35

PROCEEDINGS
OF THE
IAB CONFERENCE
OF BRYOECOLOGY

(Part A)

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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.
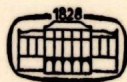
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Budapest–Vácrátót, Hungary
5–10 August, 1985

PART A

Edited by
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PREFACE

Volume 35 of the series Symposia Biologica Hungarica con-
tains the proceedings of the First World Congress of Bryoecol-
ogy organized by the International Association of Bryologists
(IAB) and held in Budapest and Vácrátót on August 5-10, 1985.
About 150 bryologists, representing the vanguard of bryoecolog-
ical research, from 30 countries attended the conference.

Bryoecology goes back only a few decades and is one of the
most rapidly developing areas of plant sciences. The founda-
tions are due to Loeske, Amann, Gams, W. Watson, and other pio-
neers, whose works were much advanced later by synbiologists,
especially coenologists and ecologists. Recently, several hun-
dred researchers have been involved in bryoecological studies,
facilitating the application of results on bryophyte popula-
tions and communities to biological basic research and nature
conservation.

Thanks to their wide geographical distribution, important
ecological and coenological role, relatively large plant sur-
face, specific water economy, and characteristic adaptive stra-
tegies, bryophytes are very sensitive indicators of environ-
mental change. The analysis of the structure and function of
these plants at population and community levels is not only of
theoretical relevance; the results promote plant physiological
studies (e.g., on resistance) and yield new bioactive sub-
stances of potential usefulness in pharmacology.

The papers presented at the first bryoecological world
congress and the discussions support the above statements. Al-
most all areas of bryoecology, including ecophysiology, repro-

duction and population biology, community ecology, population ecology, bryophytes in ecosystems, and bioindication, were represented. These main topics were discussed in six separate sessions at the conference. The structure of this volume follows the classification above: the papers are grouped according to the sessions at which they were presented.

The editing work required more time and effort than expected, over 850 manuscript pages had to be reviewed, corrected and revised. Most of the job was carried out by the conveners of sessions, M. F. Proctor, H. J. During, N. G. Slack, R. Wyatt, R. E. Longton, and J. Sarosiek, whose cooperation is gratefully acknowledged.

All final versions of papers arrived by June, 1986, although the editors received some requests for further modification even in August. The standardization of style, the solution of technical problems associated with diagrams, photographs and large tables, and typing into camera-ready form required several months.

We thank all the participants of the congress for their contribution to this volume. Special thanks are due to P. W. Richards, Honorary President of the conference, for his active presence and stimulative opening and closing remarks. We are also indebted to the members of the Advisory Committee: N. G. Slack, representative of the American Bryological Society; S. W. Greene, of the British Bryological Society; H. Ando, from the Japanese Bryological Society; G. A. M. Scott, representing Australia; G. Mogensen, from the Nordic and Nuch Bryological Society; S. Orbán, representing the Eastern and Central European Working Group; A. Borhidi, representing the Botany Section of the Hungarian Biological Society; and G. Fekete, the Ecology Section of the Hungarian Biological Society. We are obligated to R. S. Gradstein, Secretary of IAB, for his help in organizing the conference.

Many thanks are due to the host institutions of the congress, the Institute of Ecology and Botany of the Hungarian Academy of Sciences(Director: Á. Bereczik), and the Department of Plant Taxonomy and Ecology, L. Eötvös University. Moral support was received from the Biology Division of the Hungarian

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BEGRÜSSUNGSANSPRACHE

Herr Ehrenpräsident, Verehrtes Präsidium,
verehrte Teilnähmer,
meine Damen und Herren!

Es ist für mich eine angenehme Pflicht die Internationale
Bryoökologische Konferenz hier in Ungarn im Namen der Biolo-
gischen Sektion der Ungarischen Akademie der Wissenschaften
begrüssen zu können.

Zur zeit erleben wir in globalem Masse den Aufschwung
der ökologischen Forschungen. Das hangt wohl auch mit den sich
zuspitzenden Umwelschutz-Fragen zusammen. Die sich immer mehr
und mehr anhäufenden Fragen können auch von der wissenschaft-
lichen Seiteher nur mit internationaler Zusammenarbeit beant-
wortet werden.

Nun möchte ich betonen, dass Ungarn für die internationale
Zusammenarbeit, für den freien Austausch der 'Gedanken und der
Wissenschaftler - stets aufgeschlossen war. Die ungarischen
Forscher sind auch heute in den verschiedenen internationalen
Organisationen eifrig tätig. So zum Beispiel meinerseits als
Vertreter der Botanik zwischen 1967 und 1973 im Executiven
Committee der Union International des Sciences Biologiques
(siehe die Generalversammlungen in Montreux und Washington)
oder I. Láng, der Generalsekretär der Ungarischen Akademie der
Wissenschaften in den internationalen Organisationen des
Umweltschutzes.

Wir sind der Meinung, dass die bekannte ungarische Gast-
freundschaft zur guten Stimmung und gegenseitigen Verständigung

während den verschiedenen Veranstaltungen von wissenschaft-
lichen und kulturellen internationalen Organisationen stets
beiträgt. Und so wird es auch bei diesem Zusammentreffen der
IAB in Budapest und Vácrátót sein.

Bitte empfangen Sie zum erfolgreichen Gedankenaustausch,
zur Diskussion, Zusammenarbeit und zu den - gewiss wertvollen -
Ergebnissen unsere besten Wünsche.

Den Begrüssungsworten möchte ich auch etwas Fachliches
hinzuzufügen. Es sei mir gestattet darauf hinzuweisen, dass
ich meinerseits zu Ihren Exkursionen auf dem Gelände einige
Detail-Auszüge aus früheren Publikationen über die Moos-
flechten Synusien zur Verfügung stelle (Zólyomi 1943, 1958,
Debreczy 1966).

Ich hoffe, dass diese Dokumentation bzw. Konferenz (an-
gewandte Methode nach Braun-Blanquet und Gams) einen erweiter-
ten Einblick in die Lage der besuchten Gelände (National Park
Kiskunság, Balaton-Oberland) ermöglichen wird. Die allgemeinen
pflanzengeographischen und speziellen zönologischen Fest-
stellungen sind im guten Einklang mit den modernsten ökophysio-
logischen Untersuchungen von Biró - Debreczy und Tuba (siehe
Sitzungsauszüge Seite 9 und 50, Abstracta Botanica 9. suppl.
1, 1985). Meine damals publizierten Untrsuchungen der pH-
Werte und des $CaCO_3$-Gehaltes lassen auch auf einen basenreichen
Zustand schliessen.

Ich bin fest überzeugt, dass auch unsere Konferenz weitere
schöne Ergebnisse zeitigen wird. In diesem Sinne wünsche ich
weitere erfolgreiche Arbeit!

B. Zólyomi

Mitglied der Ungarischen Akademie der Wissenschaften,
Wissentschaftlicher Ratgeber des Ökologisch-Botanischen
Instituts der Ungarischen Akademie der Wissenschaften
in Vácrátót

OPENING REMARKS

P. W. RICHARDS

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This Conference is concerned with bryophyte ecology in
the present and future, but it would perhaps be appropriate to
begin with a brief glance backwards. This is, I believe, the
first conference entirely devoted to bryophyte ecology, though
at several previous international meetings there have been
sessions on the subject. At the International Botanical Con-
gress at Edinburgh in 1964, for example, there was a symposium
on the experimental ecology of bryophytes. There were eight
contributors and the papers were afterwards published (Richards
et al. 1964).

Looking further into the past, it can be seen that bryo-
logists, especially in the alpine countries and Scandinavia,
became aware quite early of what we would now call the ecolog-
ical interest of mosses and liverworts - their characteristic
communities and their sensitive reactions to climate, soil and
other environmental factors. J. R. Lorentz (1858) and P. G.
Lorentz (1860) described bryophyte associations in the eastern
Alps. Molendo (1865) in the Allgäu Alps. Pfeffer (1871) in
Switzerland classified the bryophyte associations into 'sub-
stratum groups' and drew attention to the differences between
the bryophyte flora of calcareous and non-calcareous rocks.

In the present century Loeske (1901) published an account
of the bryophyte associations of the Berlin district which
contains many interesting field observations. Later, important
works dealing wholly or partly with bryophyte ecology were
written by Gams (1927), Amann (1928), Olsen (1917, 1923) and

others. In England Tansley (1915) published an important review article on 'Recent work on the ecology of bryophytes' in the then recently established Journal of Ecology: some of the papers reviewed dealt with experimental work, e.g., Skene's on the acidification of solutions by Sphagnum and Kessler's on spore germination. At about the same time W. Watson began a series of papers in the New Phytologist and Journal of Ecology which mainly consisted of lists of species found on different soils and in various plant communities, but some included observations on successions and other ecological topics.

A further step in the development of bryoecology was the publication of Verdoorn's Manual of Bryology (1932), which included a chapter on 'Bryocoenology' by Gams and one on the 'Ecology of Bryophytes' by myself, the latter to some extent modelled on Lundegårdh's Klima und Boden in ihrer Wirkung auf das Pflanzenleben (1931).

Now, 50 years later, research on bryophyte ecology is active in many countries. Modern techniques such as chromatography, electron microscopy and radio-active tracers, as well as mathematical and computerised methods of data evaluation, are being successfully exploited. The important role of bryophytes in many kinds of ecosystems is increasingly realised even outside the ranks of specialists. The next few days will show how wide and promising a field for research bryoecology has become.

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Session 1
PHYSIOLOGICAL ECOLOGY
Convener: M.C.F. Proctor
(Exeter)

MOSS GARDENING IN JAPAN

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Mosses have been greatly appreciated as precious attribute
of Japanese gardens. First, mosses are useful as an evergreen
ground cover with varying tones, and second, they give a
peculiar beauty and ancient look to gardens by clothing trees,
rocks and stone lanterns. In a certain type of Japanese gar-
dens, mosses are the only plant element which is simply but
harmoniously arranged with stones and white sand. Many
attractive moss gardens are seen in Kyoto, an ancient capital
of Japan, where the surrounding mountains ensure constant
humidity favorable for the growth of the mosses. More important
species commonly used in Kyoto are Polytrichum commune, Leuco-
bryum bowringii, L. neilgherrense, Trachycystis microphylla,
and Rhizogonium dozyanum, but in other drier regions, Hypnum
plumaeforme and Racomitrium canescens are employed as prefer-
able material. Technical hints on moss gardening include:
preserving favourable habitat conditions, constant weeding,
moderate watering, continual care to remove fallen dead
leaves and droppings of cats, dogs and birds, and keeping away
harmful animals such as moles, slugs, crickets and ants. Use
of fertilizer is unnecessary.

1. INTRODUCTION

Mosses have usually been treated as objects of annoyance
in gardens of Western countries, but in Japan they have been
popularly used for gardening. Foreign visitors to Japan are
intrigued by the unique feature and beauty of Japanese gardens

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where mosses flourish covering the ground, rocks, and tree trunks or on occasion mosses are the only plant element. Many attractive examples of such moss gardens are to be seen at various Buddhist temples in Kyoto, an ancient capital of Japan, which fortunately escaped damage by the War. The foreigner will further be amazed to learn that an industry of moss cultivation for horticultural uses is developing in this country.

2. TRAITS OF JAPANESE GARDENS

Japanese gardens have a unique beauty and produce a special quiet atmosphere by the combination of natural rocks, sand, water, and plants, which are harmoniously and symbolically arranged with careful thought. They are quite different from western gardens where the arrangement of elements is usually geometric and showy works such as sculptured statues, fountains, and flower-beds are frequently built. An important principle of the scenic composition of Japanese gardens is the natural-looking feature in a limited space, and the background view outside the garden is sometimes employed, being integrated into the perspective of the garden.

The Japanese garden is generally divided into two styles. One is the stroll garden in which visitors walk about along the path and enjoy viewing changing scenes. The other is the contemplation garden which is the creation of a carefully composed scene suggestive of a picture and viewed from a veranda or within a room of a house by the garden.

3. MOSSES USED IN JAPANESE GARDENS

Mosses have been greatly appreciated in Japan as precious attribute of gardens. They are used as an ideal ground cover whose green colour is kept throughout the year and further well-maintained even at shaded sites. Mosses are also important as a clothing of tree-trunks and rocks, giving a subtle beauty and ancient look to gardens. In some simple gardens, mosses form the only plant element.

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The conscious use of mosses in Japanese gardens originated in the latter half of the 16th century when the tea garden, "Roji", developed (Ishikawa 1973). The tea garden is a small garden with groves of carefully trimmed trees and shrubs and stepping-stones, which is designed to harmonize with the ideals of the tea ceremony ("chano-yu", a highly structured, traditional art of ceremonial tea-preparing in company of guests). The garden is attached to a tea house which guests approach through it. The tea garden is required to be natural in appearance and to reflect a quiet mood of serenity as if guests walking the stepping stones were in the desolate tranquility of a mountain trail. For creating a calm profound atmosphere, mosses have been appraised as an effective element indispensible to the tea garden because of their serene tone of green and delicate tranquil texture. Their flourishing growth in the garden suggests the state around a mountain trail.

Many Japanese gardens with luxuriant development of mosses are seen in Kyoto, the ancient capital of Japan, where the home of the imperial court was located from 794 to 1868. The city lies on a slightly inclined plain surrounded on three sides by low rolling mountains. Such a topographic setting helps to ensure constant humidity which is favourable to the growth of mosses in Kyoto and has automatically led to the development of moss gardens in this city. Reproduction of Kyoto gardens will be unsuccessful in the drier climate of the present capital, Tokyo.

Stroll gardens in Kyoto, most of which are attached to old Buddhist temples or palaces, usually occupy comparatively large planted areas with ponds, islands, tea houses, and occasionally pavilions. Examples are gardens of Saihoji Temple (popularly called "Koke-dera" which means moss temple), Ginka-kuji Silver Pavilion, and the Katsura Rikyu Detached palace. In the stroll gardens, beautiful growths of mosses are extensive; the following species are representative (Ishikawa et al. 1953, 1954, Iwatsuki & Kodama 1961, Ando 1971):

(1) On sunny ground in open sites: Pogonatum inflexum,

Campylopus umbellatus, Racomitrium canescens;

(2) On sunny to moderately shaded ground: Polytrichum commune, Hypnum plumaeforme;

(3) On moderately shaded ground: Atrichum undulatum, Leucobryum bowringii, L. neilgherrense, Dicranum scoparium, Brotherella henonii, Bazzania japonica;

(4) On shaded humid ground: Rhizogonium dozyanum, Trachycystis microphylla;

(5) On banks of the pond and in other damp places: Sphagnum palustre, Polytrichum commune, Fissidens japonicus, Climacium japonicum.

(6) On tree trunks and exposed roots: Entodon rubicundus, Brotherella henonii, Clastobryella kusatsuensis, Hypnum plumaeforme.

(7) On stones: Herpetineuron toccoae, Thuidium glaucinum, Entodon rubicundus, Hypnum plumaeforme.

Among these species, Polytrichum commune is most commonly used in Kyoto gardens because of its balanced uniform beauty, ability to withstand sunlight, and ease of supply and transplanting. Furthermore, plants of this species are firmly attached to soil and can resist disturbance by the broom or the bamboo rake used to remove fallen leaves and other debris. Leucobryum species are also welcome and show a peculiar elegant beauty, forming gently rolling mats of silvery green.

Among the contemplation gardens seen in Tokyo, the dry garden ("Kare-sansui"), which is characterized by a simple abstract desing reflecting the spirit of Zen Buddhism, is remarkable. This style of dry garden is not found anywhere else in the world, even in China whose culture has influenced in several ways to the spirit and structure of Japanese gardens. The harmonious serene beauty of the dry garden issues from the unique pattern formed by the simple but symbolic arrangement of natural-formed stones, white sand, and a few plants, often only mosses which are in most cases represented by Polytrichum commune, rarely Leucobryum neilgherrense. The most famous example of dry garden is the stone garden ("Seki-tei") of

Ryoanji Temple in Kyoto. This garden consists solely of a rect-
angular bed of white sand and fifteen stones arranged into five
groups. No vascular plants are seen anywhere in the garden;
only small patches of moss (Polytrichum commune) surround the
groups of stones. The stones on a white bed of sand are sug-
gestive of mountains rising above the clouds or of islands
over the sea, and the moss growth recalls forest, shrubs, or
other grassland developed on them.

Another exceptionally simple but uniquely beautiful garden
is a small flat garden recently built in a corner of the main
garden of Sanboin Temple in Kyoto. It is composed of white
sand and five patches of moss, Polytrichum commune. Three of
the moss patches are circular, modelled after saké cups, and
two are guitar-shaped imitating gourds used as saké bottles
from old times. They symbolize the famous banquet sponsored in
spring of 1598 at cherry-blossom time by the famous lord,
Hideyoshi Toyotomi, the creator of the main garden of this
temple.

In other districts, the dominant moss species used in
Japanese gardens are sometimes different from those in Kyoto
gardens. For example, garden mosses are often pleurocarpous
mosses which are fully as beautiful but not welcome in Kyoto
gardens where acrocarpous mosses predominate. They are Plagio-
mnium acutum, Brotherella henonii, Hypnum plumaeforme, and H.
lindbergii, the last being frequent especially in north-eastern
cool regions towards the Japan Sea. In some sunny and dry
sandy places, a sun-loving moss, Racomitrium canescens, is
employed.

4. TECHNIQUES OF MOSS GARDENING

In many of the old Japanese gardens, mosses have first
appeared spontaneously as a result of the favourable setting
of the garden. In later years growth and maintenance of the
mosses have been encouraged by careful management and trans-
planting. Building of Japanese gardens is now often planned
with an original design to employ mosses.

Most important in moss gardening is selecting appropriate species suited to environmental conditions at the given sites in the garden. Sufficient knowledge on the ecology of each species in natural habitats is a prerequisite to make a design of moss arrangement in the garden. Transplanting of mosses, especially those characteristic of extreme conditions (for example, Rhizogonium dozyanum preferring shaded moist places and Racomitrium canescens, a sun-loving arenicolous moss), is not easy, and it will never be successful if they are planted in unfavourable places or inappropriately managed after transplanting.

When construction of a moss garden is planned, it must be kept in mind to avoid conditions unfavourable to the development of mosses, such as over-ventillation, constant exposure to afternoon sun, and poor drainage. Weedy vascular plants, such as Hydrocotyle sibthorpioides, Sagina japonica, Oxalis corniculata, and Poa annua, which often invade the moss carpet, must always be watched for and cleaned out. Chemical weed control can be applied in a moss garden, but a suitable herbicide must be selected and used with care to the rate of concentration and the time of treatment. Hypnum plumaeforme is in some places appreciated as a desirable garden moss, but in a garden where Polytrichum commune is a leading element, its invasion is unwelcome. Hypnum plumaeforme grows readily over the turf of Polytrichum and finally supersedes it. Thalloid liverworts, such as Marchantia polymorpha, Conocephalum conicum, C. supradecompositum, and Anthoceros spp., are also treated as undesirable elements and weeded out.

No fertilizer should be used and watering is usually unnecessary when growth of planted mosses is fully stabilized. Over watering should be avoided in any stage of moss development. Removal of fallen dead leaves and debris needs continual care. Droppings of cats, dogs and birds, and constant falling of heavy water drops from overhead trees in a rainy day are injurious to mosses and must be avoided. Harmful animals to be kept away include moles, slugs, crickets, and ants, and occasionally people who invade arbitrarily beyond the path.

Some useful guides to moss gardening have been published in Japan, such as those by Inoue (1976), Oishi (1981), and Inoue & Ohashi (1983).

5. CULTIVATION OF MOSSES AS GARDEN PLANTS

The elegant and quiet beauty of mosses has become more and more highly appreciated in Japan with the development of modern material civilization, and fancy for mosses in gardening has become more popular. Some architects of Japan introduce a courtyard or a show garden accentulated by mosses into their designs of buildings for a hotel, Japanese restaurant, public hall, or art museum.

A demand for mosses as garden plants has thus greatly increased recently and it has encouraged the development of moss cultivation for market. Several cultivators of garden plants are trying to grow mosses to supply them commercially. The centre of this new horticultural industry is in central Honshu including Ishikawa, Gifu, Aichi, Shiga, Kyoto and Mie Prefectures, where the climate is moderate with an annual precipitation of 1600-2200 mm. The main species of mosses cultivated are Polytrichum commune (most common with the greatest supply), Atrichum undulatum, Leucobryum neilgherrense, Racomitrium canescens, and Hypnum plumaeforme. They are culti- vated on soil in small rectangular plastic trays (example of size(30 x 60 cm) or on soil over cloth blocks. Nursery plants are raised vegetatively from cuttings (cut young shoots are planted), fragment scattering (crushed or cut fragments of moss plants are scattered on the bed, covered with soil, and then pressed down by a board) or division. The nursery (except for sun-loving mosses, such as Racomitrium canescens) is set under a grove of coniferous trees or in a field surrounded by forests on two sides at least, south and west. When moss beds are placed on open sites, the sunlight is controlled by a covering of black cheesecloth. Alternatively, the mosses may be grown in a polythene-covered greenhouse. Nursery plants of the most marketable moss, Polytrichum commune, are brought to market

in three months at the earliest from the beginning of culti-
vation.

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MICROCLIMATE AT INOTANI VALLEY NEAR NICHINAN, S. JAPAN[†]

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A two-year study was made of the microclimate in relation
to the growth of epiphytic and epiphyllous bryophytes at Ino-
tani Valley, southern Japan, where many tropical and subtro-
pical bryophytes are found. Maximum temperature in the valley
bottom is lower than on the slopes. However, minimum tempera-
ture in the bottom is almost the same as on the slopes through-
out the year. Measurements of relative humidity and evapora-
tion show that the valley bottom is always more humid than
the slopes. Thus the microclimate of the valley bottom is
both more humid and more equable in temperature than that on
the slopes, or outside the forest. It seems reasonable to
conclude that epiphytic and epiphyllous bryophytes are good
indicators of microclimate.

INTRODUCTION

There are many tropical and subtropical bryophytes grow-
ing in Inotani Valley, west of Nichinan. They include Garo-
vaglia elegans (Dozy et Molk.) Fleisch., Porotrichum graci-
lescens Nog., Tayloria indica Mitt., Colura tenuicornis
(Evans) Steph., and Frullania tenuicaulis Mitt. This area
is the northern limit of some of them.

[†] Contribution from the Phytotaxonomical and Geobotanical
Laboratory, Hiroshima University, New Series, No.   .

Inotani Valley is also characterized by abundant growth of pendulous mosses, which mostly belong to Meteoriaceae, hanging from branches of trees and shrubs along streams. Growth of these pendulous mosses indicates a warm and humid climate in the valley. They include Aerobryopsis subdivergens (Broth.) Broth., Barbella flagellifera (Card.) Nog., Floribundaria aurea ssp. nipponica (Nog.) Nog., Neobarbella pilifera (Broth. & Yas.) Nog., Pseudobarbella attenuata (Thwait. & Mitt.) Nog., P. levieri (Ren. & Card.) Broth., and P. laosiensis (Broth. & Par.) Nog.

Inotani Valley is also characterized by abundant growth of small epiphyllous hepatics which are found on living leaves of ferns, shrubs, and some herbs along streams. Growth of these epiphyllous hepatics also reflects the warm and humid climate of the valley. About 20 species of epiphyllous hepatics have been recognized in this valley. They are mostly belonging to Lejeuneaceae and Radulaceae, and include many subtropical and tropical species.

These tropical as well as pendulous and epiphyllous bryophytes are mostly found along streams or valley bottom in the area, and rarely found on slopes. To clarify the difference of climatological conditions on slopes and valley bottom, we measured temperature and humidity once a week for a period of about 18 months from 1966 to 1968.

MEASUREMENT SITES AND METHODS

Inotani Valley is situated about 15 km west of Nichinan, about 230 m alt. (Fig. 1). The area is covered by evergreen broad-leaved forests which are dominated by Quercus sessilifolia Blume, Persea japonica (Sieb. & Zucc.) Kosterm., and Castanopsis cuspidata var. sieboldii (Makino) Nakai. The forest belongs to national forest, and is mostly natural, although it was partly cut for charcoal-burning before the war. There is a stream flowing from west to east; the average width of the stream bed is about 10 m, and the actual width of the stream about 5 m at the study site (Fig. 2).

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Two thermo-hygrographs (Ohta Keiki Co. and Shimazu Co.) were set in the instrument screens at two sites: site F (about 1 m above the ground) on the valley bottom where many pendulous mosses and epiphyllous hepatics are very abundant, site G (about 19 m above the stream, and about 1 m above the ground) on a slope where the pendulous mosses and epiphyllous hepatics are poorly represented. The thermo-hygrographs were checked with an Assmann aspirated psychrometer and a standard thermometer at the Aburatsu Meteorological Station.
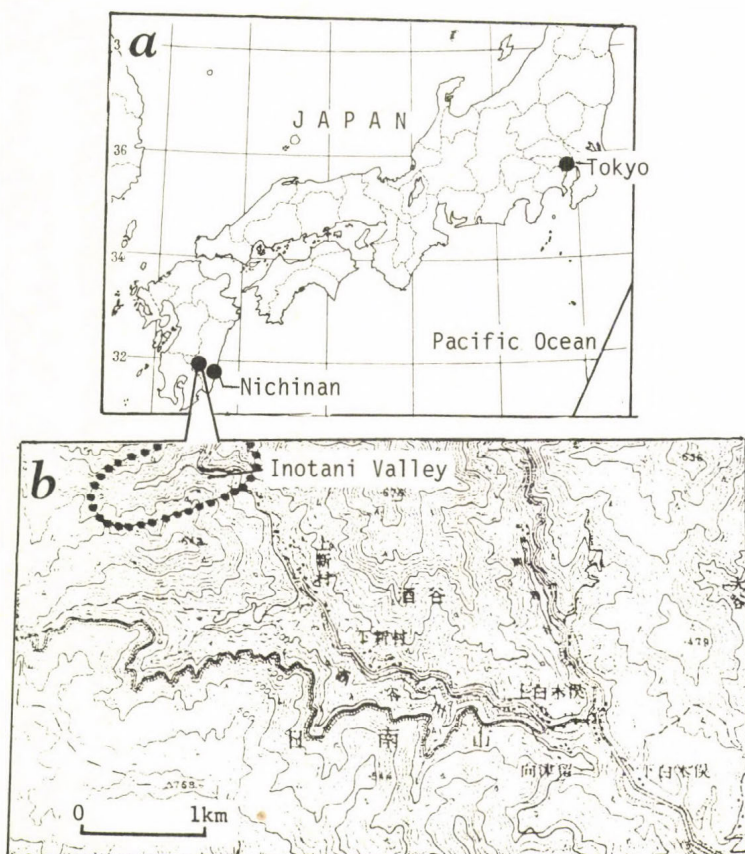
Fig. 1. a) Map showing locations of Inotani Valley and Nichinan, Japan. b) Map of Inotani Valley.
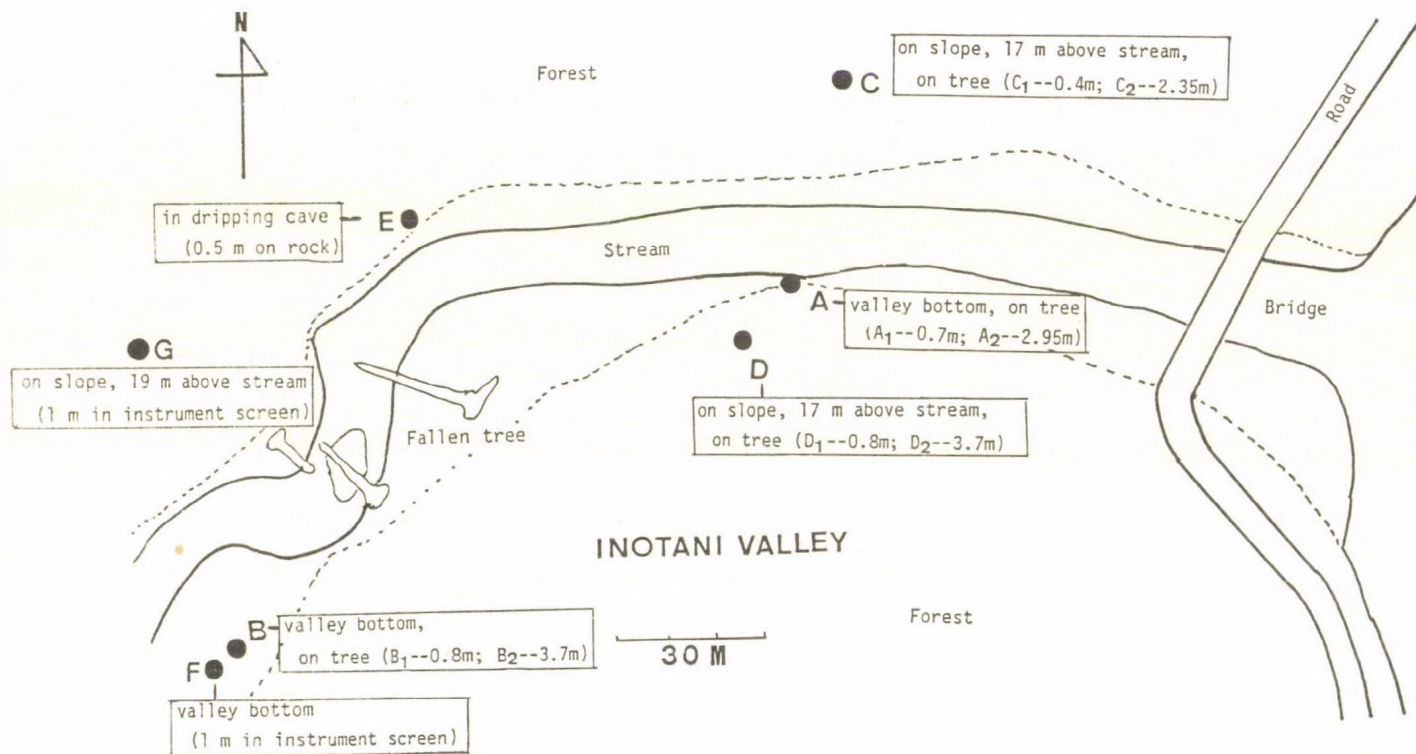
Fig. 2. Sketch of Inotani Valley showing locations of temperature stations. A-G are referred to in figures.

Twelwe maximum and minimum mercury thermometers (Tokyo AND)
were also set at different sites on the valley bottom and
slopes (Figs 2 and 3). These thermometers were checked with
a standard thermometer at the Aburatsu Meteorological Station.

Both thermo-hygrographs and maximum and minimum thermome-
ters were checked every week at around 11 a.m. from June 15,
1966 to May 31, 1968. Temperature and humidity were also mea-
sured at the sites using an Assmann aspirated psychrometer
(Yoshino Keiki Co.).

An evaporation gauge was used to compare evaporation at
valley bottom and on slope. Four petri dishes (12.4 cm diam.
and 3 cm deep) were used at sites F and G, and evaporation was
checked every week from May 1, 1968 to August 22, 1968.
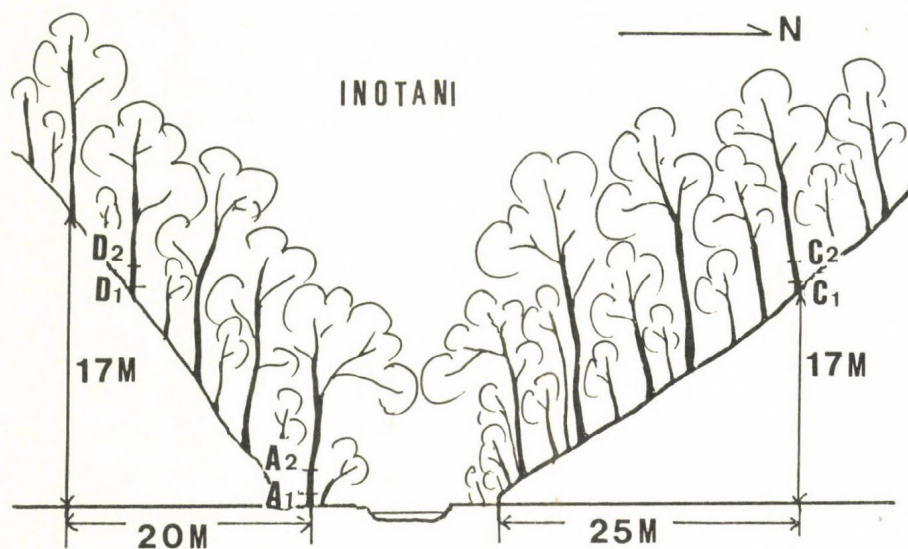
Fig. 3. A cross-section of Inotani Valley, west of Nichinan,
260 m alt. Slopes are covered by broad-leaved evergreen forests.
Abundant epiphytic and epiphyllous bryophytes are found on
trees and shrubs along the stream.

Our results were compared with measurements from Aburatsu Meteorological Station, near the coast just south of Nichinan. At Aburatsu maximum temperature often exceeds 35°C in July and August, and minimum temperature often goes down below zero in December to February. Ice and frost can be seen in winter but almost no snow. The area is known as one of the wettest places in Japan, and precipitation reaches 3000 mm a year (annual precipitation was 3875 mm in 1966 and 2267 mm in 1967).

RESULTS

1. Temperature

a. Valley bottom. Fig. 4 shows weekly maximum and minimum temperatures on trees at 0.7 m (Al) and 2.95 m (A2) above the ground on the valley bottom. Maximum temperature at Aburatsu and site A of Inotani valley differ considerably. In Aburatsu, maximum temperature generally exceeded 30°C in July and August, while it mostly stayed below 25°C during the summer season at Inotani Valley.

At the valley bottom, pendulous and epiphyllous bryophytes are usually found below 2 m above the ground. Maximum temperature at 2.95 m above ground (A2) was always 2 to 3 degrees higher than at 0.7 m above the ground. However, maximum temperaure at 2.95 m above the ground (A2) in the valley bottom is always considerably (about 5 degree) lower than those at Aburatsu.

Weekly minimum temperatures are slightly higher at Aburatsu than in the Inotani Valley in summer (June to early September). By contrast, in the winter months (November to March) minimum temperatures are almost the same at the two places although Inotani Valley is situated at 230 m alt., much higher in elevation than Aburatsu. There is hardly any difference between minimum temperatures at 0.7 m (Al) and 2.95 m (A2) above the ground in the winter.

b. Valley slopes. Fig. 5 shows weekly maximum and minimum temperatures at 0.4 m (Cl) and 2.35 m (C2) above ground level

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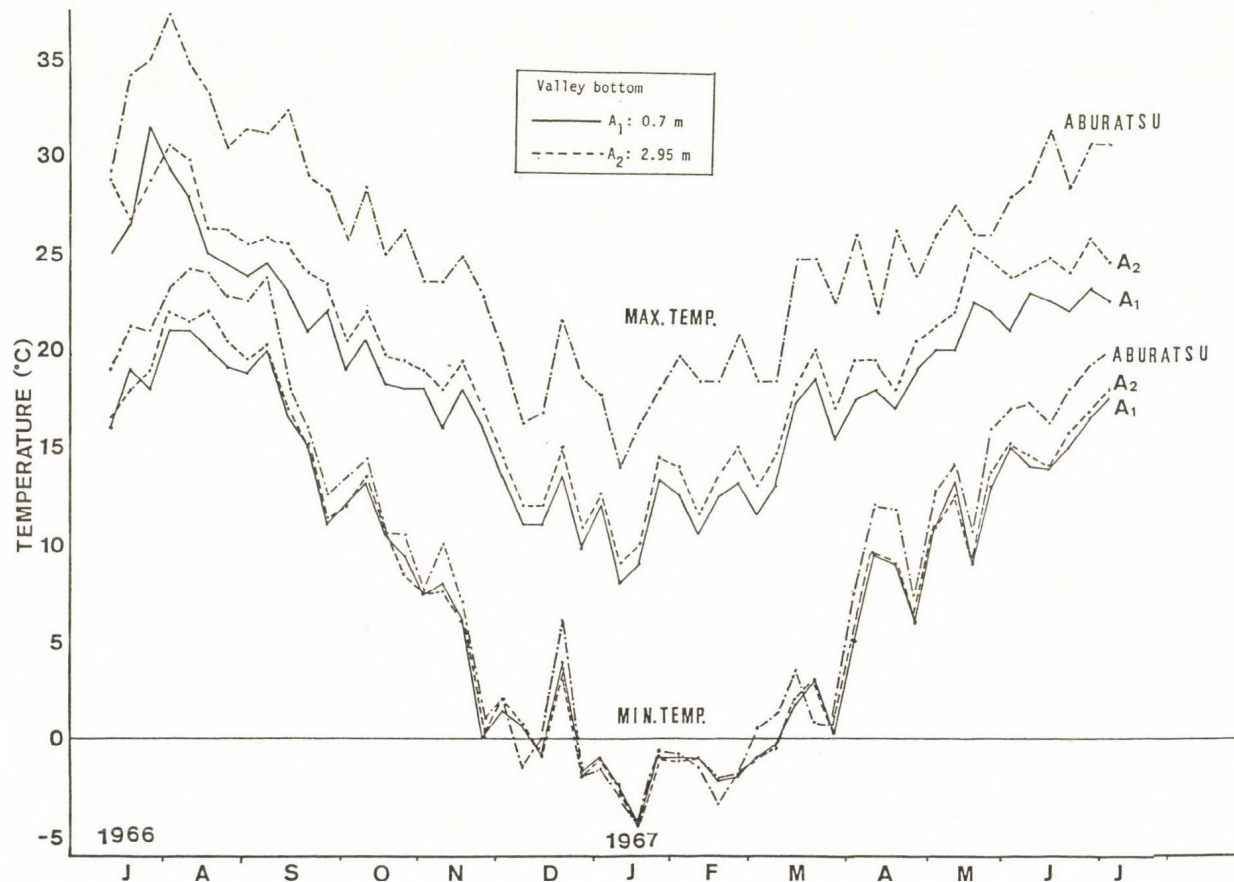
Fig. 4. Comparison of weekly maximum and minimum temperatures at Aburatsu Meteorological Station near sea coast and at station A in Inotani Valley. A1: 0.7 m above ground, A2: 2.95 m above ground, both on the same tree in the valley bottom.
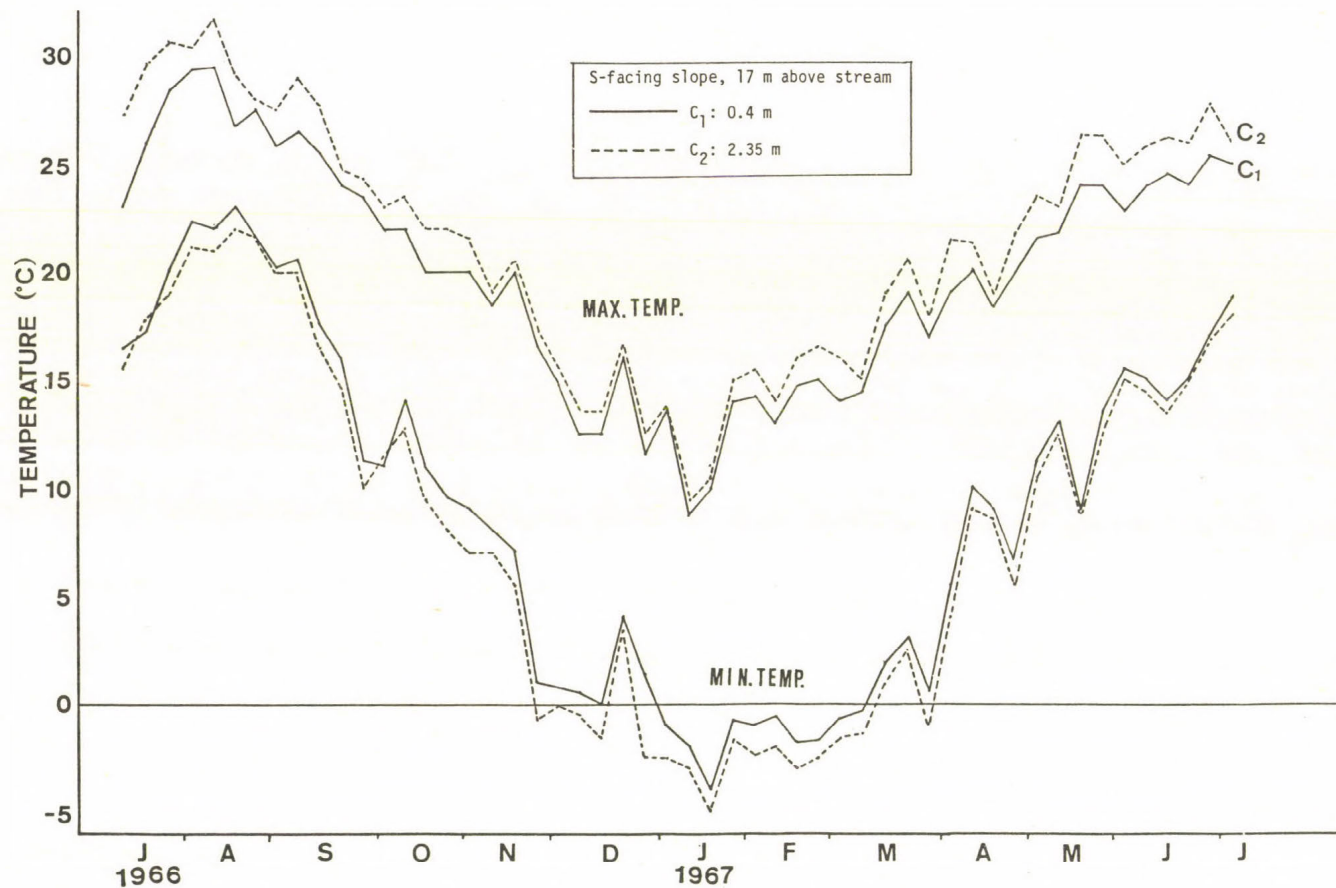
Fig. 5. Comparison of weekly maximum and minimum temperatures at two heights (C1 and C2) on the same tree on S-facing slope, about 17 m from valley bottom.
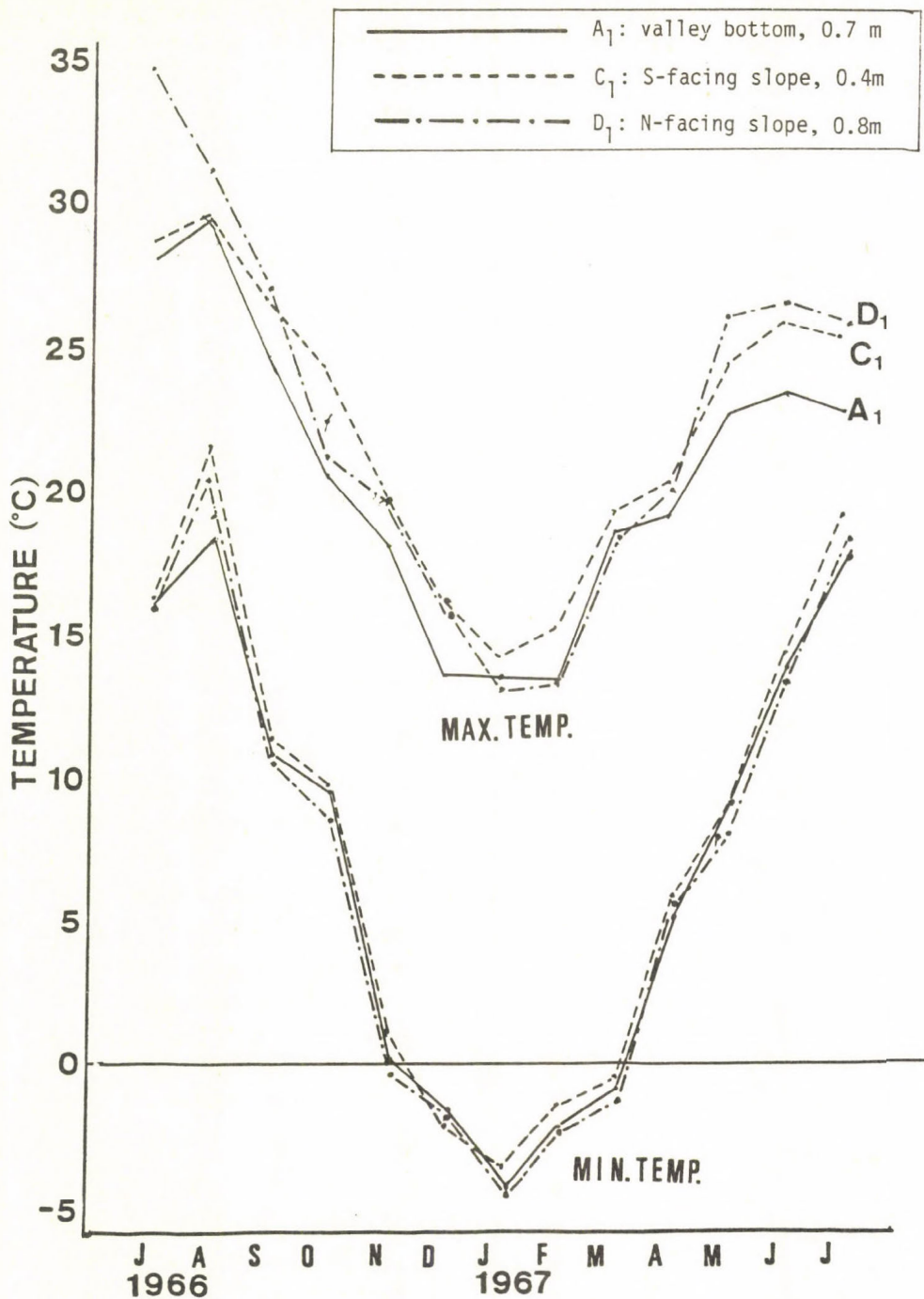
Fig. 6. Monthly maximum and minimum temperatures on tree bases in the valley bottom, and on S- and N-facing slopes.

on the south-facing slope, 17 m above the stream. Maximum temperature on the slope in the summer months is always $1-2^{O}C$ higher than on the valley bottom. This is true for both lower trunk (C1) and 2.35 m (C2) above the ground. However, it is much lower than at Aburatsu.

The weekly minimum temperature at O.4 m (C1) above the ground on the slope is almost the same as than on the valley bottom. However, minimum temperature at 2.35 m (C2) in winter (November to March) is usually $1-2^{O}C$ lower than that of the lower trunk (C1).

2. *Humidity*

Two thermo-hygrographs were set in the instrument screens located in the valley bottom and on the slope. They showed almost constant high humidity in the rainy days, but fluctuated on fine days. It is apparently more humid in valley bottom than on slope. However, it is difficult to compare measurements of the hydro-thermographs at two sites.

Fig. 8 shows relative humidity measured by Assmann aspirated psychrometer at around 11 a.m. in the valley bottom and on the slope. On rainy days, it is very equally humid both at valley bottom and on slope. On fine days, humidity is more variable, especially on the slope. It is apparently dryer on the slope than on the valley bottom.

Data obtained by evaporation gauge (petri dish) are shown in Table 1. In the valley bottom, evaporation was much higher at 1 m than at O.3 m. It is constantly humid near the ground in the valley bottom. However, on the slope evaporation is much higher than in valley bottom. Evaporation at 1 m is much higher than at O.3 m on the slope.

DISCUSSION

Epiphytic and epiphyllous bryophytes have been considered as climatic indicators (Iwatsuki 1960, Piippo 1982, and many others). Many reports have been published on microclimates in
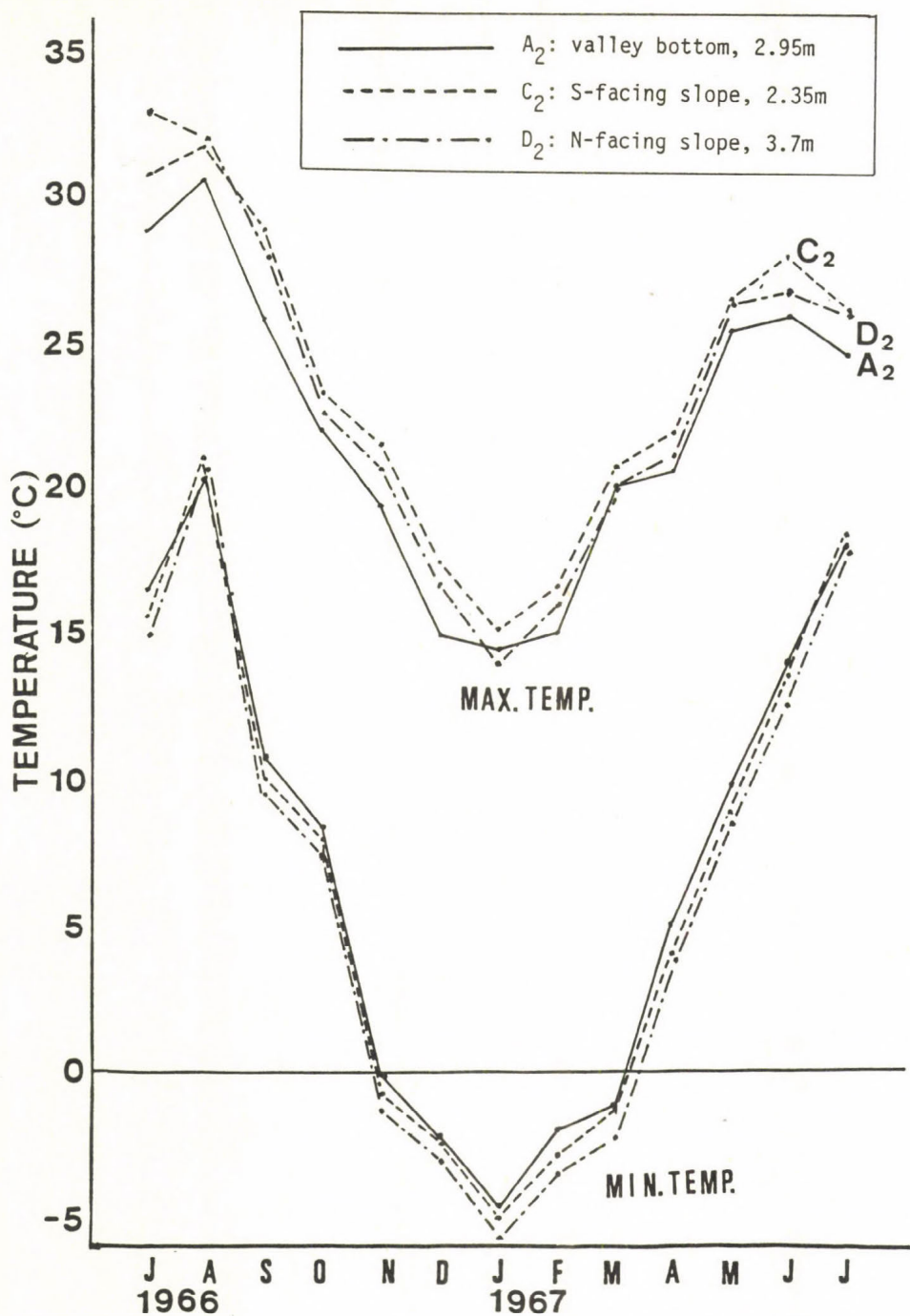
<u>Fig. 7.</u> Monthly maximum and minimum temperatures on upper trunks in the valley bottom, and on S- and N-facing slopes.
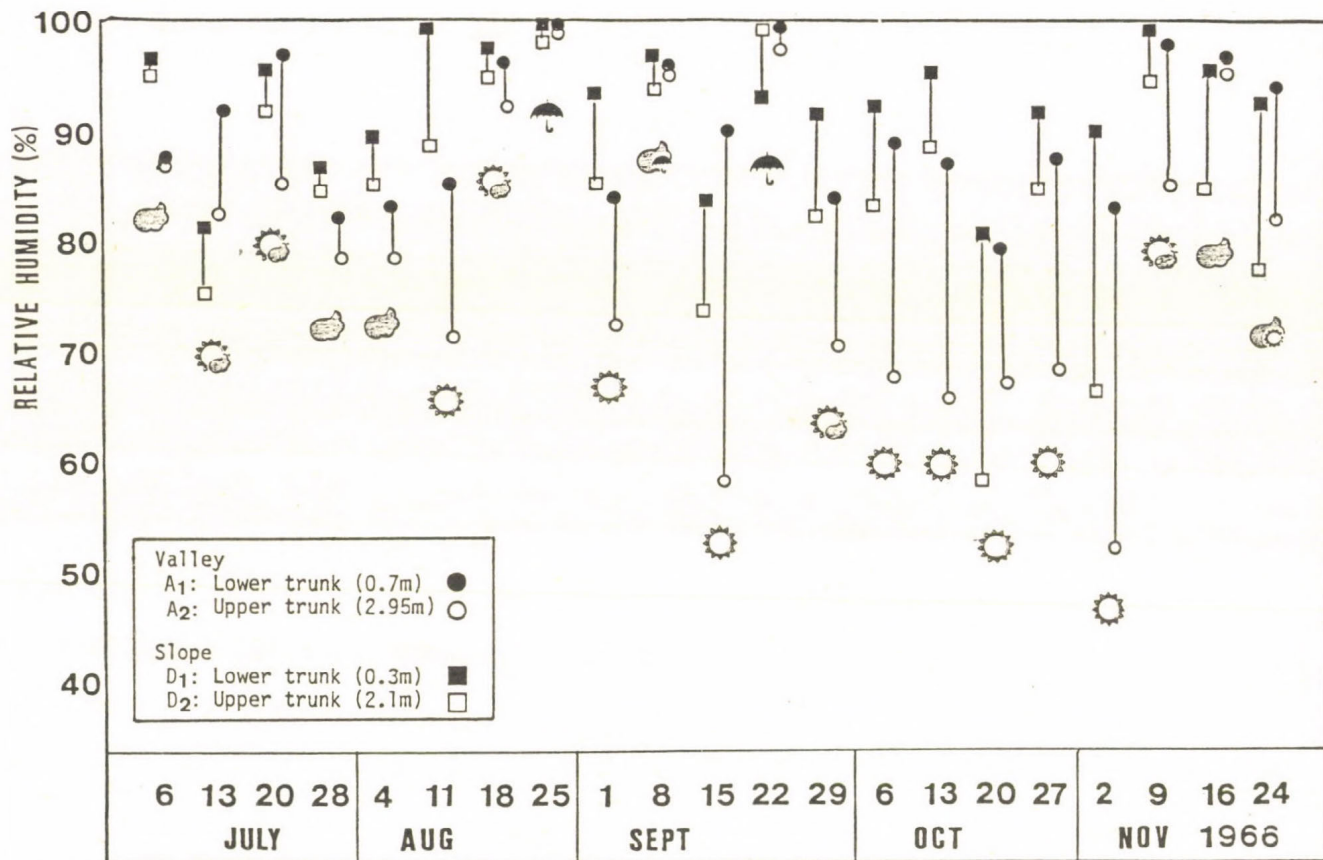
Fig. 8. Relative humidity measured by Assmann aspirated psychrometer at around 11 a.m. on valley bottom and on slope.

Table 1. Evaporation at valley bottom and on slope, Inotani Valley, west of Nichinan. Value indicates evaporation per day from 38.9 cm^2 (measured every 7 days) petri dishes which were set at 30 cm and 100 cm above the ground. (cm^3).

1968	Valley bottom		Slope	
	30 cm	100 cm	30 cm	100 cm
May 10	1.4	3.5	4.3	6.8
May 17	1.9	6.9	6.6	9.3
May 24	0	1.4	1.7	8.9
May 31	0.7	2.6	2.3	3.3
June 6	1.5	2.7	3.7	5.3
June 16	0.3	1.0	3.7	5.7
August 8	0.9	1.1	1.9	2.7
Average	0.95	2.74	3.45	6.00

forests (e.g., Wolfe et al. 1949, Osting & Hess 1956). However, almost no reports have focussed on epiphytic pendulous mosses and epiphyllous liverworts.

We have been much interested in the habitats of those tropical and subtropical epiphytic bryophytes at Inotani Valley, southern Japan. They are absent or very rare at low altitudes in this area, but are found in the deep valleys above 100 m. Furthermore, they are found usually in the valley bottom and are absent or very rare on slopes.

Measurements of temperature at different heights on trees at the valley bottom and on slopes show considerable difference in these different microenvironments. It is quite interesting that in the valley bottom minimum temperatures are almost the same throughout the year at different levels on trees, although maximum temperatures are always higher on higher level of trees. Climate in the valley bottom is quite equable, not very warm in the summer season, not very cold in winter, compared with that on slopes or even low altitude (Aburatsu).

Humidity gradients and bryophyte zonation in the Afromontane forests (South Africa) were reported by Russell (1983). Measurements of relative humidity and evaporation at Inotani Valley show that the valley bottom, where abundant growth of epiphytic and epiphyllous bryophytes is seen, is much more humid than on slopes. It is also quite clear in this area that it is much drier at high levels than at low levels on trees.

According to our field observations, many bryophytes of this area start growing in early autumn. Abundant new shoots are also observed in spring, but they do not grow in summer. Some mosses have new sporophytes in late autumn; other species have them in spring. Furness & Grime (1982) examined 40 British species of mosses, and reported the optimal temperature for growth in the majority of species under controlled laboratory conditions was between 15 and 25°C. They also said that all species were killed, often very rapidly, when maintained in a continuously moist condition at 35°C and many species died eventually when kept continuously at temperature above 30°C. In our experience in culturing bryophytes (including Takakia), temperature above 30°C is usually fatal for many bryophytes, even for many tropical species.

At the bottom of Inotani Valley, it is relatively cool in summer and relatively warm in winter, and constantly humid throughout the year. This climatic condition might be essential for abundant growth of pendulous mosses and epiphyllous liverworts. It seems reasonable to consider pendulous mosses and epiphyllous liverworts to be good indicators of a special microclimate.

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LIGHT AND EPIPHYLLOUS LIVERWORTS IN THE SUBTROPICAL EVERGREEN FORESTS OF SOUTH-EAST CHINA

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Epiphyllous liverworts are abundant in tropical and sub-tropical evergreen forests in China. In November 1983, we measured the illumination in the open and in the habitats of epiphyllous liverworts in sub-tropical evergreen forests in the Wuyi Mountains, South-east China. The ratio between light intensity outside the forest and in the habitats of epiphyllous liverworts in forested ravines varied from 1.4 to 632; it was high in the early and middle part of the day, but low in the evening. Epiphyllous liverworts appear to require about 2 hours' direct light and 10 hours' diffuse light in winter. Light, temperature and humidity are the three main factors influencing their distribution.

INTRODUCTION

Epiphyllous liverworts are one of the characteristic features of tropical rain-forests. In China, epiphyllous liverworts are abundant both in the tropical rain-forests and the subtropical evergreen forests. We still do not know in detail the relationship between habitat factors and the occurrence of epiphyllous liverworts, but light, humidity and temperature are three main factors of the environment which influence their distribution. Epiphyllous liverworts are peculiar plants ecologically. Kono (1967) studied the relationship between their occurrence and environmental factors. In an earlier study, Chen and Wu (1964) had concluded that temperature and

humidity are the main factors influencing these plants in
China. Since then, our observations have suggested that light
is one of the most important factors influencing their growth.
Up to now more than eighty species of epiphyllous liverworts
have been found in tropical and subtropical evergreen forests
in China. None of them are found in very shady or dark forests,
although temperature and humidity are still very important
factors. We were interested to compare environmental conditions
in the tropical and subtropical forests. In the winter of 1983,
from 20-30 November, we did a series of experiments on the re-
lation of epiphyllous liverworts to light in the subtropical
evergreen forests of Wuyi Mt., a representative mountain re-
gion in South-east China.

THE SITE: LOCATION AND ENVIRONMENTAL CONDITIONS

The Wuyi Mountains (Wuyi Shan) are located at the north-
west border of Fukien Province; their highest peak is 2158 m
above sea level. In the ravines of this mountain region the
main forests are subtropical evergreen forests consisting of
<u>Fagaceae</u>, <u>Cameliaceae</u>, <u>Lauraceae</u>, etc., and most of the first
stratum trees are 12-15 m high (Fig. 1). The slopes by the
streams are mostly 30-35°, with epiphyllous liverworts abun-
dant on the leaves from 0.5-2.0 m above the ground. Epiphyl-
lous liverworts grow best where the width of the ravines is
about 6-10 m. If the width of the ravine is less than about
5 m, the light is too dark, while if the width of the ravine
is more than 10 m the light becomes too strong.

Winter is the dry season in the Wuyi Mountains, and the
relative humidity in the ravines usually averages more than
80%.

METHODS

We first chose sites in the subtropical evergreen forest
beside streams in ravines where epiphyllous liverworts were
present. We did not record the individual species separately,

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but treated them as a group or population. The commonest species are <u>Leptolejeunea</u> <u>elliptica</u>, <u>Radula</u> <u>acuminata</u>, <u>Cololejeunea</u> <u>ocelloides</u> and <u>Frullania</u> <u>moniliata</u>. Generally, leaves with epiphyllous liverworts at 0.5 m, 1 m, 1.5 m and 2 m were taken as sample points for measurement, and the illumination both inside and outside the forest was recorded. We measured every sample point six times a day, at two-hourly intervals. The illumination in the forests inside and outside the ravines was also recorded.

Our measurements were made using a JP-1 photoelectric luminosity meter (Jia-Ding-Xue-Lian Instrument and Meter Plant, Shanghai). The spectral response of this instrument conforms to the standard CIE brightness curve.

Fig. 1. The landscape of the ravine of Er-Li-Ping in Wuyi Mt., SE China, showing the subtropical evergreen forest and the localities (x) of the epiphyllous liverworts.

RESULTS

In the classical subtropical evergreen forests in South-
east China, the observations show that, as a group, the epi-
phyllous liverworts need at least two hours' direct light and
about 10 hours' diffuse light per day in the winter season.
Our first daily measurement was made at 8 a.m., with successive
measurements at two-hour intervals (Fig. 2). At 8 a.m. and 6
p.m. illumination was very low, and measurements inside and
outside the forest were very close. After 10 a.m. the curve
rises immediately, with the highest period from noon to 2 p.m.
reaching 12000 lx. The lowest values (5 lx) were recorded in
the evening; equally low values would be found in early morn-
ing. The ratio of the illumination in sites with epiphyllous
liverworts in the forested ravines to that outside the forest
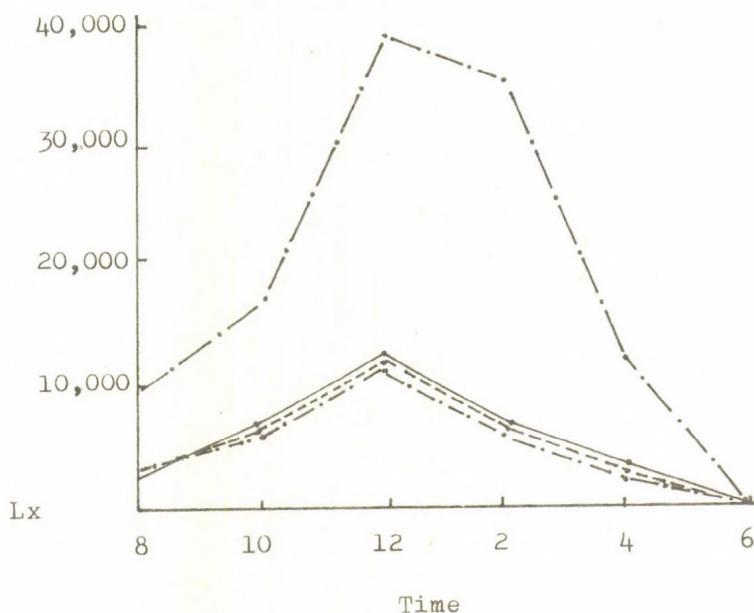
Fig. 2. Comparison of illumination at sample sites in habitats
of epiphyllous liverworts in evergreen forest in ravines with
illumination outside forest, showing variation in the course
of the day from 8 a.m. to 6 p.m. -·-·- : leaves at 0.5 m,
----: leaves at 1.0 m, ——: leaves at 1.5 m, ——·——: outside
the forest.

is 1.4-632 (Fig. 3). This ratio is high in the early and middle
part of the day (with peaks at 8 a.m. and 2 p.m.), but declines
towards evening, probably because the sun then shines directly
onto the leaves with the epiphyllous liverworts.

It is probably for this reason that the epiphyllous liver-
worts usually grow on the leaves of the second stratum of trees
facing the ravines, but not at the top of trees facing the
open slopes (Fig. 1). On the other hand, epiphyllous liverworts
could be found rarely on leaves within 10 m from the ravines.
The results from different heights in the forest are very
similar; as Fig. 2 shows, illumination at 0.5 m is very similar
to that at 1.0 and 1.5 m.

Nevertheless, in addition to light, temperature and
humidity are also very important to the epiphyllous liver-
worts, and constitute the three main factors influencing their
growth.
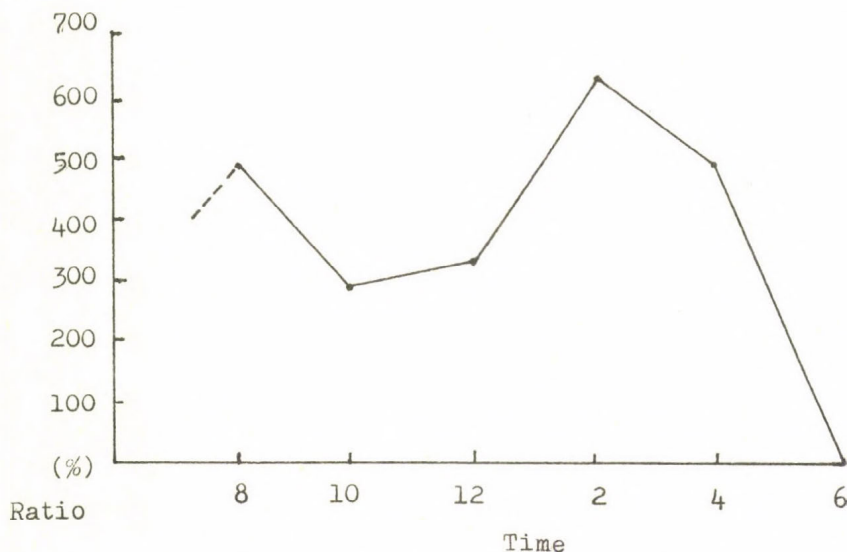
Fig. 3. Ratio of illumination outside forest and illumination
inside forest in habitats of epiphyllous liverworts.

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CHANGES IN SOIL PH ALONG THE ZONATION OF CRYPTOGAMOUS SYNUSIA AT BUGAC (HUNGARY)

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The characteristic zonation of lichens and mosses was
studied in the open Juniperus forest of sand hills at Bugac
(Kiskunság National Park, Hungary). Changes in species
composition and abundance of cryptogams throughout the zones
were detected. As an effect of cryptogam succession, changes
in soil pH values were measured.

INTRODUCTION

Cryptogamous synusia have a leading role in the initial
stages of succession of vegetation, especially in sandy
areas.

In the open Juniperus communis forest of Bugac (Kiskun-
ság National Park, Hungary) a characteristic pattern of
cryptogams can be found around the individual juniper trees
(Gallé 1976). As a result of succession, a fairly regular
zonation of the cryptogams has been formed under the shelter
of the canopy. The closer the zone to the trunk, the richer
is in species and higher in species abundance. This, to a
certain extent a retarded process of cryptogamous succession,
results a rather small-scale pattern of zonation. It has
different effects on microhabitat,   particularly on soil
characteristics. Under such circumstances, a definite gradient
of soil pH can be detected along the transect crossing the
subsequent zones.

MATERIAL AND METHODS

Bugac is situated in central Hungary in the territory of
the Kiskunság National Park, on alluvial calcareous sand from
the Danube River.

The relief formed during the Holocene. Bugac is an area
of sandy hills with relative heights of 3-10 m. The annual mean
temperature is $10.6^{\circ}C$, annual mean precipitation is 510 mm.
The zonal vegetation of this rather continental region is forest
steppe. On the sand hills (or dunes), as a result of secondary
succession, sparse stands of Juniperus communis and Populus
alba are typical (Simon 1979, Tölgyesi 1979, Simon & Rajkai
1985).

The soil formation in this area is in an initial stage;
the sandy soil has low organic matter content and water holding
capacity, so the limiting factors of succession are the low
level of soil moisture and nutrients, especially N (Snakin et
al. 1984).

In the characteristic belt of cryptogams surrounding the
junipers, one can distinguish between 2-4 zones which differ
from one another in species composition, species richness and
abundance. Most often, three zones (Tortella-dominated, lichen-
dominated, and Hypnum-dominated) can be observed. The width
of the zones depends on the height of junipers and also on the
microrelief.

We selected a well-developed four-staged zonation for the
present study. It is situated at the foot of a NE slope on a
medium-sized dune, and it was shaded by tall trees. Due to
this special position, more species were found here than usual.
The transect crossing the zones was about 6 m long and the
width of the different zones was 1.5 - 1.5 - 1.0 - 2.0 m.

In July, 1985, pH measurements were made in the four
zones under field conditions. We measured in dry soil at a
depth of 5 cm, where soil moisture content made it possible,
and after watering in mositened soil at a depth of 1 cm. For
the measurements, the "in situ" ionometric method developed
in the Soil Institute of the Soviet Academy of Sciences was

employed (Zykina et al. 1978). Glass electrodes, Ag/AgCl reference electrode and, as a detector, an I-102 ionometer were used.

RESULTS

The results are summarized in Table 1. As seen, the first zone, which represents the first successional stage from the bare sand, is characterized by the presence and dominance of extremely xerotherm species (Tortella inclinata and Diploschistes muscorum) with a cover of about 50%.

In the subsequent stages, the species richness increases. Species diversity reaches its maximum in the third zone. At the same time, a gradual shift of species is associated with an increase in total cover. It is worth mentioning that in the fourth stage the dense moss layer of Hypnum cupressiforme and Thuidium abietinum covers entirely the soil surface, and on this carpet a second layer of lichens has been formed. The lasting existence of such a zonation is likely due to the gradually weakened sheltering effect of junipers.

The zonation os cryptogams is accompanied with a pH gradient in the soil, which is the result of acidic substances produced by lichens and mosses; the beginning of a slight biological activity and the formation of humic materials in the soil. This process is the first step of soil development. The decrease in pH values during succession is more definite in the upper horizon of the soil, although the biotic effect of cryptogams can be detected at a depth of 5 cm as well. In this case the range of pH alteration is narrower. In the initial stage of succession (Tortella- and Diploschistes-dominated zone) the soil pH is the same as that of bare sand. The greatest change takes place when succession proceeds from the second to the third stage, where a leap can be measured in the pH of the soil.

Table 1. Changes in species composition, abundance and soil pH in the different zones of cryptogamous synusia at Bugac, on 5-6. 7. 1985.

Zones (successional stage)	Species present	Cover (%)	Mean pH values (based on 6 measurements each)			
			5 cm moisture = 2%		1 cm moisture = 6%	
bare sand					7.96	s = 0.70
I.	Tortella inclinata	50				
	Diploschistes muscorum	7	8.04	s = 0.20	8.00	s = 0.16
	Cladonia magyarica	5				
II.	Tortella inclinata	60				
	Cladonia magyarica	70				
	Diploschistes muscorum	15	7.90	s = 0.09	7.82	s = 0.25
	Cladonia convoluta	5				
	Toninia coeruleo-nigricans	2				
III.	Tortella inclinata	40				
	Diploschistes muscorum	30				
	Cladonia magyarica	20				
	Cladonia convoluta	40	7.69	s = 0.41	7.19	s = 0.23
	Parmelia pokornyi	1				
	Hypnum cupressiforme	10				
	Thuidium abietinum	5				
	Tortula ruralis	1				
IV.	Thuidium abietinum	60				
	Hypnum cupressiforme	40	7.33	s = 0.29	7.07	s = 0.32
	Cladonia furcata	20				
	Cladonia convoluta	10				

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WATER RELATIONS AND NUTRIENT STATUS OF BRYOPHYTE COMMUNITIES AT MARION ISLAND (SUB-ANTARCTIC)

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An outline is given of the existing phytosociological classification of bryophyte-rich communities at Marion Island. Detailed relevé data recorded at the time of the original survey indicate soil moisture as a principal factor controlling bryophyte distribution. Studies of bryophyte water relations at Marion Island support this conclusion while emphasising the additional role of nutrient status in relation to species composition, especially at biotically influenced and well-drained sites.

INTRODUCTION

The Prince Edward Island, including Marion Island ($46°54'S$, $37°45'E$), are the northernmost of the islands of the Sub-Antarctic botanical zone recognised by Greene & Walton (1975). Bryophytes are an important part of the Marion Island eco-system, contributing approximately 25 % of the total lowland plant biomass, increasing locally to 60%, e.g., in Agrostis mires (V. Smith 1978), and approaching 100% in higher altitude fellfield habitats. Bryophyte production studies were carried out by the author in 1980-1982 and results have been published along with information on bryophyte energy and chlorophyll values in Russell (1984, 1985). Supplementary data on water relations and nutrient status of the principal bryophyte species of Marion Island were collected during the productivity investigations and the results of these studies are presented here.

METHODS

Gremmen (1982) analysed 510 relevés for the phytosociological survey of Marion Island. For the bryophyte production study, 15 species with the highest cover values (greater than 75% in a high proportion of the relevés) were selected as representatives of the six major plant community complexes recognised by Gremmen. The study species are listed by community (sub-association) and community complex (habitat) in Table 1. The arrangement is based on an observed xerix-hydric soil moisture gradient, with values for each community calculated from the multiple releve data of Gremmen (1982). The liverwort Clasmatocolea vermicularis is characteristic of both biotic and saltspray zones on Marion Island. These community complexes do not form part of the xeric-hydric sequence and are shown last in the table.

Eight core samples of each of the 15 bryophyte species were collected from the production study sites on each of three dates during the first quarter of 1981 to allow for rainfall/water table fluctuations. Cores of plant material were weighed, then centrifuged at 1500 r.p.m. for one minute to remove external capillary water (Gimingham & Smith 1971). After further weighing, the cores were oven dried at $80^{\circ}C$ for 24 hours and reweighed. Marion Island soil cores required oven drying at this temperature for up to 36 hours to reach constant weight.

A crude assessment of water retention was obtained for the 15 species by weighing for water loss after air drying overnight in a controlled environment room maintained at 35% relative humidity and $20^{\circ}C$. Stems were first saturated and centrifuged to allow comparison with the data of Gimingham & Smith (1971).

For the plant chemical analyses, five replicate core samples of the 15 bryophyte species were collected from the study sites in May 1982. Samples were taken of the current year's growth as defined during the production study (Russell 1984). 200 mg subsamples of dried, ground, plant material

Table 1. Principle bryophyte species of Marion Island and the communities in which they occur arranged according to soil moisture gradient.

No.	Species	Sub-Association	Soil water content (%)	Habitat
1	Brachythecium subplicatum	Brachythecietum subplicati inops	2896	Drainage Line
2	Distichophyllum fasciculatum	Distichophylletum fasciculati	2333	Wet
3	Drepanocladus uncinatus	Junco-Drepanocladetum clasmatocoleetosum	1882	
4	Campylopus arboricola	Blepharidophyllum-Clasmatocoleetum ranunculetosum	1832	
5	Breutelia integrifolia	Bryo-Breutelietum uncinietosum	1652	
6	Ptychomnion ringianum	Uncinio-Ptychomnietum	1650	Mire
7	Clasmatocolea humilis	Blepharidophyllo-Clasmatocoleetum clasmatocoleetosum	1633	
8	Blepharidophyllum densifolium	Blepharidophyllo-Clasmatocoleetum blechnetosum	1160	
9	Jamesoniella colorata	Lycopodio-Jamesonielletum ranunculetosum	1041	
10	Jamesoniella grandiflora	Jamesonielletum grandiflorae	779	
11	Racomitrium lanuginosum	Lycopodio-Jamesonielletum catagonietosum	770	Dry
12	Brachythecium rutabulum	Isopterygio-Blechnetum brachythecietosum	588	Slope
13	Ditrichum strictum	Andreaeo-Racomitrietum crispuli	85	Fellfield
14	Andreaea acutifolia	Andreaeo-Racomitrietum crispuli	85	
15	Clasmatocolea vermicularis	Montio-Clasmatocoleetum vermicularis	1081	Biotic / Salt Spray

were digested in HNO_3-$H_2SO_4HClO_4$ mixture. P concentrations in dilutions of the digest were determined using a phosphomolybdate-blue procedure (Murphy 1962), the H^+ concentration of the colour-developing reagent being adjusted to compensate for the acidity of the digest. Ca, Mg, Na and K concentrations were determined on suitable dilutions of the digest by atomic absorption spectrophotometry, lanthanum (in HCl) suppressant being added to the aliquots for Ca determination. Kjeldahl N was measured by a modified Solorzano colourimetric procedure (V. Smith 1985), after digesting subsamples of the dried, ground plant material in H_2SO_4-K_2SO_4-$CuSO_4$ mixture.

WATER RELATIONS

Average total water content of eight cores of bryophyte material per species are graphed in Fig. 1.a for each of the three sampling dates. Total water comprises internal apoplast and symplast water plus external capillary water (Dilks & Proctor 1979). External water was measured on the last two dates only and is graphed in Fig. 1.b.

Fluctuations in the generally high level of precipitation (2500 mm p.a.) are known to affect ground water levels on Marion Island (Gremmen 1982). Such fluctuations may also have an effect on bryophyte tissue water content as suggested by the increased level of total plant water content measured in February 1981, which appears to correlate with the higher level of rainfall recorded in the preceding month. The percentage component of external water remained fairly constant in the following two months, however, with an average variation between species of only 4.9% between February and March.

The degree of variability of the inter monthly means is indicated in Table 2 and the integrated averages show clearly the lower water contents found in species of the exposed fellfield habitat. A high value was obtained in the drainage line species and an intermediate value in the slope species. Reference to these data and Fig. 1 will show that the range of water contents found in the mire species exceeds that
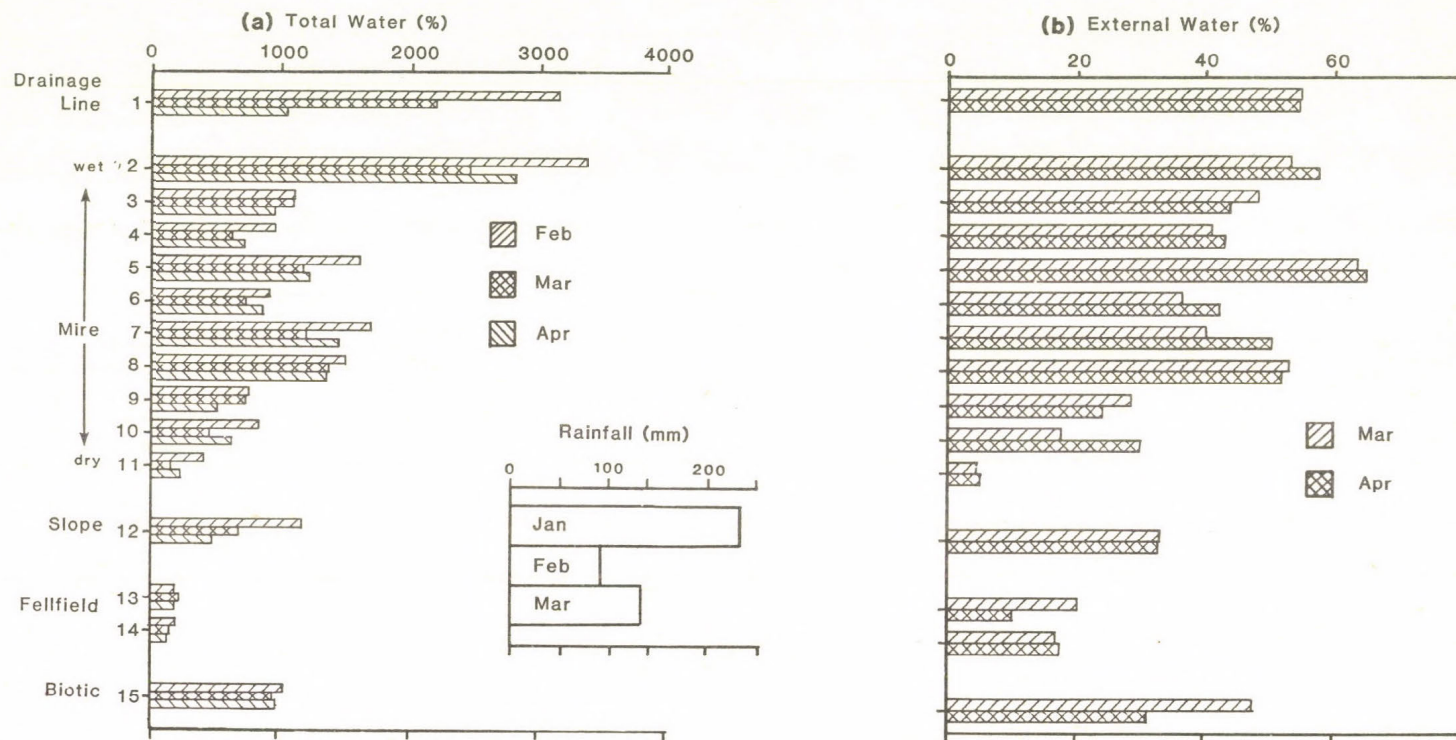
Fig. 1. a) Total field water content (% dry weight) measured on three dates, and b) external water (% of total water) measured on two dates in 1981 for Marion Island bryophytes. Total rainfall for the month before each collection date is indicated in the smaller graph. Species are numbered as in Table 1.

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Table 2. Total plant water content (%, 3-month mean ± standard deviation), external water content (%, 2-month mean ± standard deviation) and soil moisture (%) at bryophyte growth plots.

Species	Total water		External water		Soil water
Brachythecium subplicatum	2133	+ 166,5	54,8	+ 7,5	2787
Distichophyllum fasciculatum	2878	+ 137,0	55,5	+ 1,9	2396
Drepanocladus uncinatus	1058	+ 54,7	46,1	+ 4,7	1808
Campylopus arboricola	776	+ 52,5	42,0	+ 2,9	2469
Breutelia integrifolia	1339	+ 64,0	64,2	+ 1,3	1599
Ptychomnion ringianum	841	+ 91,9	39,4	+ 6,3	1480
Clasmatocolea humilis	1449	+ 47,7	45,3	+ 1,9	1417
Blepharidophyllum densifolium	1413	+ 103,4	52,5	+ 1,5	2216
Jamesoniella colorata	674	+ 76,3	26,3	+ 5,0	1299
Jamesoniella grandiflora	641	+ 29,5	23,7	+ 2,8	746
Racomitrium lanuginosum	264	+ 18,4	4,9	+ 1,9	895
Brachythecium rutabulum	781	+ 67,9	32,8	+ 5,0	649
Ditrichum strictum	202	+ 12,8	15,3	+ 3,6	260
Andreaea acutifolia	158	+ 12,6	17,1	+ 3,3	184
Clasmatocolea vermicularis	988	+ 77,5	39,3	+ 6,1	895

round between the fellfield and drainage line habitats and further reflects the xeric-hydric soil moisture gradient demonstrated by Gremmen (1982).

Water contents of soil cores collected from the bryophyte study plots are shown in Table 2. The values agree closely (r = 0.9131) with soil moisture means calculated from the relevé tables of Gremmen, for the communities in which these species are dominant (Table 1). Correlation between soil water content and plant water content is reasonable (r = 0.7640 and 0.7645, respectively, for total and external water) considering the lack of an absorptive root system in bryophytes and the susceptibility to rainfall fluctuations noted above.

The results of the thirteen-hour desiccation test are in-dicated in Table 3. Water retention appears to be closely link-ed to growth form of the species. Growth form and stem spacing data (from Russell 1984) are included in Table 3, and compari-son of the information allows the following generalisations. Those species with less robust growth form and higher areal stem densities (> 20 cm^{-2}) tend to be most resistant to drying out, i.e., the cushion and mat growth forms, all of which re-tained more than 25% of their initial water content. Those species with more robust growth form and lower stem densities (< 25 cm^{-2}) were less resistant to drying out, i.e., the carpet and weft types, which all retained less then 35% of their initial water content.

The tall-turf growth form gave variable results, but open-ness of growth habit appeared to outweigh factors such as erect, parallel branch arrangement or dense rhizoid felts where water retention was concerned. Those turfs with stem densities of more than 20 cm^{-2} retained more than 40% of the initial water, with the converse true of those with greater than 20 shoots per cm^2 spacing.

