten when offered as an alternative to the preferred young L. sativa leaf in two-choice tests (24-25). However, significant consumption of intact F. hygrometrica capsules was observed when they were offered alone (27) or with P. commune capsules (26). In the latter experiment over half the F. hygrometrica capsules were eaten or rasped, but no consumption of intact P. commune capsules occurred in comparable experiments (26, 28). Consumption of both species was greater when the capsule walls were broken, exposing the developing spores (29-30). Consumption of broken F. hygrometrica capsules was comparable, on a fresh weight basis, with that of young T. officinale leaf, and on a dry weight basis with that of L. sativa leaf in previous experiments (Tables 1-2). In both mosses, developing spores appeared to be the preferred food, but in F. hygrometrica the contents of many capsules were completely consumed leaving the wall as an empty shell, and some capsule walls were eaten leaving only the seta. The ex-

Table 3. Consumption of sporophytes in one and two-choice tests.

Experiment number	Plant material		Consumption (mg) by 10 slugs Fresh wt	Dry wt	Percentage of food items* Rasped or eaten
24	L. sativa	Y	226	15.8	65.0
	F. hygrometrica	C	0	0	0
25	L. sativa	Y	218	13.5	65.0
	P. commune	C	0	0	0
26	F. hygrometrica	C	24	4.2	65.0
	P. commune	C	0	0	0
27	F. hygrometrica	C	16	3.4	35.0
28	P. commune	C	0	0	0
29	F. hygrometrica	CB	68	25.8	57.5
30	P. commune	CB	25	21.6	15.0

Experiments 24-28 were run for 90 minutes in summer and 29-30 for 90 minutes in autumn. Y = Young leaf material; C = Intact capsules; CB = Capsules with walls broken.

* A food item as defined on page 000 comprised one L. sativa leaf disk, one P. commune capsule or two F. hygrometrica capsules; n = 20 in experiments 24-26 and 40 in 27-30.

periments on intact capsules were carried out in summer and those on broken capsules in autumn. Interpretation of the results is also complicated by lower fresh:dry weight ratios of the capsules in autumn than in summer, evident from Table 3., especially the stored P. commune capsules. Nevertheless, the results suggest that the capsules of both species are acceptable to A. hortensis to some extent, and that the outer layers of the capsule wall present a physical barrier to feeding, particularly in P. commune. The apparently lowered palatibility of F. hygrometrica shoots in autumn as compared with summer did not apply to the sporophytes.

No consumption of calcium alginate gel or filter paper disks was observed in experiments lasting 90 minutes. Results for overnight experiments are given in Tables 4-5. Technical

Table 4. Visible evidence of consumption of calcium alginate gel containing plant extracts.

Experiment number	Plant extract+	Percentage of food items* Rasped	Eaten
31	L. sativa	20	0
	control	0	0
32	P. commune	55	0
	control	0	0
33	M. hornum	25	0
	control	0	0
34	L. sativa	45	20
35	P. commune	40	0
36	M. hornum	40	0

Experiments 31-33 were run for 18 hours in summer, and 34-36 for 18 hours in autumn; * n = 20 in experiments 31-33 and 40 in 34-36; + control disks contained no plant extract.

Table 5. Visible evidence of consumption of filter paper disks soaked in plant extract.

Experiment number	Plant extract	Percentage of food items* Rasped
37	L. sativa	42.5
38	T. officinale	22.5
39	M. hornum	25.0
40	P. commune	20.0
41	A. undulatum	20.0
42	F. hygrometrica	12.5

Experiments were run for 18 hours in autumn; No samples were completely eaten; * n = 40.

difficulties such as substantial loss in the weight of control gel disks in the absence of slugs prevented expression of data in terms of consumption on a weight basis. The results for visible evidence of consumption (Tables 4-5) cannot be regarded as conclusive, but they do suggest that acceptability of arti-

ficial media containing extracts of moss gametophyte shoots may be higher than that of intact shoots.

Observations on slug behaviour were made during the 90 minute experiments. Most slugs were seen to visit all four items offered, in contrast to reports of immediate feeding under stimulated conditions (Whelan 1982b). Some angiosperm leaf disks were eaten completely but not normally without investigation of the other food items. Some of the most interesting slug behaviour was seen in the presence of M. hornum. On approaching the shoots with tentacles extended the slugs were commonly seen to withdraw their tentacles and retreat. Behaviour towards P. commune was quite different. The shoots were thoroughly investigated and apparent attempts to sever leaves were made. The leaf bases appeared to provide the greatest attraction. Some slugs were seen to settle at a cut shoot base, their head movements suggesting that they were feeding upon shoot exudates. Such behaviour has been observed in the field at the cut base of straw (G. Steele, personal communication). Slugs were observed to enter phases of inactivity during some experiments, remaining stationary with their bodies straight and tentacles withdrawn. The number of such phases increased both with length of experiment and with the quantity of moss involved. In the presence of M. hornum many slugs adopted an unusual position, remaining at rest but with their bodies curled and their tentacles only partially withdrawn.

DISCUSSION

The experiments were carried out under conditions designed to promote feeding. The slugs were kept for 24 hours without food, with darkness for the final 1-2 hours as exposure to light following a period of darkness stimulates feeding in slugs (Dainton 1954). The shorter experiments were performed under laboratory lighting to permit observations an slug behaviour, but the longer experiments provided a period of darkness to simulate nocturnal feeding conditions. Slug activity is also stimulated by temperature fluctuation at around 21 ^{o}C

(Dainton 1954, Getz 1963). Thus the present experiments were initiated in the early afternoon when laboratory temperature was normally rising. Temperatures during the experiments were in the range 19-27 ^{o}C.

That the experimental conditions were conducive to feeding is confirmed by the consistently high consumption of angiosperm leaf disks. L. sativa is particularly palatable to slugs (Dirzo 1980, Whelan 1982a) and thus the higher consumption of this species than of T. officinale was not unexpected. The preference for young over senescent material agrees with previous resluts for A. hortensis (Godan 1983). Under the same conditions, consumption of moss shoots was negligible, both in one-choice tests and where they were offered as an alternative to angiosperm leaf. Only with F. hygrometrica in summer did the results suggest consumption, given the errors in the saturation technique. Otherwise there was no evidence of seasonal variation in consumption of either moss shoots or angiosperm leaf disks, and consumption in the 90 minute and 18 hour experiments was comparable. Occasional shoots of several mosses were rasped by the slugs (Tables 1-2), buth such sporadic feeding was usually performed by small, possibly juvenile animals, and aberrant individuals that consume foods not eaten by other members of their population have been noted among slugs (Dirzo 1980, Whelan 1982a). It is conceivable that the preference for the flowering plants in the present experiments stemmed from familiarity as both species grew where the slugs were collected and L. sativa was part of their diet in stock culture. However, there is some evidence that slugs will initially eat unpleasant food items with which they are unfamiliar (Gouyon et al. 1983, Whelan 1982b), and the significant consumption of broken capsules argues against conditioning being an overriding factor.

The repsent results thus support previous observations that bryophyte shoots are not commonly grazed. Relative immunity could be due to a combination of factors including low nutrient value, physical resistance presented by the cell walls, chemical defence involving secondary compounds or unusual concentrations of certain elements (Gerson 1982, Longton 1984). The pre-

sent behavioural observations suggest that a physical barrier may be involved in the case of P. commune shoots and a volatile chemical in the case of M. hornum. Some slugs are known to respond to volatile compounds (Stephenson 1979) and L. sativa and T. officinale have been shown to release volatiles that stimulate feeding (Pickett & Stephenson 1980). Preparation of the plant extracts removed any physical barriers and might well have reduced the effectiveness of volatile deterrents, particularly where the extracts were heated to 40 ^{o}C for incorporation in the alginate gel. It is interesting that some feeding on madia containing moss shoot extracts apparently took place but the extent cannot yet be assessed. While moss gametophytes generally have a slightly lower calorific value, and thus possibly lower concentrations of organic nutrients than flowering plant shoots, the spores are rich in carbohydrate and/or lipid food reserves. The present observations on sporophyte consumption agree with earlier reports that capsules are preferred by animals and provide further evidence of physical barriers to feeding, particularly in P. commune. Cell walls of Polytrichum spp.contain holocellulose and lignin-like compounds (Erikson & Mische 1974), which could be involved in physical resistance. Capsule walls in both P. commune and F. hygrometrica contain crystals of calcium oxalate (Suire 1975) which may also act as a feeding deterrent (Gerson 1982). Low consumption of setae could be the result of thick walled peripheral cells containing callose (Watson 1971, Suire 1975). We intend to investigate moss/animal feeding relationships in greater depth in view of their ecological significance and implications for pest control.

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MITES WHICH FEED ON MOSSES

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Mites of the genus Eustigmaeus (Prostigmata: Stigmaeidae) feed on mosses in North America, Hawaii and New Zealand. Extensive collecting in North America showed the mites to be associated with 38 moss species in eight orders (Dicranales, Eubryales, Fissidentales, Funariales, Hypnobryales, Isobryales, Polytrichales, and Pottiales). Mite-moss associations were habitat-, rather than species-specific. Some mites occurred mostly on acrocarpous mosses, others on pleurocarpous mosses and one mite species on acidophilous mosses. All active stages of Eustigmaeus feed on moss leaves and stems, sucking out green cell contents whilst leaving the cell walls intact. Mosses with thickened cell walls (Atrichum, Polytrichum) do not allow feeding by mites with short mouth parts. Female mites deposit their eggs on moss leaves and stems and the entire life cycle may be passed there. Many other mite species, of most mite orders, may be found in mosses, but little is known concerning their phytophagous activities there.

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Mosses have several attributes which enable many invertebrates to live in and feed on their colonies:

1. They grow in habitats that are intermittently dry and humid, and while under the latter conditions they are capable of absorbing large amounts of water. This provides any sheltering animal with suitable humidity as well as a variety of diets.

2. They insulate invertebrates harboring within them against extreme temperatures and winds. This is of special importance when growing under very cold (i.e., polar) conditions.

3. They usually have unprotected leaves, only one cell thick, which facilitates feeding on them.

Thus it is surprising that a great many invertebrates, including arthropods, are found in mosses. The arthropods consist of the Copepoda and Malacostraca in the Crustacea, the so-called Myriapoda, representatives of 21 orders of the Insecta, as well as the pseudoscorpions, spiders and mites in the Arachnida. This paper is concerned with one group, the mites, and only with those which actually feed on mosses.

The prostigmid family Stigmaeidae contains some predaceous genera (Krantz & Linquist 1979) and at least one, Eustigmaeus, whose members feed on mosses. I have collected and reared moss-feeding species of this genus in Canada and New Zealand, and observed their behavior in the laboratory (Gerson 1972). Mites were found in 78 (49.4%) of the 158 samples collected in eastern Canada and the northeastern United States. And of the 55 moss species obtained, 38 (69%) carried one or more species of Eustigmaeus. The 38 bryophytes belong in eight orders (Dicranales, Eubryales, Fissidentales, Funariales, Hypnobryales, Isobryales, Polytrichales, and Pottiales), indicating that the association between mites and mosses is quite wide-ranging. This assumption is supported by the fact that ancestral groups, such as the Polytrichales (Smith 1978), as well as many more advanced, pleurocarpous mosses, serve as food for Eustigmaeus. The same mite species was sometimes found on members of both these bryophyte groups. The sampling data suggest that the mites are habitat- rather than moss species-specific. E. frigida, for instance, was collected only from pleurocarpous mosses growing in shaded, humid sites on rotting logs, arboreal tree roots or rocks, but never from common acrocarpous species like Bryum argenteum or Ceratodon purpureus. A different pattern was obtained in regard to E. gersoni and E. rhodomela. Both were collected mostly from colonizing bryophytes growing

on open, sometimes quite dry sand, dumped soil, broken sidewalks and on roadside gravel. Only one species, the aptly-named E. acidophila, appears to have a clear preference for acidophilous mosses, such as Polytrichum spp., Dicranum scoparium and Pleurozium schreberi. No mites were found on the few hepatics collected.

All active stages of Eustigmaeus feed on moss leaves and stems. The mites wound the thin outer cuticle, when present, and the outer cell wall, and then suck out the green contents. Although perforated, the cell walls apparently remain undamaged. Young moss shoots heavily attacked by mites soon lose their natural green colour, becoming rather greyish. The feeding site also becomes soiled with the mites' dark fecal pellets. Feeding experiments showed that mosses differ in their suitability for the various species of Eustigmaeus. Mites fed and oviposited on some mosses but only survived, without reproducing, on others.And the Polytrichaceae, with lamellae on upper leaf sides and thickened cell walls on their lower surfaces, did not allow a species of Eustigmaeus with short mouth parts to feed on them.

These mites deposit their eggs on moss leaves and stems, imparting a reddish colouration to the plants. The eggs may be washed away with water, and this is probably on dispersal mechanism; another could well be with drifting or wind-blown moss parts. Female eggs arriving singly at new sites hatch and the maturing mites produce only male progeny. These males mate with their mothers, which then produce females and thus establish new families. The same probably takes place when single, unmated females arrive at new sites.

Very few other mites are known to subsit exclusively on mosses. These probably include some species of Penthaleus, a recognised plant feeder (Krantz & Lindquist 1979) which had been collected from mosses in many parts of the world (unpubl. data), and the water mite Prohalacarus alpinus. The latter was found (Bartsch 1981) in sphagna with greenish body contents, indicating that it had fed on these plants. A vast variety of other mites, of most acarine orders, may also be

found in mosses. Most of them do not appear to subsist on these plants; the few that do probably feed on mosses in lieu of more suitable diets.

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Session 6

BRYOPHYTES AS BIOINDICATORS

Convener: J. Sarosiek
(Wrocław)

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URBAN BRYOPHYTES IN SPANISH TOWNS

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This paper presents a comparative study of the distribution/occurrence in the different habitats and the resistence to urban conditions of the bryophytes found in four towns of central Spain: Avila, Badajoz, Madrid and Toledo. Samples were collected from green and built-up areas. These towns were chosen because of their particular physiographic characteristics, air pollution and variety of habitats.

Tolerant and indifferent species common to all towns and sensitive species growing in particular habitats were detected. Similarities and differences between the urban floras are discussed.

INTRODUCTION

Bryophytes in urban environments are subjected to a special stress due to frequent physical changes in the substrata and to chemically aggressive conditions in industrialized agglomerations.

The urban bryoflora in Spain has been barely studied (Casas & Oliva 1982, Casas & Sáiz-Jiménez 1982), and almost no information is available with regard to the presence of certain species in these environments. For this reason and for a comparative study based on the richness of species, their ecology and distribution, the bryophyte flora of four towns in the center of the Iberian Peninsula has been studied. Their physiographic features are summarized in Figures 1 and 2 as well as

in the following table:

	alt.	lat.	long.	climate
Avila	1126 m	40°39'N	4°42'W	Medit. cont. extr.
Badajoz	183 m	38°52'N	6°58'W	Medit. cont. mod.
Madrid	650 m	40°25'N	3°41'W	Medit. cont. extr.
Toledo	548 m	39°51'N	4°01'W	Medit. cont. extr.

Avila, 41,735 inhabitants, is the provincial capital in Spain with the highest altitude having a cold and dry climate. The town is built on a granitic batholith and ancient stone buildings are common, many of them 700 years old. There are no polluting industries and the green areas are reduced.

Badajoz, 114,361 inhabitants, has long, dry, and hot summers and mild, humid winters. The few parks in the town are very new and trees are rarely seen in the streets. However, it

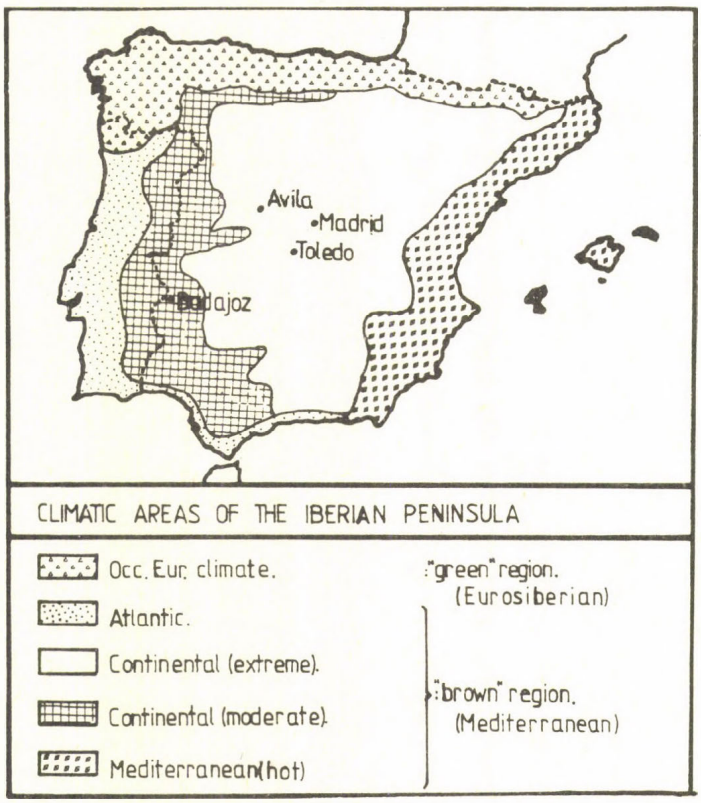

Fig. 1. Climatic areas of the Iberian Peninsula

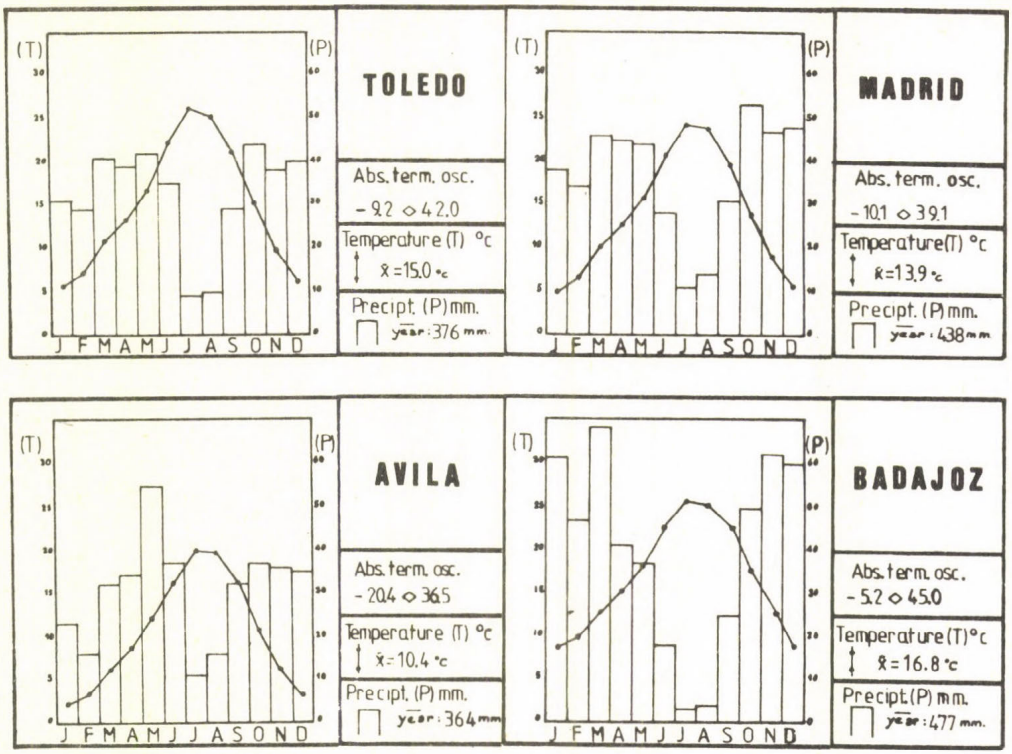

Fig. 2. Ombrothermic diagrams of the towns

has no polluting industries. Badajoz is built on alkaline materials.

Madrid, 3,188,000 inhabitants and ranked among the five most polluted capitals in Europe, has large and ancient parks in the 32 km^2 of the urban area studied, which is built on sedimentary rocks.

Toledo, 57,769 inhabitants, is built on gneiss covered by limestone. The parks are few and small and there are almost no trees in the streets. It lacks polluting industries.

MATERIALS AND METHODS

Collections were made periodically between 1982 and 1985 always in the urban area, excluding the industrial belt as well as the residential suburbs. The area studied in each town is as follows: Avila = 1.7 km^2, Badajoz = 1 km^2, Madrid = 32 km^2, and Toledo = 1 km^2.

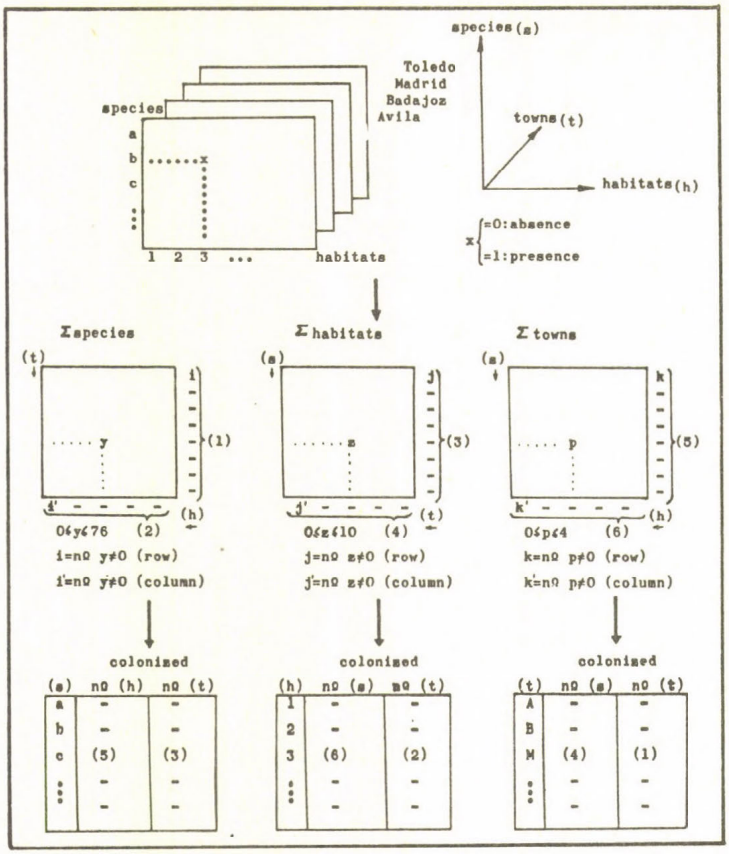

Fig. 3. Numerical treatment of the data

Ten different habitats were defined in each town in an attempt to standardize the substrata in which the bryophytes were collected. This classification was done considering the physical and chemical characteristics of the substratum as well as its moisture:

Terricolous (T): T_1 = Moist shaded soil and lawn. T_2 = Dry and exposed soil. T_3 = Waste ground and high nitrogenous soil.

Saxicolous and chasmophytes (SC): SC_1 = Damp basic rocks and walls. SC_2 = Dry basic rocks and walls. SC_3 = Mortar and concrete. SC_4 = Bricks and tiles. SC_5 = Wet acidic rocks and walls. SC_6 = Dry acidic rocks and walls.

Epiphytes (E): E_1 = On bark and tree bases.

The flora of each town is represented on a table of species/habitats which contains the total list of species. No

quantitative evaluations are made, the presence or absence of a given species in a particular habitat is represented by 1 or 0, respectively. These tables can be displayed as a tridimensional array of species/habitats/towns that can be handled in order to obtain the relationship between species/habitat, species/towns and habitats/towns (Fig. 3).

RESULTS AND DISCUSSION

Habitats. All the ten habitats previously defined were colonized by bryophytes in Madrid, but only nine of them were found colonized in Avila and Toledo, and eight in Badajoz (Table 10).

a) Terricolous. Habitats of the T_1 type and T_2 type were the richest among the habitats present in the four towns, 43 and 41 species, respectively (Table 9). Most of the pleurocarpous species were found in these habitats.

The species diversity in enriched habitats, T_3 type, is lower than that in T_1 and T_2 types (Table 2); and no species have been found occurring exclusively in the nitrogen-rich terricolous habitat.

Terricolous habitats are somewhat restricted to parks. Due to the species diversity that occurs in these habitats, the richness of species in a town depends largely on the abundance and size of its green areas. Apart from the larger area studied, this would explain partially the high number of species found in Madrid (Table 5).

Although the soil characteristics are different for each town in the study, the urban terricolous habitats do not show significant differences in the occurrence of its bryophyte species.

b) Saxicolous and chasmophytes. Except for the SC_1 and SC_6 types which were only found colonized in two towns, all the other SC habitats were colonized in the four towns, but showed a lower species diversity than the terricolous habitats (Table 9).

The SC_1 and SC_2 are poorly represented in all of the towns studied and have a low species diversity. Most of the mosses that colonized them are cosmopolitan substrate-indifferent, except for Didymodon tophaceus, which is found in SC_1, and Grimmia pulvinata, very common in SC_2 (Table 7).

The artificial substrata, SC_3 and SC_4, are obviously very well represented in all of the towns studied and show the highest richness of species among the SC substrata (Table 9), in part because of their liability to be altered.

SC_5 and SC_6, acidic materials, are almost non-existing in Badajoz and Toledo and poorly represented in Madrid. Nevertheless, in Avila they are quite abundant as construction materials as well as in the form of unaltered outcrops. However, they do not show a high number of species (Table 9).

c) Epiphytes. Trees bearing epiphytic bryophytes are found almost exclusively in parks and never in the streets. Epiphytic bryophytes were only found at the base and trunk of aged trees.

Species. A total number of 76 species of bryophytes have been found arranged as follows:

Avila = 28 species (Table 1),
Badajoz = 26 species (Table 2),
Madrid = 51 species (Table 3),
Toledo = 28 species (Table 4).

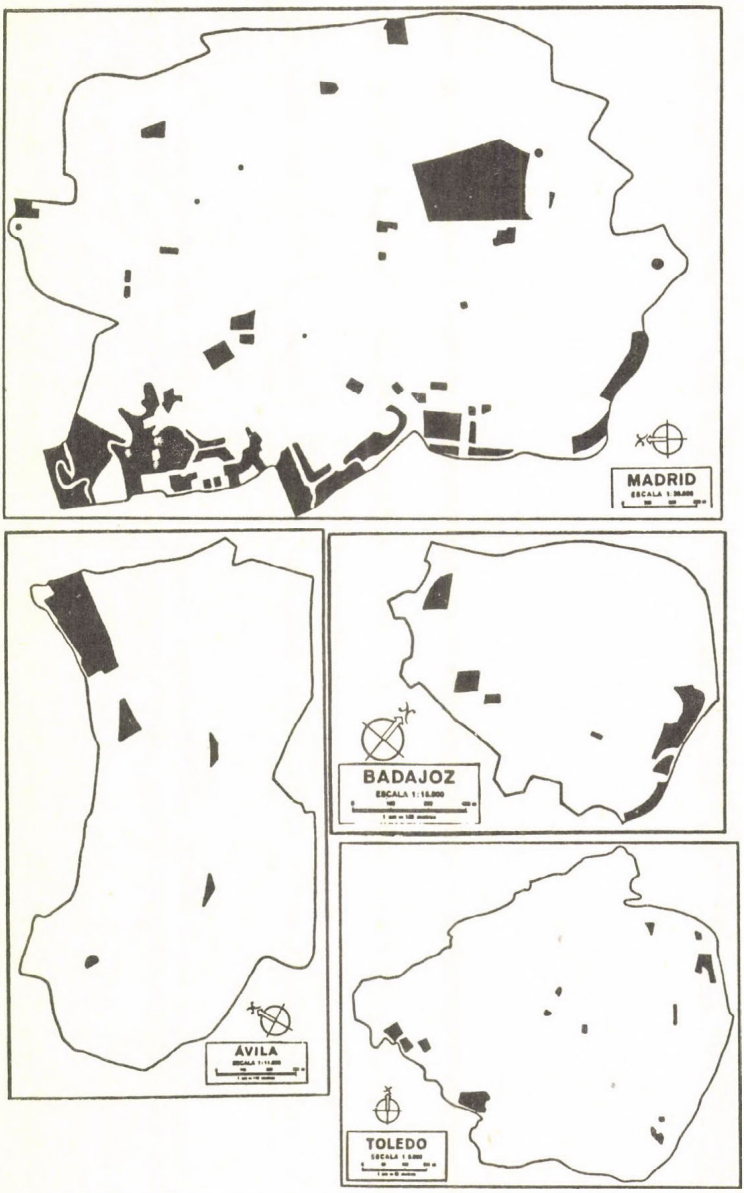

Fig. 4. Green (black) and built-up areas within the urban areas studied

Table 1. Occurrence of bryophytes in the different habitats in Avila. Presence = 1, absence = 0.

	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
1. Sphaerocarpus michelii Bell.	0	0	0	0	0	0	0	0	0	0
2. Lunularia cruciata /L./ Lindb.	0	0	0	0	0	0	0	0	0	0
3. Riccia lamellosa Raddi	0	0	0	0	0	0	0	0	0	0
4. Frullania dilatata /L./ Dum.	0	0	0	0	0	0	0	0	0	0
5. Fissidens bryoides Hedw.	0	0	0	0	0	0	0	0	0	0
6. Fissidens viridulus /Sw./ Wahlenb.	0	0	0	0	0	0	0	0	0	0
7. Fissidens taxifolius Hedw.	0	0	0	0	0	0	0	0	0	0
8. Fissidens cristatus Wils. ex Mitt.	0	0	0	0	0	0	0	0	0	0
9. Dicranum scoparium Hedw.	0	0	0	0	0	0	0	0	0	0
10. Tortula princeps De Not.	0	1	0	0	0	1	1	0	0	0
11. Tortula ruralis /Hedw./ Gaertn., Meyer & Scherb.	1	1	0	0	0	1	1	0	0	0
12. Tortula intermedia /Brid./ De Not.	1	1	1	0	0	1	1	0	0	1
13. Tortula virescens /De Not./ De Not.	0	0	0	0	0	0	0	0	0	1
14. Tortula laevipila /Brid./ Schwaegr.	0	0	0	0	0	0	0	0	0	1
15. Tortula pagorum /Milde/ De Not.	0	0	0	0	0	0	0	0	0	0
16. Tortula papillosa Wils.	0	0	0	0	0	0	0	0	0	0
17. Tortula subulata Hedw.	0	0	0	0	0	0	0	0	0	0
18. Tortula marginata /B. & S./ Spruce	0	0	0	0	0	0	0	0	0	0
19. Tortula vahliana /K.F. Schultz/ Mont.	0	0	0	0	0	0	0	0	0	0
20. Tortula muralis Hedw.	0	1	0	0	0	1	0	1	1	0
21. Aloina aloides /K.F. Schultz/ Kindb.	0	0	0	0	0	0	0	0	0	0
22. Aloina rigida /Hedw./ Limpr.	0	0	0	0	0	0	0	0	0	0
23. Pterygoneurum ovatum /Hedw./ Dix.	0	0	0	0	0	0	0	0	0	0
24. Pottia lanceolata /Hedw./ C.Müll.	0	0	0	0	0	0	0	0	0	0
25. Pottia truncata /Hedw./ B. & S.	0	0	0	0	0	0	0	0	0	0
26. Pottia bryoides /Dicks./ Mitt.	0	0	0	0	0	0	0	0	0	0
27. Phascum cuspidatum Hedw.	0	0	0	0	0	0	0	0	0	0
28. Barbula unguiculata Hedw.	0	0	0	0	0	0	0	0	0	0
29. Pseudocrossidium revolutum /Brid./ Zander	0	1	0	0	1	1	0	0	0	0
30. Pseudocrossidium hornschuchianum /K.F. Schultz/Zander	0	1	0	0	0	1	0	0	0	0
31. Trichostomopsis umbrosa /C.Müll./ Robins.	0	0	0	0	0	0	0	0	0	0
32. Trichostomopsis trivialis /C.Müll./ Robins.	0	0	0	0	0	0	0	0	0	0
33. Didymodon luridus Hornsch. ex Spreng.	0	1	0	0	0	0	0	0	0	0
34. Didymodon vinealis /Brid./ Zander	1	1	0	0	1	1	0	0	0	0
35. Didymodon tophaceus /Brid./ Lisa	0	0	0	0	0	0	0	0	0	0

36. Didymodon fallax /Hedw./ Zander	0	1	0	0	0	1	0	0	0	0
37. Pleurochaete squarrosa /Brid./ Lindb.	0	0	0	0	0	0	0	0	0	0
38. Grimmia anodon B. & S.	0	1	0	0	1	1	1	0	0	0
39. Grimmia laevigata /Brid./ Brid.	0	0	0	0	0	0	0	0	0	1
40. Grimmia pulvinata /Hedw./ Sm.	0	1	0	0	0	1	1	0	0	0
41. Grimmia trichophylla Grev.	0	0	0	0	0	0	1	1	1	0
42. Funaria hygrometrica Hedw.	0	1	0	0	0	1	0	0	0	0
43. Funaria pulchella Philib.	0	0	0	0	0	0	0	0	0	0
44. Bryum capillare Hedw.	0	0	1	0	0	1	0	0	1	0
45. Bryum canariense Brid.	0	0	0	0	0	0	0	0	0	0
46. Bryum caespiticium Hedw.	0	1	1	0	0	1	0	0	1	0
47. Bryum argenteum Hedw.	0	1	0	0	0	1	1	0	0	0
48. Bryum bicolor Dicks.	0	0	0	0	0	0	0	0	0	0
49. Bryum radiculosum Brid.	0	0	0	0	0	0	0	0	0	0
50. Rhizomnium punctatum /Hedw./ T.Kop.	0	0	0	0	0	0	0	0	0	0
51. Plagiomnium affine /Bland./ T.Kop.	0	0	0	0	0	0	0	0	0	0
52. Plagiomnium undulatum /Hedw./ T.Kop.	0	0	0	0	0	0	0	0	0	0
53. Orthotrichum lyellii Kook. & Tayl.	0	0	0	0	0	0	0	0	0	0
54. Orthotrichum rupestre Schleich. ex Schwaegr.	0	0	0	0	0	1	0	0	1	0
55. Orthotrichum anomalum Hedw.	0	0	0	0	0	1	0	0	0	0
56. Orthotrichum cupulatum Brid.	0	1	0	0	0	1	0	0	0	0
57. Orthotrichum tenellum Bruch. ex Brid.	0	0	0	0	0	0	0	0	0	1
58. Orthotrichum diaphanum Brid.	0	0	0	0	0	1	0	0	0	1
59. Thamnobryum alopecurum /Hedw./ Nieuwl.	0	0	0	0	0	0	0	0	0	0
60. Amblystegium serpens /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
61. Amblystegium tenax /Hedw./ C. Jens.	0	0	0	0	0	0	0	0	0	0
62. Amblystegium humile /P.Beauv./Crundw.	1	0	0	0	0	0	0	0	0	0
63. Amblystegium riparium /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
64. Isothecium myosuroides Brid.	0	0	0	0	0	0	0	0	0	0
65. Scorpiurium circinatum /Brid./ Fleisch. Loeske	0	0	0	0	0	0	0	0	0	0
66. Homalothecium sericeum /Hedw./ B.,S.& G.	1	1	1	0	0	1	0	0	0	0
67. Homalothecium aureum /Spruce/ Robins.	0	0	0	0	0	0	0	0	0	0
68. Brachythecium albicans /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
69. Brachythecium mildeanum /Schimp./Schimp. ex Milde	1	0	0	0	0	1	0	0	1	0
70. Brachythecium rutabulum /Hedw./ B.,S. & G.	1	1	0	0	0	0	0	0	0	0
71. Brachythecium velutinum /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
72. Rhynchostegium riparioides /Hedw./ Card.	0	0	0	0	0	0	0	0	0	0
73. Rhynchostegium megapolitanum /Web. & Mohr/B.,S. & G.	0	0	0	0	0	0	0	0	0	0

	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
74. Eurhynchium pulchellum /Hedw./ Jenn.	0	0	0	0	0	0	0	0	0	0
75. Eurhynchium hians /Hedw./ Sande Lac.	0	0	0	0	0	0	0	0	0	0
76. Hypnum cupressiforme Hedw.	0	0	0	0	0	0	0	0	0	0

Terricolous (T): T_1=Moist shaded soil and lawn. T_2=Dry and exposed soil. T_3= Waste ground and high nitrogenous soil.

Saxicolous and chasmophytes (SC): SC_1=Damp basic rocks and walls. SC_2=Dry basic rocks and walls. SC_3=Mortar and concrete. SC_4=Bricks and tiles. SC_5=Wet acidic rocks and walls. SC_6=Dry acidic rocks and walls.

Epiphytes (E): E_1=On bark and tree bases.

Table 2. Occurrence of bryophytes in the different habitats in Badajoz. Presence = 1, absence = 0

	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
1. Sphaerocarpus michelii Bell.	0	0	0	0	0	0	0	0	0	0
2. Lunularia cruciata /L./ Lindb.	1	0	0	0	0	0	0	0	0	0
3. Riccia lamellosa Raddi	0	1	0	0	0	0	0	0	0	0
4. Frullania dilatata /L./ Dum.	0	0	0	0	0	0	0	0	0	1
5. Fissidens brvoides Hedw.	1	0	0	0	0	0	0	0	0	0
6. Fissidens viridulus /Sw./ Wahlenb.	0	0	0	0	0	0	0	0	0	0
7. Fissidens taxifolius Hedw.	0	0	0	0	0	0	0	0	0	0
8. Fissidens cristatus Wils. ex Mitt.	0	0	0	0	0	0	0	1	0	0
9. Dicranum scoparium Hedw.	0	0	0	0	0	0	0	0	0	0
10. Tortula princeps De Not.	0	0	0	0	0	0	0	0	0	0
11. Tortula ruralis /Hedw./ Gaertn., Meyer & Scherb.	0	0	0	0	0	0	0	0	0	0
12. Tortula intermedia /Brid./ De Not.	0	0	0	0	0	0	0	0	0	0
13. Tortula virescens /De Not./De Not.	0	0	0	0	0	0	0	0	0	0
14. Tortula laevipila /Brid./ Schwaegr.	0	0	0	0	0	0	0	0	0	1

15. Tortula pagorum /Milde/ De Not.	0	0	0	0	0	0	0	0	0	1
16. Tortula papillosa Wils.	0	0	0	0	0	0	0	0	0	0
17. Tortula subulata Hedw.	0	0	0	0	0	0	0	0	0	0
18. Tortula marginata /B. & S./ Spruce	0	0	0	0	0	0	0	0	0	0
19. Tortula vahliana /K.F. Schultz/ Mont.	0	0	0	0	0	0	0	0	0	0
20. Tortula muralis Hedw.	0	1	0	0	0	1	1	0	0	0
21. Aloina aloides /K.F. Schultz/ Kindb.	0	0	0	0	0	0	0	0	0	0
22. Aloina rigida /Hedw./ Limpr.	0	1	0	0	0	0	0	0	0	0
23. Pterygoneurum ovatum /Hedw./ Dix.	0	0	0	0	0	0	0	0	0	0
24. Pottia lanceolata /Hedw./ C.Müll.	0	0	0	0	0	0	0	0	0	0
25. Pottia truncata /Hedw./ B. & S.	0	0	0	0	0	0	0	0	0	0
26. Pottia bryoides /Dicks./ Mitt.	0	0	0	0	0	0	0	0	0	0
27. Phascum cuspidatum Hedw.	0	0	0	0	0	0	0	0	0	0
28. Barbula unguiculata Hedw.	1	0	0	0	0	0	0	0	0	0
29. Pseudocrossidium revolutum /Brid./ Zander	1	0	0	0	0	0	0	0	0	0
30. Pseudocrossidium hornschuchianum /K.F. Schultz/ Zander	1	0	0	0	0	0	0	0	0	0
31. Trichostomopsis umbrosa /C.Müll./ Robins.	0	0	0	0	0	0	0	0	0	0
32. Trichostomopsis trivialis /C.Müll./ Robins.	0	0	0	0	0	0	0	0	0	0
33. Didymodon luridus Hornsch. ex Spreng.	0	0	0	0	0	0	0	0	0	0
34. Didymodon vinealis /Brid./ Zander	0	1	1	0	0	1	0	0	0	0
35. Didymodon tophaceus /Brid./ Lisa	0	0	0	0	0	0	0	0	0	0
36. Didymodon fallax /Hedw./ Zander	0	0	0	0	0	1	0	0	0	0
37. Pleurochaete squarrosa /Brid./ Lindb.	0	1	0	0	0	0	0	0	0	0
38. Grimmia anodon B. & S.	0	0	0	0	0	0	0	0	0	0
39. Grimmia laevigata /Brid./ Brid.	0	0	0	0	0	0	0	0	0	0
40. Grimmia pulvinata /Hedw./ Sm.	0	0	0	0	1	0	0	0	0	1
41. Grimmia trichophylla Grev.	0	0	0	0	0	0	0	0	0	0
42. Funaria hygrometrica Hedw.	0	1	0	0	0	0	0	0	0	0
43. Funaria pulchella Philib.	1	1	0	0	0	0	0	0	0	0
44. Bryum capillare Hedw.	0	0	0	0	0	0	0	0	0	1
45. Bryum canariense Brid.	0	0	0	0	0	0	0	0	0	0
46. Bryum caespiticium Hedw.	0	1	0	0	0	0	0	0	0	0
47. Bryum argenteum Hedw.	0	1	0	0	0	0	0	0	0	1
48. Bryum bicolor Dicks.	0	0	0	0	0	0	0	0	0	0
49. Bryum radiculosum Brid.	0	0	0	0	0	0	0	0	0	0
50. Rhizomnium punctatum /Hedw./ T.Kop.	0	0	0	0	0	0	0	0	0	0
51. Plagiomnium affine /Bland./ T.Kop.	0	0	0	0	0	0	0	0	0	0
52. Plagiomnium undulatum /Hedw./ T.Kop.	0	0	0	0	0	0	0	0	0	0

BADAJOZ	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
53. Orthotrichum lyellii Kook.& Tayl.	0	0	0	0	0	0	0	0	0	0
54. Orthotrichum rupestre Schleich. ex Schwaegr.	0	0	0	0	0	0	0	0	0	0
55. Orthotrichum anomalum Hedw.	0	0	0	0	0	0	0	0	0	0
56. Orthotrichum cupulatum Brid.	0	0	0	0	0	0	0	0	0	0
57. Orthotrichum tenellum Bruch ex Brid.	0	0	0	0	0	0	0	0	0	0
58. Orthotrichum diaphanum Brid.	0	0	0	0	0	0	0	0	0	1
59. Thamnobryum alopecurum /Hedw./ Nieuwl.	0	0	0	0	0	0	0	0	0	0
60. Amblystegium serpens /Hedw./ B.S., &G.	0	0	0	0	0	0	0	0	0	0
61. Amblystegium tenax /Hedw./ C. Jens.	0	0	0	0	0	0	0	0	0	0
62. Amblystegium humile /P. Beauv./ Crundw.	0	0	0	0	0	0	0	0	0	0
63. Amblystegium riparium /Hedw./ B.S., & G.	0	0	0	0	0	0	0	0	0	0
64. Isothecium myosuroides Brid.	1	0	0	0	0	0	0	0	0	0
65. Scorpiurium circinatum /Brid./ Fleisch. & Loeske	0	1	0	0	0	0	0	0	0	0
66. Homalothecium sericeum /Hedw./ B.S., & G.	0	0	0	0	0	0	0	0	0	1
67. Homalothecium aureum /Spruce/ Robins.	0	1	0	0	0	0	0	0	0	0
68. Brachythecium albicans /Hedw./ B.S., & G.	0	0	0	0	0	0	0	0	0	0
69. Brachythecium mildeanum /Schimp./ Schimp. ex Milde	0	0	0	0	0	0	0	0	0	0
70. Brachythecium rutabulum /Hedw./ B.S., & G.	0	0	0	0	0	0	0	0	0	0
71. Brachythecium velutinum /Hedw./ B.S., & G.	1	0	0	0	0	0	0	0	0	0
72. Rhynchostegium riparioides /Hedw./ Card.	0	0	0	0	0	0	0	0	0	0
73. Rhynchostegium megapolitanum /Web.& Mohr/ B.S., & G.	0	0	0	0	0	0	0	0	0	0
74. Eurhynchium pulchellum /Hedw./ Jenn.	0	0	0	0	0	0	0	0	0	0
75. Eurhynchium hians /Hedw./ Sande Lac.	0	0	0	0	0	0	0	0	0	0
76. Hypnum cupressiforme Hedw.	0	0	0	0	0	0	0	0	0	0

Terricolous (T): T_1=Moist shaded soil and lawn. T_2=Dry and exposed soil. T_3=Waste ground and high nitrogenous soil.

Saxicolous and chasmophytes (SC): SC_1=Damp basic rocks and walls. SC_2=Dry basic rocks and walls. SC_3=Mortar and concrete. SC_4=Bricks and tiles. SC_5=Wet acidic rocks and concrete. SC_6=Dry acidic rocks and walls.

Epiphytes (E): E_1=On bark and tree bases.

Table 3. Occurrence of bryophytes in the different habitats in Madrid. Presence = 1, absence = 0

	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
1. Sphaerocarpus michelii Bell.	0	0	0	0	0	0	0	0	0	0
2. Lunularia cruciata /L./ Lindb.	1	0	0	0	0	0	0	0	0	0
3. Riccia lamellosa Raddi.	0	0	0	0	0	0	0	0	0	0
4. Frullania dilatata /L./ Dum.	0	0	0	0	0	0	0	0	0	0
5. Fissidens bryoides Hedw.	0	0	0	0	0	0	0	0	0	0
6. Fissidens viridulus /Sw./ Wahlenb.	0	1	0	0	0	0	0	0	0	0
7. Fissidens taxifolius Hedw.	1	1	0	0	0	0	0	0	0	0
8. Fissidens cristatus Wils. ex Mitt.	0	0	0	0	0	0	0	0	0	0
9. Dicranum scoparium Hedw.	0	0	0	0	0	0	0	0	0	1
10. Tortula princeps De Not.	0	1	1	0	0	0	0	0	0	0
11. Tortula ruralis /Hedw./ Gaertn., Meyer & Scharb.	1	1	1	0	0	1	0	0	0	0
12. Tortula intermedia /Brid./ De Not.	0	1	0	0	0	0	0	0	0	0
13. Tortula virescens /De Not./ De Not.	0	0	0	0	0	0	0	0	0	0
14. Tortula laevipila /Brid./ Schwaegr.	0	0	0	0	0	0	0	0	1	0
15. Tortula pagorum /Milde/ De Not.	0	0	0	0	0	0	0	0	0	1
16. Tortula papillosa Wils.	0	0	0	0	0	0	0	0	0	1
17. Tortula subulata Hedw.	0	1	0	0	1	0	0	0	0	0
18. Tortula marginata /B. & S./ Spruce	0	0	0	0	0	0	0	0	0	0
19. Tortula vahliana /K.F. Schultz/ Mont.	0	1	0	0	0	0	0	0	0	0
20. Tortula muralis Hedw.	1	1	1	1	1	1	1	0	1	0
21. Aloina aloides /K.F. Schultz/ Kindb.	0	1	0	0	0	1	0	0	0	0
22. Aloina rigida /Hedw./ Limpr.	1	1	0	0	0	0	0	0	0	0
23. Pterygoneurum ovatum /Hedw./ Dix.	0	0	0	0	0	0	0	0	0	0
24. Pottia lanceolata /Hedw./ C.Müll.	0	1	1	0	0	0	0	0	0	0
25. Pottia truncata /Hedw./ B. S.	1	1	0	0	0	0	0	0	0	0
26. Pottia bryoides /Dicks./ Mitt.	0	1	0	0	0	0	0	0	0	0
27. Phascum cuspidatum Hedw.	0	1	1	0	0	0	0	0	0	0
28. Barbula unguiculata Hedw.	1	1	1	0	0	1	1	0	0	0
29. Pseudocrossidium revolutum /Brid./ Zander	0	1	0	0	0	0	0	0	0	0
30. Pseudocrossidium hornschuchianum /K.F. Schultz/ Zander	1	1	1	0	0	0	0	0	0	0
31. Trichostomopsis umbrosa /C.Müll./ Robins.	0	0	0	0	0	0	0	0	0	0
32. Trichostomopsis trivalis /C.Müll./ Robins.	0	0	0	0	0	0	0	0	0	0
33. Didymodon luridus Hornsch. ex Spreng.	0	0	0	0	0	0	0	0	0	0
34. Didymodon vinealis /Brid./ Zander	0	1	0	0	0	1	0	0	0	0
35. Didymodon tophaceus /Brid./ Lisa	0	0	0	0	0	0	0	0	0	0

MADRID	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
36. Didymodon fallax /Hedw./ Zander	1	1	1	1	1	1	1	0	0	0
37. Pleurochaete squarrosa /Brid./ Lindb.	1	1	1	0	0	0	0	0	0	0
38. Grimmia anodon B. & S.	0	0	0	0	0	0	0	0	0	0
39. Grimmia laevigata /Brid./ Brid.	0	0	0	0	0	0	0	0	1	0
40. Grimmia pulvinata /Hedw./ Sm.	1	0	0	1	1	1	0	0	0	0
41. Grimmia trichophylla Grev.	0	0	0	0	0	0	0	0	1	0
42. Funaria hygrometrica Hedw.	1	1	1	0	0	1	0	0	0	0
43. Funaria pulchella Philib.	0	0	0	0	0	0	0	0	0	0
44. Bryum capillare Hedw.	1	1	1	0	0	1	0	0	0	1
45. Bryum canariense Brid.	1	0	0	0	0	0	0	0	0	0
46. Bryum caespiticium Hedw.	1	1	1	1	1	1	1	1	0	1
47. Bryum argenteum Hedw.	1	1	1	1	1	1	0	0	1	1
48. Bryum bicolor Dicks.	1	1	1	0	0	1	0	0	1	0
49. Bryum radiculosum Brid.	0	0	0	0	0	0	0	0	0	0
50. Rhizomnium punctatum /Hedw./ T.Kop.	1	0	0	0	0	0	0	0	0	0
51. Plagiomnium affine /Bland./ T.Kop.	1	0	0	0	0	0	0	0	0	0
52. Plagiumnium undulatum /Hedw./ T.Kop.	1	0	0	0	0	0	0	0	0	0
53. Orthotrichum lyellii Kook. & Tayl.	0	0	0	0	0	0	0	0	0	0
54. Orthotrichum rupestre Schleich. ex Schwaegr.	0	0	0	0	0	0	0	0	0	0
55. Orthotrichum anomalum Hedw.	0	0	0	0	0	0	0	0	0	0
56. Orthotrichum cupulatum Brid.	0	0	0	0	0	0	0	0	0	0
57. Orthotrichum tenellum Bruch ex Brid.	0	0	0	0	0	0	0	0	0	1
58. Orthotrichum diaphanum Brid.	0	0	0	0	0	1	0	0	0	1
59. Thamnobryum alopecurum /Hedw./ Nieuwl.	0	0	0	0	0	0	0	0	0	0
60. Amblystegium serpens /Hedw./ B., S. & G.	1	0	1	1	0	1	0	1	0	0
61. Amblystegium tenax /Hedw./ C. Jens.	0	0	0	0	0	0	0	0	0	0
62. Amblystegium humile /P.Beauv./ Crundw.	0	0	0	0	0	0	0	0	0	0
63. Amblystegium riparium /Hedw./ B., S. & G.	1	0	1	1	0	0	0	0	0	0
64. Isothecium myosuroides Brid.	0	0	0	0	0	0	0	0	0	0
65. Scorpiurium circinatum /Brid./ Fleisch. Loeske	0	0	0	0	0	0	0	0	0	0
66. Homalothecium sericeum /Hedw./ B., S. & G.	1	1	1	0	0	0	0	0	0	0
67. Homalothecium aureum /Spruce/ Robins.	1	1	1	0	0	0	0	0	0	0
68. Brachythecium albicans /Hedw./ B., S. & G.	1	0	0	0	0	0	0	0	0	0
69. Brachythecium mildeanum /Schimp./ Schimp. ex Milde	1	1	1	0	0	0	0	0	0	0
70. Brachythecium rutabulum /Hedw./ B., S. & G.	1	0	0	1	0	0	0	0	0	0

71. Brachythecium velutinum /Hedw./ B.,S. & G.	1	0	0	0	0	0	0	0	0	1
72. Rhynchostegium riparioides /Hedw./ Card.	0	0	0	0	0	0	0	0	0	0
73. Rhynchostegium megapolitanum /Web. Mohr/ B.,S. & G.	1	0	0	0	0	0	0	0	0	0
74. Eurhynchium pulchellum /Hedw./ Jenn.	1	1	1	0	0	0	0	0	0	0
75. Eurhynchium hians /Hedw./ Sande Lac.	1	1	1	0	0	0	0	0	0	0
76. Hypnum cupressiforme Hedw.	0	0	0	0	0	0	0	0	1	1

Terricolous (T): T_1=Moist shaded soil and lawn. T_2=Dry and exposed soil. T_3=Waste ground and high nitrogenous soil.

Saxicolous and chasmophytes (SC): SC_1=Damp basic rocks and walls. SC_2=Dry basic rocks and walls. SC_3=Mortar and concrete. SC_4=Bricks and tiles. SC_5=Wet acidic rocks and walls. SC_6=Dry acidic rocks and walls.

Epiphytes (E): E_1=On bark and tree bases.

Table 4. Occurrence of bryophytes in the different habitats in Toledo. Presence = 1, absence = 0.

	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
1. Sphaerocarpus michelii Bell.	1	0	0	0	0	0	0	0	0	0
2. Lunularia cruciata /L./ Lindb.	1	0	0	0	0	0	0	0	0	0
3. Riccia lamellosa Raddi	0	0	0	0	0	0	0	0	0	0
4. Frullania dilatata /L./ Dum.	0	0	0	0	0	0	0	0	0	0
5. Fissidens bryoides Hedw.	0	0	0	0	0	0	0	0	0	0
6. Fissidens viridulus /Sw./ Wahlenb.	1	0	0	0	0	0	0	0	0	0
7. Fissidens taxifolius Hedw.	0	0	0	0	0	0	0	0	0	0
8. Fissidens cristatus Wils. ex Mitt.	0	0	0	0	0	0	0	0	0	0
9. Dicranum scoparium Hedw.	0	0	0	0	0	0	0	0	0	0
10. Tortula princeps De Not.	0	0	0	0	0	0	0	0	0	0
11. Tortula ruralis /Hedw./ Gaertn., Meyer & Scherb.	0	1	0	0	0	0	0	0	0	0
12. Tortula intermedia /Brid./ De Not.	0	0	0	0	0	0	0	0	0	0

TOLEDO	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
13. Tortula virescens /De Not./ De Not.	0	0	0	0	0	0	0	0	0	0
14. Tortula laevipila /Brid./ Schwaegr.	0	0	0	0	0	0	0	0	0	0
15. Tortula pagorum /Milde/ De Not.	0	0	0	0	0	0	0	0	0	0
16. Tortula papillosa Wils.	0	0	0	0	0	0	0	0	0	0
17. Tortula subulata Hedw.	0	0	0	0	0	0	0	0	0	0
18. Tortula marginata /B. & S./ Spruce	0	1	0	0	0	0	0	0	0	0
19. Tortula vahliana /K.F. Schultz/ Mont.	0	0	0	0	0	0	0	0	0	0
20. Tortula muralis Hedw.	0	1	1	0	0	0	1	0	0	0
21. Aloina aloides /K.F. Schultz/ Kindb.	0	0	0	0	0	0	0	0	0	0
22. Aloina rigida /Hedw./ Limpr.	0	0	0	0	0	0	0	0	0	0
23. Pterygoneurum ovatum /Hedw./ Dix.	0	0	0	0	0	0	1	0	0	0
24. Pottia lanceolata /Hedw./ C.Müll.	0	0	0	0	0	0	0	0	0	0
25. Pottia truncata /Hedw./ B. S.	0	0	0	0	0	0	0	0	0	0
26. Pottia bryoides /Dicks./ Mitt.	0	0	0	0	0	0	0	0	0	0
27. Phascum cuspidatum Hedw.	0	0	0	0	0	0	0	0	0	0
28. Barbula unguiculata Hedw.	0	0	0	0	0	0	0	0	0	0
29. Pseudocrossidium revolutum /Brid./ Zander	0	0	0	0	0	0	0	0	0	0
30. Pseudocrossidium hornschuchianum /K.F.Schultz/ Zander	0	0	0	0	0	0	0	0	0	0
31. Trichostomopsis umbrosa /C.Müll./ Robins.	0	0	1	0	0	0	0	0	0	0
32. Trichostomopsis trivialis /C.Müll./ Robins.	0	1	0	0	0	0	0	0	0	0
33. Didymodon luridus Hornsch. ex Spreng.	0	1	0	0	0	0	0	0	0	0
34. Didymodon vinealis /Brid./ Zander	1	0	0	0	0	1	0	0	0	0
35. Didymodon tophaceus /Brid./ Lisa	0	0	0	1	0	0	0	0	0	0
36. Didymodon fallax /Hedw./ Zander	0	0	0	0	0	0	0	0	0	0
37. Pleurochaete squarrosa /Brid./ Lindb.	0	1	0	0	0	0	0	0	0	0
38. Grimmia anodon B. & S.	0	0	0	0	0	0	0	0	0	0
39. Grimmia laevigata /Brid./ Brid.	0	0	0	0	0	0	0	0	0	0
40. Grimmia pulvinata /Hedw./ Sm.	0	0	0	0	1	0	1	0	0	0
41. Grimmia trichophylla Grev.	0	0	0	0	0	0	0	0	0	0
42. Funaria hygrometrica Hedw.	0	1	1	0	0	0	0	0	0	1
43. Funaria pulchella Philib.	0	0	0	0	0	0	0	0	0	0
44. Bryum capillare Hedw.	1	0	0	0	0	0	0	0	0	0
45. Bryum canariense Brid.	0	0	0	0	0	0	0	0	0	0
46. Bryum caespiticium Hedw.	0	0	0	0	0	0	0	0	0	0
47. Bryum argenteum Hedw.	1	1	1	0	0	0	1	0	0	0
48. Bryum bicolor Dicks.	0	1	1	0	0	0	0	0	0	0
49. Bryum radiculosum Brid.	0	0	0	0	0	1	0	0	0	0

50. Rhizomnium punctatum /Hedw./ T.Kop.	0	0	0	0	0	0	0	0	0	0
51. Plagiomnium affine /Bland./ T.Kop.	0	0	0	0	0	0	0	0	0	0
52. Plagiomnium undulatum /Hedw./ T.Kop.	0	0	0	0	0	0	0	0	0	0
53. Orthotrichum lyellii Kook.& Tayl.	0	0	0	0	0	0	0	0	0	1
54. Orthotrichum rupestre Schleich. ex Schwaegr.	0	0	0	0	0	0	0	0	0	0
55. Orthotrichum anomalum Hedw.	0	0	0	0	0	0	0	0	0	0
56. Orthotrichum cupulatum Brid.	0	0	0	0	0	0	0	0	0	0
57. Orthotrichum tenellum Bruch ex Brid.	0	0	0	0	0	0	0	0	0	0
58. Orthotrichum diaphanum Brid.	0	0	0	0	0	0	0	0	0	1
59. Thamnobryum alopecurum /Hedw./ Nieuwl.	1	0	0	0	0	0	0	0	0	0
60. Amblystegium serpens /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
61. Amblystegium tenax /Hedw./ C. Jens.	1	0	0	0	0	0	0	0	0	0
62. Amblystegium humile /P.Beauv./ Crundw.	0	0	0	0	0	0	0	0	0	0
63. Amblystegium riparium /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
64. Isothecium myosuroides Brid.	0	0	0	0	0	0	0	0	0	0
65. Scorpiurium circinatum /Brid./ Fleisch. & Loeske	0	0	0	0	0	0	0	0	0	0
66. Homalothecium sericeum /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
67. Homalothecium aureum /Spruce/ Robins.	0	1	0	0	0	0	0	0	0	0
68. Brachythecium albicans /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	0
69. Brachythecium mildeanum /Schimp./ Schimp. ex Milde	0	0	0	0	0	0	0	0	0	0
70. Brachythecium rutabulum /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	1	0	0
71. Brachythecium velutinum /Hedw./ B.,S. & G.	0	0	0	0	0	0	0	0	0	1
72. Rhynchostegium riparioides /Hedw./ Card.	1	0	0	0	0	0	0	0	0	0
73. Rhynchostegium megapolitanum /Web. Mohr/ B.,S. & G.	0	1	0	0	0	0	0	0	0	0
74. Eurhynchium pulchellum /Hedw./ Jenn.	0	0	0	0	0	0	0	0	0	0
75. Eurhynchium hians /Hedw./ Sande Lac.	0	0	0	0	0	0	0	0	0	0
76. Hypnum cupressiforme Hedw.	0	0	0	0	0	0	0	0	0	0

Terricolous (T): T_1=Moist shaded soil and lawn. T_2=Dry and exposed soil. T_3=Waste ground and high nitrogenous soil.

Saxicolous and chasmophytes (SC): SC_1=Damp basic rocks and walls. SC_2=Dry basic rocks and walls. SC_3=Mortar and concrete. SC_4=Bricks and tiles. SC_5=Wet acidic rocks and walls. SC_6=Dry acidic rocks and walls.

Epiphytes (E): E_1=On bark and tree bases.

Table 5. Number of species found in the different habitats of each town.

	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
Avila	7	17	4	0	3	20	7	2	7	5
Badajoz	8	11	1	0	1	3	1	1	0	8
Madrid	31	30	21	8	6	14	4	2	7	10
Toledo	9	11	5	1	1	2	4	1	0	4

The number of liverworts is very reduced, only four species, probably due to the dryness of the towns.

Six species of mosses: Tortula ruralis, Didymodon vinealis, Grimmia pulvinata, Funaria hygrometrica, Bryum argenteum and Ortothrichum diaphanum, occur in the four towns studied (Table 8) and are widely distributed within each of them (Table 6). This agrees with the observations for Lisbon (Sérgio 1981), Brussels (Gerard 1978), Hiroshima (Ando & Taoda 1967), Montreal (Le Blanc & De Sloover 1970) and Duisburg (Nordhorn-Richter & Düll (1982).

On the other hand, a species considered as pioneer, toxiphilous and frequent in urban habitats, Ceratodon purpureus, has not been detected, nor does it appear cited for any other Spanish town studied.

Trichostomopsis trivialis, a South African species, has been found in Toledo. Interestingly, it has previously been cited in the city of Sevilla and in the province of Toledo (Casas & Saiz-Jiménez 1982), but nowhere else in Europe.

Among the epiphytic species, propaguliferous and gemmiferous mosses are quite common: Tortula pagorum, T. papillosa, Bryum capillare, B. caespiticium, Orthotrichum lyellii and O. diaphanum. Except O. diaphanum, none of them was found fruiting.

The results obtained and their discussion allow one to conclude that the terricolous habitat, T_1 type, is the richest in species; so its presence and extension seems to condition the richness in bryophytes of a town.

Table 6. Number of habitats that a species has colonized in each town.

		AVILA	BADAJOZ	MADRID	TOLEDO
1.	Sphaerocarpus michelii Bell.	0	0	0	1
2.	Lunularia cruciata /L./ Lindb.	0	1	1	1
3.	Riccia lamellosa Raddi	0	1	0	0
4.	Frullania dilatata /L./ Dum.	0	1	0	0
5.	Fissidens bryoides Hedw.	0	1	0	0
6.	Fissidens viridulus /Sw./ Wahlenb.	0	0	1	1
7.	Fissidens taxifolius Hedw.	0	0	2	0
8.	Fissidens cristatus Wils. ex Mitt.	0	1	0	0
9.	Dicranum scoparium Hedw.	0	0	1	0
10.	Tortula princeps De Not.	3	0	2	0
11.	Tortula ruralis /Hedw./ Gaertn., Meyer & Scherb.	4	0	4	1
12.	Tortula intermedia /Brid./ De Not.	6	0	1	0
13.	Tortula virescens /De Not./ De Not.	1	0	0	0
14.	Tortula laevipila /Brid./ Schwaegr.	1	1	1	0
15.	Tortula pagorum /Milde/ De Not.	0	1	1	0
16.	Tortula papillosa Wils.	0	0	1	0
17.	Tortula subulata Hedw.	0	0	2	0
18.	Tortula marginata /B. & S./ Spruce	0	0	0	1
19.	Tortula vahliana /K.F. Schultz/ Mont.	0	0	1	0
20.	Tortula muralis Hedw.	4	3	8	3
21.	Aloina aloides /K.F. Schultz/ Kindb.	0	0	2	0
22.	Aloina rigida /Hedw./ Limpr.	0	1	2	0
23.	Pterygoneurum ovatum /Hedw./ Dix.	0	0	0	1
24.	Pottia lanceolata /Hedw./ C.Müll.	0	0	2	0
25.	Pottia truncata /Hedw./ B. & S.	0	0	2	0
26.	Pottia bryoides /Dicks./ Mitt.	0	0	1	0
27.	Phascum cuspidatum Hedw.	0	0	2	0
28.	Barbula unguiculata Hedw.	0	1	5	0
29.	Pseudocrossidium revolutum /Brid./ Zander	3	1	1	0
30.	Pseudocrossidium hornschuchianum /K.F. Schultz/ Zander	2	1	3	0
31.	Trichostomopsis umbrosa /C.Müll./ Robins.	0	0	0	1
32.	Trichostomopsis trivialis /C.Müll./ Robins.	0	0	0	1
33.	Didymodon luridus Horsch. ex Spreng.	1	0	0	1
34.	Didymodon vinealis /Brid./ Zander	4	3	2	2

ΣHABITATS	ÁVILA	BADAJOZ	MADRID	TOLEDO
35. Didymodon tophaceus /Brid./ Lisa	0	0	0	1
36. Didymodon fallax /Hedw./ Zander	2	1	7	0
37. Pleurochaete squarrosa /Brid./ Lindb.	0	1	3	1
38. Grimmia anodon B.& S.	4	0	0	0
39. Grimmia laevigata /Brid./ Brid.	1	0	1	0
40. Grimmia pulvinata /Hedw./ Sm.	3	2	4	2
41. Grimmia trichophylla Grev.	3	0	1	0
42. Funariahygrometrica Hedw.	2	1	4	3
43. Funaria pulchella Philib.	0	2	0	0
44. Bryum capillare Hedw.	3	0	5	1
45. Bryum canariense Brid.	0	0	1	0
46. Bryum caespiticium Hedw.	4	1	9	0
47. Bryum argenteum Hedw.	3	2	8	4
48. Bryum bicolor Dicks.	0	0	5	2
49. Bryum radiculosum Brid.	0	0	0	1
50. Rhizomnium punctatum /Hedw./ T.Kop.	0	0	1	0
51. Plagiomnium affine /Bland./ T.Kop.	0	0	1	0
52. Plagiomnium undulatum /Hedw./ T.Kop.	0	0	1	0
53. Orthotrichum lyellii Kook. & Tayl.	0	0	0	1
54. Orthotrichum rupestre Schleich. ex Schwaegr.	2	0	0	0
55. Orthotrichum anomalum Hedw.	1	0	0	0
56. Orthotrichum cupulatum Brid.	2	0	0	0
57. Orthotrichum tenellum Bruch ex Brid.	1	0	1	0
58. Orthotrichum diaphanum Brid.	2	1	2	1
59. Thamnobryum alopecurum /Hedw./ Nieuwl.	0	0	0	1
60. Amblystegium serpens /Hedw./ B.,S.& G.	0	0	5	0
61. Amblystegium tenax /Hedw./ C. Jens.	0	0	0	1
62. Amblystegium humile /P.Beauv./ Crundw.	1	0	0	0
63. Amblystegium riparium /Hedw./ B.,S. & G.	0	0	3	0
64. Isothecium myosuroides Brid.	0	1	0	0
65. Scorpiurium circinatum /Brid./ Fleisch. & Loeske	0	1	0	0
66. Homalothecium sericeum /Hedw./ B.,S.& G.	4	1	3	0
67. Homalothecium aureum /Spruce/ Robins.	0	1	3	1
68. Brachythecium albicans /Hedw./ B.,S. & G.	0	0	1	0
69. Brachythecium mildeanum /Schimp./ Schimp. ex Milde	3	0	3	0
70. Brachythecium rutabulum /Hedw./ B.,S. & G.	2	0	2	1

71. Brachythecium velutinum /Hedw./ B.,S.& G.	0	1	2	1
72. Rhynchostegium riparioides /Hedw./ Card.	0	0	0	1
73. Rhynchostegium megapolitanum /Web. Mohr/ B.,S.& G.	0	0	1	1
74. Eurhynchium pulchellum /Hedw./ Jenn.	0	0	3	0
75. Eurhynchium hians /Hedw./ Sande Lac.	0	0	3	0
76. Hypnum cupressiforme Hedw.	0	0	2	0

Table 7. Number of towns in which a species has been found in a particular habitat.

	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
1. Sphaerocarpus michelii Bell.	1	0	0	0	0	0	0	0	0	0
2. Lunularia cruciata /L./ Lindb.	3	0	0	0	0	0	0	0	0	0
3. Riccia lamellosa Raddi	0	1	0	0	0	0	0	0	0	0
4. Frullania dilatata /L./ Dum.	0	0	0	0	0	0	0	0	0	1
5. Fissidens bryoides Hedw.	1	0	0	0	0	0	0	0	0	0
6. Fissidens viridulus /Sw./ Wahlenb.	1	1	0	0	0	0	0	0	0	0
7. Fissidens taxifolius Hedw.	1	1	0	0	0	0	0	0	0	0
8. Fissidens cristatus Wils. ex Mitt.	0	0	0	0	0	0	0	1	0	0
9. Dicranum scoparium Hedw.	0	0	0	0	0	0	0	0	0	1
10. Tortula princeps De Not.	0	2	1	0	0	1	1	0	0	0
11. Tortula ruralis /Hedw./ Gaertn., Meyer & Scherb.	2	3	1	0	0	2	1	0	0	0
12. Tortula intermedia /Brid./ De Not.	1	2	1	0	0	1	1	0	0	1
13. Tortula virescens /De Not./ De Not.	0	0	0	0	0	0	0	0	0	1
14. Tortula laevipila /Brid./ Schwaegr.	0	0	0	0	0	0	0	0	0	2
15. Tortula pagorum /Milde/ De Not.	0	0	0	0	0	0	0	0	0	2
16. Tortula papillosa Wils.	0	0	0	0	0	0	0	0	0	1
17. Tortula subulata Hedw.	0	1	0	0	1	0	0	0	0	0
18. Tortula marginata /B. & S./ Spruce	0	1	0	0	0	0	0	0	0	0
19. Tortula vahliana /K.F. Schultz/ Mont.	0	1	0	0	0	0	0	0	0	0
20. Tortula muralis Hedw.	1	4	2	1	1	3	3	1	2	0
21. Aloina aloides /K.F. Schultz/ Kindb.	0	1	0	0	0	1	0	0	0	0
22. Aloina rigida /Hedw./ Limpr.	1	2	0	0	0	0	0	0	0	0

Σ TOWNS	T_1	T_2	T_3	SC_1	SC_2	SC_3	SC_4	SC_5	SC_6	E_1
23. Pterygoneurum ovatum /Hedw./ Dix.	0	0	0	0	0	0	1	0	0	0
24. Pottia lanceolata /Hedw./ C.Müll.	0	1	1	0	0	0	0	0	0	0
25. Pottia truncata /Hedw./ B. & S.	1	1	0	0	0	0	0	0	0	0
26. Pottia bryoides /Dicks./ Mitt.	0	1	0	0	0	0	0	0	0	0
27. Phascum cuspidatum Hedw.	0	1	1	0	0	0	0	0	0	0
28. Barbula unguiculata Hedw.	2	1	1	0	0	1	1	0	0	0
29. Pseudocrossidium revolutum /Brid./ Zander	1	2	0	0	1	1	0	0	0	0
30. Pseudocrossidium hornschuchianum /K.F. Schultz/ Zander	2	2	1	0	0	1	0	0	0	0
31. Trichostomopsis umbrosa /C.Müll./ Robins.	0	0	1	0	0	0	0	0	0	0
32. Trichostomopsis trivialis /C.Müll./ Robins.	0	1	0	0	0	0	0	0	0	0
33. Didymodon luridus Hornsch. ex Spreng.	0	2	0	0	0	0	0	0	0	0
34. Didymodon vinealis /Brid./ Zander	2	3	1	0	1	4	0	0	0	0
35. Didymodon tophaceus /Brid./ Lisa	0	0	0	1	0	0	0	0	0	0
36. Didymodon fallax /Hedw./ Zander	1	2	1	1	1	3	1	0	0	0
37. Plaurochaete squarrosa /Brid./ Lindb.	1	3	1	0	0	0	0	0	0	0
38. Grimmia anodon B. & S.	0	1	0	0	1	1	1	0	0	0
39. Grimmia laevigata /Brid./ Brid.	0	0	0	0	0	0	0	0	2	0
40. Grimmia pulvinata /Hedw./ Sm.	1	1	0	1	3	2	2	0	0	1
41. Grimmia trichophylla Grev.	0	0	0	0	0	0	1	1	2	0
42. Funaria hygrometrica Hedw.	1	4	2	0	0	2	0	0	0	1
43. Funaria pulchella Philib.	1	1	0	0	0	0	0	0	0	0
44. Bryum capillare Hedw.	2	1	2	0	0	2	0	0	1	2
45. Bryum canariense Brid.	1	0	0	0	0	0	0	0	0	0
46. Bryum caespiticium Hedw.	1	3	2	1	1	2	1	1	1	1
47. Bryum argenteum Hedw.	2	4	2	1	1	2	2	0	1	2
48. Bryum bicolor Dicks.	1	2	2	0	0	1	0	0	1	0
49. Bryum radiculosum Brid.	0	0	0	0	0	1	0	0	0	0
50. Rhizomnium punctatum /Hedw./ T.Kop.	1	0	0	0	0	0	0	0	0	0
51. Plagiomnium affine /Bland./ T.Kop.	1	0	0	0	0	0	0	0	0	0
52. Plagiomnium undulatum /Hedw./ T.Kop.	1	0	0	0	0	0	0	0	0	0
53. Orthotrichum lyellii Kook. & Tayl.	0	0	0	0	0	0	0	0	0	1
54. Orthotrichum rupestre Schleich. ex Schwaegr.	0	0	0	0	0	1	0	0	1	0
55. Orthotrichum anomálun Hedw.	0	0	0	0	0	1	0	0	0	0
56. Orthotrichun cupulatum Brid.	0	1	0	0	0	1	0	0	0	0
57. Orthotrichum tenellum Bruch ex Brid.	0	0	0	0	0	0	0	0	0	2
58. Orthotrichum diaphanum Brid.	0	0	0	0	0	2	0	0	0	4

59. Thamnobryum alopecurum /Hedw./ Nieuwl.	1	0	0	0	0	0	0	0	0	0
60. Amblystegium serpens /Hedw./ B.,S.& G.	1	0	1	1	0	1	0	1	0	0
61. Amblystegium tenax /Hedw./ C. Hens.	1	0	0	0	0	0	0	0	0	0
62. Amblystegium humile /P.Beauv./ Crundw.	1	0	0	0	0	0	0	0	0	0
63. Amblystegium riparium /Hedw./ B.,S.& G.	1	0	1	1	0	0	0	0	0	0
64. Isothecium myosuroides Brid.	1	0	0	0	0	0	0	0	0	0
65. Scorpiurium circinatum /Brid./ Fleisch. Loeske	0	1	0	0	0	0	0	0	0	0
66. Homalothecium sericeum /Hedw./ B.,S.& G.	2	2	2	0	0	1	0	0	0	1
67. Homalothecium aureum /Spruce/ Robins.	1	3	1	0	0	0	0	0	0	0
68. Brachythecium albicans /Hedw./ B.,S.& G.	1	0	0	0	0	0	0	0	0	0
69. Brachythecium mildeanum /Schimp./ Schimp. ex Milde	2	1	1	0	0	1	0	0	1	0
70. Brachythecium rutabulum /Hedw./ B.,S.& G.	2	1	0	1	0	0	0	1	0	0
71. Brachythecium velutinum /Hedw./ B.,S.& G.	2	0	0	0	0	0	0	0	0	2
72. Rhynchostegium riparioides /Hedw./ Card.	1	0	0	0	0	0	0	0	0	0
73. Rhynchostegium megapolitanum /Web. Mohr/ B.,S.& G.	1	1	0	0	0	0	0	0	0	0
74. Eurhynchium pulchellum /Hedw./ Jenn.	1	1	1	0	0	0	0	0	0	0
75. Eurhynchium hians /Hedw./ Sande Lac.	1	1	1	0	0	0	0	0	0	0
76. Hypnum cupressiforme Hedw.	0	0	0	0	0	0	0	0	1	1

Terricolous (T): T_1=Moist shaded soil and lawn. T_2=Dry and exposed soil. T_3=Waste ground and high nitrogenous soil.