Percentages of water remaining after the drying period have been graphed against the initial water content in Fig. 2 to allow comparison with the data of Gimingham & Smith (1971) from Signy Island. Species of permanently wet habitats and water tracks on Signy Island and Marion Island, e.g., certain

Table 3. Growth form, stem density and water content after a 13-hour desiccation period in Marion Island bryophytes. Water content after desiccation is expressed as a % of internal water content at the start of the experiment.

Species	Growth form*	Mean shoot density per cm^2**	Retained water (%)
Clasmatocolea vermicularis	Mat, thread-like form – tall turf	106,5	53,5
Blepharidophyllum densifolium	Tall turf, branches erect	42,0	51,7
Clasmatocolea humilis	Short – tall turf	100,0	50,8
Campylopus arboricola	Tall turf with dense rhizoid felt	26,3	49,0
Ditrichum strictum	Large cushions	23,7	48,9
Jamesoniella grandiflora	Mat, thread-like form – tall turf	40,2	47,6
Distichophyllum fasciculatum	Tall turf, branches erect	49,7	37,9
Andreaea acutifolia	Small – large cushions	280,0	35,2
Drepanocladus uncinatus	Carpet	15,8	31,7
Jamesoniella colorata	Mat, thread-like form – tall turf	47,7	28,1
Ptychomnion ringianum	Tall turf, branches erect	4,3	11,9
Racomitrium lanuginosum	Carpet	4,5	6,9
Breutelia integrifolia	Tall turf with dense rhizoid felt	16,0	4,7
Brachythecium subplicatum	Carpet	23,2	3,6
Brachythecium rutabulum	Weft	19,2	3,1

Brachythecia, occupy similar positions in the centre left of
the scatters in both diagrams (group 1). Species of drier,
mire margin habitats occur towards the lower left of the
scatter (group 2), and species of exposed, fellfield habitats
also correspond in position on the lower right of both graphs
(group 3). The species of the central groups 4 and 5 on Signy
Island (wet rocks and flushes, and peat banks, respectively)
do not have taxonomic/ecological counterparts among the species.
studied on Marion Island, and this area of the graph is cor-
respondingly blank in Fig. 2.b. Liverwort mats and turfs of
the mire habitat are, however, more important on Marion Island,
as evidenced by the group of species to the upper right of the
scatter in Fig. 2.b (group 4). Drepanocladus uncinatus also
occurs in group 4 on Marion Island as a species of the wettest
mire habitats. On Signy Island, however, the same species
occurs only on temporarily wet groun at swamp margins (group
2) according to Gimingham & Smith (1971).

NUTRIENT STATUS

The mean results of the mineral element determinations are
given in Table 4. Totals of each element for all bryophyte
species are given in the bottom row and totals of all elements
for each species in the last column. The species are arranged
in their habitat groupings on the xeric-hydric moisture gra-
dient as in Table 1. Mean values for each habitat are graphed
in Fig. 3. Values are expressed on a dry weight basis, for the
current year's growth as determined during the production
study (Russell 1984). This manner of expressing the data al-
lows easy comparison with the results of other workers in
the tundra biome but, see provisos of Brown (1982) concerning
the potential influence of differing cation exchange capacities
and acropetal nutrient translocation when making interspecific
comparisons on this basis.

Mineral nutrient levels (N, P, K and Ca) are highest in
the species of the drainage line, slope and biotic habitats.
As Walton & Smith (1979) found on South Georgia, species of
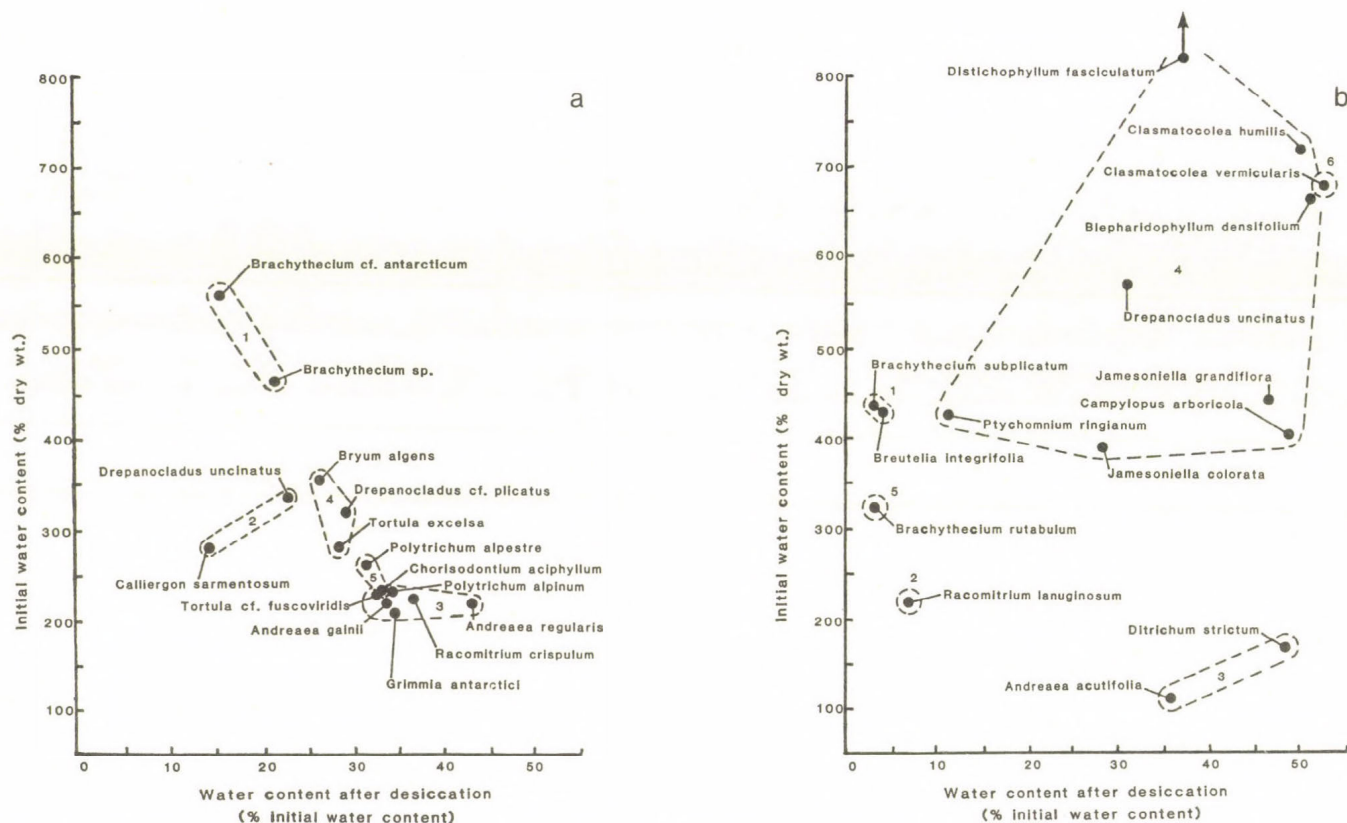
Fig. 2. Relationship between initial water content, water content after a period of desiccation and habitat occupied in 15 bryophyte species from a) Signy Island (modified from Gimingham & Smith 1971) and b) Marion Island. Numbered habitat zones explained in text.

Table 4. Mineral content (% dry weight, mean ± standard deviation) for Marion Island bryophytes.

	N	P	K	Mg	Ca	Na	Total Minerals
Brachythecium subplicatum	0.656 +0.033	0.220 +0.013	1.184 +0.052	0.326 +0.016	0.501 +0.030	0.118 +0.009	3.010
Distichophyllum fasciculatum	1.279 +0.067	0.147 +0.013	1.184 +0.086	0.668 +0.019	0.325 +0.025	0.855 +0.087	4.460
Drepanocladus uncinatus	0.995 +0.107	0.124 +0.062	0.653 +0.070	0.280 +0.006	0.175 +0.009	0.116 +0.012	2.343
Campylopus arboricola	0.596 +0.033	0.064 +0.003	0.235 +0.011	0.101 +0.012	0.173 +0.021	0.193 +0.024	1.362
Breutelia integrifolia	0.909 +0.125	0.090 +0.037	0.536 +0.201	0.463 +0.020	0.483 +0.025	0.143 +0.013	2.624
Ptychomnion ringianum	0.831 +0.102	0.068 +0.003	0.247 +0.013	0.197 +0.010	0.218 +0.005	0.060 +0.008	1.621
Clasmatocolea humilis	0.789 +0.054	0.081 +0.041	1.680 +0.106	0.207 +0.009	0.161 +0.010	0.355 +0.063	3.273
Blepharidophyllum densifolium	0.577 +0.041	0.056 +0.028	1.185 +0.067	0.425 +0.013	0.255 +0.012	0.347 +0.042	2.845
Jamesoniella colorata	0.560 +0.054	0.054 +0.027	0.349 +0.008	0.292 +0.007	0.215 +0.012	0.121 +0.005	1.590
Jamesoniella grandiflora	0.774 +0.038	0.043 +0.022	0.341 +0.032	0.294 +0.008	0.276 +0.007	0.101 +0.016	1.829
Racomitrium lanuginosum	0.645 +0.000	0.048 +0.000	0.107 +0.000	0.171 +0.000	0.120 +0.000	0.041 +0.000	1.132
Brachythecium rutabulum	1.069 +0.108	0.141 +0.010	0.796 +0.025	0.373 +0.009	0.506 +0.115	0.138 +0.019	3.023
Ditrichum strictum	0.412 +0.004	0.068 +0.034	0.099 +0.009	0.465 +0.041	0.128 +0.033	0.021 +0.017	1.193
Andreaea acutifolia	0.682 +0.000	0.093 +0.000	0.107 +0.000	0.524 +0.000	0.188 +0.000	0.075 +0.000	1.669
Clasmatocolea vermicularis	1.338 +0.032	0.183 +0.012	1.871 +0.125	0.280 +0.014	0.235 +0.023	0.489 +0.066	4.396
$\bar{x}$	0.887 +0.134	0.099 +0.027	0.705 +0.293	0.338 +0.075	0.264 +0.066	0.212 +0.111	

the fellfield habitat show the lowest values for most minerals
with the exception of Mg. R. Smith (1985) suggests that plants
of dry mineral soils may occasionally show high levels of
minerals when concentrations in the substrate rocks are high.
MgO is present in the alkali trachy-basalts of Marion Island,
at concentrations of up to 14% (Verwoerd 1971) and may there-
fore account for this result.

   Mean mineral nutrient values are generally low for the mire
species but as in the water relations study, interspecific
variability is great owing to the heterogeneity of the habitat.
For example, the lowest values of P and Mg found in this
study occurred, in dry mire habitats, in Jamesoniella grandi-
flora and Racomitrium lanuginosum respectively; whereas the
highest levels of Mg and Na were found in Distichophyllum
fasciculatum of the wettest mires.
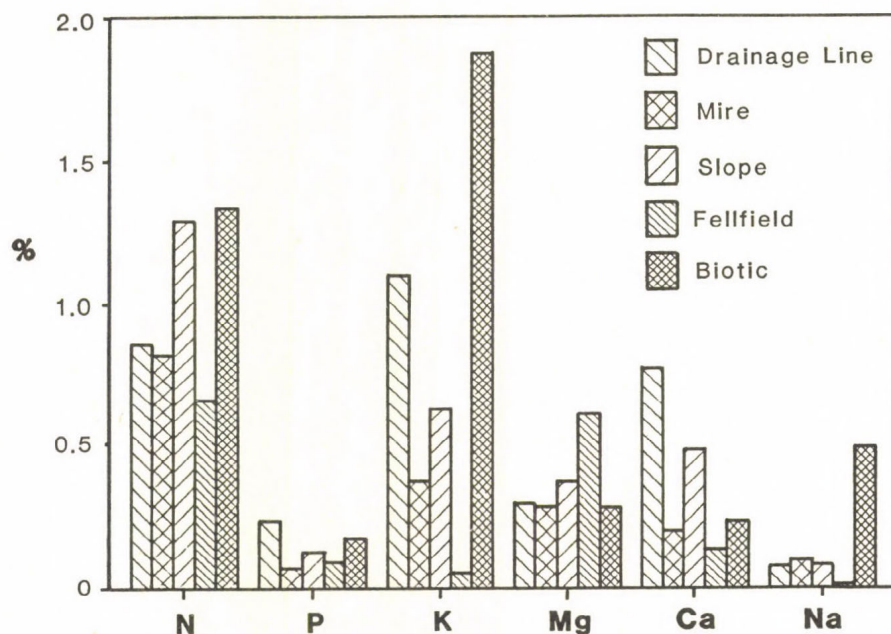
Fig. 3. Mean macronutrient levels (% dry weight) in Marion
Island bryophytes grouped according to habitat.

The biotic habitat is influenced by bird and seal manuring and by salt spray from the nearby coast. Clamatocolea vermicularis from this habitat shows correspondingly high levels of N, K and especially Na.

P and Ca levels are high in the drainage line moss Brachythecium subplicatum. This species occurs in a habitat with a near neutral soil pH, and therefore shares a more minerotrophic character with mire flushes dominated by Breutelia integrifolia (Gremmen 1982). Both these habitats have pronounced lateral soil water flow and their bryophytes show high nutrient levels.

K is the most mobile macronutrient and is strikingly accumulated by mosses (Malmer & Nihlgaard 1980, Proctor 1981). Its mean level in Marion Island mosses (0.69%) is only surpassed by N concentration (0.81%). The high level of K in the bitoc zone may be due to uptake from marine sources as suggested by R. Smith (1978) for islands elsewhere in the Antarctic.

Tundra habitats are known to be relatively N-rich (Rosswall & Granhall 1980, Sikora & Keeney 1983) especially where high concentrations of moss-epiphytic, nitrogen-fixing cyanobacteria occur, e.g., in mires (Stewart 1974, Broady 1979). Such organisms are common and active on Marion Island and according to Smith & Russell (1982), occur with greatest abundance in association with Brachythecium subplicatum in the minerotrophic drainage line habitat. The fact that plant N levels are not outstandingly high in this habitat may therefore appear anomalous. However, loss of N from the system will be promoted by denitrification which may proceed more rapidly in the aerobic regime and neutral pH of the drainage line habitat. Leaching and fixation in the underlying peat will further deplete N-levels in this habitat (Sikora & Keeney 1983). This situation has been confirmed by Smith (1985) on South Georgia, where hydrophytic mosses such as Brachythecium were also found to have high concentrations of all minerals except N.

In common with the findings of Vitt & Pakarinen (1977), N and P levels are closely correlated in Marion Island bryophytes (r = 0.8827 when the anomalous drainage line species is

excluded from the calculation). The bryophyte N levels recorded
in this study are very similar to those found by other research-
ers working in tundra habitats (Northover & Allen 1967, Vitt
& Pakarinen 1977, R. Smith 1978, Walton & Smith 1979). Overall
nutrient levels in this study fall within the ranges for bryo-
phyte material quoted by Huneck (1984), except with regard to
the maxima for Mg and Na which can be considered superabundant
in coastal sub-Antarctic habitats due to the influence of salt
spray.

Several authors have noted the lack of complementarity
between soil and bryophyte mineral element concentrations
(Walton & Smith 1979, Longton 1980, Proctor 1981), due to the
ability of bryophytes to accumulate mineral ions selectively
from very dilute solutions. However, R. Smith (1978, 1985)
has noted some proportionality with substrate levels on Signy
Island. V. Smith (1977) noted a relatively high concentration
of Ca in soils of the drainage line habitat on Marion Island,
which may account for the high plant levels recorded in this
study. Mosses have a high exchange capacity for this divalent
cation and might be expected to accumulate high levels of Ca
where continually presented with the element in the constant
water flow of the drainage line habitat. V. Smith also noted
high mineral concentrations in slope ("fernbrake") soils,
which may account for the high nutrient levels recorded in the
moss Brachythecium rutabulum of the slope habitat. For all 15
species, a limited correlation ($r = 0.4124$) exists between
soil inorganic component (Gremmen 1982) and bryophyte ash con-
tent (Russell, unpublished data).

Lack of space forbids detailed consideration of nutrient
concentrations in the part of the shoot below the current
year's growth. However, this was measured (Russell, unpubl.
data) and it was found that P, K and Na decreased in the older
portions of the stem, while small increases were noted in some
species in the cases of Mg and Ca. The latter cations are more
strongly sorbed than K and Na, and are immobilized in the old
cell walls (Dowding et al. 1981, Proctor 1981). Nitrogen was
consistently present in higher concentrations in the older

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parts of the plant, which agrees with the findings of Allen et al.(1967) and Grubb et al. (1969). Brown (1982) suggested that the increase of N with age may be due to microbial growth, which is known to be important in bryophyte communities on Marion Island (Smith & Russell 1982).

DISCUSSION

The results of this study indicate that field water content and water retention follow a trend in Marion Island bryophytes, correlated with soil moisture and growth form. Species with compact growth form, low field water contents and high water retention occupy the exposed fellfield habitats, e.g., Andreaea acutifolia and Ditrichum strictum, while species with more open growth form, high water contents and low resistance to water loss occupy drainage line and wet mire habitats, e.g., Brachy-thecium subplicatum and Bruetelia integrifolia. A large group of mire species with high cover values can also be sequenced on the soil moisture gradient, and represent an ecological group that is important on the mord northerly sub-Antarctic islands, but is less prominent in the Maritime Antarctic. These species (mainly of the liverwort genera Blepharidophyllum, Clasmato-colea and Jamesoniella) have high field water contents but also relatively high resistance to water loss, at least in the short term, due to their closely packed mat or turf growth forms. This growth habit may adapt such species to the short periods of drying out associated with fluctuating water table levels on Marion Island.

Shoot production figures from Russell (1984) were regressed against data from the present study to provide the correlation coefficients shown in Table 5. Omitting the anomalous species Distichophyllum fasciculatum from the calculation (low pro-ductivity due to total submergence of stem apices during growth season) annual shoot production shows a close relationship with water content (r = 0.7902).

As might be expected for plants with predominantly ecto-hydric mode of nutrient assimilation, reasonable correlations

Table 5. Correlation coefficients indicating relationships between annual shoot production, water content and mineral content in 15 species of Marion Island bryophytes.

		N	P	K	Mg	Ca	Na
Shoot production	Total water content	0.4165	0.5618	0.6514	0.2929	0.3239	0.7605
	0.7902	0.0557	0.5235	0.4541	0.2329	0.5238	0.1571

between bryophyte element concentrations and water contents were also found (Table 5). However, there is a less obvious relationship between nutrient content and production (Table 5). For example, little correlation is seen between growth and N, Mg and Na concentration. As already mentioned, these elements can be regarded as super-abundant on Marion Island. P, K and Ca, however, occur at levels closer to the norms quoted by Huneck (1984) and correlate more closely with growth (Table 5). The low level of P found in this study and its relatively high correlation with production may therefore be significant with regard to the proposal of P as the principal limiting nutrient for bryophyte growth (Brown 1982, Babb & Whitfield 1977).

CONCLUSION

Bryophyte communities on Marion Island are characterised by species with field water contents consistent with habitat factors, e.g., soil water, degree of exposure, at their sites of occurrence. Bryophyte production is positively correlated with field water content and high nutrient levels may also contribute to the enhanced plant performance noted in minero-trophic habitats, e.g., drainage lines and mire water tracks.

Only one bryophyte species, Clasmatocolea vermicularis, reaches high cover values in the nutrient-rich/salt spray zone at Marion Island. This species also shows a high (short term) resistance to water loss and further investigations of the physiology of this interesting salt-tolerant leafy liverwort are currently continuing.

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IN VIVO STUDIES ON THE REGULATION OF NITRATE REDUCTASE IN SPHAGNUM SPECIES*

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An in vivo assay for nitrate reductase (NR) of Sphagnum species active under dark aerobic conditions has been developed. The assay was used to study some regulatory mechanisms of NO_3^- reduction in Sphagna.

NR activity of Sphagnum spp. is substrate inducible. This induction is correlated with NO_3^- concentration of the induction medium. The non-linear shape of the Lineweaver-Burk diagram (reciprocal plot of NO_3^- reduction versus NO_3^- concentration) suggests that more than one enzyme system is involved in NO_3^- reduction, e.g., NR, NO_3^- permease and NAD(P) generating enzymes.

NH_4^+ is not a significant regulator of nitrate reduction in Sphagnum. Experiments with six Sphagnum species show that under natural conditions (concentrations not higher than 0.1 mM) ammonium has only a slight effect on induction and activity of NR.

The addition of various metabolites and inhibitors to the in vivo assay medium led to the hypothesis that mainly GAP and NAD-GAPDH are responsible for the   generation of reducing

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* Abbreviations: AA amino acids, ADP adenosine diphosphate, ATP adenosine triphosphate, DHAP dihydroxyacetonephosphate, dw dry weight, Fd ferredoxin, F-1,6-bP fructose-1,6-biphosphate, GAPDH glyceraldehyde-3-phosphate dehydrogenase, NAD nicotine adenine dinucleotide, $NADH+H^+$ reduced NAD, NR nitrate reductase, P_i inorganic phosphate.

equivalents for NO_3^- reduction. The similar reaction of NAD-GAPDH and NR to NO_3^- application gives further support to the hypothesis that carbohydrate and nitrogen metabolism are linked via $NADH+H^+$ production and consumption. This linkage might be regarded as a mechanism of regulation of NO_3^- reduction in Sphagnum spp.

INTRODUCTION

While extensive literature on nitrate reduction in higher plants is available (reviewed by Beevers & Hageman 1980) little attention has been paid to this aspect of nitrogen metabolism in bryophytes (for references see Rudolph et al., these proceedings).

Rudolph & Voigt (1986) have shown that NO_3^- is essential for cultivating Sphagnum species. Ammonium at a concentration of 225 µM caused, e.g., growth inhibition and chlorophyll degradation, while nitrate (322 µM) had a beneficial effect on growth, chlorophyll content and rate of photosynthesis.

There are two main regulatory mechanisms of nitrate reduction in plants, regulation by amount and by activity of the key enzyme of nitrate reduction, nitrate reductase (NR). NR activity of Sphagna has been shown to be substrate-inducible (Deising & Rudolph, unpubl., Woodin et al. 1985, Press & Lee 1982). The kinetics of enzyme synthesis suggest that these species are capable of metabolizing NO_3^- rapidly (Deising & Rudolph 1985). These findings are consistent with the fact that NH_4^+ is the dominating nitrogen form in bog water and that NO_3^- is not detectable despite its presence in wet deposition.

Press and Lee (1982) have found that NH_4^+ is an important repressor of NR synthesis in Sphagnum spp. NH_4^+ effects on NR were demonstrated for higher plants (Orebamjo & Stewart 1975, Timpo & Neyra 1983). If, however, ammonium would really act as a strong regulator of NR induction in Sphagna, these plants could hardly utilize NO_3^- because of high NH_4^+ concentrations in bog water. In contrast to Press & Lee (1982) Deising and Rudolph (unpublished) and Woodin et al.

(1985) have found that inducible NR activity was little affected even at high NH_4^+ concentrations.

The regulation of NR activity in plants can be achieved by linking NO_3^- reduction to carbohydrate oxidation, mediated by regeneration and consumption of reducing equivalents. Different plant species use different carbohydrate sources (Kaplan & Lips 1984, Mann et al. 1978, Klepper et al. 1971). Therefore NO_3^- reduction must alter carbohydrate metabolism.

The aim of this study was to analyze the effect of substrate and co-substrate (reducing power) as well as of NH_4^+ on activity and induction of NR in Sphagnum spp.

MATERIAL AND METHODS

In all experiments Sphagnum magellanicum Brid. was used as the representative of the genus. Experiments on the effect of ammonium on NR activity were made with the following Sphagnum species: S. compactum DC., S. cuspidatum Hoffm., S. fallax (Klinggr.) Klinggr., S. fuscum (Schimp.) Klinggr., S. magellanicum Brid., and S. subnitens Russ. & Warnst.

Precultivation and cultivation of the plants were as described by Rudolph & Voigt (1985, unpublished). Depletion of Sphagna for NO_3^-, NR induction and the in vivo assay followed Deising & Rudolph (unpublished).

In vitro NAD-GAPDH assay

Enzyme extraction. Capitula with 2 cm of green stem were homogenized in three volumes of ice-cold 60 mM Tris-HCl buffer (pH 8.75), containing (mmol·litre^{-1}) $MgCl_2$ (10), EDTA (0.27), L-Cystein (4.13) and DTE (3.24), using an Ultra Turrax homogenizer. Filtration and centrifugation (15 min at 30,000 g) resulted in a clear crude extract which was used for NAD-GAPDH determination, Enzyme extraction was carried out at 4^oC.

Determination of enzyme activity. The reactants were applied in the following concentrations (mmol·litre^{-1}): Tris-HCl (90), $MgCl_2$ (5), Na_2HAsO_4 (5), EDTA (0.92), NAD (1), GAP (10). The

crude extract (0.5 ml) was used in a total assay volume of
2.4 ml. The pH was 8.0, the reaction was carried out at 30°C
in 1 cm cuvettes.

Determination of protein

Protein determination was made following the microassay
procedure as suggested by Bio Rad Laboratories.

RESULTS

Plotting NO_3^- concentrations of the induction media versus
Sphagnum magellanicum NR activity shows a saturation curve
(Fig. 1). No further dramatic change of NR activity can be
measured above a concentration of 0.5 mM NO_3^-. The Lineweaver-
Burk diagram gives no linear relationship but it is curvilinear.
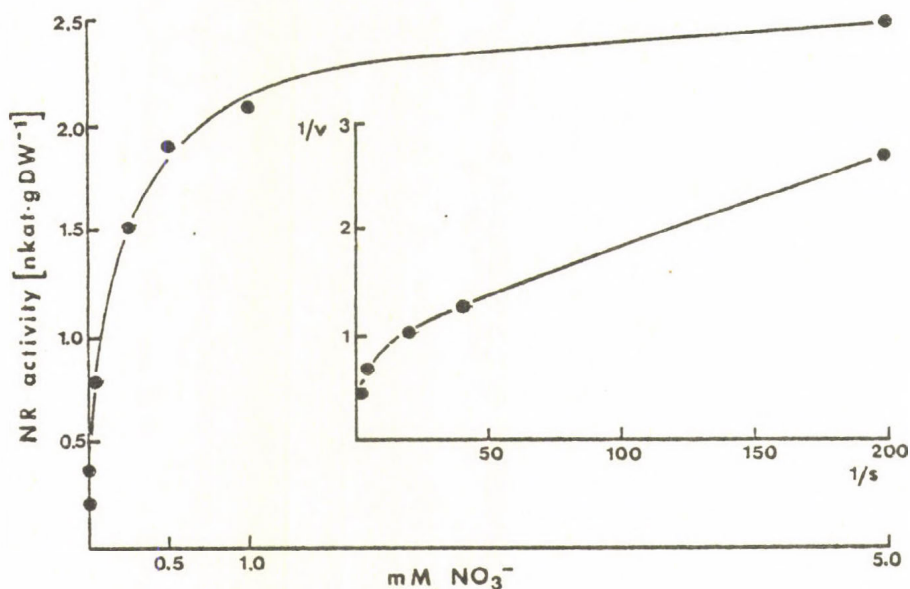
Fig. 1. Effect of various NO_3^- concentrations on the inducible
NR activity in Sphagnum magellanicum. NR activity was
measured 8 h after application of the induction media.

The effect of ammonium on NR activity and induction is shown in Fig. 2. Concentrations up to 100 μM NH_4^+ in the in vivo assay medium do not significantly influence NR activity. Even the 10-fold concentration is only slightly (16%) inhibitory (Fig. 2.A). Fig. 2.B demonstrates that NH_4^+ has little effect on NR induction. NH_4^+ and NO_3^- at 500 μM in the induction medium, respectively, (ratio = 1) result in 28% decreased

A

B
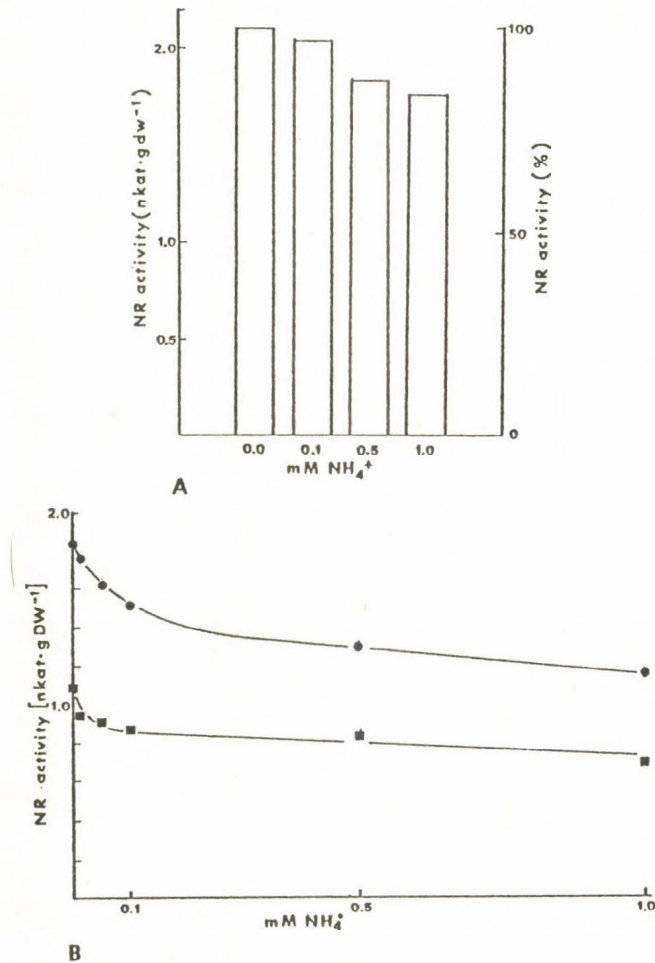
Fig. 2. Effect of NH_4^+ on activity (A) and induction (B) of Sphagnum magellanicum NR. Different NH_4^+ concentrations were given with the in vivo assay medium to investigate NH_4^+ effects on NR activity (A). Different concentrations were applied with 50 μM (■) or 500 μM (●) NO_3^- to investigate NH_4^+ effects on NR induction (B).

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NR activity. At a lower N concentration (50 µM NH_4^+ : 50 µM NO_3^-) the same ratio yields a 17% decrease.

The results of another experiment in which the NH_4^+ concentration of the induction medium was restricted to natural conditions (0.1 mM) are presented in Fig. 3. Again, the response of six _Sphagnum_ species demonstrates that NH_4^+ is not a strong regulator of NR induction in this genus. A maximum decrease of 23% was measured in _Sphagnum fallax_.
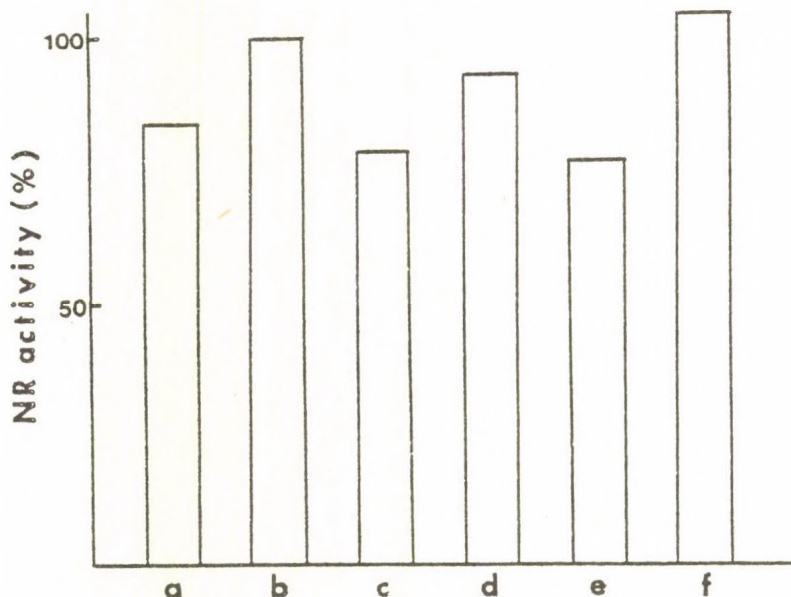
Fig. 3. Effect of NH_4^+ on NR induction in six _Sphagnum_ species, expressed as % of control. NH_4^+ (100 µM) and NO_3^- (500 µM) were applied at the beginning of the light period. A: _S. magellanicum_, B: _S. subnitens_, C: _S. compactum_, D: _S. fuscum_, E: _S. fallax_, F: _S. cuspidatum_.

Table 1 gives the effect of different metabolites and inhibitors on NR activity. The reactants were supplied with the in vivo assay medium. While NAD and phosphorylated sugars (F-1,6-bP and GAP) stimulate NO_3^- reduction, citrate, malate, glycolate and 2-P-glycolate are inhibitory. In contrast to the inhibitory ATP, ADP and arsenate promote NO_3^- reduction. Iodoacetate as an inhibitor of NAD-GAPDH completely inhibits NO_3^- reduction.

Table 1. Effect of various metabolites and inhibitors on NO_3^- reduction in Sphagnum magellanicum.

Metabolite/ inhibitor	Concen- tration (mM)	NR activity (%)	ΔNR activity (%)	Significance
NAD	1.0	117.80	+ 17.8	1 %
Glucose	10.0	99.43	− 0.6	− −
Fructose-1,6-bP	10.0	103.94	+ 3.9	− −
Glyceraldehyde-3-P	10.0	105.31	+ 5.3	− −
Malate	25.0	76.26	− 23.7	1 %
Malate	50.0	72.13	− 27.9	1 %
Citrate	10.0	78.30	− 21.7	1 %
Glycolate	10.0	93.20	− 6.8	− −
Glycolate + N_2	10.0	93.75	− 6.3	− −
2-P-Glycolate	10.0	72.48	− 27.5	1 %
ATP	10.0	89.36	− 10.6	− −
ADP	10.0	114.59	+ 14.6	− −
Arsenate	20.0	123.56	+ 23.6	5 %
Iodoacetate	10.0	0.00	−100.0	1 %
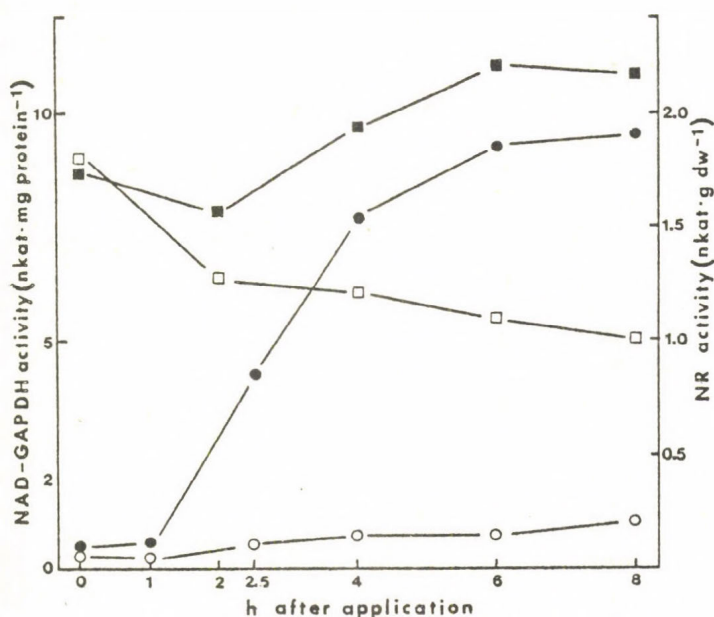
Fig. 4. Effect of NO_3^- on NR and NAD-GAPDH of Sphagnum magellanicum. NO_3^- (500 μM) was applied at the beginning of the light period. ●: NR activity in NO_3^- treated plants, o: NR in controls (dest. H_2O), ■ : NAD-GAPDH in NO_3^- treated plants, □: NAD-GAPDH in control (dest. H_2O).

The response of NR and NAD-GAPDH to NO_3^- application is given in Fig. 4. NAD-GAPDH and NR activity increase following this application, resulting in maximum activity after 6-8 h for both enzymes. Replacing nitrate by distilled water causes no induction of NR activity, and NAD-GAPDH activity, following cyclical fluctuations, is decreased.

DISCUSSION

The strong increase of NR as a response of increasing NO_3^- concentrations up to 0.5 mM in the induction medium (Fig. 1) suggests that NO_3^- from wet and dry depositions is metabolized rapidly by Sphagnum spp. This behavior is a necessary mechanism of successful competition for nitrate which is essential for growth and development of Sphagnum spp. (Rudolph & Voigt 1986, and Rudolph et al., these proceedings).

The reciprocal plot of NO_3^- reduction versus NO_3^- concentration is non-linear. Neyra & Hageman (1975) found similar correlations in corn roots. This phenomenon can be interpreted as the result of co-operation of more than one enzyme system, e.g., NR, NO_3^- permease and enzymes involved in the generation of reducing equivalents. Following the contribution of Rudolph et al. (these proceedings) on the beneficial effect of NO_3^- in contrast to NH_4^+, one would expect that the whole system of nitrate uptake and reduction would not be regulated by NH_4^+ as frequently reported (reviewed by Guerrero et al. 1981). The results shown in Figs 2 and 3 clearly demonstrate that NH_4^+ does not act as a regulator of Sphagnum NR. Since Sphagnum is a genus of ammonium rich environments with an essential demand for nitrate, these physiological reactions are reasonable. These findings are in contrast to the results of Press & Lee (1982) who, applying 1 mM NH_4^+, recognized NH_4^+ as a repressor of NR synthesis in Sphagnum cuspidatum. Because Rudolph & Voigt (1986) have shown that 225 μM NH_4^+ is high enough to cause growth inhibition and chlorophyll degradation, all higher concentrations cannot be accepted as comparable to natural conditions.

The supply of reducing equivalents could be a regulating factor in the rate of nitrate reduction (Stulen & Lanting 1976, Klepper et al. 1971). No general mechanism of generation of $NAD(P)H+H^+$ can be detected. Klepper et al. (1971) argued strongly that carbon flow through glycolysis involving $NADH+H^+$ generation by NAD-GAPDH is essential for NO_3^- reduction.

The results given in Table 1 show that malate and malate dehydrogenase probably are not responsible for the generation of reducing equivalents for NR. Glycolate, even under anaerobic conditions, failed to support NO_3^- reduction. F-1,6-bP and GAP slightly increased NO_2^- production in vivo. This increased rate of nitrate reduction could be attributed to a change of the cytoplasmic adenylate charge (Shawney et al. 1978). Using arsenate, ADP and ATP in the in vivo assay led to a different view. Arsenate prevents the formation of ATP by glycolysis without affecting the production of $NADH+H^+$. Nitrate reduction in Sphagnum magellanicum was significantly increased by arsenate and ADP but inhibited by ATP. These results and inhibition of NR by citrate support the hypothesis that in the dark $NADH+H^+$ is generated by the glycolytic pathway, namely NAD-GAPDH, and that NO_3^- reduction might be under Pasteur control. In the light, GAP which is produced by the chloroplasts, might directly serve as a NAD reductant (catalysed by NAD-GAPDH) as can be seen from Fig. 5. Iodoacetate (at 2 mM completely blocking NAD-GAPDH in vitro) was used as a tool to examine the role of NAD-GAPDH in nitrate reduction: at 10 mM the inhibitor blocked NO_3^- reduction in vivo. Furthermore, the increase of NAD-GAPDH activity as a response to nitrate application is closely correlated with the NO_3^--triggered increase of NR activity in S. magellanicum (Fig. 4). These results indicate that NAD-GAPDH and GAP could be responsible for $NADH+H^+$ generation and regulation of NO_3^- reduction (Fig. 5). However, a precise knowledge of the meachanism of generation of reducing equivalents and the enzymes involved in these processes requires the in vitro analysis of NR and especially the reaction of this enzyme with different electron donors would be of interest.
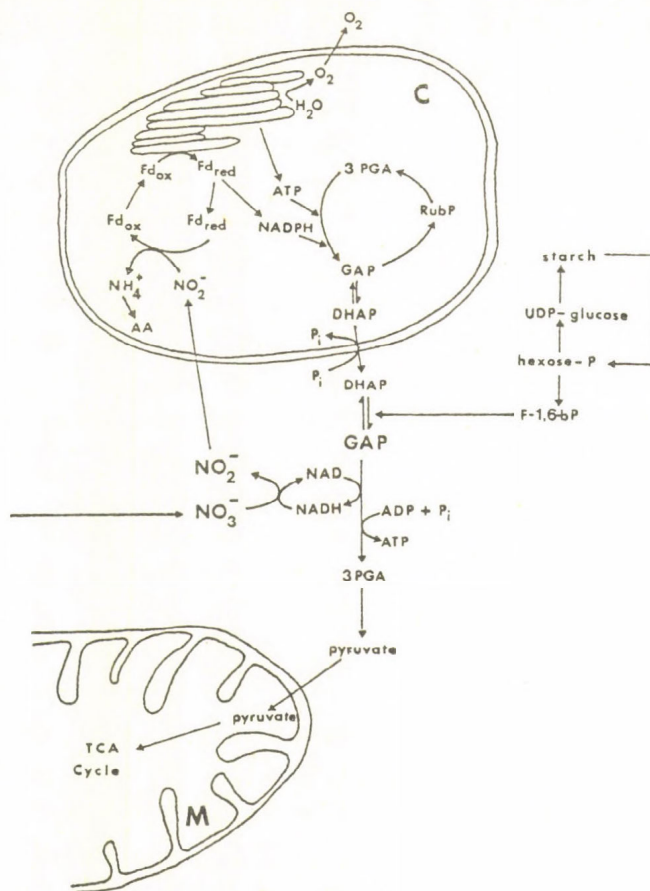
Fig. 5.

In conclusion, this work has demonstrated that NR of Sphag-
num magellanicum is regulated by the available concentrations
of substrate; the role of co-substrate (reducing equivalents)
in regulation of NR activity has been discussed. In contrast
to other reports it has been shown that NH_4^+ has no significant
effect on either induction or activity of Sphagnum NR under
natural conditions.

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THE TOLERANCE OF RAISED BOG SPHAGNUM SPECIES IN RESPECT TO INORGANIC NITROGEN

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Nine formulations of macronutrient media which have been used to culture Sphagnum species were compared and critically reviewed. In the present paper growth rate, chlorophyll content, net photosynthesis and nitrate reductase activity were used to examine the influence of NH_4^+-N and NO_3^--N on Sphagnum magellanicum cultivated under defined conditions in phytotrons. NO_3^- concentrations up to 322 µM NO_3^- were found to be favourable. Increased NH_4^+ concetrations, however, resulted in growth inhibition and decreased chlorophyll content at concentrations $\geq$ 225 µM; e.g., 600 µM NH_4^+ caused a 20% reduction of nitrate reductase activity and net photosynthesis.

INTRODUCTION

In ombrotrophic raised bogs there are only a few plant species other than Sphagnum which have the ability to tolerate a complex of factors that are usually extremely unfavourable to plant growth. Minerals are scarce, for the mosses receive nutrients almost exclusively from wet and dry atmospheric deposition and function as cation exchange columns in the recycling of minerals (Brehm 1968, 1970, 1971, Damman 1978, Rudolph & Brehm 1965).

The nitrogen balance of raised bogs and the occurrence of nitrogen in bog water almost exclusively in the ammonium form is a particular problem, however. There are numerous reports of moss-associated nitrogen fixation measured by the

acetylene reduction assay. In general, in ombrotrophic mires
the fixation rate is low compared with minerotrophic sites,
but some of the results are controversial.

To date, there are insufficient studies available on the
nutrient requirements of raised bog Sphagnum species, especial-
ly with regard to inorganic nitrogen sources. Such data are
absolutely necessary in projects designed to regenerate level-
led raised bogs (Müller 1980, Eigner & Bretschneider 1983).
To study the effect of different nitrogen sources, we culti-
vated Sphagnum under controlled conditions in phytotrons,
which maintained the natural habit of the mosses for several
years (Rudolph 1963, 1978, Rudolph & Voigt 1986).

MATERIAL AND METHODS

Nutrient solution: 10 ml of the following stock solutions
were added to 20 l distilled water: $(NH_4)_2SO_4$ 6 g/l, $MgSO_4$ x
$7H_2O$ 10 g/l, $CaSO_4$ x $2H_2O$ 5 g/l, $CaCl_2$ x $2H_2O$ 2 g/l, KH_2PO_4
2 g/l, KNO_3 2 g/l, NH_4NO_3 5 g/l, NaOH 4.4 g/l, $FeCl_3$ x $6H_2O$
1 g/l + 1.38 g EDTA, HNO_3 0.12 M, NH_3 3.6 10^{-2} M; A-Z solu-
tion (Hoagland) 10^{-1} dilution. Using a bottle top dispenser
we applied the minerals by sprinkling 100 cm^2 of moss surface
every two days with 50 ml of the nutrient solution. This
corresponds to a precipitation of 900 mm per year. The growth
rate and the chlorophyll content were then measured as de-
scribed earlier (Rudolph et al. 1977). For nitrate reductase
activity measurement an in vivo assay was developed (Deising
& Rudolph 1985). O_2-exchange was measured by an infrared gas
analyser, UNOR 2 N. The data presented are averages of three
replicates.

RESULTS

In the following experiments different concentrations of
HNO_3 and NH_3 were added to a basal nutrient solution (pH ad-
justed to 5.8).

Within five months there was a distinct effect on growth rate of Sphagnum magellanicum according to the amount and quality of the applied nitrogen source (Fig. 1).

Total growth of plants supplied with 322 μM NO_3^- and 153 μM NH_4^+ was almost three times as high as the rate of plants without mineral supply. In unsupplemented plants the growth rate had declined by the second month. On the other hand, when the NH_4^+ content in the nutrient solution was increased to 225 μM and the concentration of nitrate reduced to 82 μM, the growth rate decreased. In particular, strong depression was observed at 600μM NH_4^+ and 82 μM NO_3^-.

The chlorophyll content increased from 172 nmol Chl.a+b to 230 nmol/loo mg dry weight when a nutrient solution containing 322 μM nitrate and 153 μm NH_4^+ was used. On the other hand there was no enhancement of chlorophyll concentration when the level of NH_4^+ was increased to 225 μM and the NO_3^- concentration reduced to 82 μM. 600 μM NH_4^+ (82 μM NO_3^-) re-
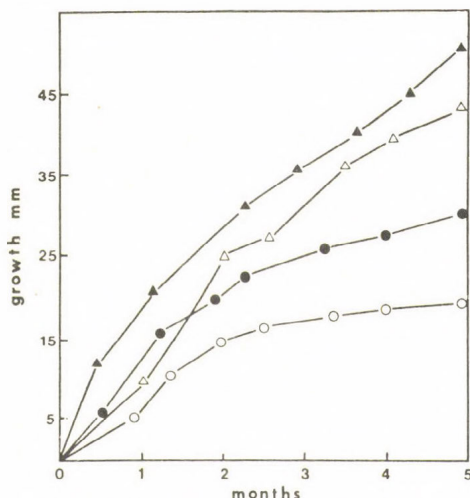
Fig. 1. The effect of NH_4^+-N and NO_3^--N on growth rate of Sphagnum magellanicum. ▲ : nutrient solution with 322 μM NO_3^- and 153 μM NH_4^+; △ : nutrient solution with 82 μM NO_3^- and 225 μM HN_4^+; ●: nutrient solution with 82 μM NO_3^- and 600 μM NH_4^+; o: no mineral supply (distilled water application).

sulted in a decrease in chlorophyll content similar to the effect measured in Sphagnum magellanicum without any mineral supply (Fig. 2).

The net photosynthesis rate increased by 17% in comparison to the control sample with a net photosynthesis rate of 1.2 mg CO_2 $g^{-1}h^{-1}$ when the nitrate concentration was enhanced up to 322 µM. In the absence of any mineral supply there was a 75% depression. 600 µM ammonium resulted in only 20% reduction of the net photosynthetic rate (Fig. 3.a).

Nitrate reductase activity was measured as 1 nkat/g dry weight after a three month application of standard nutrient solution. In the absence of any mineral supply the activity dropped by 50%. 322 µM nitrate led to an increased activity of the enzyme (1.5 nkat/g dry weight). In the presence of 600 µM NH_4^+ the enzyme activity showed a 20% reduction in comparison to the control sample (Fig. 3.b).

These results are representative for all Sphagnum species investigated. The time pattern of nitrate-triggered NR-synthesis of different Sphagnum species is shown in Fig. 4. In general, the activities were all in the same range.
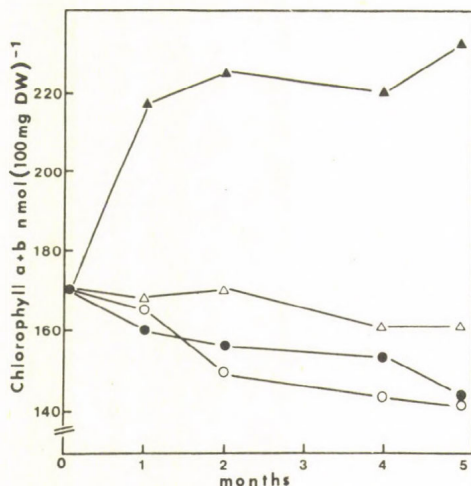
Fig. 2. The effect of NH_4^+-N and NO_3^--N on chlorophyll content of S. magellanicum. See Fig. 1 for explanation of symbols.

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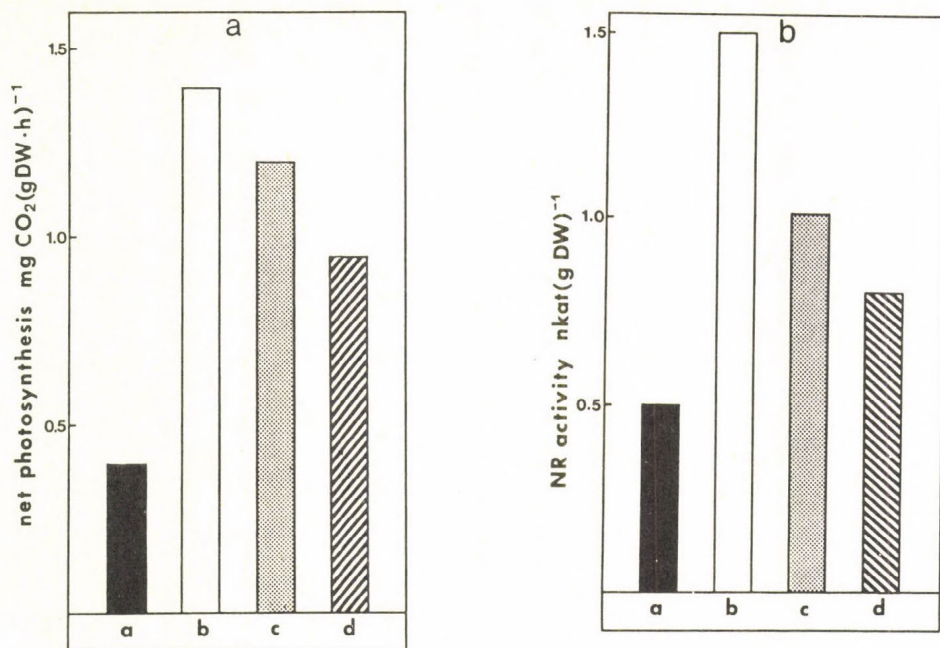
Fig. 3a. Net photosynthesis of $\underline{S}$. $\underline{magellanicum}$ after a three-month application of nutrient solution with different NO_3^- and NH_4^+ concentrations. a) no mineral supply (plants watered with distilled water); b) nutrient solution with 322 µM NO_3^- and 95 µM NH_4^+; c) nutrient solution with 100 µM NO_3^- and 95 µM NH_4^+ (standard nutrient solution); d) nutrient solution with 100 µM NO_3^- and 600 µM NH_4^+. $\underline{b:}$ Nitrate reductase activity after a three months application of nutrient solution with different NO_3^- and NH_4^+ contents to $\underline{S}$. $\underline{magellanicum}$. The explanation for letters a, b, c, and d is given above.
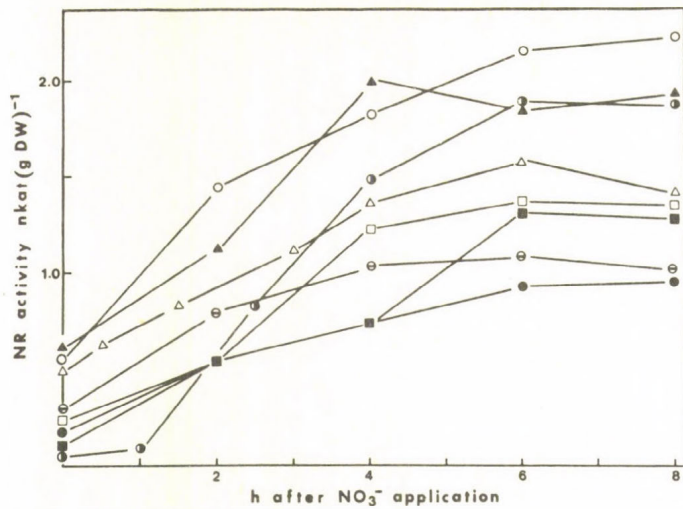
Fig. 4. Time pattern of nitrate triggered nitrate reductase (NR) activity of different Sphagnum species. For six days the mosses were rinsed with redistilled water to ensure that NR activity declined to a minimum level. For induction of NR 0.5 ml of 0.5 mM KNO_3 were applied to each plant.   o: S. rubellum Wils;. ▲: S. subnitens Russ. & Warnst.; ◐: S. magellanicum Brid.; △: S. fuscum (Schimp.) Klinggr.; □: S. compactum DC.; ■: S. nemoreum Scop.;   ⊖: S. cuspidatum Hoffm.; ●: S. fallax (Klinggr.) Klinggr.

DISCUSSION

What makes Sphagnum remarkable is that given a suitable water supply, they can create a habitat where they flourish without any apparent competition.

In discussing the effects of mineral nutrition on plant growth, a comparison of laboratory results with field experiments is only possible when the experiments are conducted under natural physiological conditions: This means that the concentration ranges and the mode of application should be comparable (Press & Lee 1982). Thus we believe that it is problematic to cultivate emersed growing species immersed. Some nutrient solutions used for culture experiments on growth, spore germination and prothallial development of Sphagnum are

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Table 1. Nutrient solutions used for Sphagnum culture experiments in comparison to rain water. * no data available; + supplied; - not supplied.

IONS	RIEHM (Rain-water) (1961) ppm	RUDOLPH et al. (present paper) ppm (μmol/l)	GILLET (1978) ppm	SIMOLA (1977) ppm	SIMOLA (1975) ppm	HINTIKKA (1972) ppm	RUDOLPH & BREHM (1966) ppm	ANDERSON & CROSBY (1965) ppm	COURTE-JAIRE (1959) ppm	BOLD (1948) ppm
Na^+	0.2-0.5	1.26 (55)	0.4	4.2	8.3	-	7.7	-	-	-
K^+	0.2-0.5	0.67 (17)	6.1	162.4	-	28.7	3.1	57.4	3.6	96
NH_4^+	0.26-0.65	1.71 (95)	1.4	45	99.2	33.7	4.5	112.4	-	-
Ca^{++}	1.0-2.0	0.86 (22)	4.4	72.2	72.2	-	1.6	27.4	13.8	193
Mg^{++}	0.2-0.4	0.49 (22)	2.5	19.7	19.7	9.9	2.0	19.7	1.2	14
Mn^{++}	*	+	-	4.9	4.9	-	+	-	-	-
$Fe^{++(+)}$	*	0.11 (2)	0.2	5.0	5.0	1.1	0.2	-	-	-
Cl^-	0.5-1.0	0.71 (20)	5.4	223	163-167	68.4	3.2	48.2	5.8	-
NO_3^-	0.89-2.22	6.26(100)	4.7	155	155	-	20.2	387.3	37.9	68.6
SO_4^{--}	3.0-4.5	5.52 (58)	20.4	95.1	95.1	38.9	7.8	77.9	4.9	56
PO_4^{---}	*	0.70(7.4)	2.1	139.6	143.2	69.8	31.6	139.5	8.7	100
trace elem.	*	+	+	+	+	-	+	+	-	-
Sucrose	-	-	-	10000	10000	-	-	-	-	-
Glc.	-	-	-	-	-	5000	-	-	-	-
pH	5.0-5.5	5.8	4.7	6.0	6.0	4.3-4.6	5.3	-	4.4	-

summarized in Table 1. The mineral content of these solutions is very different, often incomplete and in an unnatural range. The nitrogen sources vary widely; for example, in some NO_3^- is the only N-source (Courtejaire 1959, Bold 1948), while in others NH_4^+ is exclusively applied (Hintikka 1972).

In general, the mineral concentrations of most nutrient solutions are higher than those of rain water, often too high for good results in cultivation experiments. Because Sphagna do not grow in aseptic cultures without additional C-sources, - sucrose (1%) or glucose (0.5%) are occasionally added. With the application technique described there was an input of 90 mmol $NO_3^- m^{-2} yr^{-1}$, and 85 mmol $NH_4^+ m^{-2} yr^{-1}$. This corresponds to a total N input of 2.43 g $m^{-2} yr^{-1}$. This value is in the same range of the nitrogen input measures for the Honigau area in Schleswig-Holstein by Kretschmar (pers. comm.). Re-induction experiments with several Sphagnum species failed in the Holme Moss (South Pennines). In this case the bulk deposition of total nitrogen was 4.6 g N $m^{-2} yr^{-1}$ (Press & Leee 1982). Normally, the total measured N input is smaller.

For several Sphagnum species the best results were obtained with a nitrate concentration of 100 μM. Since the water filled hyaline cells of Sphagnum constitute a complex micro-habitat for various organisms, raising the nitrate concentration above this concentration caused accumulation of coccoid unicellular green algae in the hyaline cells. One major result of the presented data is the observed sensitivity of Sphagnum to ammonium ions. The effect of NH_4^+ on nitrate reductase activity and photosynthesis is observed to be small. The strong inhibition of enzyme induction by 1 mM ammonium in Sphagnum cuspidatum and the depression of nitrate-induced nitrate reductase activity in Sphagnum fuscum by 1.5 mM ammonium is, in relation to levels in precipitation, not of ecological relevance (Press & Lee 1982, Woodin et al. 1985).

The results presented indicate that the chances of success in projects designed to regenerate levelled raised bogs in cases when precipitation is high in ammonium are relatively low.

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ECOLOGICAL CONDITIONS IN A PHOTOPHILOUS-XEROTHERMOTOLERANT
MOSS COMMUNITY (MANNIO-(GRIMALDIO-) TORTELLETUM INCLINATAE
(ASSOC. NOV.) AND MICRORESPIROMETRIC TESTS OF ITS SPECIES

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The specific dimensions of the active surface depend on the
number of shoots and the leaf density which may determine the
coenological role of the species in the association. The species
which were examined did not show the photophilous type light
response curve because of their fast desiccation brought about
by parallel increases of temperature and light intensity. The
active period of mosses is restricted here to the cold part of
the year with short photoperiod and to the early hours in the
warm season. The same factors hinder their adaptation to the
higher temperature characteristic of the site. The contradic-
tion of their physiological character and their photophilous
type morphological construction - with rosette-like arrange-
ment of the leaves, high leaf area index - and also their
restricted tolerance to shade, may be explained by their
vegetation history: ancient alpine origin with subsequent adap-
tation enabled them to survive within extrazonal treeless ve-
getation at the lower edge of the woodlands.

- . -

In general, it is mainly photophilous species of mosses and
lichens which are capable of forming more or less independent
associations. Among the mosses these communities are mainly
composed of acrocarpous and Sphagnum species, whether they
grow above the upper limit of forest or lower levels, and
whether their sites are 'too cold' or 'too dry' or 'too wet'
for closed woodland (Fig. 1).

Fig. 1. Natural habitats of the photophilous mosses in the Carpatho-Pannonian region.

The association studied by the authors is developed on a barren SE dolomite slope in the Balaton upland on calcareous skeletal soil (Fig. 2). It is surrounded by xerothermo-tolerant saxicolous herbaceous vegetation (Chrysopogono-Caricetum humilis) and pubescent oak-wig tree scrub wood (Cotino-Quercetum) in an extrazonal situation within a pubescent oak - manna ash (Orno-Quercetum) climax forest belt. A characteristic of the site is that during the six summer months the temperature near the ground is much higher than in the surrounding area

Fig. 2. Gravelly-rocky dolomite slope with selective drought effect on the SE slope of Péter-hegy (Balaton Upland, 260 m a.s.l.). The scrub wood (Cotino-Quercetum) alternates with open and closed steppaceous grass-subshrub community Chrysopogono-Caricetum humilis (minuartietosum and botriochloetosum) according to the micro-relief the deepness and water retaining ability of the soil. Besides the closed and open grassy formations, also terricolous moss communities hindern sticking litter and humification (inhibition type of "succession").

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(about 32 ^{O}C on the average, instead of 18 ^{O}C) and the effective part of the precipitation of the same period is scarcely more than 100-120 mm (instead of an average of around 300 mm). The absolute maximum found here was 56 ^{O}C at ground level (Fig. 3) and even in November the temperature often reaches almost 20 ^{O}C. Precipitation falls mainly in form of summer showers but due to the skeletal soils and the continuous humus erosion the water retention capacity of the site is so bad that we may call it an "edaphic microclimatic semidesert" (see Fig. 3). Microclimate measurements with parallel field observations showed that under the conditions of this semidesert - like situation the mosses were saturated with just for the few morning hours during the warmer season (Fig. 4a).However, we do not know whether these short periods of moistening are enough for the mosses to maintain a positive carbon balance in the same way as the lichens studied by Lange et al. (1970) and Kappen et al. (1979) in the Negev Desert of Israel. Even on warm days in October and November the mosses soon desiccate as the temperature rises and remain dry during the day (see Fig. 4b-c).

On the driest patches of the site with a soil depth of 1-12 cm (average 3.5 cm) the rupicolous open grass-subshrub vegetation (the so-called "slope-steppe") thins out so much that it gives enough space for the development and survival of a xerothermo-tolerant moss-lichen association. This is mainly composed of four moss species, namely Ditrichum flexicaule, Pleurochaete squarrosa, Tortella inclinata, and Trichostomum crispulum. Other 8 species also take part in this association, these are: Bryum bicolor, Didymodon fallax, and Tortula ruralis ssp. calcicola with a constancy of II, whereas Barbula unguiculata, Bryum argenteum, Encalypta vulgaris, Mannia fragrans, and Tortella tortuosa only attain a constancy value of I but may be abundant where they occur.

Sporadically, we may find Barbula convoluta, Dydimodon vinealis, Pseudocrossidium hornschuchiana, P. revolutum, Weissia controversa, and W. fallax growing only in minute patches (Table 1). In moderately shaded places species such as Tortella tortuosa, Ditrichum flexicaule, Tortula ruralis ssp. calcicola soon overgrow the other species and the community shows a more

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CLIMATIC BORDER
ROUND COTINO-QUERCETUM
SCRUB FOREST

Microclimate at ground level:
1. within saxatilous,plant community (Chrysopogono—Caricetum)
2. Margine of the scrub-wood community
3. Inside scrub-wood community (Cotino—Quercetum)

outside Cotinetum in saxatilous pl. comm.

① ② ③

inside Cotinetum

acc. to measurements of P. Jakucs   acc. to measurements of Zs. Debreczy

constructed "microclimate diagram" of the habitat of the rupestral Chrysopogono—Caricetum humilis plant community set by dates of microclimate and water retention capability measurements
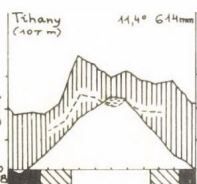
Tihany (107 m)   11,4° 614mm   ← Climate diagram of Tihany (nearby)
—4,0
—27,8

Cotino—Quercetum

Chr.—Caricetum
scrub-wood margin

Chrysopogono—Caricetum
xerothermo-tolerant / "steppaceous" rupestral (dolomite) community

scrub-wood margin "saum"

saxatilous community

Changing of the soil factors from wood to saxatilous

5.84–5.15
2.48 – 1.46   2.37   P₂O₅
1.89 – 1.02
5.65 – 3.66   0.95   NO₃
23.9 9.28
27.08   0.45   NH₃
20.03
7.36   10.51   2.06   K
(6.98)   7.62
4.65
7.44   4.19   18.12–19.9   10.51
(7.06)   13.99   Mg
7.51   —3.77   —15.56   6.20   32.7
pH   (7.16)   y₁   Humus   hy   Ca   CaCO₃

soil factors: after Jakucs, 1972

Fig. 3. The differences in the microclimate space with the climate characters and soil factors between the scrub wood, the scrub margin and the saxatilous community on the natural (extrazonal) lower woodland border on a dry dolomite slope.

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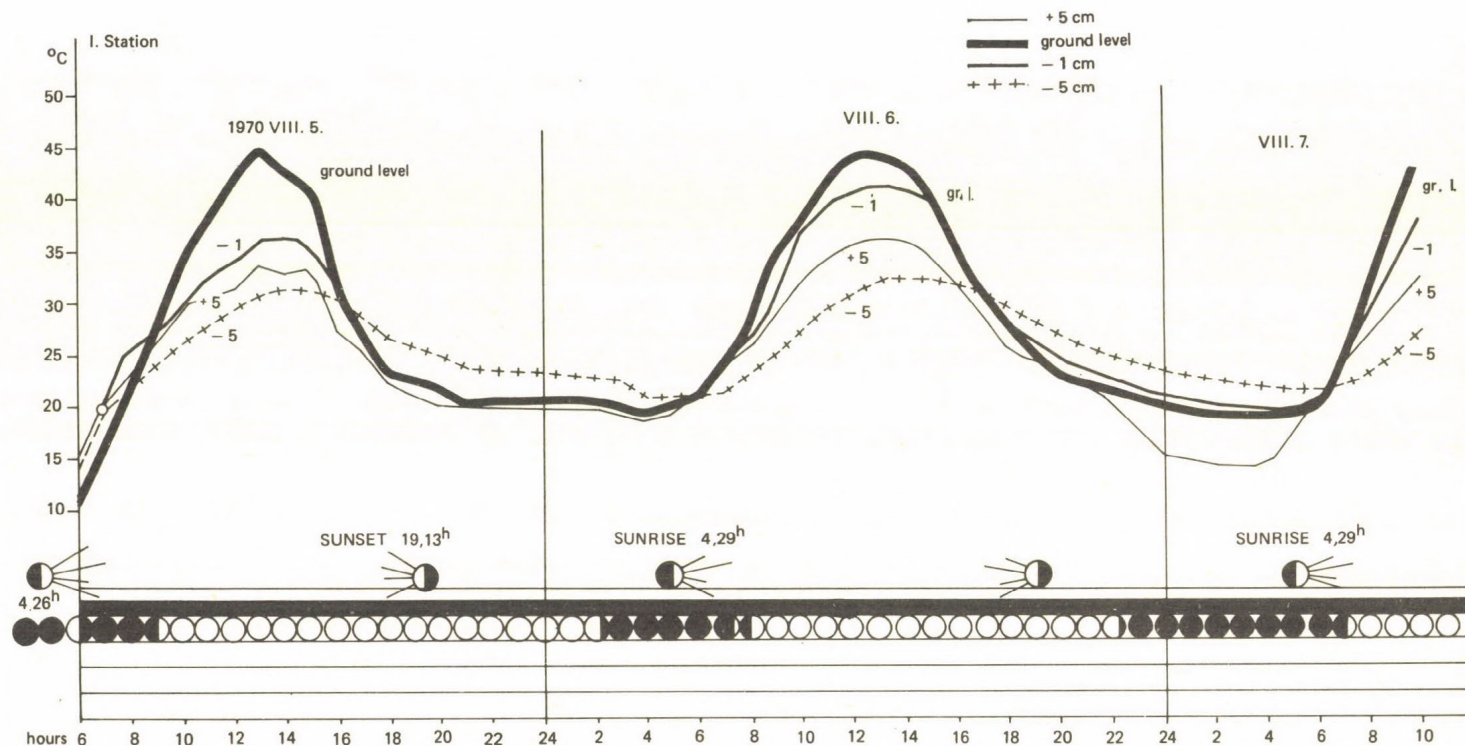
Fig. 4.a. Microclimate at different levels (-5, -1, 0, 5, 20, 100 cm) and diurnal moss behaviour. August. Full circles: mosses are saturated with water.
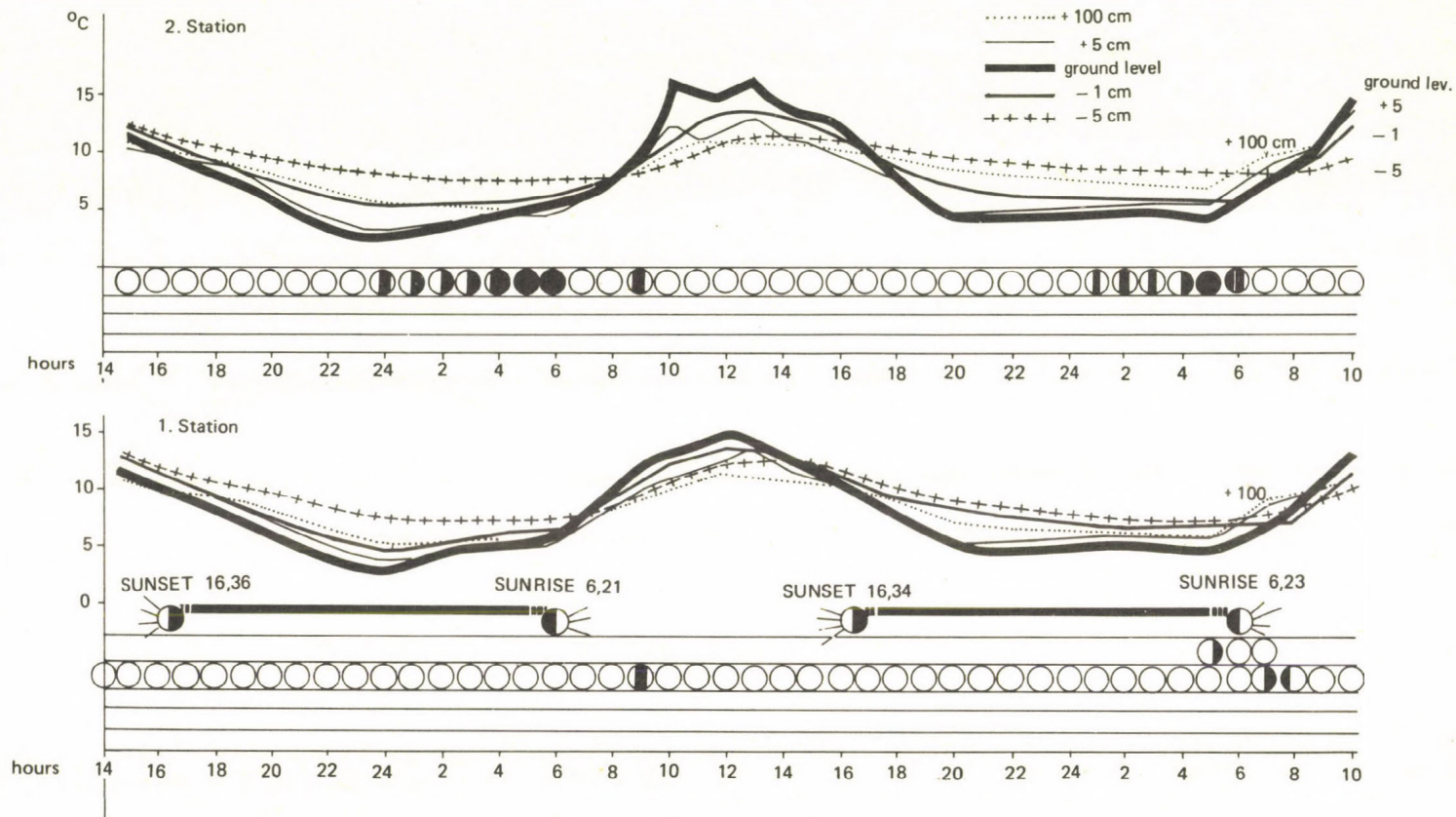
Fig. 4.b. Microclimate measurements in October (compare with Fig. 4.a)
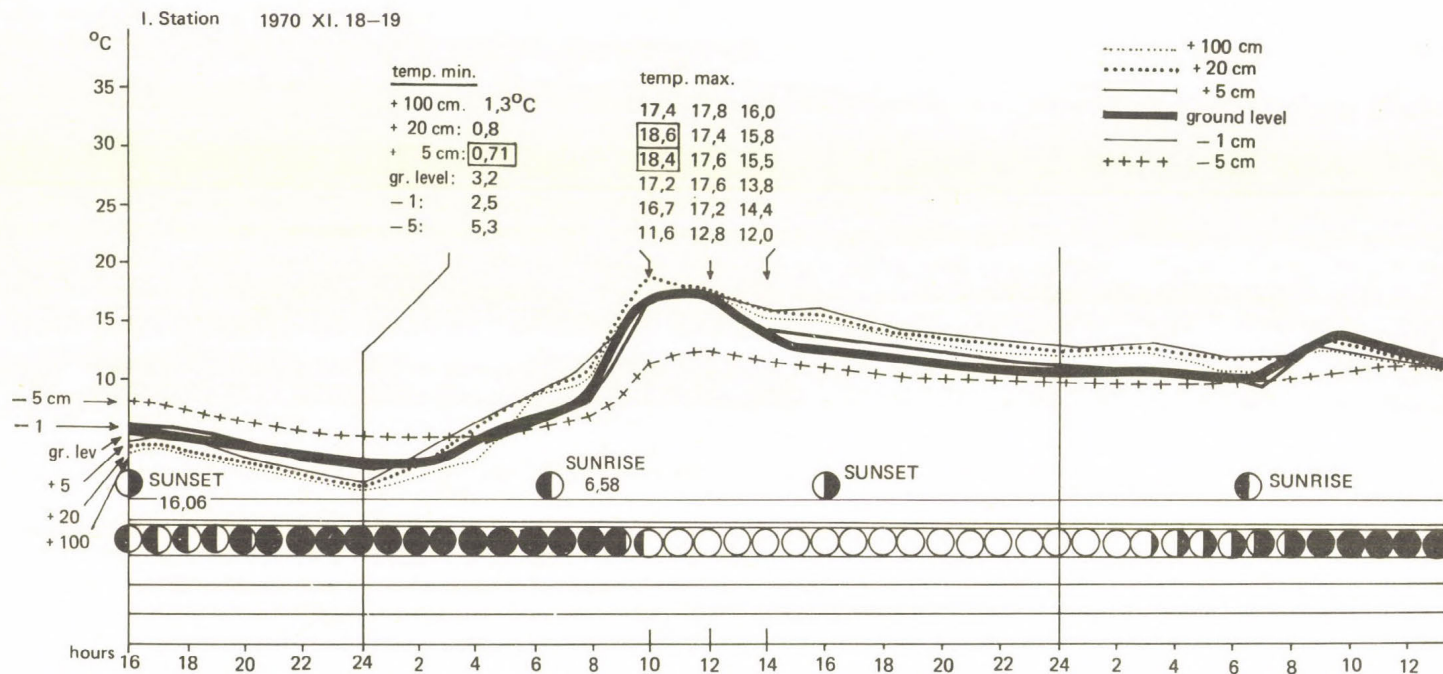
Fig. 4.c. Microclimate measurements in November (compare with Fig. 4.a).

Table 1.

S P E C I E S	K	A-D /%-
Level of mosses and lichens		
Pleurochaete squarrosa	V	P-80
Tortella inclinata	IV	P-92
Ditrichum flexicaule	IV	P-85
Trichostomum crispulum	IV	1-85
Grimmia pulvinata	II	P-5
Tortula ruralis	II	P-2
Barbula fallax	II	P-3
Bryum bicolor	II	P-2
Bryum argenteum	I	P-1
Encalypta vulgaris	I	P-5
Grimaldia fragrans	I	P-10
Tortella tortuosa	I	7-10
Barbula unguiculata	I	P
Ortotrichum anomalum	I	5
Collema tenax	III	P-4
Peltigera rufescens	II	P-10
Psora decipiens	II	P-10
Toninia coeruleonigricans	II	P-8
Squamarina lentigera	II	P-10
Cladonia symphicarpia	II	P-5
Higher (saxatilous) plants		
Fumana procumbens	IV	P-75
Thymus praecox	III	P-25
Carex liparicarpos	III	P-40
Stipa capillata	II	P-40
Globularia aphyllanthes	II	P-25
Chrysopogon gryllus	II	2-56
Poa badensis	II	P-5
Aethionema saxatilis	I	P-30
Euphorbia cyparissias	I	P-10
Festuca glauca	I	3-25
Minuartia setacea	I	1-20
Silene otites	I	2-15
Allium flavum	I	P
Potentilla arenaria	I	1-15
Teucrium montanum	I	P-25
Hippocrepis comosa	I	1-15
Sedum album	I	P-5
Helianthemum ovatum	I	P-70
Dorycnium germanicum	I	5
Veronica spicata	I	1
Hieracium pilosella	I	P-10
Aster linosyris	I	1
Paronychia cephalotes	I	2-5
Linum tenuifolium	I	30
Carex humilis	I	20

homogeneous appearance. The distribution of mosses according to their ecological characters in different associations in close proximity and the restricted areas of the photophilous species within the territory studied are clearly shown in Fig. 5.

Lichen species play a subordinate role in the association: Caloplaca fulgens, Cladonia furcata var. subrangiformis, C. symphicarpa, Collema pulposum, Dermatocarpon hepaticum, Peltigera rufescens, Psora decipiens, Squamarina crassa, Toninia coeruleonigricans occur frequently but only with a low abundance-dominance value.

The abundance of mosses and the subordinate role of lichens in the association contrast with the so-called "multicoloured lichen association", (Buntflechten-Gesellschaft, which Reimers proposed as a German terminological equivalent of the Swedish "broklavsamhallen") found in the northwestern part of Central Europe. This difference may be explained by the lower humidity of the air during the warmer part of the year and by the comparatively pronounced continentality of the cold season which particularly in a calcareous environment hinders the rapid spreading of the more vigorous lichens, which would probably otherwise soon cover the moss cushions in a more humid climate.

Because of these differences, to reflect the similarity yet make a distinction we suggest the term "multicoloured moss community" for the micro-association dominated by mosses, like the one described here, the Mannio- (Grimaldio-) Tortelletum inclinatae from the Balaton Upland. This association belongs to the terricolous Epigaetea Lichenosa class and the Toninion coeruleonigricantis series within the coenological system of Klement (1954) (see Table 2). The comparative study of the vegetation and species (both higher plants and cryptogams) clearly indicates that the species composing the associations on the sites at the dry lowland margin on barren dolomite slopes at colline elevations originate from preglacial alpine elevations (Fig. 6). It is for that very reason (despite the influence of different environmental and floristic factors today) closely related to the present Carpathian mountain rock-fissure vegetation of south-facing limestone cliffs at 800-1000 m elevation in the mixed beech-fir wood (Abieti-Fagetum) zone

photophil
xerothemo-tolerans

photophili-sciotolerans
mesophil-xerothermo-tolerans

photophil-sciotolerans
mesophil

sciotolerans
mesophil

sciophil
mesophil

sciophil
mesophil-hygrotol.

photophil
hygrophil

sciophil
hygrophil

tol. = tolerans
(incl. "frequens")

Ditrichum flexicaule
Pleurochaete squarrosa
Tortella inclinata
Bryum bicolor s. l.
Trichostomum crispulum
Weissia fallax
Encalypta vulgaris
Mannia fragrans
Pseudocrossidium hornschuchianum
P.   revolutum
Didymodon fallax
D.   vinealis
Tortula ruralis
Hypnum cupressiforme
Weissia controversa
Bryum argenteum

etc. (21. spec.)

Amblystegium serpens
Leucodon sciuroides
Campylium calcareum
Brachythecium velutinum
Plagiomnium cuspidatum
Fissidens cristatum
Abietinella abietinum

(7 spec.)

Bryum capillare
Thuidium erectum
Rhodobryum spathulatum
Scleropodium purum
Dicranum scoparium
Dicranella heteromalla
Atrichum undulatum
Eurhynchium hians
Plagiomnium undulatum
Anomodon viticulosus

etc. (15 spec.)

Neckera complanata
N.   crispa
Isothecium filescens
Leskea cathenulata
Chrysohypnum chrysophyllum
Hypnum incurvatum
Fissidens taxifolium
Scapania calcicola
Porella platyphyila
Metzgeria furcata
Pylaisia polyantha
Taxiphyllum depressum

etc. (42 spec.)

1A   1B   1C   2   3A   3B   4   5   6

Chrysopogono –
Caricetum (1A–C)
(incl.: Mannio-Tortelletum)

Cotino–Quercetum (2)

Orno-Quercetum (3A–B)

Quercetum
petraeae

Querco– Carpinetum (5)
„Koloska-völgy"
(Koloska-valley)

Phyllitidi–
Aceretum– like assoc.
fragments in ravines (6)

Orno-Quercetum

S-SW

W-NW

3 A–B
& Cult.

„Péter-hegy"
(Péter-hill) 318 m

Ladinian ·Carnian

LIMESTONE

„Nagymező"   (Upland)

(Middle Triassic

Anisian)

DOLOMITE

(Upper Triassic –Norian)

DOLOMITE

Pleistocene (loess)

Pliocene (pannonian)

Lower Triassic
Campilian

(Scythian) LIMESTONE

PLEISTOCENE (loess)

Fig. 5. Division of mosses according to ecological characters in different associations in con-
tact with other in the environs of Péter-hegy.

Fig. 6. Schematic distribution of vascular plant species which occur in the Carpathians and Balkan alpine regions and also in the Pannonian steppe-grassland of dry limestone and dolomite slopes.

and to the subalpine-alpine rupicolous communities of calcareous high mountains of the Balkans. The species partly reoccupied their previous territories in the Balkans because of the lesser influence of the glacial period and the arcto-alpine type of flora there. During the Ice Age the formerly restricted alpine flora replaced the earlier woodland belt and as an alpine re-lict survived colline and even at lower elevations within the woodland in negative extrazonal sites (in sites where the pro-

Table 2. The connection of the Mannio-Tortelletum moss-lichen association of the Balaton Upland with the lichen-moss system of Klement (1954).

```
┌─────────────┐        ┌─────────────┐        ┌─────────────┐
│  class of   │        │  class of   │        │  class of   │
│  saxicoles  │        │ terricoles  │        │ corticoles  │
│ EPIPETRETEA │        │  EPIGAETEA  │        │ ERIPHYTETEA │
│  LICHENOSA  │        │  LICHENOSA  │        │  LICHENOSA  │
└─────────────┘        └─────────────┘        └─────────────┘
```

| RHIZOCARPETALIA | | HYDROVERRUCARIETALIA | | EPIXYLETALIA |

XEROVERRUCARIETALIA

terricol lichens EPIGAEETALIA

EPIPHYLLETALIA

EPIBRYETALIA

basiphilous

| Acarosporion fuscatae | Caloplacion pyraceae | Verrucarion marinae | Toninion coeruleonigricantis | Bacidion chlorococcae | Ochrolechion tartareae |

loessophilous halophilous

| Crocyrion membranceae | Calopacion decipientis | Aspicilion lacustris | | | Loborarion pulmonariae |

Diploschiston terrestris

acidiphilous

| Rhizocarpion alpicolae | Collemion rupestris | | Solorionion croceae | | |

Leprarion

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duction os less and rapidly decreasing compared with the climax
("climate-zonal") vegetation units.