Saxicolous and chasmophytes (SC): SC_1=Damp basic rocks and walls. SC_2=Dry basic rocks and walls. SC_3=Mortar and concrete. SC_4=Bricks and tiles. SC_5=Wet acidic rocks and walls. SC_6=Dry acidic rocks and walls.

Epiphytes (E): E_1=On bark and tree bases.

Table 8. Results for the species (considering the four towns)

		nº towns colonized	nº habitats colonized
1.	Sphaerocarpus michelii Bell.	1	1
2.	Lunularia cruciata /L./ Lindb.	3	1
3.	Riccia lamellosa Raddi	1	1
4.	Frullania dilatata /L./ Dum.	1	1
5.	Fissidens bryoides Hedw.	1	1
6.	Fissidens viridulus /Sw./ Wahlenb.	2	2
7.	Fissidens taxifolius Hedw.	1	2
8.	Fissidens cristatus Wils. ex Mitt.	1	1
9.	Dicranum scoparium Hedw.	1	1
10.	Tortula princeps De Not.	2	4
11.	Tortula ruralis /Hedw./ Gaertn., Meyer & Scherb.	3	5
12.	Tortula intermedia /Brid./ De Not.	2	6
13.	Tortula virescens /De Not./ De Not.	1	1
14.	Tortula laevipila /Brid./ Schwaegr.	3	1
15.	Tortula pagorum /Milde/ De Not.	2	1
16.	Tortula papillosa Wils.	1	1
17.	Tortula subulata Hedw.	1	2
18.	Tortula marginata /B. & S./ Spruce	1	1
19.	Tortula vahliana /K.F. Schultz/ Mont.	1	1
20.	Tortula murali Hedw.	4	9
21.	Aloina aloides /K.F. Schultz/ Kindb.	1	2
22.	Aloina rigida /Hedw./ Limpr.	2	2
23.	Pterygoneurum ovatum /Hedw./ Dix.	1	1
24.	Pottia lanceolata /Hedw./ C.Müll.	1	2
25.	Pottia truncata /Hedw./ B. & S.	1	2
26.	Pottia bryoides /Dicks./ Mitt.	1	1
27.	Phascum cuspidatum Hedw.	1	2
28.	Barbula unguiculata Hedw.	2	5
29.	Pseudocrossidium revolutum /Brid./ Zander	3	4
30.	Pseudocrossidium hornschuchianum /K.F. Schultz/ Zander	3	4
31.	Trichostomopsis umbrosa /C.Müll./ Robins.	1	1
32.	Trichostomopsis trivalis /C.Müll./ Robins.	1	1
33.	Didymodon luridus Horsch. ex Spreng.	2	1
34.	Didymodon vinealis /Brid./ Zander	4	5
35.	Didymodon tophaceus /Brid./ Lisa	1	1

36. Didymodon fallax /Hedw./ Zander	3	7
37. Pleurochaete squarrosa /Brid./ Lindb.	3	3
38. Grimmia anodon S. & S.	1	4
39. Grimmia laevigata /Brid./ Brid.	2	1
40. Grimmia pulvinata /Hedw./ Sm.	4	7
41. Grimmia trichophylla Grev.	2	3
42. Funariahygrometrica Hedw.	4	5
43. Funaria pulchella Philib.	1	2
44. Bryum capillare Hedw.	3	6
45. Bryum canariense Brid.	1	1
46. Bryum caespiticium Hedw.	3	10
47. Bryum argenteum Hedw.	4	9
48. Bryum bicolor Dicks.	2	5
49. Bryum radiculosum Brid.	1	1
50. Rhizomnium punctatum /Hedw./ T.Kop.	1	1
51. Plagiomnium affine /Bland./ T.Kop.	1	1
52. Plagiomnium undulatum /Hedw./ T.Kop.	1	1
53. Orthotrichum lyelli Kook. & Tayl.	1	1
54. Orthotrichum rupestre Schleich. ex Schwaegr.	1	2
55. Orthotrichum anomalum Hedw.	1	1
56. Orthotrichum cupulatum Brid.	1	2
57. Orthotrichum tenellum Bruch ex Brid.	2	1
58. Orthotrichum diaphanum Brid.	4	2
59. Thamnobryum alopecurum /Hedw./ Nieuwl.	1	1
60. Amblystegium serpens /Hedw./ B.,S. & G.	1	5
61. Amblystegium tenax /Hedw./ C. Hens.	1	1
62. Amblystegium humile /P.Beauv./ Crundw.	1	1
63. Amblystegium riparium /Hedw./ B.,S. & G.	1	3
64. Isothecium myosuroides Brid.	1	1
65. Scorpiurium circinatum /Brid./ Fleisch. & Loeske	1	1
66. Homalothecium sericeum /Hedw./ B.,S. & G.	3	5
67. Homalothecium aureum /Spruce/ Robins.	3	3
68. Brachythecium albicans /Hedw./ B.,S. & G.	1	1
69. Brachythecium mildeanum /Schimp./ Schimp. ex Milde	2	5
70. Brachythecium rutabulum /Hedw./ B.,S. & G.	3	4
71. Brachythecium velutinum /Hedw./ B.,S. & G.	3	2
72. Rhynchostegium riparioides /Hedw./ Card.	1	1
73. Rhynchostegium megapolitanum /Web. & Mohr/ B.,S. & G.	2	2
74. Eurhynchium pulchellum /Hedw./ Jenn.	1	3
75. Eurhynchium hians /Hedw./ Sande Lac.	1	3
76. Hypnum cupressiforme Hedw.	1	2

Table 9. Results for the habitats

	No. of towns colonized	No. of species
T_1	4	43
T_2	4	41
T_3	4	24
SC_1	2	9
SC_2	4	9
SC_3	4	25
SC_4	4	12
SC_5	4	6
SC_6	2	10
E_1	4	18

Table 10. Results for the towns.

	No. of species	No. of habitats colonized
Avila	28	9
Badajoz	26	8
Madrid	51	10
Toledo	28	9

Besides, species considered to be toxitolerant and poleophyllous, have been detected in all of the towns studied, although their distribution varies within each of them.

It is also remarkable that the epiphytic species seem to increase their asexual reproduction, showing a decrease of fertility in urban environments.

However, these and other observations pointed out in this paper, will be satisfactorily explained only when data of the pollution levels of the towns are available.

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SPHAGNUM MOSS-BAGS IN AIR POLLUTION MONITORING IN THE CITY OF HELSINKI

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The moss-bag technique originally developed in Great Britain has been used in Finland since 1976 in air pollution monitoring in cities and near industrial and traffic emission sources. In this study, about 600 moss-bags were suspended for approximately 3-month periods in 1981-1983 at receptor points all over the City of Helsinki and in some background areas. Several moss species were tested for further development of the technique, but Sphagnum girgensohnii was found to be preferable. Based on the atomic absorption analysis of moss-bags, the monthly accumulation values of Cd, Cr, Cu, Fe, Pb, Ni, V, and Zn were calculated and mapped. Three main emission sources were recognized: traffic, energy supply and refuse burning.

To determine the relative significance of these emission sources at different receptor points, principal component analysis was applied, resulting in the following three factors: 1. traffic factor (Fe, Ash, Pb, Cr), 2. energy factor (Ni, V) and 3. incinerator factor (Zn, Cd).

INTRODUCTION

The use of various bio-indicators for monitoring air pollution has increased in recent years (Lötchert et al. 1975, Andersen et al. 1978, Rühling & Skärby 1979, Rambaek & Steinnes 1980). Also, this study is based on the bio-indicator method, on the moss-bag technique originally developed in

Great Britain (Goodman et al. 1974, Little & Martin 1974, Temple et al. 1981).

Most moss species absorb air pollutants efficiently, especially wet deposition, and are much cheaper to use than mechanical collectors. So, the monitoring is possible simultaneously in tens of hundreds of observation (receptor) points and the spreading of pollutants during the study period (mostly 1 - 6 months) may be mapped accurately.

The moss-bag technique is very useful, especially in such polluted areas where wild growing mosses are lacking.

This method further developed by the author has been used in Finland since 1976 for air pollution monitoring in cities and near industrial and traffic emission sources, most recently in project MIL 4 during which this material was collected (Mäkinen 1977, 1984, Mäkinen et al. 1980, Nurmi 1981, Mäkinen & Lodenius 1982, 1984, Hynninen 1983, Lodenius & Tulisalo 1984).

2. STUDY AREA

The study area comprises the whole downtown of Helsinki, Finland, but the network of measuring points is denser in industrial areas and near the vicinity in the eastern part of the city (Fig. 1).

The topography of the study area varies because the City of Helsinki is built up mainly on rocky hills lifted up from the Baltic Sea.

The densely populated old city is about one half of the whole 100 km^2 study area (Fig. 1) with approximately 260,000 residents (Statistical Center of the Helsinki City).

A great part of the study area consists of bays and parks.

3. EMISSION SOURCES

3.1 Traffic

In In the study area there are three main streets with very busy traffic (Fig. 1). The greatest density (49,400 vehicles

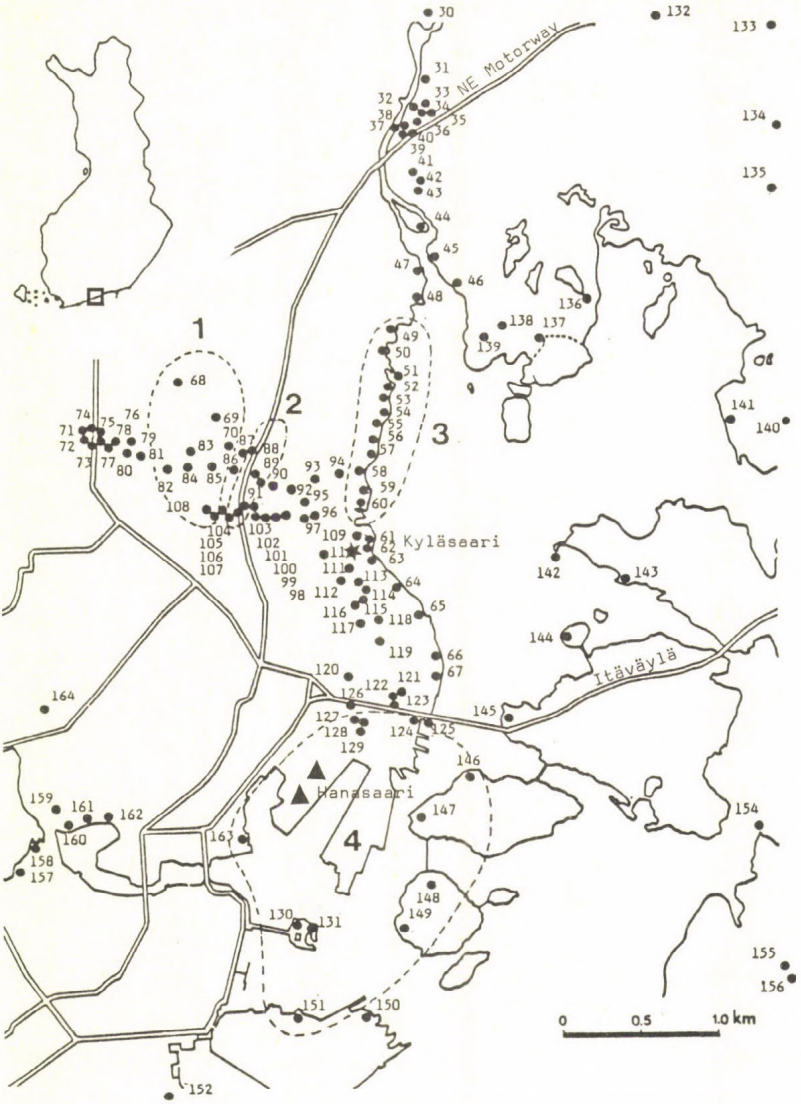

Fig. 1. Location of the receptor points and greater emission sources in the study area. The special subareas 1-4 are marked with broken line (see text). ═══ : main street, ✱ : refuse burning plant, ▲ : coal-fired power plant.

per day in 1981) was estimated on Eastern Highway (Haataja 1984).

Whereas about 70% of all vehicles in Helsinki traffic are private cars, with a significant proportion of them using until now high-octane gasoline with 0.45 g lead in 1 liter gas, they are considerable emission sources.

On the main streets of the study area, the calculated range of daily lead emissions is 0.58 - 1.00 kg/km. That makes about 500 g monthly in the study area.

3.2 Energy supply

The energy supply in the study area is based mainly on two coal-fired power plants, Hanasaari A and B, which produce a major part of the electricity and heating energy used in Helsinki (Fig. 1). Their total use of coal during the study period (October 19, 1982 - March 14, 1983) was 425,000 tons. Use of oil was about 5,000 tons. Corresponding estimated fly ash emission 1.250 tons, including about 37 tons of heavy metals.

3.3 Refuse burning

The influence of refuse burning on air pollution has been quite considerable in many cities (Heimler 1975, Jacko & Neuendorf 1977, Freeman 1978, Granath 1978, Greenberg et al. 1978a, b, Stockholms kommun 1978, Lorber 1980, Vornanen 1982). A special problem if such burning facilities is that neither has any electric filter nor smoke washing like Kyläsaari in Helsinki.

During the study period, when the burning plant was still in function, about 38,000 tons of miscellanous housing, shop and workplace waste were burned in the Kyläsaari incinerator. That made about 26% of the community waste of Helsinki city.

The smoke of that burning plant was cleaned by cyclones with a separation capacity from 37 to 73% and conducted through a smoke stack to 105 metres height.

4. MATERIAL AND METHODS

The moss-bags used in this study were made from acid-washed material consisting of two moss species: Sphagnum girgensohnii and S. angustifolium. The material was taken from Pälkäne, 150 km north of Helsinki.

More than 600 moss-bags (each about 1 g of dry weight) were suspended in nylon nets at about 3 metres height on the top twigs of young birches in 164 receptor points all over the study area (Fig. 1) and reference areas in southern Finland. Suspending of the moss-bags near the streets was avoided, where the emissions caused by traffic were not studied.

After about 5 months accumulation time, the pre-treatment of the moss-bags included two days at +40 °C temperature and dry-ashing at 450 °C. The ash was extracted with 5 ml of conc. HCl on a hot plate. From the filtrate the heavy metals were determined by a standard AAS-flame method (Allen 1974, Mäkinen 1977). The mean monthly accumulation, µg/g weight, based on 2-4 replicate analyses, was calculated at all receptor points for lead, cadmium, chromium, copper, iron, nickel, vanadium and zinc as an increase of the metal content of the moss-bag material from the beginning of the test. The monthly accumulation of ash is indicated in per cent units.

The statistical claculations of the data were carried out with BMDP and MINITAB programs at the Computer Center of the University of Helsinki.

To estimate the relative influence of different emission sources on air pollution, four representative subareas were selected on the basis of factor analysis of metal accumulation (Fig. 1).

5. ACCUMULATION OF ASH AND HEAVY METALS IN MOSS-BAGS

5.1 Background levels

The background values of heavy metals and ash accumulated in moss-bags were determined at the same time and with the same method as in the city area. These mean levels represented

Table 1. The estimated emissions of ash and heavy metals in Kyläsaari refuse burning plant during the study period (from 19th October 1982 to 14th March 1983), according to the emission measurements and neutron activity analyses of fly ash published in Aikäs & Hahkala 1982 (+) and Mattsson & Jaakkola 1979 (++).

Ash	143,200 kg(+)	Ni	151 kg(+), 22 kg(++)
Cd	164 kg(+), 37 kg(++)	Pb	3,200 kg(+), 1375 kg(++)
Cr	230 kg(+)	V	5 kg(+)
Cu	127 kg(++)	Zn	4.668 kg(+), 3222 kg(++)
Fe	1,824 kg(+)		

Table 2. Mean monthly background values (ppm dry wt, ash in %-units) of heavy metal and ash accumulation into the moss-bags in southern Finland during wintertime in 1982-1983.

Ash	Cd	Cr	Cu	Fe	Ni	Pb	V	Zn	n
0.3	0.03	0.1	0.6	74	0.4	4.3	1.5	5.5	23

in Table 2 were calculated in three relatively remote areas of southern Finland. One of them was situated in Pälkäne.

5.2 Ash

The ash content of living Sphagnum moss varies between 1.3-4.4% in the bogs in Finland (Pakarinen 1981). The original ash content of Sphagnum mosses used in this study before acid washing was about 2.1% after that 1.7%. The soluble part of ash in part consists of long-transported mineral components (cf. also Kivinen 1933).

During about a five-month collection time the ash content had increased in all receptor points by 0.5-40% units. In monthly accumulation values this corresponds to an increase of 0.1-8.3%-units. The mean increase was 1.9± 1.5 %-units (n = 164).

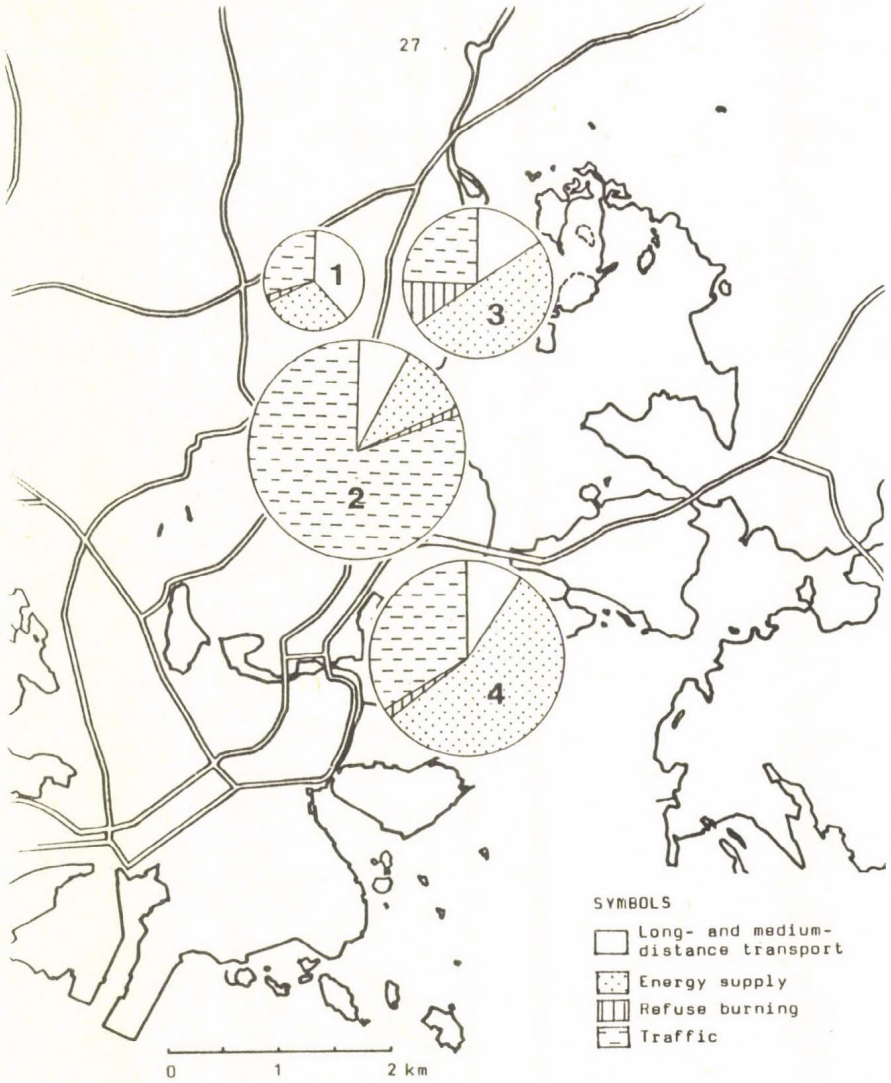

Fig. 2. Relative accumulation values of ash in moss-bags, indicating the origin of emissions in four subareas (cf. Fig. 1): 1. Central park area (Kumpula) far away from emission sources; 2. Traffic area (Hämeentie) with daily traffic intensity of 26,200 vehicles; 3. Refuse burning area (Kyläsaari) near an incenerator; 4. Energy supply area (Hanasaari) near coal-fired power plants.

In Fig. 2 the relative values of different emission sources are presented. The area of the circles is proportional to the ash accumulation in the subareas. The great proportion of the traffic on subarea 2 is particularly noticeable.

Fig. 3. Mean monthly accumulation of cadmium (ppm dry weight) in moss-bags in Helsinki during the winter of 1982/1983. Interpolated graphs of equal value are shown.

5.3 Cadmium (Cd)

The monthly accumulation of cadmium in moss bags ranges from 0.01 to 0.65 ppm/dry wt (Fig. 3). The greatest values are in the study area leewards (NE) from the Kyläsaari refuse burning plant. The mean monthly accumulation of cadmium in the whole material is 0.20± 0.15 ppm (n = 164), which is exactly the same average value as measured in autumn, 1981, in a similar study in the same area (Mäkinen & Lodenius 1982, 1984).

5.4 Chromium (Cr)

A great part of the chromium accumulated in moss-bags comes apparently from the city. This conclusion may be drawn if the accumulation values of the background area and the study area are correlated. In a great part of the study area the accumulation values of Cr were 10 times or higher higher than in background areas. The highest values (over 3 ppm) were found near the main streets and leewards from the coal-fired power plants (Fig. 4).

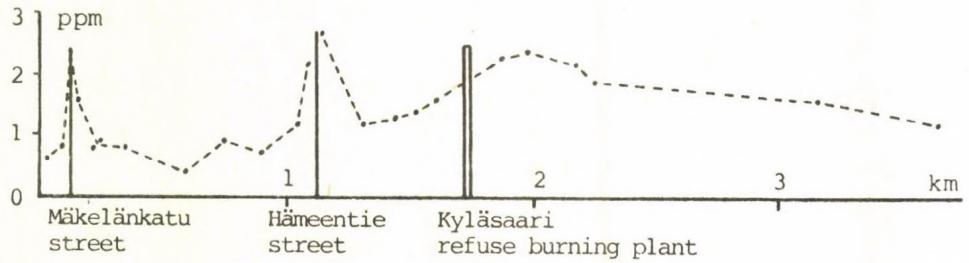

Fig. 4. Accumulation of chromium in moss-bags along a transect from west (left) to east through the study area.

5.5 Copper (Cu)

The distribution pattern of copper accumulation in moss-bags was quite similar to that of chromium, which fact may suggest a common emission source (Figs 4 & 5). The mean monthly accumulation of copper was 5.1± 2.9 ppm/dry wt (n = 164) ranging from 0.5 to 12.3 ppm.

The greatest mean values were found along main streets and near the coal-fired power plant, which may be considered as

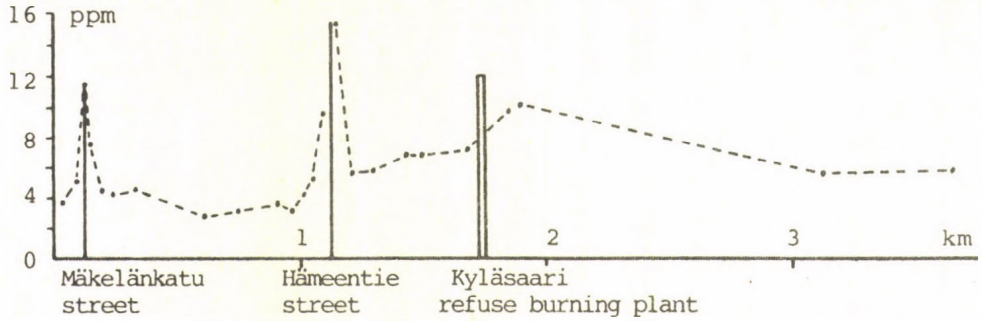

Fig. 5. Accumulation of copper in moss bags along a transect from west (left) to east through the study area.

one emission source (Fig. 5). The copper content of Polish coal used in Hanasaari is 12-15 g/ton (Lautkaski et al. 1980). In fly ash there is about 174 ppm Cu (Mäkinen 1983).

5.6 Iron (Fe)

Iron is a very common mineral in nature, both plants and soil containing plenty of this elements. From the weathering soil surface, dust is easily raised up, particularly in open places and especially in polluted areas.

Another emission source of iron is coal. The iron oxide content of Polish coal is approx. 11% and that of Russian coal about 8.3% (Keppo & Ylinen 1980, Mäkinen 1983).

In communal waste there is much iron, too. From 5,600 tons of metal waste burned in the Kyläsaari incinerator in 1981, about 95% consisted of iron.

The greatest accumulation values of iron in the study area were approximately 60-70 times higher than in the background areas (Table 2, Fig. 6). Also, inside the study area the concentrations between the subareas may vary by a factor of 20.

5.7 Lead (Pb)

The accumulation of lead in moss-bags ranges from 1.0 to 88.3 ppm dry wt/month in the whole material. The mean value ($\bar{X} \pm SD$) is 28.8 ± 17.5 ppm (n = 164).

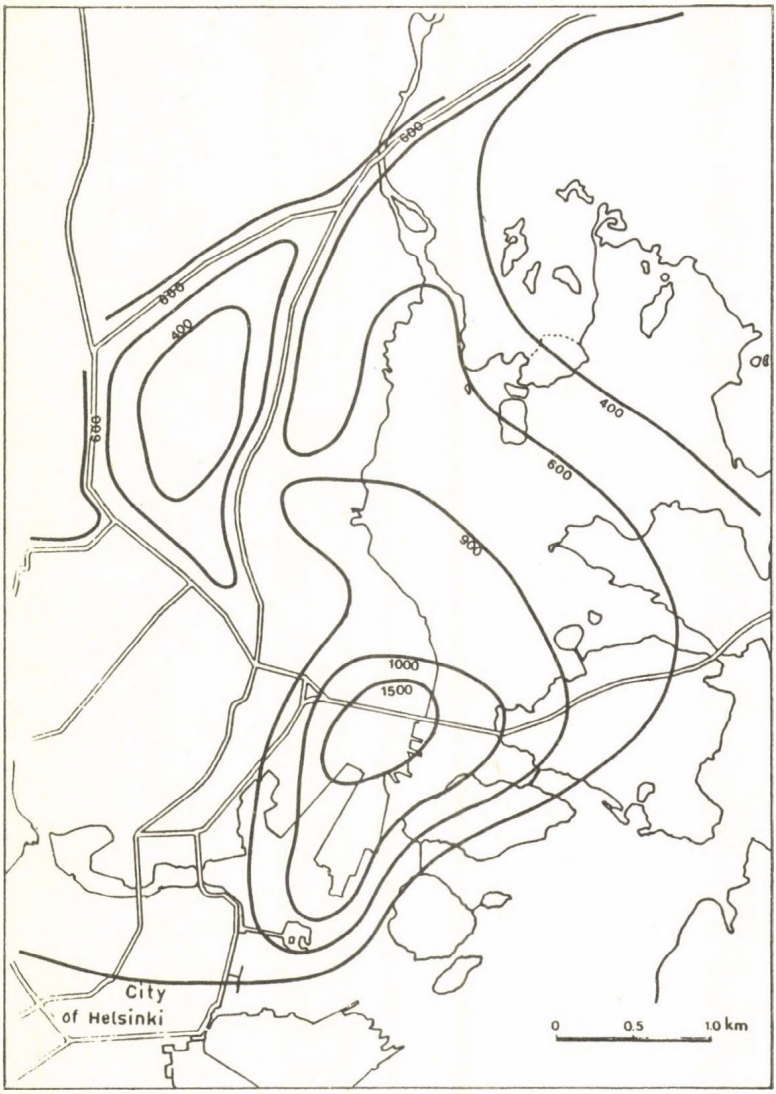

Fig.6. Mean monthly accumulation of iron (ppm dry wt) in moss-bags in Helsinki during the winter of 1982/1983. Interpolated graphs of equal value are shown.

The influence of traffic on lead accumulation is most important. That can be seen in transects shown in Fig. 7.

The influence of the main streets does not, however, extend far. At a distance of 200 m, the lead values in moss-bags

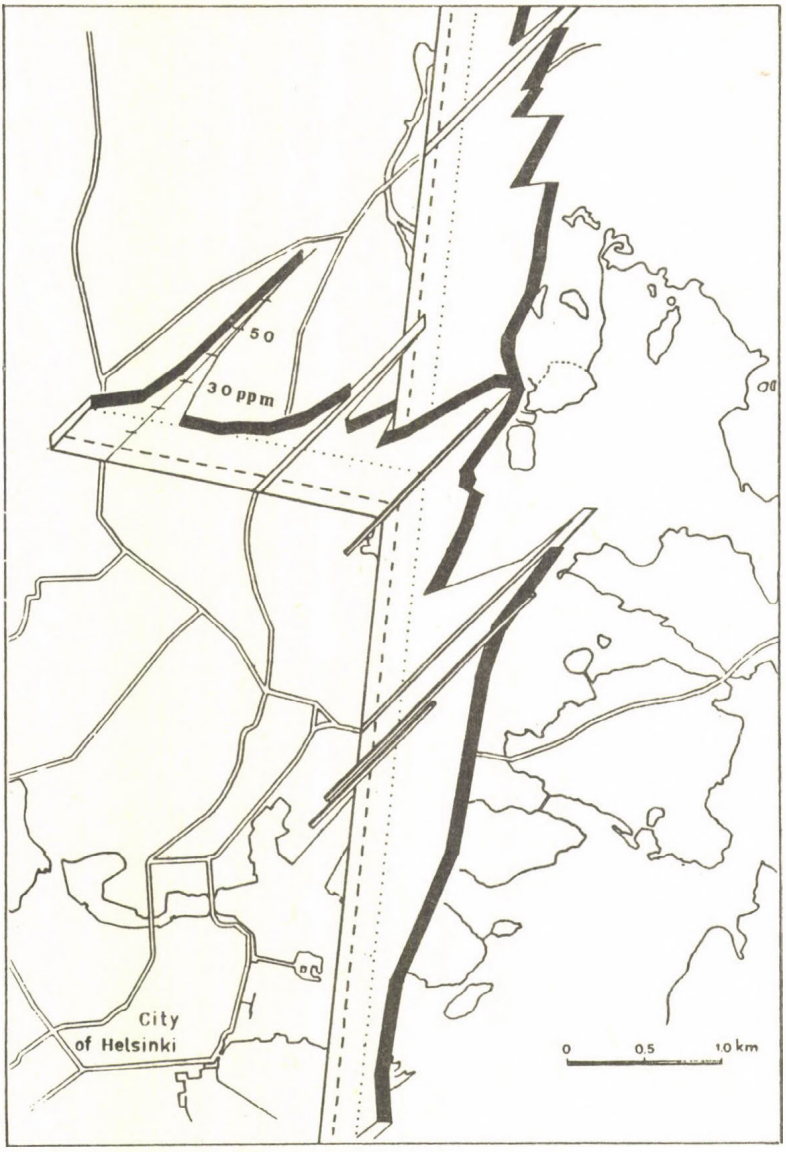

Fig. 7. Lead accumulation in moss-bags along two transects in Helsinki during the winter of 1982/1983. Further information is given in the text.

are on the average only 13% of those measured near the street (Nurmi 1981, Mäkinen & Lodenius 1982).

5.8 Nickel (Ni)

The nickel content of the Sphagnum mosses used in this study was at the beginning on average 1.6 ppm/dry wt and after about four months over 20 ppm. Converted into monthly accumu-

Fig. 8. Relative accumulation values of Ni in moss-bags, indicating the origin of emissions in four subareas. See text for further information.

lation values, that means a rate of more than 4 ppm/dry wt ranging from 0.2 ppm in remote areas to 9.3 ppm near the coal fired power plants (Fig. 8). The mean accumulation value of Ni was 2.2± 1.4 ppm. It is somewhat higher than in 1981 apparently because of the greater number of receptor points in the polluted part of the study area (cf. Mäkinen and Lodenius 1982).

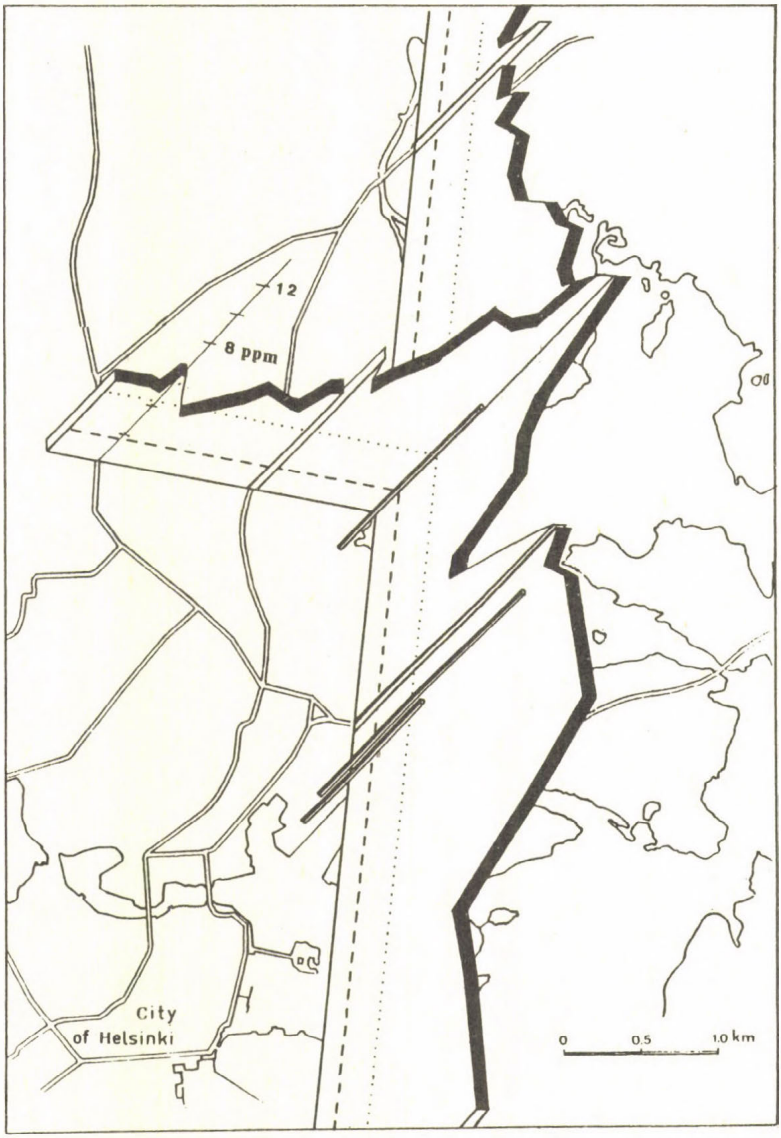

Fig. 9. Vanadium accumulation in moss-bags along two transects in Helsinki during the winter of 1982/1983. See text for further information.

5.9 Vanadium (V)

The most important vanadium source of densely populated areas is as a rule heavy fuel oil that contains approximately 150 ppm of V (Pohjola et al. 1983). When heavy oil is used as fuel of auxiliary boilers in coal-fired power plants too, elevated V concentrations are commonly found in plants around power plants using fossil fuels (Mäkinen 1982, 1983). The findings of the current study give similar results (Fig. 9). The greatest monthly accumulation values were obtained in the nearest vicinity of oil-fired power plants.

5.10 Zinc (Zn)

The mean monthly accumulation of Zn in moss-bags during the study period was 16.9 ± 11.5 ppm (n = 164), ranging between 0.9 and 66.4 ppm/dry wt. The corresponding mean value of the background stations was 5.5 ppm/dry wt (n = 23).

The two greatest emission sources in the study area are the Kyläsaari refuse-burning plant and the coal-fired power plant in Hanasaari.

A reason for great zinc values neat the incinerator seems to be the content of burned waste. It consists of about 1.2 kg zinc per ton of dry waste (Hovsenius 1977, Mroueh & Laukkarinen 1981).

The zinc content of the coal burned in Hanasaari power plant is about 50 g per ton (Pohjola et al. 1983).

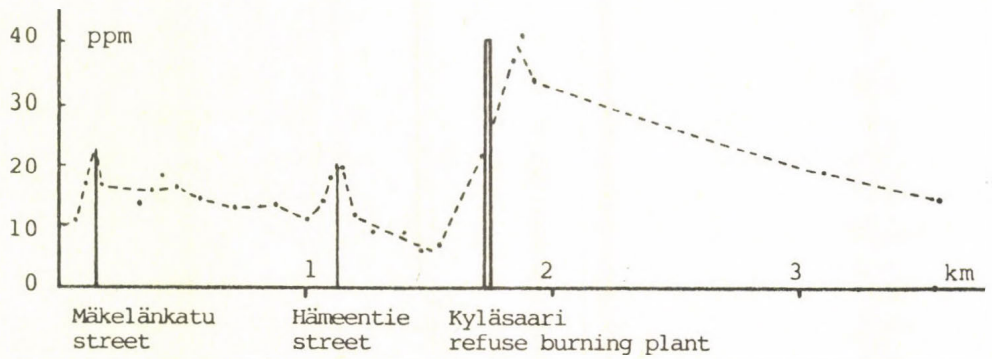

Fig. 10. Accumulation of zinc in moss-bags along a transect from west (left) to east through the study area.

6. RELATIVE SIGNIFANCE OF DIFFERENT EMISSION SOURCES FOR THE HEAVY METAL ACCUMULATION IN MOSS-BAGS IN HELSINKI

6.1 Receptor models

To determine particle sources, various receptor models have been used recently (Cooper & Watson 1980). Principal component analysis (PCA) was used in this study to categorize the chemical parameters. The primary data set consists of 164 mean monthly accumulation values of 8 heavy metals (Pb, Cd, Cr, Cu, Fe, Ni, Zn, and V) and ash in moss-bags. In computer treatment, the BMDP4M version of factor analysis converted for use on Burroughs by M. Conveney, K. Halstead and I. Liddel was used. The number of factor was limited to three.

6.2 Elemental concentrations

Between all elements a highly significant correlation ($p < .001$) was indicated. That shows that the spreading mechanism of the elements studied is quite similar. This apparently concerns the background areas, too.

The greatest correlations between element pairs indicate which components are probably spreading together or are coming from the same emission source:

Element 1	Fe	Ni	Cr	Cu	Pb	Cd
Element 2	Ash	V	Fe	Ni	Fe	Zn
Correlation	.923	.890	.852	.830	.787	.742

The highest correlation value, r = .923***, was found between iron and ash. These are including to the major components of fly ash, but also the traffic produces both elements.

6.3 Pattern recognition by PCA

The BMDP component analysis produces a rotated factor loading matrix where the variables are sorted in decreasing order according to their loadings. Thus, the elements can be grouped and the groups correlated with emissions in the study area.

The moss-bag material (n = 164) computed gives three factors when the eigenvalue is greater than 0.600. Consequently, there are three separate groups to identify. The first one named traffic factor includes iron, ash, lead and chromium. The second group named energy factor includes nickel and vanadium which occur in heavy fuel oil used in power plants. The

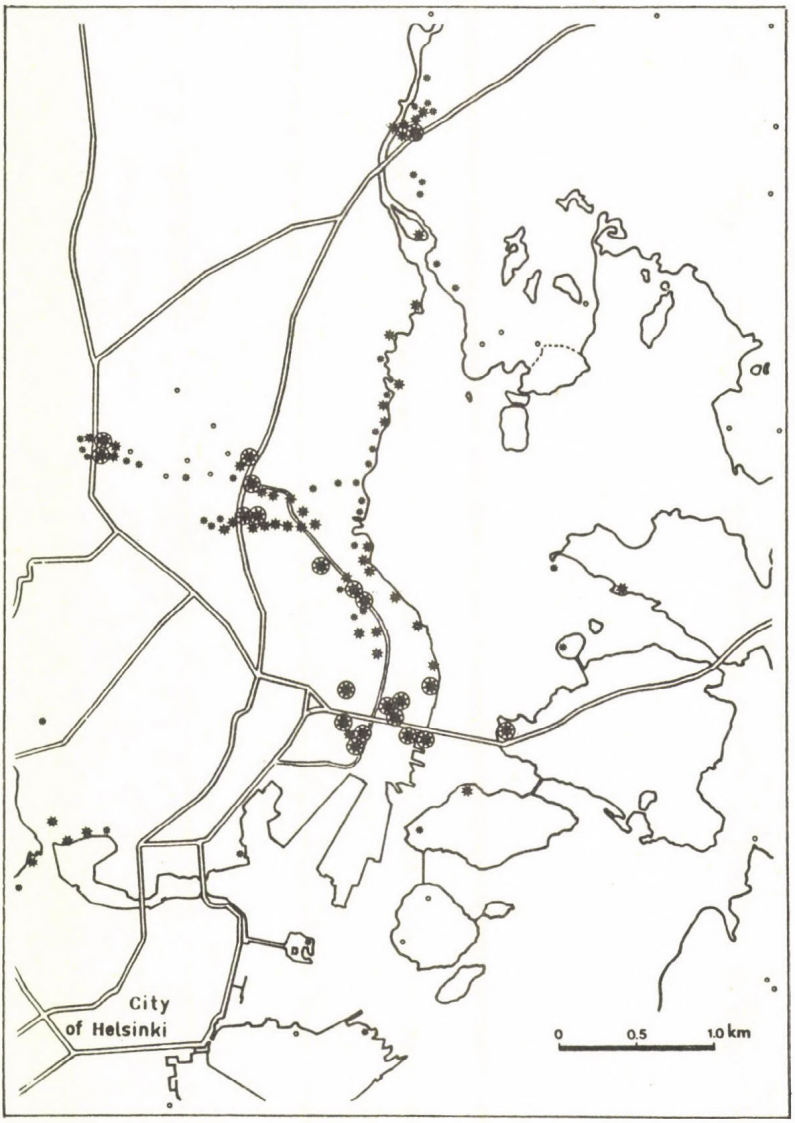

Fig. 11. The scores of factor 1 (traffic factor) indicated in four levels (limits: -0.5, 0, 1 and 4).

third group named incinerator factor includes zinc and cadmium, that very often are together in alloys. Outside the groups is copper that has a great correlation both with nickel and iron.

When the estimated factor scores of all receptor points are calculated and the scores marked on a map with symbols (limits: -o.5, O, 1 and 4), the main sources corresponding to the factors are exposed (Figs 11 and 12). The combined infor-

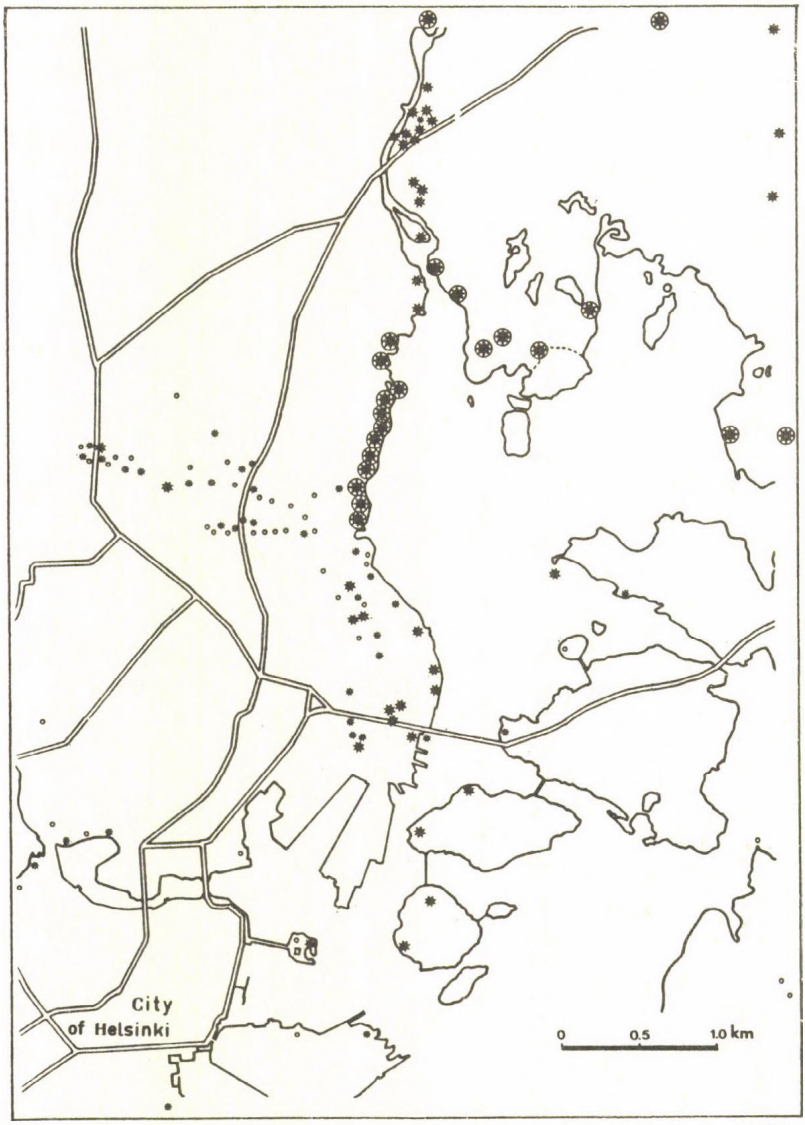

Fig. 12. The scores of factor 3 (incinerator factor) indicated in four levels. Limits as in Fig. 11.

mation of factor scores gives more condensed information on the air pollution and emission sources than concentration maps of individual elements.

Many receptor points with highest scores on factor 1 are situated on the east and north side of the main streets because the dominating wind direction is from south or southwest (Fig. 11).

The maximum values on factor 2 (the energy factor) are situated near the power plants. Equal amount of high values are to be found also in the nearest surroundings of refuse burning plant Kyläsaari.

The pattern of cadmium and zinc in factor 3 is clear. All of the greatest factor scores are situated downward northeast from the Kyläsaari incinerator where great emission values have been measured (Fig. 12). Also, the receptor points far away on higher hills get high scores. That is an evidence of longer transport of emissions.

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USE OF HYLOCOMIUM SPLENDENS FOR REGIONAL AND LOCAL HEAVY METAL MONITORING AROUND A COAL-FIRED POWER PLANT IN SOUTHERN FINLAND

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This paper reports the concentrations of eight metals (Cd, Cr, Cu, Mn, Ni, Pb, V and Zn) in a woodland moss, Hylocomium splendens (Hedw.) Br. et Sch., collected around a large coal-fired power plant in coastal southern Finland when the plant was in full function (1980) and discontinued (1982). The analyses were carried out with the atomic absorption spectroscopy (AAS flame method).

Three apical segments of the moss were used in regional metal analyses, four in local verical correlations. The leaves of H. splendens were also studied with SEM and a comparison was made with fly ash collected from electrofilters.

Elevated concentrations of Ni, Cr and V in H. splendens were found near the power plant. In vertical segments of H. splendens, the amounts of Cr, Ni and Pb increased with depth (age), whereas Cu, Mn and Zn decreased downwards in many samples.

1. INTRODUCTION

For a long time coal has been used as a fuel, but recently its influence on air pollution was studied intensively because after the oil crisis its proportion as an energy supply increased in many countries. In these air pollution studies mosses have been used successfully in monitoring, especially in Nordic countries and in Central Europe (e.g., Rühling & Tyler 1970, 1971, 1973 and 1984, Lötschert et al. 1975, Rüh-

ling & Skärby 1979, Rambaek & Steinnes 1980, Maschke 1981, Gydensen et al. 1983). The most important moss species have been Hylocomium splendens and Pleurozium schreberi. In this study, Hylocomium splendens was used.

Formerly, corresponding air pollution studies with H. splendens have been made in Finland on a small scale only (Rühling & Tyler 1973, Bramryd 1981, Rinne & Mäkinen 1985). Ombrotrophic Sphagnum mosses have been used more in air pollution monitoring (Pakarinen 1978, 1981, Pakarinen et al. 1981).

2. STUDY AREA AND ITS EMISSION SOURCES

The study area, about 2300 km^2, is located in northern shore of the Gulf of Finland about 60 km west from Helsinki on sparsely populated countryside (Fig. 1). In this area, there are a few emission sources that may cause air pollution. The greatest one is a power plant in Inkoo.

The study area slopes slightly towards the sea. The even rock cliffs in the archipelago rise less than 5 - 20 m above sea level. Most of the cliffs are covered with coniferous forest.

The inland hills are about 40 m from the sea level, and in the northern part of the study area they are about 60 m above the sea level. These hills represent the elevation range of sampling sites.

In moss collection sites on the hills, dry or moist heath forests (Vaccinium or Myrtillus types in Finnish classification of forest vegetation) (Kujala 1961) dominate. On this soil Scots pine is most common, with Vaccinium vitis-idaea, Calluna vulgaris and Pleurozium schreberi in the ground vegetation. On the hillside there is more soil and moisture. The vegetation becomes more mesic and the tree canopy is composed of Norwegian spruce and of some deciduous trees. In the undergrowth Vaccinium myrtillus and Hylocomium splendens dominate. The amount of herbs and grasses increases, but is still small. Deschampsia flexuosa is a common grass in the field layer.

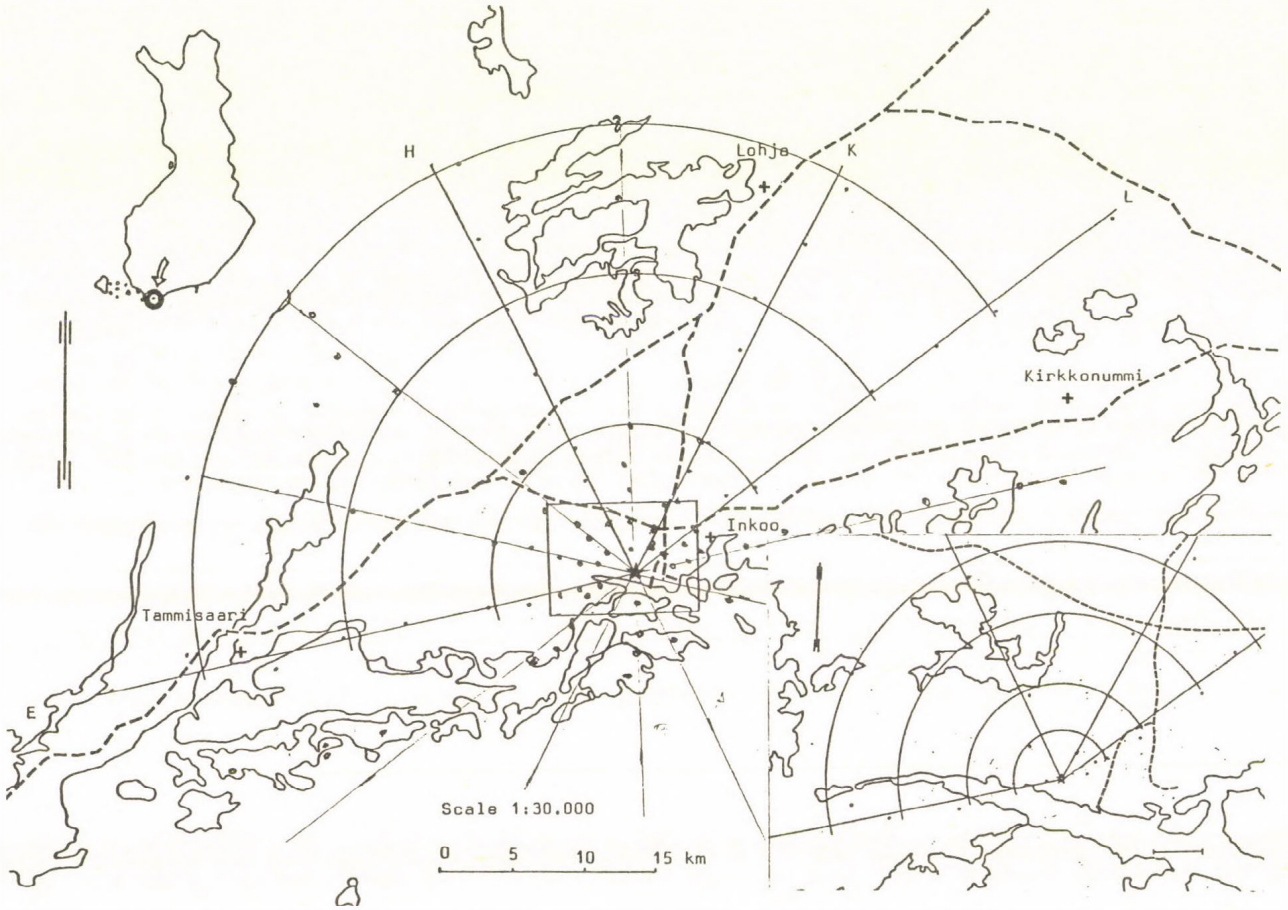


Fig. 1. Study area with moss collection sites. Power plant is marked with a star.

A great part of the study area, except the small village of Inkoo 6 km NE from the power plant, is sparsely populated, less than 20 persons/km^2. Its influence upon air pollution is slight because in the village there are fewer than 600 inhabitants and only a small textile industry.

The nearest small towns of Karjaa (about 80,000 inhabitants), Tammisaari (11,000) and Lohja (14,000) are situated in 15 km, 25 km and 27 km distance from the Inkoo power plant (Fig. 1). In these towns there are no significant heavy metal sources besides traffic, small industry and heating of settlements.

The location of the power plant is thus very favourable for air pollution studies. The deposition of the emissions can be observed under nearly virgin conditions.

The power plant, one of the greatest in Nordic countries, consists of four separate units. Each unit has a maximum net output of 250 MW. In full capacity the power plant uses 8.600 tons of coal per day. That makes 5.8 million tons during the 4.5-year study period (Fig. 2). Besides coal, the power plant uses heavy oil as a fuel in auxiliary boilers and in the starting stage corresponding to 2 - 3% of the total energy use in the plant.

The use of energy in Finland increases in wintertime for climatic reasons - the mean monthly temperature amplitude in southern Finland is more than 23 ^{o}C (from -6.5 ^{o}C in February to +16.5 ^{o}C in July, Heino 1976). This variation besides other factors is also reflected in the use of coal and emissions at Inkoo power plant (Fig. 2). Because of effective fuel gas filtration, only 0.9% of the total fly ash produced in the plant spreads into the surroundings. That means about 1 kg ash per combusted ton of coal. During the 4.5-year study period the emitted amount of ash was thus 5,400 tons.

According to the dominating wind directions during the study period, a great part of the emissions spread in the direction of NE and W.

The amount of emitted heavy metals in coal firing depends on the use of coal as well as on the chemical and physical

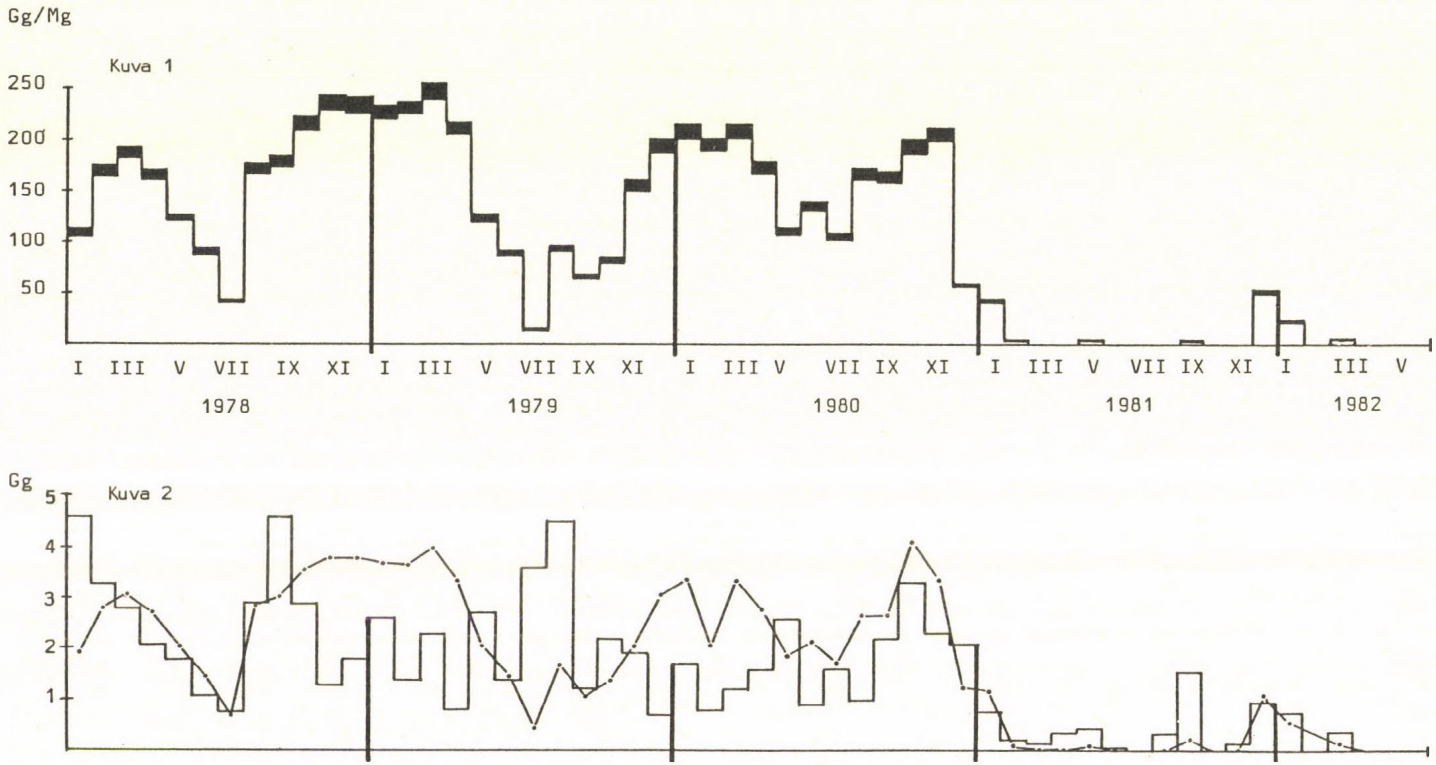


Fig. 2. The monthly use of coal (Gg = 10^3 tons) and corresponding fly ash emissions (Mg = tons) (the lower margin of the diagram) from the power plant at Inkoo. Note the decreasing use of coal after December, 1980.

Table 1. Use of fuel (coal and oil) and estimated mean ash, sulphur dioxide and heavy metal emissions from the power plant at Inkoo during the study period between 1.1.1978 - 31.5.1982. Inside brackets the metal content of the fly ash.

Coal	Year 1978	1979	1980	1981	1982	Total
Use (Gg)	1987	1781	1976	111	30	5885
Ash emission (Mg)	1860	1667	1850	104	28	5508
Heavy metal emissions (kg)						
Cd (2.0 ppm)	3.7	3.3	3.7	0.2	0.1	11.0
Cr (110.4 ppm)	205	184	204	11	3.1	608
Cu (174.2 ")	324	290	322	18	4.8	959
Mn (1270 ")	2362	2117	2349	131	35.3	6995
Ni (173.3 ")	322	289	321	18	4.8	955
Pb (162.5 ")	302	271	301	17	4.5	895
V (214.2 ")	398	357	396	22	6.0	1180
Zn (396 ")	736	660	733	41	11.0	2181
Oil						
Use (Gg)	30.0	25.3	21.3	4.9	1.1	82.6
SO_2 [x)] (Gg)	31.7	28.3	32.2	2.7	0.7	95.6
Ni (30 ppm)	900 kg	759	639	147	33	2478
V (150 ")	4500 "	3795	3195	735	165	12390

x) Including the SO_2-content of coal.

content of the ash and varies always according to the quality (origin) of the coal (cf. Pilegaard 1976, Lämpövoimalatosten ilmansuojeluselvitys 1980 and Pohjola 1981). The coal used in Inkoo power plant originates mainly (about 90%) from Poland and the rest (10%) from the Soviet Union. The amounts of emitted trace elements (mean of 12 samples) from Inkoo power plant are presented in Table 1 according to the preliminary results of Imatran Voima and project KHM. The periodical variation of fly ash emissions is presented in Fig. 2.

3. MATERIAL AND METHODS

A woodland moss Hylocomium splendens was used as a bioindicator in this study. It is quite common in moist spruce and pine forests all over the study area. H. splendens has been formerly used in large air pollution studies especially in Nordic countries (Rühling & Tyler 1970, 1984, Rambaek & Steinnes 1980, Gydensen et al. 1983) because of its commonness, growing rhythm (Lackner 1932, Tamm 1953, Busby et al. 1978) and high cation exchange capacity (Tamm 1953).

In collection 6 to 10 subsamples within an area of 0.5 ha were attached in larger samples. Because of contamination risk the hands were covered by new platic bags during collection. The vicinity of roads and other local emission sources was consciously avoided as well as the dripping water from trees. The minimum distance from the collection sites to any road or highway was 300 m.

In the laboratory, the H. splendens samples were cleaned from litter with clean hands and dried at 30 °C. Only three apical fully developed segments were used for analysis. Some analyses (e.g., Mn) were also made from the rest of the material of 1980 with dry-ashing and AAS-flame method. In 1980, wet-ashing was used with nitric and perchloric acids (proportion 4:1) for about 3 days until all the organic material was fully oxidized (Rühling & Tyler 1970, Rühling & Skärby 1979). Excess acid was evaporated to about 2 ml, distilled water was added to 50 ml and 7 elements (Cd, Cr, Cu, Ni, Pb, V, and Zn) were determined with standard AAS-flame method. The results are given in ppm/air dry (+30 °C) weight.

4. HEAVY METAL CONCENTRATIONS OF HYLOCOMIUM SPLENDENS IN THE STUDY AREA

a. Regional variation of heavy metal content in moss samples

Heavy metal concentrations of H. splendens range both regionally and in an altitudinal direction (Table 2). Most values are based on the first material collected in 1980,

Table 2. Heavy metal concentrations (ppm/dry weight) of Hylocomium splendens in the study area, regional-altitudinal variation. All values are based on analyses made from 1980 moss collections except Mn concentrations and the analysis of vertical moss segments where younger (1982) material was used.

	Cd	Cr	Cu	Mn	Ni	Pb	V	Zn
Background value Q_1	0.17	1.5	5.9	155	2.4	23.0	7.3	34.9
Mean value	0.24	2.1	7.3	244	3.8	30.3	16.1	44.9
Range	0.12-0.45	1.0-4.2	4.0-10.8	51-474	1.9-10.4	18.0-73.0	3.5-57	28.0-77.0
Last year segment 1982	0.38	1.1	6.8	212	3.7	22.1	13.5	40.8
older segments (2-4 years) 1982	0.38	1.8	6.1	275	4.8	31.4	17.4	41.0
Regional mean concentrations								
Archipelago	0.25	2.0	6.7	304	2.9	28.5	10.2	42.6
Coastal zone	0.23	1.8	6.9	252	2.7	29.3	10.0	45.4
Inland	0.26	2.0	7.1	290	2.9	28.3	9.6	42.1
1 km from the power plant	0.20	2.8	7.7	217	8.2	28.1	39.0	40.5
The nearest vicinity of Lohja	0.26	2.7	8.8	157	6.0	36.3	20.0	60.8
The region of Kirkkonummi	0.27	2.7	8.8	218	4.0	42.3	14.1	55.6

when the power plant still was in full function (Mäkinen 1983). Comparison between later (1982) collections was also made together with analyses of younger and older segments (Mäkinen 1982).

To find some areal differences in this material, all analysis values were put on separate maps and the isoritms were compared with dominating wind directions. Remote archipelago, coastal zone and inland mean values were calculated to find some seashore - inland or south - north gradient (Table 2). Corresponding values of industrial and settled areas were compared together. The mean values around Inkoo power plant were compared with the mean values of industrial and densely populated areas of Lohja and Kirkkonummi.

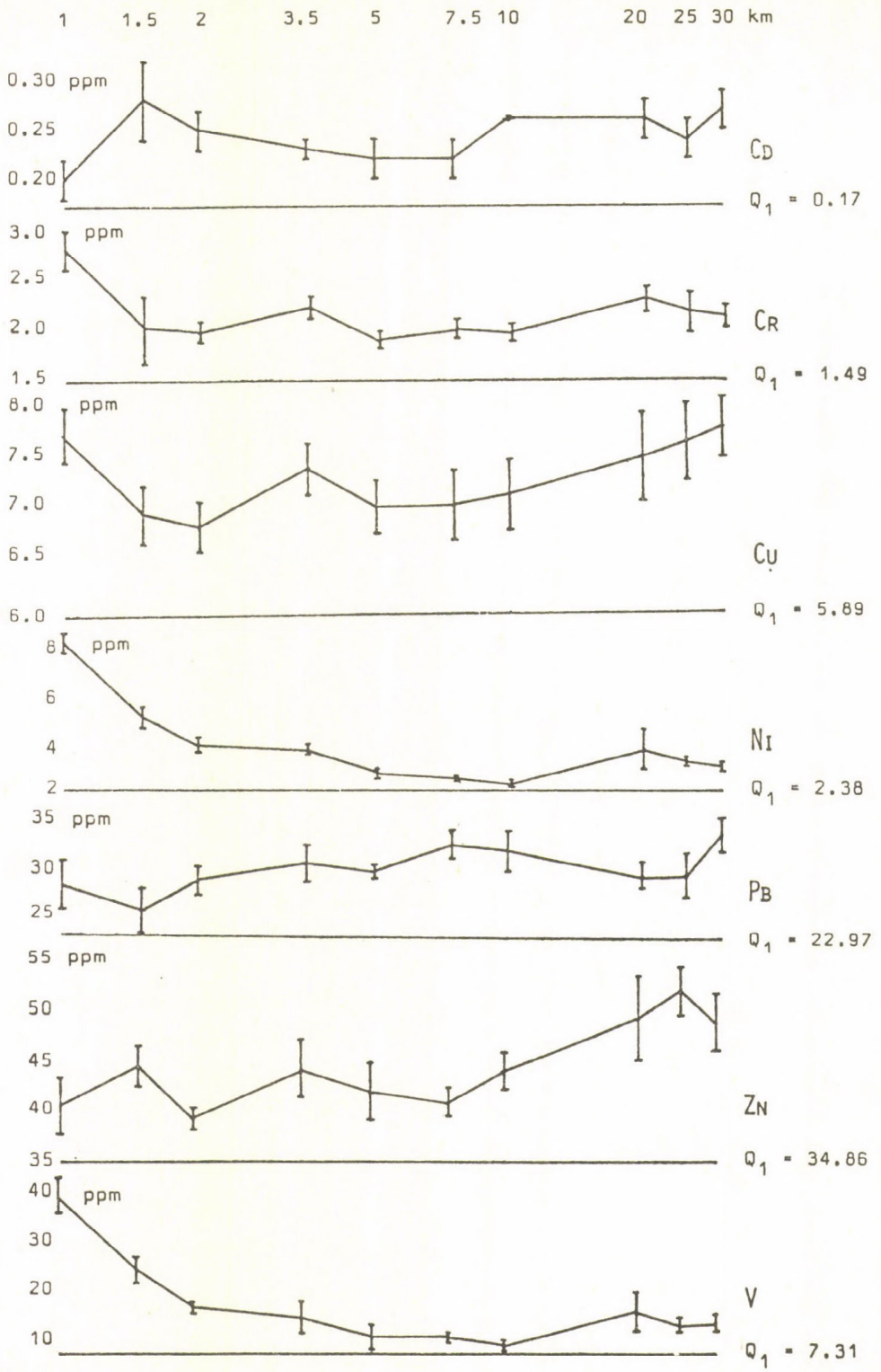
The regional variation of different elements is as follows:

Cd The variation of the cadmium content of Hylocomium in the study area is very small and different from many other metals. No local emission sources can be detected. Nor do the Cd values of Hylocomium show any clear relationship to the distance from the power plant (Fig. 3) or between the dominating wind direction, traffic and population density.

Cr The chromium content of 3-year old Hylocomium mosses ranges from 1.0 to 4.2 ppm. Both mean (2.1 ppm) and the background value , Q (=lowest quartile of all Cr values), are on the same level as the Cr concentrations in remote areas of central and northern Norway (Rambaek & Steinnes 1980). The highest mean concentration (2.8 ppm) is found in the nearest vicinity of the power plant (on the lower side of the prevailing wind) and indicates small air pollution, but a steep decrease is found to 2 km distance (Fig. 3). In later studies a decreasing gradient ranged from the power plant up to 15 km in 2-4 year-old segments of Hylocomium (Mäkinen 1982).

Cu The copper content of Hylocomium is somewhat elevated in populated and industrialized areas. The greatest values (Mean 8.8 ppm) are found around Lohja and Kirkkonummi. Also in the vicinity of the Inkoo power plant (1-2 km distance) the copper content of Hylocomium is somewhat elevated (Table 2 and Fig. 3). Because there are no other emission sources near the plant and because the values are higher, especially on the lower side of the prevailing wind, it is probable that one part of the Cu pollution may originate from the power plant. In later studies in 1982, however, such trend was not found.

The mean value of copper, 7.3 ppm, corresponds to that of background areas in northern Sweden and Norway (Rühling & Skärby 1979, Rambaek & Steinnes 1980). The highest concentrations (10.8 ppm) are similar to the mean values of southern Sweden, but much lower than near copper processing plants (Tyler 1972).


1 1.5 2 3.5 5 7.5 10 20 25 30 km
0.30 ppm
0.25
0.20
CD
Q1 = 0.17
3.0 ppm
2.5
2.0
1.5
CR
Q1 = 1.49
8.0 ppm
7.5
7.0
6.5
6.0
CU
Q1 = 5.89
8 ppm
6
4
2
NI
Q1 = 2.38
35 ppm
30
25
PB
Q1 = 22.97
55 ppm
50
45
40
35
ZN
Q1 = 34.86
40 ppm
30
20
10
V
Q1 = 7.31

Mn Manganese was not determined from older collections, but only in 1982. In concentration values there are great variations. The differences between remote and industrial or settled areas are, however, small. In the archipelago, the mean value is a little higher than in the inland (Table 2).

The lowest manganese concentration of Hylocomium occurs nearest the vicinity of Lohja and the power plant, but is not significant statistically. These values were probably higher during the full function of the power plant.