For the coenological study of the community, quadrats of
50 x 50 cm (2500 cm^2) laid down previously were divided into
9 smaller ones (Fig. 7), each with sides of 16.6 cm. Within
these smaller quadrats we estimated the proportion of the moss
and lichen species having been previously saturated by water,
and also the percentage cover of the higher plants, and the
bare rocky "dolomite-sand" patches. The results were checked
on detailed photographs to a scale of 1:1 (Fig. 9), and on the
exact map made on cellophane during field work. The results
were summarized in coenological tables and expressed by gra-
phical methods as well (Fig. 8).
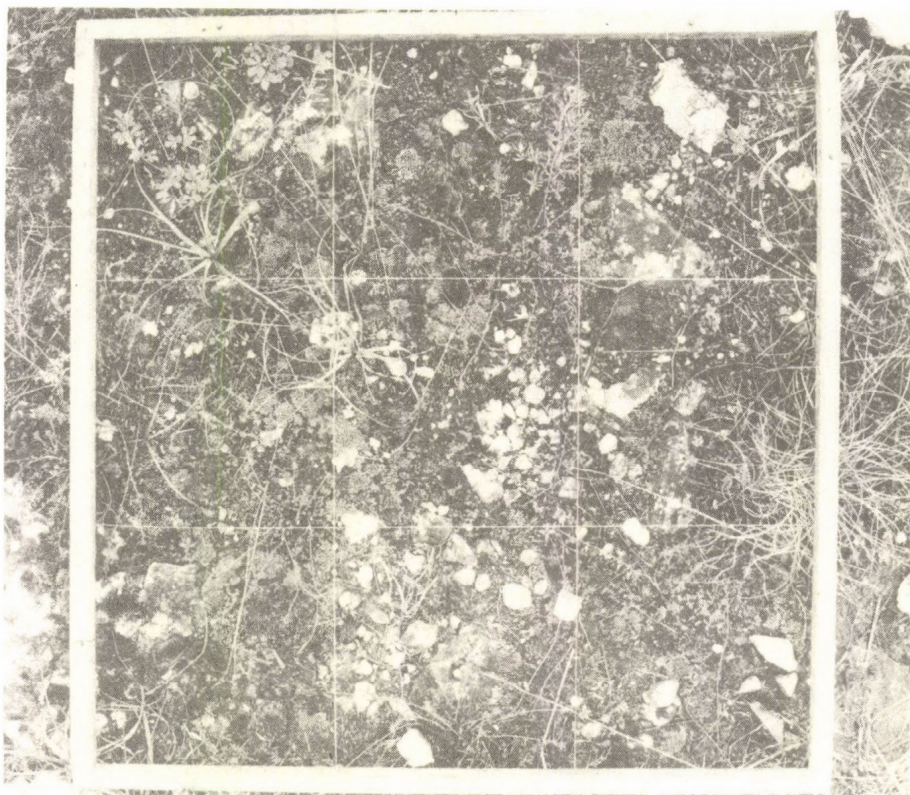
Fig. 7. Sample quadrat of Mannio-Tortelletum inclinatae in
February, 1982. See Fig. 8, for the coenological composition
of this quadrat.

The analyses of the results compared with other communities underlined the isolated position of <u>Mannio-Tortelletum inclinatae</u> from the other central European communities published (from Germany: Zechstein gypsum territory, south Harz Mts. Kyffhauser, Rhine territory, farther southeast the Pannonian Plain and colline region, - Reimers 1937, etc.). The comparison with Balkan type communities has not yet been finished, partly because of the lack of published work on the subject. Notwithstanding their small dimensions, the total surface of these minute plants is surprising large en masse. By counting the number of shoots in 1 cm^2 quadrats, which varies from 13 (<u>Tortula</u>) to 338 (<u>Trichostomum</u>), and the number of living leaves on each shoot, varying between 17 (<u>Encalypta</u>) and 104 (<u>Tortella tortuosa</u>) excluding the two plagiotropes, and by measuring the leaf surface by a combination of photographic and planimetric method we obtained total leaf surface areas over unit

Pleurochaete squarrosa
1

Tortella inclinata
2

Ditrichum flexicaule
3

Trichostomun crispulum
4

Toninia coeruleonigricans
5

Peltigera rufescens
6

Grimmia pulvinata
8

other species

cover of higher plants

barren ground (soil, stone)
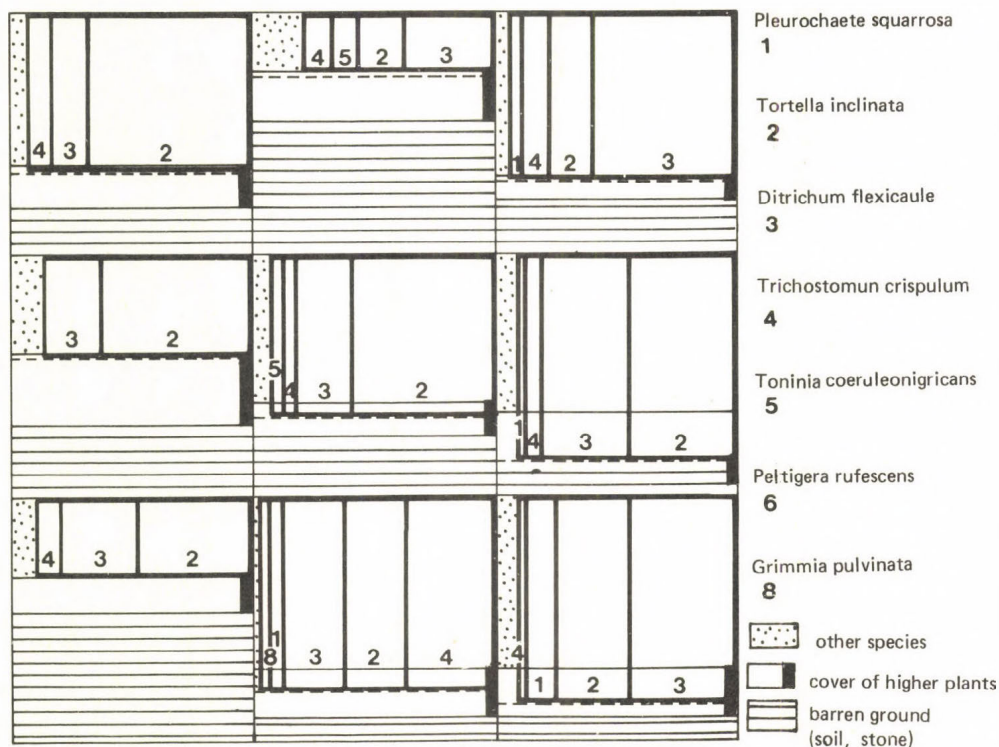
Fig. 8. Cover values (percentages) in the sample quadrat illustrated in Fig. 7.
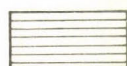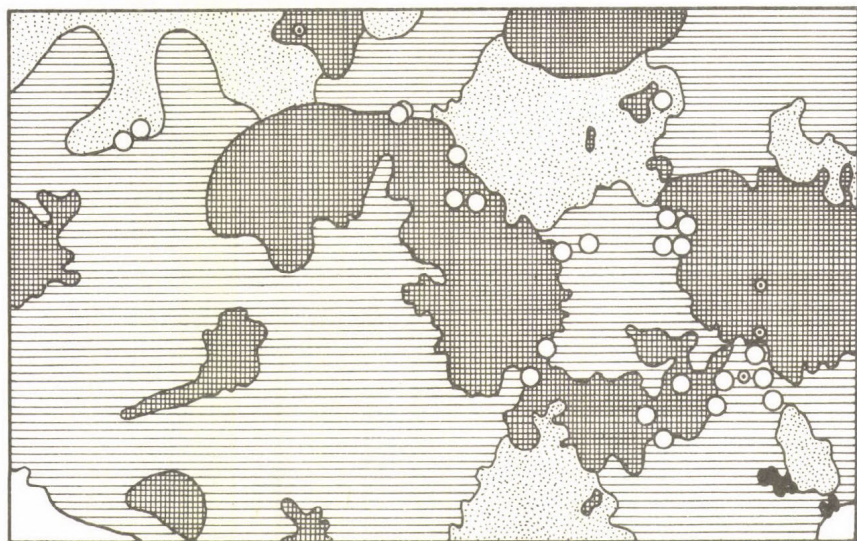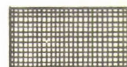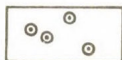
Fig. 9. The method of mapping moss micro-communities by means of 1:1 photographs.

area of ground ("leaf area index", Table 3). It is interesting that the 3 species with the largest leaf area indices dominate the association. As we found no essential differences among species in their response to light intensity and temperature during the photosynthesis studies by microrespirometer, this fact may be important and may determine their competitiveness.

Altogether 1300 measurements were made with microrespirometer technique, introduced by Zurzicky and developed by

Starzecky in 1955 (cf. Zurzicky & Starzecky 1971). The samples were taken from the Balaton Upland, while the measurements were made in the Plant Physiological Dept. of the Paedagogical College in Cracow under the instructions by Dr. J. Krupa. The microchambers of the apparatus were modified to suit the photosynthesis study of mosses.

The photosynthetic activity of leaves was studied over a range of light intensities and at various temperatures. In the case of the photophilous Tortella inclinata it may be clearly
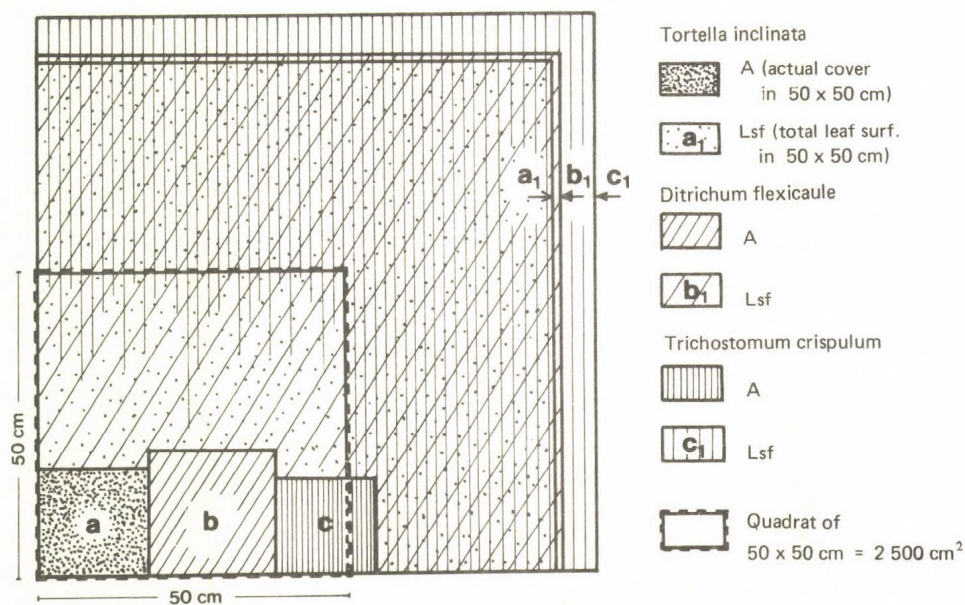
Fig. 10. The relation of the average of actual cover (A) and that of counted on the base of leaf surface (Lsf) at the three important species of Mannio-Tortelletum inclinatae.

Table 3. Shoot density, leaf number and leaf area index of mosses from the Mannio-Tortelletum inclinatae community. ⊕ : counted in autumn phase.

Species	Number of shoots in cm^2	⊕ Number of leaves on shoots			⊕ Ratio of leaves			leaves number in cm^2		Total living leaves-surface of mosses in cm^2 (L.A.I.)
		living	dead	≦	living	dead	≦	living	dead	
Ditrichum flexicaule	142	64	146	210	30.5	69.5	100	9088	20732	17.335
Tortella tortuosa	19	104	133	237	43.9	56.1	100	1976	2527	15.215
Hypnum cupressiforme	17	328	268	596	55	45	100	5576	4556	24.063
Bryum argenteum	150	20	2	22	91	9	100	3000	300	12.100
Tortula ruralis	13	46	60	106	43	57	100	598	780	6.354
Camptothecium sericeum	27	167	60	227	73.6	26.4	100	4509	1620	13.189
Encalypta vulgaris	52	17	12	29	59	41	100	884	624	5.701
Tortella inclinata	45	79	88	167	47	53	100	3555	3960	22.858
Trichostomum crispulum	358	32	29	61	52.5	47.5	100	10816	9802	31.993
Grimmia pulvinata	188	20	47	67	29.9	70.1	100	3760	8836	12.425

seen that the net photosynthetic activity of moss leaves falls
rapidly as irradiance is cut down by using filters and is zero
at filter 7 (Fig. 11). The light response is more strongly
expressed at higher temperatures. For example, the photosyn-
thetic activity of Tortella tortuosa decreases by 44.66% at
filter 7 compared with the results obtained at full light at
15 °C, while at 25 °C the corresponding decrease is 90.80%.
For most of the species the production loss between full light
(no filter) and filter 7 was around 50-60 t 10 °C, while it
was 80-90 % at 25 °C. In Bryum argenteum, Tortella inclinata
and Mannia fragrans net photosynthesis was 26-67% greater
at 25 °C than at 10 °C (Table 4). Tortella tortuosa
showed rather more rapid assimilation at 15 °C than at 25 °C.
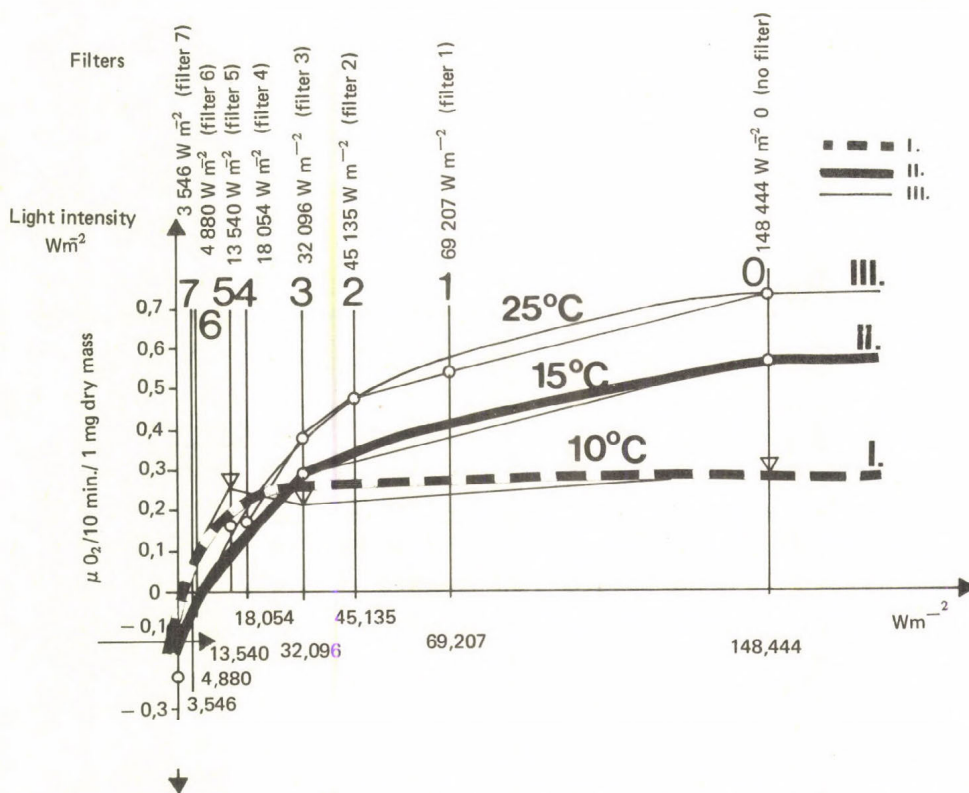
Fig. 11. Light response curves of Tortella inclinata at dif-
ferent temperatures. (Light source: 1000 W 100 V Tungsram bulb
with Schott BG-½7 filter for transferring natural light).

Table 4. Net photosynthesis expressed in μl O_2/10 min./1 mg dry mass at different temperatures by using no filter (144.444 Wm^{-2}) and filter 7 (3.546 Wm^{-2}).

S p e c i e s	filter	10 °C	15 °C	25 °C
Tortella tortuosa	0 7		0.91 0.54	0.76 0.07
Encalypta vulgaris	0 7	1.61 0.80	0.64 0.19	0.78 0.48
Ditrichum flexicaule	0 7	1.45 0.46		0.93 0.09
Trichostomum crispulum	0 7	1.24 0.52		0.85 0.14
Mannia fragrans	0 7	0.93 0.99		1.81 0.64
Tortella inclinata	0 7	0.38 0.16		0.95 0.15
Grimmia pulvinata	0 7			1.31 0.67
Tortula ruralis	0 7			0.95 0.17
Bryum argenteum	0 7	0.77 0.71		1.16 0.21

Encalypta vulgaris, Ditrichum flexicaule and Trichostomum crispulum showed highest activity at 10 °C. At higher tempera- tures of 30-35 °C the activity rapidly fell and generally stopped at 40 °C. More details on these measurements will be published in Acta Botanica Hungarica in 1987.

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SOME ECOPHYSIOLOGICAL FEATURES IN WOODLAND MOSSES
IN SW SLOVAKIA 1. WATER RELATIONS

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Ecophysiological studies were made on common moss species
of several forest communities in the Malé Karpaty Mountains,
SW Slovakia. Samples of seven species (Polytrichum commune, P.
formosum, Hypnum cupressiforme, Atrichum undulatum, Ditrichum
flexicaule, and Pohlia sp.) were collected from six study
sites in July, August and September 1984.

Moss water content and water loss ratios were determined
during desiccation of the saturated mosses in laboratory con-
ditions: $23^{O}C$ and 76% RH in July, $27^{O}C$ and 75% RH in August,
and $26^{O}C$ and 52% RH in September. Decline of the water poten-
tial of mosses was very rapid during the first minutes of de-
siccation, so the use of this characteristic was impractical.

Two groups of moss species could be distinguished:

(1) species with low water loss rates (P. commune, P. for-
mosum); they lost 50% of water content during the first 30
minutes and 90% of water content during 2-3 hrs of desiccation.
Saturated water content (% of dry matter) and maximum transpi-
ration rate at saturation (g H_2O g^{-1}d.m. h^{-1}) were 170-200%
and 2.2-2.7 in July and August, and 210-310% and 3.5-5.1 in
September, respectively.

(2) species with high water loss rates (A. undulatum, H.
cupressiforme, D. flexicaule, Pohlia sp.); they lost more
than 80% of water content during the first 30 minutes of
desiccation. Saturated water content and maximum transpira-
tion rate were 210-340% and 3.7-7.6 in July and August, and
530-550% and 11.2-12.3 (A. undulatum), 180-250% and 5.7-7.3

(D. flexicaule), and 140-195% and 4.8-6.7 (H. cupressiforme)
in September, respectively.

INTRODUCTION

Mosses (bryophytes) occur in forest communities either in
the ground layer, marked E_o (terrestrial mosses) or they
grow over the trunks of trees (epiphytic mosses), in scree
forests on larger rocks.

The ground layer of mosses is variously developed in fo-
rest communities; it usually has a mosaic structure with indi-
vidual patches of mosses. Only in acidophilous communities,
e.g., in oak-forests, is the layer strongly developed.

In forest communities mosses are part of the understorey;
they are affected by the same factors (stress of light and
water deficiency) as the other plants (herbs and woody plant
species) (cf. Eliáš 1984). It may be assumed that moss species
growing in forest stands exhibit similar ecophysiological
characteristics to herbaceous or woody species in the under-
storey. The moss leaf water content in a spruce forest in
Alaska was dealt with along these lines (Skre et al. 1983).

We present here the results obtained within the frame-
work of ecophysiological research into herbaceous layers of
various forest communities in the Malé Karpaty Mountains, SW
Slovakia.

MATERIAL AND METHODS

Mosses were collected on research areas of the Slovak
"Man and Biosphere" project, in the southern part of the Malé
Karpaty Mountains, SW Slovakia, located on a transect along
the line Bratislava-Rača-Biely Križ-Kosariská-Lozorno (the
"1st transect"). The following forest communities were in-
cluded:
- a) secondary Pinus sylvestris stand (marked as I/2),
- b) acidophilous deciduous Quercus petraea forest with
    Vaccinium myrtillus (I/3), and
- c) hygrophilous deciduous Alnus glutinosa forest (I/9).

Since mosses occur sporadically on the areas of the 1st tran-

sect, additional material was collected from three forest
stands at Bratislava - Železná studnička.

The material was sampled in three different periods: in
July, August and September 1984. Patches sized 20x20 cm were
sampled, or smaller ones, and transferred with the soil to the
site in Bratislava, where laboratory experiments were made
after some days of acclimatization. The plants were watered
so as to keep water content on a high level, and exposed out-
side at the same radiation level as in the forest stands.

The following common moss species were selected: Polytric-
hum commune Hedw., P. formosum Hedw., Atrichum undulatum (Hedw.)
P. Beauv., Plagiomnium undulatum, Hypnum cupressiforme Hedw.,
Ditrichum flexicaule (Schwaegr.) Hampe and Pohlia sp. These are
terrestrial mosses with different anatomy, structure and with
different requirements for water supplies in the soil.

H. cupressiforme also occurs as an epiphytic moss, mainly
over the trunk bases of deciduous trees (oaks).

These species were used to estimate some ecophysiological
characteristics important for comparison with vascular plants
forming the understorey in the forest communities.

For laboratory experiments the collected moss was prepared
by separating the green parts in the upper third of the indi-
viduals and putting them into an environment with 100% relative
air humidity, the lower portions being in water.

Before the experiments proper, the plants were saturated
for 24 hours.

To estimate moss water content, sets of 15 (Polytrichum),
15-25 (most other species) or up to approximately 80 shoots
(Atrichum) were weighed together to estimate fresh weight.
Dry weight was estimated after ovendrying at a temperature of
$90^{\circ}C$ for 48 hours.

The moss water potential was determined with the WESCOR
dew point hydrometer and C-52 sample chamber. Leaves (Poly-
tricum) or small moss pieces (other species) were used. Equi-
libration time was standardized to 60 minutes.

Patterns of the water loss rate were expressed as water-
loss curves. Plants were exposed in the laboratory for 3-6
hours to various temperature and air humidity levels:

July: 23°C and 76% RH,

August: 27°C and 75% RH, and

September: 26°C and 52% RH.

Parrallel samples were consecutively weighed at intervals of
0, 15, 30, 45, 60, 90, 150, 210, 270, 330, 390 minutes.
After the end of the experiment, the plants were oven dried
and dry weight was determined.

RESULTS AND DISCUSSION

By the measurements and water-loss curves the species
examined may be divided into two groups:

(1) The first group includes species with low water loss
rates and comprises the species Polytrichum commune and P.
formosum. These species lose 50% of their water content in
the course of the first 30 minutes and 90% of water content
during 2-3 hours of desiccation (Fig. 1, Table 1). These are
species with a relatively low water content at saturation
(170-200% of dry weight in July and August and 210-310% in
September, because of having a high dry matter content).
Maximum rate of water loss at saturation was 2.2-2.7 g H_2O g^{-1}
d.m. h^{-1} in July and August and 3.3-5.1 g H_2O g^{-1} d.m. h^{-1} in
September (though at a lower relative air humidity and a
higher water content).

(2) The second group includes species with high rates
of water loss during desiccation and it encompasses such
species as A. undulatum, H. cupressiforme, P. undulatum, D.
flexicaule and Pohlia sp. These species lose in the first 30
minutes of desiccation more than 80% of their water content.
These are species with a relatively high water content at
saturation. Most of the water was clearly held externally on
the shoots. High maximum water loss rates at saturation are
in agreement with this.

The last group is not entirely homogeneous, and the indi-
vidual species differ in the characteristics mentioned above.
Water content and water loss rate were highest with A. undula-
tum, lower with D. flexicaule and the lowest of all with the
epiphytic H. cupressiforme, within the same time period (Table 1).

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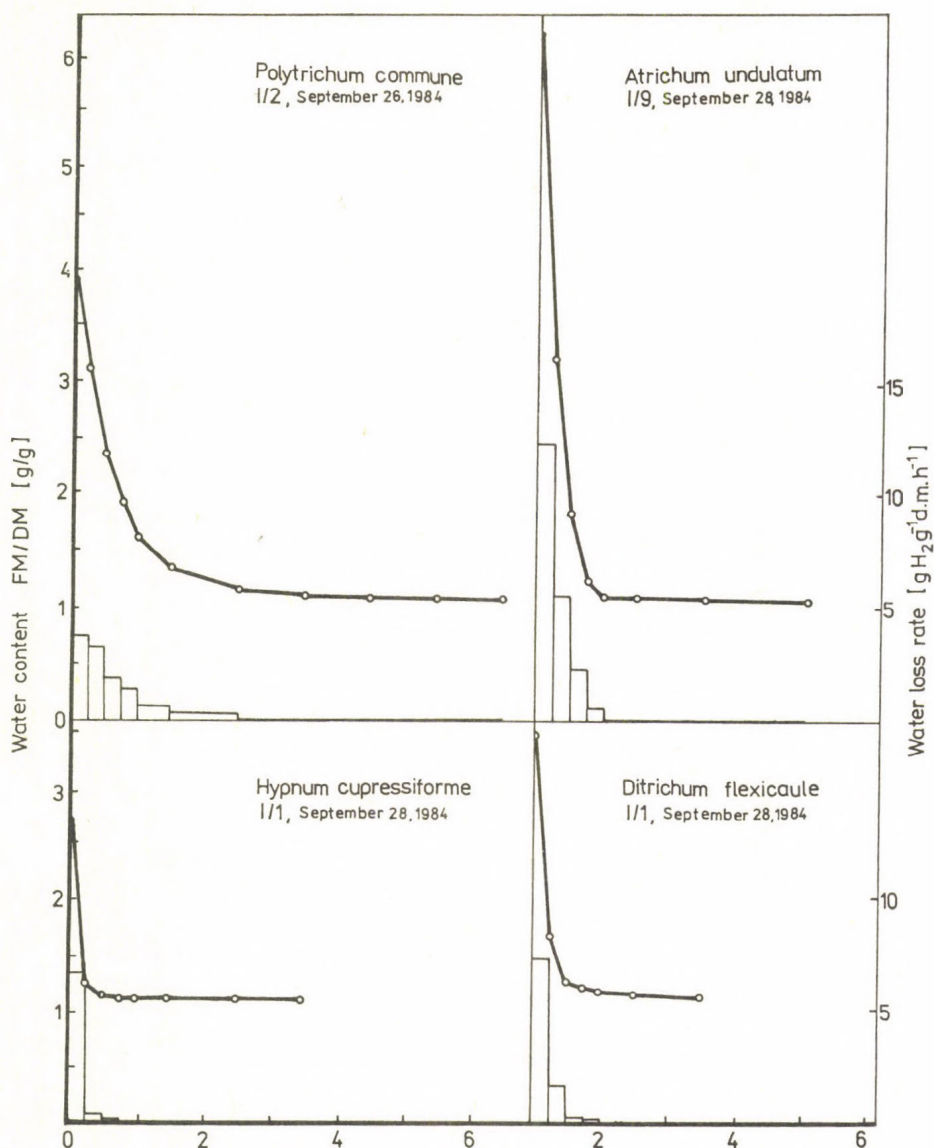
Fig. 1. Water content (lines) and rate of water loss (columns) in four moss species during desiccation in laboratory conditions (air temperature: 26°C, air humidity: ca. 50%). Samples were collected in the following communities: I/1 - oak forest, I/2 - spruce forests, I/9 - _Alnus_ stand. Time of desiccation is given in hours.

Table 1. Selected characteristics of water relations of woodland mosses collected from different forest stands in Malé Karpaty Mts., SW Slovakia (1984).

Species	Polytrichum commune			P. formosum	Atrichum undulatum	Plagiomnium undulatum		Hypnum cupressiforme	Ditrichum flexicaule
Community*	I/2		I/3	ŽS	I/9	ŽS		I/1	I/1
Date	July	Sept.	Sept.	Aug.	Sept.	July	Aug.	Sept.	Sept.
Saturated water content (FM/DM)	2.9	4.0	3.5	2.9	6.3	3.4	4.0	2.9	3.4
Saturated water content (% of dry matter)	190	305	255	190	535	246	330	193	248
Maximum water loss rate ($g\ H_2O\ g^{-1}\ d.m.h^{-1}$)	2.4	3.7 (5.1)	3.5	2.7	12.3	4.2	7.6	2.6	7.3
Relative water loss (% of initial water content) during first 30 min. of desiccation	32 (55)	55	58	53	85 (89)	85	80	90	86 (89)

* See text, for explanation.

The use of water potential as an important ecophysiological characteristic of mosses appeared to be impractical. In the course of the first 30 minutes of desiccation water potential in the moss species dropped to unmeasurable values. These practical difficulties of measurement of water potential in mosses over a wide range have been noted before (cf. Dilks & Proctor 1979, Proctor 1981).

Variations in moss water content, rate of water loss and drought tolerance among moss species have been found by different investigators. Water content of bryophytes at full turgor, free of external water, varied between 100 and 1180% of dry mass (Dilks & Proctor 1979). The rate of water loss from various moss species also differs considerably (Krupa 1977, Di Nola et al. 1983, Skre et al. 1983). Di Nola et al. (1983) concluded, from measurements of six species growing in different climatic regimes, that the mosses from the desert lost water most rapidly, while those from the humid habitat lost it more slowly. This finding appear to be in contradiction with our results on A. undulatum, a species collected in a moist alder forest stand, whose soil dries out at the surface only in the hot summer months. Irrespective of the specific structure, the saturation water content was the highest in this species, in July, August as well as in September (with the maximum of 550% of dry mass). The high water content is also matched with the high maximum rate of water loss at the saturation water content (up to 12 g H_2O g^{-1} d.m. h^{-1}). Water loss rate during desiccation was very high in this species: it was the highest in comparison with other species measured in the same period (see Fig. 1).

The moss water content after air drying (ca. 6 hours) in the seven moss species varied between 10-13% of dry mass. Di Nola et al. (1983) show similar data, from 7.4 to 15% of dry mass. Kroupa (1977) found differences in the dynamics of water loss from leaves of six moss species during a 24-hour period of desiccation at 85% and 95% RH. According to Krupa, the differences were not caused by differences in anatomical structure of the moss leaves but they were more likely due to the properties and structure of cell walls, though they might also

result from different resistance of the cytoplasm to evaporation.

The identified differences in the water-holding capacity of the moss species studied follow from differences in both the structure of mosses, in the mode of water transport, but also in the ecology and ecophysiology of the species.

Species of the genus Polytrichum belong to the endohydric species of mosses with internal water transport; they show the closest structural and functional analogies with vascular plants (Proctor 1979). The water holding capacity in the first minutes of desiccation of the Polytrichum species is therefore higher than in the other species examined.

Water relations of Polytrichum commune differ also in the field. As Skre et al. (1983) found, it showed the lowest water content at field capacity and lowest initial rate of water loss from excised green shoots among four woodland species; it also showed the shortest duration of desiccation in the field. This resulted from its ability to take up water from the soil (Bayfield 1973) and from its low water loss. It avoided moisture stress to a greater extent than the other moss species which were more dependent upon water absorption through the leaves.

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SOME ECOPHYSIOLOGICAL FEATURES IN WOODLAND MOSSES
IN SW SLOVAKIA 2. CHLOROPHYLL CONTENT AND PHOTOSYNTHESIS

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Chlorophyll content (Chl_c) per dry matter was estimated
in seven common woodland mosses in July 1984. Chl_c a varied
between 2.66 amd 908 mg/g, Chl_c b between 1.06 and 3.82 mg/g,
and total Chl_c a+b between 3.72 and 12.80 mg/g. Chl a:b ratio
ranged from 2.14 to 2.85.

Net photosynthetic rate (P_N) as a function of irradiance
was analysed in three woodland mosses (<u>Polytrichum</u> <u>commune</u>,
<u>Atrichum</u> <u>undulatum</u>, and <u>Hypnum</u> <u>cupressiforme</u>). The dark res-
piration rate (R_D) was established for the P_N/R_D ratio deter-
mination. IRGA in the open system was used ($20\pm1^{O}C$, high RH).
Water content in the moss samples was near saturation.

<u>P</u>. <u>commune</u> exhibited higher P_N sat (3.67-5.62 mg CO_2 g^{-1}
d.m. h^{-1}) and lower R_D (0.62-0.89 mg CO_2 g^{-1} d.m. h^{-1}) than
<u>A</u>. <u>undulatum</u> or <u>H</u>. <u>cupressiforme</u> (means 3.41, 2.54 and 2.56,
1.01, respectively). Photosynthetic activity in <u>P</u>. <u>commune</u>
was found to be higher in terms of the unit chlorophyll con-
tent, too (assimilation number = 0.53 mg CO_2 mg^{-1} Chl_c h^{-1}).
P_N/R_D ratio varied between 5.15 and 8.13 in <u>P</u>. <u>commune</u> and
1.14 and 1.79 in <u>A</u>. <u>undulatum</u>. The former moss exhibited
higher I_c (12 W m^{-2}), I_s (80-165 W m^{-2} PhAR) and photosynthe-
tic efficiency (17.23 mg CO_2 J^{-1}) than <u>A</u>. <u>undulatum</u> (8-10
and 65-100 W m^{-2}, respectively, 2.62 mg CO_2 J^{-1}) or <u>H</u>. <u>cupres-</u>
<u>siforme</u> (6 and 55 W m^{-2}, respectively, 6.31 mg CO_2 J^{-1}).

Dry matter per plant was higher in <u>P</u>. <u>commune</u> (13.70-
17.28 mg) than in <u>A</u>. <u>undulatum</u> (2.22-4.00 mg).

On the basis of quantitative features examined, P. commune belongs to heliophilous and A. undulatum with H. cupressiforme to sciophilous woodland mosses.

INTRODUCTION

Mosses differ from vascular plants in their generally lower photosynthetic activity and productivity. The reason for this is mainly the low chlorophyll content and the poikilohydric water economy which restrict the season of activity. Rapid drying is a mechanism of adaptation to high light and temperature conditions. Their relatively slow growth rate may also be regarded as a homeostatic mechanism for the mosses. They possess an ability for rapid reactivation without a lag phase and are able to take advantage of very short periods of temperatures suitable for photosynthesis (see e.g., Kallio & Kärenlampi 1975, Proctor 1979, 1981). In interactions with its atmospheric environment, the habit and growth form of mosses are to all intents and purposes part of their structure (Proctor 1979).

In this part of the paper we have aligned our sights upon the interspecific differences between stands in chlorophyll content, photosynthetic and respiration rates in some woodland mosses in SW Slovakia.

MATERIAL AND METHODS

Chlorphyll contents and CO_2 exchange were studied with the same mosses and at the same time as water relations (see Eliáš & Masarovičová 1986).

Chl_c a, b and a+b were determined directly in acetone extract (80% acetone). Measurements of absorbances were made in UNICAM SP 800 recording spectrophotometer. The Chl_c were calculated according to Vernon (1960). The results were expressed per dry mass.

Net photosynthetic and dark respiration rates were measured by the gasometric method in controlled environmental conditions (for details, see Masarovičová 1984). IRGA in the open

system was used. The plants were installed in the thermosta-
bilised assimilation chamber and well supplied with water. In
the case of Atrichum undulatum and Hypnum cupressiforme the
plants were measured together with soil.

Measurements were made in ranges of 5-200 X m^{-2} PhAR, air
temperature $20\pm1^{\circ}C$ and at high air humidity.

From the light response curves for CO_2 uptake the values
were extracted of the saturating (I_s), compensating (I_c) ir-
radiances, the net photosynthetic rate at I_s ($P_{n\ sat}$), the
dark respiration rate (R_D) and the photosynthetic efficiency
(slope of the initial part of the light response curve for
CO_2 uptake).

RESULTS AND DISCUSSION

Chlorophyll content and photosynthetic activity are de-
pendent on the anatomical and structural differentation of
leaves which are determined by ecological (mainly light and
humidity) conditions of the environment. The anatomical struc-
ture of moss leaves is much simpler and less differentiated
as compared with that of leaves of vascular plants (e.g.,
Proctor 1979, 1981, Krupa 1978, 1984). There should exist,
therefore, a relation between the anatomical structure of moss
leaves and their chlorophyll contents or photosynthetic acti-
vity, too.

Chlorophyll content

Chlorophyll content was measured in 7 moss species: Poly-
trichum commune Hedw., P. formosum Hedw., Atrichum undulatum
(Hedw.) P. Beauv., Plagiomnium undulatum (Hedw.) T. Kop.,
Ditrichum flexicaule (Schwaegr.) Hampe, Hypnum cupressiforme
Hedw. and Pohlia sp. growing in five forest stands with various
ecological conditions differing mainly in light and humidity.

Over all, chlorophyll a content amounted to 2.656-9.08,
chlorophyll b content to 1.06-3.82 and chlorophyll a+b to 3.72
- 13.8 mg/g d.m. The chlorophyll a:b ratio varied from 2.14 to
2.85. The highest Chl_c was found in P. undulatum (12.8 mg/g

d.m., July 31), the lowest in $\underline{D}$. flexicaule (3.72 mg/g d.m., July 27). In addition to interspecific differences within the same habitat, differences in Chl_c were also found within the same species stemming from various forest stands (Table 1). The differences appeared to be most pronounced in $\underline{P}$. undulatum, $\underline{D}$. flexicaule and $\underline{H}$. cupressiforme. Leaves differing in age, also differ in terms of Chl_c. This was borne out in the case of $\underline{P}$. commune and $\underline{P}$. formosum. the young leaves exhibiting a lower Chl_c as compared with old leaves (Table 1).

The character of concentration and quantitative relations of chlorophyll in mosses are similar to those described by

Table 1. Chlorophyll a, b and a+b contents, chlorophyll a and chlorophyll b ratio in some woodland mosses in SW Slovakia (1984).

Species		Loc.	Date	Chlorophyll content (mg/g d.m.)			
				a	b	a+b	ratio a:b
Polytrichum commune		I/2	3/7	*7.74±0.57	3.82±0.60	11.56±1.16	2.14±0.18
				**5.31±0.08	1.86±0.05	7.18±0.11	2.85±0.08
Polytrichum formosum	No.4	ŽS	27/7	*6.37±0.12	2.67±0.08	9.04±0.15	2.38±0.08
				**6.13±0.28	2.16±0.26	8.29±0.54	2.85±0.21
Atrichum undulatum		I/2	3/7	6.06±0.17	2.27±0.07	8.34±0.23	2.67±0.01
Plagiomnium undulatum	No.4 No.3	ŽS	27/7	***7.21±0.25	2.62±0.06	9.82±0.28	2.75±0.09
				9.08±1.22	3.72±0.30	12.80±1.51	2.42±0.17
Ditrichum flexicaule	No.4 No.3	ŽS	27/7 31/7	2.66±0.15	1.06±0.07	3.72±0.21	2.51±0.02
				8.41±0.25	3.33±0.09	11.74±0.34	2.53±0.01
Hypnum cupressiforme	No.1 No.3	ŽS	27/7	4.87±0.50	1.91±0.11	6.60±0.60	2.44±0.13
				7.64±0.11	3.08±0.05	10.85±0.16	2.52±0.01
Pohlia sp. No.2		ŽS	27/7	8.22±0.32	3.46±0.00	11.68±0.32	2.38±0.09

* Old plants
** Young plants
*** Generative plants

many authors in vascular plants (e.g., Krupa 1978, Aro & Valanne 1979). Conspicious is also the seasonal dynamics of Chl_c. In autumn and winter the Chl_c in the leaves of mosses (mainly epiphytic mosses) increases, whereas in the summer months a marked decrease of Chl_c is observed (Miyata & Hosokawa 1961).

Martin & Churchill (1982) found that in 20 moss species of the oak-hickory woods in north-eastern Kansas, Chl_c varied from 0.66 to 6.38 mg/g d.m. Mosses growing after full canopy closure mostly had a significantly higher Chl_c (4.36 mg/g d.m.) and a lower Chl_c a:b ratio (2.38) than before full canopy closure (1.46 mg/g d.m. and 2.51, respectively). The mean value of the Chl_c a:b ratio was 2.69 (2.29-2.99). The range of Chl_c a:b ratios for Kansas mosses was substantially higher than that reported for 11 species of mosses collected in North Carolina (1.4-2.1, Martin 1980).

However, not all mosses can alter their pigment composition following changes in the irradiance levels of the environment (Aro & Valanne 1979). This might explain the relatively low a:b ratio observed by Martin (1980) in the mosses collected in North Carolina.

Marked interspecific differences were found with 6 species of mosses also by Krupa (1984). Chl_c was highest in Mnium punctatum (14.0 mg/g d.m.), lowest in Polytrichum piliferum (3.63 mg/g d.m.). Interspecific differences in tissue chlorophyll concentration may be attributable to different morphologies (Nobel 1977). For example, the low amounts of chlorophylls per g d.m., characteristic of mosses examined in the paper of Martin & Churchill (1982), may be related to their extremely thick cell walls.

High Chl_c in shaded conditions would potentially increase the capture of available light, while a low Chl_c a:b ratio reflects an increase in size of the light-harvesting Chl a:b pigment protein complex (Alberte et al. 1976). Such changes in the characteristic of the ligh-harvesting pigment system appear to represent adaptations enhancing the efficiency of light capture (Martin & Churchill 1982).

Noteworthy are the results of experiments with Thuidium delicatulum and Leucobryum glaucum (Martin & Walker 1984). Neither Chl_c nor Chl a:b ratios were significantly correlated with the water contents for either species at either irradiance.

Photosynthesis and respiration

Mosses belong to plants whose growth and development, and occurrence in nature are closely connected with light conditions. Mosses, like vascular plants, may be divided into photo- (or helio-) and sciophilous ones. Frequently underlying such classification are the I_c and I_s values (Krupa 1978). In studying photosynthetic processes we have therefore concentrated upon the analysis of light response curves for CO_2 uptake, thus obtaining data on I_s, I_c, $P_{N\ sat}$ and α. In addition to these parameters data were gained on the assimilation number (AN), the dark respiration rate (R_D), on the balance of assimilation and dissimilation processes ($P_{N\ sat}/R_D$) and average dry mass per plant.

The above mentioned parameters were examined in three moss species: Polytrichum commune, Atrichum undulatum and Hypnum cupressiforme, differing in water relations (Eliáš & Masarovičová 1986) and Chl_c (this paper). The plants came from 6 different forest stands and measurements were made in September and October 1984.

On the basis of the quantitative features examined, P. commune belongs to heliophilous and A. undulatum and H. cupressiforme to sciophilous woodland mosses (Table 2).

Pronounced interspecific differences were found in the form of the light response curves for CO_2 uptake (Fig. 1). In P. commune a longer lasting plateau was reached, whereas in A. undulatum and H. cupressiforme P_N declined markedly after I_s was reached.

Generally, the value of I_c for sciophilous mosses range from 20 to 400 lx (Bazzaz et al. 1970) and for heliophilous species I_c lies between 1000 and 2000 lx. For heliophilous mosses I_s varies from 10-30 klx (Proctor 1981). In Ulota crispa, I_s was

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Table 2. Net photosynthetic rate at I_s ($P_{N\ sat}$), dark respiration rate (R_D), $P_{N\ sat}$ and R_D ratio, assimilation number (AN), photosynthetic efficiency (α), compensating (I_C) and saturating (I_s) irradiances, average dry matter per plant in some woodland mosses in SW Slovakia.

Species	Loc.	Date	$P_{N\ sat}$	R_D	$P_{N\ sat}/R_D$	Ass. number	α	I_C	I_s	Avg. W
			(mg CO_2 g^{-1}(d.m.)h^{-1})			(mg CO_2/mg Chl· h^{-1})	(mg CO_2 J^{-1})	(W m^{-2})		(mg(d.m.) per plant)
Polytrichum	I/3	25/9	4.554	0.885	5.146		14.30	13	110	15.250
commune	I/2	26/9	3.672	0.626	5.866	$\bar{x}$=0.532	19.08	12	110	17.280
	I/2	13/9	5.616	0.691	8.129		28.60	12	80	13.170
	ZS	1/8	5.328	–	–		11.40	12	165	15.530
Atrichum	I/9	29/9	3.492	2.829	1.234		2.68	8	90	2.224
undulatum	I/4	28/9	3.492	1.949	1.791	$\bar{x}$=0.330	3.38	8	65	4.000
	I/2	27/9	3.240	2.849	1.137		1.80	10	100	3.837
Hypnum cupressiforme	I/1	3/10	2.556	1.012	2.528	0.293	6.31	6	55	–

over 40 klx (Miyata & Hosokawa 1961). This means that I_c and I_s of heliophilous plants are, approximately, 10 times higher in comparison with sciophilous mosses. Our results are a bit higher than the generally accepted values (Table 2, Fig. 1).

Krupa (1978) analysed the light response curve for CO_2 uptake in <u>Polytrichum juniperinum</u>, <u>P. piliferum</u>, <u>Mnium punctatum</u>, <u>Catherinea undulata</u>, <u>Funaria hygrometrica</u> and <u>Aloina rigida</u>, finding <u>Mnium punctatum</u> to be a typically sciophilous plant (I_c=0.6 and I_s=15 W m^{-2}, respectively), and <u>P. piliferum</u> with <u>Funaria hygrometrica</u> typically photo- (or Helio-)philous mosses (I_c=1.8, I_s=55 and I_c=1.4, I_s above 100 W m^{-2}, respectively). The maximal gross photosynthesis values were 5-6 times higher than R_D, this being in agreement with our values (Table 2). Krupa also obtained similar response curves for CO_2 uptake in both (sciophilous and heliophilous) mosses to those in our experiments (Fig. 1). He found pro-
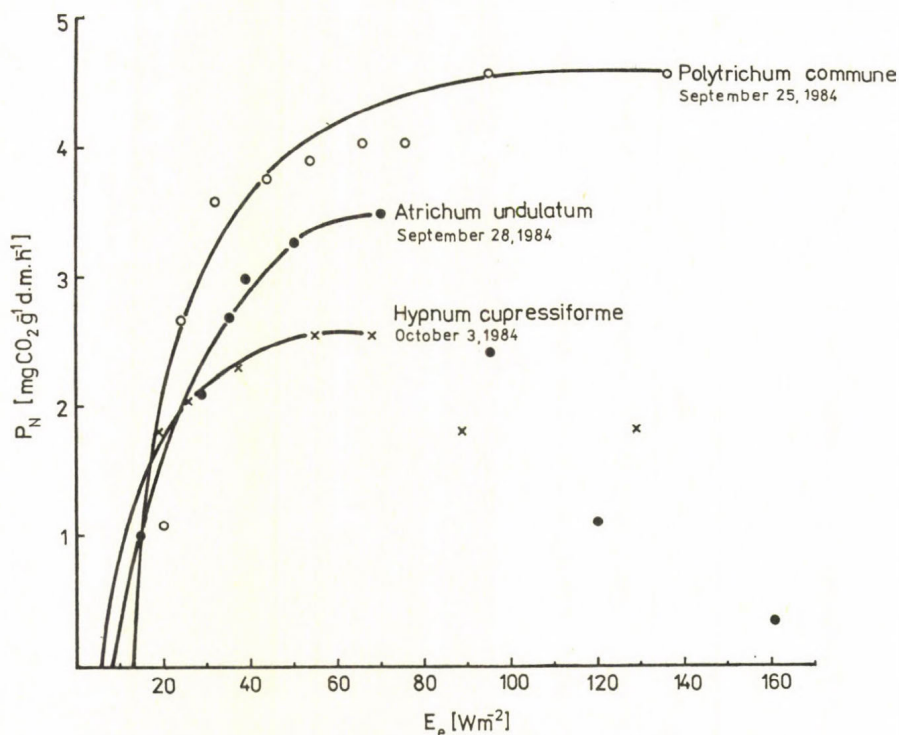
Fig. 1. The light response curves for CO_2 uptake of three moss species growing in various forest communities in SW Slovakia.

nounced differences between $\underline{P}$. $\underline{piliferum}$ and $\underline{P}$. $\underline{juniperinum}$
leaves. The different habitat of the former species and certain
differences in the morphology of its leaves find their reflec-
tion in the rate of gas exchange. At the same time, Krupa
draws attention to the cause of differences in the parameters
of the light curves of photosynthesis, namely that measurements
are made either with whole stems or with single leaves.

Proctor (1981) emphasize that I_c as such   is of little
ecological relevance; what is important is that the plant
should be able to recoup during the day the net carbon loss
due to respiration at night.

In another paper Krupa (1984) correlated the photosynthetic
activity of the leaf area with the degree of differentiation
of the anatomical leaf structure. Mnium punctatum has the
largest leaf area but the smallest P_N and R_D. Polytrichum pi-
liferum and $\underline{P}$. juniperinum exhibited a small leaf area, but
high P_N and R_D. A small leaf area ensures better water economy.
On the other hand, the leaves of Polytrichum species have on
their surface lamellae which no doubt increase the area of gas
exchange; the lamellae are partly shielded by the folded bor-
ders of the leaves. Krupa also obtained data on assimilation
number which were evidently higher in heliophilous species.
These mosses had lower Chl_c per unit d.m. So the lower acti-
vity per unit Chl_c found in the leaves of Mnium, as well as
other physiological differences between sun and shade leaves,
may be the cause of differences in the photosynthetic activity
of the leaves per unit leáf area.

The results of our research as well as other papers (e.g.,
Kallio & Kärenlampi 1975, Dilks & Proctor 1979, Proctor 1981,
Martin & Churchill 1982, Di Nola et al. 1983. Krupa 1984) em-
phasize the need for further ecophysiological investigations
into moss adaptation to different levels of irradiance or
water conditions. This is important primarily from the view-
point of completing the data on chlorophyll content, photo-
synthesis and respiration of this life form of plants in order
to gain an overall survey about the production and production
processes (i.e., carbon balance) of plants in forest ecosys-
tems.

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SOME PHOTOSYNTHESIS-ECOLOGICAL CHARACTERISTICS OF FOREST BRYOPHYTES[*]

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The total photosynthetic pigment content and light curves of net photosynthesis in three common moss species were measured by thin layer chromatography and infrared gas analysis in May and July from two forest habitats with different light regimes.

In summer the amount of each photosynthetic pigment is several times as large as it was in spring. By summer the max P_N values and P_N/R_D ratios increase and the light compensation point decreases.

In summer we have found great differences in both the pigment content and net photosynthetic rate between the populations of mosses living at the two habitats. Although in spring the light intensity in the two habitats can be considered almost the same, differences in the investigated photosynthesis parameters also can be found at this season. In the investigated bryophyte species, on the basis of our data we separated two ecotypes which are adapted to the local light intensity, very probably genetically.

[*] Abbreviations used in this paper: a = chlorophyll-a, b = chlorophyll-b, c = β-carotene, x = xanthophylls, car = carotenoids, P_N = net photosynthesis, R_D = dark respiration, RH = relative humidity, PS I = photosystem I, PS II = photosystem II, LHCP = light harvesting chlorophyll-protein complexes.

INTRODUCTION

The photosynthesis-ecological behaviour of higher plants
has been studied for a long time. The plants can adapt to
changes of the quantity and quality of light. The manifesta-
tion of helio- or sciophilous character of species or indivi-
duals is due to this adaptation. The character of the response
to the light climate is less known in mosses, although know-
ledge of this should be very important because they are very
good indicators of the environmental factors which are impor-
tant for the vascular plants and communities, too. In this way
mosses can be used for characterization of the environment of
their habitat.

One of the responses to the changes of quality and quantity
of light is the change of composition of thylakoids in the
chloroplast. This can be shown on basis of analysing of photo-
synthetic pigments. The most important functional response is
the modification of the net photosynthesis rate. By analysis
of the composition of photosynthetic pigments and character-
istic points of light-curves of net photosynthesis we tried to
answer the following questions: First: do populations of the
same moss species show adaptation to different light-ecological
environments of different habitats, or in other words, can
moss species from physiologically different ecotypes similarly
to the higher plants? Second: do certain photosynthesis cha-
racters of moss species depend on seasonal changes of light
regime?

MATERIAL AND METHODS

The ecophysiological studies were carried out on dominant,
terricolous, woodland moss species of two forest communities
(Melitti-Fagetum subcarpaticum and Quercetum petraeae-cerris
pannonicum) in Pilis Mts, northern Hungary, ca. 400 m above
sea level. It is known that there is lower daily average air
temperature, higher relative air humidity and lower light in-
tensity values in the Melitti-Fagetum (M-F) community than in

the _Quercetum_ _petraeae-cerris_ (Q.p.-c.) community. (For
example, daily average light intensities are 1,375 Klx and
3,175 Klx in M-F. and Q-P-c., respectively, in summer (see
Baló 1985 for details). The species examined are _Polytrichum_
formosum Hedw., _Atrichum_ _undulatum_ (Hedw.) P. Beauv. and _Pla-_
giomnium _affine_ (Bland.) T. Kop.

Photosynthetic pigment determination

Leaf pigments were extracted by acetone. Chlorophyll and
carotenoid components were separated by thin layer chromato-
graphy on cellulose powder (MN 300) and silica gel G to Stahl
plates (Maróti & Gabnai 1971). Chromatograms were developed
in dark at 5°C in benzene:isopropanol:water (100:12:0.25) as
solvent. Single components were eluted in ethanol (carotenoids)
and in acetone (chlorophylls) and pigment quantities were cal-
culated according to Hager & Meyer-Bertenrath (1966). The spe-
cific absorbance coefficients listed by Hager & Meyer-Berten-
rath (1966) and Grumbach et al. (1978) were used.

CO_2-_gas exchange measurements_

The net CO_2-uptake and dark respiration were measured with
an open flow infrared gas analysis system (Infralyt 4, Junka-
lor, Dessau) at 20°C $\pm$ 0.5 tissue temperature at 70% RH at
60 l·h^{-1} flow rate. For CO_2-exchange measurements the photo-
synthetically active upper leafy part of the mosses were used.
Measurements were carried out at saturated water content
(_Polytrichum_ _formosum_: 242.52%, _Atrichum_ _undulatum_: 307.89%
Plagiomnium _affine_: 434.63: dry weight^{-1}) in ventilated
chambers. Inside chamber control conditions were maintained
by Conviron E15 phytotron. The details of the system used for
CO_2-exchange are described by Tuba (this volume). Every de-
termination was repeated 3 times for each species.

RESULTS AND DISCUSSION

It is known that bryophytes have lower (net) photosynthesis
rates than the higher plants (Larcher 1980). Furthermore,

Table 1. Photosynthetic pigment contents (mg·g^{-1} dry wt) of the species examined.

	a	b	chl	c	x	car	pig
1. in spring							
a) in Melitti-Fagetum							
A. undulatum	0.67	0.26	1.03	0.19	0.27	0.60	1.63
b) in Q. petraeae-cerris							
A. undulatum	2.29	0.71	3.00	0.44	0.93	1.36	4.37
P. formosum	1.07	0.42	1.55	0.20	0.56	0.75	2.31
2. in summer							
a) Melitti-Fagetum							
F. vesca	3.54	1.26	4.80	0.35	0.76	1.11	5.91
A. undulatum	3.96	1.84	5.80	0.45	1.03	1.48	7.28
P. formosum	2.76	1.35	4.10	0.29	0.68	0.97	5.08
b) in Q. petraeae-cerris							
F. vesca	3.11	0.97	4.08	0.28	0.68	0.97	5.04
A. undulatum	4.80	1.97	6.77	0.49	1.06	1.55	8.32
P. formosum	2.50	1.24	3.74	0.39	0.83	1.23	4.97

bryophytes generally show shade photosynthesis characters, even in photophilous species (Tuba 1982). Therefore, first we have compared the photosynthesis parameters of the investiated bryophytes with the parameters of a vascular species growing in the understorey of the same community.

Comparison of pigment composition in the mosses and the higher species examined

Fragaria vesca (wild strawberry), a shade adapted higher plant (Baló 1985) from the same community contains more chlorophyll-a than P. formosum and less than A. undulatum (Table 1). We pointed out that chlorophyll-b and carotenoid content in the moss species mentioned are greater than in the shade-adapted F. vesca.

Table 2. Pigment ratios of the species investigated.

	a/b	a/c	b/c	x/c	$\frac{a+b}{x+c}$
1. in spring					
a) in Melitti-Fagetum					
A. undulatum	2.64	3.31	1.46	1.80	1.42
b) in Q. petraeae-cerris					
A. undulatum	3.25	5.27	1.63	2.13	2.20
P. formosum	2.66	5.74	1.88	2.82	1.91
2. in summer					
a) in Melitti-Fagetum					
F. vesca	2.81	10.21	3.66	2.21	4.31
A. undulatum	2.16	8.90	4.12	2.39	3.88
P. formosum	2.17	9.60	4.68	2.37	3.99
b) in Q. petraeae-cerris					
F. vesca	3.10	11.13	3.44	2.34	4.15
A. undulatum	2.45	9.85	4.05	2.16	4.41
P. formosum	2.14	6.98	3.16	2.32	2.45

This relation in the amount of pigments was the same in both habitats.

It was found that the ratio of a/b in F. vesca is greater and the ratio of b/c is smaller than in the moss species P. formosum and A. undulatum (Table 2).

It is well-known that shade-plants contain chlorophyll-a and β-carotene in smaller and chlorophyll-b and xanthophylls in greater amount than sun plants do. These results reflect the greater amount of LHCP in shade plants (Lichtenthaler 1982). The small a/b and the large b/c ratios are characteristic of shade plants because of their pigment content (Boardman 1977, Lichtenthaler 1982). By means of analysing pigmentprotein complexes it has been concluded that the PS II+LHCP/ PS I ratio is greater in shade plants than in sun plants.

On the basis of this fact, we established that the investigated woodland mosses have a greater degree of shade character in comparison with a higher plant.

Seasonal changes in the pigment composition in the mosses

We have observed that in summer the amount of each pigment is 2-8 times larger than in spring. The degree of increase is the greatest in case of chlorophyll-b and xanthophylls, especially in A. underlined undulatum.

As the amount of each pigment does not increase in the same rate, by summer the chlorophyll a/b ratio decreases and the a/c, b/c and x/c ratios increase (except x/c in P. formosum growing in Q. p-c.).

In summer the increase of average daily temperature accelerates synthetic processes. As the canopy of trees becomes closed, the decrease of light intensity leads to the high pigment content, mentioned before, and pigment ratios which are characteristic of shade plants.

The effect of light regime of the two habitats

Although the properties of the investigated moss species are similar to shade plants, great differences were found in pigment content and pigment rations between the moss species growing in the two habiats.

In summer, the chlorophyll-a content in A. undulatum growing in Q.-p-c. is much greater than in M-F. The a/b and a/c ratios were found to be greater in mosses growing in Q.p-c., and the x/c, and b/c ratios were greater in M-F. in the case of A. undulatum.

Practically there is no difference either in pigment content or in the a/b and x/c ratios in P. formosum growing in the two habitats. Nevertheless, the a/c and b/c ratios are greater in the population growing in M-F.
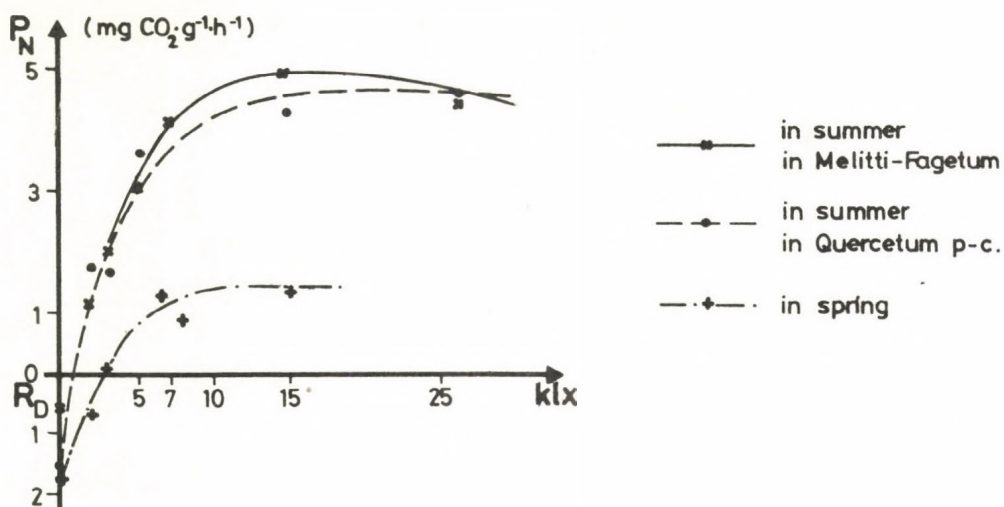
Fig. 1. Light curves of net photosynthesis of <u>Atrichum</u> <u>undulatum</u>
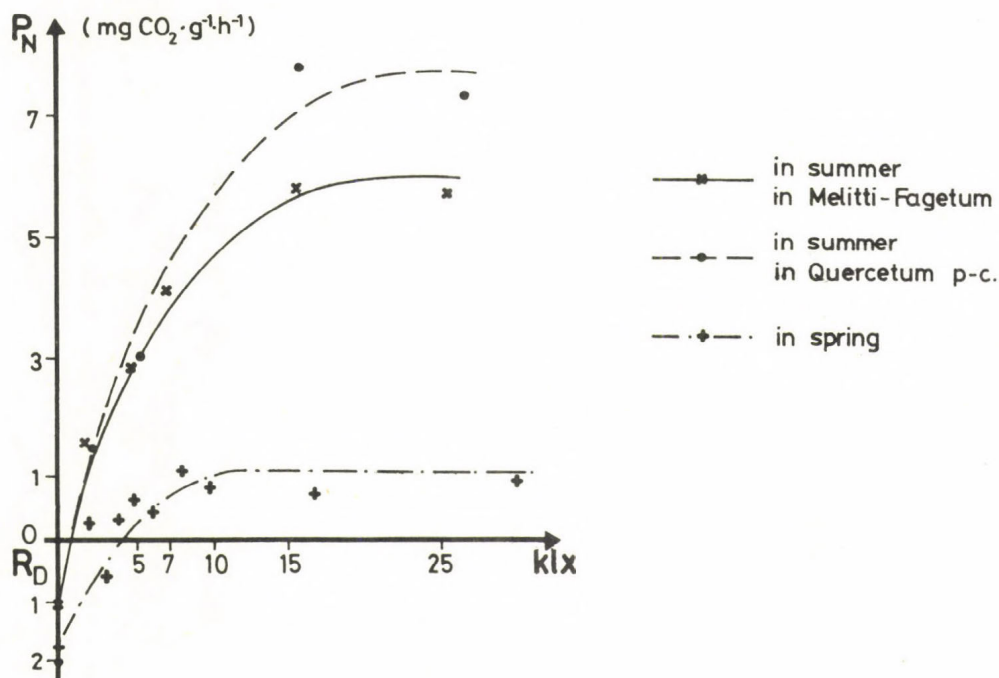
Fig. 2. Light curves of net photosynthesis of <u>Polytrichum</u> <u>for-</u>
<u>mosum</u>.

All these data correlate closely with our earlier results, namely: in summer in the herb layer the average light intensity is twice greater in Q.p-c. than in M-F (3,175 Klx and 1,375 Klx, respectively).

Although in spring the light intensity in the two habitats can be considered almost the same we found that chlorophyll-a and carotene content in both moss species is greater in Q.p-c. than in M-F. Similarly, the a/b ratio is greater in mosses growing in M-F. as in summer. This relation in the pigment content and pigment ratios between the two habitats is independent of seasonal changes of light intensity.

Comparison of CO_2-exchange in the mosses and Fragaria vesca

According to our earlier results, the maximum value of net photosynthesis for shade plants is 6 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$, and for sun plants is 11 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ in the case of <u>Fragaria</u>. In the course of our investigations, we found that the P_N max values of the three investigated species (<u>P</u>. <u>formosum</u>, <u>A</u>. <u>undulatum</u> and <u>Plagiomnium</u> <u>affine</u>) were much smaller, 4.5-7.5 mg $CO_2 \cdot g^{-1} h^{-1}$.
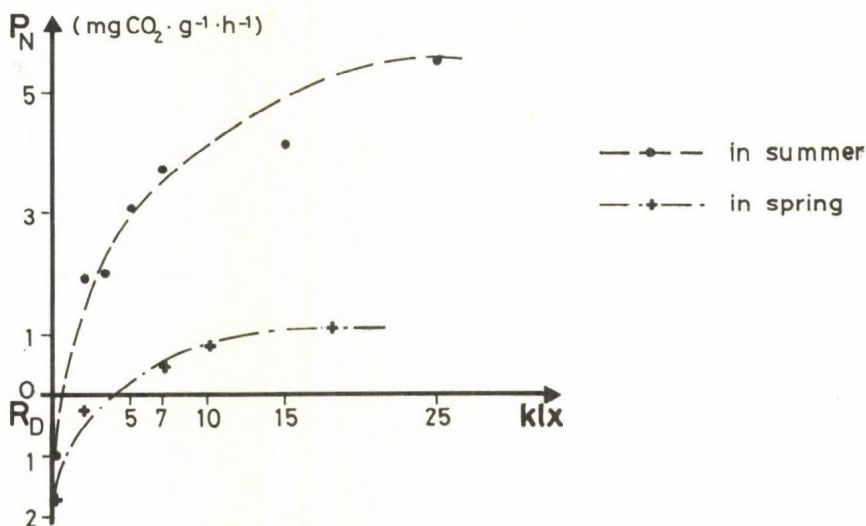
Fig. 3. Light curves of net photosynthesis of <u>Plagiomnium</u> <u>affine.</u>

It is known that the dominance of PS II and the great amount of LHCP besides other factors may cause the low maximum rate of net photosynthesis in shade plants (Boardman 1977). This statement can also be applied to the mosses investigated. In this way a close connection can be found between the pigment composition mentioned above and the low P_N max. values. On the basis of these results we can consider the investigated moss species as shade plants.

Seasonal changes of light curves of net photosynthesis

We observed three important facts in every case: by summer the light-compensation point decreases (in spring 3-4.5 klx, in summer 0.7-1 klx) and the P_N max. values and P_N/R_D ratios are many times higher than in spring (1-1.26 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$) in summer 4.5-7.6 mg $CO_2 \cdot g^{-1} \cdot h^{-1}$). Probably there is a certain connection between increase of the amount of LHCP and the decrease of light compensation point. It needs further investigations.

The effect of different light regime in the two habitats

We have not found any difference between the P_N max values of A. undulatum living in Q.p-c. and M-F. Nevertheless, at high light intensity (25 klx) the net photosynthetic rate of species from Q.p-c. remains unchanged while the photosynthetic rate of mosses from M-F. decreases. This decrease can be explained by the high light intensity, to which the plants are never exposed under natural conditions.

The light compensation point and rate of dark respiration of mosses living in M-F. are lower than in Q.p-c. and they reach the saturation point more quickly.

In the case of P. formosum higher values of P_N max. can be observed than in A. undulatum in both habitats and it is higher in Q. p-c. than in M-F. The saturation is reached more quickly and the value of R_D is lower in M-F., as in A. undulatum.

CONCLUSIONS

On the basis of the comparative analysis of the photosyn-
thetic pigment composition and light curves of net photosyn-
thesis, we can conclude that the investigated moss species have
more extreme shade-character than the shade-adapted higher
plants from the same community. The great amount of LHCP and the
low value of P_N max. all support this statement. Since other
bryophyte species show similar properties (Martin 1980, Martin
& Churchill 1982) mosses appear generally to be shade plants.
This shade character may have close connections with their
taxonomic position and their way of living (Tuba 1982). How-
ever, although mosses can be considered shade-plants, like the
higher plants, they are capable of adapting to different light
intensity to a certain extent. On the basis of our data we can
draw the conclusion that P. formosum and A. undulatum have
two ecotypes which are adapted to their local light intensity.
The difference between the two populations is less strongly
expressed in case of P. formosum because it may prefer light
spots in both habitats.
Since differences in the photosynthetic behaviour of the
moss populations can also be found in spring under the same
light regime, we concluded that the adaptation to the habitat
is genetically determined.

ACKNOWLEDGEMENTS

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LIGHT, TEMPERATURE AND DESICCATION RESPONSES OF CO$_2$-EXCHANGE IN THE DESICCATION-TOLERANT MOSS, TORTULA RURALIS

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It was hypothetized that the specific photosynthetic
("shade-like") feature of bryophytes, at least in the case of
the desiccation-tolerant mosses, is a consequence of their
poikilohydric economy. This idea was investigated on the
desiccation-tolerant photophilous Tortula ruralis, by the
elimination of desiccation, the most important poikilohydric
character, at different combinations of light and water eco-
logical situations in field experiments. Desiccation, light
and temperature responses of CO$_2$-exchange (net photosynthesis
and dark respiration) were measured under controlled condi-
tions using an open flow gas analysis (IRGA) system. The
CO$_2$-exchange investigations on T. ruralis confirm the specific
photosynthetic features of mosses. In the case of T. ruralis,
the "shade-like" characters are developed in close connection
with its poikilohydric economy. In the consequence of the
repeatedly occurring desiccation, tissue water relations that
ensure photosynthetic activity of T. ruralis, exist only at low
or moderate light intensity and in the lower temperature range.
After eliminating desiccation, with a continuous water supply,
T. ruralis shows shade and light adaptation as well. However,
T. ruralis growing at the high light intensity has extremely
low photosynthetic capacity, which is the consequence of the
specific temperature response of photosynthesis and dark
respiration, caused by the poikilohydric economy, too.

INTRODUCTION

It is generally known that the photosynthesis physiological and ecological features of bryophytes are different from those of higher C_3 species. The most striking and important photosynthetic characteristics of bryophytes can be summarized as 1) they have lower photosynthetic capacity (see e.g., comparison of Larcher 1980, Aro 1984); 2) their photosynthetic structure and function reflect shade adaptation syndromes, even in the case of the photophilous, sun-loving mosses (Proctor 1981, Aro 1982, Martin & Churchill 1982, Aro et al. 1981, Valanne et al. 1982, Tuba 1984a); 3) in relation to their poikilohydric water economy their photosynthetic activity at any moment depends on their actual tissue water relations at that time (e.g., Dilks & Proctor 1979, Tobiessen et al. 1978); 4) high tolerance' of their photosynthesis against the environmental stresses (Proctor 1981).

However, we have no evidence about the reasons responsible for these special photosynthetic features or about the factors contributing to their development. On various grounds I hypothetized that the shade-like characters, at least of the desiccation-tolerant mosses, evolved in relation to their poikilohydric economy. The photosynthetic activity, and indeed all the metabolic activity of desiccation-tolerant mosses generally takes place only at low or moderate light intensity and in the lower temperature range, because of their very rapid water loss and their frequent desiccation.

This idea was investigated on the photophilous, desiccation-tolerant _Tortula ruralis_, growing in a semi-desert grassland. According to the hypothesis, by the elimination of the most important poikilohydric character, the desiccation, _Tortula ruralis_ has to show shade, light and high light adaptation, too, and the _Tortula_ individuals growing in original field circumstances at high light intensity with frequent desiccation, haveto reflect shade photosynthetic features.

I investigated the photosynthesis responses of _T. ruralis_ growing at two levels of low irradiance with continuous water

supply without desiccation and at high light intensity with
frequent desiccation, growing in a similar situation as in
the field.

MATERIAL AND METHODS

Plant material

Tortula ruralis was grown in a semi-desert continental
perennial grassland (Festucetum vaginatae danubiale) at Vác-
rátót (19°15'E, 47°42'N, 130 m a.s.l.).

*Field experimental procedures (light and water ecological
situations)*

On 12 March 1982, the Tortula cushions were collected and
transferred together with their soil substrate into the field
experimental area of the photosynthesis laboratory of the
institute. T. ruralis cushions were divided into 4 groups
and were kept outdoors until 21 June 1985, under the following
distinct light and water conditions: 1) in deep shade, at very
low light irradiance (during the experiment the highest light
intensity was 13 Klx), without desiccation, at continuous
field water saturation level (water content 288.6-389.9% of
dry weight); 2) in shade at low irradiance (highest light
intensity during experiment 19-20 Klx), without desiccation at
continuous field water saturated level (water content 262.4-
342.0% of dry weight); 3) similar to the original field eco-
logical situation under high irradiance (daily average light
intensity during the experiment above 35 Klx and highest light
intensity 96 Klx) and under the naturally occurring water
regime, therefore exposed to repeated desiccation (water con-
tent between 15.9-356.0% of dry weight); 4) at high irradiance,
under the same light regime as described in the case of 3, but
without desiccation at continuous field water saturation level
(water content 273.5-325.6% of dry weight). The air temperature
measured 3 cm above the cushions kept in the deep shade and
shade (1 and 2) was 0.5 - 2.5°C, lower than above the cushions
kept at the high irradiance (3 and 4). Light intensity and

air temperature were measured continuously during the experiment (by a JU 16 type luxmeter and a thermometer of type TM-25).

Measurements of CO_2-gas exchange

Net CO_2-uptake and dark respiration were measured using an open-flow gas analysis system with a Peltier-module equipped Infralyt-4 (Junkalor - Dessau) differential infrared gas analyser (IRGA), at the ambient atmospheric CO_2 level (330-360 vpm). Chambers used in this system were constructed of plexiglas with the volume of 750 ml (Tuba 1984b). Flow rate through the chamber was maintained at 500 ml·min^{-1}. Ventilation inside the chamber was provided by a radial fan.

Light responses of net photosynthetic rate were measured at 20.0 ± 1.0^{o}C leaf tissue temperature at saturated water contents (which were identical with the value given in the description of the field experiments). Light was provided by F72 12-CM-WHO 100 W (Sylvania) tubes.

Temperature responses of net photosynthesis rate were examined also at saturating water contents and at saturating light intensity (30 Klx).

The adaptation to a given light or temperature condition was at least 30 minutes. Dark respiration at various temperatures was measured after half hour darkness.

During the measurements, the chamber and moss tissue temperature was maintained by the temperature controlling system of a Conviron E15 phytotron or by a refrigerator operated temperature controlled assimilation chamber (Tuba 1984b). The relative humidity of the air coming into the chamber was controlled and maintained at 70% (± 5.0%) with the relative air humidity controlling system of a Conviron E15 plant growth chamber.

Only the photosynthetically active upper leafy parts of the moss were used for the investigations to avoid the respiratory CO_2-release of the lower parts. The cut leafy parts of the individuals were kept in the chamber on moistened filter paper. During the measurements, the mosses were sprayed

with distilled water to maintain the water saturated level required. The moss tissue temperature was monitored with a thermometer (TM-25).

All measurements were repeated at least 3 times. The CO_2-exchange rates are referred to 1 g dry mass, the water content is given as a percentage of oven dry weight.

The quantity of total photosynthetic pigments (chlorophylls and carotenoids) was determined after TLC separation, as described in Tuba (1984c).

RESULTS AND DISCUSSION

Effect of desiccation on the net photosynthetic rate of Tortula ruralis

The relationship between the changes of tissue water content and net CO_2-uptake of T. ruralis growing in the original field situation can be described by a third degree polynomial function (Fig. 1). The water content compensation point of the species is 15% and the relative air humidity compensation point indicates a very frequent desiccation of the species.

The combined effect of the different irradiance level and water relations on the light and temperature responses of net CO_2-exchange

As in the literature data, the maximal net photosynthetic rate of T. ruralis growing in all of the investigated situations, is lower than for higher C_3 plants (e.g., Larcher 1980, Aro 1984), even from the same grassland (Tuba 1984b).

Light responses

The light compensation point and saturation light intensity of net photosynthesis in T. ruralis growing in similar conditions to the field (at high irradiance and exposed to repeatedly frequent desiccation) is lower than for C_3 flowering plants (Fig. 2). This light response curve reflects shade photosynthetic characters. The light compensation point of T. ruralis

growing at low irradiance without desiccation is lower than
that of material growing in field situation with desiccation
(Fig. 2). T. ruralis growing in shade shows light saturation
already at 15 Klx light intensity (Fig. 2). Among the treat-
ments investigated, T. ruralis which was growing at high ir-
radiance and continuous water supply without desiccation has
the highest light compensation point. At the same time its
photosynthesis shows saturation at the highest light intensity
(Fig. 2). On the basis of the light compensation points and
the initial slopes of the photosynthesis illumination curves,
compared with material growing in the field situation, T.
ruralis growing at low light intensity without desiccation
shows shade adaptation, while at high light intensity without
desiccation it shows high-light or sun adaptation (Fig. 2).

However, contrary to the results observed on higher plants
(Boardman 1977), the maximal net photosynthetic rate from both
of the shade adapted treatments is higher than that of the

$$y=-0.392+0.043x-0.00028x^2+0.00000052x^3$$
$$P=0.1 \%$$
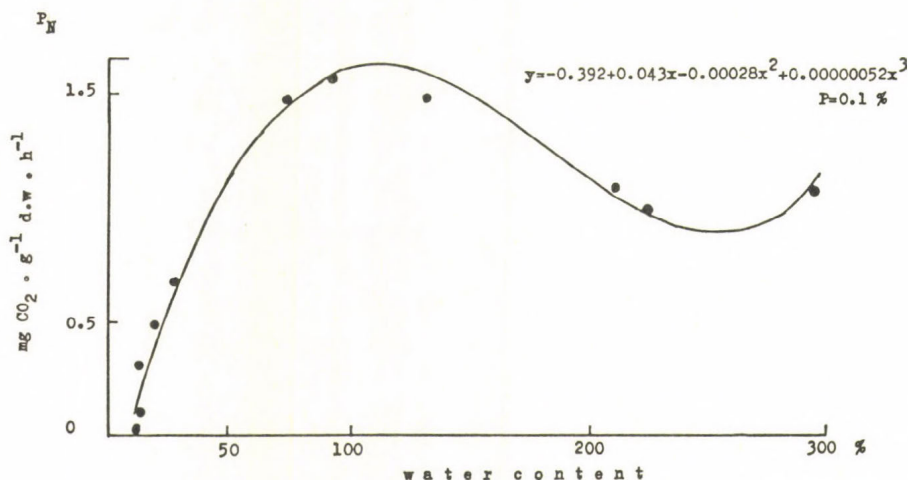
Fig. 1. Relationship between the net photosynthetic rate and
tissue water content of Tortula ruralis growing in original
field situation.

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Table 1. The total photosynthetic pigment content (chloro-phylls + carotenoids) of _Tortula_ _ruralis_, growing without de-siccation in deep shade (A) and shade (B), at high light in-tensity with desiccation (C) and at high light intensity with-out desiccation with continuous water supply (D).

	Photosynthetic pigment content $(mg \cdot g^{-1}$ dry weight)
A	2.879
B	2.778
C	1.382
D	1.112
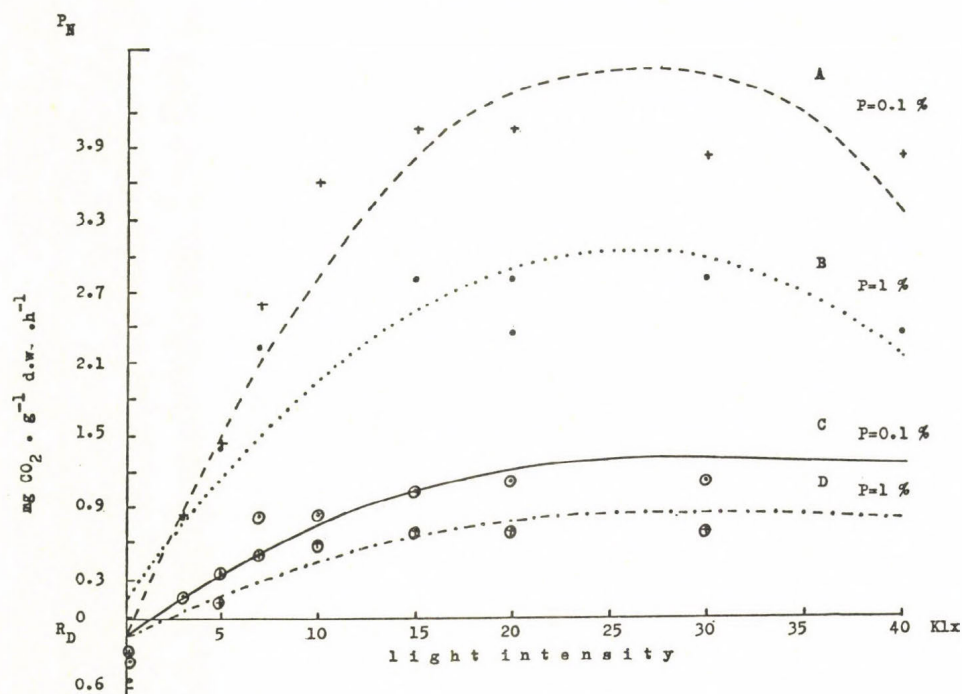
Fig. 2. Dependence of net photosynthesis upon light intensity in _Tortula_ _ruralis_, growing without desiccation at continuous water supply in deep shade (A) and shade (B), at high light in-tensity with frequent desiccation (C) and at high light inten-sity without desiccation with continuous water supply (D).

light adapted T. ruralis, growing without desiccation (see
Fig. 2). The increased photosynthetic capacity in T. ruralis
growing in shade is the consequence of the synthesis of ad-
ditional photosynthetic units, developed by continuous un-
limited water supply (Table 1). The synthesis of new photo-
synthetic units is shown by the increased amount of the photo-
synthetic pigments (total photosynthetic pigments = carotenes
+ xanthophylls + chlorophylls) - see Table 1. The synthesis of
new photosynthetic units in the moss exposed to frequent de-
siccation is much less or may even be inhibited (Table 1).
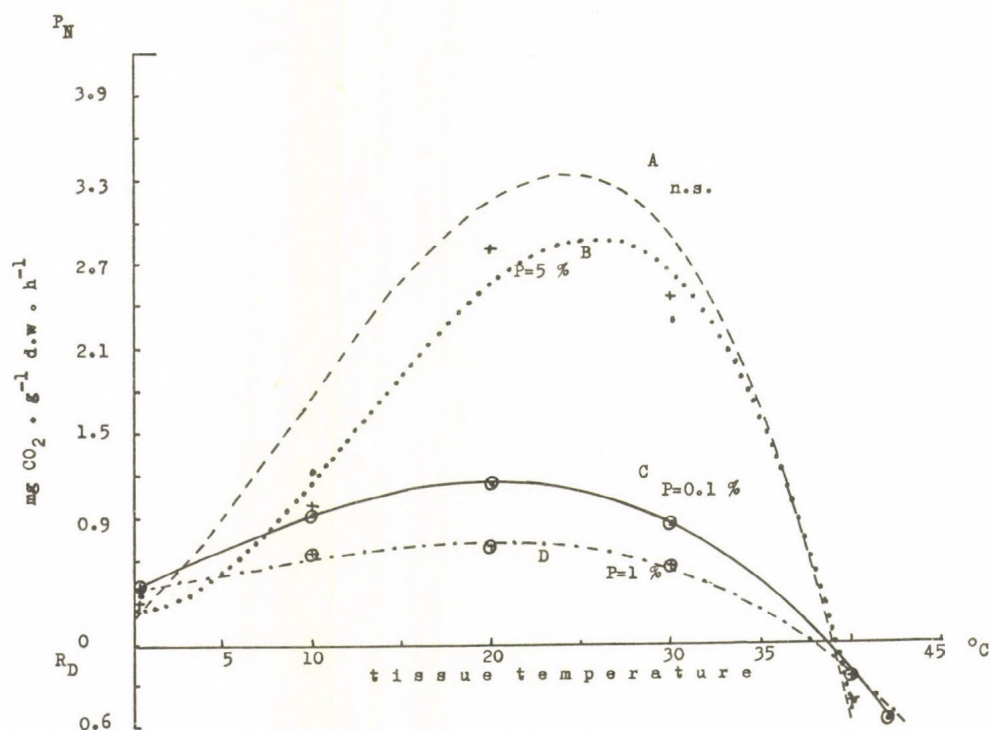
Fig. 3. Temperature dependence of light-saturated CO_2-uptake in
Tortula ruralis, growing without desiccation with continuous
water supply in deep shade (A) and shade (B), at high light in-
tensity with frequent desiccation (C) and at high light inten-
sity without desiccation with continuous water supply (D).

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At the same time, decrease in the photosynthetic unit density can be observed in the moss growing at high irradiance level and continuous water supply without desiccation (Table 1). This decrease of the density in the photosynthetic units results in a marked decline in photosynthetic capacity (Fig. 2). (The details of the photosynthetic pigment composition change with the effect of different light and water conditions; the relationship between pigment composition and net photosynthetic CO_2-uptake will be the subject of another paper).

The net photosynthetic rates in T. ruralis from all of the treatments declines very rapidly above $30^{\circ}C$, and above $37^{\circ}C$ there is only negative C-balance in every case which indicates the dominance of catabolic processes (Fig. 3). Since T. ruralis kept at high light intensity without desiccation usually exceeds $30^{\circ}C$ and often reaches the $37^{\circ}C$ upper temperature compensation point (Tuba 1984b), catabolic processes are likely to cause at least partial decomposition of the photosynthetic units, and lead to decrease of the net photosynthetic capacity, too.

Temperature responses (Fig. 3)

The characteristic temperature responses of net CO_2-exchange in T. ruralis, growing under different light and water ecological conditions, are as follows: 1) they show net CO_2-uptake already at $0^{\circ}C$, even in summer, which is highest in the material growing at high irradiance; 2) the optimal temperature of net photosynthesis in T. ruralis, growing at high light intensity is similarly low (between $13-26^{\circ}C$) than reported for other bryophytes, even for desert ones (see Proctor 1981); in the shade-grown material this temperature optimum is a bit higher ($18-30^{\circ}C$); 3) the photosynthesis of T. ruralis growing at high irradiance remains close to the maximum over a rather wider range, especially at lower temperatures; 4) the upper temperature compensation points of each of the investigated batches of T. ruralis, growing in different light and water ecological conditions, are very similar and lie between 35 and $38^{\circ}C$.