Ni The concentrations of nickel in Hylocomium samples range from 1.9 to 10.4 ppm/dry wt. The highest single values are found nearest the vicinity of the Inkoo power plant on the lower side of the prevailing wind (northeast from the power plant). They belong to the same magnitude as the Ni concentrations mentioned from the polluted industrial areas in central Sweden (Rühling & Skärby 1979), but are lower than great local industrial sources nearby (Tyler 1972). Also, the highest mean values at Inkoo are close to the Ni levels of central Sweden. The lowest single Ni contents are similar to those of northern Sweden.

In areal examination, there are distinct differences between rural and industrial or settled areas, where heavy oil is used as a fuel (Table 2).

Pb The lead concentrations of Hylocomium splendens are elevated in all populated areas. That is apparently due to their greater traffic density. Because high-octane petrol (with 0.45 g lead in one liter) is used in the majority of the cars, the deposition values are positively related to the traffic (and population) density. In this case, the distance from the nearest highways has no effect on

←

Fig. 3. Mean heavy metal concentrations (ppm) of Hylocomium splendens in relation to the distance from the Inkoo power plant. Standard errors and the background level are also indicated.

the Pb values - the samples were collected from more than 300 m away from the roads - but the regional variation is more distinct. In samples collected near the Helsinki region with the highest traffic densities, the lead concentrations are also the highest (40 to 73 ppm).

The mean lead value of Hylocomium in the study area is 30.3 ppm. That is in the same level as in the former studies made in southern Finland (Rühling & Tyler 1972, Mäkinen & Pakarinen 1977).

V After the elevated nickel concentrations were found in mosses collected near the Inkoo plant, the vanadium content of 84 Hylocomium samples was also determined. The highest values (57 ppm) were found, as assumed, in moss samples collected near the power plant (Fig. 3), and a significant correlation between Ni and V was established (Fig. 4). In remote subareas, the mean concentrations stay below 10 ppm.

From the elevated V concentrations just nearby the power plant, conclusions may be drawn that the emission would originate from the auxiliary boilers, where heavy oil is used as a fuel. The oil contains namely about 150 ppm V and 30 ppm Ni. Because the smokestacks of auxiliary boilers are much shorter (70 m high) than the main stacks (150 m), most of the fly ash particles spread into the nearest vicinity of the power plant.

Zn Regional variation in zinc concentrations of Hylocomium is not great. Near the urban areas, however, the values are somewhat elevated (Table 2). Besides industry, also traffic may increase Zn contents of the air. The Inkoo power plant has no visible influence on the Zn concentrations of Hylocomium (Fig. 3), although in fly ash there is nearly 400 ppm Zn (Table 1).

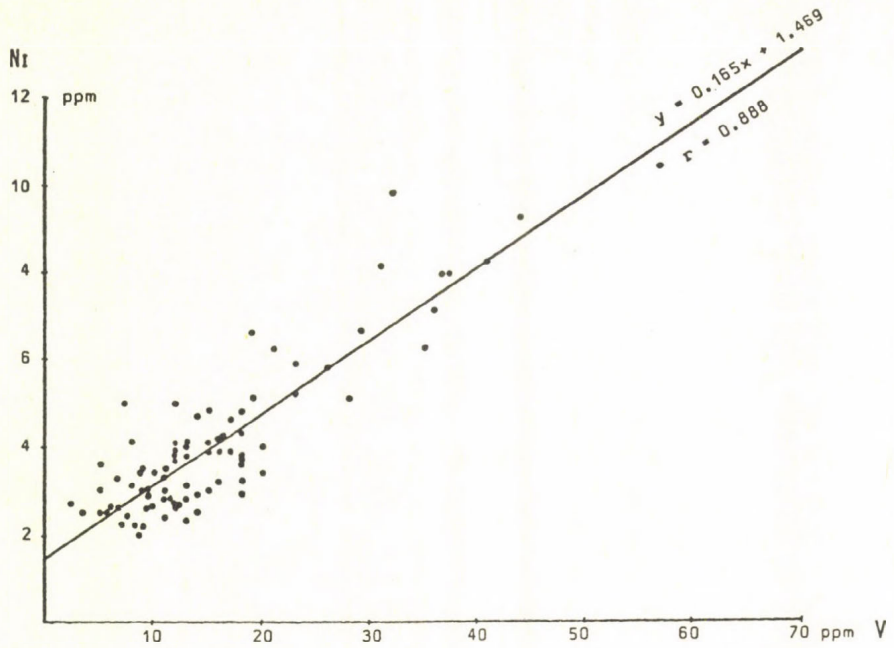


Fig. 4. Correlation between nickel and vanadium concentrations of Hylocomium splendens. The material was collected from the surroundings of the Inkoo power plant in autumn, 1980.

Table 3. Vertical variation of metal in segments of Hylocomium with different age. Mosses were collected at 0.5 to 30 km distance from the Inkoo power plant in spring, 1982.

Segment	Born	Heavy metal content (ppm dry wt)							
		Cd	Cr	Cu	Mn	Ni	Pb	V	Zn
I	1981	0.36	0.87	6.8	225	3.57	22.4	10.9	39.6
II	1980	0.37	1.37	5.1	211	3.88	27.6	12.7	32.1
III	1979	0.39	1.75	5.3	292	4.33	29.3	14.9	36.8
IV	1978	0.45	2.03	6.1	444	5.05	34.1	14.6	50.5

b. Vertical differences of heavy metal content in four apical segments of Hylocomium splendens

In order to determine yearly deposition of heavy metals from mosses, 10 large Hylocomium samples, collected in 1982 NW from the Inkoo power plant (Fig. 1, line H) were cut up to four segments. Each of them corresponded to one year's growth of Hylocomium. The youngest was born in late summer (cf. Mäkinen 1982, 1983). From each segment, the heavy metal content was analysed separately. Mean values of these concentrations are presented in Table 3.

All elements studied can be divided into two different groups in relation to their vertical distribution in moss segments. In the first group, the heavy metal content decreases downwards in all segments. To this group belong Cd, Cr, Ni, Pb, and V. In the second group, which includes Cu, Zn and Mn, the concentrations of youngest green segments are a little higher than in two-year-old segments. That may be caused by moving of these trace elements, because the same trend was also found in Sphagnum mosses (Pakarinen & Tolonen 1978).

5. IDENTIFICATION OF FLY ASH PARTICLES IN MOSS SAMPLES WITH SEM

After chemical analyses, the rest of Hylocomium samples was used for examination of fly ash particles with scanning electron microscopgy (SEM) (cf. McCrone & Delly 1973, Natusch 1976, Gibbon 1979). Air dried mosses were chafed on dense screen. Particles that fell through and moss leaves were collected and separated. The identification of particles was made by comparing them with fly ash from the Inkoo power plant, first with a stereo microscope and in colour slides. After making scanning preparations, the identification of most particles was possible. Also, X-ray microanalytical examination helped in the identification of particles (Fig. 5) (Hayes et al. 1978, Gullvåg et al. 1980). These analytical results could be correlated with the chemical analyses of the material made formerly.

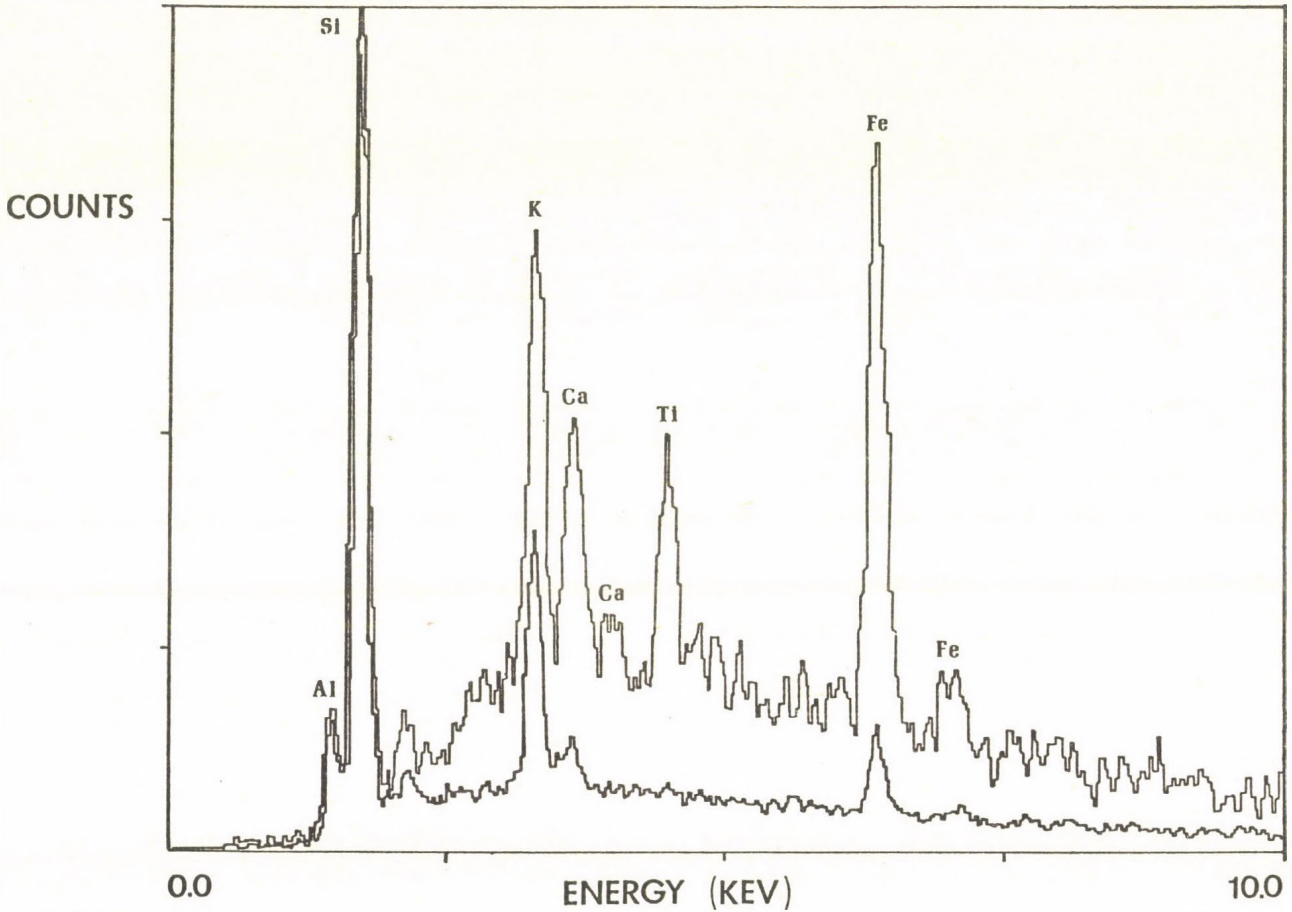


Fig. 5. X-ray spectrum from one small fly ash particle on the leaf surface of Hylocomium splendens. This sample was collected from 1 km distance of the Inkoo power plant.

Some particles originating from fly ash were found in all the samples up to 30 km distance from the Inkoo power plant. Their amount and size increased in most samples towards the plant, but their real origin or amount in the moss carpet could not be exactly determined in these preliminary studies. Also, their weathering process needs more investigations.

ACKNOWLEDGEMENTS

This study was made with the financial support of the Swedish State Power Board and the Finnish Power Company Imatran Voima. I wish to express my gratitude also to my assistants in the field and laboratory: Veikko Hynninen, Mikael Pihlström, Simo Lehtinen, Anne Nurmi, Pertti Heikkinen, Anne Sairanen and Sirpa Peltonen. Further, I am very grateful to Germund Tyler, Pekka Pakarinen and Rainer Penttila for valuable comments on the original manuscript. I am also indebted to Tarja Mäkinen for correcting the translation and to Pirkko Dookie for typing the text.

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EPIPHYTIC BRYOPHYTES AND AIR QUALITY IN THE TEJO ESTUARY*

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The epiphytic bryophyte flora of 200 sites in the Tejo estuary and the urban Lisbon areas was investigated mostly on Olea europea phorophytes. A list of 32 taxa with their percentage of presence and fertility in 6 IAP classes is given and related to the SO_2 values evaluated from a toxitolerance scale. A marked depauperisation of bryophyte species is demonstrated with transplants of Tortula laevipila. Maps of some species are presented based on presence, fertility and vitality. The decrease and extinction of some species are discussed.

INTRODUCTION

Epiphytic communities as monitors of air pollution have long been of interest to ecologists in several countries and many investigations have shown that sulphur dioxide and other pollutants are responsible for the disappearance and changes in this flora around urban and industrial complexes.

However, few studies have used bryophytes in this topic, compared to the great amount of lichenological research, which has been carried out mainly by American and North European authors.

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A survey of the epiphytic flora in the Lisbon area and all the upper parts of the Tejo estuary has been carried out as a part of a programme designed to monitor the levels of pollution in the large urban and industrial complex in Portugal (Sérgio & Bento-Pereira 1981, Bento-Pereira & Sérgio 1983, Jones et al. 1981, Sérgio 1985).

This study was conducted in the Lisbon region, in a large urbanized area around the city where some important industrial complexes are also located (Fig. 1).

The area under consideration is cca 1000 km^2, the topography is complex, in the north-western part and in the Lisbon area. Elevation ranges from about 100 m to 300 m (the 'colinas' = hills). In the south and southeast (the left side) the lowlands are situated with a more uniform altitude with no more than 50 m.

The complex relief of the region is formed by compact limestones mainly of the Cenozoic Epoch, much affected by local tectonic movements of the Sierra de Sintra. All the lowlands have a recent origin, mostly of the Pliocene, Pleistocene and Holocene, with an important humid alluvial border from the Quaternary, the 'mouchões' (areas of land with salt marsh).

The climate shows an annual rainfall of 600 to 800 mm with an average annual temperature of 15.3 ^{o}C to 16.8 ^{o}C (in January 10.5 to 11.2 ^{o}C, in July 21.4 to 22.8 ^{o}C). There is a recorded average of 12 days of fog per year. The climatic scheme for the Lisbon region (Fig. 1) and the Emberger index correspond to a typical subhumid Mediterranean climate. The annual wind conditions show a dominance from the north and the northwest, with 0.1 calm days/year (Fig. 1).

Diverse anthropogenic factors generate conditions for poor development of the potential forest vegetation. However, in protected sites in the Lisbon area and in a southern reserve (Arrábida), there are interesting examples of a sclerophyll Mediterranean forest, the Oleo-Ceratonion and Quercus faginea-suberis.

In general, the land is poorly forested. However, many mosaics of Olea europea exist in cultivated areas in the vicinity

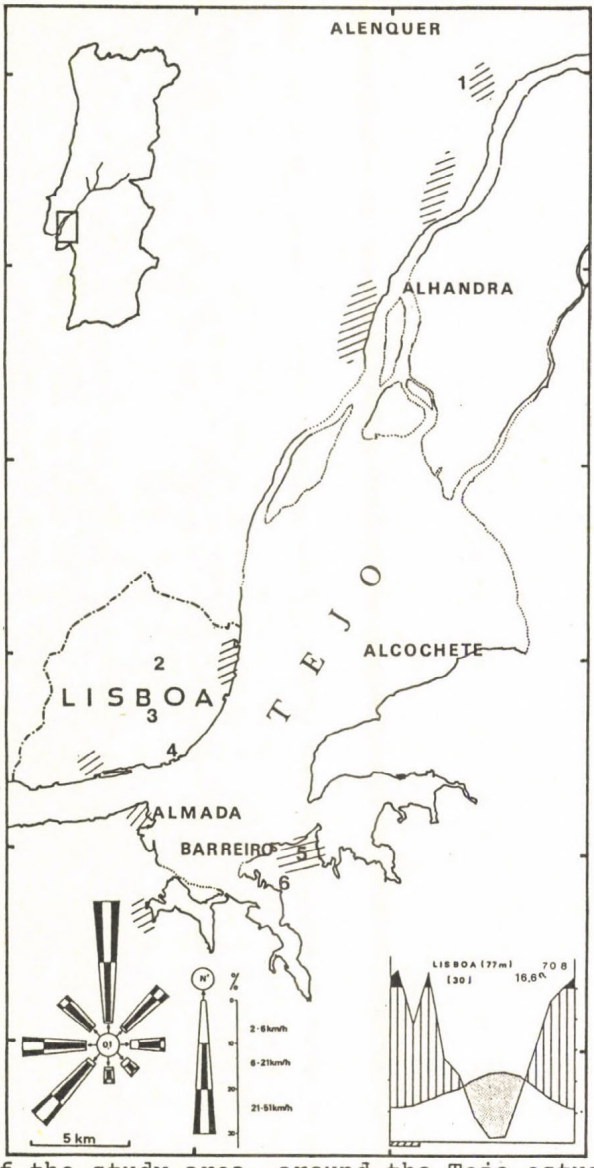

Fig. 1. Map of the study area, around the Tejo estuary, showing the annual wind conditions in Lisbon (average for 1951-1960) and climatic diagram. //// : industrial complexes. Numbers indicate air pollution monitoring stations. 1: Thermal power station (130 $\mu g/m^3$, 1979-1981, average of 3 stations); 2: urban area (38 $\mu g/m^3$, 1976-1978, 3 stations); 3, 4: Urban area with intense traffic (85 $\mu g/m^3$, 1976-1978, 5 stations); 5: Chemical industry complex (227 $\mu g/m^3$, 1977-1979, 2 stations); 6: Urban area (91 $\mu g/m^3$, 1977-1979, 2 stations). The SO_2 values are in $\mu g/m^3$, winter average.

of Lisbon and also in urban and adjacent industrial areas. In the coastal region, there are considerable areas of commercially exploited Pinus pinaster and Eucalyptus sp.

Physico-chemical measurements of SO_2 emissions only cover the past few years (1976-1982) in restricted sites (Fig. 1). The levels have decreased during the last years in some industrial areas. However, as far as the study area is concerned, it seems that in these areas there are changes of air quality due mainly to the increase of traffic.

METHODS

The study area was divided into three sub-areas (North Lisbon and South), and field work was carried out from 1979 to 1984. From about 200 selected sites, nearly 2000 trees were inspected for quantitative and qualitative investigation of lichens and bryophytes. Only bryophytes belonging to the Olea europea (90%) and, occasionally, to Ulmus spp. (10%) were selected for standardizing the method. In each case, the trunks had a diameter of 30 to 100 cm and trees situated in protected sites or sites suspected of suffering from human action and agricultural sprays were generally omitted.

With the correlation between epiphytic species distribution and the absolute degree of SO_2 pollution, and keeping in mind that all the area has quite uniform climatic conditions, it was possible to prepare a qualitative scale of toxitolerance for epiphytes in the Lisbon area (Sérgio et al. 1981). Field observations during this study were also compared with the Hawskworth and Rose (1970) scale and adapted to include bryophytes.

Clean air zones with climax vegetation in adjacent sites are studied to evaluate the more sensitive species.

For quantiative methods, we use the mathematical index of IAP (Index of Air Purity) of Leblanc & De Sloover (1970), with an introduction of a new factor, the 'vitality' of these species, in each selected site (Hoffmann 1974).

With Tortula laevipila (Brid.) Schwaegr., a supplementary study with transplants was performed. During the autumn of 1983 and winter of 1984 (6 months), tree bark patches of Ulmus spp. with Tortula tufts with 10 cm diameter were transplanted from a less polluted area to 9 different sites in the study area, with different levels of SO_2. Similar orientation and microhabitat conditions were always maintained.

RESULTS AND THEIR DISCUSSION

Optimal epiphytic vegetation and epiphytic deserts

The epiphytic vegetation is characteristic of neutrophyllous substrates and shows higher structural complexity. Different associations primarily reflect various degrees of dynamic, eutrophication exposure but also levels for pollution emissions.

Several sites in the region, just outside the geographical limits of this work, show rich communities which have more than 45 epiphytic species, with a rich cover (more than 80%), composed mainly of large foliose lichens, and present different associations in the Lobarion pulmonariae alliance Oschn. 1928, mixed with mosaics of rich bryophytic communities of Leucodontetalia (v. Hübschmann 1952) amend. Lecointe 1975.

Intermediate sites have several elements of Parmelion perlatae P. James et al. 1977 and with eutrophication species of Tortulenion laevipilae (Oschn.) Barkman 1958. Some pre-Lobarion species such as Nephroma laevigatum Ach., Homalothecium sericeum (Hedw.) B., S. G., Frullania tamarisci (L.) Dum. and Normandina pulchella (Borrer) Nyl. are present.

In more exposed sites, different associations in the Xanthorion parietinae Oschn. 1928 occur, mixed with elements of Frullanion dilatatae Lecointe 1975 and in more humid sites with Radulo-Cryphaeetum arboreae Lecointe 1975, particularly luxuriant on horizontal branches.

Depauperate vegetation, with lower diversity, was noted around the industrial areas and areas with more traffic, and contains crustose species or nitrophilous elements such as Bryum argenteum Hedw., Lecanora chlarotera Nyl., L. conizea s.

lat. etc., and frequently with minute mosaics of sterile Tortula laevipila and a filamentous alga (Chlorohormidium sp.)

Some epiphytic deserts were present in the study area; these correspond to the most heavily polluted sites (Fig. 2).

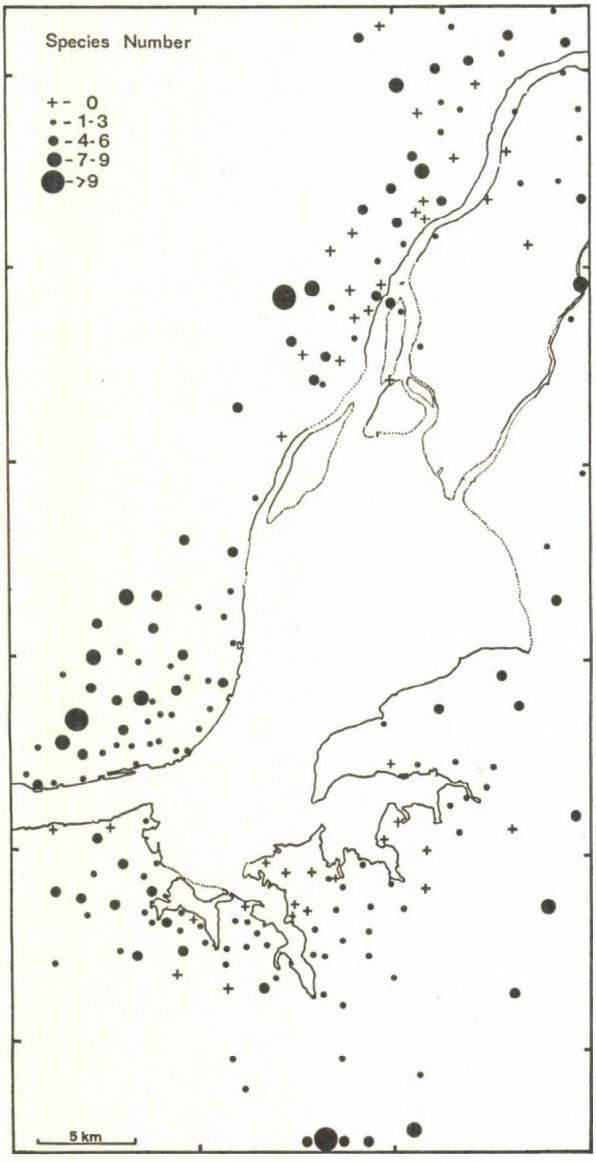

Fig. 2. Highest number of bryophyte species in the sample sites.

A high number of epiphytic species is regarded, in general, as an expression of optimal environmental conditions (De Sloover 1969). This was confirmed for the Tejo estuary (Sérgio 1982, see also Fig. 2).

Bryophytes recorded and notes on selected species

A total of 32 bryophyte species is recorded among 140 taxa of lichens in the study area from the analysis of the epiphytic flora (Table 1).

A high correlation (91%) is present between the IAP index and the air pollution ratio, directly through the observation of epiphytic vegetation using the qualitative scale for Lisbon (Sérgio et al. 1981, Sérgio 1985). On the other hand, the percentage of relative frequency of each IAP zone and the fertility of some mosses are important (Table 1). and using mapping studies it can be confirmed that resistant and sensitive species exist in the Tejo estuary.

More pollution-tolerant species were recorded in bryophyte communities, such as Bryum argenteum (Fig. 3), a nitrophilous moss with a ubiquitous distribution. This species is also common in urban areas. Chlorohormidium sp. has a similar distribution type.

Resistant species are present and have a special life strategy with asexual reproduction. They can exist close to the industrial areas. These are, for example, Tortula laevipila s. lat. (Fig. 4), Frullania dilatata (L.) Dum. (Fig. 5), and Zygodon baumgartneri Malta.

More sensitive species show no tendency to develop asexual types of propagation, and present frequently sexual reproduction: Leptodon smithii (Hedw.) Web. & Mohr, Pterogonium gracile (Hedw.) Sm., Homalothecium sericeum (Hedw.) B.S.G. (Fig. 6), Leucodon sciuroides (Hedw.) Schwaegr. and Lejeunea cavifolia (Ehrh.) Lindb. Nevertheless, others normally with gemmae seem to be very sensitive to air pollution due perhaps to their protonema stages, which have a low buffer capacity (Orthotrichum lyelli Hook. & Tayl., Radula lindenbergiana Gott. and Dicranoweisia cirrata (Hedw.) Lindb. ex Mild.)

Table 1. Relative frequency of epiphytic bryophyte species in different IAP classes in the Tejo estuary. Presence and fertility.

SPECIES	IAP classes		VI	V	IV	III	II	I
	IAP values		30	20-30	10-20	5-10	1-5	0-1
	Mean of species number incl. linchens		35	25-34	15-24	10-14	5-9	0-4
	SO2 zones in ug/m^3 (Winter average)		40	40-50	50-60	60-70	70-125	125
	Number of studied sites		18	37	54	48	38	10
Bryum argenteum HEDW.	Presence	(%)	0	8	7	4	8	0
	Fertility	(%)	0	0	0	0	0	0
Tortula laevipila (BRID.) SCHAEGR.	Presence	(%)	94	92	81	65	58	20
	Fertility	(%)	83	62	20	2	0	0
Orthotrichum diaphanum BRID.	Presence	(%)	56	68	43	38	8	0
	Fertility	(%)	56	59	33	8	0	0
Zygodon baumgartneri MALTA	Presence	(%)	61	32	24	6	3	0
	Fertility	(%)	17	3	4	0	0	0
Frullanis dilatata (L.) DUM	Presence	(%)	89	70	39	17	5	0
	Fertility	(%)	83	59	7	0	0	0
Bryum capillare HEDW.	Presence	(%)	39	27	6	10	11	0
	Fertility	(%)	6	3	0	0	0	0
Dialytrichis mucronata (BRID.) BROTH.	Presence	(%)	11	14	4	2	5	0
	Fertility	(%)	0	0	0	0	0	0
Homalothecium sericeum (HEDW.) B.,S. and G.	Presence	(%)	72	56	31	6	3	0
	Fertility	(%)	22	3	4	0	0	0
Cryphasa heteromalla (HEDW.) MOHR	Presence	(%)	11	5	2	2	0	0
	Fertility	(%)	11	5	0	0	0	0
Scorpiurium circinatum (BRID.) FLEISCH and LOEBKE	Presence	(%)	11	11	6	2	0	0
	Fertility	(%)	0	0	0	0	0	0

Eurhynchium meridionale (B.,S. and G.) DE NOT	Presence (%)	11	3	0	0	0	0
	Fertility (%)	0	0	0	0	0	0
Leucodon sciuroides (HEDW.) SCHWAEGR.	Presence (%)	39	5	6	0	3	0
	Fertility (%)	6	0	0	0	0	0
Leptodon smithii (HEDW.) WEB. and MOHR	Presence (%)	0	5	2	0	0	0
	Fertility (%)	0	0	0	0	0	0
Drthotrichum lyellii HOOK. and TAYL.	Presence (%)	6	5	2	0	0	0
	Fertility (%)	6	3	0	0	0	0
Orthotrichum tenellum BRUCH ex BRID.	Presence (%)	22	11	4	0	0	0
	Fertility (%)	17	8	0	0	0	0
Pterogonium gracile (HEDW.) SM.	Presence (%)	17	3	0	0	3	0
	Fertility (%)	0	0	0	0	0	0
Radule lindenbergiena GOTT	Presence (%)	11	3	0	0	0	0
	Fertility (%)	11	0	0	0	0	0
Brachythecium velutinum (HEDW.) B.,S. and G.	Presence (%)	17	3	0	2	0	0
	Fertility (%)	0	0	0	0	0	0
Hypnum cupressiforme (HEDW.)	Presence (%)	17	0	2	0	0	0
	Fertility (%)	0	0	0	0	0	0
Frullania tamarisci (L.) DUM.	Presence (%)	6	3	0	0	0	0
	Fertility (%)	6	3	0	0	0	0
Pylaisia polyantha (HEDW.) SCHIMP.	Presence (%)	6	3	0	0	0	0
	Fertility (%)	0	0	0	0	0	0
Orthotrichum pumilum SW.	Presence (%)	6	3	0	0	0	0
	Fertility (%)	6	0	0	0	0	0
Lejeunea cavifolia (EHRH.) LINDB.	Presence (%)	6	0	0	0	0	0
	Fertility (%)	6	0	0	0	0	0
Neckera complanata (HEDW.) HUB. a)	Presence (%)	6	0	0	0	0	0
	Fertility (%)	0	0	0	0	0	0
Zygodon forsteri (WITH.) MITT. a)	Presence (%)	6	0	0	0	0	0
	Fertility (%)	6	0	0	0	0	0

SPECIES	IAP classes	VI	V	IV	III	II	I
	IAP values	30	20-30	10-20	5-10	1-5	0-1
	Mean of species number incl. lichens	35	25-34	15-24	10-14	5-9	0-4
	SO2 zones in ug/m^3 Winter average	40	40-50	50-60	60-70	70-125	125
	Number of studied sites	18	37	54	48	38	10
Scorpiurium sendtneri (SCHIMP.) FLEISCH. a)	Presence (%)	6	0	0	0	0	0
	Fertility (%)	0	0	0	0	0	0
Homalothecium philippeanum (SPRUCE) B.,S. and G. a)	Presence (%)	6	0	0	0	0	0
	Fertility (%)	6	0	0	0	0	0
Dicranoweisia cirrata (HEDW.) LINDB ex MILDE a)	Presence (%)	6	0	0	0	0	0
	Fertility (%)	0	0	0	0	0	0
Tortella flavovirens (BRUCH.) BROTH.	Presence (%)	6	3	0	2	0	0
	Fertility (%)	6	0	0	0	0	0
Trichostomum brachydontium BRUCH.	Presence (%)	0	3	0	0	0	0
	Fertility (%)	0	0	0	0	0	0
Fabronia pusilla RADDI	Presence (%)	0	0	2	0	0	0
	Fertility (%)	0	0	0	0	0	0
Tortula muralis HEDW. b)	Presence (%)	6	0	4	2	0	0
	Fertility (%)	6	0	2	2	0	0
Bryum caespiticium HEDW. b)	Presence (%)	0	0	0	2	0	0
	Fertility (%)	0	0	0	0	0	0

a) - In the Arrabida Reserve

b) - In the vicinity of a cement industry

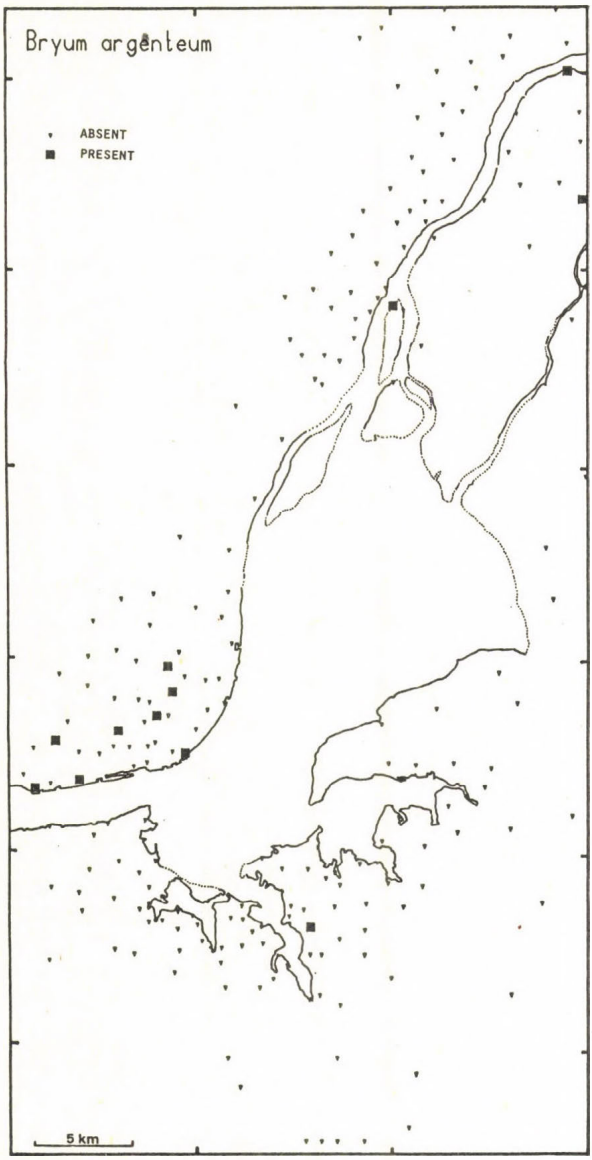

Fig. 3. The occurrence of Bryum argenteum in the study area.

It was interesting to note that some species, such as Tortula muralis Hedw., Didymodon vinealis (Brid.) Zander, Bryum cæspiticium Hedw. and Brachythecium velutinum (Hedw.) B.S.G., usually considered as terricolous or saxicolous, were present on the bark of Olea and Ulmus near a cement industry complex.

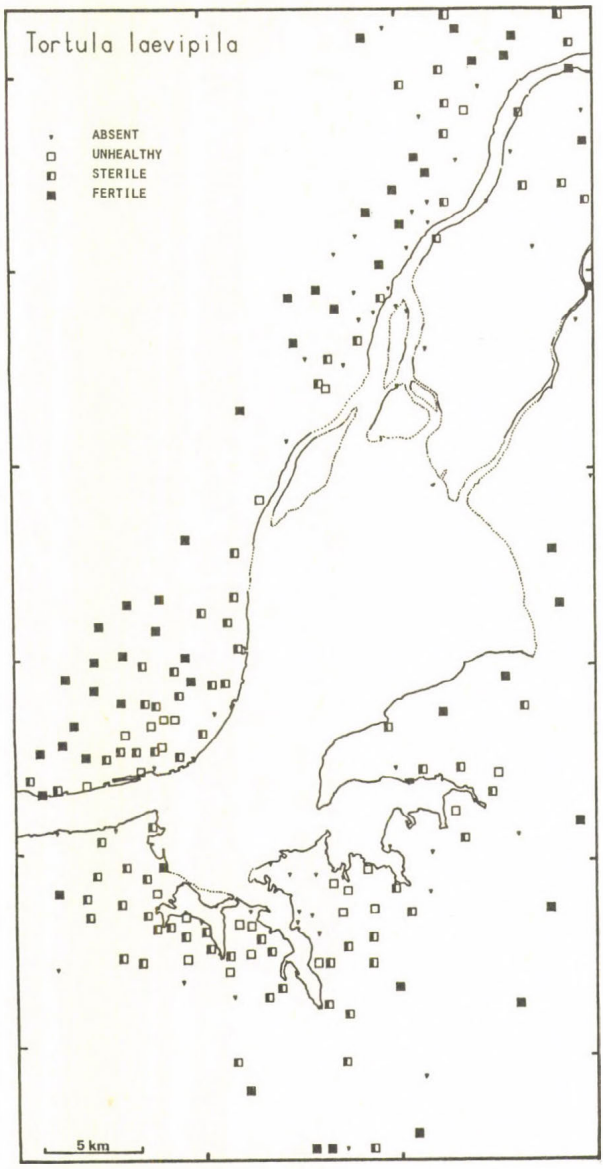

Fig. 4. The occurrence of Tortula laevipila in the study area.

Dialytrichia mucronata (Brid.) Broth., usually growing in hygrophilous communities in Europe, is present with a high frequency on Olea bark, sometimes in damaged sites (Sérgio & Sim-Sim 1984).