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These values are lower than those of the C_3 vascular
species in the same community (Tuba 1984b). This points very
clearly to the fact that T. ruralis, in its metabolically
active condition, cannot tolerate the higher temperature which
occurs after its desiccation. This seems to be genetically
fixed, since all of the investigated material from the dif-
ferent ecological conditions show similar responses in this
respect.

This is confirmed by the increase of dark respiration with
increasing temperature (Fig. 4). At 38-40°C, the mitochondrial
respiration rate is greater than the CO_2-uptake, therefore at
38-40°C there is only net CO_2 release (Fig. 4). The ratios of
net photosynthesis to mitochondrial respiration, which inform
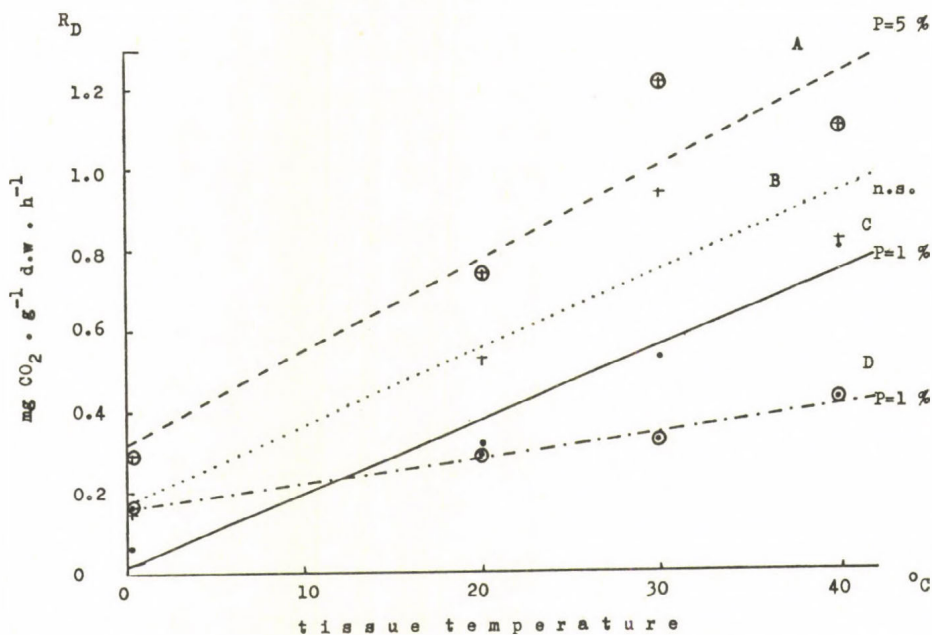
Fig. 4. Temperature dependence of dark respiration in Tortula
ruralis, growing without desiccation with continuous water
supply in deep shade (A) and shade (B), at high light inten-
sity with frequent desiccation (C) and at high light intensity
without desiccation with continuous water supply (D).

Table 2. Temperature dependence of light saturated net photo-
synthesis / dark respiration ratio in Tortula ruralis, growing
without desiccation in deep shade (A) and shade (B), at high
light intensity with desiccation (C) and at high light inten-
sity without desiccation with continuous water supply (D).

| | P_N/R_D | | | |
	$0^{\circ}C$	$20^{\circ}C$	$30^{\circ}C$	$40^{\circ}C$
A	2.0	5.3	2.6	only CO_2 release
B	1.2	5.4	1.9	
C	3.5	3.5	1.6	
D	2.4	2.4	1.7	

us about the efficiency of CO_2-assimilation, are highest at
lower temperatures (at 0 and $20^{\circ}C$); at $30^{\circ}C$ the ratio decreases
significantly due to the enhancement of dark respiration and
at $40^{\circ}C$ we find already a negative carbon-balance (Table 2).

CONCLUSIONS

    The present investigations, performed on the photophilous,
desiccation-tolerant, ectohydric moss Tortula ruralis sup-
port and confirm the specific photosynthetic features of
mosses (and other bryophytes), which differ from those of C_3
higher plants and can be summarized as shade-like photo-
synthetic features.
    According to my results, in the case of the photophilous,
desiccation-tolerant T. ruralis, the shade-like photosynthetic
characteristics are developed in close connection with the
poikilohydric water economy. In consequence of repeatedly
occurring desiccation, tissue water relations generally ensure
that photosynthetic, and indeed all metabolic activity of T.
ruralis takes place only at low or moderate light intensity
and in the lower temperature range. These limitations are

expressed by the light and temperature responses of photo-synthesis in T. ruralis, growing under field conditions. After eliminating desiccation, the most important poikilohydric feature, then on the basis of the light response of photo-synthesis, T. ruralis shows shade and high light adaptation. However, the high light adapted material growing without desiccation has much lower maximal net photosynthesis rate than the shade adapted, or even than material growing at high irradiance with desiccation. This extremely low photosynthetic capacity is nevertheless the consequence of the specific temperature response of photosynthesis, caused by the poikilohydric economy, too. Since because of its desiccation, T. ruralis during its metabolically active stage is not exposed to higher temperature than the upper temperature compensation point for net photosynthesis, adaptation to higher temperature has not yet been developed. This is reflected clearly by the temperature responses of CO_2-exchange, the temperature dependence of mitochondrial respiration and net photosynthesis/dark respiration ratio. In other words, because of desiccation, in T. ruralis adaptations were developed only to those light and temperature situations and their combinations which occur in its metabolically active hydrated stages. The nature of the adaptations to the extremely high light and high temperature, occurring after its desiccation, is anabiotic.

The above-mentioned facts probably are valid for most mosses, at least for the desiccation-tolerant species, knowing their "shade-like" characters and their rather low upper temperature compensation point of net photosynthesis, and these are probably not unimportant for the distribution of terrestrial mosses.

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THE USE OF DIMETHYL SULFOXIDE (DMSO) AS A SOLVENT TO EXTRACT CHLOROPHYLL FROM MOSSES

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Determination of chlorophyll a and b is an important parameter in ecophysiological research. The aim of this study is to develop a standardized method for the use of DMSO as a solvent to extract chlorophyll from mosses, and to compare it with the 80% acetone extraction method. Pleurozium schreberi is used as a test species. DMSO proves to be a reliable solvent: it is easier to use and gives a more complete extraction than 80% acetone, the extract has a low turbidity, and the extracted chlorophyll can be stored for 64 hrs at 4°C without degradation.

INTRODUCTION

Determination of chlorophyll content in plants is a useful estimation of primary productivity or has been used in bio-assays of environmental stresses in ecophysiological research. Extraction of chlorophyll in acetone has been the common method among bryologists (Wolf 1958, Martin 1980, Martin & Churchill 1982, Glime & Keen 1984, Penuelas 1984).

Although dimethyl sulfoxide (DMSO) was known as a solvent for proteins and starch before it was used to extract photo-pigments from algae (Seely et al. 1972), there have been no reports, until recently (Alpert 1984), on its use to extract chlorophyll from bryophytes. Hiscow & Israelstam (1979) used DMSO to extract chlorophyll from higher plants, Ronen & Galun (1984) tested DMSO to extract chlorophyll from lichens. Shoaf

& Lium (1976) extracted chlorophyll from algae in a 1:1 mixture of DMSO and 90% acetone.

The high dielectric constant of water and DMSO, in comparison to acetone, enables both molecules to pass the hydrophilic heads of the phospholipid layers of the cell membrane. However, water won't pass the hydrophobic tail of the phospholipid layers, whereas DMSO will do so because of its two methyl ($-CH_3$) groups. A result of this is that DMSO opens up the membranes and makes them permeable for other molecules, such as chlorophyll. The solubility properties of DMSO and acetone with respect to chlorophyll are less understood. We can hypothesize that acetone, because of its weaker dipole moment and smaller size, penetrates the chlorophyll-protein complexes better than DMSO. Chlorophyll might be more soluble in acetone than DMSO. However, the dielectric constant properties or the ability of DMSO to make membranes permeable is of far more importance in this context than the dipole moment interactions.

The objectives of our study were to develop a method to extract chlorophyll from mosses using DMSO, and to compare the extraction of chlorophyll a and b by DMSO with the 80% acetone method. We also tested the stability and optical characteristics of pure chlorophyll a and b in DMSO. Both extraction methods have been criticized in overestimating chlorophyll a content because of the overlapping absorption spectrum of chlorophyll a with that of other photopigment degradation products. However, prior chromatographical separation to obtain our chlorophyll pigments requires advanced techniques and is more expensive without being ecologically significant for most bioassay types of research.

METHODS

Because of our eco-physiological work on boreal bryophytes, we selected Pleurozium schreberi (Brid.) Mitt. as the test species. The bryophytes were collected under jack pine (Pinus banksiana Lamb.) in Alberta, Michigan ($88^O40'E$, $46^O40'N$). We air-dried 1 cm green stem tips in the dark for 24 hrs, weighed

them and extracted chlorophyll. Five to ten replicates were used in each experiment. We used pure chlorophyll a and b from spinach (Sigma Chemical Company) to develop standards.

Extraction of chlorophyll in 80% acetone

To soften tissues for easier maceration and facilitate more efficient extraction, we immersed three air-dried moss tips in distilled water for 15 seconds. We ground the tips in 80% acetone with a mortar and pestle and a few grains of sand. Following complete maceration, we precipitated the particles with gravity and filtered it through Whatman #1 filter paper. (Centrifugation of such a small quantity proved to be uneffective). We washed the filter paper with 80% acetone to flush remaining pigments from the filter paper thus obtaining 5 ml of the extract, measured in graduated test tubes. We read absorbance on 3-ml samples at 663 (chl a), 645 (chl b), and 750 nm (turbidity) against 80% acetone blank using a Beckman DU-8 Spectrophotometer with a slitwidth of 0.5 nm. We calculated chlorophyll concentration (mg chlorophyll/gram air-dried moss) using Arnon's equation (Arnon 1949). We worked in subdued light throughout both acetone and DMSO extraction.

Extraction of chlorophyll in DMSO

We submersed the air-dried moss tips in water for 5 minutes to insure complete hydration, then pressed them between disposable paper tissue to remove excess water. We transferred the stem tips to test tubes with 5 ml of DMSO (Fischer Scientific, d-128), closed the test tubes with aluminium caps, and placed them in the oven at $65^{\circ}C$. The extraction time differed among the various experiments. After extraction we cooled the solvent to room temperature or placed it in the refrigerator at $4^{\circ}C$ until absorption readings were taken. Absortion readings (against DMSO as a blank) and calculation of the chlorophyll concentration followed the same steps as described above for 80% acetone.

Experimental design

a. To determine extraction time in DMSO we read absorbances of extracted P. schreberi chlorophyll after 2, 4, 8, 16, 24, 32, 48, 64, and 72 hours. At each time interval we pipetted 3 ml of the DMSO to a cuvette to read absorbances, then returned the chlorophyll extract to the sampled test tube. After 72 hours, the stem tips were completely bleached and further extraction was omitted.

b. To determine stability of chlorophyll extract in DMSO after extraction for 32 hours at $65^{\circ}C$, we removed the stem tips from the solvent and stored the test tubes with the extract at $20^{\circ}C$ and at $4^{\circ}C$ in the dark. We read absorbances after 0 (immediately after DMSO extraction), 32, 64, 126 hrs, 2, and 4 weeks. We measured absorbances in three ml aliquots which we returned to the same test tubes for further storage. We stopped the experiment after 4 weeks because there were significantly lower chlorophyll concentrations compared to those at the start of the storage period.

c. To determine stability of pure chlorophyll a and b in DMSO we prepared stock solutions of 2 mg/l of chlorophyll a and b (this corresponds with the amount of chlorophyll we found in P. schreberi stem tips). Solutions of chlorophyll a and b were stored in the dark at $25^{\circ}C$ and $65^{\circ}C$ for 0, 4, 8, and 16 (period of maximum extraction) hours before reading absorbance.

d. Based on the degradation of pure chlorophyll at $65^{\circ}C$ in DMSO in experiment c, we tried to improve the extraction of chlorophyll by changing the temperature during the 16 hr extraction period. We submersed one set of P. schreberi stem tips in DMSO for 4 hrs and a second set for 16 hrs at $65^{\circ}C$. We measured absorbance at the end of the extraction period. We extracted a third set for 4 hrs at $65^{\circ}C$, followed by 12 hrs at $25^{\circ}C$. The 4 hr period was selected because no decrease of pure chlorophyll a and b in DMSO at $65^{\circ}C$ occurred within this time in experiment c.

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RESULTS

a. Substantial amount of chlorophyll a and b is extracted
by DMSO during the first two hours (Fig. 1a,b). Chlorophyll a
is optimally extracted after 8 to 16 hrs submersion in DMSO
at 65°C. Chlorophyll b tends to have a slower extraction rate,
which reaches a maximum at about 16 hrs. Further prolongation
after 16 or 24 hrs reduced the level of chlorophyll a and b
in solution, showing significant differences after 72 hrs
(chl a: p=0.001, chl b: p=0.000, t-test). Because of the dif-
ferent extraction rates of chlorophyll a and b there was a
sharp drop of the chlorophyll a/b ratios during the first 8
hours of the extraction and leveled off after 16 hrs. We
therefore selected 16 hrs as an optimal extraction time for
chlorophyll in DMSO. We found significantly higher extraction
of chl a in DMSO than in acetone (p = 0.01, t-test). No further
extraction of chlorophyll was evident when the moss tips were
kept in the DMSO after removal of test tubes from oven.

b. Chlorophyll a and b in DMSO are most stable at 4°C in
the dark, where they can be stored for 64 hrs (Figs 2 and 3).
A significant decrease of chlorophyll a and b showed up at
5 days (chl a: p = 0.007, chl b: p = 0.006, t-test), but the
chlorophyll a/b ratio remained stable for two weeks. We found
a significant decrease of chlorophyll a and b after 32 hrs
if the DMSO extract was stored at 25°C (chl a: p = 0.04, chl b:
p = 0.019, t-test). Chlorophyll a tends to decrease at a
faster rate than chlorophyll b at 25°C, and although a similar
trend seemed to occur at 4°C, we did not find significant dif-
ferences between chlorophyll a and b in this respect.

c. Although chlorophyll a remained stable for 16 hrs at
25°C, we found a significant decrease at 8 hrs if we kept the
DMSO at 65°C (p = 0.038, t-test), (Fig. 4). However, no sig-
nificant differences in chlorophyll a showed up between 25
and 65°C at any of the different time periods. Chlorophyll b
decreased significantly after 8 hrs at 65°C, (p = 0.000, t-
test), but no significant degradation occurred over a 16 hr
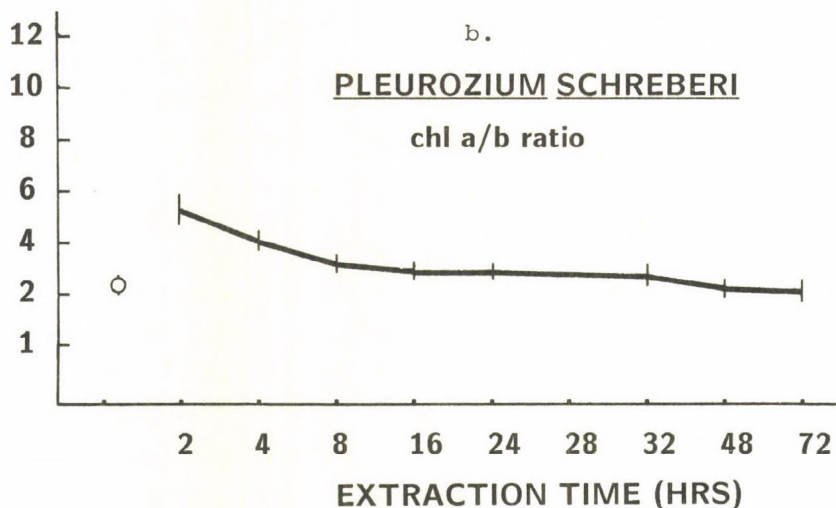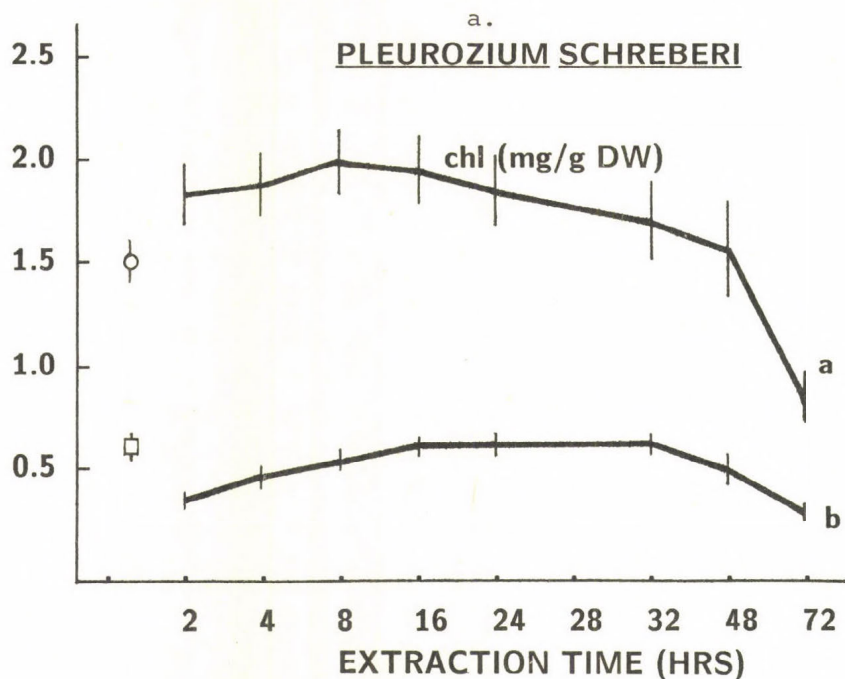
Fig. 1. Determination of extraction time in DMSO. (a) Chloro-
phyll a and chlorophyll b content (mg/g DW) in function of
the extraction time. (b) Chlorophyll a/b ratio as a function
of the extraction time. Open dots represent the 80% acetone
extraction levels. (Vertical bars represent the 95% C.I.,
n=10).

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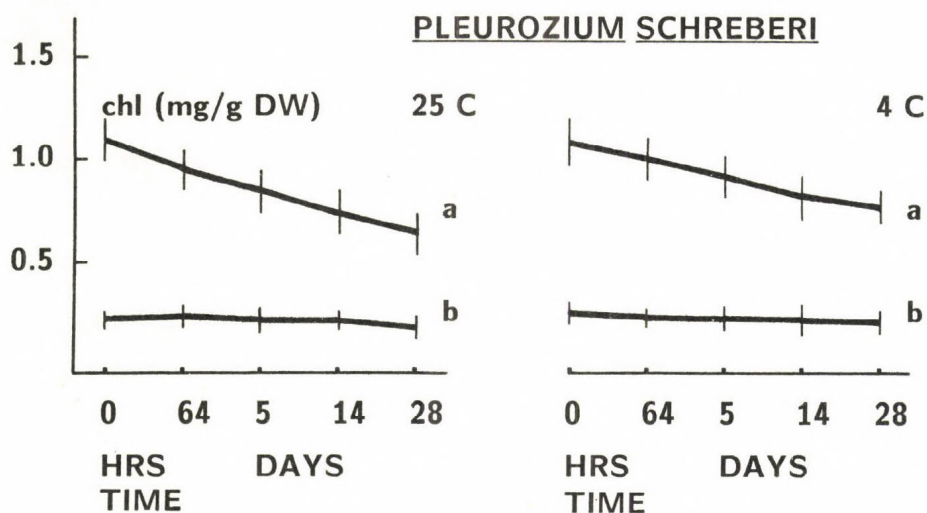
Fig. 2. Stability of chlorophyll a and b extract in DMSO.
Storage at 25°C and 4°C in dark. (Vetical bars represent the
95% C.I., n=10).

Fig. 3. Stability of chlorophyll extract in DMSO. Chlorophyll
a/b ratio. Storage at 25°C and 4°C in dark. (Vertical bars
represent the 95% C.I., n=10).
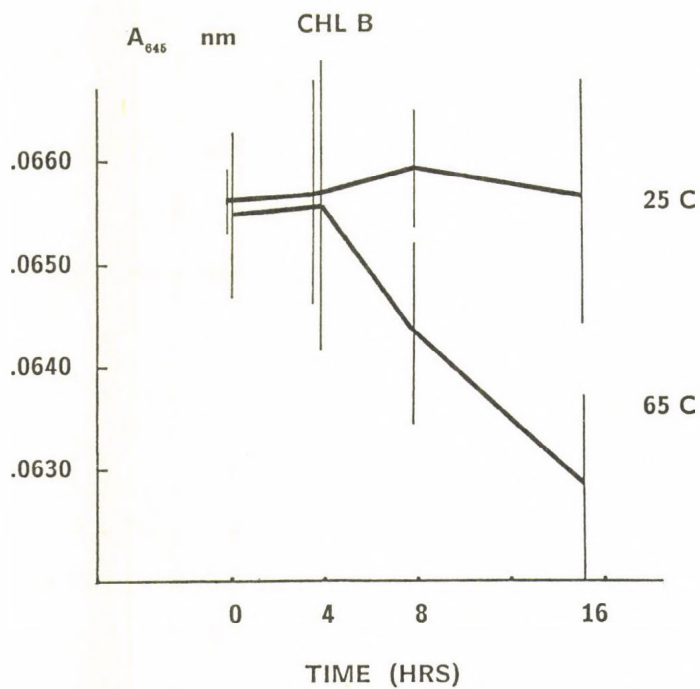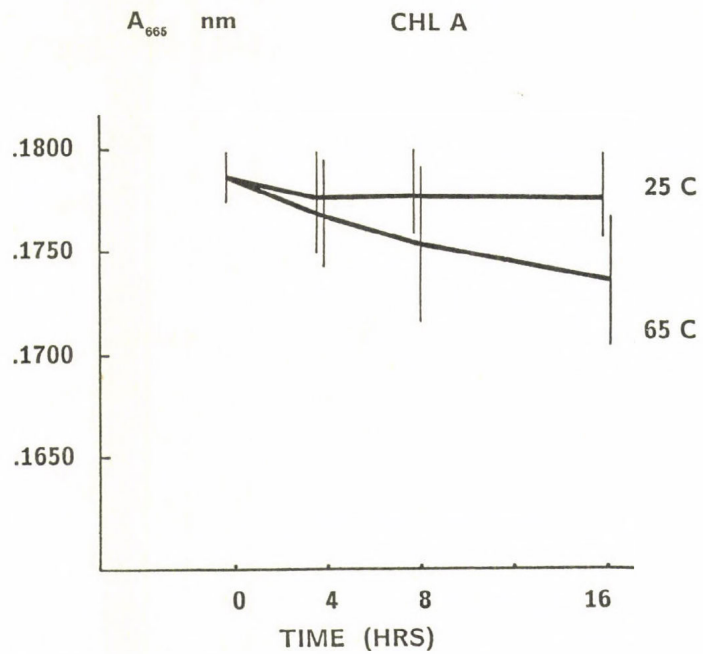
Fig. 4. Stability of pure chlorophyll a and b at 25°C and 65°C. (Vertical bars represent the 95% C.I., n=5).
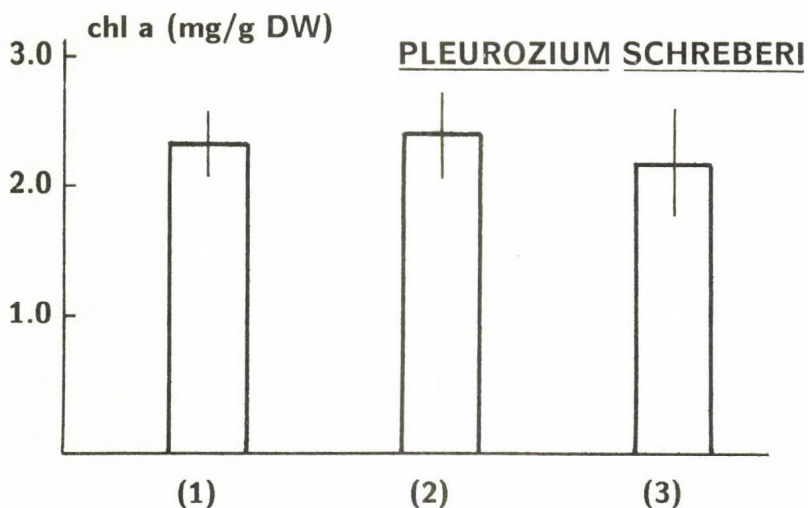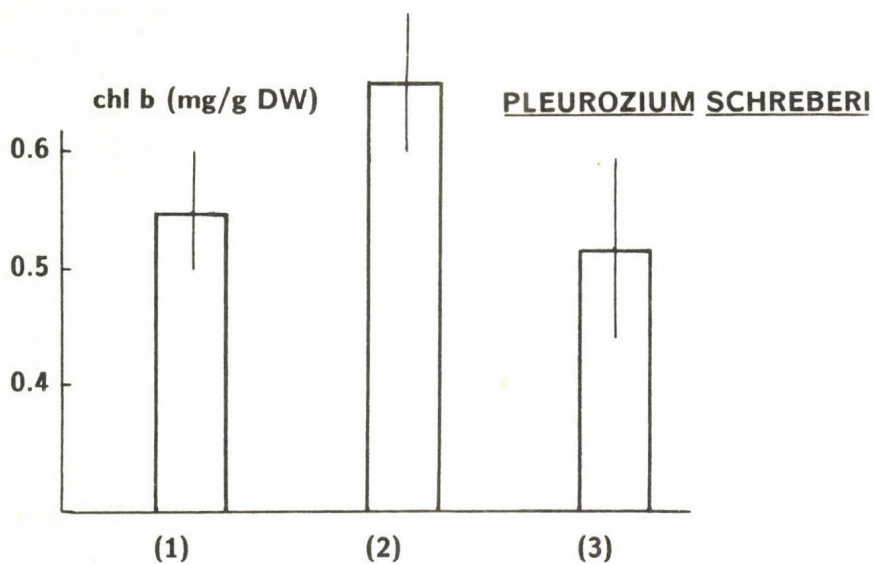
Fig. 5. Differential temperature experiment. Chlorophyll a
and chlorophyll b content (mg/g DW) under three extraction
conditions: (1) 4 hrs at 65°C, (2) 16 hrs at 65°C, (3) 4 hrs
at 65°C + 12 hrs at 25°C. (Vertical bars represent the 95%
C.I., n=5).

period at 25°C. We also found significantly less chlorophyll b at 65°C than at 25°C at 8 and 16 hrs (8 hrs: p = 0.008, 16 hrs: p = 0.000, t-test)

d. No significant differences in chlorophyll a were observed among the three extraction procedures (Fig. 5). However, we found significantly more chlorophyll b after submersion of the stem tips for 16 hrs in DMSO at 65°C than after a short submersion of 4 hrs in DMSO at 65°C (p = 0.000, t-test), even when followed by a further extraction for 12 hrs at 25°C (p = 0.034, t-test).

DISCUSSION

Submersion of mosses in DMSO for 16 hrs at 65°C proved to be a reliable, reproducible method to extract chlorophyll. We found extraction of chlorophyll by DMSO preferable over the extraction of chlorophyll by acetone. DMSO-mediated extraction does not require maceration of the plant samples. The elimination of this step reduces analytical errors and yields a solvent with less turbidity than found in the 80% acetone-mediated extraction. DMSO gives a more complete extraction of chlorophyll pigments and these are more stable over time than in 80% acetone. We also found that further extraction after 16 hours by DMSO produced no additional dissolved chlorophyll. Shoaf & Lium (1976) also observed this for algae.

To provide a consistent biomass measure, moss samples should be air-dried in the dark at 20°C or less to prevent destruction of chlorophyll. Drying of the tips at high temperatures, as reported by Alpert (1984), might degrade the chlorophyll in some species. Glime (pers. comm.) dried Fontinalis in the oven at 60°C and the color was lost in two hours. In order to be consistent with the 80% acetone extraction, we decided to re-wet the samples prior to submersion in DMSO. We often found significatnly higher chlorophyll b levels in rewetted samples, although there was no consistency among the different experiments we carried out. Glime (1984) likewise found that re-wetting greatly improved chlorophyll

extraction of _Fontinalis_ in 80% acetone.

An extraction temperature of 65°C was optimal and Ronen
(pers. comm.) did not find any detrimental effect on the
total chlorophyll content of lichens if the DMSO was heated
up to 85°C for a short period. Only a slight extraction took
place at 25°C which means that heating is probably necessary
to destroy the proteins associated with the chlorophyll mole-
cules and to put chlorophyll into solution.

The optimal extraction time in DMSO should be determined
for each species. We found 16 hours to be most effective for
the boreal pleurocarps _Pleurozium_ _schreberi_ and _Ptilium_
crista-castrensis (Hedw.) De Not. Alpert (185) found optimal
extraction between 3 and 9 hours for xerophytic bryophytes,
depending on the species. It seems that the extraction time
for bryophyte chlorophyll needs to be longer than for higher
plants. Hiscox & Israelstam (1979) submersed angiosperms be-
tween 15 minutes and 2 hours, and determined the extraction
time visually when the leaf-fragments appeared clear.

It is advisable to perform the extraction under subdued
light conditions. In a preliminary experiment we found signi-
ficantly lower chlorophyll a if the DMSO extract was kept
at "full room light" for 30 minutes.

According to Ronen & Galun (1984) Arnon's equation
(Arnon 1949, Mackinney 1941) can be used for the quantifica-
tion of total chlorophyll with DMSO. However, there is a shift
in the peak positions for chlorophyll a and b from 80%
acetone (663 and 645 nm, respectively) to DMSO (665 and 648.5
nm, respectively). This shift in the peak maxima of the red
bands is probably caused by the different refractive indices
of the two solvents (Seely & Jensen 1965). However, Ronen &
Galun (1984) did not find different extinction coefficients
for chlorophyll a and b between DMSO and 80% acetone.

DMSO extracts from mosses reveal high chlorophyll a/b
ratios (between 3 and 4). Martin (1982) and Aro (1982) re-
ported low chlorophyll a/b ratios in mosses, which are
characteristic for shade plants, even though mosses are not
obligate shade plants. The low chlorophyll a/b ratio might be

caused by the large amount of light-harvesing chlorophyll
protein complexes (LHCP) in the thylakoids from mosses compared
to higher plants (Aro 1982). LHCP complexes have chlorophyll a
and b in about equal amounts, whereas the photosystems (PS I
and PS II) have much more chlorophyll a than chlorophyll b
(Salisbury & Ross 1985). The higher chlorophyll a/b ratio in
DMSO extracts might be caused by a slower denaturation of
the LHCP complexes by DMSO than by 80% acetone, or by a con-
tinuous breakdown of chlorophyll b during extraction in DMSO
at $65^{\circ}C$ as suggested in our experiments.

We cannot assume that careful measurements using 80%
acetone or DMSO will give an unbiased measure of the true
amounts of chlorophyll a and b. Our experiments with pure
chlorophyll a and b show a significant degradation of chloro-
phyll a and b at $65^{\circ}C$, and degradation of total chlorophyll in
80%acetone has been documented by Hiscox & Israelstam (1979).

The DMSO extracts should be kept in the dark at $4^{\circ}C$ where
they can be stored up to 64 hours (a significant decrease in
chlorophyll a and b showed up after 5 days). Ronen & Galun
(1984) kept the DMSO extracts for 10 days at $4^{\circ}C$, without any
decrease in chlorophyll content. However, based on three re-
plicates, Alpert (1984) found a decrease after 18 hours, even
when stored at $4^{\circ}C$.

SUMMARY

The advantages of DMSO to extract chlorophyll from mosses
are numerous. The chlorophyll can be extracted without macera-
tion of the moss sample, rendering the method very simple.
The turbidity of the extract is very low. More chlorophyll is
extracted with DMSO than with 80% acetone, although neither
of the two solvents gives the true amounts of chlorophyll a
and b in the moss sample. Chlorophyll is more stable in DMSO
than in 80% acetone. Dry weight can be obtained after extrac-
tion, if necessary, so that chlorophyll can be extracted
immdetiately upon sampling.

ACKNOWLEDGEMENTS

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LYOPHYLLUM PALUSTRE, A PARASITE ON SPHAGNUM

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The sphagnicolous basidiomycete Lyophyllum palustre (Peck) Singer is only found in Sphagnum carpets where it causes necrotic patches. The fungus kills the moss plants by penetrating the cell wall enzymatically and digesting the protoplasm. The decay of the cell walls was studied, using light microscopy and electron microscopy, and enzymes secreted by the fungus into the cell culture liquids were investigated. A high pectinase and a low cellulase activity was found in conjunction with a considerable capacity for breakdown of Sphagnum cell walls.

INTRODUCTION

Bogs are more than any other biotopes dominated by a single genus of bryophytes, the peat mosses. Yet, Sphagnum is not only the dominating but also the determining plant in this habitat. The actively growing Sphagnum carpet causes a high water table, a low pH and an extreme microclimate (Mueller 1983). These unfavourable environmental conditions in addition to the lack of nutrients allow only a few plants and microorganisms to live in bogs (Dickinson et al. 1974, Clymo 1965). Peat accumulation is a consequence of the reduced microbiological activity, and Sphagnum is the main peat-forming plant (Given et al. 1975). Sphagnum peat shows the lowest rate of decomposition (Rakovskii et al. 1968), and during the course of decay the Sphagnum tissues are not as quickly decomposed as

those of other plants, which leads to an enrichment of Sphagnum fragments in the deeper layers (Rakovskii et al. 1968, Collins et al. 1978, Latter et al. 1967a, Rumjantzewa 1939). Both are due to a considerable resistance of Sphagnum cell walls to decay by those microorganisms that are actively growing in bogs (Coulson et al. 1978, Kilbertus 1972, Kox 1954, Wolter 1964).

Bacteria hardly play any role in decomposition of cellulose in bogs. Here, nearly the whole desctruction of cellulose is brought about by fungi (Clymo 1965, Latter et al. 1967a).. In the case of breakdown of Sphagnum cell walls only a small percentage of the loss of dry weight is due to the activity of micromycetes (Chastukhin 1967) while the predominant part is left to basidiomycetes (Chastukhin 1967, Latter et al. 1967b).

Amongst the sphagnicolous basidiomycetes Lyophyllum palustre is remarkable because of the necrotic patches in Sphagnum carpets that are always associated with the occurrence of its fruit bodies (Jahn 1964, Redhead 1981, Untiedt et al. 1985). Using axenic cultures Redhead (1981) showed that L. palustre is a parasite on Sphagnum. The fungus kills the moss plants and causes the necrotic patches. Our own research (Un-tiedt et al. 1985), using light microscopy, transmission elec-tron microscopgy (TEM) and scanning electron microscopy (SEM), revealed that intimate contact between hyphae of L. palustre and Sphagnum cells is common. The hyphae penetrate the cell walls of the moss plant and colonize the cells digesting the protoplast, thus causing the macroscopically visible discolour-ation of the plant. At the early stage of infection the plant shows the formation of an uncommon type of additional walls, that seem to be destroyed very soon after the hypha has en-tered the cell, as we never found any of these walls in cells that contain hyphae.

Furthermore, the investigations showed that infection occurs from outside as well as from neighbouring cells, and that stems are infected as well as leaves. Though hyphae were also present in mature hyaline cells, we found that living

cells are infected rather than dead ones. The cell walls of
the infected moss plants only showed signs of slight decay, but
some observations of Sphagnum plants infected by L. palustre
led us to the assumption that the fungus is able to destroy
the moss plants almost completely. However, at that time
microscopical investigations on more intensively decayed
Sphagnum plants had not yet been carried out. Results of such
research will be outlined below.

Transmission electron micrographs of hyphae penetrating
the cell wall had previously shown the dislocation of wall
layers in assocation with opaque material that may have ori-
ginated from the fungus or from both organisms. The space
that exists between the hyphal peg and the attacked wall
layer indicates that penetration is effected by enzymes. Re-
sults of the latest electron microscopical research support
this thesis. Using liquid culture, enzymes that are secreted
by the fungus into the surrounding medium are investigated.

MATERIALS AND METHODS

Microscopical research

Axenic cultures of L. palustre and Sphagnum fallax were
provided and, after three month of culture, the vigorously
growing moss was inoculated with mycelium of the fungus (Un-
tiedt et al. 1985). As soon as the plants had become chloro-
tic, and looked wet and pulpy and collapsed, branches were
fixed and prepared for investigation with light microscopy
and TEM as previously described (Untiedt et al. 1985).

Studies on enzymes in liquid culture

As a growth medium for liquid culture we used either a
hot water extract ("Sphagnum extract") of Sphagnum plants
or a synthetic nutrient solution. 20 µm Tetracyclin per ml
culture liquid was added and every 25 ml culture liquid was
inoculated with 1 ml homogenate of mycelium grown on Sphagnum
extract agar. All cultures were kept at $292^{O}K$ ($19^{O}C$) in the
dark, normally for 14 days.

Sphagnum extract: 1 g dried Sphagnum powder is extracted
with 100 ml boiling 10^{-1} M potassium phosphate buffer (ph 5.6)
for 4 minutes. The filtrate is used as the culture medium.

Synthetic nutrient medium: A mineral salt solution deve-
loped by Voigt (1981) as nutrient liquid for Sphagnum cultures
is combined with 10^{-1} m potassium phosphate buffer to a pH of
5.6. As carbohydrate source either glucose (1% (w/v)), cellu-
lose (in form of filter paper) or pectin (1% (w/v)) is added.
After sterilisation at 120°C under pressure for 20 minutes
a sterile-filtered aminoacid solution is added (100 µl/25 ml
culture liquid) that contains the aminoacids of 1 g dried
Sphagnum in 400 µl (Thoenes et al. 1983).

Experiment 1: 72 assays with 25 ml Sphagnum extract each
were cultivated for different periods of time. One half of
the assays contained cellulose in form of filter paper. My-
celial growth was recorded by measuring the dry weight of
the grown mycelium. During the first 16 days every second
day and afterwards once a week two assays of each sort were
evaluated.

Experiment 2: Carefully dried and weighed portions of
Sphagnum fragments were incubated with solutions of several
purchasable enzymes (cellulose, pectinase, pectinesterase,
hemicellulase) that might cause decay of the cell walls. The
enzymes were used alone or in combinations and at different
pH and temperatures. As a control, Sphagnum fragments were
incubated with buffers only. After a week of incubation the
dry weight of the Sphagnum fragments was recorded again in
order to establish decay of the cell walls by loss of dry
weight.

Experiment 3: Mycelium was grown in synthetic nutrient
liquid cultures, containing either glucose, cellulose or
pectin as the only carbohydrate source. As a control, the
mycelium was grown in synthetic nutrient liquid containing
dried Sphagnum powder (1 g/100 ml) and in the normal Sphagnum
extract, respectively. After 12 or 23 days of culture the

mycelium was separated from the culture liquid. Dry weight of
the grown mycelium and protein contents of the culture liquids
were determined. Further, the effects of the culture liquids
on cellulose, polygalacturonic acid and on fragments of dried
Sphagnum plants were tested. For this purpose, the culture
liquids were sterile-filtered and incubated either with
cellulose for four days at $37^{\circ}C$, with polygalacturonic acid
at $29^{\circ}C$ for 24 hrs or with dried and weighed Sphagnum fragments
at $30^{\circ}C$ for one week. As control the same assays were performed
as above but with the culture liquids heated to $120^{\circ}C$ under
pressure for 20 minutes to denature the enzymes. Breakdown of
cellulose was recorded by determining the increase of glucose
concentration, using the GOD/POD method (Werner et al. 1970).
Breakdown of polygalacturonic acid was measured by decrease
of viscosity according to Kox (1954). Decay of Sphagnum tissue
was tested by determining the loss of dry weight as described
in Experiment 2.

RESULTS AND DISCUSSION

Microscopy

Light micrographs of semi-thin sections of Sphagnum plants
that had become wet and pulpy by advanced infection show that
the cells of stems and leaves are packed with hyphae. At some
points the cell walls have been destroyed completely which
explains the collapse of the plants. The worst decay can be
observed in the centre of the branch, especially at the stems
where leaves initiate.

Transmission electron micrographs show that the destruc-
tion of the cell walls starts from the middle lamella, where
the highest concentrations of pectin should be expected, and
proceeds into the wall layers of the secondary wall that are
rich in cellulose. These pictures showing that wall layers
not in direct contact with the hyphae are destroyed first
indicate that the fungus secretes enzymes that permeate the
cell wall, thus reaching the oldest wall layers that seem to
be more easily destructible than the secondary wall. A thin

layer on the surface of the leaves, however, remains un-
destroyed and is detached from the wall that is progressively
disintegrated beneath. As this superficial layer is obviously
more resistant to decay than the other wall layers it might be
a kind of cuticle or wax layer.

Enzymes

Experiment 1 (Fig. 1) shows that during the first two
weeks mycelial growth is equal in cultures with and without
cellulose. After a lag of 3 or 4 days the dry weight increases
until the 12th to 14th day. During this time, I assume, soluble
sugars that are present in the Sphagnum extract are used up
by the growing fungus. As the culture liquids run short of
soluble sugars the mycelial growth in cultures without cel-
lulose ceases and after a few days the dry weight decreases
due to autolysis. After 6 weeks the dry weight of mycelium re-
mains constant indicating that the cultures have reached a
steady state with equal rates of mycelial growth and lysis. In
cultures with cellulose, however, the period of net growth is
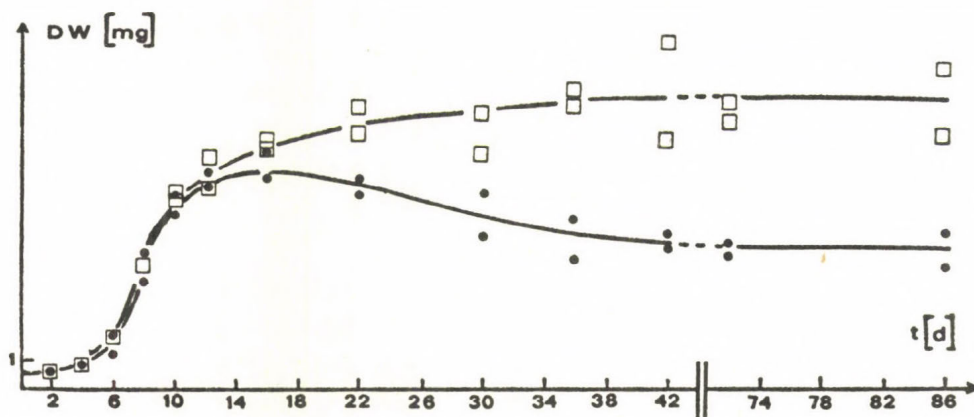
Fig. 1. Experiment 1: Time course of mycelial growth. □:
assays with cellulose, ●: asssays without cellulose.

Table 1. Results of Experiment 3.

Experiment			3a	3b	3c
Period of culture [d]			23	12	12
Growth rate (dry weight mg)	I:	NL+glucose	37.5	29.6	34.5
	II:	NL+cellulose	21.4	8.7	4.5
	III:	NL+Sph.powder	55.5	46.0	41.3
	IV:	NL+pectin	32.7	26.8	30.3
	V:	Sph.extract	64.4	37.6	46.7
Protein content [ug/ml]	I:	NL+glucose	294	319	295
	II:	NL+cellulose	208	200	220
	III:	NL+Sph.powder	203	291	265
	IV:	NL+pectin.	470	432	430
	V:	Sph.extract	291	307	285
Cellulose destruction (increase of glucose [mg/100ml])	I:	NL+glucose	0	0	0
	II:	NL+cellulose	7.6(6.8-9.1)	0	0
	III:	NL+Sph.powder	0	0	0
	IV:	NL+pectin	0	0	0
	V:	Sph.extract	0	0	0
Pectin destruction [mg/20ml]	I:	NL+glucose	0	22	0
	II:	NL+cellulose	0	24	21
	III:	NL+Sph.powder	117	107	125
	IV:	NL+pectin	110	138	137
	V:	Sph.extract	0	50	37
Breakdown of Sph.frag-ments (de-crease of dry weight [%])	I:	NL+glucose	0		
	II:	NL+cellulose	4.2(3.2-5.4)		
	III:	NL+Sph.powder	7.7(6.3-10.4)		
	IV:	NL+pectin	7.6(5.1-10.2)		
	V:	Sph.extract	0		

NL = synthetic nutrient liquid;
Sph. = Sphagnum

extended and autolysis is not obvious during the 86 days of
the experiment. This indicates that cellulose is used as a
carbohydrate source.

Experiment 2: Purchasable enzymes (cellulase, hemicellu-
lase, pectinase, pectinesterase) did not cause any breakdown
of Sphagnum tissue.

Experiment 3: Table 1 shows the results of Exp. 3a-c.
Mycelial growth had occurred in all assays. Growth was best,
and nearly equal, in cultures with Sphagnum extract (V) and

in synthetic nutrient liquid (NL) containing Sphagnum powder (III), and it was second best in assays containing glucose (I) as the only carbohydrate source, followed by the assays with pectin (IV). The lowest growth rate was recorded in assays containing cellulose (II). Comparison of Experiment 3a with 3b and 3c shows that in assays I, III, IV and V growth was rapid during the first 12 days of culture and slowed down afterwards. In assay II (cellulose), however, the growth rate was very low during the first 12 days but increased gradually, so that by the twenty-third day the dry weight of assay II was not much less than that of assay IV (pectin). Cellulase activity was only found in assays with no other carbohydrate than cellulose after 23 days of culture (3a, II). After 12 days of culture, however, the same assays did not show any cellulase activity.

Pectinase was found in all assays containig pectin or Sphagnum powder, no matter how long the culture period had been.

These findings suggest that the formation of cellulase needs a long time and is only initiated if no other carbohydrate source is available, whereas pectinase appears very soon and in any case if pectin is present. The low pectinase activities in the assays lacking pectin may be artificial, but perhaps a low pectinase production is usual.

Sphagnum breakdown was found in assays containing either cellulose (II), pectin (IV) or Sphagnum powder (III) as carbohydrate sources. Loss of dry weight of the Sphagnum fragments was equal in culture liquids of assays III and IV. It is very likely that in these cases the loss of dry weight is due to pectinase activity whereas in assay II it should be due to cellulase activity. The low rate of Sphagnum breakdown in the latter case corresponds with the low cellulase activity that had been found in this culture liquid.

The rate of breakdown of Sphagnum tissue caused by culture liquids of L. palustre seems to be very low. However, purchasable enzymes did not cause any breakdown at all. In this respect even a small capacity for Sphagnum breakdown deserves emphasis.

CONCLUDING REMARKS

The results of the enzymatic research correspond well with those of the microscopical studies. The high pectinase activities, which are quickly induced, and the low cellulose activity, which is induced only if cellulose becomes the only available carbohydrate, explain why wall layers rich in pectin are destroyed first. The results suggest a mechanism of infection and decay as follows: The hypha enters the cell penetrating the cell wall by enzymic means. The cell contents are digested very quickly and pectin serves as an additional carbohydrate source. Cellulose, on the contrary, is only destroyed when no other carbohydrates are left. This idea, however, applies to axenic cultures. In the field interactions with other microorganisms play an important role and may cause modifications.

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GENETIC VARIATION IN THE LIVERWORT GENUS PELLIA WITH SPECIAL REFERENCE TO CENTRAL EUROPEAN TERRITORY*

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Using electrophoresis in starch gel, variability of more than ten enzymes has been analyzed in Central European Pellia taxa and in Pellia samples from other geographic regions. Individual taxa of Pellia in the region of Poland have been found to exhibit differences in their genetic structure. In P. endiviifolia and P. epiphylla two enzymatic forms have been distinguished, with fixed distinct alleles in several loci. The detected enzymatic differences are correlated with complexes of other distinct biological properties of the species. Possibly, the forms represent distinct biological units (taxa?).

P. neesiana and P. borealis are very uniform in their genetic structure. Variability level in Polish Pellia populations is low. The diploid taxon of P. borealis is enzymatically slightly different from P. epiphylla S, thought to represent its parental form, which indicates that P. borealis may be an old polyploid.

INTRODUCTION

The genus Pellia is represented in Poland by two widely distributed (America, Asia, Africa) dioecious taxa, P. endiviifolia, n=9, P. neesiana, n=9, and by two monoecious taxa, P.

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* Genetic Variation and Evolution of the Liverwort Genus Pellia with Special Reference to Central European Territory. X.

epipyhlla, n=9, and P. borealis, n=18 (Schuster 1981). Pellia borealis is thought to represent an autopolyploid form of P. epiphylla and is considered to be restricted in its occurrence to Europe (Lorber 1934, Müller 1947, Paton & Newton 1967, Mendelak 1971).

Liverworts of this genus show extensive morphological plasticity, most evidently expressed in plants growing in atypical biotopes. For example, Pellia growing in water forms thalli of a very peculiar shape which are, as a rule, sterile. For the above reasons, identification of Pellia species and studies on their variability encounter several obstacles.

Individual Pellia taxa have been characterized using electrophoresis and peroxidase markers (Szweykowski et al. 1981). This has opened up opportunities to conduct broader studies on variability of the liverworts, including samples difficult for taxonomic interpretation, which might represent interesting or unique variability types. Results of studies on Pellia presented below pertain in particular to: a. genetic variability of P. endiviifolia in Poland, as compared with that of P. endiviifolia from Japan and of P. megaspora from the U.S.A.[*]; b. genetic variability in P. neesiana; c. genetic variability in P. epiphylla and in its natural diploid, P. borealis.

TWO DIFFERENT GENETIC FORMS OF PELLIA ENDIVIIFOLIA IN POLAND

Electrophoretic analysis of Pellia endiviifolia from Poland has shown than the species includes two enzymatic forms (Zieliński 1985a,b; Figs 1-2). The typical form of P. endiviifolia is identified by the peroxidase marker PxI 5,6 (band in the lower gel zone) and the new form by the PxII 1 marker (band

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[*] P. megaspora has been differentiated from P. endiviifolia in the U.S.A. on grounds of comparative morphological-anatomical studies (Schuster 1981), additional cytological studies (Newton 1981, Mendelak 1981) and by peroxidase isoenzyme patterns (Krzakowa 1981).

in the upper gel zone). Enzymatic variability of P. endivii-
folia has been noted to correlate with variability in other
characters, too. A set of traits differentiating the two forms
of P. endiviifolia has been established. Common traits in the
two forms include: a. dioecism, b.development of pitcher-like
perithecia, c. karyotype similar in respect to chromosome num-
ber (n=9) and to absolute as well as relative lengths of chro-
mosomes, d. common phenotypes of some enzymes, in particular
GOT, which differentiates the species from the remaining Pellia
taxa. Traits which are distinct in the two forms are as fol-
lows: a. fixation of distinct alleles in 16 out of 19 analyzed
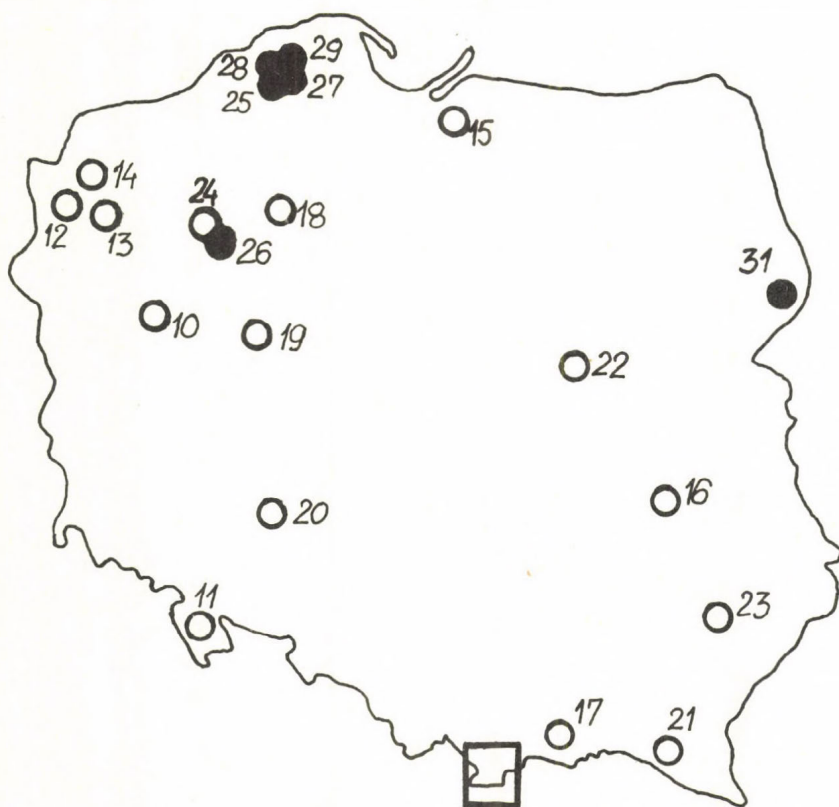
Fig. 1. Occurrence of the new Pellia form (solid circles) and
P. endiviifolia in Poland except for the Tatra Mountains.

loci (coefficient of genetic identity i=0.231). At the same
time, each of the two forms has been internally uniform and
showed no variability in respect to phenotypes of 10 enzymes,
b. distinct ecological requirements. The typical form of P.
endiviifolia grows preferentially in places of high calcium
content and even on limestone. It rarely grows directly in
water, acquiring the so-called aquatic form. The new Pellia
form grows on substrates of lower calcium content and it has
as yet never been encountered on limestone. In its ecological
requirements, the latter form resembles P. neesiana. Very-
frequently it forms mixed populations with P. neesiana, in
which the plants may grow as immediate neighbours (Zielinski
1985a). The new P. endiviifolia form occurs frequently in mires,
springs and other watery sites. Eighty percent of collected
samples have been found growing directly in water. c. in con-
trast to the typical P. endiviifolia, this plant does not form
rosette-like outgrowths in the spring in nature (even when
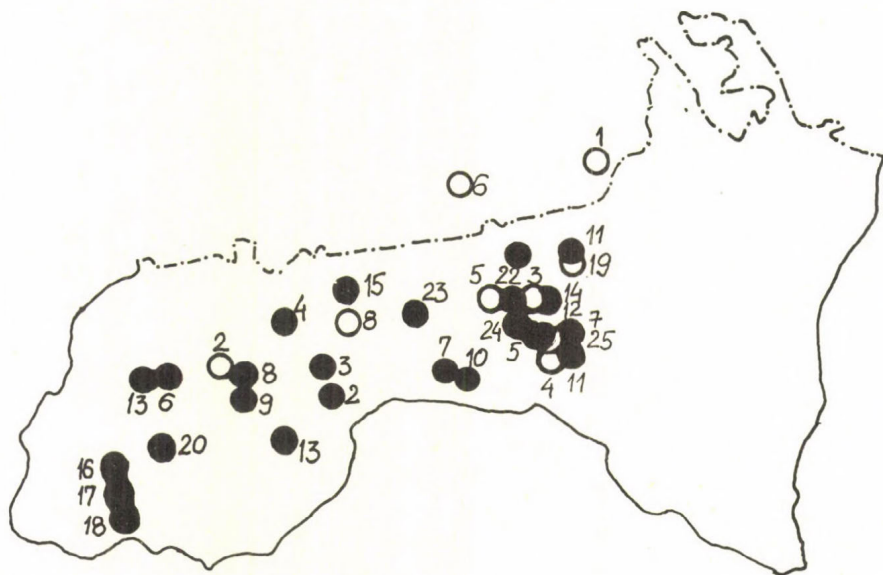
Fig. 2. Occurrence of the new Pellia form (solid circles) and
P. endiviifolia (open circles) in the Tatra Mts.

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growing out of water). However, such outgrowths are produced
in culture. d. geographical distribution. The new Pellia form
seems to be more frequent in mountain regions (e.g., the Tatra
Mountains) whereas P. endiviifolia is more frequent in the low-
lands of Poland (Figs 1-2). In the mountains the new Pellia
form has been encountered in 25 localities and the typical P.
endiviifolia in 9 localities. In the lowland, the respective
numbers of localities have been 6 and 15. The new form has
been encountered at elevations of 950-1650 m above sea level and
the typical form at 880-1300 m.

The new form of P. endiviifolia has also been detected in
Belgium (unpublished data).

COMPARISON OF THE TYPICAL AND THE NEW FORM OF P. ENDIVIIFOLIA
FROM POLAND WITH P. ENDIVIIFOLIA FROM JAPAN AND P. MEGASPORA
FROM THE U.S.A.

To assess the taxonomic value of the detected enzymatic
differences between P. endiviifolia and the new Pellia form
from Poland, I have determined, for comparison, levels of en-
zymatic differences between the well-distinguished taxa within
the P. endiviifolia complex, i.e., between P. endiviifolia and
P. megaspora (Zielinski 1985b).

Phenotype comparison for 13 enzymes in the studied complex
P. endiviifolia-megaspora has demonstrated its differentiation
into four equivalent categories, corresponding to: a. P. endi-
viifolia from Poland, b. P. endiviifolia from Japan, c. P. me-
gaspora, and d. the new form from Poland. Each of the 12 ca-
tegories featured 5 specific enzymatic phenotypes. Coefficients
of genetic identity between the examined taxa have shown low
values, ranging from 0.077 to 0.461. P. endiviifolia from Po-
land has differed in phenotypes of 9-10 enzymes of P. endivii-
folia from Japan and in phenotypes of 11 enzymes from P. mega-
spora. The demonstration of a similar level in enzymatic dif-
ferences between P. endiviifolia and P. megaspora taxa and be-
tween P. endiviifolia and the new Pellia form from Poland
allows us to suggest that the latter probably corresponds to

a new _Pellia_ taxon, overlooked until now using the classical
taxonomic methods. It is worth stressing that analysis of mixed
populations, including the new _Pellia_ form, P. _endiviifolia_
and P. _neesiana_, has demonstrated existence of a reproductive
barrier between the taxa (Zieliński 1985a).

GENETIC VARIATION IN P. NEESIANA

P. _neesiana_ exhibits a non-uniform distribution in the
area of Poland. It is much more frequent in the southern,
mountainous part of Poland than in the lowland. In mountains,
particularly in the Tatra Mountains, P. _neesiana_ not infrequent-
ly forms large populations whereas in the lowland it occurs as
isolated colonies.

Analysis of 10 enzymes in 33 samples of P. _neesiana_ from
the whole region of Poland (Figs 3-4) has demonstrated that
the genetic structure of the species is very uniform and
shows no resemblance whatsoever to the structure described
above for P. _endiviifolia_. The only variability detected in-
volves the existence of three peroxidase alleles, $Px1^n$, $Px2^n$
and $Px3^n$ (Zieliński 1985c). In the lowland stands, peroxidase
phenotype has been restricted to the single, most frequent
allele $Px1^n$. In the Tatra Mountain stands all three alleles
have been detected, occurring even within a single population.
The smaller P. _neesiana_ populations in the Tatra Mountains
also carried only a single allele, like the lowland stands.
However, apart from $Px1^n$ allele, the populations have shown
also $Px2^b$ allele which might have resulted from more extensive
P. _neesiana_ polymorphism in the Tatra Mountains. In one of the
mountain populations in Sudety Mountains, two out of three
peroxidase alleles have been encountered ($Px1^n$ 57%, $Px2^n$ 43%).

ELECTROPHORETIC PATTERNS OF THE PELLIA EPIPHYLLA AND P. BOREA-
LIS COMPLEX

The most interesting aspect of studies on P. _epiphylla-_
borealis complex involves problems associated with clarifica-

tion of the origin of the diploid form, P. borealis. Preliminary electrophoretic studies (Zieliński 1984b) have demonstrated that P. epiphylla includes in the area of Poland two different multi-enzyme forms and that the only one of them (P. epiphylla S) corresponds to the variability type noted in P. borealis (see also Szweykowski et al. 1981, Zieliński et al. 1985, Zieliński 1985, in prep.). The conclusion has also been confirmed by cytological studies on the complex (Zieliński 1984b).

The distribution of the forms is allopatric: P. epiphylla S occurs mainly in southern Poland and P. epiphylla N in the centre and north of the country (Figs 5-6).
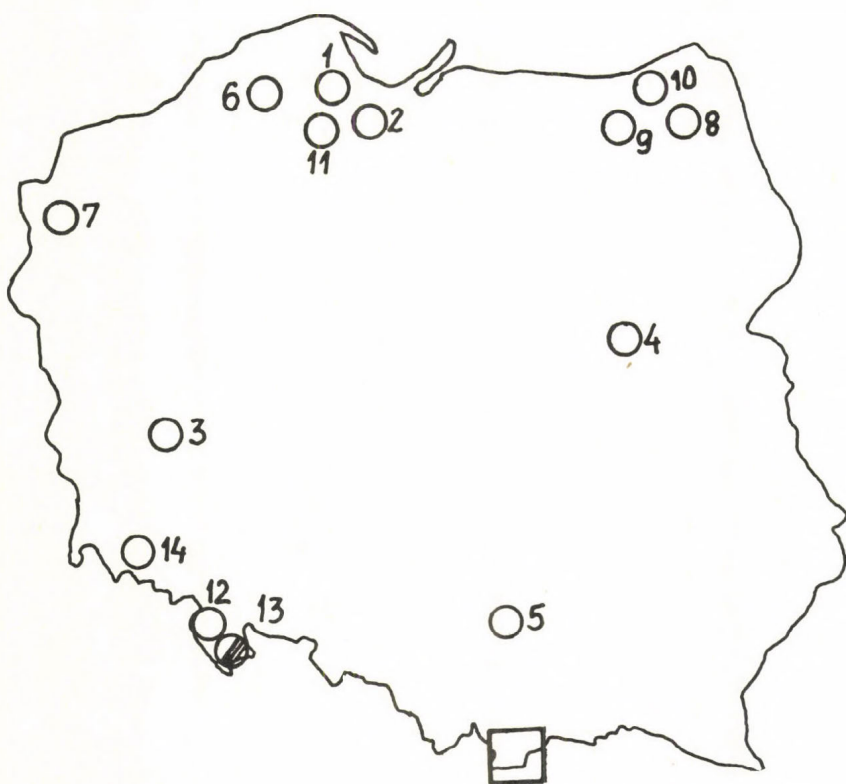
Fig. 3. Occurrence of peroxidase alleles in lowland (1-11) and mountain (12-14) stations of Pellia neesiana in Poland, except for the Tatra Mts. o: $Px1^n$, •: $Px2^n$, ⊘: $Px3^n$.

Comparison of 17 enzymes in the P. epiphylla-borealis complex (Table 1) showed that P. epiphylla S differs from P. borealis in phenotypes of two enzymes (PX, GDH) and P. epiphylla N in phenotypes of six enzymes (AF, EST, ME, HEX, PX, GDH). The results confirm the assumption that P. epiphylla S may represent the parental form for P. borealis.

In artificial diploids developed from P. epiphylla S and N (Zieliński 1984b), the analyzed phenotypes have not been altered by polyploidization.

Distinct phenotypes of peroxidases and glutamic acid dehydrogenase in P. borealis, as compared to P. epiphylla, may indicate that P. borealis is an old polyploid. This is indicated also by geographic distribution of the two taxa. In Poland, P. borealis is more frequent than P. epiphylla S (Figs 5-6) and occurs in all regions of the country whereas P. epiphylla S manifests itself mainly in southern Poland.
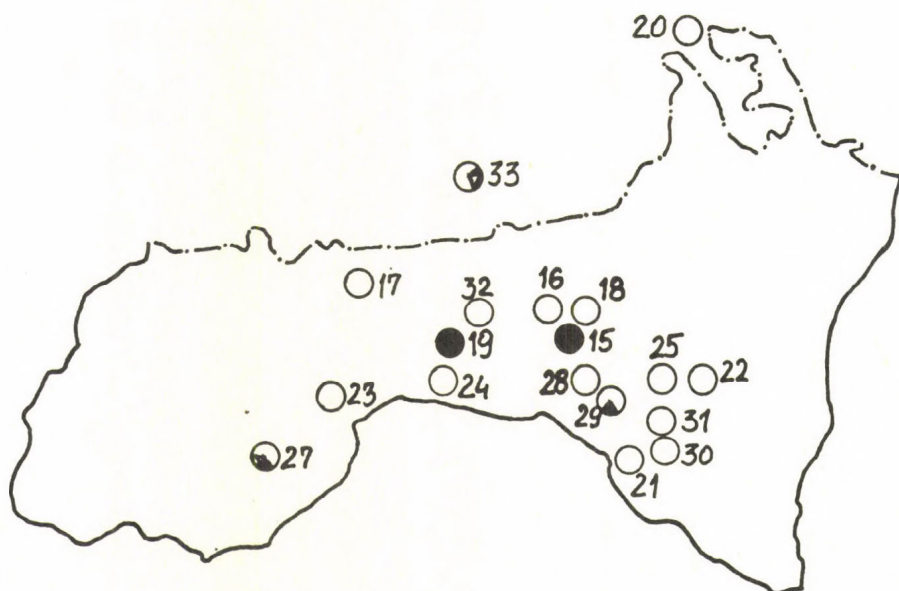
Fig. 4. Occurrence of peroxidase alleles in Pellia neesiana in the Tatra Mountains. o: $Px1^n$, •: $Px2^n$, ⊙: $Px3^n$.

Fig. 5. The geographic distribution of Pellia epiphylla (o)
and P. borealis (●) in Poland (a) and in the Tatra Mountains
(b).

Table 1. Electrophoretic phenotypes of 17 enzymes in two Pellia epiphylla forms, P. epiphylla S and N, and in P. borealis (based on the Polish plants studied).

Enzyme	P. epiphylla S	P. borealis	P. epiphylla N
AF	1	1	2
EST	1	1	2
ME	1	1	2
HEX	1	1	2
PX	1^a, 2^a	1^b, 2^b	3
GDH	1	2, 3	2'
SHI	1, 2	1	1
LAP	1	1	1
GOT	1	1	1
EST FE	1	1	1
MDH	1	1	1
G-3	1	1	1
ALD	1	1	1
PGM	1	1	1
PGI	1	1	1
GPGD	1	1	1
IDH	1	1	1

Fig. 6. The distribution of two <u>Pellia</u> <u>epiphylla</u> forms, <u>P.</u> <u>epiphylla</u> S (o) and <u>P.</u> <u>epiphylla</u> N (●) in Poland.

DISCUSSION

One of the most interesting results obtained in studies on the enzymatic variability of <u>Pellia</u> involves discovery of two levels of genetic variability.

At the first, polymorphic loci are present (Zieliński 1984a, 1985c,d,e, 1986). Several genotypes can arise. In <u>P.</u> <u>neesiana</u> one polymorphic locus has been detected with three peroxidase alleles while ten remaining enzymes examined have proven monomorphic. In <u>P.</u> <u>borealis</u>, 2 polymorphic loci, each with two alleles have been described, with four possible geno-type combinations while 11 loci have been monomorphic. In

particular _Pellia_ populations a few genotypes only (1-4) were
detected. This situation is probably connected with the predo-
minantly vegetative propagation of those liverworts. The va-
riability type detected in _Pellia_ is analogous to those found
in other organisms and used to be given the term of polymor-
phism. However, an evidently lower level of the variability is
noted, as compared to higher plants, particularly when ex-
pressed by the genetic diversity index H. Genetic diversity
index, H_T, amounts to 0.025 in _P._ _neesiana_ and 0.045 in _P._
borealis against an average of 0.1-0.2 in flowering plants
(Nevo 1984, Zieliński 1985, in prep.).

The second level is associated with complex differences in
multi-enzyme phenotypes, noted in _P._ _endiviifolia_ and _P._ _epi-
phylla_ within Poland. Such differences allow us to distinguish
two enzymatic forms of _P._ _endiviifolia_ and _P._ _epiphylla_, with
fixed distinct alleles in multiple analyzed loci. For example,
in _P._ _endiviifolia_, the two forms distinguished have carried
distinct alleles in 16 out of 19 analyzed loci (genetic iden-
tity coefficient I = 0.231).

The differences detected in multi-enzyme phenotypes cor-
relate with distinct biological properties in the species
examined.

In the two _P._ _endiviifolia_ forms from Poland, not only
structural gene differences (fixation of distinct alleles)
but also differences in regulatory genes (differential expres-
sion of peroxidase isoenzymes, lack of rosette-like outgrowths
in the field in the new _P._ _endiviifolia_ form) have been noted
as well as distinct ecological requirements. Enzymatic dif-
ferences noted between _P._ _endiviifolia_ from Poland, that from
Japan and the new _P._ _endiviifolia_ form detected in Poland are
of the same rank as differences between individual _Pellia_ taxa
or between flowering plant species (in the latter the res-
pective genetic identity coefficient I is lower than 0.65, cf.
Crawford 1983).

The variability detected at the molecular level within the
_P._ _endiviifolia_-_megaspora_ complex is much greater than the de-
scribed morphological (Schuster 1981) and cytological variabi-

lity (Newton 1981, Mendelak 1981) within the complex. Using
enzymatic analysis, P. endiviifolia from Poland, P. endivii-
folia from Japan and P. megaspora and the new Pellia form
have been shown to represent equivalent units, each exhibiting
differences of a similar level, while morphological studies
have distinguished only P. endiviifolia and P. megaspora (va-
riability noted in P. endiviifolia has been of a lower rank).

Two similar groups have been distinguished in cytological
studies.

In P. epiphylla, not only have differences of geographic
distribution of its S and N forms been noted, but also mor-
phological-anatomical variability (Zieliński, unpubl.) and
distinct reactions at the cytological level after their arti-
ficial polyploidization (Zieliński 1984b) have been detected.
P. epiphylla N has a wider geographical range as noted in
Sweden and U.S.A. Pellia epiphylla S has been demonstrated in
Western Europe. In U.S.A., another, totally distinct form of
P. epiphylla has also been noted (Zieliński 1985, in prep.).

The results obtained indicate that liverworts of the Pellia
genus exhibit extensive variability and further, particularly
morphological and cytogenetical studies should establish the
taxonomic rank of the detected forms. Indispensably, the
studies should also be extended to other geographical regions.
As demonstrated by samples of the material from Japan and U.S.A.
significant genetic variability of Pellia occurs in these
regions.

However, the evidence already available gives us substan-
tial ground to treat the detected forms as separate biological
units and to regard the individual taxa as complex species.

ACKNOWLEDGEMENT

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LIFE HISTORY OF THE MOSS, ATRICHUM UNDULATUM (HEDW.) P. BEAUV.

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A wide-ranging study enables us to present the following account of the life history of Atrichum undulatum in Britain. A. undulatum is a colonist of disturbed soil in woodland or open habitats, forming tall, loose turfs of parallel, erect, predominantly unbranched shoots. The turfs are capable of rapid expansion but normally persist for only 2-3 years at a given point. They consist primarily of first year shoots, and older shoots, many with sporophytes, that are no longer actively growing. Sexual reproduction follows a clearly defined annual cycle and sporophytes may develop within 12 months of colony establishment. Annual spore output reaches at least 449 million per m^2 of turf. Most are released from January to March. They are deposited at high density in and immediately outside the parent colony, but over half the spores appear to be transported to distances greater than 2 metres. Spores collected in winter germinate on agar, but viability declines after 8 months air-dry storage. Asexual reproduction appears to be the principal method of colony development and maintenance, due to failure in spore germination and early stages in protonema development under field conditions. Experimentally planted spores have only rarely given rise to shoots at field sites. There are no specialized asexual propagules but juvenile shoots arise as buds on gametophyte fragments, at the base of established shoots, or several centimetres away on rhizoid wicks. A. undulatum is monoecious, but most individual shoots produce gametangia of only one sex each year, and many sporo-

phytes clearly arise following cross-fertilization between shoots. There is considerable electrophoretic variation within British material, and the occurrence of genetic variation in some colonies, combined with the sex distribution pattern, suggests that inbreeding is unlikely to be obligatory.

INTRODUCTION

Reproductive biology of selected mosses is being studied to establish the influence of the reproductive system on variation in these haploid organisms (Longton & Miles 1982). Particular interest lies in determining the effectiveness of reproduction by spores and the incidence of inbreeding in monoecious taxa (Longton & Schuster 1984, Wyatt & Anderson 1984). This presentation summarises the results for Atrichum undulatum. More detailed accounts of the methods and data for this and other species will be given in future papers. In Britain, A. undulatum is common in rich woodland, occurring less frequently in open habitats. It is most abundant as a colonist of disturbed soil where it forms extensive tall turfs of parallel, erect, rather loosely packed shoots.

METHODS AND RESULTS

Reproductive phenology

A. undulatum is monoecious and regularly produces sporophytes. The seasonal pattern of reproductive development has been determined by the methods of Longton & Greene (1969). Juvenile antheridia are first seen in January and archegonia in April, with fertilization following during May and June. Sporophytes develop rapidly, and mature spores are present by September. Spore release begins in December or January, and continues for two to three months.

Colony development and longevity

Little information is available on the rates at which bryophyte colonies develop, or on their stability in time.

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We have obtained data relevant to these points through obser-
vations extending up to five years on eleven 50-cm square
quadrats in typical woodland habitats. Twice yearly, the cover
of A. undulatum and other species was recorded and the quad-
rats were photographed overlain with a 5 cm wire grid. More
detailed information was gained from photographs of individual
grid squares. The sporophytes in each grid square were counted
annually.

Results for a quadrat on an unstable soil slope in the
Aber Valley, north Wales, are summarized in Fig. 1. In Decem-
ber 1980, cover of A. undulatum was 40%, with the remainder of
the quadrat bare ground. A. undulatum cover increased to 60%
by autumn 1981: it remained roughly constant until early 1983
and then declined to 5% by spring 1985. Other bryophytes be-
came established and bare ground decreased to 10% in 1983, sub-
sequent data indicating disturbance. Sporophytes of A. undula-
tum were produced abundantly during the two successive annual
cycles corresponding with maximum cover, and their frequency
also subsequently declined. Observations on 5 cm squares show-
ed that sporophytes may develop within 12 months of gameto-
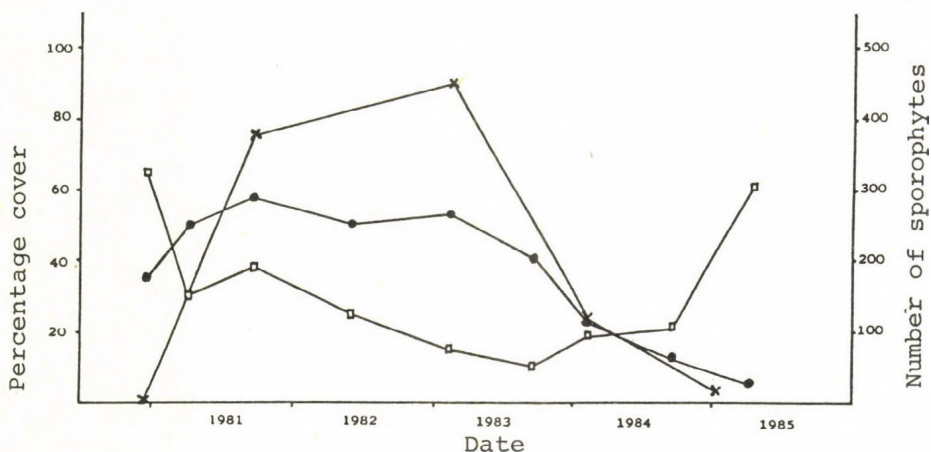
Fig. 1. Variation in the performance of Atrichum undulatum in a
50-cm square quadrat on an unstable soil slope in deciduous
woodland in the Aber Valley, North Wales, showing percentage
cover of A. undulatum (●), number of sporophytes (x), and the
percentage of bare ground (□).

phytes becoming established, indicating that gametangia are sometimes produced during the first six months of growth. The pattern of rapid colony expansion but limited longevity at a given point was repeated in other quadrats, suggesting that turfs of A. undulatum normally persist for only to to three years. In some parts of the quadrats, A. undulatum was replaced immediately by other mosses, but elsewhere it gave way to bare ground indicating that its decline was not due solely to competition. In no quadrat has A. undulatum yet become extinct: rather, it has persisted as isolated shoots among other mosses.

Spore output and deposition

The counts of sporophytes in the quadrats, combined with haemacytometer estimates of spore content in individual capsules, gave values for spore output per unit area of moss turf. The mean number of spores per capsule was 381,000 in plants from Aber, and 145,000 in plants from Sulhamstead, near Reading, in southern England. Spore output per square metre of turf at these sites was estimated at 449 million and 116 million, respectively, being higher in freely fruiting parts of the colonies (Longton & Miles 1982).

The pattern of spore deposition was investigated to determine whether spores land sufficiently close to the parent colony to play a role in its expansion, or whether they could act as vectors in gene flow over greater distances. Circular portions of turf 20-30 cm in diameter were transplanted from deciduous woodland at Padworth to a similar habitat 11 km away on the Reading University campus during November in 1981, 1982 and 1983 to provide an isolated source of spores. After preliminary studies in 1982, spore trapping was carried out during January and February for 30 days in 1983 and 34 in 1984 using microscope slides coated with petroleum jelly and placed horizontally on the ground, a technique considered effective in assessing spore deposition (Gregory 1979). Similar records were obtained during 10-11 days in 1983 and 1984 at an undisturbed colony at Sulhamstead. One slide was placed in the centre of the colony, with 28 others radiating to distances of 2 m from its edge. Slides were replaced daily and the spores

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on a 2 cm^2 area of each one were counted microscopically. The preliminary observations showed that heavy rain removed the petroleum jelly. Accordingly, in 1983 and 1984 each slide was sheltered by a 9 cm diameter petri-dish lid suspended 15 above it on a thin cane. It is not clear what influence the shelters had on air movement, but the effects may have been comparable with those of angiosperm leaves that overlie many natural colonies.

The capsules were initially undehisced, and spore content of ten capsules was estimated each year using a haemacytometer. At the end of the trapping period the numbers of spores remaining in ten dehisced capsules were also estimated. Spore release during the trapping period was calculated as the product of the number of sporophytes and the difference between the initial and final mean spore content per capsule.

Some spores were caught on all the slides. The mean catch per unit area throughout the 1984 trapping period at Reading, for different distances from the colony, is shown in Fig. 2. The pattern is markedly leptokurtic. The catch was high in, and at the edge of the colony, but fell dramatically with distance. There was little directional bias in the results. A computer was used to integrate the curve through 360° and thus estimate the number of spores deposited within the trapping area, i.e., a circle extending for 2 m from the edge of the colony. In 1984, 41,419 spores were trapped and it was estimated that 8.2 million spores were deposited in the trapping area, a figure equivalent to 12% of the estimated spore release of 66.3 million. In 1983, the estimated deposition in the trapping area was 16% of the estimated spore release. These figures suggest that spores are deposited in large numbers within and immediately outside the parent colony, but also that the majority of spores travel to distances greater than 2 m.

The form of the curve (Fig. 2), which was repeated at the undisturbed colony at Sulhamstead, suggests that the maximum dispersal distance may be substantial.
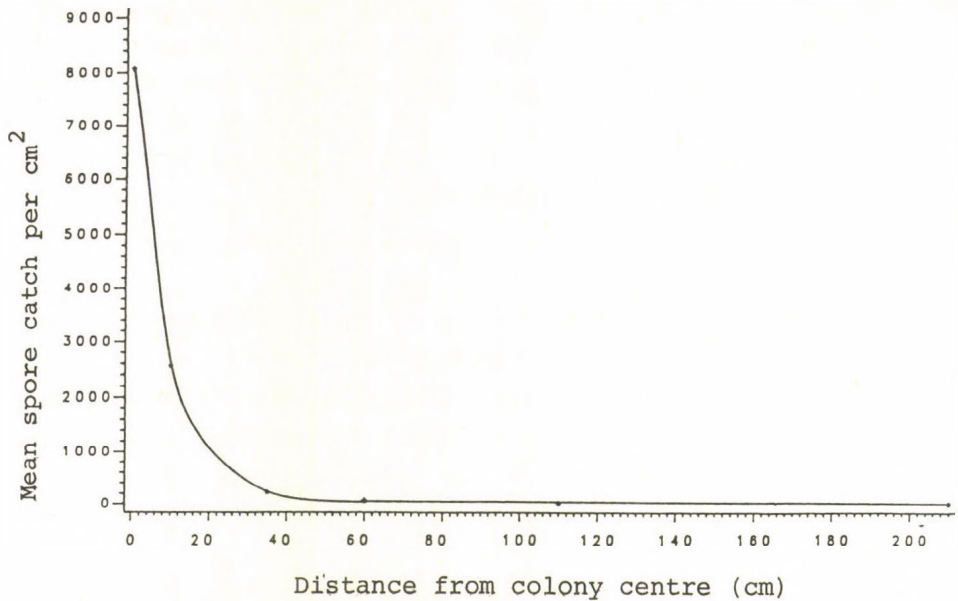
Fig. 2. Variation in mean spore catch per unit area of trapping surface with distance from the centre of an A. undulatum colony, based on 29 traps. The point at 0 cm represents the centre, and that at 14 cm the edge of the colony. The data are based on total spore catch during 34 days in 1984. The curve was fitted by hand.

Methods of colony expansion

A. undulatum turfs are clearly capable of rapid expansion (Fig. 1), and scattered juvenile shoots are frequently present several centimetres outside the area of continuous cover. The deposition study suggests that such shoots could arise from spores liberated by the adjacent colony. On the other hand, A. undulatum is known to undergo asexual propagation through buds arising either at the base of established shoots, on rhizoid wicks extending for several centimetres from existing shoots, or less commonly on detached shoot fragments. The potential for establishment of closed turf through asexual reproduction from single shoots has been demonstrated in greenhouse culture (Longton & Miles 1982). Observations were therefore made

to investigate which method of reproduction predominates under natural conditions.

The occurrence of spore germination was investigated by microscopic examination of spores and sporelings present on the surface of shoots from four fruiting colonies and from adjacent soil. In all, 11,490 spores were detected on leafy shoots and of these 5.4% were germinated, the figures for soil being 747 spores with 27.5% germination. However, none of the sporelings was more than seven cells in length.

A total of 513 juvenile shoots was carefully dissected from portions of A. undulatum turf and adjacent soil from six colonies. The shoots fell into three categories: first, 49% were attached to older shoots, usually by rhizoid wicks; second, 42% were similar, but the rhizoid wicks, after dissection, did not extend to older shoots; third, 9% were attached to green protonema, single-stranded rhizoid or both. Shoots in the first category had clearly arisen by vegetative reproduction. Given the fragility of the rhizoid systems and the ease with which they are broken during dissection, it seems likely that most of the shoots in category two had also arisen asexually. Protonema was commonly present near the colonies. In some cases its origin and identity were unclear. In others, it had been initiated as branches of single-stranded rhizoids or rhizoid wicks. Therefore one cannot conclude with certainty that shoots in the third category had arisen from spores.

Experimental establishment of colonies

The observation that at least half, and possibly all the juvenile shoots examined had arisen asexually agrees with the fact that no sporelings more than seven cells long were recorded from the field. However, it is not clear whether larger sporelings would have been recognised as such or classed as unidentified protonema. Because of these uncertainties, experimental planting of spores and fragments of gametophyte was carried out. Spore germination leading to protonema development and initiation of leafy shoots took place in experiments both on agar, and on soil in a cool greenhouse. However, the viability of spores in undehisced capsules collected in

December declined after eight months air-dry storage at laboratory temperature, falling to 1% after 14 months (Table 1).

Of greater interest, however, are the results of experimental plantings under field conditions. In the first experiment, 10 ml of suspensions containing ca. 10,000 spores per ml of deionised water was applied to the soil surface in a total of 40 10-cm square quadrats at four sites in woodland and a fifth on a ditch bank in an open habitat. Other spores from the same suspensions germinated when planted on agar, but no evidence of germination and protonema development visible to the naked eye was observed at the field sites.

In other experiments, spores were planted at intervals under laboratory conditions so that cultures at different stages

Table 1. Variation with time in percentage germination of spores in undehisced capsules collected at Padworth, near Reading, in December 1983.

Date	Max	Mean	Min
January 1984	92	88	81
March 1984	98	93	90
May 1984	99	97	95
July 1984	89	82	71
August 1984	67	47	34
October 1984	30	18	1
December 1984	15	8	0
February 1985	1	1	0

Based on spores from five capsules for each date. The spores from each capsule were dispersed onto a plate of 2% agar with half strength Knop's solution of macronutrients. The plates were maintained at $20^{o}C$ night/$10^{o}C$ day with a 16 hour photoperiod at irridance of 240 μE m^{-2} sec^{-1} PhAR. Records are based on at least 100 spores per plate after 7 days. Similar results were obtained after 14 days. Axenic culture techniques were employed.

of development became available for planting into the field
to determine at what stage development under natural conditions
is blocked. Soil from field sites was placed in 5 cm square
plastic pots lined with nylon net so that the contents of the
pots could subsequently be removed intact. Cultures were initi-
ated by scattering spores onto the soil, two pots being in-
oculated per capsule. The pots were kept moist in a growth
chamber under the conditions indicated in Table 1. Field ex-
periments were set up by immersing the contents of the pots
to the level of the surrounding soil. Similar plantings of
freshly sown spores and of gametophyte fragments were made at
the same time. In all, six experiments involving 180 plantings
were established at three sites. Seasonal effects were tested
by initiating experiments both at the time of spore release
and later in the year. Soil from pots containing protonema and
ungerminated spores was collected periodically for microscopic
examination. Some of the freshly planted spores germinated,
but the largest sporelings recovered were only three cells
long (Table 2). Where sporelings were planted they developed
slightly, but did not give rise to shoots. Shoot production
was sometimes recorded where older protonema was planted, and
cultures planted as protonema with young shoots gave rise to
closed turf. These experiments thus gave no evidence that
spores can germinate and give rise to gametophore colonies in
the field. In contrast, regeneration and the development of
closed turf occurred readily from gametophyte fragments. Rapid
onset of fruiting in the artificially established turfs (Table
2) agrees with results from the permanent quadrats.

In another experiment, 34 pots of soil from Sulhamstead
were inoculated with spores as described above. The contents
of ten pots were immediately immersed in soil at the field
site, eight pots were placed on a tray standing on the ground
at the field site, and 16 pots were placed on trays on a con-
crete path at Reading. Half the Reading pots were covered with
nylon net to provide shade and shelter from direct rainfall.
No development was recorded in either treatment at Sulhamstead,
but at Reading sporelings were present after seven days, and
shoots after 96 days in all the pots both covered and exposed.

Table 2. Summary of results from experimental planting of Atrichum undulatum in the field.

Material planted	Age of culture when planted (days)	Result
Ungerminated spores	O	Some sporelings up to 3 cells long present after 7-64 days. No further development recorded.
Sporelings 2-3 cells long	7	Sporelings up to 12 cells long present after 54 days. No further development recorded.
Protonema	24 - 45	Shoots produced after 28-128 days.
Protonema with shoots	38 -146	Shoots survived and gave rise to closed turf in some cases. Sporophytes developed after 1 and 2 years in one experiment.
Shoot fragments up to 1 cm long or individual leaves planted at varying density	O	Regeneration occurred leading to shoot formation. Closed turf developed and produced sporophytes after one year, in one experiment in which shoot fragments were planted.
Controls without an innoculum of A. undulatum	O -146	No plants of A. undulatum developed.

No development occurred in control pots without an inoculum of spores. This result suggests that neither gross climatic nor edaphic factors are responsible for the inhibition of protonema development noted in the field.

Finally, ten nylon net bags, ca. 10 x 3 cm, were filled with soil from Padworth and a capsule was opened inside each bag. The bags were immersed in soil at the Padworth site during January 1981. After 154 days spores, sporelings, protonema and over 20 juvenile shoots of A. undulatum were present in two of the bags. This is the only occasion when shoots appear to have arisen from spores planted in the field, and even here no material of A. undulatum was recovered from the eight other bags, or from 15 bags in a similar experiment.

Considered overall, the experimental results agree with the observations on naturally occurring spores and sporelings in suggesting that failure in germination and early stages of protonema development reduces the effectiveness of sexual reproduction in A. undulatum. The ease with which colonies were established from fragments of gametophytes supports the conclusion that vegetative propagation is important in colony expansion. However, the net bag experiment suggests that reproduction by spores may occur occasionally under as yet undefined circumstances, and the possibility that spores are effective in the initiation of new populations cannot be excluded.

Electrophoresis and inbreeding

Although A. undulatum is monoecious, most individual shoots produce gametangia of only one sex during a given year. Indeed, 84 of 101 young sporophytes examined in four populations had clearly resulted from cross-fertilisation between shoots (Longton & Miles 1982). However, the possibility remained that reproduction was functionally by inbreeding if each colony normally contained plants representing only one genotype. Abderrahman & Smith (1982) have commented that British material of A. undulatum shows little morphological variation although three levels of ploidy occur. Therefore, enzyme electrophoresis

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was employed as a means of detecting genetic variation. Turf
from 18 colonies in 11 populations in England and Wales was
collected and cultured in a cool greenhouse to reduce the
likelihood of environmentally induced variation, and then 158
shoots from this material were ground individually in extrac-
tion buffer. The extracts were absorbed in paper wicks and run
in 12% starch gels. Fourteen enzymes were surveyed and acti-
vitiy was detected in Esterase (Est), Glutamate oxaloacetate
transaminase (Got), Malate dehydrogenase (Mdh), Malic enzymes
(Me), 6-Phosphogluconate dehydrogenase (6-Pgdh), Phosphoglu-
cose isomerase (Pgi), Phosphoglucomutase (Pgm), and Shikimic
dehydrogenase (Skdh). Variation in bending pattern was seen
in Est, Mdh, 6-Pgdh and Pgi, being evident between populations,
between colonies from the same populations, and between shoots
from five of the 18 colonies. The data suggest that a minimum
of 12 genotypes was present in the material analysed.

DISCUSSION

Clearly defined seasonal patterns of reproductive develop-
ment have been demonstrated in many mosses, though often with
minor variation in relation to climatic differences between
sites or from year to year, but there is considerable varia-
tion between species in the timing and duration of the
cycles. There have been fewer studies of temporal aspects of
the development and decline of bryophyte colonies. Rapid turn-
over of colonies was reported in several successional communi-
ties in Scotland (Watson 1960), but other colonies may persist
for long periods. We have observed specific hummocks of Poly-
trichum alpestre over five years in Welsh blanket bog, and
radiocarbon dates from the base of peat profiles suggest that
stands of this species have persisted more or less continuously
for 5,000 years in the maritime Antarctic (Smith 1979). A. un-
dulatum normally persisted for only two or three years at a
given point in the permanent quadrats. This result is consis-
tent with an analysis of age distribution, since most shoots
examined were either in their first year of growth, or were
older but no longer actively growing, in many cases having

sporophytes at the apices (Longton & Miles 1982). It is not clear why shoot replacement by basal branching should not continue on an annual basis, particularly where there is no evident competition from other species, and it is possible that rapid colony turnover is an intrinsic feature of A. undulatum.

The data for spore content in A. undulatum capsules are within the range commonly recorded for other mosses (Longton & Schuster 1984). There is considerable variation between capsules, however, and thus the data for spore release from colonies where trapping was undertaken, as well as estimates of deposition within the trapping area, are to be regarded as first approximations. This does not invalidate the conclusion that spores are deposited at high density within and immediately outside the parent colony and that the majority of spores are nevertheless transported outside the trapping area. A leptokurtic pattern of spore deposition has been reported for pollen grains and pteridophyte spores (Proctor & Yeo 1973). There are no published data for bryophytes, but the present results appear to be in broad agreement with a preliminary report for A. angustatum (Wyatt & Anderson 1984).

The observational and experimental studies of spore germination and colony expansion point strongly towards asexual reproduction as the principal method of colony maintenance and expansion in A. undulatum, despite the abundant output of viable spores, although there is some evidence that spores may occasionally give rise to protonema and shoots under field conditions. The reasons for the general failure in germination and early stages of protonema development in the present experiments are obscure. The fact that spores germinated and gave rise to protonema and shoots on soil from natural habitats under laboratory conditions, and also in pots placed on a concrete path under the prevailing climatic conditions, leads us to suspect that chemical inhibition may be involved in natural environments. In this context, it should be noted that the experimental plantings were normally placed with 10 m of established colonies of A. undulatum. Other possible explanations include subtle microclimatic requirements and the possi-

bility that substrate instability disrupts protonema develop-
ment under natural circumstances.

Despite the apparent prevalence of asexual reproduction,
the electrophoretic studies indicate the presence of sub-
stantial genetic variation in British populations, and, com-
bined with the data on sex distribution, suggest that inbreed-
ing is unlikely to be obligatory, at least in some colonies.
The occurrence of electrophoretic variation in A. undulatum
is in agreement with data for other bryophytes (Daniels 1982,
Szweykowski 1984), including the related, dioecious species A.
angustatum (Cummins & Wyatt 1981).

These observations, together with the previous report
(Longton & Miles 1982) contribute towards a broad outline of
the reproductive biology of A. undulatum in Britain, as sum-
marised in the Abstract. It may be noted that the life his-
tory pattern of this species differs in several significant
respects from each of the strategies proposed by During (1979),
indicating that bryophytes may be more variable in this res-
pect than previously realized.

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THE BIOLOGY OF LETHOCOLEA SQUAMATA

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Lethocolea squamata (Tayl.) Hodgson, a species with an un-
usually wide ecological amplitude, is shown to comprise three
different species. A form in mallee vegetation is probably
Gongylanthus scariosus (Lehm.) Steph. A form in sclerophyll
forests and swamps is a true Lethocolea, L. pansa (Tayl.)
comb. nov. hitherto known as L. squamata Tayl. A third, pre-
dominantly thallose form with uncertain morphological varia-
tion and biology, appears to be a new genus.

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Lethocolea squamata (Taylor) Hodgson, a leafy liverwort
in the family Arnelliaceae or Acrobolbaceae, has been recorded
from a wide range of forest habitats in the State of Victoria,
Australia, and has come to be regarded as one of the most
widely distributed and ecologically tolerant Australian liver-
worts. In particular, there are four habitats, differing in
moisture regime and forest type (Groves 1981), each
apparently characterised by a different form of the plant.

1. Swamps of the myrtaceous shrubs Leptospermum and Mela-
leuca, with an understorey of dense Restionaceae, such as Hy-
polaena. These swamps are enclaves in dry sclerophyll forest
(see 3. below), caused by impeded drainage, sheltered from
wind by the surrounding forest and sheltering the bryophytes
from insolation in the dense restionaceous undergrowth. The
plants here are deeply crimson-brown tinted, forming densely

overlapping mats and, in extreme cases, may be loose and free-floating among the sedges. This particular form of the plants seems to be always sterile and is, so far, only known from the Grampian Mountains of Victoria.

2. Wet sclerophyll (tall open) forest, dominated by very tall trees (up to ca. 100 m) of Eucalyptus regnans. The rainfall in such forest is high, from 1000 mm (but more usually from 1500 mm) to 2000 mm. On relatively dry and open clay banks in this wet forest, Lethocolea forms prostrate green Lophocolea-like mats. It lacks crimson colouration and reproduced both by discoid gemmae and by very long marsupia, up to 2 cm long, driving down into the soil. The leaves are clearly alternate, circular or lingulate and horizontally spreading. There are no underleaves. This is by far the commonest form of the species.

3. Dry sclerophyll forest (open forest), dominated by a range of Eucalyptus spp. such as E. obliqua, with usually a rich shrub understorey of leguminous, myrtaceous and proteaceous shrubs. Rainfall here is generally less than 1000 mm. In relatively wet parts of this dry forest a flat thallose form occurs, more or less invariably associated with the leafy forms, with similar oil-bodies, and often with traces of leaves very much like a moribund Lethocolea squamata.

4. Mallee. This is an endemic type of low shrubland (up to ca. 8 m) confined to dry areas (mostly 25o-450 mm rainfall) dominated by many species of Eucalyptus with a characteristic multi-stemmed growth form, sprouting from a lignotuber (burl) at or below ground level as a post-fire response. In this habitat, there are plants where the leaves are concave, silvery, erect and rather densely imbricate in most cases; but where there is extra moisture they become more spreading, flat and green.

We have investigated this unusually wide ecological range and come to the, not surprising, conclusion that three species are involved.

1. As a result of culture experiments, we have recently
come to believe that the mallee form (4) is possibly Gongylant-
hus scariosus (Lehm.) Steph. hitherto considered to be endemic
to South Africa. It differs from Lethocolea squamata in having
sub-opposite leaves which are more concave, less wettable
(probably because of very finely verruculose surface) and in
the oil bodies which tend to be more numerous and hyaline
rather than slightly brownish. The marsupium is similar to that
of Lethocolea and the tube of this is lined with the same kind
of swollen, almost hair-like cells. One of the puzzles of
mallee bryophytes has been the appearance of isolated marsupia
in cultured mallee soil, not attached to any liverwort stem.
These turn out to be the marsupia of this plant and are clearly
capable of persisting after the parent shoots have decayed and
disappeared. This plant shares with Cephaloziella arctica the
distinction of being virtually the only leafy liverworts in
the soil crusts of these dry areas which are otherwise dominated
by Fossombronia, Riccia and many mosses, as well as lichens
and blue-green algae (Scott 1984).

2. In 1846, Taylor described Podanthe squamata from speci-
mens collected by Drummond in Western Australia (Swan River
Colony as it was known then) and known by the herbarium name
of Riccia squamata. Taylor pointed out that the plant had a
marsupium ("receptacle") like Gymnanthe, but it was Mitten
(1854-5) who first synonymised his own Gymnanthe drummondi
from New Zealand, with Taylor's Podanthe squamata. He later
(1867) .gave it separate generic status as Lethocolea drum-
mondii, without commenting on the fact that Taylor used the
word frons in his Latin description, thus implying that it
had a thallose rather than leafy axis. It was not until 1958
that Mrs Hodgson took the final step of transferring Podanthe
squamata to the genus Lethocolea, the genus Podanthe being
treated as an othographic variant, and hence homonym, of the
earlier name Podanthes Haworths (Asclepiadaceae). Mitten gave
no reasons for uniting Podanthe and Lethocolea but we believe
he was right to do so. The presumed holotype material in the
Farlow Herbarium contains a Riccia as well as Lethocolea squa-

mata and it seems probable that Taylor confounded the two plants in his description, hence his use of the word frons. Surprisingly, however, the specimen does not contain any of the thalloid plant which hitherto has been associated with the name Lethocolea (see 3 below). Moreover, it seems clear after the Sydney amendments to the ICBN that the genus Podanthe is not a homonym of Podanthes, but a valid genus. Since the name has been in abeyance for the past 100 years we believe that the name Lethocolea should be conserved against it and will be submitting a proposal to that effect.

A slightly earlier name, Jungermannia pansa Taylor was dubiously proposed as a synonym of Gymnanthe drummondii by Mitten (1854-5). Gottsche (1880) concurred but without the examination of the type of J. pansa, and his views have been accepted by Hodgson (1958) and Grolle (1965). Examination of isotype material in the British Museum confirms this. The specific epithet pansa, however, since it appeared in the first part of Taylor's (1846) paper and therefore presumably was published earlier than the second part, must take priority over squamata. The name of the leafy liverwort is therefore Letho- colea pansa (Tayl.) G.A.M. Scott & K. Beckman comb. nov. (Ba- sionym: Jungermannia pansa Taylor. London J. Bot. 5:275. 1846).

The plant of sclerophyll forests and swamps is the true Lethocolea squamata, more correctly named L. pansa. This seems to be always leafy, but produces discoid gemmae which germi- nate by direct growth of a new leafy shoot from the centre rather than the rim of the disc as Goebel (1906) illustrates. These gemmae are produced from the upper stem surface among the leaves, but on only a minority of plants.

In winter the stems and leaves may enlarge greatly and among the terminal leaves is produced a very long marsupium, up to 2 cm long, sunk into the ground, appearing more like an angiosperm root with a swollen tip (enclosing the sporophyte). The marsupium tube is lined with swollen hairs, similar to those of Gongylanthus.

The ecological amplitude of this species therefore extends from dry forests to free-floating; no small range, but much less than had formerly been thought.

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3. The thallose plant we are concerned with seems likely to be not _Lethocolea_ but a new genus. It is not uncommon in herbaria, masquerading as "Riccia sp." The plant is extraordinarily interesting. In the resting stages it consists of a yellowish green, ± homogeneous discoid thallus, sometimes with traces of scales or leaves near the apex. What happens to this later is not yet certain but in autumn new plants arise which are clear green, instead of yellowish, and have a very curious upper surface of loosely arranged turgid cells. At the apex two rows of semicircular leaves (or scales) develop, which may straddle a large patch of gemmae near the apex; when plated on agar, these gemmae are more angular than those of _Lethocolea_ and develop directly into similar thalli. Alternatively the thallus apex between the scales may become depressed, indicating the formation of a robust marsupium beneath. It is too soon, from our cultures, to say what the sporophytes produced in these will be like. Until then it is not possible to be certain that the plant is basically a leafy rather than a thallose one, _Jungermanniales_ rather than _Metzgeriales_, but we suspect this to be true. The marsupium tube is lined with swollen hairs of the _Lethocolea_/_Gongylanthus_ type, which strongly suggests a relationship within the _Arnelliaceae_.

Probably, with age at the end of the season, the thallus will thicken up and turn yellowish, and the leaves will tend to erode, producing the familiar _Riccia_-like stage. Whether this can act as a tuber, producing new young growths in the following year, we cannot yet say but are following marked colonies in the field to determine this.

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ON THE GEMMAE OF WEST TROPICAL AFRICAN MOSSES

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There is a great multiplicity of forms in gemmae of West
Tropical African mosses from globose and stellate (Hyophila),
spherical or pyriform (Bryum cruegeri) to elongated forms in
the Calymperaceae. Gemmae are often borne on specific diag-
nostic portions of the gametophyte but sometimes more than one
gametophytic portion are gemmate (Bryaceae). Both leaf and
axillary gemmae have diagnostic values at specific level. Con-
currently gemmae are of immense ecological importance to tro-
pical mosses especially in stressed environments. They occur
and regenerate readily on sterile as well as fertile plants
while the pH for optimum regeneration parallels the substrate
pH of the shoots. The alternate production and dispersal of
gemmae and spores in the Calymperaceae during wet and dry
seasons of the year, respectively, suggest a maximum input to
the reproductive effort ensuring a successful spread of the
species.

INTRODUCTION

Reproductive biology is gradually becoming a new line of
study in biology. This is a significant shift in bryophyte
systematics as it is now increasingly clear that features of
the reproductive biology and life history do influence evo-
lutionary processes within bryophytes (Anderson 1963, Longton
1976).

Sporophyte production, especially in dioecious bryophytes, is an indication of genetic variability within the group. But the loss of the capacity to produce sporophytes is a common and widespread tendency in bryophytes. This has been due mainly to massive regression in sexual reproduction (Longton & Schuster 1984) and/or spatial separation of ♂ and ♀ plants. In cases where sporophytes are freely produced successful spore germination on artificial or natural media in the laboratory has not been widely repeatable on the field and there has been no frequent occurrence of gametophyte establishment from sporelings in nature.

A whole array of asexual reproduction methods in mosses provides 'reliefs' for the development and spread of populations in the face of various setbacks in sexual reproduction. There are records of the occurrence of specialized asexual propagules in 15% and 17% of the moss floras of eastern North America (Crum 1972) and the British Isles (Smith 1978), respectively. The bryophyte flora of tropical Africa is susceptible to the prevailing harsh environment, e.g., drought, desert encroachment, and insolation. These most probably elicit adaptive features in the flora. Various specialised asexual propagules abound in the moss species and these play a vital role in their reproductive biology. This account represents an initial study in the documentation of propaguliferous mosses of West Tropical Africa.

RESULTS

Calymperaceae

Edwards (1980), in a revision of West Tropical African Calymperaceae, considered the heterogeneous family as containing five genera: Calymperes, Syrrhopodon, Mitthyridium, Calymperopsis, and Hypodontium. The family is mainly lowland pantropical and subtropical but occasionally extending well beyond the equator to Cape of Good Hope in the South and Majorca in the north. In the Americas the family is represented by the genera Calymperes, Syrrhopodon and Mitthyridium (Reese 1979)

which all bear foliar gemmae on both sides of the Atlantic.

Hypodontium, mainly subtropical in distribution, is about the only genus lacking gemmae. Foliar gemmae are papillose in Mitthyridium and when present in Syrrhopodon (as in S. armatus from the delta plains of southern Nigeria, Odu No. 638) are usually borne terminally on otherwise undifferentiated leaves. In Calymperopsis the leaves are characteristically dimorphic: those that bear gemmae ('comal') and the non-gemmiferous type ('cauline') (Richards & Edwards 1972). The needle-like and variable gemmae range from 420 to 900 μm and are usually bunched laterally on both sides of the costa in the mid-lamina region of the 'comal' leaves.

The genus Calymperes is very diversified in the humid forests of West Tropical Africa mainly as epiphytes but occasionally on earth-covered rocks in less shady habitats. Calymperes is basically dioecious and dimorphic producing gemmiferous and non-gemmiferous leaves on the same shoots. In the former, the gemmae ($>$ 20) are variously arranged in clusters on the proboscis, a specialized extension of the costa. In some cases all leaves on particular mature shoots may lack gemmae but the opposite has been rarely observed in nature. The gemmae are generally clavate, multicellular and consist of 6-10 uniseriate cells (Fig. 1a, b, e). They are green, mostly 150-300 (-500) x 25-30 μm with no stalks.

Gemmae germinate very readily within 1-2 days after dislodgement from the leaves. Protonemal filaments grow from both ends and rarely form the lateral sides (Fig. 1d, f). This mode of gemma germination appears to be different from that in the obclavate protonemal gemmae of Schistostega pennata where protonemal filaments develop laterally from one or both larger basal cells (Edwards 1978).

Reproduction in most of the Calymperaceae would partly be by means of the elongated gemmae judging from the observed viability of the propagules both in the laboratory and on the field. Moreover, while most plants of Calymperes produce fruits quite freely, sporophytes seem to be rare in both the African and Asiatic species of Calymperopsis (Richards & Edwards 1972).

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The Bryaceae is a very large cosmopolitan family noted among others for the high frequency of occurrence of asexual propagules (Hart & Whitehouse 1978, Lewis & Smith 1978, Smith & Whitehouse 1978, Nordhorn-Richter 1984). Field studies have revealed propagules on some African bryoid mosses and further work is in progress in this respect.

Bryum nitens Hook. (B. cruegeri Hampe) is a highly variable, tuberous moss known from the American tropics, Florida, Bermuda (Whitehouse 1978) and also from Liberia, Ghana
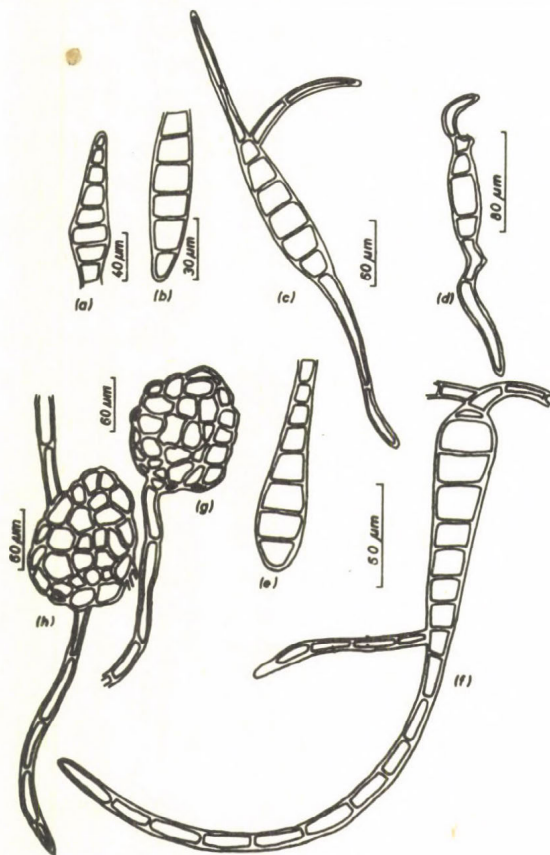
Fig. 1. Asexual propagules. a-d. Foliar gemmae of Calymperes rabenhorstii. c-d. 2-day old germinating gemmae, e-f. Foliar gemmae of Calymperes afzelii. f. 12-day old germinating gemma. g-h. Rhizoid gemmae of Bryum cruegeri. h. 3-day old germinating gemma.

and Nigeria. In West Africa, it occurs commonly on pH-neutral unstable habitats in open situations. Tubers are character- istically multi-cellular, brownish, rhizoidal in origin and may be spherical, 125-200 μm in diameter (Fig. 1g) or some- times ellipsoidal to pyriform. The great variability of the species is pronounced, sometimes to the extent of separating the habitat variants into seemingly distinct species. The same plant may bear gemmae on the stem in leaf axils and on rhizoids. Axillary gemmae, however, possess very short stalks. B. nitens is commonly sterile and reproduction is no doubt is through the dispersal and germination of the tubers. Gemmae detach quite easily from the shoots and germinate within 2-3 days, radially, producing eventually up to 5(-8) protonemal fila- ments (Fig. 1h). Asexual reproduction is accentuated by the additional occurrence of numerous bulbils (Fig. 2d) on the shoot tips of variants in drainage culverts. In some po- pulations of this species it seems that stem gemmae occur much later in the season on the older parts of stems leaving the current season growing portions free of gemmae (Fig. 2b, c). This apparent rhythm of gemmae production, endogenously or environmentally controlled or both is comparable to the pe- riodic production of foliar gemmae in Calymperes species (Odu & Owomoto 1982). However, there is a distinction in the latter species where gemmae develop simultaneously with the leaves on the upper, younger parts of the shoots (Fig. 2a).

Pottiaceae

Among the Pottiaceae, Barbula and Hyophila produce diag- nostic and ecologically differentiated axillary gemmae in southern Nigeria. Barbula indica (Hook.) Spreng. occurs com- monly on basic soils, mortar walls and concrete slabs of cul- verts in open environments. It is pantropical in distribution occurring in southern and central Africa, the Indian subcon- tinent, southern and southeast Asia and Japan (Magill 1981). Its colonisation and fast spread within weeks on uncompleted buildings, cement blocks in building sites and drainages has put this species into the class of weedy plants in urban areas.

Fig. 2. a-c. Seasonal development of gemmae in (a) Calymperes erosum, b-c. Bryum cruegeri. Single line = non-gemmiferous zone; double line = gemmiferous zone. d. Axillary bulbil of Bryum nitens.

Although it is dioecious, most plants are female. Sporophytes and male plants are rare.

The fast spread of B. indica is attributable to the dispersal and subsequent germination of numerous gemmae from each shoot (ca. 50-100 . Gemmae are obovate, multicellular (8-10 cells), greenish-brown, shortly stalked and measuring 50-100 µm across (Fig. 3a, b). Leaves are arranged on the lower parts of the stem in such a way that the gemmae are freely exposed.
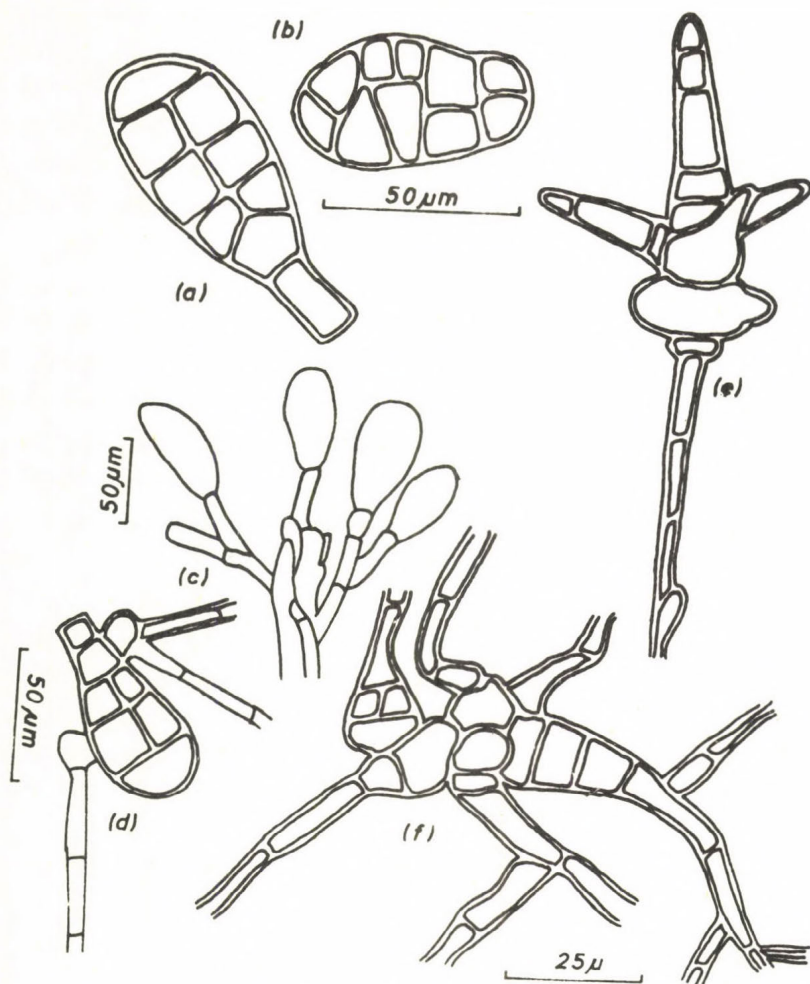
Fig. 3. Asexual propagules. a-d. Gemmae of Barbula indica. c.
Stem apex with multiple budding of gemmae. d. 2-day old ger-
minating gemma. e-f. Hyophila involuta. f. 5-day old germinat-
ing gemma.

At the shoot tips leaves are crowded together forming "gemma-
cup' structures. The propagules which bud off copiously at the
stem apices (Fig.3c) most probably collect into these "gemma-
cups' and at the appropriate time are dispersed as powdery
masses. Germination occurs within 2 days, protonemal filaments
forming radially on the propagules (Fig. 3d). The basic nature
of the plant's substrates must have favoured the initial es-

tablishment of the gemmae which germinated well at high pH
whereas germination of propagules of Bryum nitens is suppressed
at high pH (Fig. 4).

Hyophila involuta (Hook.) Jaeg. produces highly polymorphic
multicellular axillary gemmae with long rhizoidal stalks (Fig.
3e). The species is generally characteristic of shady habitats.
Although dioecious and always producing seasonal crops of
sporophytes the species also bears 16-20(-25) greenish, axil-
lary gemmae along the whole length of each shoot. The gemmae
are distinctly stellate with 5-11 multicellular uniseriate
arms (lesser variations from this type may occur). The mode
of germination of the gemmae is through the elongation of all
the stellate arms (Fig. 3f) producing a network of protonemal
filaments within 5 days. The rhizoidal stalks in all cases are
multi-seriately branched, each branch terminating in a gemma.
An abscission cell, or 'tmema', separates each gemma from the
branch as in the protonemal gemmae of Schistostega pennata
(Edwards 1978). Hyophila crenulata has been reported by
Olarinmoye (1981) to produce polymorphic axillary gemmae in
Nigeria. But the nearly similar habitat conditions, morpholo-
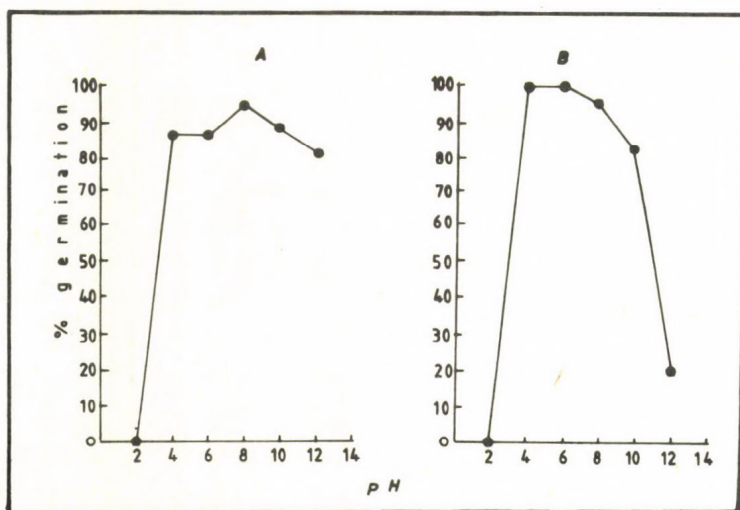
Fig. 4. Influence of media pH on germination of gemmae. A. Bar-
bula indica, B. Bryum nitens.

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gies and dioecity suggest that H. involuta and H. crenulata
are synonyms or at least the latter species is a variant of
typical H. involuta (Odu, in press). H. involuta is a largely
tropical species which Magill (1981:230) says is probably new
to Africa, having been previously known from Europe, southern
Asia and India, Micronesia and North, Central and South Ameri-
ca.

DISCUSSION

The varied forms of gemmae in West African mosses play
vital roles in the dispersal and maintenance of bryophyte po-
pulations in the alternating humid and dry environment of tro-
pical Africa. These propagules undoubtedly disperse the plants
judging from the rapid spread of many non-fruiting weedy
species into new areas. The distribution pattern of the gem-
mae agrees with the existing opinion in literature about the
occurrence of asexual structures in temporary unstable sub-
strates (Whitehouse 1966) where they would survive field dis-
turbance in a dormant state and then regenerate from tubers
at the advent of suitable growing conditions. In addition,
the propagules are advantageous to non-fruiting or sterile
plants where they could compensate for lack of spores in re-
productive spread. Even when sporophytes are produced propa-
gules could still out-score spores in plant dispersal. Bryum
coronatum, a dioecious, widespread commonly fruiting weedy
species in Nigeria propagates more efficiently by axillary
propagules than by spores (Egunyomi 1982). Occurrence of gemmae
in non-fruiting plants seems not to be as significant as oc-
currence in dioecious plants. The production of asexual pro-
pagules in mosses is associated more directly with the dio-
ecious condition than with failure to fruit (Longton & Schus-
ter 1984).

Gemmae polymorphism in Hyophila involuta is probably
due to the micro-climatic effects. Zander & Ireland (1979)
reviewed cases of environmental effects on the expression of
asexual reproduction in otherwise potentially fertile mosses.
The West African species of Calymperes exhibit a regular pe-

riodicity in the development of foliar gemmae (Odu & Owotomo 1982). This biological rhythm is endogenously determined but likely subject to environmental modification. The result is that while lighter spores are dispersed in the dry season gemmae formed at the onset of the rainy season mature, are dispersed and would be able to germinate in mid-rainy season.

Gemmae are generally larger in size than bryophyte spores and therefore are less likely to be involved in long range dispersal. The only possible option is local dissemination of species by short range dispersal of propagules. If this is possible a gemmiferous species such as Barbula indica can cover considerable wall surfaces through step by step dispersal. The large-sized gemmae may contain considerable stored food materials which would be of value to their early and rapid germination in unstable temporary habitats. Alternately, the gemmae could act as survivors or, perennating structures in stressed environments.

ACKNOWLEDGEMENTS

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PROTONEMA-GEMMAE IN EUROPEAN MOSSES

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A range of moss species has been tested for the occurrence
of gemmae on the protonema by growing the plants on Knop's
agar. Any species that produces gemmae on the leaves or in the
leaf axils seems also able to produce similar gemmae on the
chloronema. Numerous other species, not known to produce gem-
mae elsewhere on the plant, have been found to produce gemmae
on the protonema in culture. If, as seems likely, similar
gemmae are produced in nature, they are likely to be important
for the life strategy of the species.

INTRODUCTION

Gemmae arising on moss protonema, as distinct from rhi-
zoids, have been reported in several species: Pseudocrossidium
revolutum* (Müller 1874), Tortula muralis (Müller 1874, Maheu
1908), T. ruralis (Müller 1874, Maheu 1908), T. papillosa
(Maheu 1908), Zygodon forsteri (Malta 1926), Gyroweisia tenuis
(Monkemeyer 1927), Orthodontium lineare (Whitehouse 1961), Eu-
cladium verticillatum (Dalby 1926, Vajda 1966), Bryum kling-
graeffii (Chopra & Rawat 1973) and Schistostega pennata (Edwards
1978). Five years ago I reported their occurrence in Didymodon
luridus and also in 18 European species with gemmae found
elsewhere on the plant (Whitehouse 1980). Three of the species
mentioned above also fall into this category (P. revolutum,

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* Nomenclature follows Corley et al. (1981).

<u>T</u>. <u>papillosa</u>, <u>B</u>. <u>klinggraeffii</u>). I have now tested some additional species of mosses for the occurrence of gemmae on the protonema in culture.

METHODS

The technique I have used to start cultures is top dip a fragment of the plant - leaves, shoots, capsules, or gemmae if present - in 1.5% sodium hypochlorite solution for a few seconds to sterilize the exterior, and then to use sterile needles to place the material in a drop of sterile distilled water on the surface of Knop's agar in a petri dish. With capsules, the spores are then released by puncturing it with the needles. Within a few days protonema should emerge from the moss material. It is then transferred with needles to an agar slope in a 10 cm tube plugged with cotton wool. If alga or fungus is present it will be necessary to repeat the sterilization process when moss shoots have appeared.

RESULTS

The results I have obtained concerning the occurrence of gemmae have surprised me.

First, mosses with gemmae formed on the leaves or in leaf-axils seems always to produce similar gemmae on the protonema. This does not apply to species with bulbils. I have seen protonema-gemmae in culture in the following 26 European species already known to be gemmiferous on leaves or in leaf axils:

Dicranaceae: <u>Dicranoweisia</u> <u>cirrata</u>, <u>Dichodontium</u> <u>pellucidum</u>, <u>Ceratodon</u> <u>purpureus</u>;

Encalyptaceae: <u>Encalypta</u> <u>streptocarpa</u>;

Pottiaceae: <u>Tortula</u> <u>latifolia</u>, <u>T</u>. <u>papillosa</u>, <u>Scopelophila</u> <u>ligulata</u>, <u>Pseudocrossidium</u> <u>revolutum</u>, <u>Didymodon</u> <u>nicholsonii</u>, <u>D</u>. <u>cordatus</u>, <u>D</u>. <u>rigidulus</u>, <u>D</u>. <u>glaucus</u>, <u>Leptodontium</u> <u>gemmascens</u>, <u>Gymnostomium</u> <u>luisieri</u>, <u>Anoectangium</u> <u>warburgii</u>;

Bryaceae: <u>Bryum</u> <u>pallens</u>, <u>B</u>. <u>flaccidum</u>, <u>B</u>. <u>pseudotriquetrum</u>;

Orthotrichaceae: Zygodon viridissimus, Z. baumgartneri, Z. conoideus, Orthotrichum lyellii, O. pumilum, O. diaphanum;

Leskeaceae: Habrodon perpusillus;

Plagiotheciaceae: Plagiothecium latebricola.

Many species with rhizoid gemmae also produce similar gemmae on the protonema (Chopra & Rawat 1973, Whitehouse 1980).

Secondly, numerous species have gemmae on the protonema even though gemmae, or at least gemmae of this morphology, have not been recorded elsewhere on the plant. Within these species, two categories of protonema gemma can be recognised on the basis of their morphology.

1. Gemmae little differentiated

Segments of aerial protonema, little differentiated from normal aerial filaments, become detached. Such gemmae, which usually consist of 3-6 cells and measure 150-200 x 20-40 µm, seem to occur particularly in the Bryaceae. In addition to the species with axillary filamentous gemmae, I have seen filamentous protonema-gemmae in cultures of the following 10 species:

Dicranaceae: Dicranella staphylina;

Splachnaceae: Splachnum sphaericum, S. luteum;

Bryaceae: Orthodontium lineare, Leptobryum pyriforme, Bryum radiculosum, B. ruderale, B. klinggraeffii, B. sauteri;

Orthotrichaceae: Zygodon forsteri;

In Dicranella staphylina the protonema-gemmae have thicker walls to the filament cells than is usual with this type of propagule. In Bryum radiculosum the filament cells are strongly papillose. In B. klinggraeffii and B. sauteri the filamentous protonema-gemmae have one or more short branches ending in a gemma resembling those on the rhizoids.

2. Gemmae well differentiated

Protonema gemmae well differentiated by rounding off and detachment of individual cells or groups of cells seem to be of

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widespread occurrence in mosses. I have seen such gemmae in cultures of the following 36 species:

Dicranaceae: Ditrichum pusillum;

Encalyptaceae: Encalypta rhaptocarpa;

Pottiaceae: Tortula ruralis, T. ruraliformis, T. intermedia, T. virescens, T. subulata, T. marginata, T. vahliana, T. muralis, T. stanfordensis, Aloina ambigua, A. brevirostris, Barbula unguiculata, Leptobarbula berica, Pseudocrossidium hornschuchianum, Didymodon luridus, D. sinuosus, D. spadiceus, D. fallax, Eucladium verticillatum, Gyroweisia tenuis, G. reflexa, Gymnostomum calcareum, G. aeruginosum;

Bryaceae: Bryum alpinum;

Orthotrichaceae: Zygodon gracilis, Orthotrichum rupestre, O. cupulatum, O. rivulare, O. sprucei, O. tenellum, Ulota crispa;

Leucodontaceae: Cryphaea heteromalla, C. lamyana;

Neckeraceae: Homalia trichomanoides.

When unicellular, the gemmae usually measure about 25-45 μm in diameter. When multicellular, measurements of 60-120 x 25-45 μm are usual. The cell walls in some species are strongly thickened, for example, up to 4.5 μm thick in Didymodon sinuosus.

DISCUSSION

Protonema-gemmae arise on primary or secondary chloronema and are often produced in large numbers in culture. For example, in Eucladium verticillatum I estimated that there were at least 100 per mm^2 (Whitehouse 1980). I assume that they also occur abundantly in nature under suitable conditions, although this will be difficult to establish. In culture, the thicker-walled gemmae arise when the culture starts to dry up and are presumably adaptations to survive desiccation. On the other hand, the thinner-walled gemmae arise when the chloronema is actively growing and are perhaps primarily adaptations for short-range dispersal.

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From the lists of species in which protonema gemmae have been observed it is evident that they occur in species from a great diversity of habitats. It would be of interest to look at their occurrence in relation to the life strategy of the species (During 1979). It seems likely, in particular, that primary colonizers of open habitats might gain a considerable advantage from the rapid spread made possible through the production of protonema-gemmae before leafy shoots have appeared.

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THE BRYOPHYTE PROPAGULE BANK OF ANTARCTIC FELLFIELD SOILS

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In the Antarctic the totally cryptogamic fellfield eco-
system is dominated by lichens and bryophytes. Colonisation of
recently deglaciated substrata is dependent on the immigration
of propagules from both local and remote sources. Soil samples
from unvegetated areas of fellfield on Signy Island were in-
cubated at temperatures from 2 to $25°C$ for up to 23 weeks to
determine the colonisation potential of the soil propagule
bank. Numerous bryophyte colonies, belonging to a total of
14 taxa, developed from buried spores and gametophyte fragments.
Species diversity and production was greatest between 10 and
$20°C$ but growth of some taxa occurred at the extreme tempera-
tures. A much greater incidence of colonisation occurred in
superficial than in sub-surface samples, but amending the soils
with nutrients did not increase the number of species or pro-
ductivity. Most were typical fellfield taxa, but the dominant
species were not represented. The propagule bank also contained
an element of exotic species providing evidence of long-distance
wind dispersal. The importance of this reservoir of diaspores
in the soil with regard to primary colonisation and succession
is discussed.

INTRODUCTION

A knowledge of plant colonisation and early successional
processes is important in understanding the development of com-
munities. In most systems this is a complex series of inter-

actions between a wide range of plant, and subsequently animal, species and their environment. There are therefore distinct advantages in investigating ecosystem dynamics and testing ecological hypotheses in biologically simple systems. Thus a community of low species diversity and reduced interactions lends itself to ecological interpretation much more readily than one comprising high diversity and complex interrelationhsips. In this context the Antarctic biome offers ideal opportunities for such research. Here, the terrestrial biota are restricted to cryptogam-dominated vegetation and a small number of invertebrate taxa belonging to a few phyla. Unlike the Arctic biome where vascular plants dominate most systems, the Antarctic supports only two vascular species (Colobanthus quitensis and Deschampsia antarctica) which are confined to the most favourable habitats in the maritime Antarctic. Communities composed entirely of bryophytes, lichens and algae are widespread and locally extensive throughout this region and also occur more sparsely in suitable ice-free habitats on continental Antarctica (Smith 1984a).

In this environment it is possible to follow the course of colonisation and succession from the earliest stages without them being overwhelmed and obscured by the development of vascular plants or by being affected by herbivory. Most accounts of primary colonisation and succession, even in extreme environments, relate to higher plants and the occurrence of avascular cryptogams is usually reported merely as incidental associates. However, these lower plants and micro-organisms are undoubtedly the true primary colonists followed closely by phanerogams in the more advanced ecosystems. In the Antarctic biome communities of bryophytes and lichens represent the climax vegetation type, and therefore it is possible to examine and assess their role in the process of ecesis and possibly determine what autogenic changes they induce which enhance secondary development.

While there is a growing awareness of the importance of the pool of buried seed in maintaining stability, continuity and recovery from perturbarion in phanerogamic communities (Roberts 1981), very few studies refer to the bryophyte com-

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ponent of the soil diaspore* bank (e.g., Leck 1980, During & ter Horst 1983). However, no comparable studies have been made of unvegetated soils. It is in such a substratum that any viable propagules* present must play a crucial role as potential colonists, and those for which the prevailing conditions favour germination and development will be the pioneer macrophytes of any subsequent succession. The work reported here is a preliminary assessment of the composition of viable propagules present in skeletal Antarctic soils to test the colonising potential of the soil propagule bank. The study was carried out as part of the British Antarctic Survey's Fellfield** Ecology Research Programme at Signy Island, South Orkney Islands (lat. $60^{O}43'S$, long $45^{O}38'W$) (Smith 1985).

DESCRIPTION OF SITES

The two study sites, each over 1 ha in area, represent fellfields undergoing primary colonisation, but of different age (since ice retreat) and nature of instability. The Jane Col site (150 m altitude) is a level saddle uncovered by the receding ice cap about 25 years ago. Much of the site is devoid of macroscopic vegetation but primary colonisation by cryptogams occurs very sparsely in several places; a slight rise at the west has been ice-free for longer and supports patches of relatively abundant vegetation. Denser vegetation occurs several hundred metres to the north and east. The site is extensively patterned with small sorted circles and stripes. The Moraine Valley site (35-60 m) is an unstable

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* Diaspore, propagule, disseminulate - any spore (seed or fruit) or vegetative portion of a plant capable of being dispersed and able to produce a new plant.
** Fellfield is the dominant ecosystem in the Antarctic biome, comprising a continuum of communities of sparse bryophytes and lichens on dry exposed mineral substrata subjected to continual freeze-thaw and desiccation-hydration cycles.

slope, adjacent to a glacier, and ice-free for several centuries. It has sparse vegetation on the more stable sorted stripe margins and scattered boulders. The higher eastern slope of the valley is extensively vegetated.

METHODS

At each site in February 1981 samples of fine mineral soil from periglacial features were placed in 5 cm diameters by 2 cm deep polystyrene petri dishes and their lids sealed with adhesive tape in the field. Within a few hours of collection the dishes were stored in darkness at -20°C until required for culture in England several months later.

At the Jane Col site the surface 0.1-0.5 cm was sampled from five sub-sites:

Soil A: fine soil from the centre of a sorted gravel stripe c. 25 m from the nearest visible very sparse bryophyte or lichen colonies and close to the receding ice edge at the north-east of the site;

Soil B: an accumulation of black detritus washed down from an adjacent ice slope at the south side of the site; also c. 25 cm from the nearest sparse vegetation;

Soil C: fine soil from the centre of a sorted circle near the centre of the site and surrounded by very sparse bryophytes;

Soil D: as Soil C towards the south-west of the site;

Soil E: barren fine soil from the centre of a sorted circle at the west side of the site, and with relatively dense bryophytes and lichens around the margin and beyond.

At the Moraine Valley site a sorted stripe 130 wide and 10 m long was sampled from five positions at 0.1-0.5 cm and 4-5 cm depths along a transect across the feature. Some sparse bryophyte and lichen colonies occurred on the stable coarser stripe margins, but the progressively finer and more mobile material towards the centre was barren.

Prior to culturing the soils on a thermogradient incubator similar to that described by Grime & Thompson (1976), the

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plates were thawed slowly at 2°C for several days. Duplicates of each soil were then arranged along five parallel aluminium bars 70 cm long and 8 cm wide, each of which provided a temperature gradient from 2-5 to 25°C which was maintained 24 h d^{-1}. The plates were kept moist by the addition of deionised water as required. In the Jane Col series a duplicate set of plates was treated weekly with a fertilizer solution ("Phostrogen") containing N (10% of dw), P (10%), K (27%), Mg (1.3%), Fe (0.4%), Mn (trace) diluted 0.5 g l^{-1}. Illumination was by two HQI lamps providing c. 175 μE $m^{-2}s^{-1}$. The plates were cultured for up to 160 d and the percentage cover afforded by different algae and bryophytes was recorded at intervals (usually every two weeks). The identities of all taxa were determined when the experiments were terminated.

RESULTS

Development of bryophyte colonies from buried or superficial spores or vegetative propagules on the various soil plates is illustrated in Figs 1 and 2 (that of the algae will be reported elsewhere). In each series bryophytes appeared on many of the plates throughout the range of temperatures tested, although the amount of growth and diversity of species were much less at 2-5°C and 25°C. The optimum temperature for most species was between 10 and 20°C, a range commonly attained for several hours per day on many summer days at the soil surface ·in the field. Development also usually commenced earlier at these medial temperatures, although the first appearance of protonemata on some plates occurred after two weeks and the first gametophytes by the third week (notably Ceratodon cf. grossiretis and Bartramia patens). The abundance of shoots increased steadily with time on most soils, but in a few instances at the highest and lowest temperatures the shoots died after a few weeks. Maximum growth (as percentage cover) was achieved at 10-20°C by several species after about 10-15 weeks but slightly later at the more extreme temperatures.
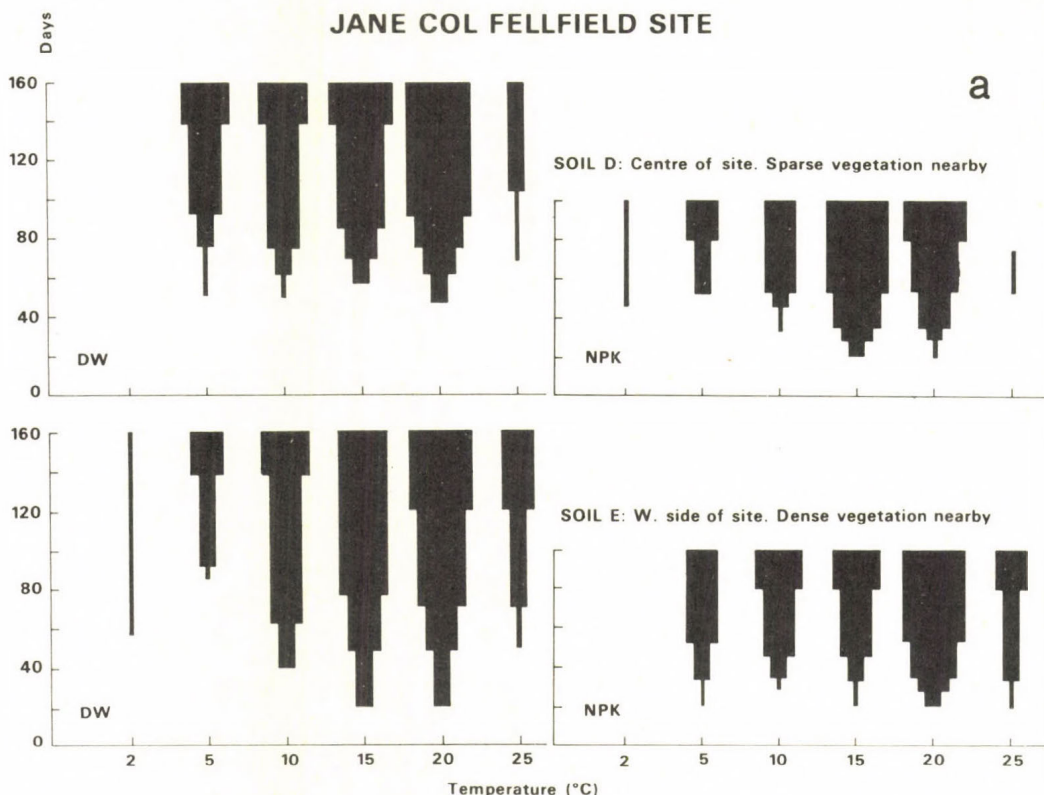
Fig. 1. The development of bryophytes on soils from five un-
vegetated sub-sites at Jane Col and incubated at a range of
temperatures. DW: soils treated with deionised water; NPK:
soils treated with a nitrogen, phosphorous and potassium-rich
nutrient solution.

Jane Col experiment (Fig. 1a-b).

The cultures revealed that even soils remote from any
established vegetation (soils A and B) contain a pool of viable
propagules. Several bryophyte taxa appeared on soil B (which
was formed by the down-washing of detritus blown onto the ice
field south of the site and which was prominent as accumula-
tions on melting ice and in cryoconite holes following periods
of melt - see Wharton et al. 1981). Additional culturing of
such debris from the ice cap also yielded gametophytes of se-
veral bryophyte taxa. Although the greatest production of

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JANE COL FELLFIELD SITE

b

SOIL A: N.E. side of site near ice margin.
Unvegetated

SOIL B: S. side of site below ice slope.
Unvegetated

SOIL C: S.W. side of site. Very sparse
vegetation nearby

50—100+ shoots
25—50 shoots
10—25 shoots
5—10 shoots
<5 shoots

Days

Temperature °C
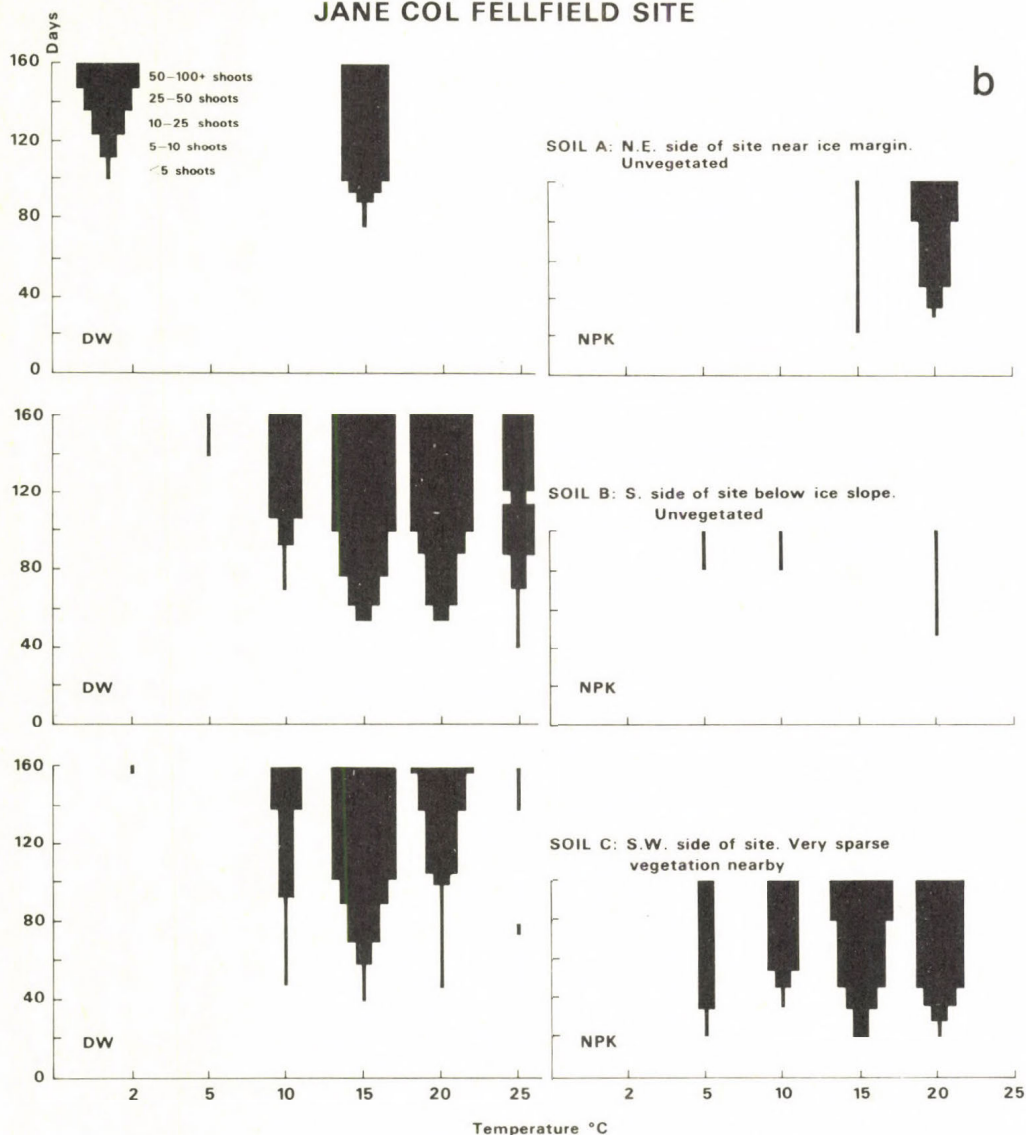
shoots occurred on soils associated with neighbouring vegeta-
tion, notably soil E which was surrounded by a relatively dense
bryophyte stand, the greatest diversity of taxa (eight of the
12 recorded on all the plates from this site) was on soil B,
indicating the importance of the ice cap as a reservoir of
viable propagules which can eventually reach terrestrial sub-
strata during the course of spring and summer melt. The prin-
cipal effect of enriching replicate samples with NPK was to

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accelerate development, i.e., protonemata and gametophytes appeared earlier than in the deionised water treatment. Increasing the nutrient status did not increase biomass nor species diversity.

Moraine Valley experiment (Fig. 2).

This illustrates the low frequency of viable propagules in the sub-surface soil compared with corresponding surface samples. It also demonstrates the reduced abundance and species diversity towards the unstable centre of the sorted stripe, indicating that dispersal of diaspores decreases rapidly with increasing distance from nearby potential sources (here, only 65 cm from the very sparse bryophyte colonies along the stable stripe margins). Development from all surface samples was considerable between 7 and 20°C, but only slight in the sub-surface samples cultured at 13 and 20°C and with no growth at 7 or 25°C. Of the ten taxa recorded from all the plates, seven and five occurred on the two marginal soils, respectively, but only four from the centre samples.

Species composition of soils.

A total of 14 bryophyte taxa was recorded from all the soil cultures. The most commonly occurring in each experiment was a taxon provisionally identified as <u>Ceratodon</u> cf. <u>grossiretis</u>, a highly variable species in the field and in these cultures often exhibiting atypical leaf characters (e.g., short or occasionally excurrent nerve and toothed margin at the apex); these may be environmental modifications resulting from the culture conditions provided (J. S. Burley, pers. comm.). It grew well at all temperatures from 2 to 25°C. <u>Bartramia</u> <u>patens</u> was abundant on some soils from 7 to 25°C, growing particularly well at the lower temperatures. <u>Pohlia</u> <u>nutans</u> also occurred frequently on many soils, with greatest development at higher temperatures, <u>Lophozia</u> cf. <u>propagulifera</u> (possibly including <u>Barbilophozia</u> <u>hatcheri</u> and <u>Cephaloziella</u> <u>varians</u>) developed well from 5 to 20°C. NPK enrichment favoured the growth of the more calcicolous <u>Bryum</u> cf. <u>algens</u>, <u>Distichium</u> <u>capillaceum</u>,
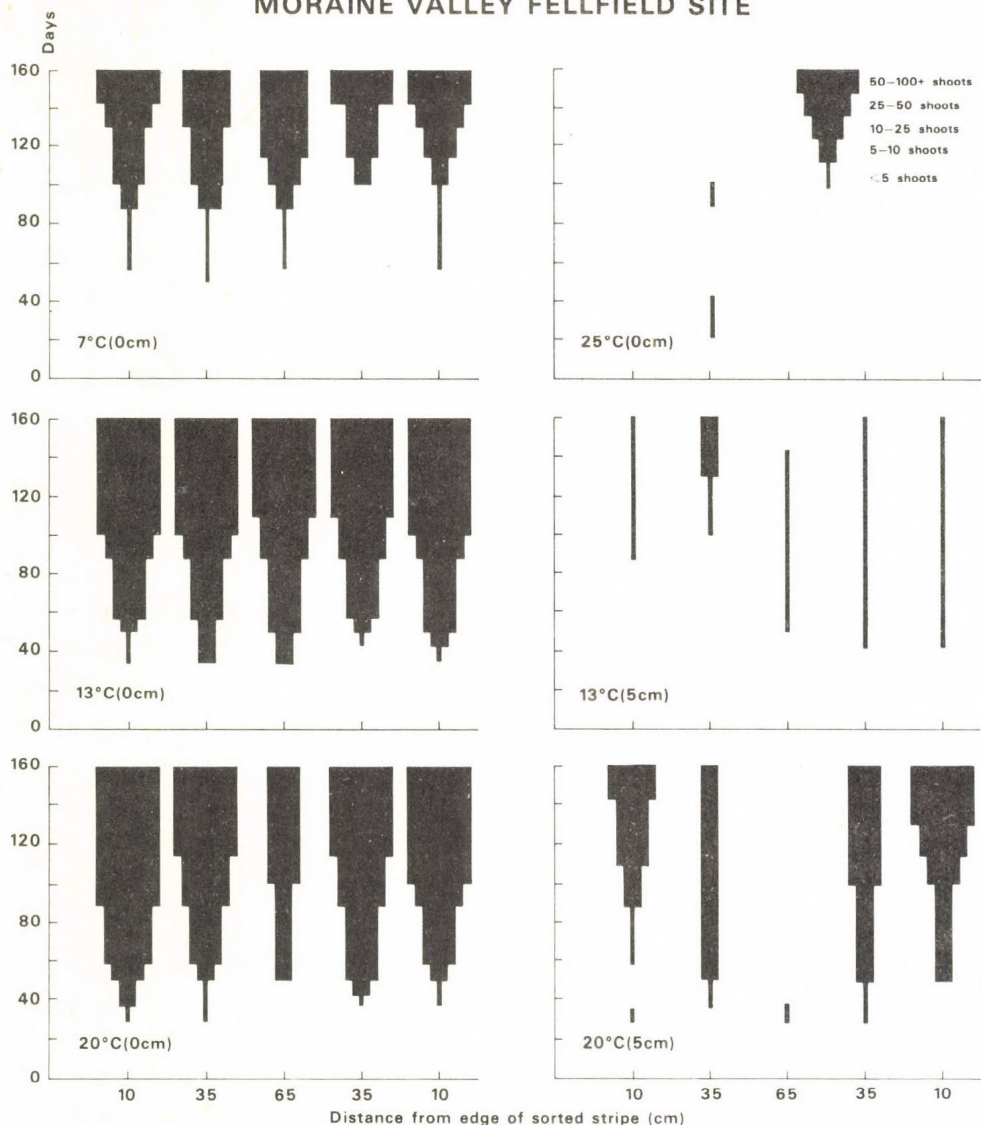
Fig. 2. The development of bryophytes on unvegetated soil sampled at 0.1-0.5 cm and 4-5 cm depths across a sorted stripe in Moraine Valley and incubated at a range of temperatures. No growth was recorded in the sub-surface samples at 7 and 25°C.

Pohlia cruda, Campylium polygamum, Schistidium antarcticum and Tortula cf. princeps, the latter three occurring only very rarely. Of the species cultured only Bartramia, Schistidium and Pottia austrogeorgica commonly produce sporophytes on Signy Island and Bryum and Tortula are occasionally fertile (Webb 1973). Ceratodon produces filamentous propagula and Lophozia forms clusters of two-celled gemmae on its leaf tips. These latter species and Bartramia are the most frequently occurring bryophytes on the soil plates. Most of the taxa readily proliferate from detached leaves or shoot fragments, but the pleurocarps, typical of wetter habitats, are less conducive to such development.

The soils were only mildly acidic (pH 5.5-6.5), which probably favoured the growth of several calciculous bryophytes. Most of these occurred close to the sample areas. There is an extensive sparsely vegetated area of marble and amphibolite scree and calcareous soil on the slope of Jane Peak c. 400 m east of Jane Col on which most of the calcicolous flora of Signy Island occurs (see Smith 1972). However, none of the principal calcifuge fellfield species (notably Andreaea spp., Dicranoweisia grimmiacea, Polytrichum alpinum, Racomitrium austro-georgicum, Herzogobryum teres, Pachyglossa dissitifolia) appeared on any of the soil plates, yet several were present within a metre of several of the soil samples and the others occurring within 100 m of the sample areas. Of these species only the Andreaeas have failed to develop in separate growth trials using leaf and shoot fragments and, for A. gainii and A. regularis, spores cultured under a range of temperature, moisture and nutrient conditions and preconditioning treatments. This genus, despite its abundance and widespread occurrence in several of the island's communities, appears to have special requirements for germination and vegetative establishment.

DISCUSSION

The preliminary experiments reported here demonstrate that unvegetated soil, both near to and remote from established vegetation, contains a reservoir of viable bryophyte propagules, although the nature of these was not ascertained. Although several major components of the local vegetation could not be detected it seems unlikely that their propagules do not occur in these soils. Clearly, the soil propagule bank serves an important role in providing a source of potential primary colonists. A proportion of these probably remain viable for several years despite being frozen for up to nine months per year; tests have indicated that fragments of several Signy Island bryophytes can proliferate after ten years at $-20^{\circ}C$. In the field these propagules may develop under favourable conditions and, in association with the soil particles stabilised by meshes of Cyanobacteria and algal filaments (Wynn-Williams in press) and by the cementing of microbial mucilaginous carbohydrate secretions (P. V. Tearle, pers. comm.), they initiate the process of primary macroscopic colonisation. As their combined influence on soil stability increases, secondary colonisation, including lichens, leads to increasingly complex phases of succession and ultimately, after a very long time span, to the climax sere.

Since few are fertile in the Antarctic, the most likely form of propagation is by leaf and shoot fragments. The ability of such gametophyte fragments to proliferate has been proven in separate experiments similar to those described by Bayfield (1976). The provenance of the propagules is most likely to be local, mainly from within a few hundred metres of the site of deposition. The use of fixed and rotating sticky slides to trap wind-borne disseminules on Signy Island has yielded numerous fragments of identifiable bryophytes and unidentified moss spores. Rudolph (1970) reported trapping leaves and buds of Bryum argenteum at a continental Antarctic site where the moss is locally frequent. Wind-blown debris containing viable propagules is deposited on the ice cap and glaciers of Signy Island and, during periods of melt, this accumulates in patch-

es and cryoconite holes. Similar occurrences have been reported from Arctic and alpine glaciers and late snow beds (e.g., Warren Wilson 1958, Bonde 1969, Teeri & Barrett 1975, Miller & Ambrose 1976).

There was also evidence of long distance dispersal of propagules, presumably spores, as three soil plates from Moraine Valley yielded Campylopus cf. canescens, a species not known on Signy Island and, indeed, recorded only very rarely from areas of geothermal activity in the South Sandwich Islands (Longton & Holdgate 1979), Deception Island, South Shetland Islands (Smith 1984b, c) and possibly also near the summit of Mt Melbourne in Victoria Land, continental Antarctica (A. Fife, pers. comm.). A sample of the glacial downwash soil (B) on Lane Col produced basidiocarps of Coprinus sp., a genus unknown in the Antarctic biome but occurring on sub-Antarctic South Georgia. The phenomenon and significance of long distance transport of spores to Antarctica from other land masses, notably southern South America, has been discussed by Smith (1984a, b, c).

ACKNOWLEDGEMENTS

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REPRODUCTION AND DISPERSAL OF MOSSES ON MACQUARIE ISLAND

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Reproductive strategies of some moss species on subantarctic Macquarie Island are described together with a general discussion of reproduction of mosses on the island. The resistance of propagules of two species of moss to salinity, and of one species to drying and low temperature, is discussed. Implications for long-distance dispersal mechanisms are explored.

INTRODUCTION

Macquarie Island ($154°57'E$, $54°30'S$) is one of seven small isolated islands in the subantarctic zone. Occupying a total area of 120 km^2, the island is 1130 km SW of New Zealand and 1580 km SSE of Tasmania. The closest land is oceanic Auckland Island.

The island is now recognised as a fragment of ocean floor, uplifted as a result of interactions between the Indian-Australian and Pacific tectonic plates (Christodoulou et al. 1984). The island's ophiolite complex is estimated as of mid-Tertiary (17-20 Ma) age (Wlliamson 1974, Quilty et al. 1973, Griffin & Varne 1980).

Uplift of the island is more recent, quite rapid and probably still continuing (Selkirk et al. 1983). One estimate is of post-last glacial appearance of the island (Ledingham & Peterson 1984). The island has never been part of, or in contact with, any other land mass. There seems, therefore, no alternative to the conclusion that all biota present on the

island arrived via some form of long distance, transoceanic dispersal.

The island's flora consists of about 45 vascular plant species and 110 bryophyte species growing in supralittoral zones, tussock grasslands, herbfield, mires and fellfield (Taylor 1955, Seppelt 1981, Seppelt et al. 1984). Bryophytes are an important component in the vegetation formations on the island (Seppelt et al, this volume) and in some communities such as the supralittoral zones, mires and fellfield, bryophytes are possibly on a par with vascular plants, in terms of biomass. Similar results have been gained from Marion Island (Russel, this volume). The threefold difference in species number between vascular plants and bryophytes suggests that bryophytes have been more successful in terms of dispersal, arrival and establishment.

Several authors have discussed the phenomenon of long distance dispersal by bryophytes (e.g., van Zanten & Pócs 1981, Longton & Schuster 1983, Schuster 1983). The geological age and isolation of Macquarie Island allow an examination of reproduction and dispersal in selected populations of bryophytes without the credibility of long distance dispersal shadowing the discussion.

There are three possible means of dispersal to Macquarie Island by spores and asexual propagules:

> 1. aerial transport,
>
> 2. animal transport, and
>
> 3. ocean current transport.

These possibilities have been substantially reviewed by the above authors, with aerial transport being the most favoured candidate.

REPRODUCTION IN SELECTED SPECIES

Transportation and arrival of a diaspore in a new area does not guarantee successful introduction of a species. It is also necessary for germination and establishment of the spore or sprouting of the asexual propagule to occur, followed by

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a period of growth and some form of local dispersal. Case studies of the reproductive strategies of several species from Macquarie Island were conducted with these ideas in mind.

Features examined included germination success or germination capacity of spores from two years' collection of capsules, possible modes of asexual reproduction and also a variety of conditions which could possibly be encountered during long distance dispersal to Macquarie Island.

Eleven species whose populations are extensive on the island were examined. Amongst these species, a range of habitats from supralittoral to fellfield, were covered. Table 1 summarises information about the species and results of germination trials conducted on Bold's Basal Medium (BBM) (Bold 1967).

The species studied exhibit three reproductive strategies (Table 2).

Species exhibiting strategy 1 have two modes of reproduction, sexual and asexual, available to them for survival. The dioicious Dicranella cardotii is the most aggressive of the species studied, with five different forms of asexual propagation. Similar strategies have been reported by Longton & Schuster (1983) in mosses and hepatics associated with habitats of limited duration.

Species of strategy 2 have never been recorded with sporophytes, and appear to rely entirely on copious gemma production for dispersal and propagation.

How Andreaea mutabilis, A. acuminata and Ditrichum strictum (strategy 3) effectively reproduce is still a mystery. Sporophyte production is abundant in their environmentally extreme fellfield. It may be possible that the low germination capacity of their spores permits the obvious success of these tolerator species only because there is a lack of plant competitors in their habitat.

On Macquarie Island, Muelleriella crassifolia and Ulota phyllantha occur in supralittoral and coastal habitats which are occasionally inundated by the sea and always subjected to wind-blown sea-spray. The former moss produces spores abundantly whereas the latter produces gemmae. The tolerance of their diaspores to saline conditions is therefore of interest.

Table 1. Germination capacity and asexual reproduction in 11 species of moss on Macquarie Island.

Species	Habitat	Means of asexual reproduction	Produces sporophytes on island	Germination capacity *
Amblystegium serpens (m)	T	pg	no	–
Andreaea acuminata (m)	F	none	yes	O (10 capsules)
Andreaea mutabi utabilis (m)	F	none	yes	4 ± 2 (6 capsules)
Bryum argenteum (d)	T,C	b	no	–
Bryum dichotomum (d)	C	b	no	–
Dicranella cardotii (d)	T,W	ag,pg,rg l,s	yes	79± 7 (9 capsules)
Ditrichum strictum (m)	F	none	yes	O (10 capsules)
Muelleriella crassifolia (m)	S,C	l	yes	72± 9 (8 capsules)
Pottia heimii (m)	C	l	yes	high (3 capsules)
Tayloria octoblepharis (m, possibly d**)	T,W,C	l	yes	28+5 (6 capsules) 80±14 (4 capsules)
Ulota phyllantha (d)	S,C	lg	no	–

* mean percent germination ± standard deviation, ** Koponen (1977).
Code: m = monoicous, d = dioicous;
C = coastal, F = fellfield, S = supralittoral, T = tussock grassland, W = water courses;
ag = axillary gemmae, pg = protonemal gemmae, rg = rhizoidal gemmae, lg = leaf gemmae, b = bulbils, s = deciduous stem tips, l = leaf fragments

Table 2. Reproductive strategies of selected mosses on Macquarie Island.

Strategy	Sporophytes produced	Spore germination capacity	Asexual reproduction known	Monoicous* or dioicous	Species studied
1	yes	high	yes	either	Dc, M, P, T
2	no	no fruit	yes	either	U, A, Ba, Bd
3	yes	low	no	monoicous	Ds, Aa, Am

* Sainsburg (1955).
Code: Dc = <u>Dicranella</u> <u>cardotii</u>, M = <u>Muelleriella</u> <u>crassifolia</u>, P = <u>Pottia</u> <u>heimii</u>, T = <u>Tayloria</u> <u>octoblepharis</u>, U = <u>Ulota</u> <u>phyllantha</u>, A = <u>Amblystegium</u> <u>serpens</u>, Ba = <u>Bryum</u> <u>argenteum</u>, Bd = <u>Bryum</u> <u>dichotomum</u>, Ds = <u>Ditrichum</u> <u>strictum</u>, Aa = <u>Andreaea</u> <u>acuminata</u>, Am = <u>Andreaea</u> <u>mutabilis</u>.

The experiments detailed in Table 3 were carried out on freshly-collected spores and gemmae from living plants, either on Macquarie Island or in the laboratory (Sydney) where plants collected from the island were grown at 4°C.

Both spores and gemmae are resistant to prolonged immersion in dilute salt solution and, in fact, germinate in them. These conditions would be analogous to conditions occurring naturally on the island, where the plants are commonly inundated with salt water and regularly by rain. Similar results to those obtained from the seawater experiments were obtained when solutions with appropriate concentrations of NaCl were used.

Spores of <u>Muelleriella</u> <u>crassifolia</u> are tolerant of prolonged exposure to saline conditions. They remained green after immersion in seawater for 6 weeks, although spores did not germinate under experimental conditions after 14 days immersion. The spores will withstand very low temperatures if wet.

Tolerance of propagules to cold and saline conditions would be important in considering the possibility of long distance dispersal of such species to subantarctic islands.

Table 3. Survival of propagules as shown by germination after 14 days.

Treatment	Muelleriella spores	Ulota gemmae
1 seawater	-	-
2 10^{-1} seawater	+	+
3 10^{-2} seawater	+	+
4 10^{-3} seawater	+	+
5 soaked seawater 5 days	+	no further data
6 air dried 45 hours	+	
7 frozen in water 36 hours	+	
8 frozen air-dry 36 hours	-	

Notes: Treatments 1-4: immersion for 14 days; treatments 5-8: after treatment, removed to BBM for 9 days; treatments 7-8: air dried 9 hours after removal from capsule before treatment. Frozen at -30°.

Table 4. Known reproductive modes of 83 moss species on Macquarie Island.

	Mode of asexual propagation known	Number of species			
		Monoicous*	Dioicous*	Both	Sexuality unknown
Species which fruit on the island**	yes	3	6	1	0
	no	11	11	1	3
Total (=36)		14	17	2	3
Species which do not fruit on the island	yes	2	13	1	1
	no	7	19	1	3
Total (=47)		9	32	2	4
Total (=83)		23	49	4	7

* Sainsburg (1955).
** Data from collections by R. D. Seppelt, 1979-1985, and D. M. Bergstrom, 1983-1984.

GENERAL COMMENTS ON BRYOPHYTE REPRODUCTION ON MACQUARIE ISLAND

It is likely that the same strategies shown in Table 4 will be found amongst other moss species on the island. Table 3 summarises what is known of their modes of reproduction. Similarities with other comparable bryophyte floras are apparent: 60% of New Zealand mosses and 56% of Marion Island mosses are dioicous while 51% of Marion Island mosses form sporophytes (van Zanten & Pócs 1981). It is noteworthy that on Macquarie Island, of the taxa known to develop sporophytes, 44% are known to be dioicous (suggesting that at least one male and one female plant had become established on the island). 36% are monoicous (theoretically requiring the establishment of only a single fertile individual). Thus more dioicous taxa have been "effectively" dispersed to Macquarie Island than monoicous taxa, where "effective" refers to Schuster's (1983) establishment of a new reproductive centre.

The converse is true of some other isolated island floras: on Marion Island, 29 (=94%) of sporophyte-forming mosses are monoicous and only 2 (=6%) are dioicous (van Zanten & Pócs 1981); on Signy Island, in the maritime Antarctic, 13 (=7%) are monoicous (Webb 1973).

While Table 4 summarises what is known of modes of reproduction amongst Macquarie Island moss taxa, it also reveals interesting gaps in our understanding. Why, for instance, have 9 monoicous species not been found with sporophytes? It is unlikely that plants producing sporophytes regularly and reasonably prolifically have been overlooked in the field, as extensive collections have been made at the appropriate season over six years (Seppelt et al., this volume). It seems likely that some environmental condition or conditions prevent or limit sporophyte production in these monoicous species, as has been suggested for <u>Amblystegium</u> <u>serpens</u> (Selkirk 1981). For the 32 dioicous species not known to produce sporophytes, inadequate collection, environmental limitation of some stage in the reproductive cycle or the presence of only one sex on the island remain possibilities awaiting investigation.

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IMPLICATIONS FOR LONG-DISTANCE DISPERSAL

It is interesting to speculate on the means by which spe-
cies arrived on the island. Of the three possible modes of long
distance dispersal mentioned above, aerial transport has been
most favourably regarded by reviewers. Van Zanten & Pócs (1981)
estimate the maximum spore diameter compatible with aerial
transport over long distances to be 25 µm; Crum (1972) cal-
culated that spores of 8-12 µm could be transported 18,200 km.
Forty-nine (82%) of 60 moss species for which spore measure-
ments were available have spores below the 25 µm limit pre-
dicted for long distance dispersal. For these, aerial dispersal
of spores seems a likely means of arrival on the island.

Each of the 11 species whose spores are of greater dia-
meter than 25 µm (Table 5) has an extensive range, and 9 of
the 11 produce sporophytes on the island. Three of the species,
Dicranella cardotii, Pottia heimii and Muelleriella crassifo-
lia were the species described in strategy 1 and are very
successful. It is possible that the strong winds over the
Southern Ocean are able to transport these relatively large
spores and that Schuster's (1983) suggestion that "large
durable spores" could be "just as dispersable as small ones"
may apply here. The results of the experiments outlined in
Table 3 showed that spores of M. crassifolia were able to
germinate after treatments of air-drying and wet-freezing at
-30°C. Such conditions are reported to be similar to those
encountered in airstreams at low altitudes and in wet air-
streams at high altitudes (van Zanten 1976).

Van Zanten & Pócs (1981) were of the opinion that the
spores of M. crassifolia were too large for long distance
aerial dispersal and remarked that birds and ocean currents
as dispersal mechanisms were untested possibilities. Our re-
sults do not eliminate ocean currents.

We have no data that fully substantiate long distance
dispersal by birds. If spores of Muelleriella crassifolia
became attached to feet of feathers, our results suggest that
the spores could survive short-term immersion in seawater
should a bird alight at sea. Macquarie Island is visited by,

Table 5. Mosses from Macquarie Island with spore size greater than 25 μm.

Species	Size range (μm)*	Sporophyte production	Vegetative reproduction	Distribution
Ditrichum strictum	25-45	+		SH
Dicranella cardotii	20-30	+	+	A,NZ
Trematodon flexipes	25-32	+		A,NZ AI
Pottia heimii	29-34	+	+	C
Macromitrium longirostre	20-40	+		Sub
Muelleriella crassifolia	40-80	+	+	Sub
Entosthodon subattennuatus	30-33	+		SH
Bartramia papillata	∼26	+		SH
Philonotis scabrifolia	24-32			SH
Eurhynchium praelongum	11-33			C
Andreaea acuminata	24-41	+		A,Sub

* Sainsbury (1955)

Distribution code: A = Australia, AI = Auckland Island, C = cosmopolitan, NZ = New Zealand, Sub = circum-subantarctic, SH = Southern Hemisphere.

and is a nesting site for, thousands of migratory sea birds and, furthermore, there are many records of vagrant land birds such as ducks, starlings, hawks, egrets and others reaching the island (Warham 1969). Most of these must reach the island in a single flight.

If large spores are dispersable, it is also possible that large asexual propagules may be carried over long distances.

They are certainly wind-dispersed locally on the island. Gemmae of <u>Ulota</u> <u>phyllantha</u>, which grows in the supralittoral zone on Macquarie Island, have been trapped from the air at a fellfield site more than 200 m above sea level (Selkirk 1984).

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ECOLOGY OF THE MOSS VEGETATION IN THE SYOWA STATION AREA, ENDERBY LAND, ANTARCTICA

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The moss vegetation in the Syowa station area, Enderby Land, continental Antarctica, was observed in relation to some ecological aspects during 1982-1984. Seven moss sociations were recognized at the outcrops on the Soya Coast. Some colonies of Bryum spec. were found with sporophytes. Furthermore, life history characteristics and ecology of six species are described.

1. INTRODUCTION

An ecological study of mosses around the Syowa Station area, Enderby Land, continental Antarctica (lat. 69°00'S, long. 39°35'E) was initiated in the summer of 1964-1965 (Matsuda 1963, 1968). Subsequent investigators have further studied moss distribution and made a phytosociological classification of the vegetation, describing ang grouping their habitats (Shimizu 1977, Nakanishi 1977, Kanda 1981a).

The author studied the vegetation in the Syowa Station area during 1982-1984 with special reference to the life history characteristics of six moss species distributed throughout this area.

2. MATERIAL AND METHODS

The six species of moss known in the Syowa Station area are Bryum argenteum, B. pseudotriquetrum, Ceratodon purpureus,

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<u>Pottia</u> <u>heimii</u>, <u>P</u>. <u>austro-georgica</u>, and <u>Grimmia</u> <u>lawiana</u>. Based
upon the herbarium specimens collected during the past 20
years, and housed in the National Institute of Polar Research
(NIPR), the distribution of these mosses has been mapped (Fig.
1). The vegetation of some ice-free sites, namely Rundvågshetta,
Strandnibba and Einstöingen was studied applying Braun Blaun-
quet's (1964) phytosociological methods.
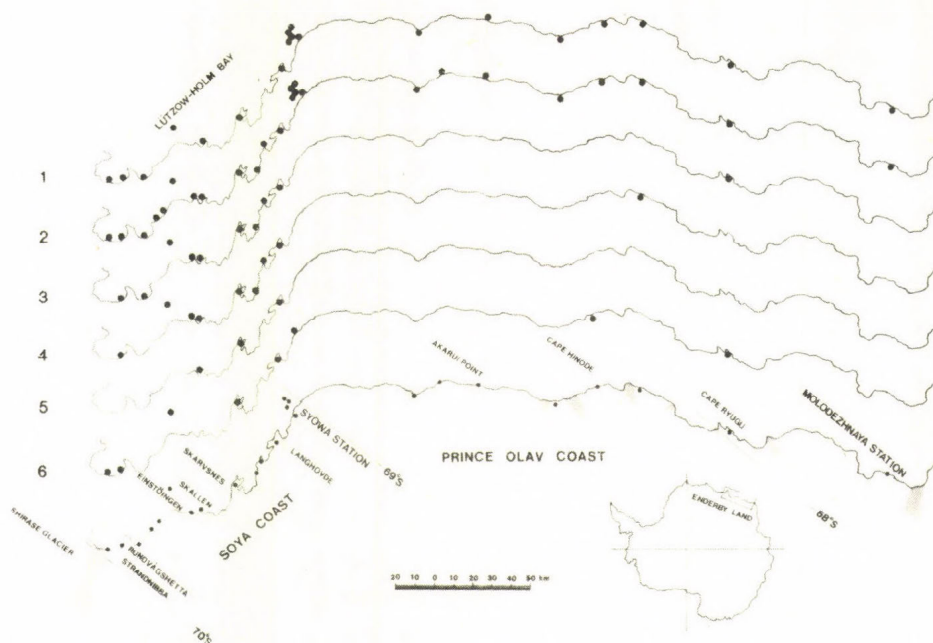
Fig. 1. Distribution of mosses on Soya Coast and Prince Olav
Coast, Enderby Land. 1. <u>Ceratodon</u> purpureus, 2. <u>Bryum</u> pseudo-
triquetrum, 3. <u>Bryum</u> argenteum, 4. <u>Pottia</u> heimii, 5. <u>Pottia</u>
austro-georgica, 6. <u>Grimmia</u> lawiana.