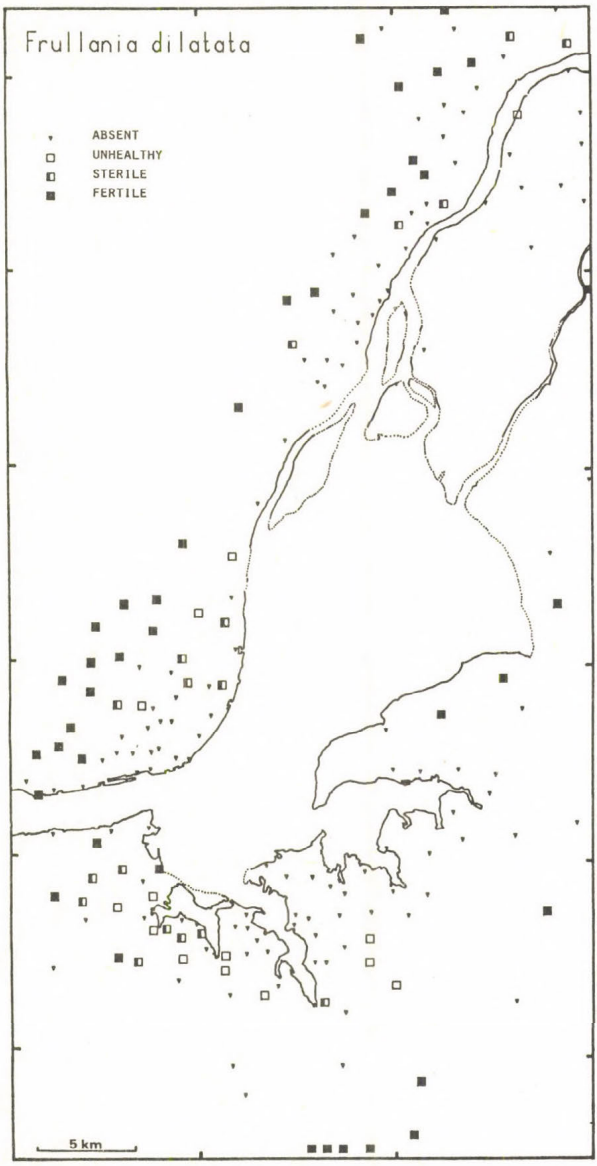

Fig. 5. The occurrence of Frullania dilatata in the study area.

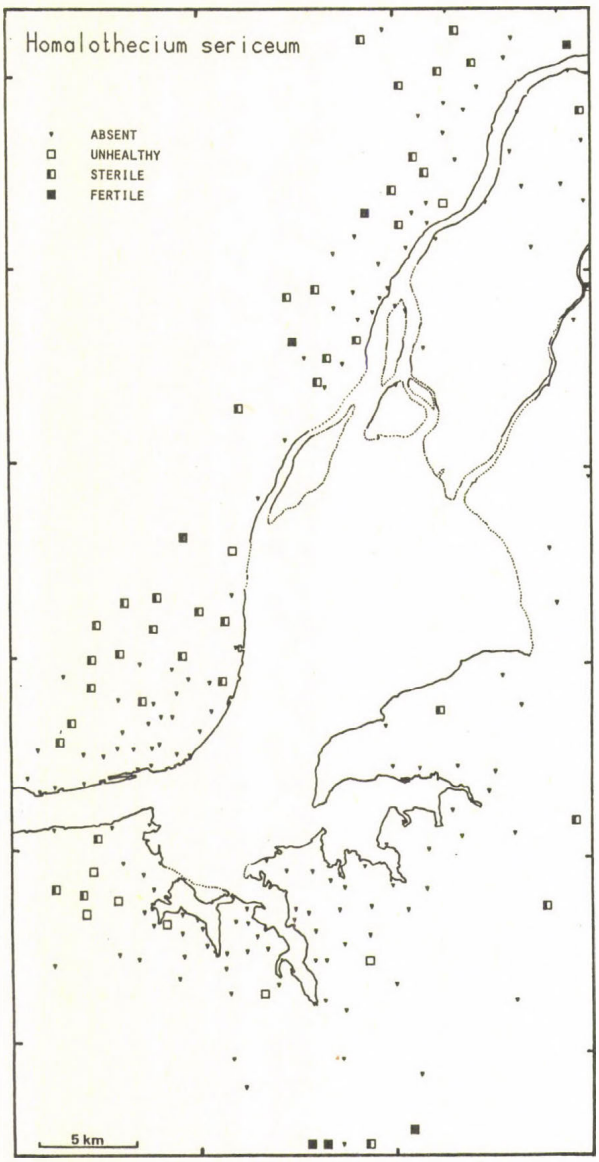

Fig. 6. The occurrence of Homalothecium sericeum in the study area.

Transplants

In the present study we have attempted to correlate the injury symptoms of SO_2 in Tortula laevipila as Brodo (1961) did for lichens and Leblanc & Rao (1973) for mosses and lichens.

Injury effects on Tortula transplants have been analysed with IAP zones and SO_2 level. The 9 bark discs with Tortula

Table 2. Results of Tortula laevipila trasplants (after 6 months). Relation to IAP values and to SO_2 doses at different sites in the Tejo estuary.

Transplant sites (1)	IAP/Values		SO_2 Zones µg/m³ wint.average	Ph Thallus	Injury Symptoms	
					Shoot and Leaves	Gemmae
S63 (a)	VI	30	< 40	5.57	not evident (Fig. 7)	rares
L8	V	21	40-50	5.41	not evident	present
L45	IV	15	50-60	5.42	not evident	present
L12 (b)	III	5	60-70	5.31	some damage, some basal leaves necrotic	present, more evident
L39	I	1	± 125	5.22	some damage, more leaves necrotic	present. more evident
L25 (c)	I	1	± 125	5.70	some damage, more leaves necrotic	present, more evident
S18 (d)	II	2	± 125	5.88	almost completly destroyed (Fig. 7)	present, with evident damage
S52 (e)	I	1	> 125	5.12	completly destroyed or dead (Fig. 7)	not present or destroyed
S65 (e)	I	0	>125	4.75	completly destroyed or dead (Fig. 7)	not present or destroyed

(1) Sérgio et al. (1985), (a) near the Arrabida reserve, (b) area with intense traffic, (c) near a railway station, (d) near a steel and iron industry, (e) in the vicinity of a chemical industry complex.

fertile material were sent out from a poorly polluted area (40 $\mu g/m^3$) and individually photographed. Each disc was exposed in 9 selected sites.

After 6 months of exposure, some changes occurred. External morphology, fertility and acidity were compared and correlated with material with normal vitality. All the discs were rephotographed.

The results (Table 2) show that Tortula laevipila has a lethal limit of SO_2 level at about 70 to 125 $\mu g/m^3$. A visible effect is the dark appearance and necrotic leaves, sometimes only the cup of gemmae remain green. New sporophytes were not observed in the transplanted material.

The surface wax of Tortula laevipila leaves also shows important differences after 6 months of transplantation, when observed dehydrated by scanning (Fig. 7).

Due to this observation and the particular strategy of Tortula laevipila , that develops sporogons mainly in unpolluted areas, and present asexual reproduction by terminal leaf-form gemmae with the SO_2 injury, and a known lethal limit of SO_2 level, it can be considered as a good monitor of SO_2 zones.

Many infraspecific taxa were described by Barkman (1963) for this species, considering only the presence and morphology of gemmae. In studying all the Lisbon material of T. laevipila, including a Welwitsch specimen of 1844 that has no gemmae, we can state that this moss shows a tendency to survive in polluted areas by an increase in regeneration of the apical cells as in Funaria hygrometrica (Comeau & Leblanc 1971).

Only using cultivation methods and with fumigation studies will it be possible to clarify this taxonomic problem.

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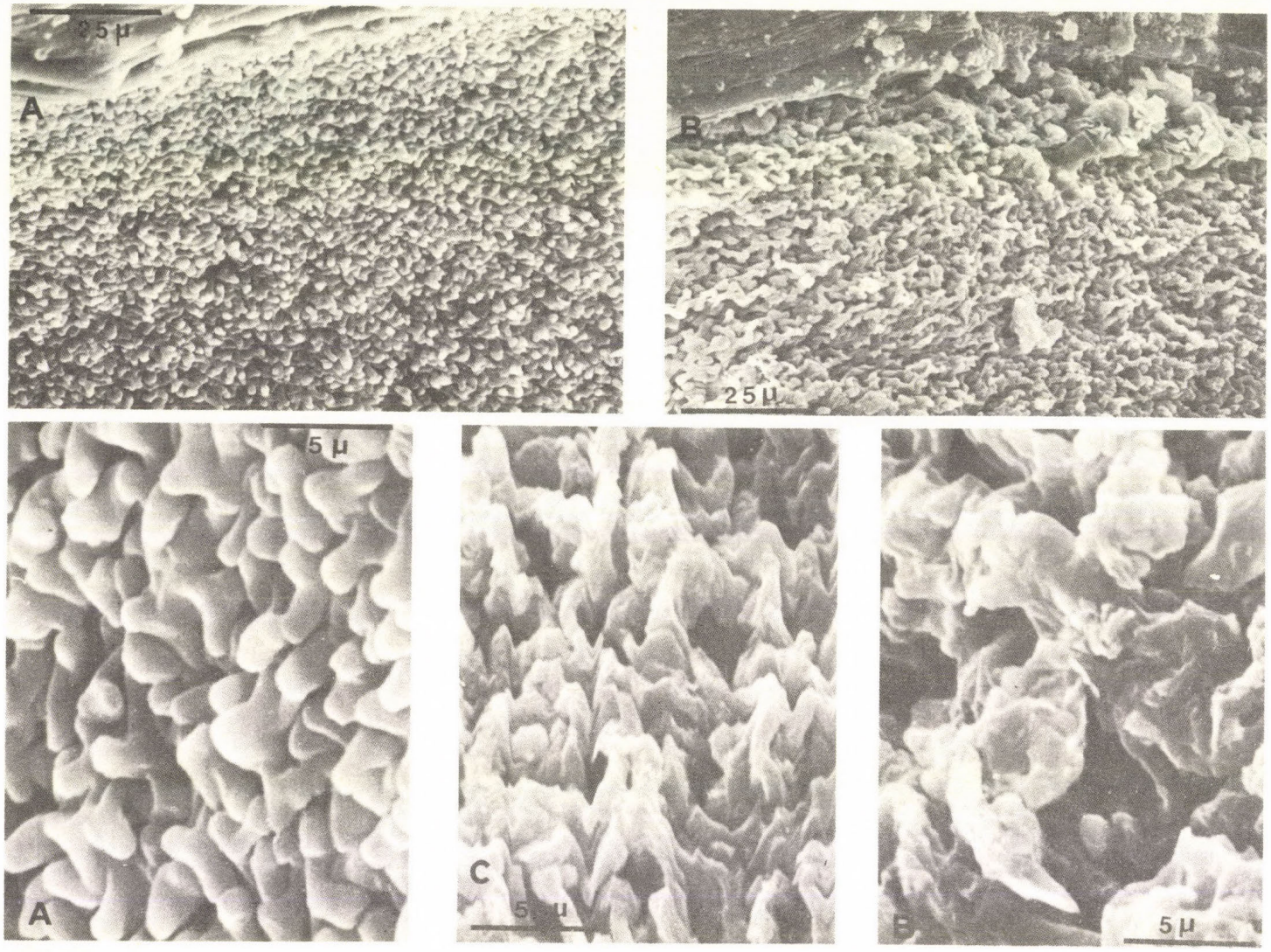
Fig. 7. Micrographs of the abaxial surfaces of Tortula laevipila leaves. A: with no evident injury; B: with evident damage; C: showing accumulated particles and damage.


25 µ
A
B
25 µ
5 µ
A
C
5 µ
B
5 µ

Now we can conclude that the production of apical propagules and their different morphology can appear as an adaptation to stress by air pollution or to mechanical damage.

Changes in the bryophyte flora

In many Portuguese regions it is very difficult to be certain that a species is really extinct, due to the deficient state of knowledge and distribution maps in the past. However, in studying herbarium material it was possible, in some cases, to confirm that some species became extinct in the Lisbon area (Sérgio 1981).

In Britain (Rose & Wallace 1974), the main factor causing extinction is air pollution by SO_2 and the species affected are mainly the same sensitive mosses found in the Tejo estuary (Cryphaea heteromalla, Frullania tamarisci, Orthotrichum lyelli, O. pumilum, Pterogonium gracile, etc.).

Cololejeunea minutissima (Sm.) Schiffn., which was present in 1949 in a locality nowadays with a SO_2 level of about 125 $\mu g/m^3$, is now extinct.

Homalothecium philippeanum present in Lisbon in 1847 is found now only in the Arrabida reserve.

Some surrounding undamaged areas, such as the Arrabida reserve, provide a constant supply for dispersal of spores or propagules of mosses, and are a very important niche for diaspores.

FINAL REMARKS

In the Lisbon area, the high diversity of epiphytic bryophyte species is regarded as an expression of less polluted air, and one of the features of the epiphytic pollution-sensitive species appears in the reduction in the number of species in time and space.

The high correlation shown in this work between the bryophyte communities and the air pollution ratio suggests that with only the survey of bryophytes of Olea europea we can limit

zone-maps of pollution levels (40 to 125 $\mu g/m^3$) in regions with similar topography and climatic situations.

The present work should be considered as a preliminary study in Portugal, and as a baseline for the selection of sensitive species of epiphytic bryophytes.

We hope we can extend the scope of this investigation to other areas, where air pollution impact exists, and also to regions with future ecological problems.

ACKNOWLEDGEMENTS

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RADIOECOTOXICOLOGICAL INFLUENCE OF A POWER STATION ON MOSSES

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This work presents the results of observation of change in the ^{226}Ra, ^{228}Ra and ^{137}Cs content in the moss Polytrichum commune in the region of Beskidy. It was found that influence of mineralization was directly and inversely proportional to annual rainfall at a power station nearby. It was confirmed through analysis on contamination in the region. The results were analysed in relation to distance from a coal power station.

INTRODUCTION

The first specific radioactivity in mosses in southern POland was measured by Grossman & Kwapuliński (1970). Many moss species accumulate radioisotopes as ^{137}Cs, ^{60}Co and ^{226}Ra. They have been found to be especially sensitive to artificially induced changes and have been employed to determine the impact of air pollution on environment. Their ability to accumulate makes them suitable organisms for monitoring anthropogenically derived radioisotopes in the air, either as a result of long-term emission of dust or as secondary emission of dust.

The retention of ^{137}Cs by mosses is higher than that of ^{90}Sr. The $^{137}Cs/^{90}Sr$ ratio, which in atmospheric fallout is in the range 1.4 - 2.0 according to different investigators, is usually 5- 8 times as high in mosses.

The influence of habitat in southern Poland was very pronounced: mosses in 1970 from the pine forest contained 1221 Bq $^{137}Cs \cdot kg^{-1}$ dry weight, from the deciduous forest 1036 Bq $^{137}Cs \cdot kg^{-1}$ dry weight. The uptake of ^{137}Cs and ^{90}Sr does not relate to potassium content; it is very important information for monitoring radioactive substances. Accumulation of radioisotopes by mosses is a long-term process, A number of authors have observed the concentration of ^{137}Cs and ^{90}Sr for several years after a fallout maximum.

Because of the variability of factors decisive in the mechanism of contamination of a given environment, radioecological investigations are always of regional character (Włodek 1971).

The facts mentioned above prompted the authors to investigate the changes in concentration of radium in the moss Polytrichum commune in several districts of the Beskidy Mountains and Karkonosze for comparison.

METHOD

Material was collected from the foothills through to higher altitudes of the Beskidy Mountains, mainly in the Silesian Region. For comparison, mosses were collected from several localities in the Karkonosze region in southwestern Poland. A basic investigation was carried out in the industrial region near Katowice.

Moss samples were first cleaned of soil, washed in distilled water, dried at 378 ^{o}K and pulverized in a mortar.

The concentration of radioisotopes in mosses was determined by a modification of the method described by Goldin (1961).

As a basic preliminary, tests were carried out to establish the absolute minimum quantity of moss required for sampling; this was found to be equal to 6 g dry matter. Measurements were repeated six times, using a scintillator produced by Tesla, Czechoslovakia. The measurement error of radioactivity was found to be 15%.

Concentrations of ^{137}Cs were determined by the method of sorption on the ion exchange phosphate molybdate bed (Włodek et al. 1970), the average standard deviation being equal to 5 - 6%.

^{228}Ra content was determined by conventional radiometers produced in Poland, and the method elaborated by the Central Laboratory of Radiological Protection in Warsaw.

RESULTS

Soil

The α-radioactivity of the soils in Karkonosze region are presented in Table 1. The specific alpha radioactivity of a particular fraction varied from 499.5 to 2434 $mBq \cdot g^{-1}$. Measurement of specific radioactivity of a particular fraction of soil does not reveal a relationship between the alpha radioactivity and the diameter of soil granules. The highest radioactivity was found in soils from under mosses, for example, 2330 $mBq \cdot g^{-1}$. This can attribute to the protective role of mosses, for example, against the secondary emission of radioactive substances. One should say that soil from under mosses contains many organic and mineral substances that together provide a much greater sorption capacity.

The average β-radioactivity ranged from 740 to 1295 $mBq \cdot g^{-1}$. In the case of soil near the power station, the α-radioisotopes were 20 times higher than for Beskidy, at a distance of about 80 km from the center of the Katowice region. Also, the specific beta radioactivity of soil was equal to 1925 - 4406 $mBq \cdot g^{-1}$.

The measurements in soils show the following sequence of alpha radioisotope accumulation:

Chorzów - 8349 $mBq \cdot g^{-1}$
Katowice - 4035 $mBq \cdot g^{-1}$ > Goczałkowice - 1925 $mBq \cdot g^{-1}$ (50 km) >
Zabrze - 5886 $mBq \cdot g^{-1}$

> Wapiennica - 1111 $mBq \cdot g^{-1}$ (70 km)

Table 1. Specific radioactivity of soil in Karkonosze

	alpha-radioactivity		beta-radioactivity	
	soil from under moss	surface soil	soil from under moss	surface soil
0.43	2330.	740.0	1184.0	947.0
0.385	1221.0	1856.0	1483.3	384.8
0.30	1406.0	1184.0	2368.0	962.0
0.25	1739.0	1591.5	1295.8	963.0
0.2	1369.0	1202.5	1285.1	952.0
0.12	499.5	2434.0	1538.0	925.0
0.102	1865.0	1170.0	2775.0	444.8
0.088	1776.0	1665.0	986.8	746.3
0.075	1480.0	999.0	848.7	848.0
0.06	1702.0	1520.0	1543.1	1287.1
0.06	1368.0	1586.0	1867.0	687.0

Moreover, the level of radioactivity of the soil influenced the meterorological condition.

Air

Radium and other radioisotopes enter the natural environment mainly with fly ashes produced during coal combustion. Power coals contain various amounts of radium compounds, generally not more than 148 $Bq \cdot kg^{-1}$ of coal.

The air of the industrial region contains relatively great amounts of alpha-radioactive substances. In Katowice and other cities the alpha-radioactive substances in the air were about:

0.12 - 0.21 Bq $^{214}Pb/m^3$
0.15 - 0.22 Bq $^{228}Ra/m^3$
0.07 - 0.24 Bq $^{232}Th/m^3$
0.18 - 0.29 Bq $^{226}Ra/m^3$
0.29 - 0.38 Bq $^{238}U/m^3$

The concentrations of these radioisotopes in rain were as follows:

^{226}Ra: 129.5 - 166.5 MBq/km^2

^{228}Ra: 125.9 - 144.3 MBq/km^2

^{238}U: 185.0 - 355.0 MBq/km^2

^{228}Th: 103.6 - 129.5 MBq/km^2

Generally, in the industrial region the air contains long-term alpha-radioactive substances at c.0.11, beta-radioactive substances at c.0.09 Bq/m^3. In this same region, the concentration of short-term alpha-radioisotopes in the air equals about 37 Bq/m^3. In general, it may be stated that in localities characterized by greater amounts of dust fallout, the concentration of ^{226}Ra and ^{228}Ra is also higher. There is a positive correlation between the two parameters.

Moss

The above facts justified our investigations on the concentrations of radiactive substances in mosses of the Katowice and Bielsko districts. Investigations were conducted in the years 1979-1984.

The radium content in a particular kind of moss has a wide range from 18.3 to 1272 mBq·g^{-1} of ash (Tables 2-4). The radium concentration in mosses is many times higher than in the soil. It is characteristic that mosses accumulate much more radium than ferns, bilberry or spruce.

The results in Tables 2-4 show selective preservation of mosses in accordance with radium. Generally, in cases where in some areas the rain or dust contained more radium than the moss, in that case the moss contained more radium than in other localities. The data we have gathered so far convince us that radium concentration in the soil does not determine the radium concentration invarious kinds of moss that absorb mineral salts from the atmosphere. These observations confirm data of radium concentrations in moss and rain or snow (Table 5).

Table 2. Concentration of radioisotopes in Polytrichum commune in the industrial region (mBq·g^{-1} of ash)

Locality	^{226}Ra	^{228}Ra	^{137}Cs	^{40}K
Mysłowice	1191.3	68.1	65.3	247.0
Bedzin	181.3	40.6	87.1	187.3
Katowice	1102.1	53.6	92.4	196.3
Chorzów	1303.4	103.8	98.3	190.8
Bytom	1272.3	108.3	95.8	203.5
Gliwice	1203.4	136.3	92.8	187.3

Table 3. Concentration of radioisotopes in Polytrichum commune in the Silesian Beskidy region (mBq·g^{-1} of ash).

Locality	^{226}Ra	^{228}Ra	^{137}Cs	^{40}K
Wapienica	461.3	48.3	83.4	250.3
Ustroń	631.3	51.2	87.8	190.6
Mount Równica (883 m)	624.3	41.3	90.3	185.5
Mount Soszów Big (884 m)	729.3	26.3	97.4	184.0
Mount Czantoria (995 m)	825.3	83.4	90.3	217.3
Mount Kiczor (989 m)	729.3	86.2	105.6	168.3
Brenna	152.3	75.6	80.6	178.3
Szczyrk	166.8	80.6	68.3	192.4

Radium accumulation by Polytrichum commune decreases proportionally to the distance from the power station. Careful observations of Polytrichum commune show that the average accumulation factor oscillates from 21 to 81 times. In the period investigated the precipitation in industrialized localities contained 5-8 times greater amounts of radium than in the agricultural localities. We observed similar variations for mosses in which the radium content was proportional to their mineralization. The coefficient of variation in radium

Table 4. The radioisotope content of mosses in the High Beskidy region.

Locality	^{226}Ra	^{228}Ra	^{137}Cs	^{40}K
Mount Pilsko (1583 m)	18.3	34.3	80.3	295.6
Mount Babia Góra (1725 m)	12.3	22.2	103.6	243.6
Mount Szelust (923 m)	20.3	26.6	203.8	189.6
Jaworzyna (1173 m)	127.3	48.6	123.6	200.3
Kondratowa (1170 m)	33.4	37.8	168.3	243.8

content in the moss Polytrichum commune was equal to 0.68 ± 0.13 in industrial regions and 0.20± 0.03 on recreational grounds.

Of several ways by which radium enters the moss, the most important are precipitation and sorption from soils. Their contribution to the pollution of the moss with radium are different and may be established by analysing the relation

$$C_m = C_p , K_p + C_s \cdot K_s$$

where C_m is the element concentration in mosses, C_p is the elemental concentration in the precipitation, and C_s is in the soil. The coefficients K_p and K_s denote the contributions of the respective ways of radium penetration into mosses from precipitation (K_p) and from soil (K_s).

By means of successive transformations we obtain

$$\frac{C_m}{C_p} = \frac{C_s}{C_p} \cdot K_s + K_p$$

The answer to the question concerning the amounts of a given element coming either from precipitation or from soil we must analyse the plots shown in Figure 1.

K_s denotes the portion of radium contributed by soil to its total content in mosses, whereas K_p denotes the direct contri-

Table 5. Radium concentration in the precipitation in several localities.

Parameter	Industrial region			Recreational region			
	Chorzów	Katowice	Kozłowa Góra	Wapienica	Strumień	Kobiernice	Goczałkowice
Dust fall ($t \cdot km^2 \cdot month$)	43.9	26.4	20.1	8.2	12.0	8.6	9.2
Precipitation (mm/year)	697	698.6	769.8	1425.0	899.4	1386.0	873.0
Mineralization ($mg \cdot dm^{-3}$)	805-1123	46.5-658.7	43.6-259	23.6-78.3	39.6-90.4	28.4-67.9	37.6-83.4
^{226}Ra (rain)	12.58	14.85	28.84	5.14	12.0	5.14	5.0
^{226}Ra (snow)	699.9-2719.5	241.0-1484	689.5-1073	352.-1036.7	388.-747.	355.-767.0	362.6-1095.2
	1961.5	740.9	740.	629.	529.1	388.	481.

bution of radium from precipitation.

From the comparison of lines a and b it follows that the quantitative predominance of radium migration from the soil is more than from precipitation. In places situated at a certain distance from the Upper Silesian Region Industry, due to a characteristic 'wind-rose', the course of radium migration to mosses may be more complex. From the data obtained, it follows that the contribution of radium migration from soil is 23 times, and from precipitation 5 times higher in industrial regions than on recreational grounds. The radium transfer from soil to mosses is given by K_s = 0.8 for industrial regions, and by K_s = 0.034 for recreational areas.

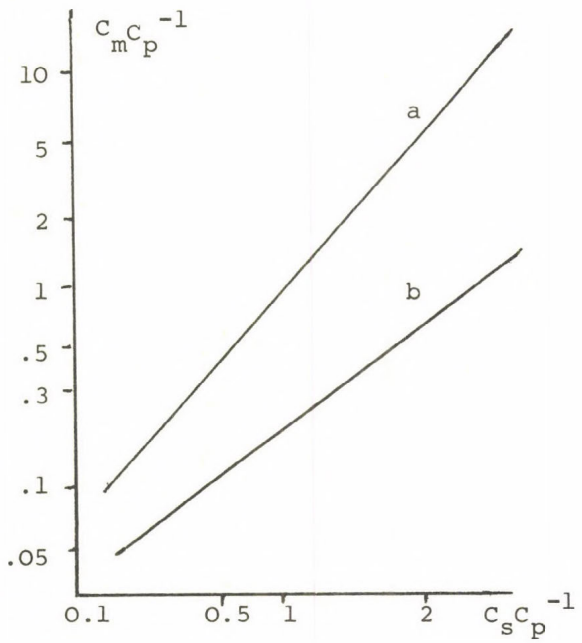

Fig. 1. Migration of radium to mosses in the industrial region (a) and in the recreational region (b). C_m - ^{226}Ra in mosses; C_p-^{226}Ra in the precipitation; C_s - ^{226}Ra in the soil.

Table 6. The radioisotope content in Polytrichum commune near a power station ($mBq \cdot g^{-1}$ of ash)

	Distance from power station				
	1 km, N	3 km, N	4 km, N	1 km, S	10 km, N
^{226}Ra	2889.3	2348.5	2438.0	2002.4	918.3
^{228}Ra	807.3	902.3	483.3	503.8	138.8
^{137}Cs	118.3	134.3	93.4	83.4	50.3
^{40}K	186.3	153.4	193.6	180.0	175.8

Table 7. Specific beta-radioactivity of mosses in Karkonosze in 1970.

Locality	Altitude (m)	Beta-radioactivity (pCi/g)	(mBq/g)
Samotnia	1300	114.1	4221.7
Snieżka	1600	401.7	14862.9
Wielki Szyszak	1509	924.7	34213.9

In case of precipitation, the respective values are 0.06 and 0.012. Based on these results some generalizations concerning the ways of pollutant transport and radioecotoxicological estimation can be made. A strong correlation between the analysed $\frac{C_m}{C_p}$ and $\frac{C_s}{C_p}$ values is described for the upper Silesian Industrial region and recreational areas by the positive coefficient of correlation equal to about 0.83. This fact allows us to forecast the changes in contamination depending on the varying concentration of dust or radium in the precipitation.

The data illustrating variations of some radioisotopes accumulated by mosses near a power station are presented in Table 6. Near the power station, the concentration of ^{226}Ra in mosses is 3 times higher than at a distance of about 10 km. The similar relationship we observe for ^{229}Ra. Concentration of ^{228}Ra in mosses ranged from 138.8 to 807.3 $mBq \cdot g^{-1}$ of ash.

The ^{137}Cs content of the mosses investigated is shown in Tables 2-4. The highest concentration of ^{137}Cs from fall-out was found in the Beskidy Mountains rather than in the Upper Silesian Industrial Region. The average ^{137}Cs content ranged from 30.7 to 348.9 $mBq \cdot g^{-1}$.

The ^{137}Cs concentration of mosses is about 30 times higher than in corn, vegetables and pine needles collected from a similar, unpolluted upland region experiencing a comparable radioactive fallout level.

The small variability in ^{137}Cs content for Polytrichum commune together with a small variation in the coefficient of accumulation demonstrate the advantage of using this species of moss as bioindicator of ^{137}Cs. The effective half-life of ^{137}Cs in mosses collected from different geographical regions of southern Poland varied from 3 to years. We suggest that as time elapses from the moment of fall-out this half-life for mosses will increase.

It is likely that mosses, like lichens, will exhibit a seasonal cycle of radiocesium, with maximum values in the summer and minimum in mid-winter.

CONCLUSIONS

1. Concentrations of ^{228}Ra, ^{226}Ra and alpha-radioactive substances in mosses resulting from coal combustion are many times higher than the average geochemical concentrations of elements in soil and water.

2. The moss genus Polytrichum can play an important role as a bioindicator of radium contamination in the environment, particularly in providing useful information on previous levels of airborne radioactivity.

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BIOINDICATION OF HEAVY METAL TOXICITY OF WATER BY THE LIVERWORT RICCIOCARPUS NATANS (L.) CORDA

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It was determined in the performed experiment that sensibility of the liverwort Ricciocarpus natans (L.) Corda to the toxicity of heavy metals (Zn, Cu and Pb) may be used in bioindication of these metals in water. Ricciocarpus natans demonstrates symptomatic reaction at a given concentration of the above mentioned metals, especially in growth and survival rate. The liverworts were cultured in vitro for 14 days with various doses of $ZnSO_4 \times 7H_2O$, $CuSO_4 \times 5H_2O$ and $Pb(NO_3)_2$. Lethal doses (DL_{100}) for Ricciocarpus natans were 20 mg Zn/dm^3 of nutrient medium, 10 mg Cu/dm^3 of nutrient medium and 30 mg Pb/dm^3 of nutrient medium. Symptomatic reactions of Ricciocarpus natans depending on concentration of the given metals were as follows: under the influence of Zn the plants turn brown, reduce rhizoids and have wrinkled thalli; under the influence of Cu thalli deform and reduced rhizoids develop, under the influence of Pb plants show symptomatic sectoral necrosis, wrinkled, asymmetric and diminished thalli and peculiarly twisted rhizoids.

INTRODUCTION

Increase of environmental pollution threatens the natural populations of Ricciocarpus natans (L.) Corda. The number of stations and abundance of the species occurrence have decreased in recent years. This paper aims at determining the sensibility of Ricciocarpus natans to environmental pollution by heavy metals.

METHODS

For the investigations, the populations of Ricciocarpus natans were chosen from the natural station in Grabnowo Wielkie (Lower Silesia). The plants were gathered in August, 1984. The experiment was carried out from 27 August to 12 September, 1984.

Designation of sensibility to toxic effects by heavy metals consists in specifying proper growth reactions of plants and their survival rate at a definite concentration of a given element. This was determined by experiments in which the lethal doses were estimated.

The plants were cultivated on Hoagland's medium with the addition of microelements in the Gorham set (Landolt 1957). The plants were cultivated in a glass-house, under constant conditions of lighting and temperature. Experimental plants, 5 initial segments each, were placed in beakers containing 400 ml of nutrient medium with a proper amount of the standard solution of the compound under investigation, with three beakers for each condition. In the experiment, salts of the following compounds were used: $ZnSO_4 \times 7H_2O$, $CuSO_4 \times 5H_2O$, $Pb(NO_3)_2$. Standard solutions were prepared in such a way that 1 ml of the solution contained 1 mg of Zn, 1 mg of Cu and 1 mg of Pb. The pH was constantly 5.7. The following concentrations were applied for $ZnSO_4 \times 7H_2O$: 0.1, 0.2, 0.5, 1, 2, 5, 10, 20, and 30 mg Zn/l; for $CuSO_4 \times 5H_2O$: 0.1, 1, 2.5, 5, 10, 20, 30, 40, and 50 mg Cu/l; for $Pb(NO_3)_2$: 0.1, 1, 2, 3, 5, 10, 20, 30, and 50 mg Pb/l.

The experiments continued for 14 days. After this time, the number of plants, the biomass expressed in fresh mass and the length of plant rhizoids were investigated.

The results were analysed by statistical methods.

RESULTS

Tolerance of Ricciocarpus natans to Zn

The changes in the number of plants, biomass and the length of rhizoids from the investigated population of Ricciocarpus

Table 1. Changes in the length of rhizoids, the number of segments and biomass of Ricciocarpus natans under the influence of Zn.

Dose in mg/l	The length of rhizoids in cm	The number of segments	Biomass in g
Control	0.57	45	0.0328
0.1	0.54	42	0.0383
0.2	0.40	37	0.0299
0.5	0.37	34	0.0222
1	0.27	23	0.0193
2	0.20	21	0.0114
5	-	13	0.0098
10	-	6	0.0081
F est.	224.	119	324.45
F tab.	3.11	2.66	2.66
LSD	0.084	3.3	0.0015

natans, at various concentrations of zinc, in cultures in vitro, after 14 days of cultivation, are presented in Table 1. The results show that a concentration of 20 mg Zn/l is a lethal dose for Ricciocarpus natans. A concentration of 0.1 mg/l of nutrient medium stimulates an increase in the number of plants. Low concentrations (0.2 and 0.5 mg Zn/l) slightly decrease the number of plants. Higher concentrations of zinc in the nutrient medium cause a gradual decrease in the number of plants.

Average values of biomass at various zinc concentrations in the nutrient medium are correlated with the changes in the number of plants under investigation.

The length of rhizoids az 0.1 mg Zn/l of nutrient medium decreased slightly. Further increase of zinc concentration caused a clear reduction of rhizoids. At the concentration of 5 mg Zn/l, complete reduction of rhizoids occurred.

In addition to quantitative changes of the number of plants, of their biomass and the length of rhizoids under the influence

of increasing Zn concentration, changes of colour and shape of plants as well as of their rhizoids were observed. At the concentration of 0.1 mg Zn/l, part of the rhizoid was brown. At 0.2 mg Zn/l and over, plants had a darker green colour, becoming more intense with the increase of concentration in the nutrient medium. At the concentration of 2 mg Zn/l, the surface area of plants decreased, and deformations occurred. A concentration of 5 mg Zn/l induced great changes in plant shape, deep incision of the thallus, reduction of rhizoids and wrinkling of the thallus surface.

Tolerance of Ricciocarpus natans to Cu

The influence of various copper concentrations in cultures in vitro on survival rate, biomass and rhizoid length of the plants are presented in Table 2.

On the basis of mean values of the number of plants, all the applied copper concentrations caused a decrease in biomass production and the number of segments. The number of plants decreased proportionally to the increase of copper concentration in the nutrient medium. Total mortality of plants is caused by the concentration of 10 mg Cu/l.

Together with the increase of copper concentration, the production of Ricciocarpus natans biomass decreased gradually. The dose of 1 mg Cu/l decreased the mean biomass value by 50%, and consecutive higher copper concentrations caused its further diminishing.

An increase of copper concentration in culture caused shortening of the rhizoids. Only at the lowest copper concentration of 0.1 mg/l, the length of rhizoids was slightly larger.

Additionally, at the concentration of 1 mg Cu/l, considerable wrinkling of thallus surface was observed, as well as occasional reduction in the number of rhizoids, deformation of thalli and production of brown colour. The tendencies quoted above became more intense with the increase of copper concentration in the nutrient medium.

Table 2. Changes in the length of rhizoids, the number of segments and biomass of Ricciocarpus natans under the influence of Cu.

Dose in mg/l	The length of rhizoids in cm	The number of segments	Biomass in g
Control	0.57	45	0.0328
0.1	0.59	36	0.0232
1	0.37	14	0.0159
2	0.30	12	0.0118
3	0.23	9	0.0027
5	0.13	6	0.0023
F est.	31.04	288.83	312.02
F tab.	3.11	3.11	3.11
LSD	0.094	2.907	0.00018

Table 3. Changes in the length of rhizoids, the number of segments and biomass of Ricciocarpus natans under the influence of Pb.

Dose in mg/l	The length of rhizoids in cm	The number of segments	Biomass in g
Control	0.57	45	0.0328
0.1	0.63	32	0.0219
1	0.40	26	0.0199
2	0.30	22	0.0194
3	0.23	19	0.0179
5	0.20	17	0.0150
10	0.13	15	0.0130
20	-	12	0.0106
30	-	-	-
F est.	25.67	110.52	541.85
F tab.	2.85	2.66	2.66
LSD	0.077	3.08	0.0087

Tolerance of Ricciocarpus natans to Pb

The lethal dose (DL_{100}) for Ricciocarpus natans was 30 mg Pb/l. The changes in the number of plants, biomass and rhizoid length at various lead concentrations in the cultures are presented in Table 3. Together with an increase of lead concentration, a decrease in the number of plants occurred. The lowest Pb concentration applied diminished the number of plants by about 30%. Analysing changeability of Ricciocarpus natans biomass under lead influence, we may observe that its value correlates with the decrease in the number of plants at the same doses.