3. RESULTS AND DISCUSSION

3.1 Phytogeography and ecology of the bryoflora

a. Distributional pattern of mosses in Enderby Land

The distribution of mosses on the Soya Coast and the Prince Olav Coast, Enderby Land, has been studied by Naka-nishi (1977) and Kanda (1981a). The Prince Olav Coast has re-latively small ice-free areas trending in a west to east di-rection. On the Soya Coast, which runs north to south in Lüt-zow-Holm Bay, the ice-free areas are strongly affected by maritime factors, namely nesting colonies of sea birds and their rich nutrient input, or air-borne salt spray carried in-land by the prevailing wind from the sea. In general, Bryum pseudotriquetrum and Ceratodon purpureus are distributed on both coasts. Bryum argenteum and Pottia heimii appear to be restricted to the Soya Coast, whereas Grimmia lawiana is dis-tributed principally in sites adjacent to the continental ice sheet of both coasts. Although Pottia austro-georgica has not been recorded on the Prince Olav Coast, it is known in Amunzen Bay farther east. The influence of the sea or the continental ice sheet is also related to topographic and geological as-pects, and this has a direct or indirect effect on the charac-teristics of the vegetation.

b. Distribution of moss communities in Einstöingen, Strand-nibba and Rundvågshetta

On individual outcrops in the ice-free areas along both coasts there are distinct trends in the relationship between species and the localities. Most of the regions in Soya Coast such as Rundvågshetta, Strandnibba, Einstöingen, Skallen, Skarvsnes and Langhovde have abundant moss vegetation, though the species composition is different between sites compared with that of the Prince Olav Coast.

Einstöingen: This is a small island about 0.5 km long about 15 km from the continental ice-free areas. In general, other nearby small isolated islands like Ongulkalven, Mame-zima and

Rumpa have very sparse moss vegetation comprising only one or two species. In contrast, Einstöingen has five moss species distributed in relatively extensive stands. The abundance of vegetation on this island is probably related to increased water availability and the many ponds scattered there, high nutrient status provided by colonies of breeding snow petrels, and the calcareous substratum. The moss community is composed of five sociations characterized in particular by the Bryum argenteum sociation and the B. pseudotriquetrum-Pottia heimii sociation.

Strandnibba: This coastal area is located at the east side of the Shirase Glacier, the largest in Enderby Land. Owing to numerous steep cliffs, this outcrop is characterized by many swift streams and waterfalls. Grimmia lawiana always occurs close to the continental ice sheet. Colonies of this species are also distributed along stream margins, often growing on the submerged rocks at higher elevations. Bryum pseudotriquetrum grows around ponds and long stream sides at lower elevations or near the sea shore. In contrast, Ceratodon purpureus always grows on drier sandy soil near the sea shore. The moss community is composed of five sociations but dominated by the Grimmia lawiana sociation.

Rundvågshetta: Pottia heimii occurs as small colonies on patterned ground with silty substrata on the moraines. Bryum pseudotriquetrum and Ceratodon purpureus are distributed throughout the area, with the most extensive stands beside streams near the sea shore. Pure colonies of Grimmia lawiana also occur on the rock covered partly by mineral-rich sandy soil extending in a south-west direction over a broad area about 1 km wide. This moss community is composed of seven sociations characterized by the Grimmia lawiana sociation, the Bryum pseudotriquetrum-B. argenteum sociation, the B. pseudotriquetrum-Pottia heimi sociation and the Pottia heimii sociation.

3.2 Occurrence of fertile Bryaceous mosses

In the stream sites of Rundvågshetta, Strandnibba, Ein-
stöingen and Langhovde, fruiting colonies of moss were recorded
for the first time in the Syowa Station area. Filson & Willis
(1975) reported fruiting specimens of Bryum algens from Fold
Island, Kemp Land. Their description and illustrations are
similar to the specimen collected in the Syowa Station area,
especially as regards the arrangement of the peristome teeth,
the inner part being in contact with the outer. Rastorfer
(1971) had previously succeeded in producing sporophytes in
artificial culture of a moss, from the McMurdo region, which
he determined as Bryum antarcticum (= Pottia heimii, sensu
Kanda 1981b). However, Rastorfer's specimen clearly belonged
to the genus Bryum according to his description and photo-
graphs.

The fruiting specimens collected from the Syowa Station
area are referred to Bryum pseudotriquetrum. The sporophytic
characters, however, are different from those of B. pseudo-
triquetrum from the Northern Hemisphere. It is also necessary
to investigate the variation of sporophyte characters of plants
grown in the severe environment of continental Antarctica.

Fruiting material of this species often occurs on wet soil
at the foot of cliffs or beneath the edge of boulders on the
banks of streams. Water content, soil temperature, substrate
type and nutrient availability are considered to be important
factors for the development of fruiting plants. Although most
spores from the specimens collected were not fully mature,
it is considered possible that they do mature and germinate
under field conditions, and that the germinated protonema or
young shoots will develop and grow during late summer and
autumn.

The occurrence of sporophytes on Bryum antarcticum was
reported by Nakanishi (1977); the species was synonymized to
Pottia heimii by Kanda (1981b) based upon some sporophytic
characters. In addition, the author found young sporophytes
of Pottia austro-georgica in the Amunzen Bay, which is about
500 km east of the Syowa Station. This species has an extremely

discontinuous distribution, being known from the Antarctic
Peninsula including its neighboring islands, Syowa Station
area and Amunzen Bay. Colonies fruit abundantly in January
and February on South Georgia, South Orkney and South Shetland
Islands. Thus the presence of sporophytes in Bryum pseudo-
triquetrum, Pottia heimii and P. austro-georgica is note-
worthy in the discussion on the life history of continental
Antarctic mosses.

3.3 Ecology of the six moss species in the Syowa Station area

Bryum argenteum: This species is found in small patches,
5-20 cm in diameter, and usually on soils near snow petrel
nest sites. The colonies are often overgrown with epiphytic
lichens. This moss is quite rare in the Syowa Station area,
but occurs frequently throughout continental Antarctica. Its
local occurrence is probably dependent no so much upon water
supply from melting snow or streams, but more by nitrogen en-
richment by birds. The species is dioicous and fruiting plants
are unknown in Antarctica. In Antarctica it has often been
confused morphologically with B. pseudotriquetrum. Leaves on
the upper portion of the stems of B. pseudotriquetrum are
often so damaged by strong winds or epiphytic organisms that
they resemble leaves of B. argenteum. Horikawa & Ando (1961)
referred such specimens to B. argenteum. However, the chro-
mosome number is a useful key to the identity of the two spe-
cies: B. pseudotriquetrum is n=20, whereas B. argenteum is
n=10 (Ochi 1979).

Bryum pseudotriquetrum: This plant, together with Ceratodon
purpureus, has the broadest distribution in the Syowa Station
area. These species often exist together. However, B. pseudo-
triquetrum prefers a rather moister substratum than the latter
and grows along the margins of relatively large streams. In
vertical cross sections of tufts or turves, B. pseudotriquetrum
exhibits hotizontal bands formed by aggregations of rhizoids
or innovation of stems (Matsuda 1968). This layering appears
to represent the period of annual growth and the growth in-

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vestment seems to be greatest in plants growing in the wetter sites by streams.

Asexual reproduction appears to be common in this species. On the surface of moss colonies usually lots of bud-like fragments of 0.1-1.0 mm long are present which have become detached from the upper portions of stems. These fragments are disseminated locally by the wind and are important for the establishment of moss colonies at the other sites. Rudolph (1970) considered the role of bud-like fragments, which he trapped on sticky slides in the field, as one form of local dissemination. Furthermore, the present author found tubers borne on the rhizoids of aquatic B. pseudotriquetrum. This plant is very similar to B. korotkevicziae described by Savicz-Lyubitskaya & Smirnova (1959). Recently, Seppelt (1983) noted that aquatic plants collected from Vesfold Hills should be B. algens and he reduced B. korotkevicziae to synonymy with B. algens. However, such tubers on aquatic specimens of B. pseudotriquetrum have not been reported previously.

Ceratodon purpureus: This plant prefers rather dry soil along banks of streams. When the surface of the turf dries out it becomes cracked. This appears not to damage the turves, and it is considered to be indicative of high tolerance of desiccation in this species. Occasionally, propagula such as brood bodies or gemmae are present in specimens from temperate regions. The present author observed gemmae on upper portions of the protonema borne from stems of C. purpureus growing along the banks of a melt-water stream running from snow drifts. The plants growing on the dry sites had more abundant gemmae than those on moist sites. Zander & Ireland (1979) suggested that the presence of propagula on plants growing in riparian habitats pointed to the possibility of some degree of ecotypic differentiation in this species. Thus the characteristics of the propagula may vary according to different moisture regimes.

Pottia heimii and P. austro-georgica: These two species are known in the coastal regions of Lützow-Holm Bay, Prince

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Olav Coast (Kanda 1981a). They always grow on sandy soils mixed with fossil shellfish, or on silty soil deposited by streams or glaciers. The two species usually occupy different habitats though they often exist together near the sea shore. P. heimii grows in extensive stands, up to 10 m^2, and is often fruiting along banks of drainage lines running from ponds. P. austro-georgica usually forms small colonies of 5-20 cm in diameter. In the maritime Antarctic, both species are distributed from South Georgia to the southern Antarctic Peninsula where they occupy similar habitats to those in the Syowa Station area.

Grimmia lawiana: This plant occurs beside swift flowing streams running from the continental glacier, and on moraines and areas of patterned ground. It is most abundant in the ice-free area of Strandnibba, adjacent to the Shirase Glacier. It does not grow in areas entiched by sea birds or marine salts deposited by wind; however, it appears to prefer nutrient deficient soils at higher altitude, where there is no marine or biotic influence. At Rundvågshetta, G. lawiana grows along streams containing minerals derived from various rocks, conditions which do not occur near the sea shore.

The composition of the bryophyte flora and their distribution patterns throughout Enderby Land are influenced by global geographic aspects. Similarly their distribution within individual sites is affected by environmental factors such as water and nutrients supply, nature of substratum, wind direction, temperature and topography. The moss vegetation also possesses various modes of sexual and asexual reproduction which are important in their life history for establishment, development and dissemination of their colonies around continental Antarctica.

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REPRODUCTIVE PROCESSES OF BRYOPHYTES IN AN URBAN ENVIRONMENT

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After removal of the bryophyte layer in experimental plots in different bryophyte communities at the university campus, in most cases the same community re-established itself in 1-2 years. Generally, thalloid hepatics and pleurocarpic mosses regenerated faster than acrocarpic mosses. Regrowth mainly took place in spring and autumn. Test tubes with glycerin were placed at the stands to trap airborne diaspores. Bryophyte diaspores were caught in much smaller amounts than phanerogamic pollen grains. Still, it is suggested that such airborne diaspores are effective in the process of recovery of the bryophyte communities. Seasonal variation in the amount of airborne diaspores was small, except for the Reboulia hemisphaerica stand, where a peak was observed at the time of spore release of R. hemisphaerica and Barbula unguiculata.

INTRODUCTION

Bryophytes, spreading by means of sexual as well as asexual reproduction, are widely distributed in various environments in the world. Especially asexual vegetative reproduction is an important means of multiplication for most bryophytes (Anderson 1963, Longton 1976, Longton & Schuster 1983). In polar regions, Miller & Ambrose (1976) and Selkirk (1984) studied windblown bryophyte fragments retrieved from snowdrifts and found a proportion to be viable. But very little is known about how diaspores are dispersed and established on land.

The present paper deals with dispersal dynamics of the bryophyte disseminules in reference to regrowth of the vegetation.

STUDY SITES AND METHODS

To investigate the reproductive processes in bryophytes, eleven stands of eight bryophyte communities were chosen at sites on the University campus as an urban environment during two years from July, 1982, to June, 1984 (Table 1).

Field

To know the regeneration of bryophyte communities, five quadrats of 10x10 cm^2 (only in <u>Bryum</u> <u>argenteum</u> comm. 3x33 cm^2) in each stand were made bare by stripping the aboveground bryophyte vegetation in 1982 on June 28, September 22, December 24, and in 1983 on March 15 and June 18. Abundance of the recovery of the species was estimated using a phytosociological method in each bare quadrat. Species composition of bryophytes and phanerogamous plants was also recorded.

Sampling

Airborne diaspores (spores, vegetative propagules, gemmae, stem and leaf fragments, etc.) were collected at each stand in the field using 3 cm diameter test tubes of 20 cm length. Each test tube contained about 10 ml glycerin. The airborne diaspores trapped were centrifuged and treated with an acetolysis method, as used in pollen analysis. Most airborne diaspores are too simple in structure to permit identification of the species, but it was possible to guess their identity from the surrounding bryophyte vegetation.

RESULTS AND DISCUSSION

In one year, recovery rates in the <u>Marchantia</u> <u>polymorpha</u> comm. are 98% and 84%. In the <u>Hypnum</u> <u>plumaeforme</u> comm. under trees and the <u>Atrichum</u> <u>undulatum</u> comm. under trees these are

Table 1. Representative data for the vegetation recovery at stripped bare lands of bryophyte communities.

Habitat	Vegetation	Place	Growth[1]	Growing season	Change of vegetation[2] '82 '83 '84		
dry sunny disturbed ↑	Bryum argenteum comm.	on roof	+	spring	BA → BA → BA		
	Brachymenium exile comm.	on roof	+	spring	BE → BE → BE		
	Barbula unguiculata comm.	in courtyard	++	spring	BU → BU → BU		
	Reboulia hemisphaerica comm.	in courtyard	++	spring / autumn	RH → RH → RH		
	Marchantia polymorpha comm. (male)	in courtyard	+++	spring / autumn	MP → MP → MP		
	Marchantia polymorpha comm. (female)	in courtyard	+++	spring / autumn	MP → MP → weeds		
	Haplocladium angustifolium comm.	in courtyard	+++	spring / autumn	HA → HA → grasses		
	Haplocladium angustifolium comm.	under tree	+++	spring / autumn	HA → HA → HA		
	Hypnum plumaeforme comm.	under tree	+++	spring / autumn	HP → HP → HP		
	Atrichum undulatum comm.	in courtyard	++	spring	AU → AU → AU		
wet shady natural ↓	Atrichum undulatum comm.	under tree	+++	spring / autumn	AU → AU → AU		

1) +: fair, ++: good, +++: very good

2) BA: Bryum argenteum comm., BE: Brachymenium exile comm., BU: Barbula unguiculata comm.,
   RH: Reboulia hemisphaerica comm., MP: Marchantia polymorpha comm., HA: Haplocladium angustifolium comm.,
   HP: Hypnum plumaeforme comm., AU: Atrichum undulatum comm.

93% and 95%, respectively. These communities have high recovery
rates. The Barbula unguiculata comm. (27%) show a comparatively
delayed development. In the Reboulia hemisphaerica comm., the
recovery rate is about 45% (Fig. 1). The Haplocladium angusti-
folium communities show 98% in a courtyard and 61% under trees.
The Bryum argenteum community on roof shows 64%. In the re-
growth of bryophyte communities, thalloid hepatics and pleuro-
carpous mosses generally do better than acrocarpous mosses.
At all stands, there seem to be two growing seasons in spring
and autumn after the rainy period. The results of growth and
the growing season are represented in Table 1.

Concerning the species composition in most bryophyte com-
munities, after one year the bared plots show almost the same
composition as the original (beginning) one before the above-
ground vegetation was stripped (Table 1). But in two years, the
Marchantia polymorpha comm. has changed into a weed vegeta-
tion. Probably an environmental change had occurred, such as
from wet to dry condition, or it was strongly disturbed by
human impact.

In the test tubes, airborne diaspores of bryophytes were
caught with many pollen grains (Fig. 2). In general, pollen
grains are very abundant, while bryophyte spores are less so,
but in the Reboulia hemisphaerica stand, spores were very
abundant with a peak in the time of spore dispersal from
spring to early summer (Fig. 3). For phanerogamous pollens, it
is clear that two dispersal seasons of spring and autumn
occur. They seem to be mostly of Pinus densiflora, Cryptomeria
japonica, Cedrus deodara and some Gramineae. In the Haplo-
cladium angustifolium comm. under a Liquidambar tree many
pollen grains of Liquidambar are found. In the Hypnum plumae-
forme comm. under an olive tree, pollens of this tree were
also abundant.

As mentioned above, airborne spores were found in much
lower quantities than airborne pollen. Although poor in quan-
tity, the bryophyte disseminules appear to be very effective
for the recovery of the bryophyte vegetation (Fig. 4).
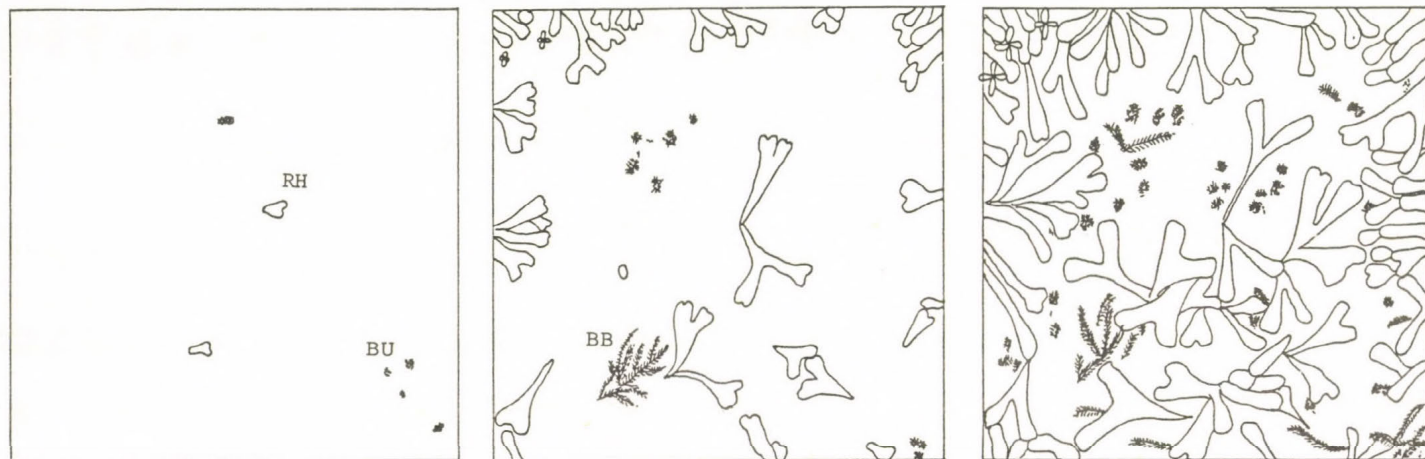
Fig. 1. Regrowth process of a <u>Reboulia</u> <u>hemisphaerica</u> community at a bare quadrat of 10x10 cm^2. Left: one month later (July 30, 1982), 1% cover; middle: 6 months (December 24, 1982), 13%; Right: 12 months (June 6, 1983), 45%. RH: <u>Reboulia</u> <u>hemisphaerica</u>, BU: <u>Barbula</u> <u>unguiculata</u>, BB: <u>Brachythecium</u> <u>buchananii</u>.
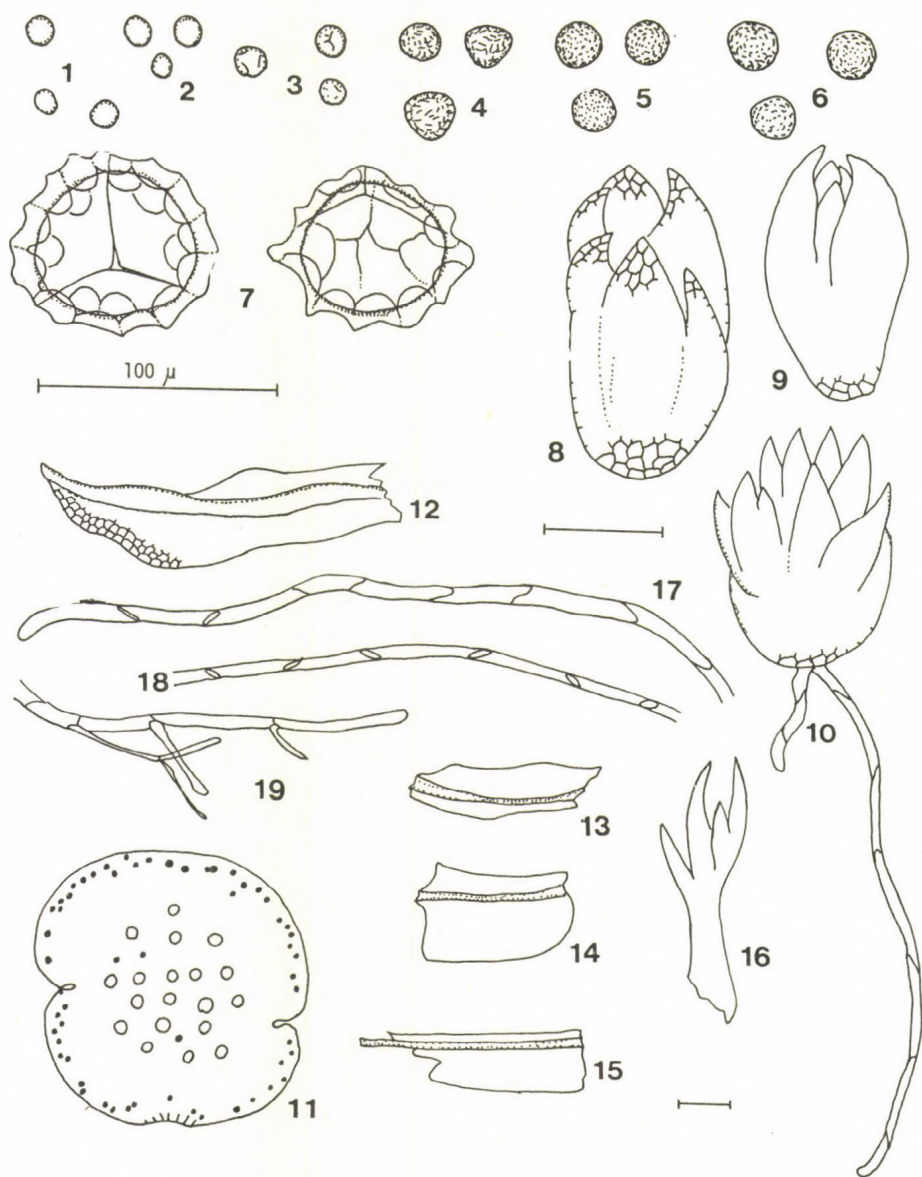
Fig. 2. Airborne diaspores trapped at the sites. 1-5: Moss spores (<u>Barbula</u> <u>unguiculata</u>, <u>Bryum</u> <u>argenteum</u>, <u>Haplocladium</u> <u>an-gustifolium</u>, <u>Rhynchostegium</u> <u>pallidifolium</u>, <u>Atrichum</u> <u>undulatum</u>), 6: <u>Marchantia</u> <u>polymorpha</u> spores, 7: <u>Reboulia</u> <u>hemisphaerica</u> spores. 8-10; Moss propagules, 11: <u>Marchantia</u> <u>polymorpha</u> gemma, 12-15: Moss leaves, 16: Apical part of a moss stem, 17-19: Moss rhizoids.
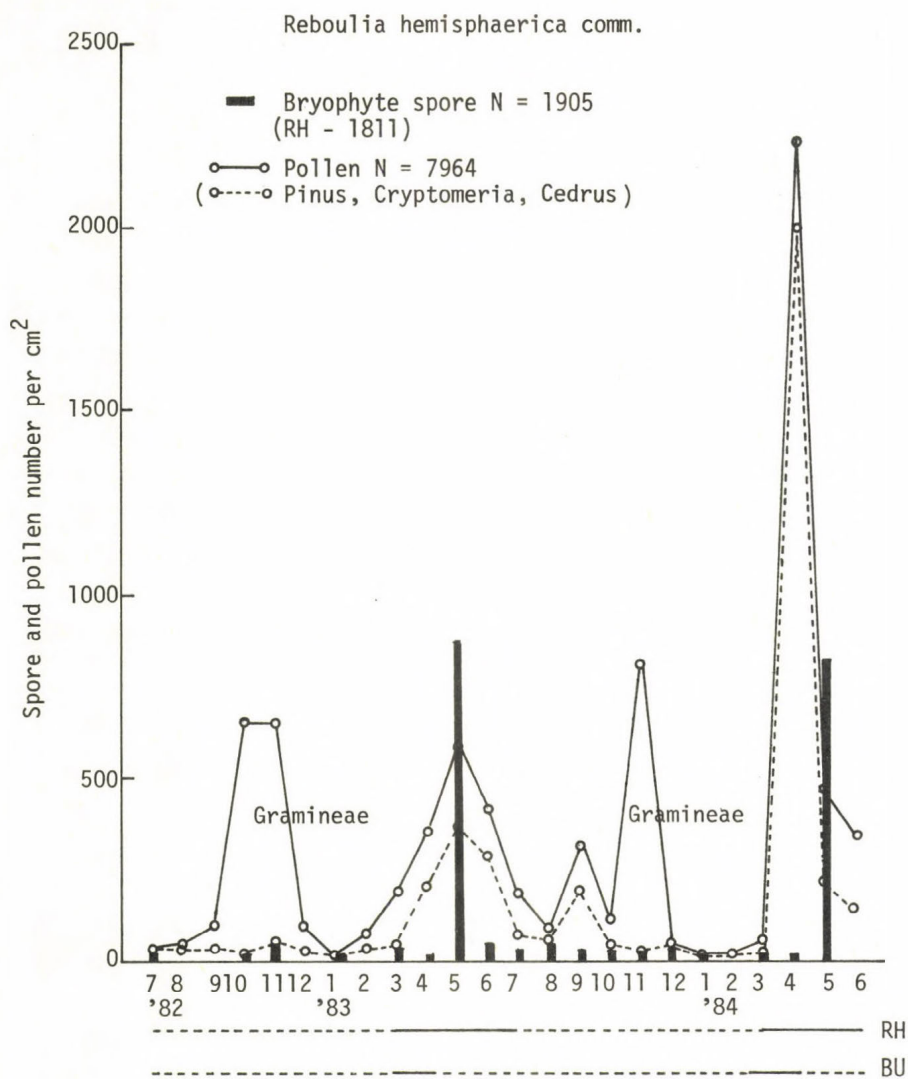
Fig. 3. Monthly fluctuation of airborne spores and pollen at the Reboulia hemisphaerica comm. during two years. Full lines in the bottom show the time of sporophyte maturation in Reboulia hemisphaerica (RH) and Barbula unguiculata (BU).

Seasonal variation in airborne bryophyte diaspores is very
low except for the Reboulia hemisphaerica community and the
Marchantia polymorpha community. In the former, there is a
peak after the sporophyte maturation stage and in the
dispersal season. In the latter, the gemmae are more effective
for the recovery of the Marchantia polymorpha vegetation.
The Marchantia polymorpha gemmae are mostly found in spring
(Table 2). In the female population of Marchantia polymorpha,
phanerogamous plant seeds are very abundant. This seems to be
related to a changeable environment. As in the Marchantia
polymorpha community, in the Haplocladium angustifolium com-
munity also many seeds, mostly of Gramineae were found. This
agrees with the observation that the bryophyte community has
changed into the grass one in two years. Both Bryum argenteum
and Brachymenium exile usually have many bud-like axillary
propagules on their stems. But in the present study these
are not found as airborne diaspores. They may occur as sur-
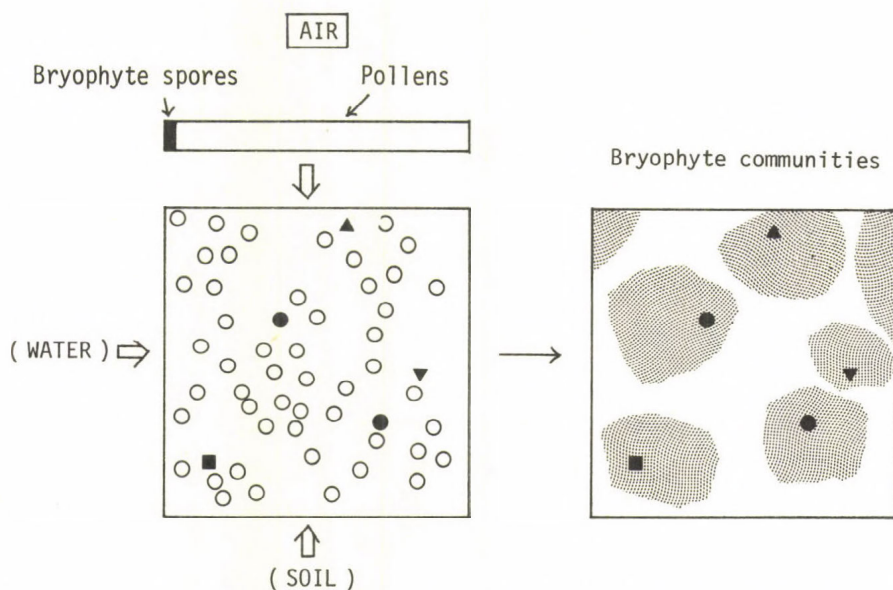
Fig. 4. Schematic diagram showing that diaspores are very ef-
fective for the recovery of a bryophyte community. (●: spore,
■ : gemma or propagule, ▲: leaf or stem fragment, ▼: rhizoid,
o: pollen).

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Table 2. Airborne diaspores in bryophyte communities.

Bryophyte vegetation	Airborne diaspores of bryophytes						Phanerogamous plants	
		Vegetative reproduction per tube.yr⁻						
	Spores per cm^2.yr⁻	Pro.[1]	Gemmae[2]	Leaf and stem fragments		Sporophyte fragments	Pollen per cm^2.yr⁻	Seeds per tube.yr⁻
				Ac.[3]	Pl.[4]			
Bryum argenteum comm.	9	0	0	0	0	0	897	0
Brachymenium exile comm.	9	0	0	0	0	0	355	0
Barbula unguiculata comm.	112	2	0	29	4	0	3675	11
Reboulia hemisphaerica comm.	952	2	0	12	1	0	3982	11
Marchantia polymorpha comm.	30	0	245	3	1	0	3727	25
Marchantia polymorpha comm.	43	0	53	2	2	0	2885	12
Haplocladium angustifolium comm.	117	0	0	2	32	2	4905	95
Haplocladium angustifolium comm.	68	0	0	7	36	2	5870	203
Hypnum plumaeforme comm.	101	0	0	0	1	0	6437	9
Atrichum undulatum comm.	41	0	0	0	0	0	1764	4
Atrichum undulatum comm.	162	0	0	0	2	2	3777	8

1) Pro.: propagules of Bryum argenteum or Brachymenium exile
2) Marchantia polymorpha gemmae
3) Ac.: acrocarpous mosses
4) Pl.: pleurocarpous mosses

face disseminules in soil. Concerning the diaspore bank in the soil, there seems to be little information except for a study in chalk grassland (During & Horst 1983). In studies of the reproduction of bryophytes, this should be investigated in the future.

In bryophytes, it is a very important problem how diaspores get detached from the parent plant, disperse and transfer. There seems to be two ways of dispersal in bryophytes. One is dissemination by wind (airborne), as in the present work, the other is by water (waterborne). In the latter case, through rain water diaspores may be dispersed over a half-long distance, because they can float and drift over land by the water. Therefore, in the present experiment with the trapping technique, bryophyte propagules might also have got into the tubes with splash water, Finally, one has to check whether the diaspores are viable or not in the field.

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SPECIES DISTRIBUTION WITHIN A MOSS BED IN GREATER ANTARCTICA

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On Bailey Peninsula, near Casey Station in Greater Antarctica, bryophytes most commonly grow in crevices between rocks but extensive moss beds occur in a few favourable sites. Species composition and soil moisture levels were examined along a line transect across a moss bed. It appears that dispersal to and within the site has influenced the pattern of distribution of the 3 species present, whereas their growth-form is determined by the moisture regime of the substratum.

INTRODUCTION

In continental Antarctica, vegetation occurs on various ice-free areas or oases around the coast. One such oasis, the Windmill Islands area of Wilkes Land, consists of five small peninsulas and a large number of small islands which become free of snow and ice-cover to varying extents during the summer.

The three peninsulas (Clark, Bailey, Mitchelll) to the west of the Løken Moraines have a generally undulating topography. Amongst this glacial debris are some depressions containing lakes which melt, or partly melt, in summer. Snow melt generates some run-off which flows as melt streams along drainage lines into lakes, and out of lakes as temporary overflow streams.

The known flora of the area comprises four species of bryophytes (<u>Bryum</u> <u>pseudotriquetrum</u>, <u>Ceratodon</u> <u>purpureus</u>, <u>Grimmia</u> <u>antarctica</u> and <u>Cephaloziella</u> <u>exiliflora</u>), approximately 25 species of lichens and an unknown number of algal species.

Bryophytes grow in small colonies in sheltered situations among rocks on some slopes and ridges, but in more extensive stands, or moss beds, in some of the moister depressions. One such moss bed, on the Bailey Peninsula near Casey Station (66°17' S, 110°32'E) was investigated for species composition, for species distribution within the bed and for factors which might affect this distribution. This study was conducted during the southern summer from December 1982 to January 1983.

SITE AND METHODS

The moss bed, approximately 80 x 30 m, is on a gently sloping north-facing site. A drainage line, along which water flowed very gently after a heavy snowfall, ran across the bed.

At six points along an 80 m long, east-west transect, 5 replicate core samples of moss and underlying gravel were collected using a 1 cm diameter, 9 cm long metal tube. Samples were placed immediately in plastic vials. In the laboratory, on the day of collection, species in each core were identified and the moisture content of each sample determined by a gravimetric method.

The samples consisted of moss turf plus underlying fine mineral soil and gravel. Heterogeneity was thus introduced, as the deeper the moss turf the smaller the amount of underlying gravel in the core. An attempt was made to measure depth of the moss turf from the cores but compression in length during sampling made this unreliable.

Since it was assumed that the moisture content of the moss turf and that of its underlying gravel would vary according to the stage of melting of the residual snowbanks and the degree of melt on recent snowfalls, soil moisture was determined three times during the summer (14/12/1982, 25/12/1982, 9/01/1983).

On 12/12/1982 there was a heavy snowfall overnight, cover-
ing the moss bed completely. Melting occurred rapidly, but by
14/12/1982 about 30% of the area was still snow-covered with
some meltwater lying in hollows between rocks. The snow cover
from 31-52 m along the transect prevented samples being
collected from that segment. On 24/12/1982, there was another
snowfall, resulting in residual snow and meltwater lying on
or gently flowing across the bed. There was neither snow
nor water on the moss bed at the time of the final sampling.

RESULTS AND OBSERVATIONS

The moisture content of samples from a particular position
along the transect was consistent between successive samplings
(Table 1), irrespective of the recent precipitation pattern.
Moisture content of the samples can be taken as an indicator
of moisture available to plants at the site.

In the low-lying area adjacent to the drainage line across
the moss bed, where the moisture content was consistently high-
er than in the other areas, a lush mixture of Grimmia antarcti-
ca and Bryum pseudotriquetrum occurred (Fig. 1). To the west-
ern end of the moss bed, on an elevated, terraced area with
consistently low moisture content, brown Ceratodon purpureus
predominated. At one site (58.1 m from western end of tran-
sect line) some short, brownish Bryum pseudotriquetrum was
intermixed with Ceratodon. The gently sloping western end of
the transect was generally moister than the terraced eastern
end, but without the pools of meltwater which occurred on
several occasions in the lowest areas of the moss bed. At
this western end, turfs of green Ceratodon purpureus occupied
spaces between large rocks and the bare gravel of frost boils.

DISCUSSION

In any desert area, water availability is important in
plant distribution. In Antarctica, available free (melted)
water, together with a suitable substrate, are essential for

Table 1. Species composition and moisture content along transect.

Distance along transect (m)	East					West
	7.3	22.0	28.8	53.7	58.1	63.6
Moss species present	C	G,B	G,B	C	C,B	C
Moisture 14/12/1982 (g H_2O/g d. wt.)	3.1 (2.2)	7.3 (2.4)	6.5 (1.1)	0.2 (0.1)	1.7 (0.6)	0.4 (0.1)
Moisture 25/12/1982	3.4 (2.1)	8.8 (2.9)	6.1 (2.6)	0.6 (0.2)	2.2 (0.8)	0.5 (0.2)
Moisture 9/1/1983	2.5 (0.9)	9.0 (1.5)	6.7 (0.8)	0.2 (0.0)	1.2 (0.4)	0.3 (0.2)

Moisture data are mean of 5 samples; values in brackets are standard deviations of the means. Code: C = Ceratodon purpureus, G = Grimmia antarctica, B = Bryum pseudotriquetrum.
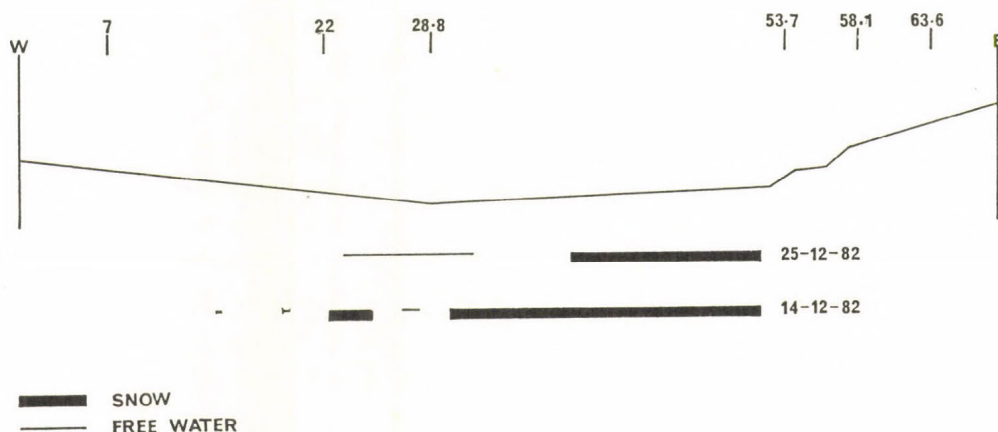
Fig. 1. Profile of 80 m transect across moss bed. Distances of sampling sites shown in m from W end of transect. Drainage line crosses transect at lowest point of profile, 29 m. Snow cover and free water indicated for dates shown.

bryophyte growth. Within the area studied, the level of available moisture clearly influences the distribution of species within the community, with Grimmia antarctica and Bryum pseudotriquetrum occupying the very moist sites adjacent to the drainage line and Ceratodon purpureus dominating the remaining drier areas. This suggests that Grimmia and Bryum prefer or require a higher moisture content for growth than does Ceratodon. However, an examination of the surrounding area upstream in the drainage line indicates otherwise. There, Bryum pseudotriquetrum occasionally grows in quite exposed situations. Although the moisture content of these areas was not measured, it is probably similar to that of the eastern terraced end of the moss bed transect, where Bryum pseudotriquetrum grows in small quantities (58.1 m position).

Perhaps the abundance, at least of Bryum, along the drainage line and in periodically flooded low-lying areas is a reflection of the readily dispersed abundant vegetative propagules (deciduous shoot tips and axillary shoots) downslope via water and their concentration in low-lying areas. In Grimmia and Ceratodon, isolated leaves and stem fragments serve as vegetative propagules (Selkirk 1984). These leaf and stem fragments are certainly blown around by wind and probably are most commonly dislodged from the plant by wind and ice abrasion rather than by water, making their dispersal independent of flowing meltwater. Bryum propagules are also wind-dispersed to a variety of exposed sites, but on this particular moss bed they may be concentrated by water in low-lying areas.

Moisture availability certainly affects the growth form and appearance of the 3 species in this community. So great is the difference in appearance between plants of Bryum pseudotriquetrum from dry and moist sites that the two growth forms were initially interpreted as separate species (Seppelt & Selkirk, this volume).

It seems that, in the moss bed studied, the lottery of local dispersal may be responsible for species distribution, while moisture availability is the principal determinant of growth form.

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EXPANSION OF BRYOPHYTES ON AREAS TREATED WITH HERBICIDES

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The mass appearance of bryophytes has been noticed in places, where herbicides have been applied in great degree. This phenomenon is especially striking in some cultivations of decorative monocotyledonous plants, in orchards as well as on railway and tramway lines. The dense carpets of bryophytes can cover hectares in such habitats. They are composed mainly of cosmopolitan mosses of wide ecological amplitude. The share of vascular plants in such communities is very small. More frequent are only annual recent immigrants (kenophytes).

The investigations showed that the very specific form of anthropopressure, namely the treatment with chemicals, contributes to the origin and spread of eusynanthropic, strongly specialized ruderal plant communities with dominance of bryophytes.

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The vegetation surrounding us is formed by more and more factors dependent on man and thus it deviates from natural systems. The observed changes very often take on a dramatic character since they are the result of a total battle against all spontaneous vegetation.

For description of vegetation of urban areas the term "desert" is sometimes used (e.g., "lichen desert") and the phenomenon of acquiring the characteristics of a steppe by agricultural areas in the middle-European forest zone is more and more common. The impoverishment of the flora is accompanied

by the parallel phenomenon of the replacement of some species by others, through which the expansive character of some plant groups comes to light.

A new way of fighting against weeds by means of chemicals has recently joined the traditional forms of anthropopressure. Herbicides are applied quite often on cultivated fields and also in orchards as well as on both sides of the tramway and railway tracks and even on town squares and sport fields. These substances effectively lower the amount of weed growth on the fields, as well as the number of species of vascular plants, but they also contribute to the development of a moss layer.

The expansion of bryophytes is clearly visible when such herbicides as, e.g., Gramoxone, Reglone, Atrazin and Simazin 50 are applied. The dense carpets of bryophytes (mainly mosses) cover very often many hectares of soil surface in orchards and in cultivations of ornamental flowers as well as many kilometers along railway and tramway tracks. The composition and structure of moss communities which develop in the habitats listed above are demonstrated in Tables 1-2. Table 1 shows moss communities in cultivations of ornamental monocotyledonous plants and in orchards, whereas Table 2 shows the vegetation on railway and tramway lines.

Dominating and of frequent occurrence are cosmopolitan bryophytes such as Bryum argenteum, Funaria hygrometrica, Bryum caespiticium, B. bicolor, Ceratodon purpureus, Barbula convoluta, and Marchantia polymorpha. Combinations of these species were described as phytocoenoses of the Funarietum hygrometricae Gams 1927 occurring on sites of fires and on soils rich in the following cations: Ca, N, Na, and K (von Hubschmann 1957). The species listed above are also components of the association Sagino-Bryetum Diem., Siss. & Westh. 1940. Phytocoenoses of these communities never covered, however, significant areas (they developed only on small surfaces).

As a result of the application of herbicides, the herb layer of the communities shown in the tables is poor. Especially worth emphasizing is the participation of annual, recent

immigrant anthropophytes (kenophytes, Kornaś 1968), such as
Erigeron canadensis, Amaranthus retroflexus, Epilobium adeno-
caulon and Eragrostis minor (Table 2). These species were not
present in the majority of relevés, but since they were destroy-
ed by herbicides, they were not noted at the beginning of our
studies. Additional observations not taken into account in the
tables show that also some species (e.g., Sisymbrium altissi-
mum, Amaranthus blittoides and A. albus) may be placed into
this group. They form a combination of characteristic species
of the alliance Sisymbrion and especially of the association
Erigeronto-Lactucetum Lohm. 1950. Their presence is not closely
connected with railway transportation, for they occur also on
tramway tracks in the centre of the city.

The greatest role in the vegetation of areas treated with
herbicides mentioned above is, however, played by bryophytes.
They occur very often in facies (Tables 1-2) and show great
vitality, producing sporogonia and bulbils. Differentiation
at the level of variants or facies in the tables is a result
of natural variability of the habitats and not of the type of
the herbicide applied. It mainly depends on the mechanical
composition, humidity and pH of the soil. For example, the form
in which Ceratodon purpureus is found on loose soils, the form
of Marchantia polymorpha in damp places and that of Barbula
convoluta on neutral or alkaline ground.

No detailed studies have been made as yet on the direct
indluence of herbicides on mosses. It seems, however, that
their mass occurrence on areas sprayed with herbicides is
mainly caused by the lack of competition by vascular plants
and by the great ease of spreading of bryophytes. This group
of plants needs a relatively short time for full development.
In our climatic zone, their growth is less dependent on the
season of the year. Such an explanation gets support from the
fact that among vascular plants growing in the patches studied
only short-lived therophytes are of some importance.

Preliminary studies have shown, however, that bryophytes
are much more resistant to herbicides than vascular plants.
During the experiments, Gramoxone (a herbicide which scorches
the aboveground parts of plants) was taken and used in a dose

Table 1. Moss communities in orchards and

Succesive number of record	1	2	3	4	5	6	7
Number of record	19	11	7	12	14	2	18
Cover of moss layer "d" in %	80	95	100	90	90	90	10
Cover of herb layer "c" in %	–	–	min	min	min	min	5
Area of record in m^2	0,8	20	1	2	0,5	0,3	1
Locality/Cultivation	Pu/R	P/O	N/F	P/O	P/O	S/F	P/O
d BRYUM ARGENTEUM	5.5	5.5	5.5	2.3	4.4o	5.5	5.4
FUNARIA HYGROMETRICA	.	.	1.2	2.2	3.2	+	1.1
BRYUM BICOLOR	.	.	.	3.3	1.1	+	+
MARCHANTIA POLYMORPHA	.	.	+	.	.	.	2.2
BRYUM CAESPITICIUM	.	.	.	.	.	.	.
GERRONEMA MARCHANTIAE	.	.	.	.	.	.	.
CERATODON PURPUREUS	.	.	.	.	.	.	.
CHLOROPHYCEAE	.	1.2	.	1.2	1.1	.	+
PHYSCOMITRIUM PYRIFORME	.	.	2.2	.	.	r	.
BARBULA CONVOLUTA	.	.	(+)	.	.	.	.
c TULIPA	.	.	.	.	.	r	.
NARCISSUS	.	.	+	.	.	.	.
EROPHILA VERNA	.	.	.	.	+	.	1.1
TARAXACUM OFFICINALE	.	.	r	.	.	.	.
POA ANNUA	.	.	r	.	.	.	.
STELLARIA MEDIA	.	.	.	.	.	.	.
ULMUS LAEVIS juv.	.	.	.	.	.	.	.
CAPSELLA BURSA-PASTORIS	.	.	.	.	.	.	.

Sporadic species (according to successive no of record):
BRACHYTHECIUM ALBICANS 10; BRYUM CAPILLARE 14; BRYUM sp. 10,
20; CHENOPODIUM ALBUM 17; CONVONVULUS ARVENSIS 4; DESCURAINIA
SOPHIA 12; EQUISETUM ARVENSE 7, 21; ERIGERON CANADENSIS 8,
21; FRAXINUS EXCELSIOR juv. 3, 12; GLECHOMA HEDERACEA 6, 18;
LAPSANA COMMUNIS 18; LOLIUM PERENNE 20/r^o); MYOSOTIS MIC-
RANTHA 16; POTTIA sp. 10; RUMEX ACETOSELLA 16; SYNAPIS
ARVENSIS 9, 13; URTICA DIOICA 11; VIOLA ARVENSIS 16, 17.

in cultivations of monocotyledonous ornamental plants

8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
207	36	4	5	6	13	17	9	8	10	1	3	20	15	16
80	100	98	95	85	95	100	100	100	95	90	80	80	100	90
5	min	10	10	7	min	min	−	10	min	2	40	min	15	−
3	6	2	3	2	0,5	0,3	0,3	1	20	0,6	0,2	0,2	0,7	1
P/O	P/O	N/F	N/F	N/F	P/O	P/O	P/O	P/O	P/O	S/F	S/F	Pu/O	P/O	P/O
3.3	1.2	2.1	2.1	2.2	2.2	4.4	5.4°	5.5	5.5	5.5	3.3	3.4	2.3	2.1
1.1	.	1.2	+	1.2	+.2°	3.3	2.2	1.1	r	2.2	3.3	3.3	5.4	5.5
2.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3.3	5.5	5.5	5.4	1.1	.	.	.	.	.	.	.	.	.	.
+	+	+	r	.	.	r	.	.	.	.	.	.	.	.
.	.	1.1	+	.	.	.	.	.	.	.	.	.	.	.
.	.	1.2	2.2	4.4	4.4	+	+	r	.	.	.	.	.	.
1.2	.	.	.	1.2	2.1	2.2	1.2	+	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	1.1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	r	+°	.	.	.
.	.	2.1	2.1	1.1	.	.	.	.	.	.	3.3	.	.	.
.	+	.	.	.	.	.	.	2.3	r°	.	.	.	2.1	.
.	.	+	+	+	.	.	.	.	.	r	+	.	.	.
.	r	r	r	.	.	.	.	.	.	+	+	.	.	.
.	+	+	+	.	.	.	.	.	.	.	.	.	.	.
.	.	+°	+	+	.	.	.	.	.	+	.	.	.	.
.	.	r	.	r	.	.	.	.	.	.	r	.	.	.

Explanations: N - Poznan-Naramowice, P - Paczkowo near Poznań,
  Pu - Puszczykowo, S - Siemionki near Kruszwica; O - orchard,
  F - flowers cultivation, R - field road.
Dates: records: 1, 20 - 1980.0516; records: 2, 4-5, 7-9, 13-17,
  21,22 - 1980.05.07; records: 6, 18, 19 - 1979.05.05; records:
  3, 10-12 - 1979.04.21; records: 8,9 - 1985.05.22.

Table 2. Moss communities on the tracks

Succesive number of record	1	2	3	4	5
Number of record	26	23	34	32	37
Date	29 05 80	16 05 80	23 09 84	23 07 85	23 07 85
Cover of moss layer "d" in %	75	40	80	90	80
Cover of herb layer "c" in %	min	–	10	20	30
Area of record in m^2	10	1	5	8	2
Locality	T-T	R-T	T-T	R-T	R-T

	1	2	3	4	5
d BRYUM ARGENTEUM	4.4	3.3	2.2	1.1	1.1
FUNARIA HYGROMETRICA	2.2	2.3	+	2.2	.
BRYUM BICOLOR	.	+.2	4.4	4.4	.
MARCHANTIA POLYMORPHA	.	.	.	.	4.4
BRYUM CAESPITICIUM (var. CAES-PITICIUM et var. IMBIRICATUM	.	.	.	+	.
BARBULA CONVOLUTA	.	.	.	+	.
PHYSCOMITRIUḾ PYRIFORME	.	.	.	.	.
CERATODON PURPUREUS					
c ERIGERON CANADENSIS	.	.	2.1	2.1	+
AMARANTHUS RETROFLEXUS	.	.	.	1.1	2.2
EPILOBIUM ADENOCAULON	.	.	.	.	1.1
SETARIA VIRIDIS	.	.	.	+	.
ACER PLATANOIDES	r	.	.	+	.
CHENOPODIUM ALBUM	r	.	.	.	.
SEDUM ACRE	r	.	.	.	.

Sporadic species (according to succesive no. of record): ACER
PSEUDOPLATANUS 13; ERAGROSTIS MINOR 9; POA ANNUA 5, 10;
SALSOLA RUTHENICA 5; SENECIO VISCOSUS 3; STELLARIA MEDIA 9;
TARAXACUM OFFICINALE 4, 9.

of railways and tramways

6	7	8	9	10	11	12	13	14	15	16
36	40	39	33	38	35	30	29	31	28	27
23	23	23		23		9	9	9	29	29
07	07	07	09	07	09	09	09	09	05	05
85	85	85	84	85	84	80	80	80	80	80
50	60	80	50	90	60	70	95	60	85	80
25	20	5	20	5	15	–	min	–	–	5
2	3	1,5	4	1,5	10	5	2	5	2	2
R/T	R/T	R/T	R/T	R/T	T-T	S	T-T	S	T-T	T-T
3.2	4.2	5.5	2.2	2.2	.	2.2	+.2	2.2	+.2	2.4
.	.	+	.	.	.	.	5.5	1.2	+	4.4
.							.	.	.	.
2.2										
.	.	1.1	3.3	4.4	4.4	3.2	1.2	1.2	.	.
.	.	.	.	.	.	2.2	1.2	3.4	5.4	1.2
.	.	.	.	.	.	+	.	.	.	.
.	.	+	.	.	.	.	.	.	.	.
2.1	2.1	1.1	2.1	1.1	2.1	.	.	.	.	.
(+)	2.1	+	+	+	.	.	.	.	.	.
2.1	+	.	.	.	.	.	.	.	.	.
.	.	+	+	.	.	.	.	.	.	.
.	.	.	.	.	.	.	r	.	.	r
.	.	.	.	.	.	.	r°	.	.	r
.	.	.	.	r	.	.	.	.	.	r

Explanations: R-T - rail trackway, T-T - tram trackway,
  S - Square.

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of 5 cm^3 per 100 cm^2 of surface. It was applied in 5 concentrations: 1:200, 1:133, 1:100, 1:67, 1:10. The vascular plants (Poa annua, Taraxacum officinale, Galinsoga parviflora) started to yellow and dry out when the lowest concentration of the herbicide was used. After treatment of mosses with Gramoxone, a brown colour in 20% of the cushions of Bryum argenteum was observed only when the highest concentration (1:10) was used.

Worth mentioning is also a case we know when a preparation named Simazin was accidentally spilled on a garden road. It happened in 1977, and phytosociological relevés were taken at the same place in 1980 (nos 1 and 20 in Table 1). The situation presented there has continued without changes until this year (1985). This shows that mosses very quickly colonise and dominate polluted areas, while the vascular plants, in spite of the passage of more than 8 years, were unable to return to the previously occupied places.

There were also attempts to use herbicides for destroying the green coating of mosses which appeared, especially in spring, on tennis courts covered with gravel. According to the report of the members of the service of the court of the Academic Sport Union in Poznań, the treatments did not give the desired results; just the opposite happened: mosses started to develop on a greater scale.

These preliminary investigations showed that the particular form of anthropopressure by chemicals contributes to the origin and spread of eusynanthropic (Faliński 1969), strongly specialized ruderal communities. The characteristic feature of some phytocoenoses of that type is the dominating role of bryophytes together with a significant participation of kenophytes of North American origin. It seems that just such phytocoenoses (Table 2) deserve distinction in a separate syntaxon, e.g., as the association Erigeronto-Bryetum.

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MICRODISTRIBUTION OF SPHAGNUM SPECIES IN RELATION
TO PHYSICAL ENVIRONMENT AND COMPETITION

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Sphagnum species growing on ombrotrophic mires occupy
different levels along the hummock-hollow gradient. Photo-
synthesis measurements after field experiments suggest that
hollow species cannot tolerate the drier hummock habitat.
Desiccation experiments reveal that the uppermost levels above
the water table reached by the four species studied are cor-
related with their ability to keep moist during dry periods of
the summer. However, a hollow species can keep moist better if
it is surrounded by a hummock species with superior water
transport ability. This is interpreted as a case of commen-
salism, explaining for instance the occurrence of the hollow
species S. balticum as single individuals within a S. fuscum
hummock at a higher level above the water table than were
monospecific carpets of S. balticum are found. The hummock
species can tolerate the hollow environment, and they were
found to be excluded from the hollows because of interspecific
competition.

1. INTRODUCTION

It has been stated that the more taxonomically related the
plant species, the less likely they are to be found in the same
habitat (Werner 1979). A quick glance at for example mire
ecosystems which are often totally dominated by species from
the families Amblystegiaceae and Sphagnaceae indicates that
the opposite may be true for bryophytes. Where closely related

plant species are found to be coexisting in an area they are
sometimes separated along some resource or environmental gra-
dient (e.g., Harper & Sagar 1953, Werner & Platt 1976).

To understand the microdistribution of the species it is
necessary to study the relationship between the actual distri-
bution of a species and its potential (in the absence of other
species). The difference between the fundamental and realized
niches (Hutchinson 1958) may provide an indication of the
occurrence of interspecific competition (cf. Werner 1979),
especially if predation can be assumed to be of minor importance
(Wiens 1977) as in bryophytes (Richardson 1981).

I have studied the relationship between tolerance to phy-
sical environment and interspecific competition for one set
of closely related coexisting species, namely Sphagnum species
occurring along a water level gradient on ombrotrophic mires
(bogs) in eastern Sweden. I will here rely on data presented
elsewhere (Rydin in prep., Rydin in press, Rydin & McDonald
1985a,b), and the aim of this paper is to present a synthesis
of these earlier reports. The overwhelming importance of this
water level (or topographic) gradient has long been recognized
(see e.g., Osvald 1923). I will here discuss separation along
this gradient, and refer to it as a niche axis, i.e., an intra-
community environmental variable in the sense of Whittaker et
al. (1973, 1975).

2. STUDY SITES AND SPECIES INCLUDED

Analyses and experiments were made on two bogs in eastern
central Sweden: Ryggmossen (province of Uppland, 25 km NW of
Uppsala) and Kulflyten (province of Västmanland, 100 km W of
Uppsala). Both mires are characterized by a pattern of hummocks
and hollows. On Ryggmossen the hummocks are formed by S. fuscum*
and the hollows occupied by S. balticum with some S. tenellum.
At low levels of the hummocks S. rubellum occurs but it is
always rare. Kulflyten has got hollows of the same type as

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* Nomenclature of Sphagnum follows Nyholm (1969).

Ryggmossen, but S. rubellum is the most important hummock-building species, although S. fuscum is common on the highest hummocks. Beside these four species, which were included in the study, the wettest hollows are dominated by S. cuspidatum, on Kulflyten often together with S. majus and S. magellanicum. Important vascular plants are Calluna vulgaris and Eriophorum vaginatum.

3. FUNDAMENTAL NICHES OF THE SPECIES

The approximate tolerance limits of the species (Fig. 1) are based on data in Rydin & McDonald (1985a). In that study we grew samples of the four species at different constant levels above the water table in bog pools on Kulflyten, and at different fluctuating levels in reciprocal transplant experiments on Ryǵgmossen. This design made it possible to analyse effects of growth height above the water table under natural conditions of water chemistry and climate. After 3 and 14-15 months, samples of the species were brought to the laboratory and their photosynthetic rate measured under standard conditions with an open gas analysis system.
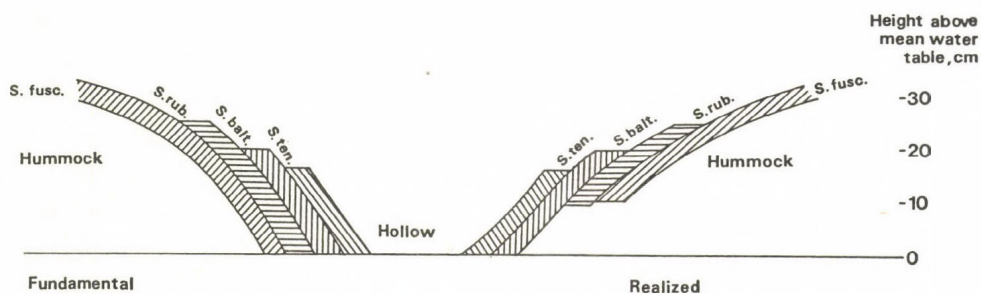
Fig. 1. Schematic view of the occurrence of four Sphagnum species along the water level gradient illustrating their fundamental niches (tolerance ranges) and realized niches (actual range, outside which they occur only occasionally, cf. Fig. 3). Based on data in Rydin & McDonald (1985a) and Rydin (in prep.).

The general trend was a decrease in photosynthetic rate
with increasing height above the water table. The hummock
species could well tolerate a treatment in which they were
placed nearer to the water table than they normally grow,
both at constant and fluctuating water levels. They are thus
potentially capable of growing in the hollows. The hollow
species showed very low photosynthetic rates when grown at
high levels above the water table. They cannot tolerate this
environment and are excluded from the hummocks.

4. REALIZED NICHES OF THE SPECIES

Based on transect studies in hummock-hollow transitions
(Rydin in prep.), the occurrence of the species on Ryggmossen
is described in Fig. 1. Although S. fuscum and S. rubellum are
able to tolerate the conditions of the hollows they are not
found there. S. balticum and S. tenellum does not seem to be
separated along the gradient, but the realized niche of S.
balticum is larger than that of S. tenellum.

5. WHY CANNOT HOLLOW SPECIES GROW ON THE HUMMOCKS?

There are several studies indicating that photosynthesis
and growth are water-limited in dry periods of the summer (Over-
beck & Happach 1957, Pedersen 1975). This suggests three hypo-
theses which may explain why there is an upper limit of occur-
rence of hollow species: (i) hollow species are less tolerant
to desiccation than hummock species; (ii) photosynthesis of
hollow species is more sensitive to low water content than that
of hummock species; (iii) hollow species have a less effective
water transport and will encounter more frequent and severe
desiccation than hummock species at a given level above the
water table.

Regarding the first hypothesis, experiments have been made
by Clymo (1973). The capitula of a number of species were sub-
ject to various humidity conditions and his results indicate
that there is no simple correlation between desiccation tole-
rance and natural habitat of the species.

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To investigate the response of photosynthesis to low water contents, we used the above-mentioned gas analysis system to measure photosynthetic rates at different water contents in S. fuscum, S. balticum and S. tenellum (Rydin & McDonald 1985b). The only statistically significant difference found was that between S. tenellum and S. balticum: S. tenellum needed a higher water content than S. balticum to maintain 50% of its photosynthetic rate.

These findings can be compared with those of Titus et al. (1983) who found that the hollow species S. fallax was more efficient than the hummock species S. nemoreum at low water contents. In contrast. Silvola & Aaltonen (1984) found that S. fuscum was superior to the hollow species S. angustifolium (Russ.) C. Jens. in this respect. In conclusion, data on the photosynthetic water response cannot explain the vertical distribution of the species.

To test the effect of height above the water table on water content, the water table in Sphagnum samples was gradually lowered from 5 to 22 cm below the surface in a laboratory experiment. At the end of the experiment the ranking in water content was S. fuscum S. rubellum S. balticum S. tenellum (Rydin, in press). After a period with dry weather, the same ranking was found in a field study at Ryggmossen (Rydin, in press). The third hypothesis is thus the only one which could not be rejected: the higher up on a hummock a species is found, the better its ability to supply its photosynthetically active parts in water.

6. EVIDENCE OF COMMENSALISM

It is noteworthy that when S. balticum occurs at high levels above the water table it is not forming monospecies carpets, but grows as single individuals within the S. fuscum hummock.

In laboratory experiments I studied desiccation in two-species mixtures of Sphagnum and an example of striking neigh-

bour effect is shown in Fig. 2 (based on data in Rydin, in press). Shoots of S. balticum surrounded by S. fuscum had a much higher water content than shoots surrounded by other shoots of S. balticum. These observations were also supported by field data (Rydin, in press). In this way S. balticum may grow at higher levels above the water table in the presence of S. fuscum than otherwise. Stated in another way: due to the commensal effect (assistance in water transport) the realized niche of S. balticum in the presence of S. fuscum is larger than its fundamental one.

7. NICHE SHIFTS INDICATING COMPETITION IN SPHAGNUM

In different parts of the mire there are either three, four or five Sphagnum species replacing each other along the gradient between hummock and hollow. It is thus possible to investigate to what extent the species have different patterns of distribution along this gradient when growing in contact with different congeners; in other words, to look for the occurrence

S. BALTICUM ○   S. FUSCUM ⊗

Surrounded by S. balticum: 37 ± 8.4 %   Surrounded by S. balticum: 300 ± 54.9 %

Mixed surrounding: 179 ± 22.8 %   Mixed surrounding: 384 ± 19.9 %

Surrounded by S. fuscum: 257 ± 24.5 %   Surrounded by S. fuscum: 423 ± 15.9 %
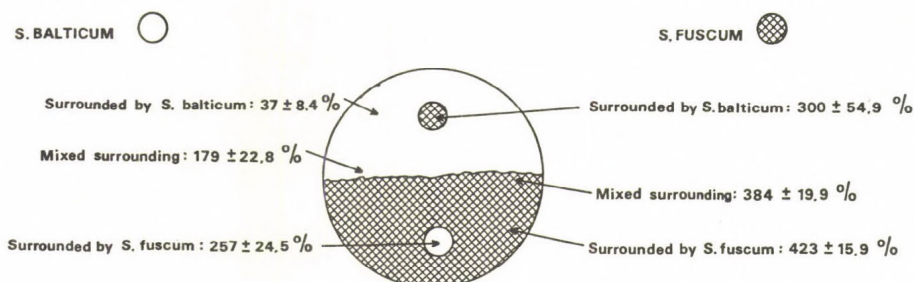
Fig. 2. Water content (mean +/- S. E. M.; n=6) in capitula of Sphagnum fuscum and S. balticum after desiccation in a laboratory experiment. The figure shows a schematic picture of an experimental plot in which the water content of individual capitula was found to be dependent on the specific identity of surrounding plants. Details about the experiment are given in Rydin (in press).

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of niche shifts resulting from interspecific competition
(Diamond 1978). I did this by analyzing transects on Rygg-
mossen in hummock-hollow transitions with different species
combinations, and the following discussion is based on
results in Rydin (in prep.).

Most commonly, S. fuscum and S. balticum are the only
species with a high cover in the transition between hummock and
hollow (Fig. 3a). When S. rubellum occurs (Fig. 3b), it oc-
cupies part of the gradient otherwise covered by S. fuscum,
but it does not affect S. balticum. If, on the other   hand,
there is a great amount of S. tenellum present (Fig. 3c), it
partly replaces S. balticum without affecting S. fuscum.
Finally, hollows where S. cuspidatum dominates (Fig. 3d) are
wetter than other hollows, so there the gradient is extended.
S. cuspidatum also partly excludes S. balticum from the wettest
parts of the range of the latter species. Thus, it is suggested
that the species are replaced at their lower limit by a stronger
competitor from lower down the gradient: S. fuscum is outcom-
peted by S. balticum or S. rubellum, S. rubellum by S. balti-
cum, and S. balticum by S. cuspidatum or S. tenellum.

8. EXPERIMENTAL EVIDENCE OF COMPETITION IN SPHAGNUM

I also studied competition over time in experiments in
which the species were grown in different combinations and at
different levels above the water table. The outcome of com-
petition was measured as an increase or decrease in area co-
vered by the different species in experimental plots. These
experiments (see Rydin, in prep. for details) generally support
the results of the transect analyses, but there are two ex-
ceptions: S. rubellum did not replace S. fuscum from S. rubel-
lum habitat and, on average, S. tenellum lost area to S. bal-
ticum, regardless of the habitat involved. The dominance of
S. rubellum and S. tenellum could not be explained by compe-
tition or response to any factor other than height above
water table. The occurrence of patches covered by these spe-
cies may thus indicate the importance of priority of coloniza-
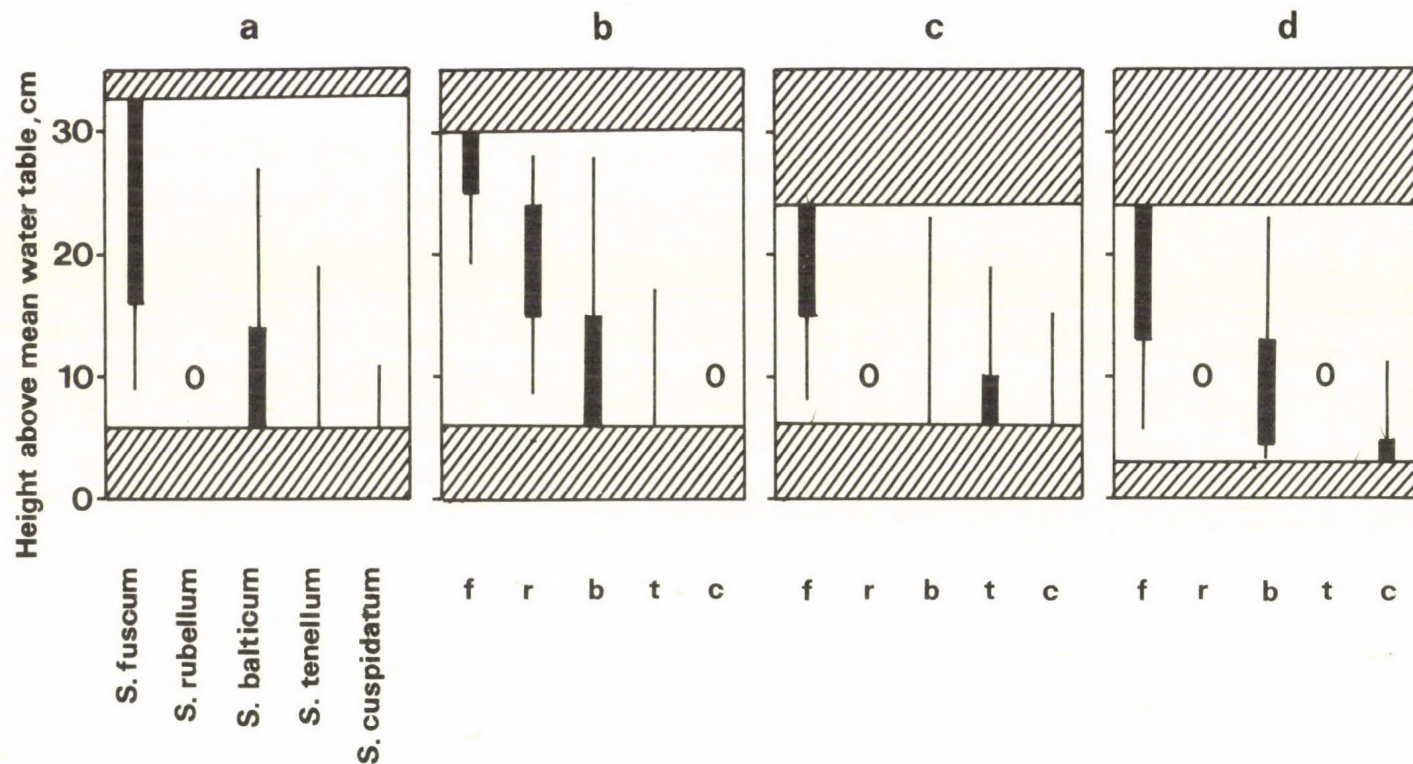
Fig. 3. Occurrence of Sphagnum species in different hummock-hollow transects on Ryggmossen. The different transects are dominated by different combinations of Sphagnum species. A wide bar indicates that the species occupies more than 50% of the total Sphagnum cover, thin bar indicates a lower cover. An open circle means that the species does not occur in the transect. Data extracted from Rydin (in prep.).

tion rather than competition, or preemtive rather than inter-active competition (Werner 1979).

The species composition in the hummocks seems to be mainly determined by tolerance of the species to the physical environment. However, it is obvious that in hollow communities competition is important, in contrast to suggestions found in other studies of bryophytes (Slack 1977, Watson 1980). Although the occurrence of competition is demonstrated by niche shifts (cf. Diamond 1978), observational data alone failed to give a complete understanding of species interactions, and I conclude that experiments are a necessary component in competition studies (cf. Simberloff 1982, Connell 1980).

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THE EFFECTS OF MAJOR IONS ON THE GROWTH OF SPHAGNUM PROTONEMATA

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The protonemata of 10 species of Sphagnum were grown and monitored over a period of 32 days to assess the effects of different ions on their growth. Although the pattern of development was similar for nearly all species, they differed in their rates of growth. Dilution of the nutrient solution severely limited the growth of most species. The effect of independently reducing the concentration of the major ions was also investigated. At low concentrations $H_2PO_4^-$ severely limited the growth of nearly all species. Reducing the concentrations of Ca^{2+} and Mg^{2+} also limited growth of the protonemata. However, lowering the concentration of K^+ had little effect on growth. Ombrotrophic species, such as S. nemoreum, S. fuscum, and S. rubellum, are very sensitive to varying concentrations of ions. More minerotrophic species, such as S. russowii, S. girgensohnii, and S. centrale, can tolerate a much broader range of ion concentrations.

INTRODUCTION

Many species of Sphagnum are frequently observed with sporophytes and presumably release large numbers of spores, but very little is known of the ecology of the protonemata. In fact, protonemata arising from spore germination has been rarely observed in the field. Vegetative reproduction, from repeated branching, is cited as the most common means of reproduction in Sphagnum (Lane 1977, Clymo & Hayward 1982).

It is unlikely that the spores are not viable since the growth
and development of the protonema for a number of species have
been documented on a variety of media (Schimper 1858, Goebel
1889, Ruhland 1909, 1924, Bold 1948, Noguchi 1958, Nishida &
Saito 1961, Nehira 1963, Anderson & Crosby 1965, McQueen 1985).

Boatman & Lark (1971) reported the development of protone-
mata for the three species they studied to be very similar
although they found differences in rates of development and
in response to varying concentrations of ions. They observed
growth only when nutrient solutions were supplied, none
occurring on natural waters.

The studies of Boatman & Lark (1971) are interesting be-
cause differential growth rates to varying concentrations of
ions in natural waters and substrates may determine what spe-
cies will eventually become established in a particular area.
The present study is a preliminary investigation of growth
rates of the protonemata of 10 species of Sphagnum in varying
concentrations of ions.

METHODS AND MATERIALS

Capsules of Sphagnum nemoreum Scop., S. subtile (Russow)
Warnst., S. russowi Warnst., S. girgensohnii Russow, S. fuscum
(Schimp.) Klinggr., S. rubellum Wils., S.angustifolium (Rus-
sow) C. Jens., S. fallax (Klinggr.) Klinggr., S. centrale C.
Jens., and S. magellanicum Brid. were collected from several
different peatlands in northern Vermont. The capsules were
placed in plastic bags and stored in a refrigerator. All ex-
periments were started within 30 days of the collection of
the capsules.

The standard solution of Boatman & Lark (1971) was used
as the basic solution for this investigation. This solution
contains 208 ml/l $NaH_2PO_4-2H_2O$, 236 mg/l $Ca(NO_3)_2-9H_2O$, 225
mg/l $MgSO_4-7H_2O$, 202 mg/l KNO_3, 5.6 mg/l NaCl, 2.2 mg/l
$MnSO_4-H_2O$, 0.24 mg/l $CuSO_4-5H_2O$, 0.29 mg/l $ZnSO_4-7H_2O$, 1.86
mg/l H_3BO_3, and 0.035 mg/l $(NH_4)_6Mo_7O_{24}-4H_2O$, giving concentra-
tions of 4 m-equiv./l of NO_3^-, 2 m-equiv./l of Ca^{2+}, Mg^{2+}, K^+,

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and SO_4^{2-}, and 1.3 m-equiv./l of Na^+ and $H_2PO_4^-$. Iron was added as Fe-EDTA prepared according to Hewitt (1966). One ml of the Fe-EDTA solution, containing 2.8 mg Fe-EDTA, was added for each liter of the standard solution. The pH of the final solution was 5.1.

Spores were germinated in aqueous solutions to facilitate sampling. Single unopened capsules were crushed and the spores were dusted into small petri dishes filled with the basic nutrient solution. Three replicates were set up for each species. The cultures were placed in a room at $25^{O}C$ and sub-jected to 18 hours of light per day at an intensity of about 142 μE m^{-2} sec^{-1}.

The number of cells per protonema was counted as a growth index. Sampling was started 7 days after setting up the cul-tures. Every 2 to 3 days a random sample of 20 protonemata per petri dish was scored. Ungerminated spores were scored as zero. Scoring was terminated after 32 days because it became difficult to accurately determine the number of cells per protonema.

In supplemental experiments the effect of varying the con-centration of the standard solution (S) was tested. Cultures with diluted solutions of 0.1 S and 0.01 S were set up. The effect of varying the concentrations of K^+, Mg^{2+}, Ca^{2+}, and $H_2PO_4^-$ were also tested. The concentration of each ion was in-dependently reduced to 0.1 m-equiv./l. Anions were maintained at the standard level by supplying them as sodium salts when the concentrations of cations were varied and cations were supplied as chlorides when anions were varied. The set up and sampling procedures were the same as those of the standard solution cultures.

RESULTS

The basic pattern of development on the standard nutrient solution was similar for most species and resembled reports for other species by Bold (1948), Anderson & Crosby (1965), and Boatman & Lark (1971). However, the species differed in their
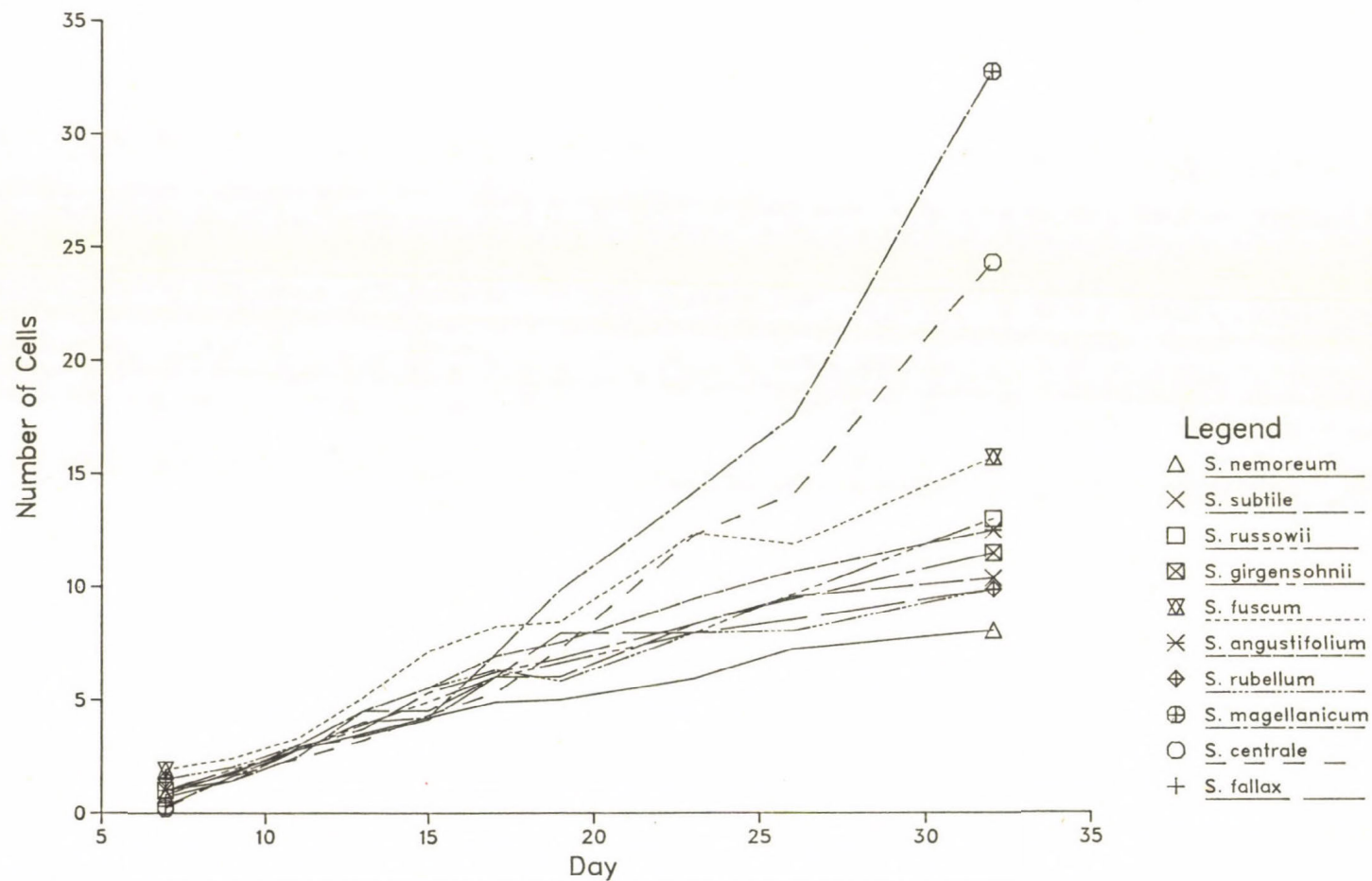
Fig. 1. Sphagnum protonemata growth in the standard nutrient solution.

Legend
△ S. nemoreum
✕ S. subtile
□ S. russowii
⊠ S. girgensohnii
⊠ S. fuscum
✳ S. angustifolium
⊕ S. rubellum
⊕ S. magellanicum
○ S. centrale
+ S. fallax

rates of development (Fig. 1). Differences among species were noticeable after seven days, but became more pronounced by the end of the third week. Sphagnum magellanicum and S. centrale developed the largest thalloid protonemata by the end of the sampling period. Sphagnum fuscum was the only species that did not produce thalloid protonemata. The protonemata of this species remained filamentous and were extensively branched. Protonemata of the remaining species were very similar. Most of them were predominately thalloid with a few three to four-celled rhizoids extending from the basal cell. A decrease in the number of cells per protonema during the sampling period was due to the death of primarily rhizoid cells.

The spores of all species germinated in the O.1 S and O.O1 S solution, but only three species survived throughout the sampling period (Table 1). Of the species that failed to survive, none of them had protonema with more than six cells and all were dead by the third week. The effect of the lower concentrations of ions was enhanced growth for S. fallax and S. girgensohnii and reduced growth for S. centrale. S. fallax and S. centrale developed thalloid protonemata with rhizoids as in the standard solution, whereas S. girgensohnii protonema did not develop any rhizoids at all. S. centrale protonemata became progressively chlorotic during the last two weeks.

The reduced concentration of K^+ had little effect on the growth of the protonemata of different species compared to the standard solution treatment. The overall number of cells per protonema was slightly less for S. magellanicum and S. centrale, but the remaining species were similar in size to those grown in the standard solution (Table 1). As in the standard solution, S. fuscum did not produce any thalloid protonemata.

In the reduced Ca^{2+} solution the spores of all species germinated, but only six species survived the sampling period (Table 1). S. fallax produced considerably larger thalloid protonemata in this solution than in the standard solution. Growth was also enhanced for S. girgensohnii and S. angusti-folium. The reduced level of Ca^{2+} had no observable effects on S. centrale.

Table 1. Mean number of cells per protonema after 32 days.

Species	S	0.1 S	0.01 S	low K^+	low Ca^{2+}	low Mg^{2+}	low $H_2PO_4^-$
S. nemoreum	8.0±1.6	-	-	8.2±1.1	-	-	-
S. subtile	10.3±1.4	-	-	9.9±1.0	9.9±0.8	-	3.0±0.1
S. russowii	12.9±1.0	-	-	12.0±1.4	13.0±1.8	12.0±1.2	-
S. girgensohnii	11.4±0.4	12.9±0.6	16.0±0.9	13.3±1.1	15.6±1.0	11.5±0.9	6.1±0.4
S. fuscum	15.6±0.7	-	-	15.1±1.3	-	-	-
S. angustifolium	12.4±0.4	-	-	12.2±0.9	18.1±2.0	-	-
S. rubellum	9.8±0.4	-	-	10.3±1.2	-	-	-
S. magellanicum	32.6±1.5	-	-	29.1±1.7	-	-	-
S. centrale	24.2±1.1	13.3±0.5	5.9±0.7	23.8±1.4	24.2±1.0	19.0±1.8	-
S. fallax	9.8±0.4	11.0±0.6	24.1±1.3	11.2±0.8	25.0±1.4	14.1±1.2	-

The spores of all species germinated in the reduced Mg^{2+} solution, but only four species survived the sampling period (Table 1). $\underline{S}$. $\underline{centrale}$ produced the largest thalloid protonemata although they were smaller than those grown in the standard solution. The growth of $\underline{S}$. $\underline{fallax}$ was enhanced although the rhizoids became chlorotic during the third week. The protonemata of $\underline{S}$. $\underline{russowii}$ and $\underline{S}$. $\underline{girgensohnii}$ differed little from those grown in the standard solution.

Only two species survived the sampling period in the reduced phosphate solution (Table 1). The spores of most species germinated, but most did not produce more than three cells per protonema. Growth was reduced in $\underline{S}$. $\underline{subtile}$ and $\underline{S}$. $\underline{girgensohnii}$. The protonemata of both species failed to produce rhizoids and thalli.

DISCUSSION

$\underline{Sphagnum}$ species definitely differ in their responses to varying concentrations of ions. Most of the species tested were very sensitive to changes in ion concentrations. The concentration of the $H_2PO_4^-$ ion was primarily responsible for limiting the growth of the protonemata when the nutrient solution was diluted since only two species were able to grow in solutions where the concentration of this ion was independently reduced. However, it is apparent that the other ions tested were also partly responsible for the limited growth of protonemata in the diluted nutrient solutions.

These results are similar to what Boatman & Lark (1971) described for $\underline{S}$. $\underline{papillosum}$ Lindb., $\underline{S}$. $\underline{magellanicum}$ Brid., and $\underline{S}$. $\underline{cuspidatum}$ Ehrh. They reported reduced growth with a progressive reduction in the size of the thalloid portion and an increase in the filamentous portion of the protonemata when the culture solutions were progressively diluted. As in this study, they found that varying the concentrations of K^+ had little effect on the growth of protonemata. The only ion they found to produce an increase in growth with a rise in concentration was $H_2PO_4^-$. They also reported that lowering the

concentration of Mg^{2+} had little affect on growth, whereas
concentrations of Ca^{2+} above 0.2 m-equiv./l. inhibited growth.
However, the results of this investigation indicate that in-
dependently lowering the concentration of Mg^{2+} inhibits growth
in some species and has a more severe effect on growth than
Ca^{2+}. This is not surprising since it is apparent that con-
centrations of ions influence the growth of the protonemata
of different species in different ways.

There seems to be a relationship between the general habitat
of the species and their response to varying concentrations of
ions. $\underline{S}$. $\underline{nemoreum}$, $\underline{S}$. $\underline{fuscum,}$ and $\underline{S}$. $\underline{rubellum}$, which are pri-
marily ombrotrophic species (Andrus 1980), appear to be very
sensitive to changes in ion concentrations. The more minero-
trophic species, such as $\underline{S}$. $\underline{russowii}$, $\underline{S}$. $\underline{girgensohnii}$, and $\underline{S}$.
$\underline{centrale}$, are more tolerant of a wide range of ion concentra-
tions. The remaining species, which are more common in tran-
sitional habitats, show varying tolerances of ion concentra-
tions. In light of the sensitivity of the more ombrotrophic
species to varying concentrations of ions, it seems unlikely
that their protonemata would be found in these habitats since
the nutrient solution used in this investigation provides K^{+},
Mg^{2+}, Ca^{2+}, and $H_2PO_4^{-}$ in excess of what is generally found in
transitional and rich fens (Sjors 1950, Bellamy 1968). This
may account for the apparent absence of protonemata in the
field despite the presence of large numbers of sporophytes.
It is possible that habitats condusive to protonemata growth
are very different from those of mature gametophores, espe-
cially in light of the ability of $\underline{Sphagnum}$ to acidify its
environment. However, this hypothesis should be tested by sim-
ulating the habitats more closely than in the present investi-
gation. Protonemata grown in aqueous solutions tend to have
smaller thalloid portion and develop slower than those grown
on solid substrates (Boatman & Lark 1971). Thus, they may not
accurately reflect growth and development in the field.

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FEASIBILITY OF LONG-DISTANCE TRANSPORT
IN COLOMBIAN HEPATICS,
PRELIMINARY REPORT**

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Environmental conditions affecting spores of 61 Colombian
hepatics during aerial transport were simulated in laboratory
experiments. Transoceanic species had a better resistance to
desiccation and to dry-freezing than endemic species, whereas
the resistance to wet-freezing is nearly the same in both
groups. Nearly all the 61 species were also subjected to
experiments on the wing-tips of an airplane. All spores died
except those of Marchantia chenopoda. Death rates were very
high for spores transported in the wing of the plane. The
results suggest that wet air-currents at high altitudes
offer a good possibility for most hepatics to disperse; dry
air-currents are much less favourable; whereas jet-stream
altitudes do not play a role in the dispersal of nearly all
the hepatics examined.

INTRODUCTION

    The distribution patterns of Colombian Hepaticae can
roughly be divided into two types, viz.:
1. species only occurring in South America, some also in
   Central and/or North America (called in this paper
   "endemic");
2. species also occurring outside the Americas (called "trans-
   oceanic").

** A more detailed account on this matter will be published
   elsewhere.

The species of the first type can have established their present day distribution by means of step by step dispersal (thus without the necessity of aerial transport over long distances) following geological and/or climatic changes. The ancestral stock of these species may either have reached America from other continents by means of step by step dispersal before the disruption of Gondwanaland (100 million years ago), or the species evolved in the Americas.

The species of the second type occur also outside the Americas, mainly in tropical and/or southern Africa, some also in Australasia or Europe (see Gradstein et al. 1983). These species may either have established their range by aerial, transoceanic long-range transport in relatively recent times (e.g., following the climatic changes as a result of Pleistocene glaciations), or the species remained unaltered since the rupture of Gondwanaland.

Effective aerial long-distance transport may be effected by the following types of air-currents (Van Zanten 1976):

A. Dry air-streams at relatively low altitude (e.g., 2000-3000 m). During this transport the spores would be subjected to desiccation. Wet air-streams at relatively low altitude are probably less effective for dispersal because of a high rate of precipitation.

B. Hurricanes, tropical storms or depressions. During this transport the spores would be subjected to wet-freezing, low pressure, and different composition of the air.

C. Dry air-streams at high altitude (e.g., jet-streams at c. 10-12,000 m). During this transport the spores would be subjected to dry-freezing, low pressure, different composition of the air (high O_3 concentration) and strong U.V. radiation.

For a more detailed discussion on this matter see Van Zanten (1976, 1978) and Van Zanten & Pócs (1981).

METHODS AND MATERIAL

To simulate the above-mentioned environmental conditions during aerial transport, laboratory experiments with spores of 61 Colombian hepatics (collected by J. Aguirre and the authors in September - October, 1984) were carried out, viz.:

1. Desiccation without any further treatment for various periods of time, imitating dry air-streams at relatively low altitude;
2. Desiccation with subsequent wet-freezing (c. -30°C) for four days, imitating wet air-streams at high altitude;
3. Desiccation with subsequent dry-freezing (c. -30°C) for four days, imitating dry air-streams at high altitude.

The duration of four-day freezing was chosen because four days is the absolute minimum to reach Africa from America or vice versa.

In these experiments, the lower air pressure, the different composition of the air and the higher U.V. radiation were not taken into account.

A combination of desiccation, dry-freezing (c. -60°C), low pressure, different composition of the air (high O_3 concentration) and high U.V. radiation was tested in a device mounted on the two wing-tips of a Boeing 747 of the Royal Dutch Airlines (KLM). The "spore-flights" from Sciphol, Amsterdam, to Los Angeles and back, were carried out during October, 1984, and received c. 6-8 hours of sunshine. Apart from the device on the wing tips (spores receiving direct sunlight and U.V. radiation), there is another device mounted in the wing (spores receiving the same environmental conditions but without direct light and U.V. radiation). This last device is used as a parallel test in order to be able to examine whether U.V. radiation, or other factors, causes a possible death of the spores.

The experiments were carried out with c. 80, mainly montane and tropical subalpine hepatics from Colombia. Because not all specimens were identified at the time of the congress in Budapest, the results presented here relate only to 61

species. Of these species 28 are transoceanic and 33 endemic to America.

RESULTS

Laboratory tests

As can be seen from Table 1, the results are as follows:
1. The viability of fresh <u>spores</u> is nearly the same for transoceanic and endemic species (rate   1.1 x);
2. The resistance to wet-freezing of fresh <u>spores</u> is somewhat higher in transoceanic than in endemic species (rate 1.3 x);
3. The resistance to dry-freezing of fresh <u>spores</u> is distinctly higher in transoceanic species (rate c. 3 x);
4. The resistance to wet- and dry-freezing of <u>spores</u> which have been dry for 1-2 weeks is somewhat higher in transoceanic than in endemic species (rate c. 1.3 x and c. 1.5 x, respectively);
5. The percentage of <u>species</u> of which the spores survive 4 days of wet-freezing is 95% for transoceanic, and 83% for endemic species (rate c. 1.1 x);

————————►

<u>Table 1.</u> Germination spectrum of 61 Colombian <u>Hepaticae</u>. Above the horizontal line in the middle of the table the percentages of <u>living spores</u> which survive the various treatments are given (germination percentage of a blanco test with fresh spores and without any treatment taken as 100%). Of several species more than one specimen was used; "average" means that the average of all specimens of a certain species was used, and "highest" means that, if more than one specimen of a certain species was checked, only the highest score was used for the calculation.

Below the double line the percentage of <u>species</u> of which the spores survive the various treatments are given. Germination " 1%" and " 5%" means that if less than 1% (5% resp.) of the spores of a species did germinate, the spores of the species are considered as being dead.

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Germination spectrum of 61 Colombian Hepatics		Rate between transoceanic and endemic species		Transoceanic 28 species		Endemic 33 species	
		average	highest	average of each species	highest score of each sp.	average of each species	highest score of each sp.
S P O R E S	Average number of spores of fresh material germinating	1.1 x	1.1 x	70%	78%	62%	69%
	Average number of living spores of fresh material surviving 4 days of wet-freezing (-30° C)	1.3 x	1.3 x	58%	73%	44%	57%
	Average number of living spores of fresh material surviving 4 days of dry-freezing (-30° C)	3.4 x	2.9 x	17%	26%	5%	9%
	Average number of living spores surviving 1-2 weeks of desicc. and subsequent 4 days wet-freezing (-30° C)	1.3 x	1.3 x	58%	65%	46%	51%
	Average number of living spores surviving 1-2 weeks of desicc. and subsequent 4 days dry-freezing (-30° C)	1.4 x	1.7 x	14%	26%	10%	15%
		germ. > 1%	germ. > 5%	germ. > 1%	germ. > 5%	germ. > 1%	germ. > 5%
S P E C I E S	Number and percentage of species of which the spores survive 4 days of wet-freezing (-30° C)	1.1 x	1.2 x	25 96%	25 93%	28 88%	25 78%
	Number and percentage of species of which the spores survive 4 days of dry-freezing (-30° C)	1.5 x	1.5 x	22 81%	18 67%	17 53%	14 44%
	Average number of days of resistance of spores to desiccation	1.8 x	2.1 x	46 days	35 days	25 days	17 days
	Number and percentage of species of which the spores survive desiccation periods of at least: — 5 days	1.1 x	1.2 x	23 82%	23 82%	24 73%	22 67%
	10 days	1.1 x	1 x	20 71%	18 64%	22 67%	21 64%
	20 days	1.2 x	1.6 x	18 64%	18 64%	17 52%	13 39%
	30 days	1.9 x	2.9 x	13 46%	12 43%	8 24%	5 15%
	40 days	3.8 x	4.8 x	13 46%	12 43%	4 12%	3 9%
	50 days	4.3 x	11 x	11 39%	9 32%	3 9%	1 3%

6. The percentage of <u>species</u> of which the spores survive 4
   days of dry-freezing is somewhat higher for transoceanic
   than for endemic species (rate 1.5 x);
7. The average number of <u>days</u> of resistance to desiccation is
   twice as high in transoceanic than in endemic species;
8. The resistance to desiccation for periods longer than 4 days
   (5-50 days) is higher in transoceanic species, especially
   when the desiccation periods exceed c. 20 days.

In short: transoceanic species have a better resistance to
desiccation and to dry-freezing than endemic species, whereas
the resistance to wet-freezing is nearly the same in both
groups.

Aeroplane tests

Nearly all the 61 hepatic species were also subjected to
the experiments <u>on</u> the wing-tips of a KLM plane. The results
were very uniform; all spores died, except those of <u>Marchantia
chenopoda</u> (an endemic species with spores probably too large
for aerial long-distance transport). The parallel test <u>in</u> the
wing also had a very high death rate. This could be expected
because the survival rate of <u>spores</u> subjected to dry-freezing
only is also rather low (c. 20% in transoceanic species and c.
7% in endemics), and because the environmental conditions in
the wing test are more severe (extra thawing and freezing in
Los Angeles, higher O_3 concentration and low pressure).

CONCLUSIONS

1. Effective aerial long-distance transport by wet air-currents
(hurricanes, tropical storms and depressions) at high altitudes,
is a good possibility <u>for</u> <u>most</u> hepatics (high resistance to
wet freezing in transoceanic as well as in endemic species);

2. Effective aerial long-distance transport by dry air-currents
at relatively low altitude (e.g., 2000-3000 m) is a possibility
<u>for</u> <u>some</u> hepatics, especially for transoceanic species (better
resistance to desiccation than endemic species);

3. Effective aerial long-distance transport at jet-stream al-
   titude is very unlikely for nearly all hepatics.

   Although a good resistance to desiccation, whether or not
combined with dry-freezing, is of some advantage for effective
transoceanic dispersal (results 3 and 6-8), this factor is
only of limited importance in hepatics, because in our experi-
ments the differences in germination rates between transoceanic
and endemic species are not very high. Moreover, most of the
endemic species (52%) survive 20 or more days of desiccation,
a period of time very probably enough for transoceanic trans-
port from America to Africa, or vice versa. Other factors
(such as quantity and size of spores, competitiveness, avail-
able niches, etc.) may be also involved in determining the
chances for effective long-range dispersal (see Van Zanten
& Pócs 1981, p. 545).

   However, the most likely explanation for the transoceanic
distribution of many Colombian hepatics is an effective long-
distance transport by hurricanes, tropical storms or de-
pressions, because the spores of a very high percentage of the
species survive wet-freezing (c. 19%).

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THE ECOLOGY OF THE INVASION OF ORTHODONTIUM LINEARE SCHWAEGR. IN CENTRAL EUROPE

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Orthodontium lineare, an adventive moss, has been spreading in Central Europe and attained a second ecological optimum in sandstone rock formations. This optimum is associated with a massive colonization of sandy soil, uncommon in other parts of Central Europe. Its occurrence is limited by low illumination levels and by extremes in moisture regime. This limitation may take place in the juvenile phase. Differences in substrate reflect differences in moisture regime of localities. Orthodontium lineare is a good colonizer of bare ground. Permanent plot observations showed that three types of communities invaded by Orthodontium lineare may be distinguished according to the mechanism of its persistence. The main processes responsible for its establishment and diversity maintenance are temporal changes in species competitive ability and external disturbance.

INTRODUCTION

Since the beginning of this century, the Southern Hemisphere moss Orthodontium lineare has been spreading in Western, Northwestern and Central Europe (for recent distribution map, see Ochyra 1982). Though its frequency declines with the distance from the Atlantic, it attained a second ecological optimum in sandstone rock formations in Northern Bohemia, Southwestern Poland and East Germany. Unlike other adventive species, such as Lunularia cruciata, this species does not

grow in made-made habitats, but predominantly colonizes natural habitats of coniferous forests, peatlands, etc. Such invasions are of great interest because
(1) they allow to study directly the factors limiting the spread and distribution of the invading species, and
(2) they may help to explain the structure and organizing forces of the invaded community.

In this paper, I shall concentrate mainly on biotic interactions accompanying the invasion using permanent plots. Unfortunately, the process of invasion seems to be almost completed in Czechoslovakia. Therefore, I could study only places already invaded by Orthodontium and not to observe directly the process of invading of this species into communities; instead, I studied mainly the dynamics of already colonized stands.

METHODS

Vegetation sampling was done at subjectively chosen plots of an area of 0.04 · 0.06 m^2, where all cryptogam species were recorded and their relative cover estimated. To assess the seasonal course of soil moisture, samples were taken at 7-14 day intervals during the 1983 vegetation season and their water content was estimated gravimetrically. The values obtained were expressed as percentage of maximum capillary capacity of the soil.

About 30 permanent plots (area 0.03-0.08 m^2) were made in various communities invaded by Orthodontium. The vegetation of these permanent plots was recorded by drawing contours of cushions of all species present on a transparent foil pressed to the moss surface. The vegetation of these plots was recorded twice a year for three years. The areas occupied by individual species were measured using a planimeter. When individual cushions could be distinguished, the effect of neighbour competition on the change in their area was calculated using the modified method of Hallett & Pimm (1979). To study the colonizing ability of Orthodontium, the original bryophyte

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cover was removed in three permanent plots in autumn, 1983.

For a rough assessment of the long term dynamics of the stands, moss cushions from the immediate vicinity of the permanent plots were collected, dissected along vertical planes and the remnants of dead mosses studied. In most cases, these remnants could be easily identified. However, the time scaling of these observations is difficult. When Orthodontium was present, the time scale could be determined by counting the successive generations of antheridia and capsules.

AUTECOLOGICAL OBSERVATIONS

There are four main substrate types colonized by Ortho-dontium in Central Europe (Reimers 1954, Muhle 1970, Fut-schig & Kurková 1977): rotten wood, tree bases, sandstone rocks (rarely), and more or less humic sandy soils. There is a marked ecological difference between these substrate types: whereas rotten wood and tree bases are the common substrate throughout Central Europe (e.g., Pankow & Lindner 1965, Muhle 1970), colonization of the latter two substrates is confined to sandstone rock areas. In contrast to non-sandstone areas, Orthodontium spreads massively here, becoming the most common bryophyte species in some parts of the sandstone rocks. It shows ecological specialization there: it prefers to grow in rather light places (but protected from direct sunlight during most of the day) on northern and eastern expositions.

As pointed out by many authors (e.g., von Hübschmann 1970), its spreading is limited by humidity conditions. Indeed, the soil moisture regime of places colonized by Orthodontium did not exhibit fluctuations as extreme as those not colonized by this species, though this difference was not particularly pronounced. Observations on permanent plots showed its considerable ability to regrow from persistent protonema after desiccation stress and apparent death (Fig. 2a). This may result in retreat and invasion cycles reflecting the weather of the year (as observed by Pankow & Lindner 1965), common in semi-arid sandstones of Central Bohemia. This behaviour in-

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dicates that the adult phase is not very sensitive to drought. The limitation by drought could occur at the juvenile phase; in favourable years without summer desiccation stress, Orthodontium would be capable of colonizing places drier on the average and could persist there later in the adult phase.

The difference in substrate preference between sandstone and non-sandstone areas (as well as between Western and Central Europe) is due to a different rate of water loss from these substrates in similar ambient conditions.
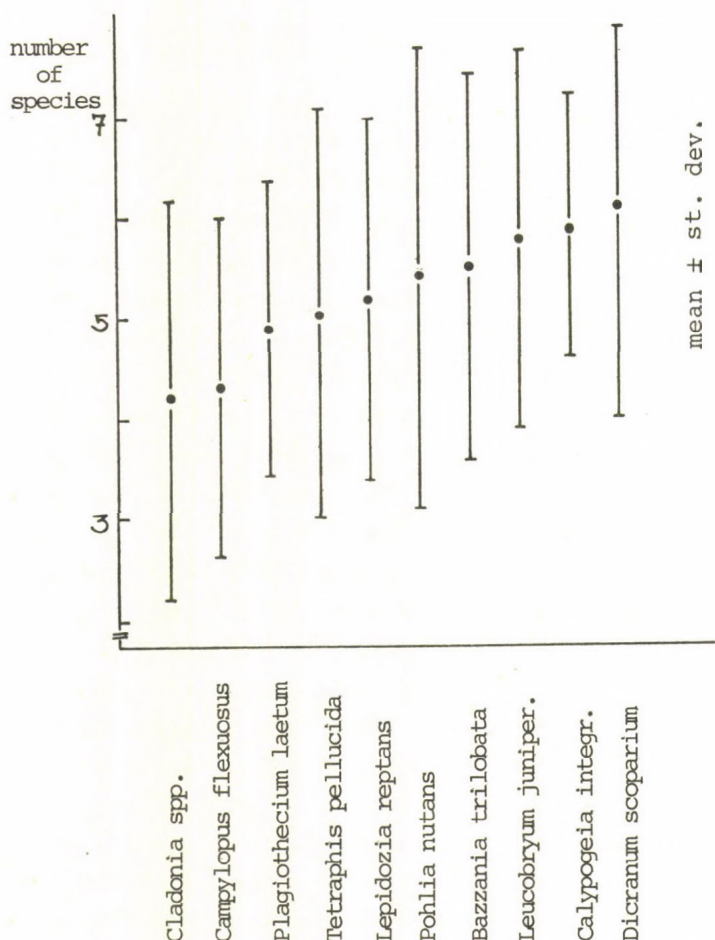
Fig. 1. Mean species richness in terricolous communities containing Orthodontium lineare together with other dominant species.

DYNAMICS OF COMMUNITIES INVADED BY ORTHODONTIUM LINEARE

In sandstone rock areas, Orthodontium is a rather good colonizer of bare soil. When the moss cover at sandy soil occupied by various communities including Orthodontium was removed, Orthodontium reappeared regularly (Fig. 2b). The first gametophores formed on the newly developed protonema carpet in less than a year; in the second year, they covered a substantial part of the free space and began to form capsules. It is by far the best colonizer of bare ground among the species present in these communities (Calypogeia integristipula, Tetraphis pellucida, Dicranella cerviculata, Pohlia nutans); these do not appear regularly and grow much more slowly (except Dicranella at one permanent plot). The progress of colonization does not depend on the type of the community present prior to the removal: both species rich communities and almost monospecific stands of Orthodontium were colonized primarily by Orthodontium.

So far little is known about competition of Orthodontium with other bryophytes. Phytosociological papers (von Hübschmann 1970, Hedenas 1981) report data on concomitant species, i.e., possible competitors in various habitats. These are mostly common acidophilous species which do not differ very much from those recorded in this study (Fig. 1).

Observations on species competition in permanent plots showed that there is no clear deterministic hierarchy of overgrowings. The outcome if competition depends on the season and may be different at different permanent plots. Furthermore, an important role is played by the size of the individual species patches. Principal trends of overgrowing are shown in Fig. 3.

According to their dynamics, three types of communities with Orthodontium lineare may be distinguished:

(1) species rich communities composed of rather large (diameter > 2 cm) patches of individual species, mostly Orthodontium, Leucobryum juniperoideum, Pohlia nutans, Plagiothecium
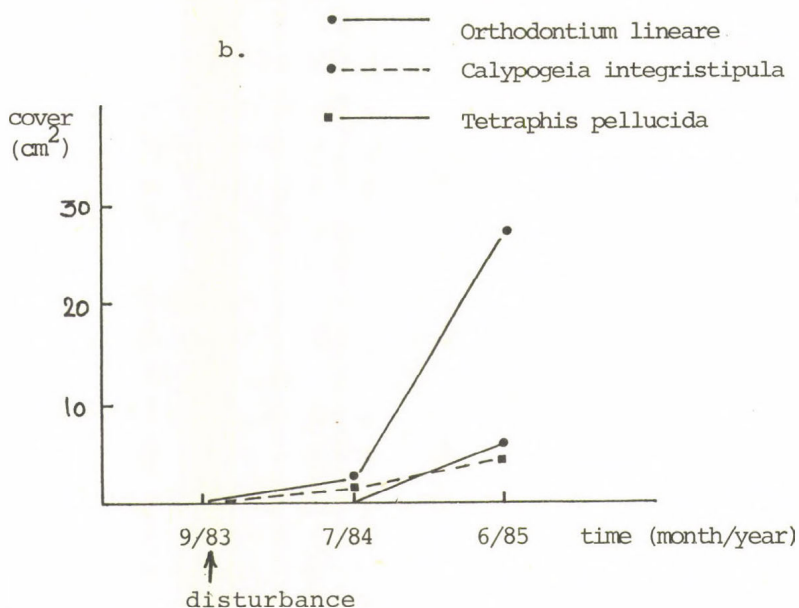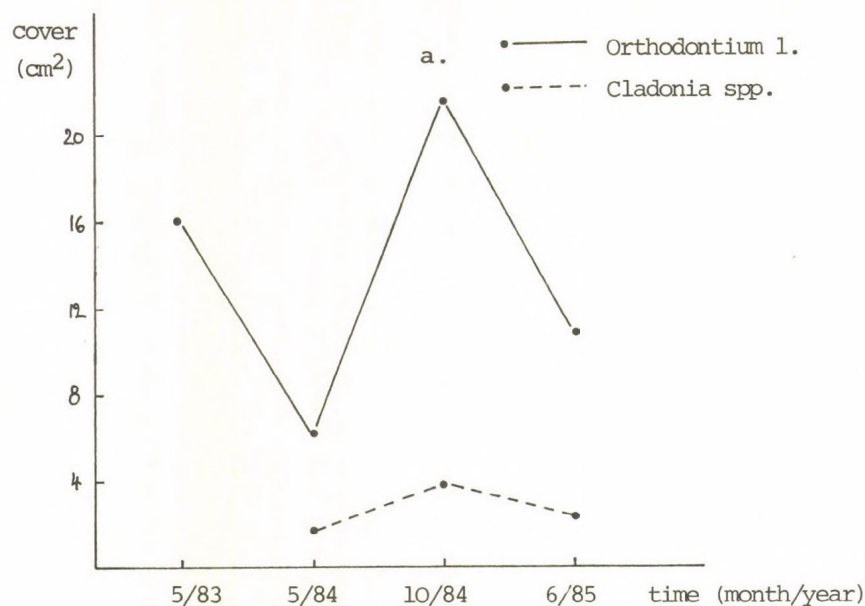
Fig. 2. Dynamics of <u>Orthodontium lineare</u> stands. a) species-poor
stand with <u>Cladonia</u> exhibiting death and regrowth cycles, b)
colonization of bare ground following disturbance of a species
rich community, c) dynamics of a species rich stand composed
of large patches, d) species rich stand of small patches.

c.

● ———	Orthodontium lineare
● - - - - ●	Leucobryum juniper.
■ ———	Pohlia nutans

d.

● ———	Orthodontium lineare
■ ———	Lepidozia reptans
⊗ ———	Dicranodontium denud.
● - - - -	Calypogeia integrist.
■ - - - -	Leucobryum juniper.
⊗ - - - -	Tetraphis pellucida
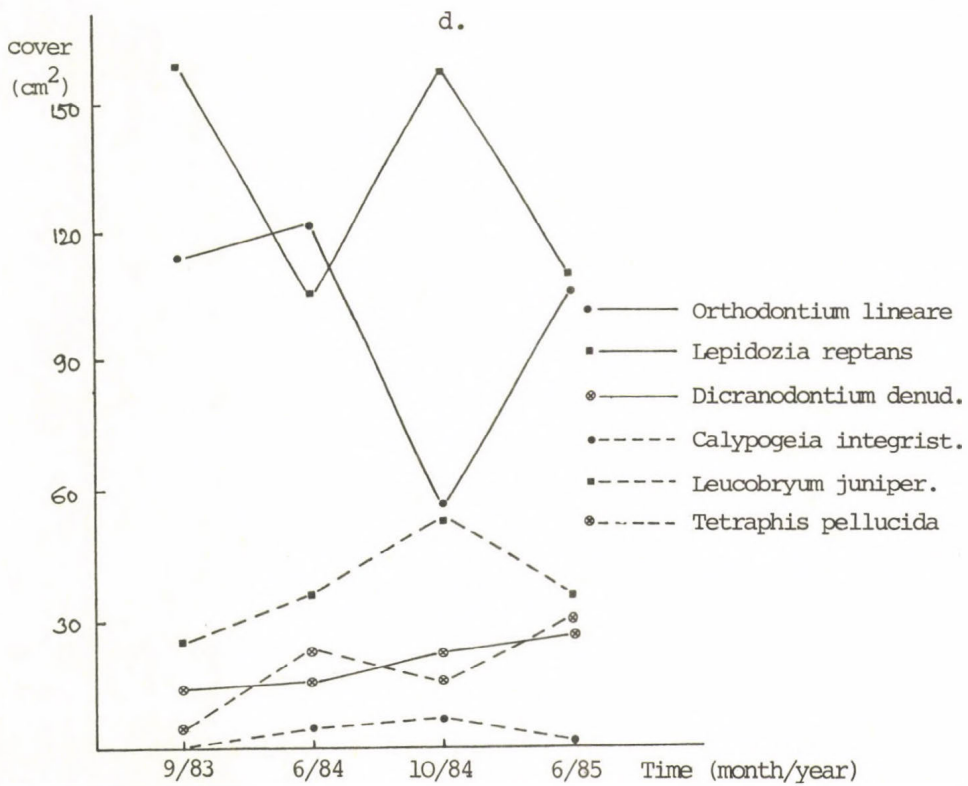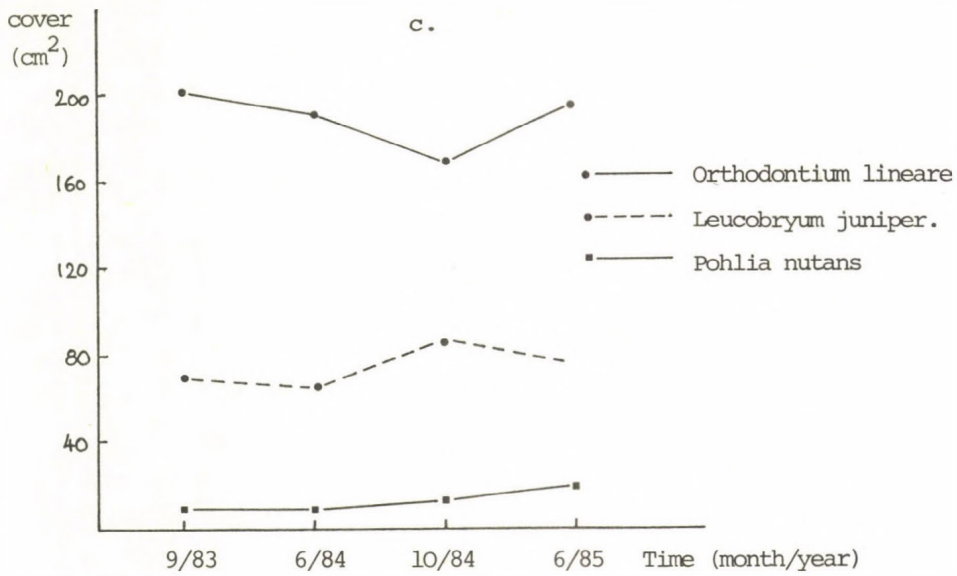
laetum (Fig. 2c). They exhibit a pronounced, but rather slow
change, consisting mainly in lateral overgrowing of cushions
(change does not exceed 20% per year). Analysis of bryophyte
remnants showed that the observed overgrowings are really uni-
directional and may result in profound change of the community
composition.

(2) species rich communities consisting of a fine scale
mixture of species, mainly Orthodontium, Tetraphis pellucida,
Calypogeia integristipula, Dicranodontium denudatum, Lepidozia
reptans, Bazzania trilobata, etc. (Fig. 2d). Their short term
rate of change is rapid, depending on the season and vertical
growth rate of species. Changes in cover may be great, but
the analysis of moss remnants does not show radical changes.
In the long run, the composition of these communities is prob-
ably more stable than that of the previous type, though it
undergoes short term quasi-cyclic changes induced by external
factors, such as climate, season, etc.

Cladonia spp.   Pohlia nutans

decreasing
overgrowing
ability

Orthodontium lineare ⇄ Lepidozia reptans

Leucobryum juniperoideum   Tetraphis pellucida
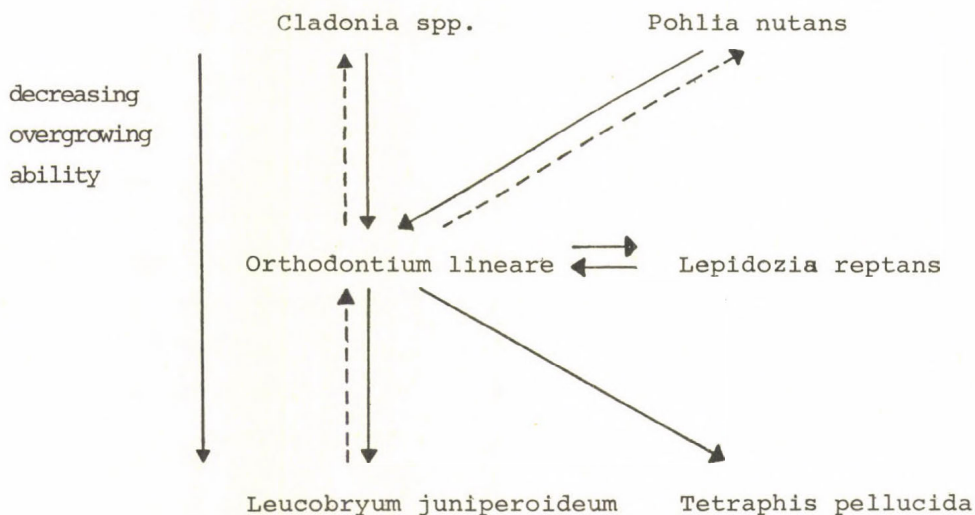
Fig. 3. Summary of the competitive interactions of Orthodontium
lineare. Arrows point to the competitively weaker species.

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(3) species poor communities of drier habitats formed by
patches of Orthodontium, Cladonia sp. div., Campylopus flexuo-
sus, Pohlia nutans (Fig. 2a). In these communities, species
composition does not play such an imprtant role as in the
previous two; change in composition is mainly due to dif-
ferent mortality of species and their regrowth after climatic
disturbances.

There is still no consensus among ecologists concerning
invasibility of communities, but it is becoming increasingly
clear that no general rule will probably be found (Robinson
& Dickerson 1984). In a very restricted theoretical case of a
system of Lotka-Volterra competitive equations, a general
criterion for invasibility is given (Shigesada et al. 1984);
nevertheless, experiments conducted in an aquatic system
gave equivocal results (Robinson & Dickerson 1984).

Further, the scenario of global competition as modelled
by Lotka-Volterra equations and aquatic systems is not a good
model for sessile bryophyte communities, where only pairwise
interactions may occur and dynamics depends strongly on the
spatial pattern. There is a growing awareness of fundamental
similarity of all such communities like lichen, marine in-
vertebrates, colonial algae, etc. (e.g., Karlson & Buss 1984,
Paine 1984), for which the same theoretical approach may be
used. According to current theory, the mechanisms of species
coexistence in these communities are constituted mostly by
non-equilibrium processes and may vary widely among the com-
munities (Seed & O'Connor 1981, Paine 1984). The invasibility
conditions are thus contingent on the particular mechanism
of community organization. There are several possible mecha-
nisms (predation is not taken into account here):
- (1) competitive non-hierarchy (Karlson & Jackson 1981);
- (2) asynchronous disturbance (Sousa 1984); and
- (3) temporal change in competitive ability (Ågren & Fager-
     ström 1984, Namba 1984), this change may be extrinsic
     (climate) or intrinsic (ageing) to the community.

All available data indicate that even in such a small
group of bryophyte communities the principal diversity main-

taining mechanisms vary greatly and cannot be easily singled
out. There is a positive evidence for the temporal change in
competitive abilities (especially in types 1 and 2), which is
probably the most common mechanism. Asynchronous disturbance
is involved in types 1 and 3. In contrast to the assertion of
Watson (1981), species coexistence in these communities is
maintained by non-equilibrium processes based on competitive
interactions between species. Such mechanisms were already
demonstrated in bryophyte communities by Kimmerer & Allen
(1982). A study of cyclic processes was done by Jahns (1982).

In such systems, the invasibility of a community need not
be easily studied. Studying structurally similar communities
of marine fouling invertebrates, Sutherland (1974) demonstrated
the existence of several stable states, differing in their
invasibility, whose development depended only on random events
at the beginning of colonization. In case of Orthodontium,
its invasion seems to be favoured mainly at the disturbed
places because of its high colonizing ability and ability to
regenerate from persistent protonema. In other communities,
Orthodontium may also perform well, but its success depends
on many factors hard to predict.

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PROGRESS WITH KNOWLEDGE OF THE SUBMERGED GENUS RIELLA (HEPATICAE) IN ARGENTINA

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An account is provided of the areas where the 5 species of Riella, known from Argentina, occur. Several were obtained from cultures of marginal sediments of lagunas, the method employed being described. Two species, R. chochonensis Hassel and R. undulata Hassel, are described for the first time.

INTRODUCTION

Riella, because of its growth habit fixed to the bottom of shallow depressions, ponds, lagoons or lakes, is seldom conspicuous and is frequently found only by accident. For example, the genus appeared in cultures of mud brought from Turkestan to Copenhagen (Porsild 1902) and from South Africa to England (Cavers 1909, Wigglesworth 1937). A review of the habitats and distribution of the genus in the world was given by Persson & Iman (1960). These authors assumed that in the genus, and in particular in R. helicophylla, growth started after the rainy season. They also described competition with vascular plants.

In Argentina, the first findings of Riella were also accidental (Hässel de Menéndez 1959, 1972). A species appeared in cultures of Ruppia cirrhosa from the Laguna Luro in the Provincia La Pampa (Gamerro 1968), but unfortunately these specimens were lost. Fresh cultures, started by the author, with sediment obtained from the margins of the same laguna, revealed plants belonging to a different species from the

two already known (Hässel de Menéndez 1979). As salt lakes or
"salinas" are plentiful in Argentina, the author decided to
sample marginal sediments from 12 lagunas in the provinces of
La Pampa and Buenos Aires in July 1983 (Fig. 1). Cultures of
Riella were obtained from only two of these lagunas: Cochicó
and Salinas Chicas. Salinity estimates and pH measurements
were available from the cultures and the natural habitats. One
new species, Riella undulata, appeared in the cultures from
Laguna Cochicó. A limnological study carried out on the Embalse
Ramos Mexia by F. Kaysin revealed the presence of another new
species, R. choconensis Hässel. In this case the plants were
collected from the benthos using the normal methods in this
kind of study.

METHODS

Sediments with crystalline efflorescences of margins of
apparent salt lakes, or saline water ponds, were collected in
plastic bags, especially from the debris area carried by waves
to the shore. Sediments were either air dried or kept moist if
the cultures were to be started immediately. The sediments
were passed through a screen of about 100 µm with tap water in
order to separate, mostly, seeds of vascular plants and eggs
of crustacea and snails. Two cultures were set up for each
sample, one containing all elements under 100 µm and the se-
cond with the larger objects. The sediment was spread in a
layer 1-2 cm thick in common aquarium containers with or with-
out aeration and located by a window facing SE, i.e., not in
direct sunlight. The purpose of the granulometric separation
was to avoid future overgrowth by vascular plants, pullulating
crustaceans and snails, and to obtain information on associated
species.

In two weeks, in sutable samples, the first nearly hyaline
germ tubes of Riella appear, and fully developed sporophytes
can be obtained in 8-10 months. If gemmae develop, as in R.
undulata, the whole bottom of the container is covered in a
short time by new plants, the gemmae becoming detached by the

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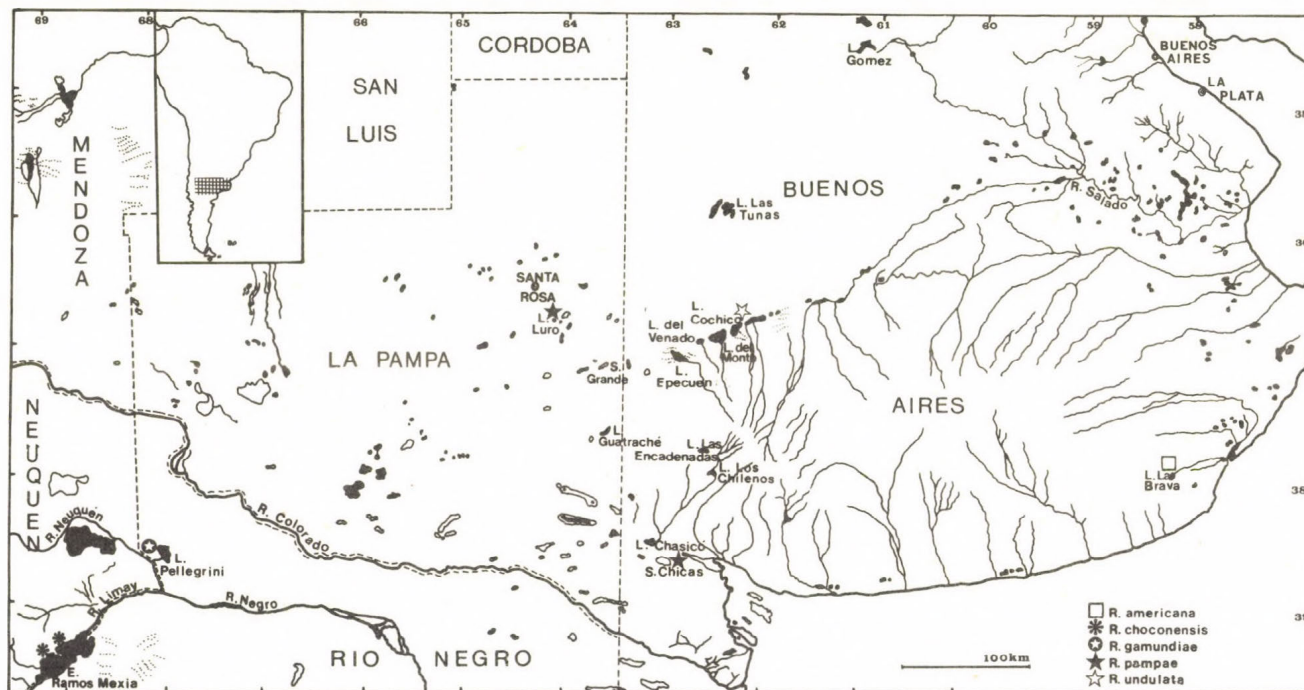
Fig. 1. Map of the distribution of the genus _Riella_ in Argentina.

addition of more water to the container. Initially, Riella
plants grow fairly quickly, but after a year they become over-
grown by algae. If erect Riella plants are too crowded and
attain great height, e.g., 7-9 cm as in R. pampae, the basal
portions of the plants die and the remainder becomes detached
and floats freely below the surfaces with stems hotizontal.
Aeration does not induce better growth.

DESCRIPTION OF LOCALITIES

Provincia Buenos Aires

This province with 900 mm (NE) to 400 mm (SW) rainfall, is
the phytogeographic "provincia pampeana", also called the
"pampa húmida". It has two mountain systems of low elevation
(300 to 1,239 m above sea level) where permanent or temporary
rivulets have their origin, some ending in closed depressions
while others continue flowing further after first forming a
lagoon. Such is the case of the Laguna Brava (see Fig. 1), sur-
rounded by low hills and with a maximum depth of 4.38 m.
Riella americana Howe & Underw. was found submerged with Lam-
prothamnium longifolium var. bulbilliferum (Dont.) Daily, as a
low carpet, towards the centre of this laguna which has a
border association of Scirpus californicus and Jussieua repens.
Cordini (1942) has given details of salinity and a pH of 6.7-
9. Laguna Cochicó (pH 8.59, salinity 15 mg/OO), a laguna de-
rived from the Sierra de la Ventana system at its N, is several
km in length and very close to Laguna del Monte. Sediment
obtained from its shore (by ruta 33, close to the bridge) yield-
ed Riella undulata Hassel, Zannichellia palustris, Scirpus
californicus and Characeae. Salinas Chicas (ph 8.10, salinity
22 mg/OO), in the SW, is a shallow laguna. Riella pampae and
Ruppia cirrhosa were obtained from cultures of marginal sedi-
ment.

Provincia La Pampa

Due to the soil constituents and climatic conditions, as
well as a rainfall of 700 mm (NE) to 150 mm (SW) a semi-arid

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to arid environment develops, recognized as the phytogeographic provinces "del espinal" to the E and "del monte" to the SW (Eskuche 1982). The highest elevations are in the centre and the S and reach 598 m. Most "lagunas" and "salinas" are closed water systems, permanent or temporary, their water supply coming either from rain or springs. Their salt content is high because of the white crystalline efflorescences at their borders. In many the water mirror (level) is only visible in the centre and the shores are of a dangerous, muddy consistency. Laguna Luro, divided by ruta 35 where the water flows under the bridge, is an example of this type. Riella pampae Hässel was obtained from cultures of the mud of the channel which runs under the bridge but was not observed in situ. The water here has a pH of c. 11, and a high Na^+, K^+ and Cl^- content (Gamerro 1968).

Provincia Rio Negro

The vegetation in the N of this province is quite similar to that of Provincia La Pampa, except for the presence of a permanent river, the Rio Negro. The Lago Pellegrini, the site of R. gamundiae, located in NW on a meseta of 300 a.s.l., is a reservoir built around 1926 connected to the Rio Negro and used to regulate its flow for agricultural purposes.

Provincia Neuquén

This territory is limited to the W by the Andes and to the E by the Rio Limay, which is fed by melting snow. In 1972, a dam was built on this river for the hydroelectric plamt known as "El Chocón", and it was in the artificial lake which formed, called Embalse Ramos Mexia, that F. Kaysin twice found R. choconensis Hässel in January, 1984, within the benthos, with Characeae on slime. The pH was estimated at 7.6 and the salinity at 8.9 mg/OO, the temperature varying from 3.5-21°C (personal communication from F. Kaysin). Where the Riella individuals were found the depth of the water varied from 0.5 to 5.80 m.

The other lagunas investigates gave negative results. Sediments from the margins of a number of lagunas with high salt content (the "salinas") were also cultured as described above, but no Riella plants developed. At other lagunas with low salinity and a high pH, from which sediment cultures were set up, no development of Riella was obtained. The author considers that in some of these cases the sampling was probably incomplete and that eventually it will be found that more lagunas are inhabited by the genus Riella.

CONCLUSIONS

The Argentinian representatives of the genus Riella, the only ones so far found in South America, do not grow in temporary dry ponds. On the contrary, they grow in lagunas or lakes, deeper than the pond described by Persson & Iman (1960), most of which are actually increasing in depth, As shown by the cultivation results, Riella individuals are capable of surviving below the surface of water, and the same situation could be expected in the field. Possibly there is continuous propagation, if space is available, by spores as well as by gemmae. Limiting factors for their development seem to be the organic components of the water, as no brackish water is preferred, and a high salinity; while pH 7 to 11 are the degrees of alkalinity observed in their natural habitat. The attachment of Riella plants seems to be possible only on fine sand and on slime, no plants having been found on rocks. Because of the great size of most of the lagunas, it was not possible to generalize about optimum basal soil conditions from soil maps. Thus, complex combinations of soil can be expected in and around them, with conditions varying during the different seasons due to the nature of the water supply. The appearance of R. choconensis and R. gamundiae, not previously known from other localities, in two artificial lakes, the first gathered 12 years after the basin was filled by the Rio Limay, suggests that spores of these species might have been transported from other lagunas by wind from marginal sediments or by birds from bottom sediments. The large number of lagunas in the area of

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34 to 40° S lat. and 57 to 70° W long. raises the possibility that other colonies of _Riella_ await discovery. For example, the presence of _Lamprothamnium haesseliae_, an associate of _Riella pampae_ (Donterberg 1984), in Laguna Salada, in the S of the prov. Buenos Aires, is regarded as a hopeful sign.

DESCRIPTIONS OF NEW SPECIES

Riella choconensis Hässel spec. nov.

Plantae dioicae erectae; lamina unilateralibus helicoidalibus, cellulis marginalibus elongatis. Antheridiis aggregatis 1-10 serialibus. Involucra ovata laevia rostrata. Sporae 117-131 μm diam., bacculis distalibus conicis truncatis 11-19 μm longis; superficie proximalibus minute vermicularibus, bacculus 9-21 μm longis.

Holotypus: Argentina, Neuquén, Embalse Ramos Mexia, estación muestreo A 10, bentos, F. Kaysin 7-I-1984 (BA 33608). Additional specimens: Ibid, II-1984 (BA 33609); Ibid, VI-1984 (BA 33610).

This species can be distinguished from the other species of the genus _Riella_ known from Argentina by its rostrate involucra and by the densely bacculate spores with a vermiculate folded proximal surface.

Riella undulata Hässel spec. nov.

Plantae dioicae erectae; lamina unilateralibus solum undulata, cellulis marginalibus breviora quam cellulis centralibus; margine minute crenato. Antheridiis aggregatis 1-6 serialibus. Involucra quasi sphaerica. Sporae 84-94 μm diam; superficie distalibus bacculis conicis truncatis 4.7-9.4 μm longis; superficie proximalibus verrucis 2.3-3.5 μm longis.

Holotypus: Argentina, Buenos Aires, Laguna Cochicó, G. Hässel de Menéndez III-1984 (Ba 33612).

This species is easily recognized by its lamina being only undulate. From R. gamundiae, which also has short bacculate spores, it differs in having a smooth involucra, the latter being keeled in R. gamundiae.

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LATE QUATERNARY FOSSIL MOSS FLORAS OF
EASTERN NORTH AMERICA:
EVIDENCE OF MAJOR FLORISTIC CHANGES
DURING THE LATE PLEISTOCENE
- EARLY HOLOCENE TRANSITION

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New data about late- and postglacial moss floras of regions
near the southern limit of continental glaciation in eastern
North America establish the widespread occurrence of calcico-
lous mosses during late-glacial times and indicate the pre-
dominance of base-rich conditions. Where calcareous bedrock,
till, or ground water are present, calcicoles remain a part
of the flora. However, even in areas of acidic soils and bed-
rock, there was an early period following deglaciation when
calcicoles prevailed. Two depositional basins in acidic regions
(Upper South Branch Pond, Maine; Tom Swamp, Massachusetts)
provide stratigraphic records of the shift from base-rich
to base-poor conditions in the early Holocene or late Pleisto-
cene. The transitions were not synchronous at these sites but
reflected instead local vegetational, edaphic, altitudinal,
and latitudinal differences. A confounding factor is that
inorganic sediments ceased being deposited during the transi-
tions. The shift in depositional mode signaled the end of
transport of materials from surrounding surfaces and the
start of autochtonous sedimentation. The floristic change is
marked by the loss of calcicoles, the elimination of arctic,
arctic-alpine, and subarctic elements, and the gain of North
Temperate Zone calcifuge mosses.

INTRODUCTION

The late Pleistocene history and paleoecology of the
eastern North American bryoflora is becoming better understood

as studies of fossil mosses in radiocarbon dated deposits increase in number. Recent work (e.g., Birks 1976, Miller 1980, Janssens in Mott et al. 1981, Tolonen & Tolonen 1984, Watts 1979) has shown not only the feasibility of obtaining large series of identifiable moss fossils from late-glacial lacustrine and fluvial deposits but also that mosses can provide paleoenvironmental information otherwise unobtainable from the more commonly undertaken studies of pollen and vascular plant macrofossils. Late-glacial fossil moss assemblages in eastern North America contain numerous terrestrial and aquatic calcicoles, although some species of acidic habitats are consistently present also. Most of the published studies have involved fossils from regions of calcareous bedrock and/or glacial drift, and the extant local bryofloras of these areas have a conspicuous calcicolous element consisting in large part of the same species that were present during late-glacial time. However, it is now apparent that even in areas where the bedrock and drift are noncalcareous and the present flora contains calcicoles, there was a period immediately following deglaciation when a diverse flora of calcicolous mosses existed. Therefore, while differing in species composition, late-glacial bryofloras of eastern North America were consistent in the presence of species characteristic of wet to dry, base-rich habitats. The loss of calcicoles from acidic areas within this region must therefore postdate this early period of widespread calcicolous floras. These relationships among late-glacial and contemporary floras of eastern North America are examined here in the light of new and already published paleobotanical and paleoecological data.

METHODS

Cores of lake sediment from Upper South Branch Pond (Maine) and Tom Swamp (Massachusetts), two sites on acidic bedrock and glacial drift, were raised with Livingstone piston samplers (internal diameter = 4.7 or 10 cm). The Upper South Branch Pond (USBP) core was subdivided into segments of known volume, which were disaggregated in warm 5% KOH and sieved. Core segments from Tom Swamp (TS) were broken down in tap water or warm 2.5% KOH; a few samples were also treated

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with 5% Na_2CO_3. All material retained by a 180 μm screen
(USBP) or a 250 μm screen (TS) was examined microscopically
and sorted into identifiable components. The fossil mosses
were dissected or sectioned as necessary and mounted on slides
in Hoyer's solution. A reference collection of Hoyer's solu-
tion mounts of plants from herbarium specimens was used to
facilitate comparisons of microscopic details. The number of
fragments (leafy plants, individual leaves, or in a few cases
parts of leaves bearing diagnostic features) per sample were
tallied. Because the number of fragments per sample was rela-
tively low (1 to 275) and varied greatly between samples,
the data were standardized to the number of fragments per 10
cm^3 (USBP) or per 100 cm^3 (TS). Actual sample volumes were
17, 26, 43, 69, or 139 cm^3 (USBP) and 121, 173, 191, or 243 cm^3
(TS).

The following information describes the study sites (Fig.
1):
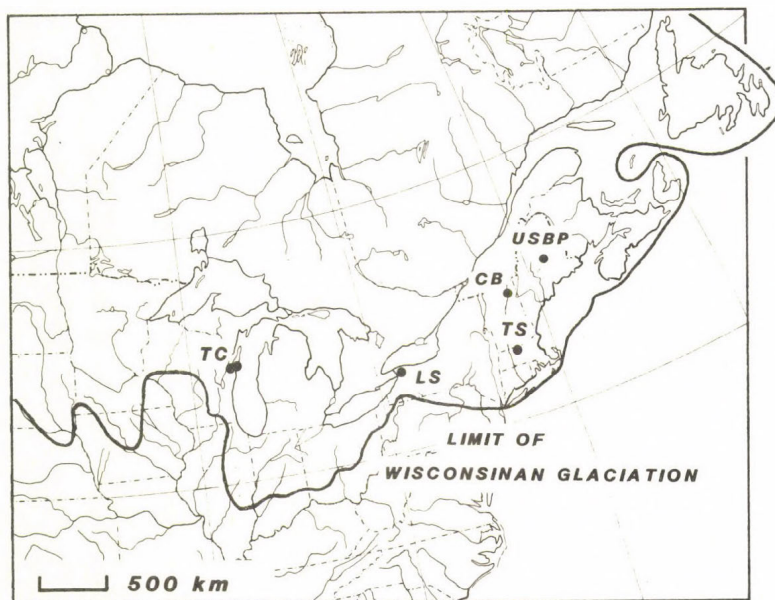
Fig. 1. Map showing location of sites discussed in text. Key:
USBP = Upper South Branch Pond, Maine, CB = Columbia Bridge,
Vermont; TS = Tom Swamp, Massachusetts; LS = Lockport Site,
New York; TC = Two Creeks Forest Bed, Wisconsin.

Upper South Branch Pond, Piscataquis County, Maine (46°5'
N Lat, 68°54'W Long) is a 34 ha lake at 300 m elevation in a
watershed of 1720 ha; local relief is 682 m; bedrock is
Traveler rhyolite (Devonian), and where exposed, the glacial
drift is noncalcareous. The existing forest vegetation is of
the hemlock-white pine-northern hardwoods type with abundant
aspens (Populus grandidentata and P. tremuloides), balsam fir
(Abies balsamea), red spruce (Picea rubens), and paper birch
(Betula papyrifera), the origin of which can be traced to an
extensive forest fire in the watershed in 1903. Further back-
ground information including Pleistocene and Holocene pollen
and plant macrofossil stratigraphies and their interpretation
is found in Anderson et al (1985).

Tom Swamp, Worcester County, Massachusetts (42°32'N Lat,
72°13'W Long) is a large (250 ha) peatland located in a valley
and occupying the divide between two drainage systems; the
peatland surface is at an elevation of ca. 232 m, and local
relief does not exceed an additional 150 m. Bedrock is alumi-
nous mica schist, quartose schist, and aluminous phyllite of
the Littleton Formation (Lower Devonian: Zen 1983); glacial
drift is composed mainly of locally derived rock material
(Alden 1925). The forest vegetation on slopes adjacent to
the peatland belongs to the hemlock-white pine-northern
hardwoods type with mesic, late successional stages predominat-
ing and Quercus spp. common on drier sites. The peatland is
largely a Larix laricina - Picea mariana treed bog. Davis
(1958) has published a pollen diagram for Tom Swamp based on
sediment samples taken from a slightly deeper part of the
basin, ca. 200 m west of the sampling site reported here.

RESULTS

The bryophytes identified and their stratigraphic occur-
rences are shown on Figures 2 and 3. Late-glacial sediments at
TS yielded materials of 32 species of mosses. Additional
fossils representing species of Encalypta and Mnium (s. lat.)
were recovered also, as were plant fragments referrable to the
following liverwort genera: Anthelia, Cephaloziella, Soleno-
stoma (or Jungermannia), and Scapania. These Hepaticae are

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Fig. 2. Moss and other plant macrofossils in late-glacial sediments at Tom Swamp, Massachusetts, U.S.A. The circled numbers 1-5 refer to moss associations and the inferred habitat types (see text); associated macrofossils of selected vascular plants are graphed under the circled 6. Column "a" at left describes the sediments (see key at bottom of diagram); column "b" is the sample interval (in black).

Fig. 3. Mosses in late-glacial and Holocene sediments at Upper South Branch Pond, Maine, U.S.A. The circled numbers refer to moss associations and inferred habitat types (see text).

noteworthy because of the apparent rarity of Pleistocene and Holocene fossil liverworts (Miller 1984). At USBP 24 species of mosses (plus Arctoa/Kiaeria sp., Encalypta sp., Grimmia sp., Sphagnum sp.) were recovered from late-glacial sediments, and an additional seven were present in the Holocene lake muds (Fig. 3). These seven species plus Sphagnum sp. are presented in groups 4-6 on Fig. 3. Group 5 contains Eurhynchium riparioides, a moss of wet rocks ar running water of streams, group 6, Sphagnum, the sparse record of which is probably a reflection of species growing on wet rocks or soil but not in mires. The composition of the late-glacial assemblages is summarized in Tables 1 and 2.

At TS an abrupt decline in the representation of mosses occurred during the radiocarbon dated interval, 12,830± 120 yBP, which also marks the first appearance of spruce needles in the sediment column (Fig. 2). These changes took place after the deposition of autochtonous organic material had begun in the basin, but while a large amount of clay was still accumulating. The spruce zone ended at 10,080 ± 100 yBP (WIS-1212), 1.9 m higher in the core (7.7 m; Bender et al. 1982). Three fossil assemblages can be recognized in the TS sedimentary record: an older late-glacial one rich in terrestrial mosses (Fig. 2), a younger late-glacial assemblage with a few fen mosses and various Sphagna (Fig. 2), and a postglacial assemblage with Brachythecium sp., Climacium americanum, Sphagnum centrale and S. subsecundum (which is based on analyses of Holocene peats at 7.11, 6.6, and 3.25 m).

Table 1. Summary statistics: eastern North American late-glacial moss floras.

Site	# species	% reported from local flora	% reported from regional flora	(a) % calcicoles	%(a) reported from local flora	%(a) reported from regional flora
Upper South Branch Pond, Maine	24	38(9/24)	75(18/24)	38(9/24)	0	22(2/9)
Tom Swamp, Massachusetts	32	41(13/32)	75(24/32)	47(15/32)	20(3/15)	60(9/15)
Columbia Bridge, Vermont	45	82(37/45)	82(37/45)	71(32/45)	75(24/32)	75(24/32)
Lockport Site, New York	32	63(20/32)	84(27/32)	69(22/32)	59(13/22)	82(18/22)
Two Creeks Forest Bed, Wisconsin	39	74(29/39)	82(32/39)	67(16/39)	73(19/26)	77(20/26)

Data on extant floras from Lowe (1939) and Parlin (1939) for Maine, Hilferty (1960) and Mishler and Miller (1983) for Massachusetts, my unpublished studies of the northern Vermont bryoflora, Ketchledge (1980) for New York, and Bowers and Freckmann (1979) for Wisconsin.

Table 2. Presence (+) of mosses in late-glacial sediments at Upper South Branch Pond, Maine (USBP), Tom Swamp, Massachusetts (TS), Columbia Bridge, Vermont (CB), Lockport Site, New York (LS), and Two Creeks Forest Bed, Wisconsin (TC).

	USBP	TS	CB	LS	TC
Andreaea rothii	+	.	.	.	.
Amblystegium serpens	.	.	.	.	+
Atrichum angustatum	.	+	.	.	.
Aulacomnium acuminatum	.	.	.	+	-
A. palustre	+	+	*	+	+
A. turgidum	+	+	.	+	+
Brachythecium salebrosum	.	.	.	.	+
B. turgidum	.	.	+	.	+
Bryoerythrophyllum recurvirostrum	+	.	+	+	+
Bryum pseudotriquetrum	+	.	+	+	+
B. tortifolium	.	.	.	.	+
Calliergon cordifolium	.	.	.	.	+
C. sarmentosum	.	+	.	.	.
C. stramineum	.	.	.	.	+
C. richardsonii	.	.	+	.	.
Campylium chrysophyllum	.	+	.	+	.
C. polygamum	.	.	.	.	+
C. stellatum	+	+	+	+	+
Catoscopium nigritum	.	.	+	.	.
Ceratodon purpureus	+	+	+	+	.
Cirriphyllum cirrosum	.	+	.	.	.
Cratoneuron commutatum	.	.	+	.	.
Dichodontium pellucidum	+	.	*	.	.
Dicranella heteromalla	.	.	.	.	+
D. schreberiana	.	.	.	+	.
D. varia	.	.	+	+	.
Dicranum fuscescens	.	.	.	+	.
Didymodon asperifolius	+	.	.	.	.
Distichium capillaceum	*	*	*	*	*

Table 2 (continued)

	USBP	TS	CB	LS	TC
Ditrichum flexicaule	+	+	+	+	+
Drepanocladus aduncus	.	+	+	+	+
D. exannulatus	.	+	+	+	.
D. fluitans	.	.	.	+	.
D. revolvens	.	.	+	+	+
D. sendtneri	.	.	.	.	+
D. uncinatus	+	.	.	.	+
D. vernicosus	.	.	+	+	+
Encalypta alpina	.	.	+	.	.
E. procera	.	.	*	.	+
Eurhynchium pulchellum	.	.	.	.	+
Fissidens bryoides	+	+	+	.	.
F. osmundioides	.	+	*	+	.
Gymnostomum aeruginosum	.	.	.	+	.
Hygroamblystegium tenax	.	.	+	.	.
Hygrohypnum luridum	.	.	+	.	.
Hylocomium splendens	+	.	.	+	+
Hypnum bambergeri	.	.	.	.	+
H. lindbergii	.	.	+	.	.
H. pallescens	.	.	.	.	+
H. pratense	.	.	+	.	.
H. revolutum	+	+	+	.	.
H. vaucheri	.	.	+	.	.
Meesia longiseta	.	+	.	.	.
M. triquetra	.	.	.	+	.
M. uliginosa	.	.	+	+	.
Mnium marginatum	.	.	.	.	+
M. pseudopunctatum	.	.	.	+	.
M. thomsonii	.	.	+	.	.
Myurella julacea	.	+	+	.	+
Orthotrichum obtusifolium	.	.	.	.	+
Paludella squarrosa	.	+	.	.	.
Philonotis fontana	+	+	+	.	.
Pogonatum alpinum	+	+	.	.	.
P. dentatum	.	+	.	.	.

Table 2 (continued)

	USBP	TS	CB	LS	TC
P. urnigerum	+	+	+	.	.
Pohlia cruda	.	.	*	.	.
Polytrichum commune	.	+	.	.	.
P. juniperinum	+	+	+	+	.
P. piliferum	+	+	+	.	.
Pseudocrossidium revolutum	.	.	+	.	.
Rhacomitrium canescens	+	.	.	.	.
Rhytidium rugosum	+	+	.	.	.
Scorpidium scorpioides	.	+	+	.	+
S. turgescens	.	.	+	+	+
Sphagnum capillifolium/fuscum	.	+	.	.	.
S. magellanicum	.	+	.	+	.
S. papillosum	.	+	.	.	+
S. teres	.	+	.	.	.
Thuidium abietinum	+	.	+	+	+
T. recognitum	.	.	.	.	+
Timmia novegica	.	.	+	.	.
Tomenthypnum nitens	.	+	.	+	+
Tortella fragilis	.	.	+	.	+
T. inclinata	.	.	+	+	+
T. tortuosa	.	.	.	+	+
Tortula ruralis	+	.	*	+	+
Trichostomum crispulum	.	.	+	.	.
T. tenuirostre	.	.	.	.	+
Weissia controversa	.	.	+	.	.

*Identification probable.

DISCUSSION AND INTERPRETATION

Paleofloristics

At both TS and USBP mosses are most diverse and numerous
during late-glacial time prior to the appearance of spruce in
the watershed as documented by the presence of needles or
fossils otherwise indicating trees. The zone of maximum bryo-
phyte occurrence appears to reflect the ease with which the
plant materials were washed into the basins from the surround-
ing slopes together with sand, silt, and clay. These upland
surfaces provided inorganic sediments and plant materials in-
dicative of open terrestrial habitats over a rather long
stratigraphic interval. Some of bryophyte and vascular plant
macrofossils belong to extant species of subarctic, arctic, or
arctic-alpine regions. These include the mosses Aulacomnium
turgidum (TS, USBP), Calliergon sarmentosum (TS), Cirriphyllum
cirrosum (TS), Didymodon asperifolius (USBP), the hepatic
Anthelia sp. (TS), and the seed plants Cassiope hypnoides
(leaves; TS), Dryas integrifolia (leaves and fruits; TS, USBP),
Oxyria digyna (fruits; USBP), and Silene acaulis (seeds, TS)
(see Fig. 2, group 6). The present North American ranges of
most of the other identified mosses are broadly northern (wide-
spread in the boreal forest zone and into the subarctic/arctic);
many reach their southern distributional limits as places in
the Great Lakes region.

The diversity and abundance of mosses recovered from Holo-
cene sediments at TS and USBP is low. The species represented
are either known from or expected components of the present
floras of areas bordering the depositional basins.

Paleoecology

The floristic and sedimentary evidence indicates that
early late-glacial upland surfaces near the sampling sites
were prone to erosion and had an incomplete plant cover of
low, light-demanding shrubs and herbs and associated bryophytes.
Physiognomically and floristically the plant cover was similar

to areas of existing tundra in the northeastern North America. Because the habitat specificities of extant populations of the mosses are known at least qualitatively and also because of the good representation of mosses, it is possible to recognize a number of distinct late-glacial plant communities and associated edaphic features (substratum type, pH, moisture) within this general vegetation type. These are designated with circled numbers in Figures 2 and 3. The habitats are (1) acidic rock and/or soil, xeric (TS, USBP); (2) calcareous rock or soil, xeric to mesic (TS, USBP); (3) rock or soil, pH indifferent, mesic (TS, USBP); (4) fen peat or calcareous flushes, minerotrophic (TS) and soil or rock, calcareous to acid, wet but not aquatic (USBP). The existence during late-glacial time of numerous species associated with dry to moist, calcareous upland soils or rocks at both TS and USBP and of base-rich fen peat or calcareous flushes at TS is significant in view of the absence of such plants (and habitats) from their present respective floras. Conditions were appropriate for these mosses until the remains of trees (particularly spruce) entered the sedimentary record, an event that is roughly correlated with the cessation of clay deposition and the onset of gyttja accumulation. At TS these changes took place at 12,830 ± 120 yBP, while at USBP the transition was at least 1800 radiocarbon years later, viz. after 10,965 ± 230 yBP (see Anderson et al. 1985).

It is unclear whether the development of forest communities and the attendant accumulation of a humus layer (sensu Berglund & Malmer 1971) or other changes in the soil, for example, the leaching of calcium, resulted in the loss of calcicoles at USBP and TS. Through chemical analyses of lake sediments at sites in northwestern Europe, Berglund & Malmer (1971) and others have shown a significant reduction in the annual deposition of calcium following the late-glacial/postglacial transition. Experiments suggest that mosses restricted to calcium-rich saxicolous habitats have a greater calcium requirement for cell membrane permeability control than do calcifuges (Bates 1982). Thus the elimination of calcium from

soils and glacial drift through leaching, precipitation, and deposition may account for the loss of calcicoles from upland habitats. A lowered pH would be expected with the loss of calcium, and for lakes in the Adirondack Mountains, U.S.A., diatom analyses have in fact shown that the waters were initially alkaline (pH=7-8) and that acidification began during late-glacial and early postglacial time (Whitehead et al. 1985).

In contrast to the TS and USBP records, which are in regions now supporting few calcicolous bryophytes, the late-glacial moss assemblages from Columbia Bridge, Vermont (Miller & Thompson 1979), Lockport, New York (Miller 1973), and the Two Creeks Forest Bed, Wisconsin (Miller 1976) contain many calcicoles that are still represented in the three local floras (Table 1). This presumably relates to the abundance of calcareous bedrock (calcareous schists, limestone, dolomite) and till, as well as to the presence of other appropriate habitat factors. Whether local populations of the species were maintained throughout the Holocene is unknown because complete stratigraphic records covering the entire late Quaternary are presently not available. However, Holocene fossils of some rich fen mosses have been discovered at a few places in the upper Great Lakes region, including Manitoulin Island (Ontario, Canada; _Calliergon_ _trifarium_, _Scorpidium_ _scorpioides_ at ca, 6790 ± 100 yBP; Warner et al. 1984), Gleason Bog (Chebogan County, Michigan; _Calliergon_ _trifarium_, _Drepanocladus_ _revolvens_, _Scorpidium_ _scorpioides_ at ca. 7670 ± 90 yBP), and Lake Sixteen (Chebogan County, Michigan; _Calliergon_ _trifarium_, _Drepanocladus_ _revolvens_, _Meesia_ _triquetra_ and _Scorpidium_ _scorpioides_, younger than 3030 ± 70 yBP). These records indicate the widespread spatial and temporal occurrence of rich fens in northern Michigan and adjacent parts of Canada during the Holocene.

THE BRYOFLORA OF GLACIATED EASTERN NORTH AMERICA: TOWARD AN
UNDERSTANDING OF ITS DEVELOPMENT DURING THE LATE QUATERNARY
TIME

Sufficient information is now available for glaciated
portions of temperate eastern North America to establish that
a floristically and ecologically diverse moss flora became
established soon after glacial ice disappeared. Moss fossils
from more than 15 late-glacial deposits, located in the region
between Maine and Minnesota southward to Pennsylvania and
southern Michigan, document the existence of floras with nume-
rous calcicoles, both terrestrial species and those of fens
influenced by minerotrophic ground water and/or of base-rich
seeps. In two edaphically acidic areas, north-central Maine
and central Massachusetts, calcicoles dropped out of the fossil
record during the transition from tundra to spruce woodland.
In Maine the calcicoles were replaced by a smaller assemblage
of mosses typical of the late Holocene acidic forest soils of
the region. The loss of calcicoles took place some 1800
radiocarbon years later at USBP than at TS, which corresponds
to the time required for spruce to migrate from southern to
northern New England. Habitat and climatic differences between
the two sites, which are 500 km apart, may also account for
some of the difference. While there is no evidence at USBP of
the presence of a peripheral fen or bog mat stopping the move-
ment of water-carried plant material from upland slopes into
the basin (and therefore biasing the record), at TS the occur-
rences of brown mosses and Sphagnum leaves above the early
late-glacial moss assemblage (see Fig. 2, groups 4 p.p. and 5)
may indicate the existence of fens or bogs at the margin of
the basin. However, because spruce needles and various other
plant macrofossils (not shown in Fig. 2) continued to be re-
presented in the sediments, plant materials did not in fact
cease being transported to the basin from the upland. There-
fore the loss of calcicoles from the Tom Swamp watershed at
12,830 yBP does not appear to be an artifact of depositional
processes.

The three late-glacial fossil floras from sites associated
with calcareous substrata also contain numerous calcicole

mosses, and many of these are represented in the extant local floras. In the absence of long stratigraphic records from appropriate sites it is impossible to know whether any of these mosses were lost from the floras during late- or early post-glacial environmental changes. That many (and in particular species of rich fens) remained in the region seems likely because of Holocene fossil occurrences. Thus at least some of the differences between the bryofloras of calcareous and acidic regions in glaciated eastern North America appear to be traceable to changes that took place during late- or early postglacial time when calcicoles appear to have been lost from areas where acidic substrata are now prevalent.

For acidic regions, the data support the following pattern: loss of the calcicolous element during late-glacial time and the gain of more calcifuges in the Holocene; for calcareous regions, the pattern is persistence of calcicoles through the Holocene and the postglacial addition of species of base-poor soils. These patterns suggest many additional questions about the migrational history of the various floristic components, questions that may be answered by analyses of additional lake and peatland sediment samples from critical locations and sites.

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ENDEMISM OF THE BRYOPHYTE FLORA IN NEW GUINEA

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The endemism of 22 hepatic families and 8 moss families occurring in New Guinea, and the ecology of 52 endemic bryophytes were studied. 48% of the hepatic species and about 23% of the moss species are endemic. Most of the endemic species occur at the altitudes of 1500-3500 m. The Frieda River Area in West Sepik Province is an exception with a high level of endemism at 200-1350 m. This may be in connection with the high concentration of heavy metals in the Frieda River Area. Three groups of endemics can be distinguished on the basis of their habitat ecology: (1) species confined to open habitats, mostly alpine and open grasslands (11), (2) species with a wide ecological amplitude (4), and (3) species almost confined to tropical rain and moss forests (37).

MATERIAL AND METHODS

In 1981, two of us (Koponen and Norris) made an expedition to the Huon Peninsula in Papua New Guinea. We collected about 17,500 specimens of bryophytes (see Koponen & Norris 1983a). The work based on these collections is mainly taxonomic. However, the material is also sufficient to be used for ecological and plant geographical studies.

The present study on the habitat ecology of 52 endemic bryophyte species is based on the information given by Koponen & Norris (1983b, 1984, 1985a,b), Frahm et al. (1985), Piippo (1984a,b, 1985a,b,c,d), Grolle & Piippo (1984b) and Norris &

Koponen (1985a,b). The percentages of endemism are based on
22 hepatic families and 8 moss families. Most of the informa-
tion on the hepatics is based on the studies by Piippo and
Grolle & Piippo (see above), but the numbers for the Frullania-
ceae are based on Hattori (1982); Plagiochilaceae on Inoue
(1982); and Radulaceae Yamada (1979, 1982). The information
about Bazzania (Lepidoziaceae) was gathered from Kitagawa's
(1979, 1980) studies and from Grolle & Piippo (1984a). Data
on the mosses is based solely on the studies by Koponen &
Norris; Norris & Koponen and Frahm et al. (see above).

RESULTS

Percentage of endemism

The endemism based on 22 hepatic families out of the 39
families known from Western Melanesia is 48% (Table 1). The
genera Bazzania, Frullania and Radula are included because
they show a high percentage of endemism. Especially in Frul-
lania and Plagiochila the degree of present-day evolution of
new taxa is high. Lejeuneaceae is the family considered the
most rapidly evolving group among Hepaticae. However, this
family has not yet been studied by us, and the previous
studies are regarded as too scattered to be useful here.

The percentage of endemism of the mosses is 23% on the
basis of only eight moss families (Table 2). The figure is
obviously tentative, and some of the most rapidly evolving
groups such as the Sematophyllaceae and Hookeriaceae are not
included.

The altitudes and habitat ecology of the endemic species

The study of the habitat ecology of the endemic species
is based on 52 bryophyte species. They occur almost exclusively
at high altitudes, mostly between 1500 and 3500 m. The Frieda
River Area in West Sepik is an exception. There the endemics
occur at clearly lower altitudes, 200-1350 m (Appendix 1, 2),
than elsewhere in New Guinea.

Table 1. The endemism of _Hepaticae_ in 22 families in Western Melanesia (for further information see text).

	Number of species	Number of endemics	% of endemism
Haplomitriaceae	1	-	-
Lepicoleaceae	2	-	-
Herbertaceae	5	-	-
Pseudolepicoleaceae	3	1	33
Trichocoleaceae	2	-	-
Lepidoziaceae (Lepidozioideae, Zoopsoideae, Bazzania)	89	37	51
Calypogeiaceae	3	-	-
Adelanthaceae	1	-	-
Cephaloziaceae	7	-	-
Jackiellaceae	1	-	-
Scapaniaceae	2	-	-
Geocalycaceae	27	6	22
Plagiochilaceae (Plagiochila)	59	47	78
Arnelliaceae	1	-	-
Acrobolbaceae	3	-	-
Schistochilaceae	19	14	74
Balantiopsaceae	2	1	50
Pleuroziaceae	2	-	-
Radulaceae	34	7	21
Porellaceae	4	2	50
Frullaniaceae	77	48	62
Jubulaceae	2	1	50
Total:	346	165	48

	Number of species	Number of endemics	% of endemism
Thuidiaceae	12	1	8.3
Meteoriaceae	16	1	6.3
Hylocomiaceae	2	1	50.
Rhytidiaceae	1	-	-
Dicranaceae (Atractylocarpus, Bryohumbertia, Campylopodium, Campylopus)	12	2	17.
Leptostomataceae	2	2	100.
Bryaceae	35	12	34.
Mniaceae	7	1	14.

On the basis of the habitat ecology, the endemics can be grouped as follows:

1. *Species confined to open habitats, mostly alpine and open grasslands (11 species)*

Hepaticae

    <u>Heteroscyphus</u> <u>sarawaketanus</u> Piippo

    <u>Lepidozia</u> <u>gwamii</u> Piippo

Musci

    <u>Anomobryum</u> <u>bulbiferum</u> Barts.

    <u>A</u>. <u>hyalinum</u> T. Kop. & Norris

    <u>A</u>. <u>ochii</u> T. Kop. & Norris

    <u>Brachymenium</u> <u>huonii</u> T. Kop. & Norris

    <u>B</u>. <u>gracile</u> Bartr.

    <u>Bryum</u> <u>pseudoblandum</u> T. Kop. & Norris

    <u>B</u>. <u>sclerodictyon</u> Dix.

    <u>Campylopus</u> <u>austrosubulatus</u> Bróth.& Geh.

    <u>Leptostomum</u> <u>perfectum</u> Bartr.

2. *Species with a wide ecoloigical amplitude* (*4 species*)

Hepaticae

    Leptoscyphus huonicus Piippo

Musci

    Bryum perdecurrens Bartr.

    Leptostomum intermedium Broth.

    Plagiomnium cordatum T. Kop. & Norris

3. *Taxa almost confined to tropical rain and moss forests*
(*37 species,* * = *not completely confined*)

Hepaticae

    Balantiopsis ciliaris Hatt. ssp. novoguineensis Hatt.

    Kurzia longicaulis Piippo

  *K. pallida Piippo

    Lepidozia bursifera Hatt. & Grolle

    L. lacerifolia Steph.

    L. loriana Steph.

    Mastigophora sepikiana Piippo

    Metahygrobiella macgregorii (Steph.) Schust.

    Lophocolea morobeana Piippo

    L. teptepensis Piippo

    L. wambana Piippo

    Porella grollei Hatt.

    P. viridissima (Mitt.) Grolle var. novoguineensis (Hatt.)
       Hatt.

  *Pseudolepicolea grolleana (Schust.) Grolle

    Schistochila antara Grolle

    S. schultzei Steph.

    S. undulatifolia Piippo

    Telaranea kaindina Grolle

    T. lawesii (Steph.) Grolle

    T. trisetosa (Steph.) Grolle

Musci

    Aerobryidium fuscescens Bartr.

  *Brachymenium nepalense Hook. var. globosum Bartr.

B. <u>wabagense</u> (Bartr.) T. Kop. & Norris

<u>Campylopus</u> <u>clemensiae</u> Bartr.

<u>Chaetomitrium</u> <u>friedense</u> Norris & T. Kop.

<u>Distichophyllum</u> <u>albomarginatum</u> Norris & T. Kop.

<u>D</u>. <u>leskeodontoides</u> Norris & T. Kop.

<u>Ectropothecium</u> <u>giganteum</u> Norris & T. Kop.

<u>Glossadelphus</u> <u>ovatus</u> Norris & T. Kop.

<u>Leptocladiella</u> <u>flagellaris</u> T. Kop. & Norris

<u>Mastopoma</u> <u>parvidentata</u> Norris & T. Kop.

<u>Plagiomnium</u> <u>integrum</u> (Bosch & Sande Lac.) T. Kop. var.
    <u>subelimbatum</u> (Dix.) T. Kop. & Norris

<u>Taxithelium</u> <u>friedense</u> Norris & T. Kop.

<u>Thuidium</u> <u>longissimum</u> Herz.

<u>Trichosteleum</u> <u>fuscescens</u> Norris & T. Kop.

<u>T</u>. <u>pendens</u> Norris & T. Kop.

<u>Vesicularia</u> <u>ectropotheciopsis</u> Norris & T. Kop.

No remarkabe differences could be noticed in substrate selec-
tion of the species in different habitats.

DISCUSSION

According to Schultze-Motel (1963) the percentage of en-
demism of New Guinean mosses is ca. 50%, and according to van
Zanten & Pócs (1981) it is 40%. However, according to the
present study, it is 23%. The figure is still preliminary but
shows how the so-called "geographical species" turn out to
be taxonomic synonyms of species of other areas. However, new
species are continuously being described from New Guinea. There
occur five endemic moss genera in New Guinea (<u>Werneriobryum</u>,
<u>Pseudopiloecium</u>, <u>Leskeodontopsis,</u> <u>Orthothuidium</u> and <u>Crepido-</u>
<u>phyllum</u>), but none of the hepatic genera are endemic. The
percentage of endemism of the hepatics is almost double that
of mosses. This is surprising, because mosses are generally
regarded as evolving more rapidly than hepatics. However,
among these presumably "conservative" hepatics are groups
which are rapidly evolving (cf. e.g., Schuster 1969). Such

groups are Frullaniaceae, Lejeuneaceae, Plagiochilaceae, Porellaceae and Radulaceae. New Guinea has obviously been an active speciation centre of many genera (cf. van Zanten & Pócs 1981). For example, of the 18 species of Schistochila, 13 are endemic. According to many previous studies, the evolutionary rate of the bryophytes is very slow (see van Zanten & Pócs 1981). According to Longton (1976), there is, however, evidence of microevolutionary processes in bryophytes similar to those in angiosperms, and Vries et al. (1983) point out that the evolutionary rate apparently is more rapid than has been assumed. For comparison it may be noted that the endemicity percentage of New Guinean angiosperm flora (ca. 9,000 species) is 90% (Walker & Hope 1982).

The circumstances for rapid evolution leading to endemism have been especially favourable in New Guinea. The area has a lively geological history and it has received taxa both from the Indo-Malaysia and from Australia (Axelrod & Raven 1982). Among the angiosperms the former element dominates at lower altitudes. The Australian elements are found on the eucalypt savannahs around the Fly River and Port Moresby. Gondwanaland elements now occur mainly in the montane zones. The central mountain was uplifted in the Pliocene and Pleistocene, and this supports the hypothesis that most of the New Guinea endemics arose within the last 10 million years (cf. van Zanten & Pócs 1981). Most of the endemic New Guinean bryophyte species occur at the altitudes of 1500 to 3500 m. This is in accordance with earlier studies on the endemicity of tropical bryofloras from other areas (Iwatsuki 1972, Schuster 1983), and has been noted for New Guinea by van Zanten & Pócs (1981).

In New Guinea the Frieda River area in West Sepik Province has a high level of endemism at only 200-1350 m. The reason for these low elevation endemics is still uncertain. It may be due to the high percentage of heavy metals there. On the other hand, this high endemism may relate to a greater age of the area. It is close to one of the ancient low-lying islands. which appeared above sea level in the Middle Miocene and has been available for land plants ca. 15 m. y. In the Frieda River

area, there is an exceptionally high concentration of minerals, such as gold, silver, lead, copper, molybdenum, arsenic, and zinc. In addition to the endemism, the bryoflora of the Frieda area presentsan unusual combination of species (cf. Norris & Koponen 1985b, Piippo 1985d). We wonder whether the rich concentration of heavy metals could have any influence on the speciation and diversity of the bryophyte flora of this area.

On the basis of the habitat ecology, three groups of endemics can be distinguished according to the present study: (1) species confined to open habitats, mostly alpine and open grasslands; (2) species with a wide ecological amplitude and (3) species almost entirely confined to tropical rain and moss forests. Endemic species are most numerous in the last category, perhaps because they can find many ecological niches on tree trunks. Species with a wide ecological amplitude have few endemics and these may later be found outside of New Guinea.

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Appendix 1. Endemism and altitude of Western Melanesian
hepatics. ——— : on the Huon Peninsula, △△△ : in Frieda River,
▲▲▲ : elsewhere in Western Melanesia.