The influence of lead ions on the rhizoid length of Ricciocarpus natans is similar to the influence of copper ions. At the lowest concentration of 0.1 mg Pb/l, explicit stimulation of growth in rhizoid length could be observed. Starting from the concentration of 1 mg Pb/l, a decrease in rhizoid length was noticed together with increasing concentrations and there was total decline at the concentration of 20 mg Pb/l which caused asymmetry of thalli in the plants under investigation. At the concentration of 1 mg Pb/l, necrosis at the border thallus fragments was observed, and at the concentration of 3 mg Pb/l, rhizoids became red, and the border fragments of thalli declined. A concentration of 5 mg Pb/l caused wide necroses and wrinkling of thallus surfaces and specific twisting of rhizoids. A concentration of 10 mg Pb/l caused a clear decrease od thallus surface area and a tendency to reduce rhizoids, which totally declined at 20 mg Pb/l.

DISCUSSION

In the following investigations, crucial differences were stated in the degree of reaction plants from natural population of Ricciocarpus natans to different doses of copper, zinc and lead. Toxic influence of heavy metals on this species was revealed, just as it was stated in the case of other land and freshwater species (Scharrer 1955). Critical and lethal doses for test plants (cultivated) given by Meinck et al.

(1975) are lower than those we observed for Ricciocarpus natans, approximating, however, the critical and lethal dose for the Lemna minor populations (Sarosiek et al. 1982). This testifies to a greater tolerance of Ricciocarpus natans in relation to phytotoxic activity of these heavy metals. Probably, Ricciocarpus natans has the ability of accumulating zinc and copper, as has been stated for other water plants, especially macrophytes (Riemer & Tóth 1969) existing in an environment contaminated with these metals.

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THE BIOINDICATION OF ETHYLENE GLYCOL IN WATER BY THE MOSSES FONTINALIS ANTIPYRETICA L. AND PLATYHYPNIDIUM RUSCIFORME (NECK.) FLEISCH.

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Studies were made on the aquatic mosses Fontinalis antipyretica L. and Platyhypnidium rusciforme (Neck.) Fleisch. affected by ethylene glycol and their ability to decompose it. The experiments were run on isolated fragments of gametophytes cultured under sterile conditions in various concentrations of ethylene glycol. It was found that these two species differ in vulnerability to the toxic action of ethylene glycol. Populations of these mosses show ecological susceptibility to ethylene glycol and they are able to decompose it.

INTRODUCTION

The aim of this paer was to ascertain whether the aquatic mosses Fontinalis antipyretica and Platyhypnidium rusciforme possess the ability to break down ethylene glycol. It was also of interest to learn about the possible innate reaction of these mosses to ethylene glycol, including their susceptibility to this substance and their ecological vulnerability. Hitherto published papers lack information on the relationship between the susceptibility of mosses to ethylene glycol and their mineral nutrition under a given habitat condition.

MATERIAL AND METHODS

Three populations of Fontinalis antipyretica and Platyhypnidium rusciforme were selected from forest mountain brooks

except for one population of F. antipyretica (number 5) from a stonepit. Microhabitat number 4 is common to both species. In microhabitat numbers 1 and 3 grows P. rusciforme.

The plants were collected during spring, several days prior to the start of the experiments.

Since bacteria and fungi actively break down ethylene glycol (Kamshilov 1977), the experiments had to be carried out under sterile conditions.

For the experiments, main gametophyte stems of F. antipyretica and P. rusciforme with intact growing points were used. The mosses were thoroughly washed in distilled water. Then, the plants were sterilized with 30% ethyl alcohol for 2 s., rinsed with distilled water, submerged in 2% solution of monochloramine for about 25-35 s., rinsed three times with sterile distilled water and placed in Erlenmeyer flasks with sterile water originating from a pond. The experiments were run under sterile conditions in a chamber sterilizied for at least 13 hours with UV rays. Flasks with distilled and pond water were sterilized in an autoclave under pressure of 1 atm. for 60 minutes.

In order to check whether mosses are able to decompose ethylene glycol, young shoots cultured under sterile conditions were cut off (about 3 cm in length) and seven were placed into each flask containing 100 cm^3 of sterile ethylene glycol solution at concentrations of 781, 1562, 3125, 6250, 12500, 25000, 100000 mg/dm^3 of water (in five replicates). The flasks were closed with cotton pad and plastic foil cap. The experiment ran for 14 days, the flasks being kept in a chamber with constant light of 1200 lux and a temperature of about 20 ^{o}C. After this time the amounts of ethylene glycol were determined according to Lurje & Rybnikova (1966), the number of dead plant shoots was determined and the growth of mosses in all concentrations observed.

Analysis of variance was applied to the data. The significance of difference was checked by Snedecor's F-test, at a probability level of $p = 0.05$ (see Oktaba 1966).

RESULTS

The lethal concentration of ethylene glycol (48 h LC 100) was 100000 mg/dm^3 of water for F. antipyretica from microhabitat 4 and 5 and P. rusciforme from microhabitat number 1 and 4. Lethal concentrations of ethylene glycol for F. antipyretica from microhabitat number 2 and P. rusciforme from microhabitat number 3 was 50000 mg/dm^3 of water. Mosses originating from microhabitats 2 and 3 were more susceptible to the toxic activity of ethylene glycol. At the lethal concentration no ethylene glycol decomposition was observed. At a concentration of 25000 mg of ethylene glycol/dm^3 of water from 17.1 to 54.3% of F. antipyretica died and from 25.7 to 80% of P. rusciforme (Table 1). At this concentration F. antipyretica decomposed from 8.2 to 15.1% of ethylene glycol and P. rusciforme from 5.6 to 13.7% (Table 2). At a concentration of 12500 mg/dm^3, F. antipyretica decomposed from 17.6 to 26.2% of ethylene glycol and P. rusciforme from 15.3 to 29.8%. At concentrations of 6250, 3125, 1562, 781 mg ethylene glycol/dm^3 and in the control with no ethylene glycol, where all moss stems survived, F. antipyretica decomposed from 23.1 to 32.5%, from 27.9 to 39.1%, from 32.3 to 49%, from 40.1 to 59.3%, respectively. At a concentration of 3125, 1562, 781 mg of ethylene glycol/dm^3 and in the control, where all P. rusciforme stems survived, this moss decomposed from 28.7 to 41.5%, from 33.4 to 46.9%, and from 39.2 to 53.8%, respectively. The decomposition by mosses became higher as the doses of ethylene glycol decreased. Different susceptibility of the examined populations appeared in efficiency of ethylene glycol decomposition. The highest amounts of ethylene glycol were decomposed by F. antipyretica and P. rusciforme possessing the least susceptibility to its toxic influence. Analysis of variance has shown that different experimental populations of the two moss species responded differently to ethylene glycol toxicity. Mosses of the same species originating from different microhabitats decomposed different amounts of ethylene glycol at equal concentrations, thus they showed ecological susceptibility. At a concentration

Table 1. The effect of ethylene glycol on the mortality (%) of Fontinalis antipyretica and Platyhypnidium rusciforme.

Species	Sampling station	Ethylene glycol concentration				LSD	F est.	F 0.05 (2.12)
		50000	25000	12500	6250			
Fontinalis antipyretica	2	100.0	54.3	14.3		3.06	1861.24	3.89
	4	51.4	17.1	0		4.39	338.31	3.89
	5	54.3	25.7	2.9		4.89	262.97	3.89
LSD		3.21	5.74	3.06				
F est.		685.45	109.12	57.95				
F 0.05 (2.12)		3.89	3.89	3.89				
Platyhypnidium rusciforme	1	62.9	31.4	5.7	0	4.69	335.85	3.24
	3	100.0	80.0	48.6	2.9	7.04	324.82	3.24
	4	54.3	25.7	0	0	3.65	450.03	3.24
LSD		4.26	5.64	8.03	2.27			
F est.		308.67	265.42	103.69	5.03			
F 0.05 (2.12)		3.89	3.89	3.89	3.89			

LSD = the least significant difference

F est. = estimated F

Table 2. The degree of biological decomposition of ethylene glycol (%) by Fontinalis antipyretica and Platyhypnidium rusciforme

Species	Sampling station	Ethylene glycol concentration (mg/dm^3)							LSD	F est.	F 0.05 (6.28)
		50000	25000	12500	6250	3125	1562	781			
Fontinalis	2	0	8.2	17.6	23.1	27.9	32.3	40.1	3.39	147.7	2.45
anti-	4	1.8	13.2	26.2	32.5	39.1	49.0	59.3	1.76	1079.2	2.45
pyretica	5	1.3	15.1	20.1	27.0	32.8	45.1	54.5	1.59	1086.2	2.45
LSD		0.18	1.56	1.69	1.95	2.18	1.95				
F est.		598.3	49.6	65.2	55.8	63.1	152.7	249.6			
F 0.05 (2.12)		3.89	3.89	3.89	3.89	3.89	3.89	3.89			
Platyhypnidi-	1	1.5	9.3	23.4	31.4	38.3	43.8	48.7	2.41	451.4	2.45
um rusci-	3	0	5.6	15.3	22.8	28.7	33.4	39.2	1.97	454.9	2.45
forme	4	2.4	13.7	29.8	36.9	41.5	46.9	53.8	7.66	47.0	2.45
LSD		0.39	3.68	2.18	2.18	1.91	1.87	2.18			
F est.		89.6	11.5	105.6	101.0	115.8	358.9	109.8			
F 0.05 (2.12)		3.89	3.89	3.89	3.89	3.89	3.89	3.89			

LSD = the least significant difference

F est. = estimated F

of 25000 mg ethylene glycol/dm^3, the linear growth of the gametophyte stem was at a minimum and no lateral growth appeared. At a concentration of 12500 mg/dm^3, the growth of the main gametophyte stem was also negligible, but lateral branches increased in numbers. At concentrations from 781 to 3125 mg/dm^3, where all moss stems survived, a clear linear growth has been observed and lateral branches appeared; their number in P. rusciforme was higher than in F. antipyretica.

DISCUSSION AND CONCLUSIONS

According to Łebkowska (1975), the lethal dose of ethylene glycol for Pseudomonas bacteria is 250 mg/dm^3 and for the Oligochaeta worm Tubifex tubifex it is much higher: 50000 mg/dm^3. This dose for Daphnia magna is 30000 mg/dm^3. The authors have also reported that Pługin (1968) proposed 1 mg of ethylene glycol per 1 dm^3 water as a maximal admissible dose of this compound for the surface waters. Lethal concentration of ethylene glycol for the examined mosses was 100000 or 50000 mg/dm^3, depending on the microhabitat where the plants were collected. At a concentration of 6250 mg/dm^3 for F. antipyretica, and at 3125 mg/dm^3 for P. rusciforme all moss stems survived, so the ethylene glycol was much more concentrated than the dose proposed by Pługin (Łebkowska 1975), which was completely harmless for both mosses. F. antipyretica and P. rusciforme showed ability to decompose ethylene glycol at a concentration of 25000 mg/dm^3, this ability being higher with the lower doses of ethylene glycol.

Both mosses examined in sterile cultures originated from chemically different microhabitats which corresponded to a great extent with the differentiation of natural populations. These chemical differences were expressed in different resistances of F. antipyretica and P. rusciforme populations to the toxic influence of ethylene glycol and were reflected in the efficiency of its decompositions. The highest amounts of ethylene glycol were decomposed by both mossess possessing the least susceptibility to its toxic influence.

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THE ELECTRIC PROPERTIES OF THE AQUATIC MOSS FONTINALIS ANTIPYRETICA L. IN THE BIOINDICATION OF ENVIRONMENTAL CONTAMINATION BY ETHYLENE GLYCOL

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Frequency-dependence of electric parameters (impedance and physe shift) of plants may be considered as quantitative characteristics of their physiological states and their disturbances. Distinct changes in the values of these parameters take place when the plants are subject to some physical and chemical factors. Determination was made of changes in electric parameters of the aquatic moss Fontinalis antipyretica L. due to contamination of water by ethylene glycol. The individual plants taken from a natural population were grown on Hoagland's medium. The experiment was conducted with the addition of a critical dose of ethylene glycol (6250 g/dm^3) and without it (control). Electric parameters of plants growing on the medium with ethylene glycol differ significantly from those of controls, where the values of impedance and phase shift of the control plants vary within a broader range than those of the experimental plants. Frequency-dependent changes in impedance and phase shift of plants due to glycol present in the medium are indicative of physiological disturbances manifested in the changes of elongation growth and biomass of the plants. Thus, electric parameters of plants may be used in bioindication of surface water contamination with ethylene glycol.

INTRODUCTION

Limiting physical and chemical factors, such as electromagnetic field, ionizing radiation or phytotoxic substances

explicitly influence the electric parameters of a plant. The value of the bioelectric potential of an organism, as well as the frequency relationship of impedance, phase shift, resistance or capacity, can be used as quantitative characterization of their physiological condition.

In this paper, the influence of ethylene glycol contamination on the impedance and phase shift of the aquatic moss, Fontinalis antipyretica in the frequency range from 5 Hz to 500 kHz is investigated. The results suggest also the possibility pf applying the measurements of electric parameters to the biotechnical indication of environmental contamination.

METHODS

The plants derived from a natural population were cultivated on Hoagland's nutrient medium with the addition of microelements in the Gorham set (Landolt 1957). The nutrient medium of combination I was supplemented with a dose of ethylene glycol, critical for mosses (6250 mg/l) according to Samecka (1984). After 21 days from starting the experiment, measurements of impedance and phase shift of 20 moss plants were taken. The experiments were conducted three times.

For the measurement of impedance and phase shift, the Hewlett-Packard Vector Impedance Meter 4800 A was used, comprising the frequency range from 5 Hz to 500 kHz, impedance range from 1Ω to 10MΩ, with a reading accuracy of 5%, and phase shift in the range from -90^{o} to $+90^{o}$ with a reading accuracy of 6%. The measurements were conducted on an electrostatic screen (Faraday cage) at 20 ^{o}C. Measurement electrodes made of silver were fixed directly, without supply counduits, to the instrument's input terminals. Spacing of electrodes was 20 mm. The electrode points of 0.5 mm diameter were introduced to the gametophyte tissue in 1 mm depth.

RESULTS

Impedance of Fontinalis antipyretica was in the range from 411 kΩ at the lowest frequency, to about 82.9 kΩ at the highest

Table 1. The influence of ethylene glycol on the impedance of Fontinalis antipyretica

Frequency (Hz)	Impedance (kΩ)	
	Control	Ethylene glycol
5	411	340
10	284.5	262
20	220.5	215
50	181	187.1
100	170.6	174.6
200	162	168.9
300	160	165.5
400	159.7	164.2
500	157.4	163.4
750	154.3	162.2
1000	151.4	163.2
2000	144.4	158.1
3000	142.1	156.9
4000	138.3	157
5000	133	155
7500	128.3	152.2
10000	124.1	149.4
20000	113.4	143.1
30000	118	139.6
40000	108	138.6
50000	103.2	137.4
75000	101.4	135.5
100000	97.9	132.3
200000	90.5	128.8
300000	84.8	124.6
400000	82.4	122
500000	82.9	119
X	148.3	163.5
F est.	25.11	22.6
F tab. (0.05)	1.55	1.55
LSD	38.5	27.1

measurement frequency of 500 kHz. Impedance of plants cultivated on the nutrient medium with ethylene glycol changed from 340 kΩ at 5 Hz, to 119 kΩ az 500 kHz (Table 1).

Impedance of plants cultivated on the nutrient medium with ethylene glycol at the lowest frequencies was lower than in the case of the control plants. On the other hand, in the range of the highest frequencies, impedance of the control plants was lower than in the plants cultivated on the nutrient medium with ethylene glycol.

Table 2. The influence of ethylene glycol on the phase shift of Fontinalis antipyretica.

Frequency (Hz)	Phase shift (in degrees)	
	Control	Ethylene glycol
5	-50.3	-41
10	-42.7	-34.7
20	-32	-26.3
50	-20.6	-19.2
100	-13.9	-12.6
200	- 9.5	- 9.5
300	- 9	- 6.3
400	- 8.3	- 5.6
500	- 7.9	- 5.4
750	- 7.5	- 3.6
1000	- 7.1	- 3.6
2000	- 8.4	- 4.2
3000	- 9	- 4.5
4000	- 9.3	- 4.8
5000	-10.1	- 5
7500	-11	- 5.6
10000	-11.8	- 6.2
20000	-12.5	- 6.4
30000	-12.8	- 6.4
40000	-12.5	- 6.3
50000	-11.3	- 6.3
75000	-11.3	- 7.1
100000	-11.6	- 8.1
200000	-11.5	- 9.9
300000	-12.4	-12.1
400000	-13.3	-13.8
500000	-12.7	-15.8
X	-14.4	-10.7
F est.	77.05	80.69
F tab. (0.05)	1.55	1.55
LSD	3.1	2.93

The phase shift was in the range from -50.3° at 5 Hz to -12.7° at 500 kHz. Phase shift of plants cultivated on the nutrient medium with ethylene glycol is -41° at 5 Hz to -15.8° at 500 kHz (Table 2). In the range of lower frequencies, phase shift of the control plants was larger and, conversely, in the range of higher frequencies, phase shift of control mosses was lower.

DISCUSSION AND CONCLUSIONS

Impedance and phase shift have been measured in a simple electric scheme arranged in series RC. Musil & Marha (1979) and Paszewski et al. (1984) proposed a simple electric model RC for vegetal tissue characterizing passive electric properties of plants. Zawadzky (1979) has revealed that the stem of Lupinus angustifolius L., when electrically stimulated, behaves as the electric circuit RC.

Paszewski (1984) has shown that the electric model elaborated by him for the thallus of Marchantia polymorpha corresponds to the general electric model for plants in the range 15-300 Hz, elaborated also by him. Over this frequency, the electric model quoted above is difficult to evaluate because of the low impedance value and phase shift. At frequencies below 25 Hz, however, there are strong dependencies in intercellular connections, as the object under investigation was multicellular, and according to Akimov(1975) and Pliquet (1969), dispersion of resistance and capacity of cellular membranes influence considerably the electric properties mentioned above.

Samecka (1984), investigating the influence of ethylene glycol on Fontinalis antipyretica plants at the dose 6250 mg/dm^3, did not report any dead plants. However, microscopic observations have revealed plasmolysis of cells, and chloroplasts turning brown, as well as their diminishing and changing their shape. Additionally, change in the rate of moss growth has also been reported.

Quantitative changes of phase shift and impedance and the changes in frequency characterization of these parameters under the influence of ethylene glycol testify to chemical changes indicated macroscopically (changes in the rate of growth) and microscopically (plasmolysis, decrease and deformation of chloroplasts) and, consequently, also the electric changes of the intracellular and extracellular environment are, speaking more precisely, the changes in resistance of integuments and cell walls, intracellular and extracellular

liquids, changes in the capacity of integuments and cellular walls as a result of the changes in their dielectric constant and their measures due to plasmolysis.

Investigations on impedance and phase shift according to the methodology given in this paper create the possibility of using the electric properties for comparative investigations. Crucial differentiation of these electric properties of plants cultivated on nutrient media contaminated with ethylene glycol or with other organic substances helps us to evaluate quantitatively the physiological state of the plants. It seems that the data given above speak in favour of using the described investigation as a method for bioindicating contamination of plants.

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THE EFFECTS OF NON-IONIZING RADIATION ON THE AQUATIC LIVERWORT RICCIOCARPUS NATANS (L.) CORDA

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Determination was made on the sensitivity of the liverwort Ricciocarpus natans (L.) Corda in experimental conditions to nonionizing radiation, in various intensities of electrostatic field and broad-band noise-like electromegnatic field. An electromagnetic field was obtained by a noise generator producing a flat-band frequency spectrum ranging from 1 Hz to 30 MHz. The shape of frequency characteristic of the generator resembled that of the atmosphere. An electrostatic field was obtained from a d. c. feeder, its negative pole being grounded in conformity with the polarity of the natural electrostatic field of the Earth. The electromagnetic field and electrostatic field in various intensities has significant influence on the quantity, biomass and mortality of Ricciocarpus natans populations. Reported symptomatic developmental reactions of plants (developmental anomaly of the thallus) to the non-ionizing radiation, are different for the electrostatic field and for the electromagnetic field, and are dependent on intensity. Thus, symptomatic reactions may be used in the bioindication of non-ionizing radiation.

INTRODUCTION

This paper aims at determining the sensitivity revealed by a selected population of the liverwort Ricciocarpus natans to the radiation of an electrostatic field as well as to a broad-band noise-like electromagnetic field of a continuous

spectrum from acoustic to short radio waves. Electric field parameters in the experiment were chosen in order to simulate the parameters of fields occurring in the natural environment according to Rotkiewicz (1978). Others have shown the influence of electrostatic fields on plants (Mùrr 1963, 1966) and electromagnetic fields of industrial frequencies: 50 Hz (Nosol 1984), 60 Hz (Miller et al. 1980, 1983, Robertson et al. 1981) and 75 Hz (Miller et al. 1979). The influence of the broad-band noise-like electromagnetic field of a continuous spectrum on biological systems is not known, and this factor is a constant element of our environment.

The choice of a liverwort for investigations was prescribed due to its simple construction that was presumed to influence great sensitivity of the plant to non-ionizing radiation.

METHODS

The plants from a natural population of Ricciocarpus natans were cultivated in vitro on Hoagland's nutrient medium with the addition of microelements from the Gorham set (Landolt 1957). The experiment was carried out in constant lighting and temperature conditions in the glass-house of the Botanic Garden, Wrocław.

a) Plants under the influence of an electromagnetic field were placed in an electromagnetic field of differentiated intensity: 28.1, 34.5, 42.4, 63.3, 95 and 380 V/m. As a source of radiation a noise generator producing a flat-band frequency spectrum was used. Frequency characterization of the amplifier was created to approximate the frequency spectrum of atmospheric discharge in the range of radio frequencies. Frequency spectrum of the output voltage of the generator comprised the frequency range from 1 Hz to 30 MHz. The resulting voltage of noise was 9 V.

The plants under investigation were placed in condenser's electromagnetic field. An antenna fixed above the plant cultures constituted one plate of the condenser, a grounded metal plate was the other. On this plate were located the cultures examined.

b) The plants under the influence of an electrostatic field were placed in an electrostatic field of various intensity: 3.2, 3.8, 4.6, 6.6, 10.3 and 46.5 kV/m. A generator of constant voltage (900 V) was the source of radiation. An antenna that hung above the plants was connected with the positive pole of the generator, the metal plate on which the plants were located - with its negative pole.

The intensity of fields (E), both electrostatic and electromagnetic, at the measurements and calculations, was designated according to the relationship U/d, where d expresses the distance from the antenna to the water surface, and U is the output voltage of the generator. The experiment continued for 21 days. The plants examined were influenced by proper fields for all the time of the experiment, the field intensity did not change during this time. After 21 days from the start of the experiment, the number of plants and the biomass were determined. In addition, developmental disturbances were also investigated.

RESULTS

The sensitivity of plants to non-ionizing radiation in the present study was designated on the basis of the biological effect of the radiation, finding its manifestation in the numbers of plants, their biomass and developmental anomalies compared to the control populations in a definite time (21 days).

Sensitivity of Ricciocarpus natans to the activity of broad-band noise-like electromagnetic field

On the basis of measurements, an electromagnetic field of differentiated intensity was found to have crucial influence on the number of plants and their biomass (Table 1). Increase in the intensity of the electromagnetic field from 28.1 V/m stimulated the number of growing segments by 22.5%, and the growth of biomass by 8%. Increase in field intensity to 34.5 V/m caused increase of plant number by 50% and biomass by 22.8%.

Table 1. Changes in the number of segments and biomass in a Ricciocarpus natans population under the influence of an electromagnetic field.

Dose (field intensity in V/m)	Biomass (g)	Number of segments	Mortality
control	0.0311	40	0
28.15	0.0336	49	3
34.55	0.0382	60	4
42.2	0.0426	72	6.7
63.33	0.0367	61	8.3
95	0.0343	48	10.3
380	0.0211	34	12.3
F est.	3.39	74.95	72.46
F tab.	2.85	2.85	2.85
LSD	0.0208	5.058	1.476

At the intensity of the electromagnetic field of 42.2 V/m, the number of plants increased by 80%, and the biomass by 36.9% in relation to the control. Further increase of field intensity to 95 V/m restricted the increase of plant number to only 20% and of biomass to 10%. At 380 V/m intensity, a clear limitation of the number of plants and biomass was observed. The number of plants at 380 V/m decreased by 15%, and the biomass by 32%. 42.2 V/m was the optimum intensity of the broad-band noise-like field for the increase in the number of plants and their biomass.

Mortality of plants increased regularly with the growth of field intensity. In the range of electromagnetic field intensity from 28.1 to 380 V/m, the mortality of plants increased from 5.9% at the lowest field intensity value to 26.6 at the highest value of electromagnetic field intensity.

Starting from the intensity 34.5 V/m, developmental anomalies in the plant deformations were observed in the experimental cultures, getting more intense as field intensity increased.

Table 2. Changes in the number of segments and biomass in a Ricciocarpus natans population under the influence of an electrostatic field.

Dose (field intensity in kV/m)	Biomass (g)	Number of segments	Mortality
control	0.0291	34	1
3.2	0.0303	40	2.3
3.8	0.0318	43	3
4.6	0.0481	51	7
6.6	0.0316	38	8.7
10.3	0.0257	33	10
46.5	0.0157	24	11.7
F est.	4.88	10.23	72.28
F tab.	2.85	2.85	2.85
LSD	0.0133	8.249	1.525

At 42.2 V/m intensity, the surface of the majority of plants was slightly wrinkled. Increase in field intensity causes plicating of all plant surfaces. At 380 V/m intensity, a strong diminishing of all plant surfaces and deformation of their shape was also observed.

Sensitivity of Ricciocarpus natans to the influence of an electrostatic field

On the basis of the experiment, an electrostatic field of differentiated intensity was found to have a crucial influence on the number of plants and their biomass (Table 2). At the increase in electrostatic field intensity to 3.2 kV/m, increase in the number of plants by 17.6% was found, and in biomass by 4.1%. Further increase in field intensity to 3.8 kV/m caused increase in plant number by 26.5%, and biomass by 9.3%. At electrostatic field intensity equal to 4.6 kV/m, the number of plants was noted to increase by 50% and biomass by 65% in

relation to the control. At the intensity of 6.6 kV/m, increase in plant number resulted only in 11.8%, and biomass in 8.6%. Further increase in field intensity to 10.3 kV/m restricted the increase of the number of plants by 3%, and the biomass by 11.7%. At 46.5 kV/m intensity, the number of plants decreased by 30% and biomass by 46% in relation to the control. 4.6 kV/m was the optimum intensity of electrostatic field for increase in numbers and biomass of the mosses investigated.

Starting from the intensity 6.6 kV/m in experimental cultures, induction was observed of developmental anomalies comprising a greater number of plants with increasing electrostatic field intensity. At 6.6 kV/m, point chloroses of individual plants were observed, and, in addition, the thalli became more etiolated at higher intensities. At 10.3 kV/m, several plants were found to have boundary crevices of the thalli. At the highest field intensity, despite strong decrease in the surface of thalli and general chlorosis, the crevices mentioned above occurred in the majority of plants.

In the range of electrostatic field intensity from 3.2 to 46.5 kV/m, mortality of plants increased from 2.8 to 32.8%.

DISCUSSION

The capacity of a tissue to pass an electric current is determined by the structure of that structure (Deno 1975, Ivanova & Goncarik 1979, Kouwehoven 1974). Thus, a change in that tissue will result in a change in the passage of current. Such a change is thereby indicative of the damage of the tissue. Flow current, induced by external electric field, influenced the morphogenesis of plants through changes in the ion permeability and in the selectivity of cellular integuments (Miller et al. 1980, 1983, Robertson et al. 1981). In the present paper, applying an electromagnetic field of a continuous spectrum and the range of frequencies from 0 to 30 MHz and intensity from 28.1 to 380 V/m changes in the number of plants and their biomass were obtained, probably as an effect of changes in the permeability of cellular membranes.

Current density between the electrodes in an electrostatic field of several intensity values applied in the present experiment from 3.2 to 46.5 kV/m, is in the range $(1.5\text{-}5)10^{-13}$ A/cm^2. The values given are 500 times larger than current density at the natural electric field of the Earth, comprising the range of intensities from 100 V/m to 130 V/m. Current density in the atmosphere, induced by the natural electrostatic field, results in $(3\text{-}10)\ 10^{-16}$ A/cm^2 (Feynman 1977). At present, there is no technical possibility of direct current measurement of such a small value.

According to Murr's observations (1966), current values induced by the field intensities used in the experiment should act as a stimulant on the growth of plants. Damage of plants, according to the author, occurs at an electrostatic field intensity of 100 kV/m, at continuous exposure for 10 hours. In our study, increase of the number of plants and biomass took place to 4.6 kV/m intensity; above that value, not only a decrease of numbers and biomass, with a considerable increase of plant mortality was noted, but also induction of developmental anomalies.

Miller et al. (1983) says that 150 V/m intensity is a minimal value of an electromagnetic field intensity of 60 Hz frequency, at which favourable influence on Pisum sativum growth is observed. However, the roots of Vicia faba under the influence of an electromagnetic field of 75 Hz frequency and 10 V/m intensity for 6 days did not reveal differences in growth and in mitotic index in relation to the control. Miller et al. (1976) did not state chromosome anomalies.

In the present paper, incrase in the number of plants and biomass was noted, with the growing intensity of electromagnetic field to the value of 63.3 V/m. Further increase of field intensity limits increase of biomass and number of plants and, simultaneously, causes considerable increase of mortality and induction of developmental anomalies.

Developmental anomalies of Ricciocarpus natans induced by an electromagnetic field, observed as wrinkles and plications of the surface, and changes induced by an electrostatic field

in the boundary crevices of thalli may be considered peculiar reactions of the plants that are symptomatic for the electric fields defined in the experiment.

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THE EFFECT OF HEAVY METALS ON THE DYNAMICS OF A RICCIOCARPUS NATANS (L.) CORDA POPULATION

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Experiments were conducted on the effects of heavy metals (V, Ni, Cr, Co) on the dynamics of a Ricciocarpus natans population. The tolerance of Ricciocarpus natans to these heavy metals has been determined (LD 50, LD 100). The relationship between plant number of the population and biomass and the levels of metals in the environment was reported.

The symptomatic reactions of Ricciocarpus natans depending on heavy metal levels were investigated. The characteristic reactions of Ricciocarpus natans can be utilized for the bioindication of water pollution by these metals.

INTRODUCTION

The liverwort Ricciocarpus natans is less and less frequent in its natural stands. This species occurs over a wide range of ecological conditions and can be found in various habitats. Thus, it may be expected that Ricciocarpus natans in both its land and aquatic form, ecotypes or ecophenes. An urgent need arises to determine its sensitivity to various kinds of human activity, chemical pollution of water being of primary importance. Sensitivity of Ricciocarpus natans has not been determined yet. The effect of different heavy metals on the dynamics of population size and its biomass has been considered. In the experiment there were applied metals characterized by a very high degree of potential menacing (chromium) as well as harmful ones (vanadium, nickel and cobalt, Kabata Pendias & Pen-

dias 1979). All those metals as micronutrients are essential for the growth of plants. In high concentrations, however, they are highly toxic. Nowadays, environmental pollution with heavy metals constantly increases, also in Poland (Stasiak & Stasiak 1983).

METHODS

The plants of Ricciocarpus natans used for the investigations were collected in the peat bog in Grabowno Wielkie, Lower Silesia. Ricciocarpus natans was cultivated in 400 cm^3 beakers on Knop medium enriched with 1 cm^3 of Gorham microelements per 1 dm^3 of medium. The basic medium contained some heavy metals (in the form of salts, i.e., $CoSO_4 \times 7H_2O$, K_2CrO_4, $NiSO_4 \times 7H_2O$ and NH_4VO_3) in the following doses: 0.1, 1, 5, 10, 20 and 30 mg/dm^3 of medium. Moreover, the medium was enriched by adding 50 mg Ca/dm^3 in the form of $Ca(NO_3)_2$, the critical dose of metals being 20 mg/dm^3. Each experiment was carried out in 3 replications, i.e., in 3 beakers each containing 5 plants. The experiment, conducted under constant light and temperature conditions (5000 lux, 24 ^oC) continued for 14 days. After that time the lethal dose of heavy metals, number of plants and biomass of R. natans population were determined. During the experiment, the development of plants was observed and their size after 3, 7 and 14 days was determined. The results were subjected to a statistical analysis.

RESULTS AND DISCUSSION

Survival of R. natans at different concentrations of cobalt, chromium, nickel and vanadium in in vitro cultures after 14 days are presented in Table 1.

Chromium was found to be the most toxic metal for R. natans, whereas vanadium and cobalt were less harmful. The changes in the number of plants of R. natans populations at various concentrations of heavy metals are presented in Table 2. Analysis of variance showed that at different concentrations of heavy metals the populations are significantly different in size.

Table 1. Mortality of Ricciocarpus natans.

Metal	Lethal dose (LD), mg/dm^3	
	LD 50	LD 100
Co	10	30
Cr	5	10
Ni	10	20
V	20	30

The concentration of 0.1 mg Co/dm^3 results in a negligible increase of population size compared with the control. At concentrations higher than 1 mg Co/dm^3, the size of the population gradually diminishes. The concentration of 30 mg/dm^3 causes the total mortality of R. natans plants. By analogy, if the dose of cobalt incrases, biomass production of this species will decrease (Table 3). Addition of calcium to the medium containing 20 mg Co/dm^3 allows the survival of 13% of the plants. Cobalt, especially in concentrations higher than 1 mg/dm^3, causes a considerable miniaturization of plants. Simultaneously, marginal necroses of thalli are observed. According to Kabata Pendias & Pendias (1979), plants can tolerate high concentrations of cobalt in polluted waters. Its concentrations amount to 1 - 70 ppm. Under experimental conditions, R. natans survives the cobalt concentrations in the range of 0.1 - 20 ppm.

Low concentration of chromium (o.1 mg/dm^3) in the medium has no effect on population size, the plants, however, are somewhat larger, which is also confirmed by the increment of plant biomass (Tables 2 and 3). Concentrations of chromium higher than 1 mg/dm^3 cause a sudden decrease of population size and biomass. The dose of 5 mg/dm^3 is considered to be lethal (LD 50). At this dose the number of plants decreases by 60%. The total mortality of plants occurs at the dose of 10 mg/dm^3 of chromium. A the same time, some specific responses of R. natans to toxic action of chromium are observed, i.e., strong dichotomy of thallus, necroses, point chloroses, conglomera-

Table 2. The effect of heavy metals on the number of plants of Ricciocarpus natans (after 14 days of culture)

Metal	Dose (mg/dm^3)								$\bar{x}$	LSD	Snedecor's F test	
	0	0.1	1	5	10	20	30	20+Ca			$F_{emp.}$	$F_{tab.}$
Co	15	16	14	10.6	6	4	0	2	8.57	1.09	285.1	2.66
Cr	15	15	10	6	0	0	0	0	5.75	0.86	551.1	2.66
Ni	15	15	13	10.3	5	0	0	2	7.54	0.65	921.1	2.66
V	15	16	14.6	11	10	8	2	5	10.19	1.08	209.8	2.66
$\bar{x}$	15	15.5	12.9	9.5	5.2	3.0	0.5	2.25				

Variabilities		Snedecor's F-test		
		LSD	$F_{emp.}$	$F_{tab.}$
	metal	0.319	272.74	2.76
	dose	0.45	1439.5	2.17
Interactions	metal x dose	0.9	23.64	1.74

LSD = least significant difference

Table 3. The effect of heavy metals on the biomass of Ricciocarpus natans (after 14 days of culture)

Metal	Dose (mg/dm^3)								$\bar{x}$	LSD	Snedecor's F-test	
	0	0.1	1	5	10	20	30	20+Ca			$F_{emp.}$	$F_{tab.}$
Co	86	88	82	64	56	28	0	24	53.5	3.515	785.2	2.66
Cr	86	90	70	37	0	0	0	0	35.4	1.368	4859.8	2.66
Ni	86	88	80	64	40	0	0	20	42.2	1.935	335.1	2.66
V	86	84	78	63	52	44	10	32	56.1	1.224	4309.7	2.66
$\bar{x}$	86	87.5	77.5	57	37	18	2.5	19				

Variabilities		Snedecor's F-test		
		LSD	$F_{emp.}$	$F_{tab.}$
	metal	0.62	1783.9	2.76
	dose	0.87	1188.3	2.17
Interactions	metal x dose	1.74	325.3	1.74

LSD = least significant difference

tion of thallus, and shortening of rhizoids. Plants can tolerate chromium dissolved in concentrations varying from 0.06 to 50 ppm (Kabata Pendias & Pendias 1979). R. natans is not so resistant to toxic action of chromium as Lemna minor (Sarosiek & Wożakowska Natkaniec 1980).

Low concentrations of nickel in the medium (0.1 mg/dm^3) affect neither the decrease of population size nor the reduction of population biomass. At the concentration of 1 mg Ni per dm^3, the size as well as biomass of the population slightly decrease. The dose of 5 mg Ni/dm^3 of medium decreases the size and biomass of the R. natans population by cca 30%, and the dose of 10 mg NI/dm^3, by 67% compared to the control. Total plant mortality occurs when the medium contains 20 mg Ni/dm^3. Addition of Ca to this medium allows the survival of 13% of the plants. Nickel doses higher than 10 mg/dm^3 cause considerable miniaturization and deformation, as well as necroses of the plants.

Low vanadium concentration (0.1 mg/dm^3) stimulates a slight increase in the size of R. natans. The dose as high as 10 mg V/dm^3 reduces the population size by cca 33% if compared with the control. Concentration of 20 mg V/dm^3 causes 50% mortality of the plants, whereas a 30 mg concentration of V corresponds to LD 100. Although R. natans is able to survive at the concentration of 20 mg V/dm^3, this metal is harmful for plants because of its inhibiting effect on growth. Plants under such circumstances are characterized by low biomass, relatively large population size (Tables 1 and 2), decrease of terminal dichotomy, inclination to thallus conglomeration, as well as point necroses. At the concentration of 20 mg V/dm^3, the thallus produces anomalous progeny thalli. Shortening of rhizoids is also observed.

The changes in population size of R. natans during 14 days of the experiment are different in the case of Cr and V, Co and Ni. Those changes and the changes in biomass are highly dependent of the sensitivity of R. natans to the metals applied.

CONCLUSIONS

The responses of R. natans to the presence of heavy metals (cobalt, chromium, nickel and vanadium) are specific and differ with metals. Therefore, this plant can be used in the bioindication of chemical water pollution both at the individual and the population levels.

The sensitivity of R. natans to toxic metal activities may be considered as one of the factors which cause this species to disappear from Poland.

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REGRESSIVE SUCCESSION INDUCED BY ACID RAIN IN CRYPTOGAMIC COMMUNITIES INHABITING JUGLANS BARK

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Significant correlations between the pH of bark and SO_2, between the pH of rain and SO_2, as well as between bark pH and rain pH reflect direct and indirect effects of pollutants on epiphytic plants and the substratum. The thalli are directly exposed to the harmful effects of sulphurous acid. Pollutants are absorbed by the bark and thus have an indirect effect on plants through the acidification of the substratum. The acidification of melting snow also has an impact on epiphytes. The most serious damages on lichen thalli and on bryophytes are observed after the melting of snow, at the end of January or in February.

The regressive succession of lichen communities was expressed by the degeneration and extinction of foliose thalli and the gradual decrease of the generative and vegetative reproductive potential of populations. In case of bryophytes, except Hypnum cupressiforme, only the colonists were able to survive pollution stress.

INTRODUCTION

Complaints about smoke and sulphurous fumes have been recorded since the 13th century. "In 1306, Londoners were forbidden to burn sea-coal because of the type of smoke it produced" (Elsworth 1984). The term "acid rain" was introduced by R. A. Smith in 1872 in his publication entitled "Air and Rain; Beginnings of a Chemical Climatology". Besides this important

report, many interesting observations have been made on dying or declining sensitive lichen species (Grindon 1859, Nylander 1866, Britzelmayer 1875, Arnold 1891-1901, etc.), indicating the increase of pollutants in the atmosphere. Arnold has also referred to the direction of the process, which was the first step towards the recognition of the so-called regressive succession.

The development of actual successional studies in lichenology was inspired by the results of terrestrial plant ecology (e.g., Clements 1916, Gleason 1917, etc.) and some brilliant studies reflecting dispersal processes (e.g., Du Rietz 1924) in connection with air pollution. The first report on regressive succession in lichenology was reported on by Schultz (1931). He detected that in the vicinity of towns and factories the increase of air pollution causes a gradual replacement of the Physcietum ascendentis and other lichen communities by the Pleurococcetum association. Barkman (1958) analysed the different types of epiphytic lichen succession, including the regressive one, and attracted the attention to "partial serule". Felföldy (1941) observed that in extreme cases the pioneer stage becomes permanent on the trees. In consequence of air pollution, only the crustose thalli of Lecanora carpinea occurred on the trees.

These earlier studies on lichen succession served many new viewpoints concerning the relations between the dynamic processes and air pollution levels although, later, this topic remained largely neglected in lichenology (cf. Kiss 1982, 1983). There is also little attention to the effect of acid precipitation or deposition on the epiphytic lichens and bryophytes (Dollard et al. 1983 with lichenological comments in British Lichen Society Bull. No. 52. 1983, Rose 1985). It is particularly interesting to show what is usually considered as a "protecting factor" against freeze. Cohen & Ruston (1925) pointed out the harmful effects of melting snow in polluted areas. Investigating the chemical composition of snow, collected in polluted areas around Leeds, they found ammonium sulphate and chloride, calcium sulphate and free sulphuric acid in the solution. The snow collected four days after snow-

fall was "quite opaque", nearly black after melting, because of the intensive soot fall.

It is also well-known that the physico-chemical factors of the substratum play an important role in the establishment, growth and survival of lichens and bryophytes, especially in polluted areas. The dry or wet deposition of pollutants modify the buffer capacity and the H^+ concentration of the substrata and plants (Gilbert 1968, 1970, Türk & Wirth 1975). Therefore, the effects of acid rain and snow need more consideration.

METHODS

This study examines regressive succession in cryptogamic epiphytic communities on 26 Juglans regia trees in a polluted area in the town of Szombathely, western Hungary, between 1979 and 1984.

The investigations aimed at the synergistic effect of acid precipitation, SO_2 and NO_2 on the communities. The studies were carried out in permanent quadrats, 400 cm^2 each, on the northern and southern faces of the trees. To the tracing of lichen thalli, sheets of cellophane were pinned up with steel needles to the surface of the bark (Rydzak 1961). Cover change and the perimeter of populations were measured annually and evaluated by computer. The fruiting zone of populations was also measured.

The life strategy of lichens was investigated on the basis of the life strategy system developed by the author (Kiss 1985). In this system, two well-observable phenetic attributes were used for the interpretation of the response of populations to stress by air pollution.

The degeneration of bryophytes was also observed. The life-strategy system of brophytes used here follows During (1979) and Orbán (1984). The T, W, R values (Zólyomi & Précsényi 1964) of species were also considered. The SO_2 and NO_2 measurements are derived from surveys performed by the "Health Service" of Szombathely.

Rain was collected into plastic containers and immediately was transported to the laboratory. Snow was collected from bark surfaces into plastic containers. In the laboratory, snow was melted at 10-15 ^{o}C. pH measurements were carried out using a Radelkis 205 Precision pH Meter with combined glass electrodes.

For interpreting the relationship between measured variables the correlation coefficient, r, was used.

RESULTS

Table 1 shows that the values of SO_2 and NO_2 increased steadily during the past six years. In 1979, the mean SO_2 value was 50 $\mu g/m^3$; which became nearly twice as much after five years (88 $\mu g/m^3$).

The pH values of the rain (Table 2) show a marked decreasing tendency (from 5.02 to 3.26) and at the same time the values of standard deviation (s) changes irregularly. On the contrary, the s values of the bark pH show a monotone increase (Table 3a).

Figure 1.a shows significant correlations ($p = 0.05$) between bark pH and SO_2: $r=-0.969$, rain pH and SO_2: $r=-0.985$, and between bark pH and rain pH as well: $r=0.955$.

The bark pH of southern faces (Table 3b) shows a different picture. The increase in pH is due to the intensive constructing activity. The dust enrichment of the bark is caused by deposition of road-dust, gravel, etc. Mortar, which is also present, has a pH of 9.0, which is harmful to lichens (see Türk & Wirth 1975).

Fig. 1b also shows a significant negative correlation between sulphur dioxide and rain pH values. However, in this case the most important stress factors derive from building operations resulting in colony as well as community degradation. The most tolerant species of these surfaces are: Bryum argenteum, Candelariella vitellina and Lecanora carpinea. It seems that an increase in either acidity or alkalinity can be harmful to lichens and bryophytes. Pleurozium schreberi became extinct from the southern faces in 1980.

Table 1. Annual mean values of SO_2 and NO_2 in Szombathely

Year	SO_2 ($\mu g/m^3$)	NO_2 ($\mu g/m^3$)
1979	50	28
1980	60	25.5
1981	75	26.2
1982	80	25
1983	85	27
1984	88	30

Table 2. The pH of rain in Szombathely. $\bar{x}$ = means, s = standard deviation.

	Months												$\bar{x}$	s
	1	2	3	4	5	6	7	8	9	10	11	12		
1979	4.1	4.4	4.7	5.2	5.7	6.2	6.4	5.4	5.3	5.4	3.8	3.7	5.02	0.890
1980	2.9	3.4	4.1	4.6	5.0	5.4	5.1	4.9	5.2	5.1	3.5	3.0	4.35	0.921
1981	2.4	3.0	3.5	4.0	4.5	4.0	4.8	5.0	5.1	4.1	3.0	2.4	3.81	0.957
1982	2.5	3.1	3.0	3.1	4.0	3.9	4.5	4.7	5.0	4.0	2.9	2.6	3.60	0.850
1983	2.6	2.9	2.9	3.5	4.1	3.8	4.4	4.5	5.1	3.7	2.8	2.7	3.58	0.822
1984	2.4	2.5	2.7	3.1	3.7	3.8	4.6	4.8	4.0	3.1	2.4	2.1	3.26	0.902

In winter, snow is also a very important factor. Table 4 shows significant differences between snow pH values within a 5-day period. The pH values of the fresh and melted snow, after 5 days, occupy two different regions (Fig. 2). The lowest snow pH ever measured in this area was 4.5 in January, 1984. Table 5 shows that the differences between the fresh and 5-day old pH values are ever increasing between 1979 and 1984. It means that the acidification of the snow became more and more serious.

Table 3. The pH of bark on Juglans regia trees in Szombathely. a) Northern faces, b) southern faces. $\bar{x}$ = means, s = standard deviations.

	Year	$\bar{x}$	s
a)	1979	5.82	0.045
	1980	5.68	0.102
	1981	5.49	0.163
	1982	5.34	0.241
	1983	5.25	0.223
	1984	5.05	0.430
b)	1979	5.10	1.070
	1980	5.73	2.402
	1981	5.93	2.675
	1982	5.91	2.975
	1983	6.30	2.788
	1984	6.51	3.348

Table 4. Changes of the mean pH of snow within a 5-day period in Szombathely in 1979-1984. f=fresh snow, 5=5 days after snowfall, J=January, F=February, N=November, D=December, d=difference.

Year	J-f	J-5	d	F-f	F-5	d	N-f	N-5	d	D-f	D-5	d
1979	6.75	6.34	-0.41	6.83	6.68	-0.15	-	-	-	6.82	6.59	-0.23
1980	6.84	6.54	-0.30	-	-	-	6.69	6.36	-0.33	6.53	6.14	-0.39
1981	6.67	6.25	-0.42	6.71	6.46	-0.25	6.50	6.26	-0.24	6.37	5.89	-0.48
1982	6.50	6.07	-0.43	6.58	6.19	-0.39	-	-	-	-	-	-
1983	-	-	-	6.48	6.02	-0.46	-	-	-	6.44	5.94	-0.50
1984	6.58	6.48	-0.10	6.67	5.30	-1.37	-	-	-	6.06	5.63	-0.43

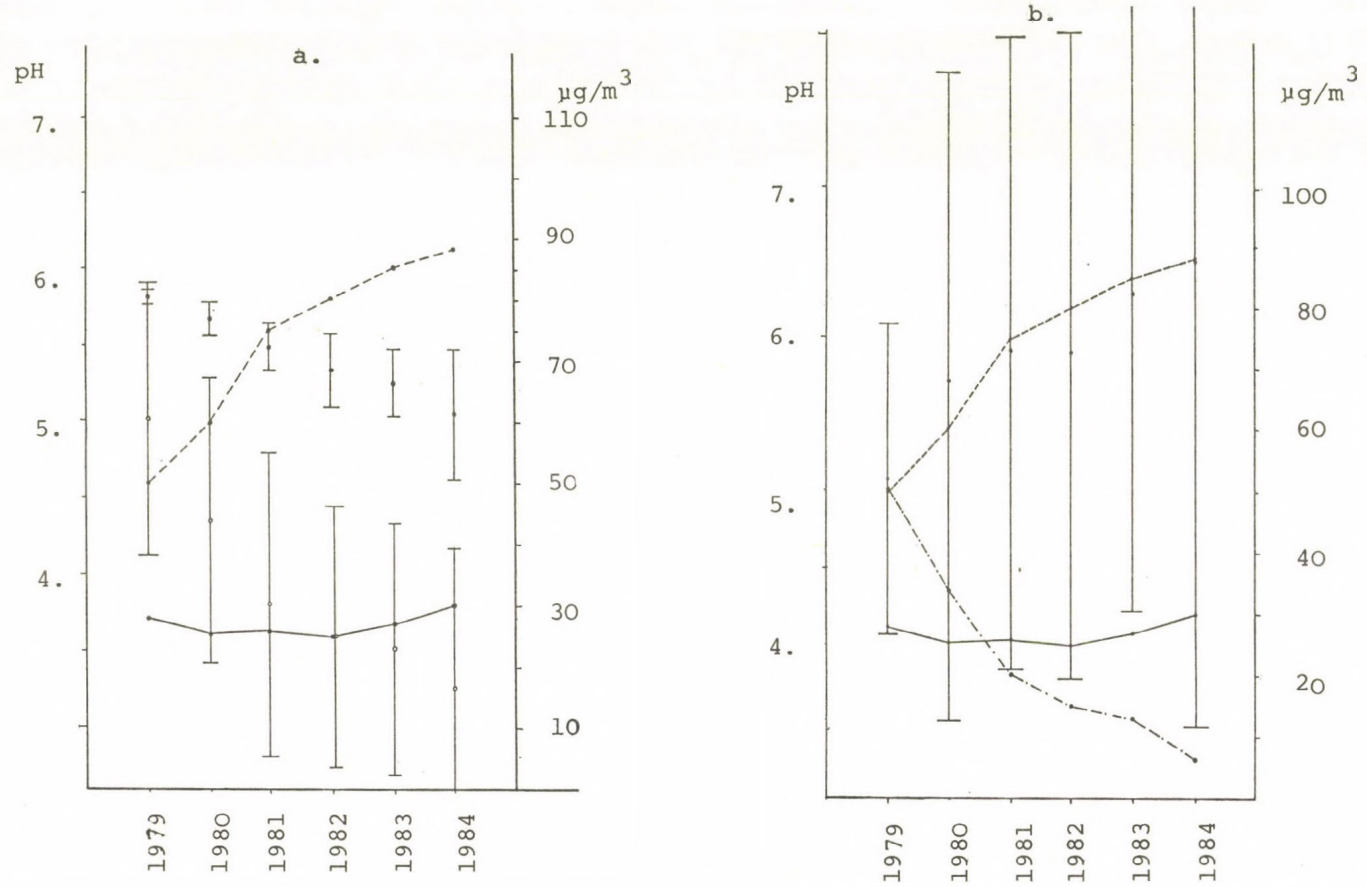


Fig. 1. Annual means of SO_2, NO_2, and the pH of bark and rain in a polluted zone of Szombathely. a) Northern faces, b) southern faces. ●: bark, ○: rain, ---: SO_2, ——— : NO_2

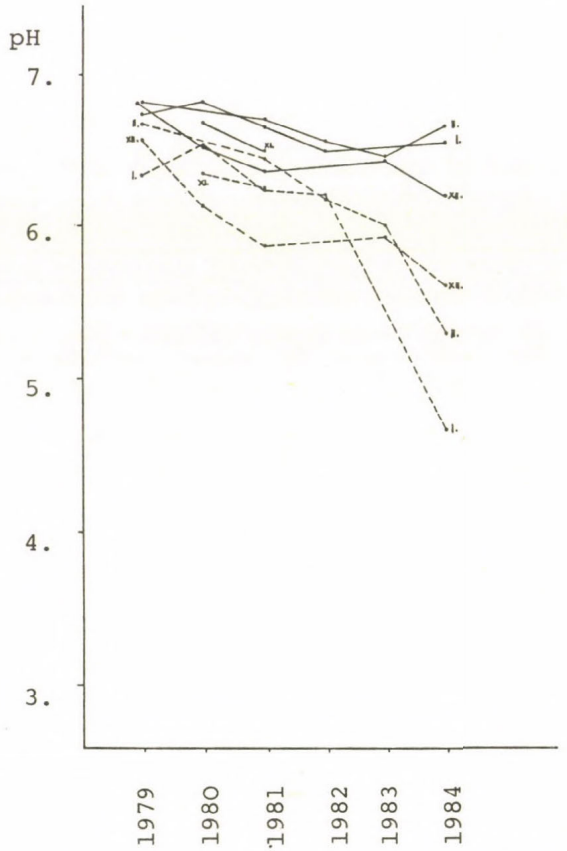


Fig. 2. Monthly means of the pH of snow between 1979 and 1984. ——: fresh, ---: 5-day

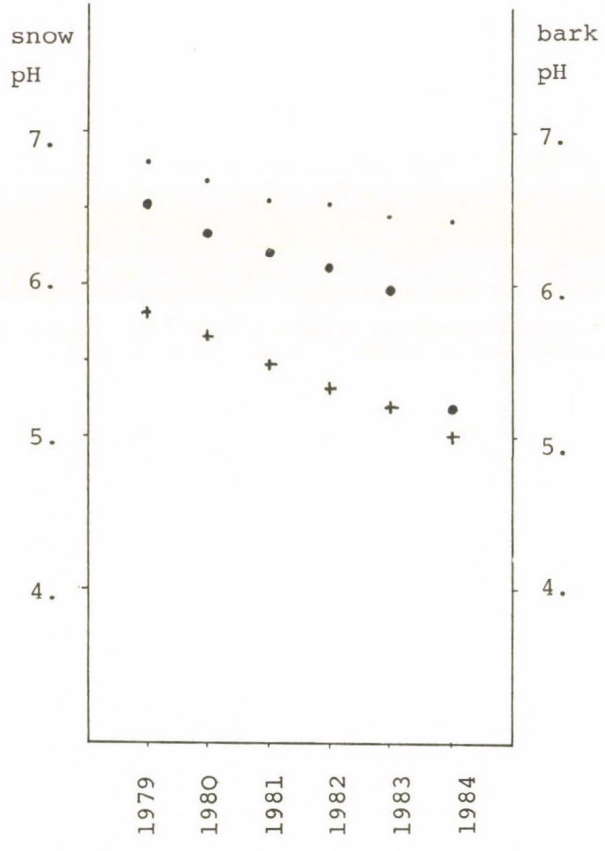


Fig. 3. Annual means of the pH of snow (•) and bark (+) between 1979 and 1984. ● : 5-day

Table 5. Differences between annual means of pH of snow in Szombathely.

Year	Fresh snow	5 days later	Diff.
1979	6.80	6.53	-.27
1980	6.68	6.34	-.34
1981	6.56	6.21	-.35
1982	6.54	6.13	-.41
1983	6.46	5.98	-.48
1984	6.43	5.2	-1.23

In addition to the pH values of snow, Figure 3 contains the pH of the bark. There is a close correlation ($p=0.05$) between the pH of fresh snow and bark ($r = 0.969$) and between the pH of 5-days old snow and bark ($r = 0.908$).

It is quite possible that, besides acid rain, the acidification of melting snow may cause harmful effects or stresses in the metabolism of lichen colonies and in bryophytes. Smith (1979) mentioned that "Rewetting of dry thalli is probably the period of greatest metabolic stress for a lichen." In these cases "respiration rates rise very rapidly to levels well above undried controls; so there is a period of net carbon loss." Pollutants are regularly absorbed on the bark and on the surfaces of bryophytes and lichens. Therefore, epiphytes are in a very intimate contact with the substrate and the atmosphere. As Rao (1982) notes: "...air pollutants, either in a gaseous state mixed with air or in a liquid state affected by dew, rain or snow, will be noxious to bryophytes attached to the bark."

Sulphur dioxide within the plant acts as sulphurous acid, so the higher the level of moisture in the tissues the more serious the degeneration.

Significant changes were observed in the lichen and the bryophyte flora and in the life strategies during the 6-year period.

During the study, seven lichen species became extinct, most of them by 1982 or 1983. Only 8 species were able to survive (see Table 6).

The most tolerant populations were the crustose ones spreading with spores and the small foliose types propagating with soredia. Spreading with thallus fragments became even more important because of the degeneration of dispersing propagules such as isidia and soredia.

The small, compact and convoluted thalli of Hypogymnia physodes were not able to develop soredia and the thalli of Physcia aipolia were also unable to produce apothecia.

Fig. 4 shows the degradation of a lichen community, together with the degeneration fo the colonies. The change of species pattern informs us about the degeneration process. It is a regressive succession during which the large and small foliose thalli disappear and the crustose type becomes dominant by the end of the process. In 1984, the most tolerant lichen species such as Lecanora conizaeoides and Lepraria incana colonized the trees.

Table 7 contains information on the performance of populations. In case of small foliose taxa, the reproductive and the whole area of populations were considered with equal weight.

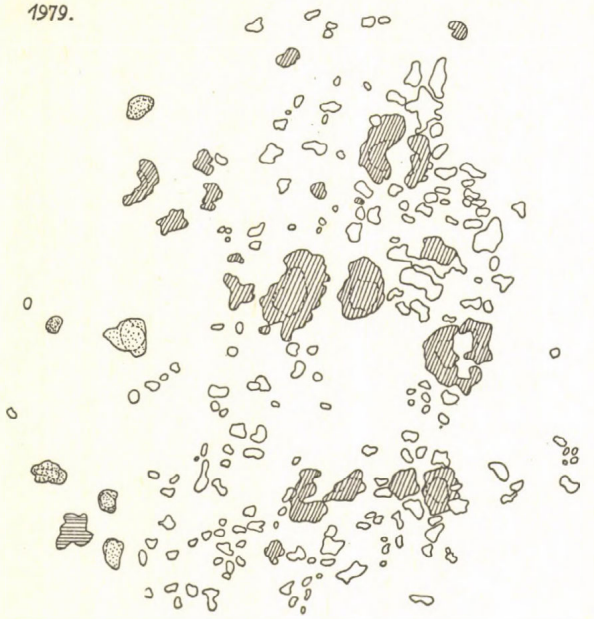
The results show that degeneration, in case of crustose colonies spreading with spores, was concentrated first of all in the reproductive area. Crustose colonies are in a very intimate contact with the substratum. The less protected area is the reproductive one because the apothecia stand out of the thalli. The A/A_{rz} values also reflect this fact. If the degeneration of the vegetative zone of thalli is less serious than that of the reproductive zone, the value of this ratio shows an increasing trend (e.g., Lecanora carpinea in Fig. 4a). The values of C reflect the physical condition of the thalli. The degeneration in a polluted environment is not a one-way process, namely: from inside to outside. As it is well-observed, in Fig. 4 the large or small foliose thalli of Hypogymnia physodes and Xanthoria parietina are fairly indented. During the

Table 6. Changes in the lichen flora and in lichen life strategies in a polluted region of Szombathely on 50-year old Juglans regia trunks between 1979 and 1984

Species	1979		1984		1979		1984	
	N	S	N	S	N	S	N	S
Buellia punctata	+		+		Sp_{EpCr}		Sp_{EpCr}	
Candelaria concolor		+		-(1982)		So_{Sf}		
Candelariella vitellina	+	+	+	+	Sp_{EpCr}	Sp_{EpCr}	Tf_{EpCr}	Sp_{EpCr},Tf_{EpCr}
Hypogymnia physodes	+		-(1983)		Tf_{Sf}			
Lecanora carpinea	+	+	+	+	Sp_{EpCr}	Sp_{EpCr}	Sp_{EpCr},Tf_{EpCr}	Sp_{EpCr},Tf_{EpCr}
Lecidella elaeochroma	+	+	+	+	Sp_{EpCr}	Sp_{EpCr}	Sp_{EpCr},Tf_{EpCr}	Sp_{EpCr}
Parmelia exasperatula	+		-(1983)		Is_{Sf}			
P. sulcata	+	+	+	+	So_{Lf}	So_{Lf}	Tf_{Lf},Tf_{Sf},So_{Sf}	So_{Lf},So_{Sf},Tf_{S}
Phaeophyscia orbicularis		+		-(1982)		So_{Sf}		
Physcia adscendens	+	+	+	-(1983)	So_{Sf}	So_{Sf},Tf_{Sf}	So_{Sf},Tf_{Sf}	
P. aipolia		+		+		Tf_{Lf}		Tf_{Lf},Tf_{Sf}
P. tenella	+	+	-(1984)	-(1982)	So_{Sf}	So_{Sf},Tf_{Sf}		
Physconia grisea	+		+		Is_{Lf}		Is_{Lf},Is_{Sf}	
Xanthoria parietina	+	+	+	-(1981)	Sp_{Lf},Sp_{Sf},Tf_{Sf}	Tf_{Sf}	Tf_{Sf}	

Abbreviations: N = north facing, S = south facing, + = present, - = extinct
Morphology: Cr = crustose, Ep = epicortical, Lf = large foliose, Sf = small foliose
Propagation: Is = isidia, So = soredia, Sp = spores, Tf = thallus fragments

a.



b.

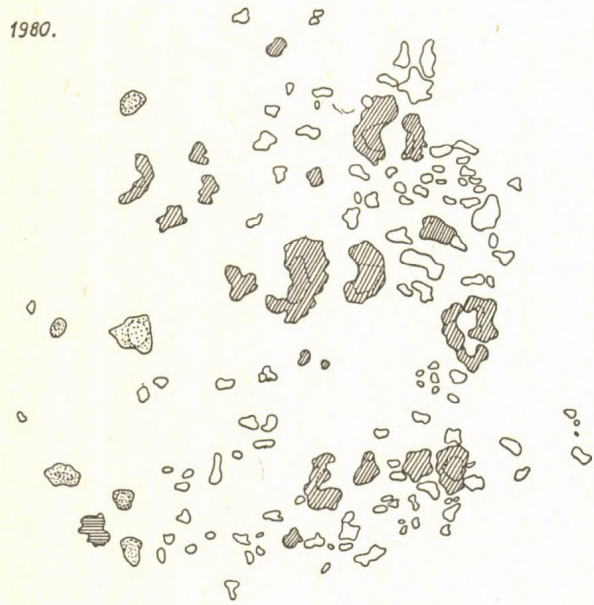
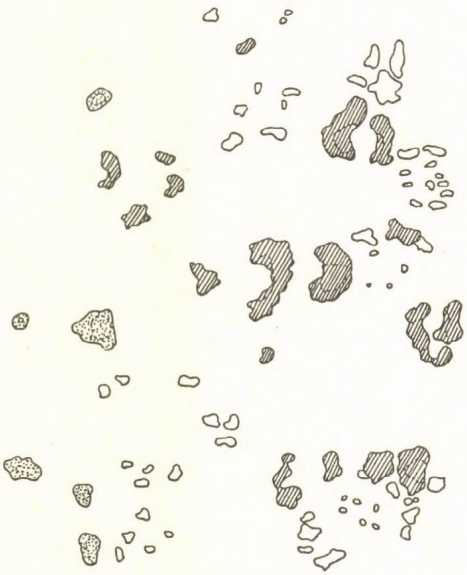


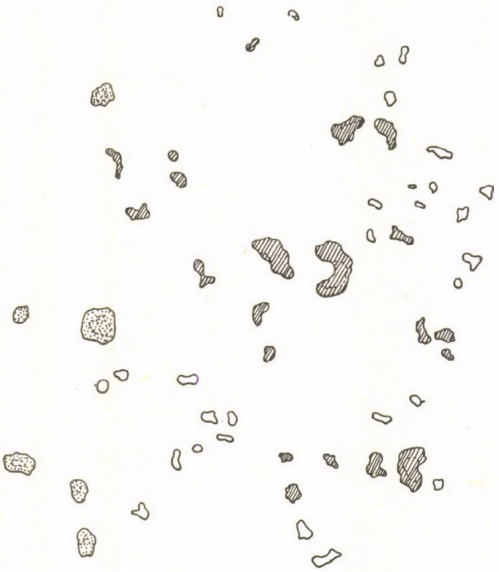
Fig. 4. The regressive succession of a lichen community between 1979 and 1983. Note the degeneration of thalli. (Physcietum ascendentis) in a polluted region of Szombathely

(Cont. on next page)

c. 1981.



d. 1982.



e. 1983.

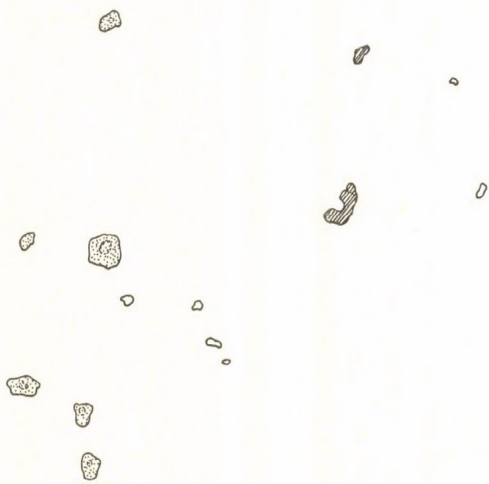


Table 7. The performance of populations and patterns.

Values Populations and patterns	A (cm^2)	A_{rz}	C (cm)	$\frac{A}{C}$
1. 1983				
Physcia adscendens	0.262	0.262	6.004	0.043
Xanthoria parietina	0.788	0.520	5.555	0.141
Lecanora carpinea	2.286	0.179	14.084	0.162
2. 1982.				
Physcia adscendens	20.421	20.421	91.517	0.223
Xanthoria parietina	7.448	3.078	36.089	0.206
Candelariella vitellina	0.341	0.341	5.388	0.063
3. 1983.				
Physconia grisea	41.534	-	88.341	0.470
Xanthoria parietina	1.322	-	6.706	0.197
Physcia adscendens	12.592	12.592	26.901	0.468
Buellia punctata	13.239	13.239	35.318	0.374
Physcia tenella	24-520	24.520	93.812	0.261
4. 1982.				
Physcia adscendens	9.135	9.135	55.625	0.164
Parmelia sulcata	11.246	-	45.496	0.247
Xanthoria parietina	16.245	6.019	55.183	0.294
Parmelia exasperatula	1.442	-	8.009	0.180
Hypogymnia physodes	0.697	-	6.342	0.109
5. 1984.				
Lecanora carpinea	9.124	1.566	30.819	0.296
Lecidella elaeochroma	0.710	0.185	5.754	0.123
6. 1983 - 1984.*				
Physcia adscendens	0.492	0.492	8.275	0.059
Parmelia sulcata	1.346	-	9.425	0.142
Xanthoria parietina	0.138	-	1.718	0.080
Lecanora carpinea	0.352	-	7.484	0.047
Lecidella elaeochroma	0.720	-	3.501	0.205
Buellia punctata	0.718	0.718	5.769	0.124
7. 1984.				
Lecanora carpinea	2.630	0.451	18.212	0.144
8. 1984.				
Buellia punctata	13.286	13.286	44.839	0.296
Candelariella vitellina	0.334	0.334	5.892	0.056
Lecanora carpinea	0.771	0.063	3.597	0.214

*No change between 1983 and 1984

R.D.R. = relative rate of decay. R.G.R. = rel. growth rate

$\frac{A}{A_{rz}}$	Decay of $A_{(cm^2)}$	Decay of A_{rz}	R.D.R. or R.G.R. A	R.D.R. or R.G.R. A_{rz}
1.0	-17.429	-17.429	-0.365	-0.365
1.515	-18.792	- 3.444	-0.278	-0.176
12.770	- 0.984	- 2.300	-0.211	-0.070
1.0	-26.892	-26.892	-0.091	-0.091
2.419	- 5.498	- 2.655	-0.06	-0.067
1.0	- 1.115	- 1.115	-0.157	-0.157
-	-72.606	-	-0.073	-
-	- 0.134	-	-0.010	-
1.0	+ 6.845	+ 6.845	+0.068	+0.068
1.0	-	-	-	-
1.0	-	-	-	-
1.0	-47.353	-47.353	-0.197	-0.197
-	-23.400	- 2.048	-0.122	-
2.699	-14.533	- 3.196	-0.069	-0.046
1.552	-11.272	- 2.471	-0.236	-
-	- 3.413	-	-0.114	-
5.826	- 1.669	- 7.092	-0.012	-0.197
3.837	- 0.724	- 0.129	-0.001	-0.205
1.0	-19.742	-19.742	-0.269	-0.269
-	-18.492	- 2.3	-0.194	-
-	-	-	-	-
8.186	- 0.041	- 0.350	-0.295	-0.295
-	- 0.412	- 0.786	-0.014	-
1.0	-	-	-	-
5.831	- 0.837	- 1.374	-0.101	
1.0	- 1.591	- 1.591	-8.166	-8.166
1.0	- 3.127	- 3.127	-0.169	-0.169
12.238	- 0.353	- 1.061	-0.208	-0.208

six years of the study, most large foliose thalli became either extinct or showed a a serious damage.

The bryophytes also suffered from damage caused by acid precipitation or deposition. Table 8 shows the list of species, life strategies and the T, W, and R values of the taxa. Funaria hygrometrica and Marchantia polymorpha are very common in courts and gardens.

The colonists represent the early stages of succession; they have high reproductive effort both in sexual and asexual diaspore production. The age of first sexual production is low and the growth-form is predominantly short turf. These taxa were able to withstand the harmful effects of pollution,

Table 8. Changes in the bryophyte flora and in life strategy composition. Life strategies: P = perennial stayer, C = colonist, + = present, - = extinct.

Species	Life str.	T	W	R	- or +
Amblystegium serpens	P	5	4	0	-(1982)
Brachythecium salebrosum	P	5	5	0	-(1982)
Bryum argenteum	C	5	3	5	+
Ceratodon purpureus	C	0	2	0	+
Hypnum cupressiforme	P	0	3	0	+
Pleurozium schreberi	P	4	5	2	-(1983)
Tortula muralis (mainly on walls)	C	5	2	0	+

the acidification of melting snow, although necrotic brown spots occurred on some leaves. These species are "... remarkably tolerant of the atmospheric pollution that occurs in large towns." (Watson 1980).

Four species are included in the perennial stayer group. As During (1979) notes, "... sexual and asexual reproductive effort is rather low to nearly absent ... age of first reproduction variable,several years at least... growth forms wefts, dendroids, mats, also large cushions." These plants never pro-

duced sporophytes in the study area. Hypnum cupressiforme was the only species in the P group, which was able to survive the stress. At the end of 1984, only small patches of colonists were seen on the trees. The only perennial stayer was confined to a single Juglans tree.

The observed signs of the degeneration of bryophytes were as follows:

- loss of colour on the tips of leaves; light brown spots on the tips,
- discolouration gradually extended downwards,
- the leaves turn brown and lose all the chlorophyll.

Regarding growth forms and tolerance, my results agree with those of Gilbert (1970, in Smith 1982): the short tufts and thalloid growth forms are less sensitive to pollution than tall tufts.

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CONCLUDING REMARKS

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Our Conference, the first ever to be held entirely concerned with the ecology of bryophytes, has covered a remarkably wide field. Ecology is not easily defined. My late brother, the entomologist O.W. Richards, once said ecology was anything on which a paper could be published in the Journal of Ecology. Tansley, rather more profoundly, wrote, 'Ecology is not a subject, it is a point of view'. However you try to define ecology, I can think of hardly any aspect of bryoecology which has not been dealt with in one or more papers in this conference. Dr. George Scott once compared bryoecology to a pile of bricks with no mortar. Have we added a little mortar to the bricks?

A scientific conference does not consist merely of reading and discussing papers. It should provide both informal and formal opportunities for exchanging ideas and information - it should be a meeting of minds. The members of this conference are of many nationalities and have many different points of view and scientific backgrounds. What unites us is what is common to all scientists, curiosity and a passion for exploring and trying to understand the natural world. We also share a love for mosses and liverworts. Botanists and zoologists have and advantage over most other scientists that they really love the things they study. I sometimes feel sorry for physicists and chemists: it must be difficult to love an atom or a molecule!

Fortunately today is not the end of our conference. We have three more days to share our ideas and enthusiasms. For these opportunities, and for all they have done to make this meeting

a success, we are deeply indebted to our Hungarian friends, especially the organizers of the meeting, Drs Pócs and Simon, and to the Hungarian Academy of Sciences. We are also grateful to the authorities of the Eötvös Loránd University for making this excellent auditorium available for our Conference.

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