Balantiopsis ciliaris subsp.
        novoguineensis
Heteroscyphus sarawaketanus
Kurzia longicaulis
K. pallida
Lepidozia bursifera
L. gwamii
L. lacerifolia
L. loriana
Leptoscyphus huonicus
Lophocolea morobeana
L. teptepensis
L. wambana
Mastigophora sepikiana
Metahygrobiella macgregorii
Porella grollei
P. viridissima
      var. novoguineensis
Pseudolepicolea grolleana
Schistochila antara
S. schultzei
S. undulatifolia
Telaranea kaindina
T. lawesii
T. trisetosa

Appendix 2. Endemism and altitude of Western Melanesian mosses.
────── : on the Huon Peninsula, ⋀⋀⋀⋀ : in Frieda River, ▲▲▲▲ :
elsewhere in Western Melanesia.

0   1000 2000 3000 4000 m

Aerobryidium fuscescens
Anomobryum bulbiferum
A. hyalinum
A. ochii
Brachymenium gracile
B. huonii
B. nepalense var. globosum
B. wabagense
Bryum papuanum
B. perdecurrens
B. pseudoblandum
B. sclerodictyon
Campylopus austro-subulatus
C. clemensiae
Chaetomitrium friedense
Distichophyllum albomarginatus
D. leskeodontoides
Ectropothecium giganteum
Glossadelphus ovatus
Leptocladiella flagellaris
Leptostomum intermedium
L. perfectum
Mastopoma parvidentata
Mielichhoferia novoguineensis
Orthothuidium curtisetum
Plagiomnium cordatum
P. integrum var. subelimbatum
Taxithelium friedense
Thuidium longissimum
Trichosteleum fuscescens
T. pendens
Vesicularia ectropotheciopsis
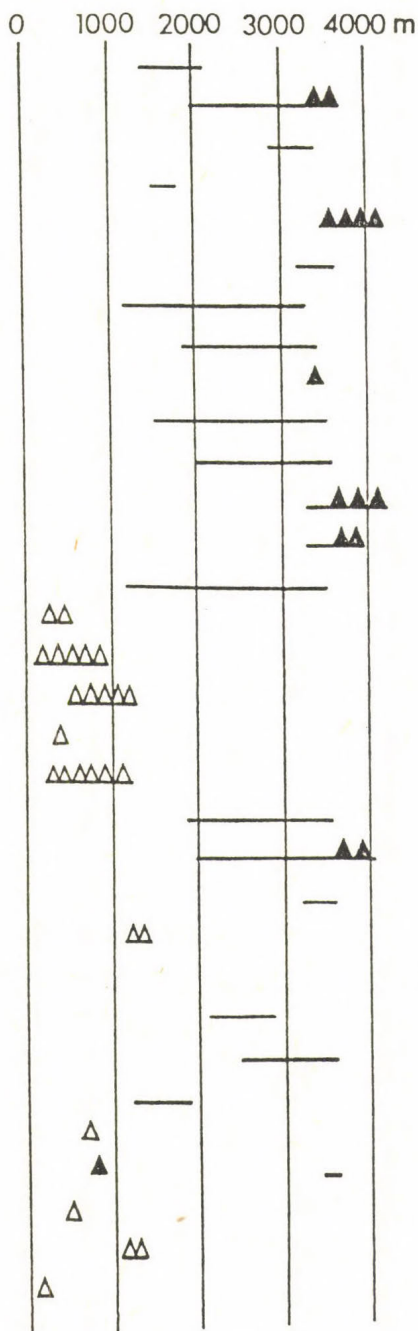
Session 3
COMMUNITY ECOLOGY
Convener: N.G. Slack
(Troy)

BUNTFLECHTEN-MOOS UND LEBERMOOS SYNUSIEN

B. ZÓLYOMI

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Moss-lichen synusia of five typical plant communities
(Festucetum glaucae hungaricum from the Budai Mts., the same
community from the Keszthelyi-, Bakony- and Vértes Mts.,
Chrysopogono-Caricetum humilis, Festucetum vaginatae danubiale,
and Diplachno-Festucetum sulcatae) from Hungary are character-
ized. The description of these synusia has previously been
published only in Hungary, in journals and books hardly avail-
able for foreign scientists.

- . -

*Festucetum glaucae hungaricum resp. Seseleo leucospermi – Festucetum
pallentis*

In "Naturbeschreibung von Budapest", Akademie Varlag 1958, 6.
Kapitel: Natürliche Pflanzendecke von Budapest u. seiner Un-
gebung, von B. Zólyomi (nur in ungarischer Sprache pp. 509-
642).

"Eine endemische Pflanzengesellschaft im Transdanubischen
Mittelgebirge in Ungarn, ausschiesslich auf Dolomit. Im der
Moosschicht Bunflechten-Moos Synusie resp. p.p. Fulgensio-
Psoro-Toninion Gams 1938. Diese charakteristische einschichtige
Vergesellschaftung zieht sich von den Hakbwüsten des Mediter-
raneums auf speziellem Grundgestein (Dolomit, Gyps) bei xero-
thermem Mikroklima bis zum südlichen Mittel- und Osteuropa. In
den kontinentalen inneralpinen Tälern hat es auch einige
Beziehungen zu den subalpinen Felsenrasengesellschaften. Bei

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klimatisch-morphologischer Betrachtung ist es merkwürdig, das-
durch die speziellen Eigenschaften des Dolomitgrundgesteins
verursacht - von den Abtragungsformen der gemässigten Zone
abweichende, extrazonale Halbwüsten-Mikroformen auf tauchen
(physische Zerbröckelung, Deflation)"

Caloplaca fulgens-Tortella inclinata synusium

Zusammensatzung auf Grund von 10 Aufnahmen im Budaer
Gebirge. Siehe Kolumne 1 in der Tabelle.

mit Ditrichum flexicaule

Wie No. 1 9 Aufnahmen aus der Moosschicht des Seseleo leu-
cospermi - Festucetum pallentis. Lokalität: Vértes-Bakony-
Keszthelyer (am Balaton) Gebirge. Zólyomi ined. - Siehe Ko-
lumne 2 in der Tabelle.

Chrysopogono-Caricetum humilis minuartietosum setaceae

In der Moosschich die selbe Synusie. Zs. Debreczy: Die
Xerothermen Rasen der Péter- und Tamás-Berge bei Balatonarács.
Ann. Hist. Nat. Mus. Nat. Hung. Pars Bot. 1966. pp. 227-228,
232-235.

Zusammensetzung auf Grund von 40 Aufnahmen. Siehe Kolumne
3 in der Tabelle. (Besichtigung bei der Exkursion zum Balaton-
See).

Festucetum vaginatae danubiale

Endemische pflanzengesellschaft im Donau-Theiss Zwischen-
stromland auf basischem Flugsand (Besichtigung bei der Ex-
kursion im National Park Kiskunság).

Siehe Zólyomi apud J. Zsolt 1943 und Zólyomi Budapest l.c.,
p. 621-623. "Mit einer der Dolomit-Synusie nahestenden Zusam-
menzetzung bildete sich eine Buntflechten - Moos-Synusie aus.
Hier steigert sich der Halbwüstenaspekt durch die Erscheinung,
dass ein Teil der Flechten vom Wind bewegt frei an der Sand-
fläche liegt (Manna-Vegetation). In etwas degradierter Sand-
vegetation ist ähnlich auch Cornicularia tenuissima, eine
Flechte, die mit Cladonia foliacea (ohne Ditrichum).

Syntetische Vergleichstabelle.

	1	2	3	4	5
!*Tortella inclinata*	V,1-2	V,+-2	IV,+-3	IV,+-1	.
!*Pleurochoete squarrosa*	II,+-2	II,+-1	III,+-3	X	II,-1
Ditrichum flexicaule	V, +-1	V,+-2	IV, +-3	.	.
Tortula ruralis	IV,+-1	II,+-2	II,+-2	IV,+-2	IV,+-2
!*Barbula convoluta*	X	.	I,+-1	II,-1	.
B. fallax	.	.	I,+-2	.	I,+
B. hornschuchiana	X	.	I,+-2	.	.
B. revoluta	I,+	.	II,+-2	.	.
B. vinealis	.	I,+	I,+-1	.	.
Encalypta contorta	.	I,+	.	.	.
E. vulgaris	X	I,+	II,+-2	II,+-1	I,+
Grimmia commutata	.	.	I,+-1	.	.
G. pulvinata	.	.	.	.	III,+
Weisia tortilis	I,+	.	III,1-2	.	.
Bryum sp. div.	.	I,+	.	.	.
B. bicolor	.	.	III,+-2	.	.
!*Grimaldia fragrans*	I,+	I,-2	II,+-2	.	IV,+-3
!*Tesselina pyramidata*	.	.	.	.	II,1-2
Riccia sp. div.	.	.	.	.	I-,+-
Camptothecium sericeum	.	.	I,+-1	.	IV,+-
Trichostomum brachiodontium	.	.	I,+-2	.	.
Thuidium abietinum	.	II,+-1	.	.	.
Hylocomium proliferum	.	I,+	.	.	.
Hypnum cupressiforme	.	.	I,1-2	.	.
Tortella tortuosa	.	II,1-2	II,+-3	.	.
Squamaria crassa	II,+-1	III,1-2	.	.	III,+-1
!*S. lentigera*	III,+-1	III,+-1	X	V,+-2	.
!*Caloplaca fulgens*	IV,+(1)	IV,+-1	.	V,+-2	.
!*Toninia coeruleo-nigricans*	IV,+	V,+	X	III-,+	.
!*Psora decipiens*	III, +-1(2)	III,+-2	.	III,+	.
Collema sp.	II,+	.	.	.	.
C. cf. granulatum	.	.	.	III,-1	.
Dermaticarpon sp.	I,+-1	I,+	.	.	.
Diploschistes scruposus var. parasiticus	.	.	.	II,+	.
Psora lurida	I,+-1	.	.	.	.

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	1	2	3	4	5
Cladonia foliacea var. convoluta	.	II,+–2	X	IV,+–1(3)	I,–2
C. pyxidata	III,+	III,+–1	.	.	IV,+–1
C. furcata	.	.	X	.	.
C. symphycarpia	.	.	X	.	.
C. subrangiformis	.	.	X	III,+–2	.
C. magyarica var. pocilliformis	.	.	.	I,+(3)	.
Peltigera canina var. rufescens	I,+	II,+	X	X	III,+–1

I–V   Konstanzwerte

+–3   Abundanz-Dominanz-Werte

!   bezeichende Arten

Zusammensetzung auf Grund von 5 Aufnahmen auf der Szentendre Insel bei Budapest. Siehe Kolumne 4 in der Tabelle.

Diplachno-Festucetum sulcatae

Siehe Zólyomi Budapest l.c., pp. 560–563. "Extrazonale Steppengesellschaft im Transdanubischen Mittelgebirge auf Dachstein-Kalk bzw. Protorendzina. Moosschicht eine submediterran getönte Lebermoos-Synusie.

Zusammensetzung auf Grund von 6 Aufnahmen im Budaer Gebirge. Siehe Kolumne 5 in der Tabelle (Syntetische Vergleichstabelle).

Mannia fragrans - Oxymitra paleacea - Riccia ciliifera Synusium

THE USE OF BRYOPHYTES FOR ECOLOGICAL COMPARISON OF VEGETATIONAL UNITS AND OF HABITATS

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The method is based on the old indicator concept of bryo-
phyte species. The numerical scales of ecological values (T,
W, R) elaborated for phanerogams by Zólyomi (1964) were
adopted to bryophytes. The ecological structure and habitat
of plant communities may be characterized with the aid of a
10-degree T (temperature ecology number) scale (1-10 from
arctic to equatorial), a 12-degree W (water ecology number)
scale (0-10 from xerophyton to hygrophyton) and a 6-degree
R (soil reaction number) scale (1-5 from acidic to basic).
The application of numerical scales of ecological values and
the calculation of ecological species group coefficients lead
to abstract numerical values instead of species or groups of
species. Thus, a comparison, on the basis of bryophytes, of
vegetational units and of habitats and the use of statistical
methods are possible.

INTRODUCTION

The article published by Zólyomi (1964) gives the T, W
and R values of phanerogams. The T, W, R is an ecological in-
dex which expresses the adaptation of the plants to the tem-
perature zone (T), to the moisture level of the environment
(W) and to the acidity of the soil (R).

The method is based on the old concept of plant species
as indicators of habitats. The ecological structure and ha-
bitat of plant communities may be characterized by the aids of

Table 1. The T scale.

Number	Vegetation zone
1	ice - tundra
2	woody tundra
3	coniferous forests - taiga
4	mixed coniferous-deciduous forests
5	subcontinental-atlantic deciduous forests
6	submediterranean deciduous forests
7	mediterranean-atlantic evergreen forests
8	mediterranean-continental warm steppe and deserts
9	tropical savanna and deserts
10	equatorial forests

Table 2. The W scale.

Number	Ecological meaning
0	extremely dry
1	very dry
2	dry
3	temporarily dry
4	semi-dry
5	mesic
6	damp
7	moist
8	very moist
9	irrigated or waterlogged
10	semi-aquatic
11	aquatic

a 10-degree T (temperature ecological number) scale (1-10 arctic - equatorial) (cf. Zólyomi 1964). For example, 5 is the index of the subcontinental-atlantic deciduous forest zone, 4 is the index of the mixed coniferous-deciduous forest zone and 6 is the index of the submediterranean deciduous forest zone (Table 1). If the plant has no indicator character the value of T is zero.

Moreover, the ecological structure may be characterized by a 12-degree W (water ecology number) scale refined from Podgrebniak (1930) by Zólyomi (1964) and Zólyomi et al. (1966). The W scale gives the indication from the extremely dry environment (marked by 0) to the very moist one (10, 11, see Table 2).

The soil or substrate of the community may be characterized by the 6-degree R (soil reaction number) scale of Ellenberg (1950). If the value of R is 0 then these plants have no indicator character. If the value of R is 1 then the plant is an indicator of very acidic soil, if R is 2 acidic, if 3 slightly acidic, if the index is 4 slightly basic, if 5 basic soil or substrate.

Ecological structure is to be understood as the proportion of indicator values, respectively, of species groups partaking in the plant association. All species as well as their occurrence in the phytocoenological table are thus taken into account, cf. Zólyomi (1964). Employing a characteristic traced curve abstracted from the species, we may effect a global comparison of habitats (cf. Zólyomi 1964). This method has often been used by coenologists in Hungary (Jakucs 1967, Kovács 1968, Horváth 1972, etc.).

METHODS

The T, W and R values of the species of the Hungarian Bryophyte flora (Orbán & Vajda 1983) were identified by the author on the basis of the method presented. Thus, the bryophytes may be used as indicators of habitats and for comparison and ecological analysis of the micro-communities of bryophytes or of the bryophyte layer of plant communities. The list of the T, W and R values of the Hungarian bryoflora was published by the author (Orbán 1984).

Employing the complete list of T, W and R values of the Hungarian bryoflora, the percentage distributions of the T, W and R values were analysed separately. The mean values of T, W and R were also given for the Hungarian bryoflora.

The whole bryophyte layers of four plant communities (Melitti-Fagetum, Querco-Carpinetum, Seslerio-Quercetum and Cotino-Quercetum) were studied for the comparison. In addition, the characteristic curves of T, W and R distribution were drawn for the comparison of the communities and habitats examined. The multidimensional ecostructure diagram was used for the same purpose.

Some simple methods are published by the author in this paper only for the comparison of communities and habitats. But if many data and replicates are available from one or several types of micro-communities or from the bryophyte layer of macro-communities we can use statistical methods (e.g., ANOVA, χ^2 test) or cluster analysis on the basis of the frequency of T, W and R data.

RESULTS

The percentage distribution of the T, W and R values and the mean values of T, W and R indices are presented in Table 3.

The percentage distribution of the temperature ecological index T of the species of the Hungarian bryoflora shows that in Hungary the species of subcontinental and subatlantic deciduous forests are characteristic. Its value is 50.3%.

The species of the coniferous mixed forest zone follow this. Its value is 27.6%. The species of submediterranean deciduous forest zone have a value of 13.3%. The others have values from 0.3 to 3%.

The percentage distribution of the water ecology index (W) seems similar, because these two indices are correlated with each other. The mesic (marked by 5) species are dominant in our bryophyte flora with a 48.4% value. The second type is the xerophyte (2) which is frequent. Its value is 14.2%. The others have 0.5-7.3%.

The percentage distribution of the soil reaction index (R) seems to be different. The species of acidic soil have a 36.3% proportion, the species of basic soil have 25%, whereas 27.2% of the species have no indicator character.

Table 3. The percentage distribution of the T, W and R values of the Hungarian bryoflora and the mean values.

	Number											
	0	1	2	3	4	5	6	7	8	9	10	11
T%	3.3	0.0	2.7	1.4	27.6	50.3	13.3	1.1	0.3	-	-	-
W%	0.5	2.5	14.3	4.6	2.9	48.4	7.3	5.0	0.5	5.0	5.5	3.2
R%	27.2	3.2	36.3	5.5	2.7	25.0						

Means: T = 4.5; w = 5.2; R = 3.1.

On the basis of this analysis, the most frequent indicator groups have 452, 550, 552, 620, 625 and 655 index number combinations in Hungary.

The mean values of T, W and R are given in Table 3. These means can be compared with the values of other territories.

The comparison of the four plant communities studied is given with the aid of characteristic curves (Figs 1-3) and with a multidimensional ecostructure diagram (Fig. 4).

It appears from the T characteristic curves (Fig. 1) that the species marked by 5 are dominant in all communities. If the community is very closed, the proportion of species marked by 5 is higher. Thus, the proportion is 60.5% in the very open Cotino-Quercetum and 92% in the very closed Melitti-Fagetum.

The curves of W values are also characteristic (Fig. 2). The mesophyte species are dominant (5) in all communities, but from Melitti-Fagetum to Cotino-Quercetum the proportion of the mesophytes decreases and the proportion of the xerophytes increases.

The curves of R values (Fig. 3) show that the four communities as habitats of bryophyte species are very different. The species of basic soil are dominant in Cotino-Quercetum and the species of slightly acidic and acidic soil are found in Querco-Carpinetum and Melitti-Fagetum.

Table 4. The mean values of T, W and R indices of four plant communities in Hungary.

Communities	Means		
	T	W	R
Cotino-Quercetum	5.1	3.2	4.7
Seslerio-Quercetum	4.9	4.5	4.1
Querco-Carpinetum	4.7	4.8	3.3
Melitti-Fagetum	4.2	4.8	3.4
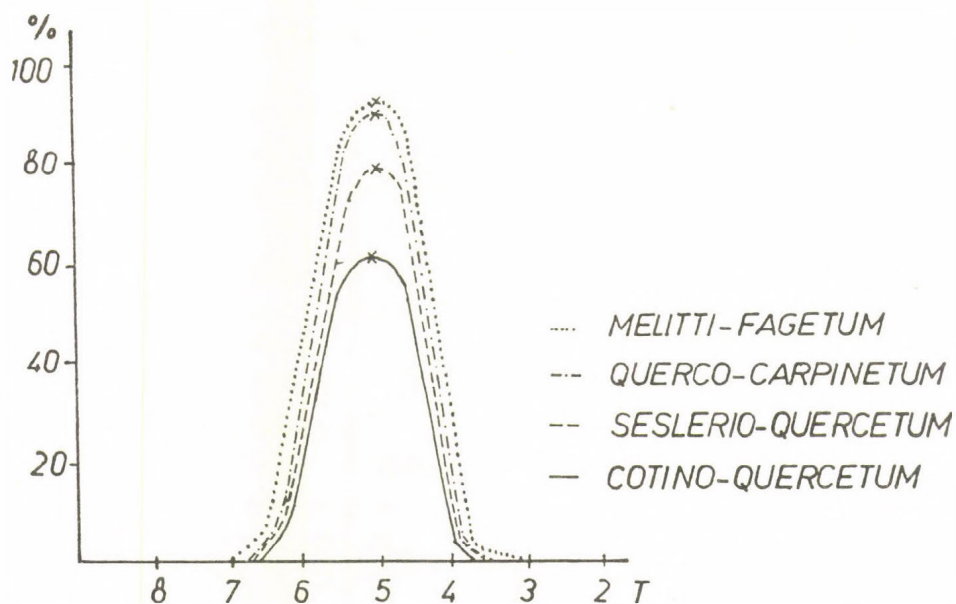
Fig. 1. The characteristic curves of the percentage distribution of the T values in the four communities examined.
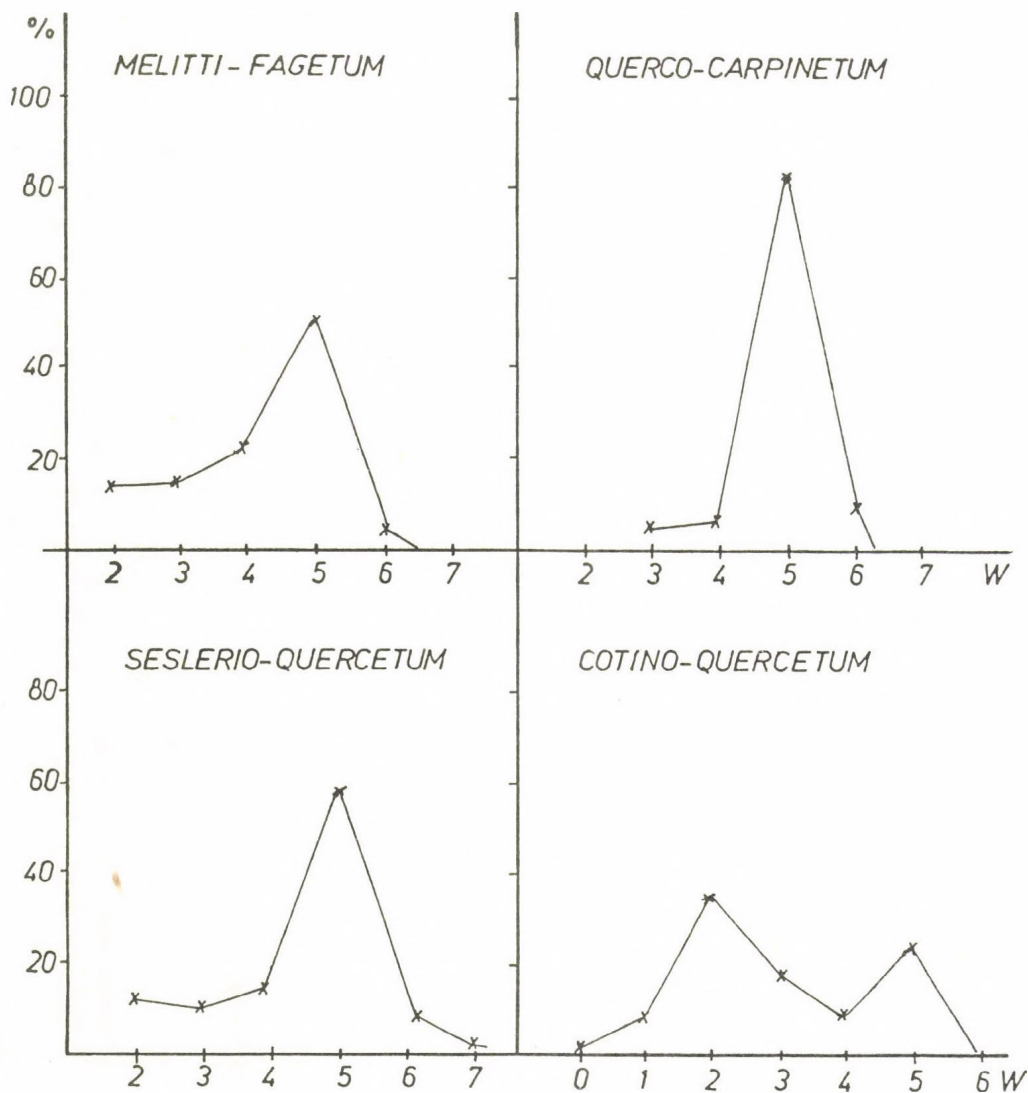
Fig. 2. The characteristic curves of the percentage distribution of the W values in the four communities examined.
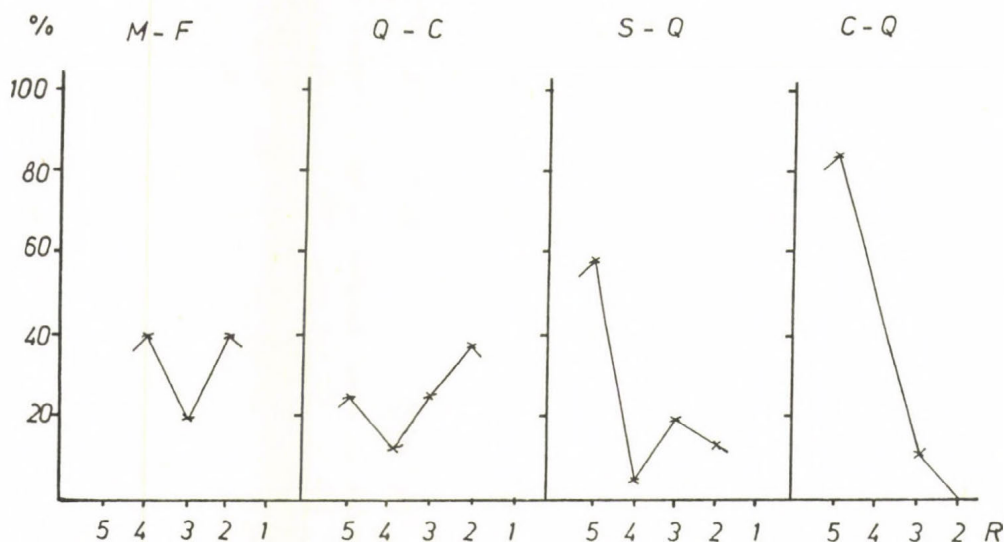
Fig. 3. The characteristic curves of the percentage distribution of the R values in the four communities examined.
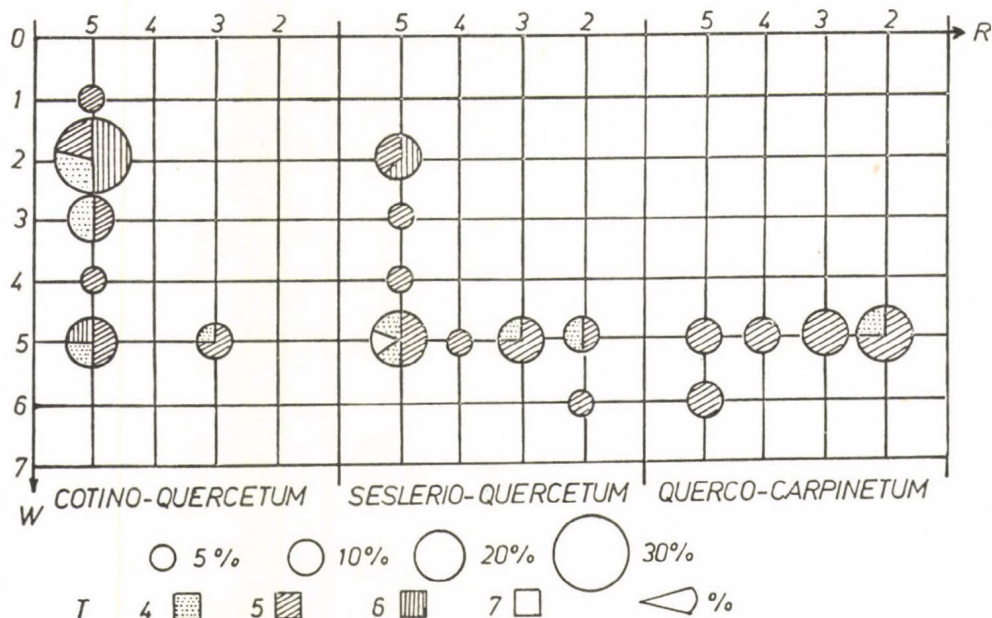
Fig. 4. The multidimensional ecostructure diagram of three communities examined.

The multidimensional ecostructure diagram (Fig. 4) which includes the proportion values of T, W and R indicates the same results.

The mean values of T, W and R of four plant communities (Table 4) show that the mean value of T index decreases from the open community to the closed community; thus, the proportion of southern elements decreases, mutually increases the proportion of mesophyte elements by the W value, thus the mean values of W increase from 3.2 (Cotino-Quercetum) to 4.8 (Melitti-Fagetum). The mean value of R increases from the Melitti-Fagetum to the Cotino-Quercetum community.

CONCLUSIONS

The results seem to show very well that the indicator values (indices) of bryophytes are suitable for the ecological comparison of vegetational units, especially if phytosociological tables or lists of bryophytes in communities of higher plants are available for analysis or comparison. With this method bryophytes may be used similarly to phanerogams.

Moreover, this method is also suitable for the comparison of bryophyte synusia and micro-communities.

The analysis of W and R indices makes it possible to compare the habitats of bryophyte species.

The method, as indicated by Zólyomi (1964), mediates between the "tabular plant coenology" of Central Europe and the English-American "plant ecology".

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LES HÉPATIQUES ET LA PINÈDE MEDITERRANEENNE DE PINUS HALEPENSIS MILLER

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The relations of hepatics and Pinus halepensis pinewoods are studied with BRYOMED, a bryoecological data bank that contains 97 relevés of this plant community. Pinus halepensis has a wide ecological tolerance, and grows in varied habitats. A floristic analysis of the hepatic flora shows that it is heterogeneous. Hepatics are sparse but species diversity is high. Only two taxa appear statistically linked to the pinewoods. All species belong to the most common and ecologically most tolerant Mediterranean hepatics. A comparison of their ecological profiles individualizes four groups. If their simultaneous presence in the pinewoods is taken into account, the same four groups individualize, hence these groups are not bound to the Pinus halepensis community.

INTRODUCTION

BRYOMED est une banque de données**contenant les observations phytosociologiques et écologiques sur les hépatiques recueillies lors des missions de S. Jovet-Ast et H. Bischler dans le bassin méditerranéen et de J. P. Hébrard dans le sud de la France (Baudoin et al. 1984). Pour des raisons d'homogénéité, nous avons choisi de n'utiliser, dans ce travail,

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** créee sur MINI 6 (Bull) au centre enformatique du Muséum National d'Histoire Naturelle à Paris.

que les 2800 relevés phytoécologiques des missions Jovet-Bischler. Chaque relevé, réalisé suivant la méthode sigmatiste, se compose de la liste des espèces présentes sur une certaine surface de substrat et de la description de leur environnement écologique qui doit être homogène pour un même relevé. L'ensemble des relevés regroupe 11400 spécimens qui se répartissent en 160 taxons.

Pour étudier la composition, l'écologie et les affinités des espèces de la flora hépaticologique des pinèdes de Pinus halepensis, nous avons extrait de l'ensemble des relevés ceux réalisés dans cette formation phanérogamique. La figure 1 montre la distribution géographique de ces 97 relevés que se répartissent ainsi:

Algérie	21	Espagne-Portugal	10	Sardaigne	3
Yugoslavie	18	Crète	4	Albanie	3
Israël	16	Sicile	4	Chypre	3
Tunisie	11	France	3	Libye	1
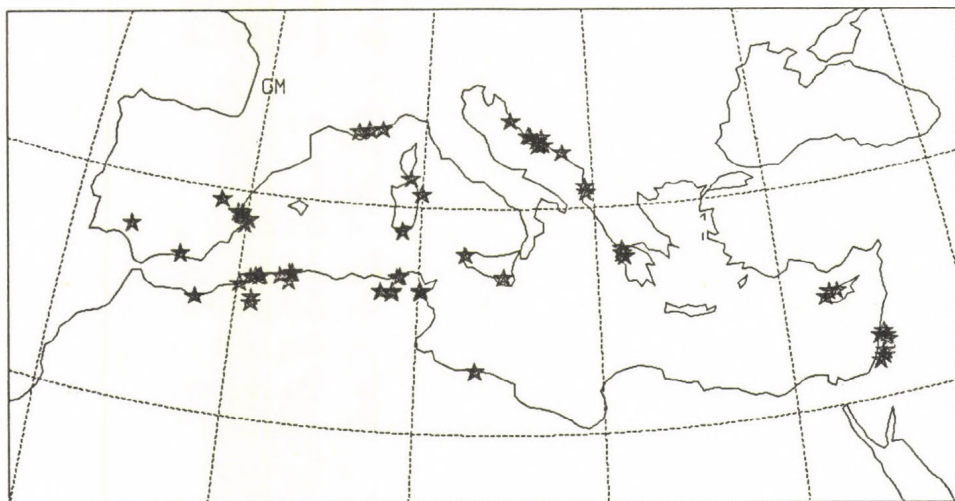
Fig. 1. Répartition des relevés de la pinède a Pinus halepensis.

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ANALYSE FLORISTIQUE DES RELEVÉS

L'ensemble des relevés effectuées dans les pinèdes de Pinus halepensis rassemble 292 spécimens d'hépatiques. Ces relevés, avec une moyenne de 3 taxons par relevé, se révèlient plus pauvres que ceux de BRYOMED en général (4 taxons par relevé).

Les spécimens se répartissent en 50 taxons (tab. 1). Ces pinèdes qui, avec seulement 3% des relevés, possèdent 30% des espèces de BRYOMED, sont par contre floristiquement très diversifiées. En outre, 2758 relevés de BRYOMED (soit 96%) renferment au moins un des taxons d'hépatiques notés dans les pinèdes depin d'Alep.

Du point de vue de la composition floristique, les Marchantiales sont ici les mieux représentées, en particulier par rapport aux Jungermanniales dont le pourcentage est nettement inférieur à celui que nous avons observé pour l'ensemble des milieux méditerranéens prospectés jusqu'à présent. Ainsi que l'on pouvait s'y attendre, cette différence s'accentue encore si on le compare à celui de la flore hépaticologique de l'Europe tempérée.

	pinède de pin d'Alep	BRYOMED	Europe tempérée
Marchantiales	54%	36%	15%
Ricciineae	78%	70%	59%
Marchantiineae	22%	30%	41%
Metzgeriales	8%	10%	7%
Jungermanniales	30%	49%	75%
Anthocerotaceae et			
Sphaerocarpales	8%	5%	3%
	100%	100%	100%

Les Marchantiales sont pour la plupart reviviscentes et supportent de longues périodes de sécheresse, tandis que les Jungermanniales, en majorité hygrophiles et sciaphiles, s'accomodent difficilement d'un environnement aride. Ainsi, l'aridité des pinèdes de pin d'Alep (fig. 2) est confirmée par la structure floristique de leur flore hépaticologique.

Tableau 1: Liste des taxons récoltés dans la pinède de Pin d'Alep et classés suivant leur affinité décroissante avec celle-ci. A gauche, le coefficient de corrélation de points mesure la liaison espèce-pinede; à droite figure la fréquence des taxons dans l'ensemble de BRYOMED et dans les relevés de la pinède.

Coef. de corrélation de points	T A X O N S	fréquences dans BRYOMED	pinède
0.109 *	*Cephaloziella baumgartneri* Schiffn.	357	33
0.088 *	*Southbya nigrella* (De Not.) Henr.	299	24
0.063	*Cololejeunea minutissima* (Sm.) Schiffn.	8	2
0.033	*Fossombronia caespitiformis* De Not.	545	25
0.022	*Southbya tophacea* (Spruce) Spruce	113	6
0.019	*Targionia hypophylla* L.	650	27
0.018	*Fossombronia pusilla* var. *decipiens* Corbière	12	1
0.016	*Petalophyllum ralfsii* (Wils.) Nees & Gott.	13	1
0.015	*Cephaloziella calyculata* (Durieu & Mont.) K. Müll.	34	2
0.015	*Riccia crustata* Trab.	14	1
0.013	*Anthoceros punctatus* L.	15	1
0.013	*Riccia gougetiana* var. *erinacea* Schiffn.	15	1
0.013	*Riccia lamellosa* Raddi	349	14
0.012	*Riccia warnstorfii* Limpr.	16	1
0.006	*Lunularia cruciata* (L.) Dum.	760	27
0.005	*Phaeoceros laevis* (L.) Prosk.	159	6
0.001	*Riccia sommieri* Levier	28	1
0.000	*Fossombronia angulosa* (Dicks.) Raddi	147	5
-0.003	*Riccia sorocarpa* Bisch.	640	21
-0.004	*Riccia ciliata* Hoffm.	192	6
-0.004	*Riccia crystallina* L.	36	1
-0.005	*Riccia cavernosa* Hoffm.	39	1
-0.005	*Riccia subbifurca* Warnst.	38	1
-0.009	*Riccia trichocarpa* Howe	47	1
-0.010	*Plagiochasma rupestre* (Forst.) Steph.	85	2
-0.011	*Lophocolea heterophylla* (Schrad.) Dum.	52	1
-0.011	*Riccia gougetiana* Durieu & Mont.	290	8
-0.012	*Riccia macrocarpa* Levier	160	4
-0.014	*Riccia beyrichiana* Hampe	98	2
-0.015	*Sphaerocarpos michelii* Bellardi	64	1
-0.016	*Phaeoceros bulbiculosus* (Brotero) Prosk.	66	1
-0.017	*Frullania dilatata* (L.) Dum.	253	6
-0.017	*Radula lindenbergiana* Gott.	108	2
-0.018	*Radula complanata* (L.) Dum.	72	1
-0.018	*Riccia atromarginata* Levier	113	2
-0.020	*Lophozia turbinata* (Raddi) Steph.	158	3
-0.021	*Riccia trabutiana* Steph.	83	1
-0.023	*Mannia androgyna* (L.) Evans	133	2
-0.025	*Cephaloziella stellulifera* (Tayl.) Schiffn.	293	6
-0.025	*Riccia bicarinata* Lindb.	222	4
-0.027	*Cephaloziella turneri* (Hook.) K. Müll.	109	1
-0.028	*Riccia crozalsii* Levier	115	1
-0.028	*Riccia michelii* Raddi	456	11
-0.029	*Lejeunea cavifolia* (Ehrh.) Lindb.	162	2
-0.033	*Gongylanthus ericetorum* (Raddi) Nees	185	2
-0.034	*Frullania tamarisci* (L.) Dum.	168	1
-0.034	*Oxymitra paleacea* Bisch.	273	4
-0.037	*Riccia nigrella* DC.	371	6
-0.048	*Reboulia hemisphaerica* (L.) Raddi	521	9
-0.049	*Corsinia coriandrina* (Spreng.) Lindb.	452	6

* liaison significative avec la pinède à *Pinus halepensis* avec un seuil d'erreur de 5%.

La plupart des taxons sont communs dans la région médi-
terranéenne. On trouve, dans la liste du tableau 1, les 25
espèces les plus fréquentes dans BRYOMED (fig. 2). Chacun des
50 taxons qui y figure, regroupe en moyenne presque trois fois
plus de spécimens que l'ensemble des autres espèces de
BRYOMED.

Dans le tableau 1, les espèces sont classées suivant leur
liaison décroissante avec la pinède de pin d'Alep. Cette liai-
son est appréciée par le calcul d'un coefficient de corrélation
da points (Dagnelie 1960) dont la formule est proche de celle
du khi deux (χ^2/n). Ce coefficient (colonne de gauche du tab-
leau 1) varie entre +1 et -1, la valeur 0 signifiant une ab-
sence de liaison (indépendance), et le signe, le sens de la
liaison.

Les faibles valeurs obtenues sont naturellement en relation
avec la forte représentation de ces taxons dans la région médi-
terranéenne. Ainsi, la plupart des espèces ne sont pas liées
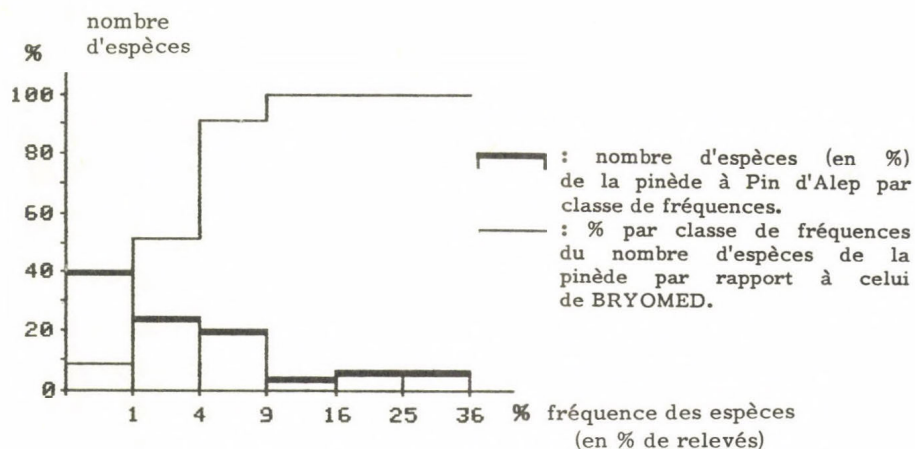
Fig. 2. Répartition des espèces en fonction de leur fréquence
dans la pinède de Pin d'Alep (en gras) et comparaison avec
BRYOMED de la composition spécifique des classes de fréquencies
(trait fin). Les classes de fréquencies suivent une progres-
sion parabolique.

a la pinède. On remarquera même, pour la majorité d'entre elles, que la valeur négative révelerait plutôt une affinité pour d'autres groupements phanérogamiques. Seules deux espèces, Cephaloziella baumgartneri et Southbya nigrella, peuvent être considérées comme statistiquement liées à la pinède (au seuil d'erreur de 5%). Ce sont des espèces écologiquement assez spécialisées (rochers calcaires et talus ombragés) dont, en fait, l'apparition est indépendante de la présence du pin d'Alep. Cololejeunea minutissima a également un coéfficient positif, mais sa fréquence trop faible dans la pinède enlève toute signification à la valeur du test utilisé (test du χ^2).

ÉCOLOGIE DES RELEVÉS DE LA PINÈDE DE PIN D'ALEP

Seules les pinèdes possédant une bryoflore ont été échantillonnées. Leur diversité spécifique en hépatiques correspond à une diversité des conditions écologiques. Les histogrammes de la figure 3 montrent la variation de quelques facteurs écologiques utilisés pour décrire le milieu. Il est intéressant de superposer l'écologie de la pinède à celle de la région méditerrannéenne représentée par l'analyse de BRYOMED (en trait fin sur les histogrammes de la fig. 3).

Sur les histogrammes de la figure 3, on remarquera l'importante amplitide des variables climatiques (de 12° à 21°C pour les températures annuelles moyennes, de 400 à 1500 mm pour la pluviométrie) et l'exclusion des conditions extrêmes.

Un grand nombre de nos relevés ont été effectués dans la partie méridionale de l'aire du pin d'Alep ou le climat est surtout de type méditerranéen chaud (température moyenne annuelle 15-21°C) et relativement sec (300-600 mm), ce que confirme le calcul du coefficient bioclimatique (Q) d'Emberger (1930), pour lequel le maximum de répartition se situe entre 21 et 55 (climat méditerranéen tempéré). Notons que plus au nord, et notamment dans le sud-est de la France (Loisel 1976), l'aire du pin d'Alep s'étend aussi sur les étages humide (variantes à hiver tempérés et chaud, Q entre 100 et 140) et subhumide (variantes a hiver tempéré at frais, Q entre 55 et
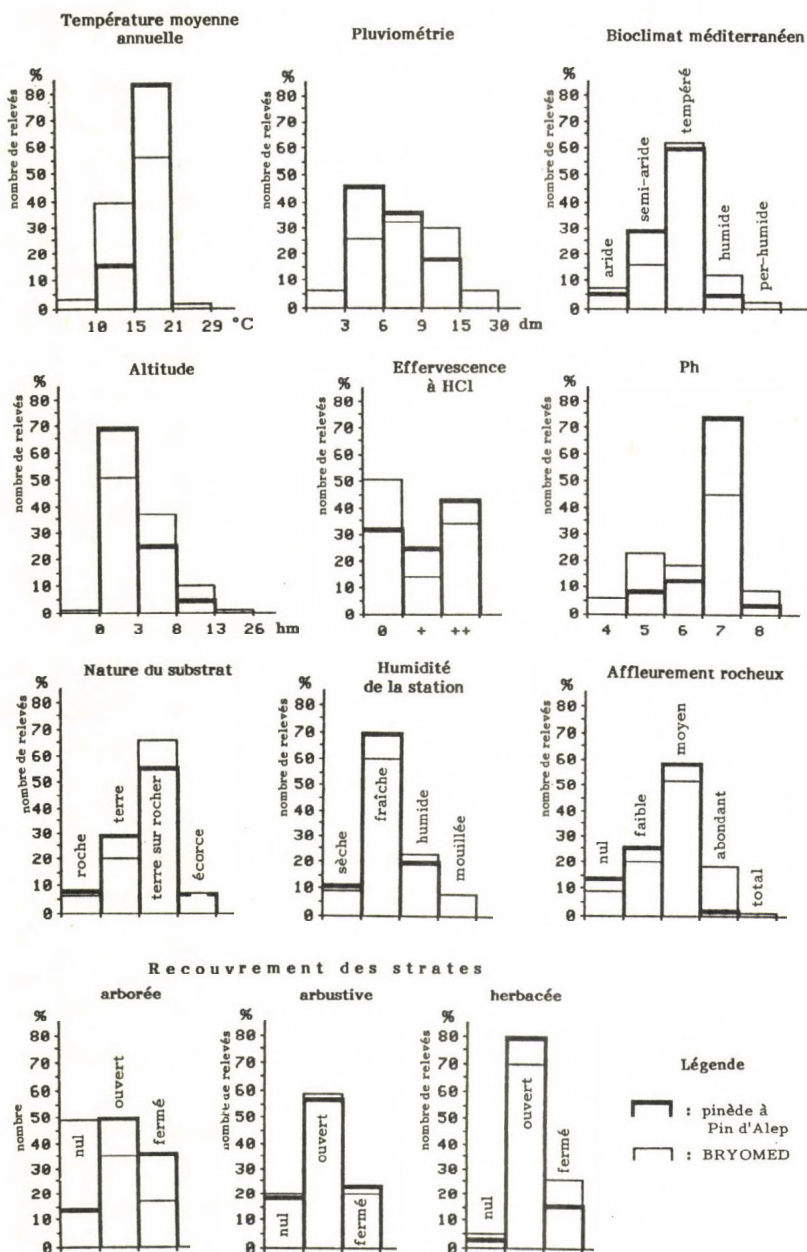
Fig. 3. Caractéristiques écologiques de la pinède de Pin d'Alep pour quelques variables descriptives du milieu (en gras). Comparaison avec les données contenues dand BRYOMED (trait fin).

95), dans les secteurs où la température moyenne annuelle se
situe entre 12° et 17°.

Pour Loisel (1976), une valeur moyenne des températures
minimum du mois le plus froid égale à 0° limite l'aire générale
du pin d'Alep, ce qui explique que la pinède s'observe préféren-
tiellement à basse altitude (0-300 m, mais des reboisements
sont pratiqués jusqu'à 1200 m en Algérie). Enfin, l'essence est
indifférente à la nature de la roche-mère et à la réaction du
substrat (pH compris entre 5 et 8), bien de sols dégradés ou
pauvres. Par contre, ce pin s'implante difficilement sur les
roches compactes et peu fissurées où sur du sable ou l'alimen-
tation en eau devient insuffisante.

LES GROUPEMENTS HÉPATICOLOGIQUES DE LA PINÈDE DE PIN D'ALEP

La pinède de pin d'Alep, parce qu'elle est peu exigeante
vis-à-vis des conditions écologiques, peut s'établir spontané-
ment ou par suite de reboisements sur une grande diversité de
milieux. En ce qui concerne les hépatiques, cela se traduit
par une composition floristique elle aussi très diversifiée.
Il s'agit de taxons très communs, car la pinède se recontre
dans des biotopes typiquement méditerranéens, donc les plus
fréquents et les mieux échantillonnés. On peut aussi penser
que les conditions offertes par la pinède ne sont pas très
favorables au développement des hépatiques, puisque seules s'y
maintiennent les espèces les moins exigeantes et qui sont les
plus largement répandues. D'ailleurs, beaucoup de pinèdes, qui
ne sont pas prises en compte dans ce travail, sont totalement
dépourvues d'hépatiques.

Il semblait intéressant de dégager les différents bio-
topes colonisés par les hépatiques de la pinède de pin d'Alep,
et les espèces qui caractérisent ces milieux. Nous avons donc
effectué des traitements statistiques sur, d'une part, les
connées floristiques de la pinède, et, d'autre part, les pro-
fils écologiques des espèces de la pinède, établis sur l'en-
semble des données de BRYOMED.

ANALYSE ÉCOLOGIQUE

La liaison entre une espèce et chaque modalité écologique
est exprimée par le calcul du taux de fréquence relative (TFR),
pourcentage de la fréquence relative de l'espéce dans la mo-
dalité (nombre de présences de l'espèce dans la modalité,
divisé par le nombre de relevés effectués dans cette modalité)
par rapport à la somme des fréquences relatives pour l'ensemble
des modalités d'une même variable (Baudoin et al. 1979). L'en-
semble des TFR d'une espèce constitue son profil écologique.
Pour rassembler les 50 espèces de la pinède suivant la res-
semblance de leur profil, nous avons employé une classification
hiérarchique ascendante (Jambu 1978), utilisant comme critère
de distance interspecifique, la métrique de khi carré, et comme
critèrie d'aggrégation, la maximisation de la variance. Le
résultat de ce traitement s'exprime sous forme d'un dendro-
gramme.

Quatre grands groupes écologiques s'individualisent nette-
ment (50% de l'inertie totale), alors qu'à l'interieur de ces
groupes, les espèces ont des exigences assez proches (fig. 4,
5). Le premier (A) qui apparaît, rassemble les espèces se
développant préférentiellement dans un climat méditerranéen
semi-aride à aride. Excepté Sphaerocarpos michelii, toutes
appartiennent au genre Riccia. Nous avons déjà mis ce groupe
en évodence dans l'analyse du peuplement hépaticologique de
la région méditerranéenne (Jovet-Ast et al. 1976). Outre ces
facteurs thermo-climatiques, ses principales caractéristiques
sont: - association hygrophile en milieu steppique - couvert
arboré ou buissonant très faible - strate herbacée bien re-
présentée - peu de bryophytes - substrat terreux (parfois
terre sur rocher), non humifère, à effervescence à HCl forte
et à pH supérieur à 7.

A l'opposé se rassemble un groupe B de Jungermanniales
à affinités corticoles. Il correspond naturellement à un milieu
forestier, surtout de feuillus, à strate arborée et buisson-
nante bien développée, avec une strate herbacée ouverte et une
présence importante de bryophytes. A ceci s'associent une

0   % d'inertie   100

Riccia atromarginata
Riccia cavernosa
Riccia crustata
Riccia crystallina   **groupe A**
Riccia lamellosa
Riccia trabutiana
Sphaerocarpos michelii

Anthoceros punctatus
Cephaloziella calyculata
Cephaloziella stellulifera
Cephaloziella turneri
Corsinia coriandrina
Fossombronia angulosa
F. pusilla var. decipiens
Gongylanthus ericetorum
Oxymitra paleacea
Petalophyllum ralfsii
Phaeoceros bulbiculosus
Phaeoceros laevis
Riccia beyrichiana   **groupe D**
Riccia bicarinata
Riccia trichocarpa
Riccia ciliata
Riccia crozalsii
Riccia gougetiana
Riccia g. var. erinacea
Riccia macrocarpa
Riccia michelii
Riccia nigrella
Riccia sommieri
Riccia sorocarpa
Riccia subbifurca
Riccia warnstorfii

Cephaloziella baumgartneri
Fossombronia caespitiformis
Lunularia cruciata
Mannia androgyna
Plagiochasma rupestre
Reboulia hemisphaerica
Southbya nigrella
Targionia hypophylla   **groupe C**

Lophozia turbinata
Southbya tophacea

Cololejeunea minutissima
Frullania dilatata
Frullania tamarisci
Lejeunea cavifolia
Lophocolea heterophylla   **groupe B**
Radula complanata
Radula lindenbergiana

Fig. 4. Dendrogramme issu de la C.A.H. des taxons de la pinède d'après leur profil écologique dans BRYOMED. Le % inertie (échelle du haut) mesure la ressemblance des groupes entre eux.

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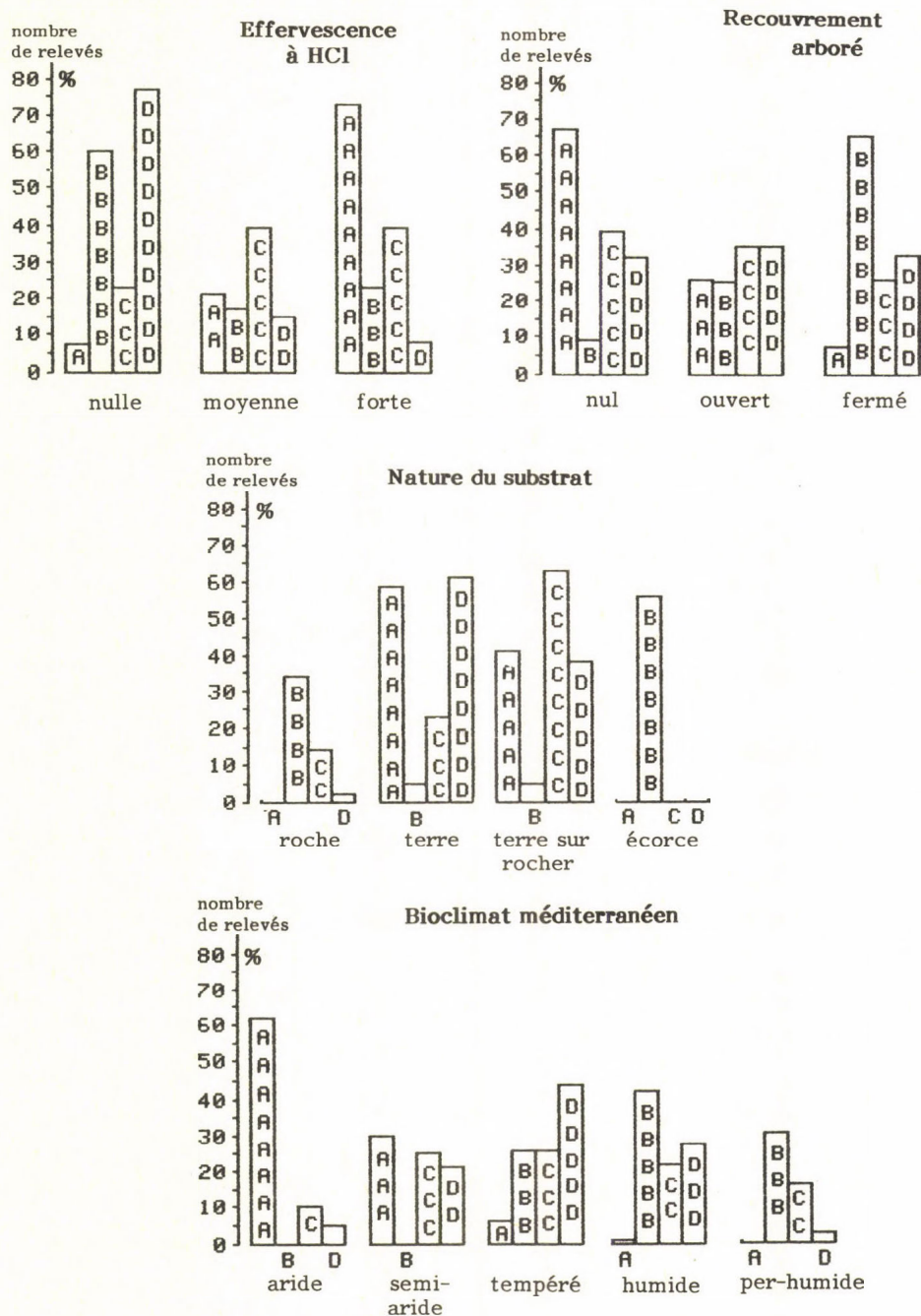
Fig. 5. Profils écologiques moyens des 4 groupes (A,B,C,D) mis en évidence par la C.A.H. de la figure 4. Moyenne des T.R.F. des taxons.

pluviosité souvent plus importante (>1000 mm), une température
moyenne du mois le plus froid inférieure à 9°C, avec ou sans
enneigement hivernal. Ces espèces peuvent, dans certaines
conditions d'humidité, s'établir directement sur les rochers.
Ce groupe préfère un climat plus tempéré, comme le révèle d'ail-
leurs une amplitude thermique annuelle plus faible (<10°C).

Les espèces restantes sont des terricoles et, bien qu'elles
se répartissent en deux groupes, on peut leur reconnaître
d'autres exigences écologiques communes qui confèrent à cet
ensemble une relative homogénéité. Ces plantes préfèrent une
température moyenne annuelle comprise entre 10° et 21°C et
une pluviosité au moins égale à 400 mm. Généralement non mon-
tagnardes, elles évitent les altitudes supérieures à 1400 m, et
on les trouve peu en forêt (feuillus et résineux), mais sur-
tout dans le maquis et la garrigue. Ce sont en fait des médi-
terranéennes typiques; c'est pour cette raison que s'y trou-
vent les espèces les plus fréquentes de BRYOMED.

La séparation de cet ensemble en deux groupes se réalise
en fonction d'affinités édaphiques et, le substrat étant dif-
férent, les formations phynérogamiques le sont aussi. Comparons
leur écologie:

variables écologiques	groupe C	groupe D
nature du substrat	terre sur rocher	terre
topographie	escarpement	plateau
microtopographie	fente de rocher	replat,rigole,cuvette
affleurement rocheux	important	nul à faible
pente	forte	nulle à faible
effervescence à HCl	moyenne à forte	nulle
pH	> 7	< 7
groupement phanéro- gamique	garrigue, assoc. rupicoles	maquis, prairies, pe- louses

Parmi les espèces du groupe C, Lophozia turbinata et
Southbya tophacea s'individualisent par leur préférence vis-à-
vis des stations humides (rochers suintants). Les grandes
Marchantiales sont majoritaires parmi les autres espèces de

ce groupe auquel appartiennet Cephaloziella baumgartneri et Southbya nigrella espèces dont on a montré la liaison avec la pinède de pin d'Alep. Il est remarquable de n'y trover aucune Ricciineae.

A l'inverse, dans le groupe D, toutes des Marchantiales, à l'exception de Corsinia coriandrina, sont des Ricciineae qui constituent presque 60% de ce groupe.

ANALYSE COENOLOGIQUE

Nous avons voulu vérifier si les regroupements écologiques établis précédemment se retrouvaient dans les combinaisons spécifiques de la pinède. Pour cela, une classification hier-archique, avec les mêmes caractéristiques que la précédente, a été réalisée sur les espèces, mais cette fois d'après leur présence simultanée dans les 97 relevés de la pinède. Pour des raisons techniques, nous n'avons pas traité les espèces récoltées une seule fois. Cette analyses est évidemment très sensible à l'échantillonnage de la pinède et ne presente pas la même stabilité que la classification effectuée sur les profils écologiques. Pour cette raison, les premières dicho-tomies apparaisent à un taux d'inertie beaucoup plus faible (fig. 6). On y retrouve les groupes écologiques précédents, mais assemblés de façon différente. Le groupe A, caractéris-tique des pinèdes méditerranéennes arides at semi-arides, est représenté uniquement par Riccia atromarginata et R. la-mellosa, et s'associe au groupe D en fonction des affinités communes vis-à-vis de la nature du substrat (terre), de la topographie (sol plat), avec une strate arborescente réduite et une strate herbacée bien développée. En fait, le groupe A ramplace le groupe D dans les cas d'une évolution du milieu vers l'aridité.

Sur l'autre branche du dendrogramme, les deux espèces re-présentant le groupe B (Cololejeunea minutissima et Frullania dilatata) s'inscrivent dans le groupe C, car il n'y a pas, pour ces taxons, de séparation nette entre corticole et rupicole. Cette branche correspond à la flore typique de la

pinède de pin d'Alep. Les hépatiques terricoles se retrouvent sur les blocs rocheux et non sur le sol (espèces du groupe C). Dans des régions à climat plus humide, apparaissent les espèces à affinités corticoles du groupe B.
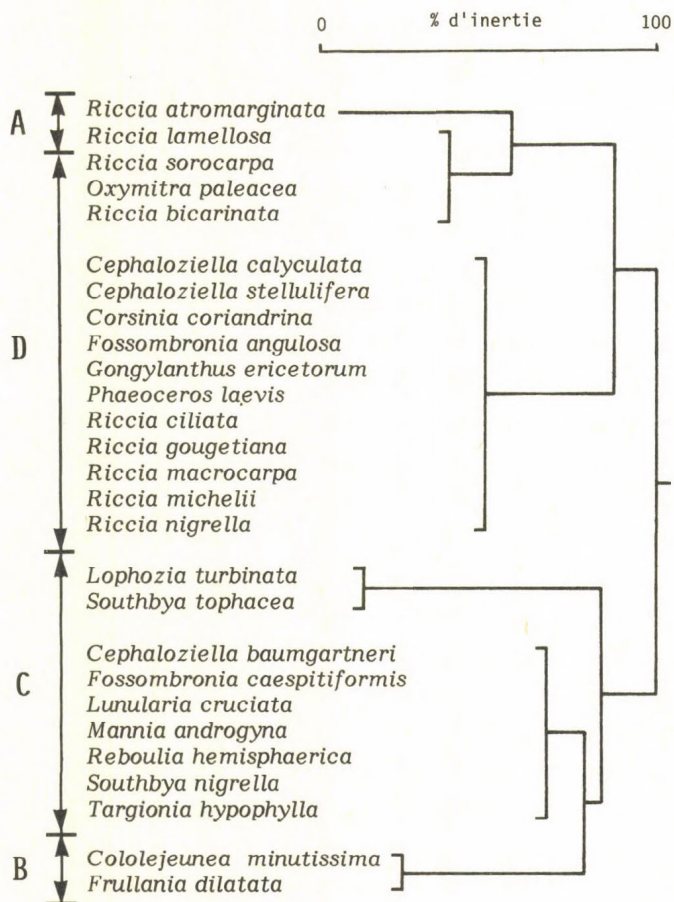
Fig. 6. Dendrogramme issu d'une C.A.H. des taxons d'après leur présence dans les relevés de la pinède a Pin d'Alep. Les groupes A, B, C, D sont définis dans la C.A.H. précédente (Fig. 4).

En résumé: Si la pinède de pin d'Alep se développe sur sol calcaire, les hépatiques, même terricoles, ne s'installent pas sur le sol, mais sur les affleurement rocheux, à la faveur d'une humidité locale de la station. Ces observations concordent avec les résultats obtenus par l'un d'entre nous (Hébrard 1984) pour les forêts de pin d'Alep de basse Provence calcaire (Bouches-du-Rhône et partie sud-occidentale du Var) dont la végétation bryophytique présente à la surface du sol n'est composée que de mousses. Le sol, très sec en surface, n'accumule que peu ou pas d'humus à cause de la décomposition trop lente des aiguilles du pin. Or seuls les quelques millimètres superficiels du substrat permettent aux hépatiques de s'établir. A la faveur de stations plus humides (sources, bords de ruisseaux, rochers suintants), un groupement à _Lophozia_ _turbinata_ et _Southbya_ _tophacea_ peut s'individualiser. Si la pinède se dégrade par une aridité croissante, les hépatiques du groupe A apparaissent. A l'inverse, une humidité croissante (influence atlantique, altitude plus élevée) permet l'installation des espèces du groupe B. Sur substrat non calcaire, une forme dégradée de la pinède laisse se développer, outre les herbacées qui deviennent très nombreuses, les taxons terricoles du groupe D.

Dans une étude des pinèdes à _Pinus_ _sylvestris_ L. et _P._ _uncinata_ Mill., Roux & Salanon (1974) remarquent que les cryptogames n'apportaient pas de modifications majeures dans la nature et le degré d'individualisation das groupmenets phanérogamiques. Réciproquement, nous venons de mettre en évidence que les groupements d'hépatiques ne sont pas liés à la pinède de _Pinus_ _halepensis_ Miller et qu'ils se définissent en dehors de celle-ci. Cela vient confirmer les conclusions de ces deux auteurs: "il faut considérer une surface de végétation comme constituée d'un assemblage d'associations de végétaux vasculaires, de Bryophytes, de Champignons, de Bactéries du sol, etc.".

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BETRACHTUNGEN UND VORSCHLÄGE ZUR ABGRENZUNG EINIGER MOOS-ASSOZIATIONEN UND IHRE ÖKOLOGISCHE EINGLIEDERUNG IN DAS BRYOZÖNOTAXONOMISCHE SYSTEM

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Based on ecological, coenological and syndynamical data the epixylous and epiphytic moss communities of forests have generally been defined considering the structure of the community, the dominant and co-dominant species and the succescional series. In fact, the epixylic and epiphytic moss communities can be separated from each other both ecologically and coenologically, although there are transitional types as well. Starting from this assumption, it seems appropriate to distinguish among 5 large bryocoenotaxonomic groups. According to the author's view, group 5 contains the epixylic moss communities. These are clearly distinguished from the epiphytic moss communities. Examples and a successional series demonstrate the findings of the paper.

I. EINLEITENDE DATEN

Die biologischen Typen (Bioformen) wurden bei den Bryophyten schon in der zweiten Hälfte des vorigen Jahrhunderts nach morphologischen (Warming, Drude) , physiognomischen (Humboldt, Grisebachm Hult) und ökologischen (Kerner, Gams) Gesichtspunkten eingeteilt.

Wir beziehen uns auf die von Geographen, Phytogeographen und Phytosoziologien besonders in den gemässigen und kalten Zonen Europas an Bryophyten ausgeführten Untersuchungen. Eine erste Einteilung der Bryophyten nach morphologisch-ökologischen Kriterien wurde von Lorenz (1860), dann von Grebe

(1917), Amann (1928) u.a. vorgenommen. Gams unterscheidet in
seiner ökologischen Klassifizierung drei Kategorien, denen wir
noch einige charakteristiche Determinanten, wie: freie, nicht
fixierte; auf feste Substrate (Gestein, Rinde, Holz) fixierte;
und auf verhältnismässig weichen Substraten fixierte (terri-
cole) Formen hinzugefügt haben.

Synökologisch gesehen, unterscheidet Herzog (1926) bei den
baumbewohnenden Bryozönosen folgende drei Kategorien: die vom
unteren Teile des Stammes (Wurzeln), die von den Stämmen und
die vom verwesenden Stämmen getroffenen. Amann (1928) stellt
zwei Kategorien auf: baumbewohlende und lignicole, mit der
Einteilung in Gesellschaften ("sociationes"), die Laubmoos-
synusien darstellen (nach Gams 1932) (z.B. Leucobryinae),
Moosgesellschaften, die ausschliesslich aus Bryophyten gebildet
sind (z.B. Sphagnaceae, Polytrichaceae, Grimmiaceae, u.a.) und
Bryophytenaasoziationen, an denen auch andere Kryptogamen-
gruppen Pilze, Flechten und Kormophyten teilnehmen, solche-
stellen z.B. die Assoziationen der Tundra, der Torfmoore, der
Wälder u.a. dar, denen die mengenmässig vorherrschenden Kryp-
togamen den Charakteristichen physiognomischen Aspekt auf-
prägen. Unter den Autoren über die Zönologie der Kryptogamen
im allgemeinem (insbesondere inbezug auf die Flechten und
Moose) sind zu nenne: Lippmaa, Gams, Braun-Blanquet, Tüxen -
Hübschmann - Pirk, Hübschmann u.a.

Die bei der Untersuchung von Moosgesellschaften und zwar
besonders von dene, die streng von einem gewissen Substrat ab-
hängen (epiphytische, epixylische, saprolignische, koprophile
u.a.) methodisch und statistisch angewandten qualitativen und
quantitativen Analysen, erlauben es, die dominanten und ko-
dominanten ± konstanten, oft monospezifischen Arten derselben
zu identifizieren und zu bestimmen. Die Beobachtungen betref-
fend des Ausmasses der ökologischen Anpassung einiger Bryo-
phyten führte zur Begrenzung und Eingliederung der Bryozönosen
in ein natürliches, ökologisches, bryozönotaxonomisches Sys-
tem.

Indem sich Gams etwas später (1932) mit der Eingliederung
der Bryozönosen nach ökologischen Kriterien eingehender befas-

ste, stellte er einen Schlüssel mit 12 Bryophytentypen, die
verschiedenen Standorte (Biotope) in Betracht ziehend, auf. Er
reiht die epiphytischen (auf der Rinde und den Blätterns vor-
handenen) und die saprolignischen (auf morschem Holz angesie-
delten) Bryozönosen in die Gruppe der Epiphytia (mit den Un-
terabteilungen Epixylia und Epiphyllia) ein, ohne aber eine
getrennte, ökologisch gesonderte Kategorie der saprolignischen
Bryozönosen vorzusehen.

Barkman 1958 teilt die Kryptogamen taxonomisch in die
Kategorien Algen, Flechten und Moose ein, welche zönologische
Einheiten vom Range der Ornungen darstellen. Der gleiche Ver-
fasser teiilt die von einem bestimmten Substrat abhängugen
Bryozönosen in zwei getrennte, den betreffenden Biotopen
entsprechende Typen und zwar in die Moose des morschen Holzes
und in die epiphytischen Moose der Bäume ein.

Erwähnenswert ist die SpeżifitäT vieler Bryophyten gegenü-
ber der physikalischen und chemischen (biochemischen) Beschaf-
fenheit des Substrates. Aus der ökologischen Analyse sowie
auch aus der Analyse einiger im Lande ausgeführten experimen-
tellen Untesuchungen (Stefureac 1941) geht die ausgeprägte
ökologische Affinität gegenüber der Substratbeschaffenheit
hervor, so dass die Bryophyten dadurch mit ihren erdbewohnenden
Formen gute ökologische und pedoklimatologische Indikatoren
und die baumbewohnenden u.a. im algemeinen gute klimatologische
Indikatoren derstellen.

Einige der Bryophytenarten (einschliessich der Infrataxa),
wachsen nur auf der Rinde der Bäume (Ulota crispa, Orthotrichum
speciosum, O. lyellii, Zygodon viridissimus, Z. dentatus u.a.),
andere wieder nur auf Gestein (Ulota hutchinsiae, Zygodon gra-
cilis, Orthotrichum anomalum u.a.). So sind innerhalb derselben
Gattung, ja innerhalb derselben Arten, ökologisch differen-
zierte Taxa vorhanden, die sich auf verschiedenen Substraten
entwickeln. Unter den Bryophyten gibt es baumbewohnende Formen,
die in ihrem Variabilitätskreis adaptiv gesteinsbewohnende
Infrataxa gebildet haben (z.B. Neckera pennata auf Baumrinde
und ihre Abart saxicola auf Gestein). Das felsenbewohnende
Moos Orthotrichum alpestre besitzt als infraspezifisches

Taxon die corticole Abart _laricinum_. Ahnliche Fälle sind auch
bei einigen erdbewohnenden Arten anzutreffen (z.B. die erdbe-
wohnende Art _Hypnum_ _lindbergii_ besitzt die holzbewohnende
Abart _lignicola_) oder bei Arten derselben Gattung (z.B. das
auf Humus vorkommende _Leucobryum_ _glaucum_ und das felsenwohnende
(Gnais) _L._ _albidum_).

Die ersten in Europa durchgeführten territorial-monogra-
phischen bryozönologischen Untersuchungen, die sich auf lang-
jährige Beobachtungen und auf zönotaxonomische Abgrenzungen
und Eingliederungen der Bryozönosen stützen, sind im Zeitraum
zwischen 1936-1947 veröffentlicht worden. Da diese Untersuchun-
gen sich auf phytozönologisch-methodologische Auffassungen
stützten, waren sie Anlass zu neuen Orientierungen und gaben
die erste Anregung zu bryozönologischen Untersuchungen, Von
diesen haben wir die von Greter (1936), Ştefureac (1941),
Waldheim (1944-1947), Demaret(1945), Krusenstjerna (1945),
Giacomini (1945) u.a., einschliesslich von diesen einheimischen
und auswärtigen Verfassern angeführte ind im Schrifttum der
vorliegenden Arbeit verzeichnete Literatur hervor.

Dank der Anhäufung von Daten und Fakten aus diesem
Gebiet haben sich in letzter Zeit die ökologischen Untersuchun-
gen der Bryophyten verstärkt und zwei Richtungen eingeschlagen:
die eine bezieht sich auf die eigentliche Bryozönologie und
die andere auf die allgemeine Phytozönologie. Beide Richtungen
haben für die methodische Erforschung der Vegetation wertvolle
Ergebnisse gebracht. Die Bryophyten besitzen, dank ihres
prägnant ökologischen und besonderen phytosozialen Charakters,
für einige Formationen (Wälder, Tundren, Sümpfe, Moore, u.a.)
oft eine vorherrschend funktionelle polyvalente und für einige
komplexe Ökosysteme (Moore, Wälder, u.a.) eine determinierende
Eigenschaft. Die bryozönologischen Untesuchungen erforderen
sowohl auf dem Gelände, als auch im Labor eine unvergleichlich
lange Zeit.

II. ALLGEMEINE BETRACHTUNGEN ÜBER DIE EPIPHYTISCHEN UND SAPROLIGNISCHEN BRYOZÖNOSEN, TERMINOLOGIE

Einige Bryologgen reihen die gesamte Mooswelt des Waldes
und zwar die epiphytischen Bryozönosen (von lebenden Bäumen)
sowie die saprolignischen (von totem, morschem Holz) in ein
und dieselbe zönotische Gruppe, und zwar in die 4. Gruppe ein
(Hübschmann 1973). Andere widere vereingen sie sogar alle zu-
sammen in derselben Ordnung (Barkman 1958). Wir sind der
Meinung, dass diese Eingliederung, die weder das ökologische,
noch das bryozönologische Kriterium beachtet, keinem natür-
lichen bryozönologischen System entsprechen kann. Daraus ist
die Schwierigkeit und Unsicherheit betreffend die Begrenzung
und Eingliederung dieser Bryozönosen im europäischen geo-
graphischen Raum zu erklären (Stefureac 1941, 1967, 1972,
1980) u.a.

Was die Terminologie der für morsches Holz charakteristi-
schen Bryozönosen anbelangt, so wurden verschiedene Fachaus-
drücke eingeführt, wie z.B. "Stock- und Baumleichen" (Glo-
wacki 1918), "bryocadaveric" (Stefureac 1941), "saprolignicol"
(Gaume 1950), "peuplement saproxyle" (Doignon 1954) u.a., von
denen häufig und singemäss der Ausdruck saprolignicol (sapro-
lignisch) verwendet wird, der physiologisch und biochemisch den
adaptiven saprophytischen Stoffwechsel als zusetzliche Er-
nährung der Bryophyten auf diesem spezifischen Substrat zum
Ausdruck bringt.

Was den Sinn einiger Begriffe anbelangt, so erachten wir
es als inkorrekt, epixylischen und saprolignischen Bryozönosen
den Charakter von Epiphyten zuzuschreiben und sie so zu den
Epiphytia einzugliedern. Die Ausdrücke epixylisch und sapro-
lignisch sind nicht gleichbedeutend, sondern unterscheiden
sich ökologisch und bryozönologisch voneinander, indem sie
syndynamisch stadial abgegrenzte, untereinander verschiedene
Bryozönösen bezeichnen, von denen die ersteren sich auf
hartem Holz und die letzteren sich auf morschem Holz ent-
wickeln.

III. KRITERIEN ZUR UNTERTEILUNG UND NATÜRLICHEN EINGLIEDERUNG
DER EPIPHYTISCHEN UND SAPROLIGNISCHEN BRYOZÖNOSEN

Wird das syndynamische öko-zönologische Kriterium der
Struktur der Bryozönosen sowie die phytozönotischen Beziehungen
zwischen den einzelnen Komponenten derselben in Betracht ge-
zogen und gleichzeitig auch der Spezifität. Affinität und Ho-
mogenität der Bryozönosen gegenüber einem bestimmten Substrat
Rechnung getragen, wobei besonders die charakteristischen
(dominanten und kodominanten) Arten beachtet werden, so scheint
die Behauptung rechfertigt, wonach die epiphytischen (baumrin-
denbesiedelnden) Bryozönosen und die saprolignischen (von
morschem Holz) aus dem phytoklimatischen Milieu der Fichten-
wälder europäischer Gebirgslagen in zwei voneinander ver-
schiedene zönotische Gruppen und zwar einerseits in die
Gruppe der epiphytischen und anderseits in die Gruppe der
saprolignischen Bryozönosen einzugliedern sind. Diese Ein-
gliederung kann im allgemeinen auch auf die extrakontinentalen
(tropischen, äquatorialen) Waldformationen erstneckt werden.
In diesem Sinne bringen wir folgende Beweise und Beispiele:
- Sowohl die epiphytischen, als auch die saprolignischen
Bryozönosen bilden einheitliche Zönosen, die unter den mikro-
klimatischen Bedingungen der Waldökosysteme von ihrem spezi-
fischen Substrat (strenger) Abhängigkeit stehen.
- Die Lage des Substrates, an welche sich diese Bryozö-
nosen anhaften und auf den sie sich dann weiter entwickeln,
kann verschieden sein, ist bei den epiphytischen im allgemeinen
vertikal und bei den saprolignischen ± horizontal.
- Die epiphytischen Arten sind dank des gut entwickelten
Rhizoidsystems, das ihnen eine dauerhafte Fixierung an die
Unebenheiten des Rhytidoms sicherstellt; sie haben im allge-
meinen eine ausgeprägte Anpassungsfähigkeit, ökophysiologisch
gesehen einen positiven Geotropismus und wachsen oft in herab-
hängender Form. Die saprolignischen Bryozönosen sind ökophy-
siologisch durch ein unterschiedliches Ausmass des Sapro-
phytismum ihres Stoffwechsels gekennzeichnet.

- Die den epiphytischen Bryozönosen charakteristischen Moose fehlen im allgemeinen aus der Zusammensetzung der eigentlichen epixylischen und saprolignischen Bryozönosen und umgekehrt.

- Die Zahl der zu den epixylischen und saprolignischen Bryozönosen gehörenden Bryophyten der Fichtenwälder ist unvergleichlich grösser, als diejenige der epiphytischen Bryophyten. Eine von uns aufgestellte Statistik über einige europäische Veröffentlichungen, einschliesslich derer aus Rumänien, bestätigen die Anwesenheit von cca 30 Arten (besonders Laubmoose und weniger Lebermoose) in den epiphytischen Bryozönosen, im Vergleich zu den cca 70-90 (epixylischen und saprolignischen) Arten der saprolignicolen Bryozönosen. Die Mehrzahl von diesen ist obligatorisch saprolignisch, häufig und oft qunatitativ vertreten, andere sind lediglich fakultativ oder sogar nur zufälligerweise anwesend (indifferent-polyedaphisch), wobei die meisten acidophil, torfliebend, silicophil und kalkmeidend.

- Es gibt Bryophyten mit einer ausgeprägten Spezifität für bestimmte Baumarten (Laubbäume, Nadelbäume), besonders im Rahmen der epiphytischen Bryozönosen (zum Teil auch bei den saprolignischen); so wachsen z.B. Apometzgeria pubescens, Porella platyphylla u.a. auf Laubbäumen und ganz besonders auf Acer pseudoplatanus.

- Zahlreiche europäische Autoren haben sich auch tatsächlich bryofloristisch und zönologisch etweder mit epiphytischen (wie z.B. Hilitzer, Ochsner, Wisniewski, Ştefureac, Felföldy, Gams, Hübschmann, Peciar, Mihai, Michiewicz, Slack, u.a.) oder mit saprolognischen Arten (wie z.B. Pichler, Ştefureac, Jovet, Doignon, Raschendorfer, Gams, Gaume, Philippi, u.a.) beschäftigt.

IV. BESTIMMENDE UND ABGRENZENDE ÖKOLOGISCHE FAKTOREN DER EPIPHYTISCHEN UND SAPROLOGNISCHEN BRYOZÖNOSEN

Vom ökologischen Standpunkt her, sind einige grundlegende Unterschiede zwischen den Faktoren, welche die Ansiedlung und Entwicklung der epiphytischen und saprolignischen Bryozönosen hervorzuheben:

- Die Luftfeuchtigkeit ist relativ höher und ± kontinuier-
lich mit einer gewissen Beständigkeit unter den ökologischen
Bedingungen der Biotope mit saprolignischen Bryozönosen, da sie
im Vergleich zu den epiphytischen näher dem Boden zu liegen.

- Der Feuchtigkeitsgehalt des Substrates mit vorherrschen-
der Rolle hängt von den Stadien der Holzzersetzung ab, dieses
ist fast ständig mit Niederschlagswasser, oft bis zur Uber-
sättigung getränkt, die Bryophyten dieses vermodernden Holzes
gehören den mezophilen, den mezohygrophilen und einige sogar
(zeitlich) den ± hygrophilen Formen an, während die Formen der
epiphytischen Bryozönosen das Wasser periodisch zurückhalten
und Mezo-, Mezoxerophyten und einige sogar Xerophyten darstel-
len, die manchmal adaptive morphologische Vorrichtungen zur
Zurückhaltung des Wassers (Wasserspeicherung) aufweisen.

- Der Wassergehalt des Substrates des saprolignischen Bryo-
zönosen schwankt zwischen 84 und 26% und weist einen Durch-
schnittswert von 77.97% auf, der aus der Analyse von 50 Proben
ermittelt wurde, was ungefähr 80% des Gewichtes des Substrates
ausmacht. Bei den epiphytischen Bryozönosen schwankt der Feuch-
tigkeitsgehalt des Substrates in Abhängigkeit von der Beschaf-
fenheit der Baumrinde, von der Intensität der physiologischen
Funktionen und der Widerstandskraft derselben, von den saison-
bedingten Niederschlagsmengen und von der Luftfeuchtigkeit
(Ştefureac 1941).

- Der pH-Wert des Substrates der saprolignischen Bryozöno-
sen schwankt zwischen 6,0-4,0 und liegt damit etwas höher, als
derjenige des Substrates der epiphytischen Bryozönosen (6,0-
5,5); der Säuregrad hängt von der betreffenden Baumart ab (z.B.
4,2 - 6,5 - Fagus sylvatica, 4,4 - 5,0 - Picea abies, 5,0 -
5,8 - Abies alba, 5,4 - 6,0 - Acer pseudoplatanus).

- Die verringerte Helligkeit verleiht ber Mehrzahl der
saprolignischen Arten einen skiaphilen Charakter, während die
epiphytischen Arten schattenliebend und ± lichtliebend und aus-
geprägteren Schwankungen unterworfen sind, die auch von den
klimatischen Elementen des Waldes, von der Höhe und von der
Lage desselben bedingt werden.

V. BRYOPHYTENZÖNOLOGISCHE ASPEKTE BETREFFEND DIE SUKZESSIONS-
PHASEN DER EPIXYLISCHEN UND SAPROLIGNISCHEN BRYOZÖNOSEN
(SCHEMA)

Von diesem Gesichtspunkte aus betrachtet, bemrken wir, dass
die epiphytischen Moosgesellschaften einen einheitlichen ±
homogene Charakter aufweisen, im Gegensatz zu den saproligni-
schen, die einen heterogenen Charakter haben und deren Struk-
tur und Zusammensetzung von den Sukzessionsstadien abhängen,
die durch den von komplexen mikrobiellen Macerationsprozessen
am lignitischen Substrat hervorgerufenen Vermoderungsgrad und
Säuregehalt bedingt werden. Die epiphytischen Moosassozoationen
unterscheiden sich klar von den epixylischen und den sapro-
lignischen. Die für die epiphytischen Moosassoziationen cha-
rakteristischen Arten gehören zu einer relativ geringen Zahl
der Lebermoose, im Vergleich zu den epixylischen und saprolig-
nischen Moosgesellschaften, die unter Bedingungen starker
Feuchtigkeit eine grosse Zahl von Lebermoosen - einige eu-
tallisch, die meisten aber cormoidisch - aufweisen und zeit-
lich verschiedenartige Bryozönosen bilden.

Was die Sukzessionsphasen anbelangt, so unterscheiden
einige Bryologen in der Dynamik der Bryozönosen, die morsches
Holz besiedeln (epixylische und saprolignische) vier Stadien
(Gams 1928, Ştefureac 1941). Bei den in den rumänischen
Karpaten ausgeführten Analysen wurden in Abhängugkeit von den
pH-Werten vier Phasen mit den für sie charakteristischen
Arten aufgestellt: I. Phase (pH-Wert 6,0 - 5,4) mit Hypnum
cupressiforme var. filiforme, Orthodicranum montanum; II.
Phase (pH-Wert 5,4 - 4,8) mit Herzogiella seligeri; III. Phase
(pH-Wert 4,8 - 4,0) mit Tetraphis pellucida, Dicranodontium
denudatum; die IV. Phase ist ausser diesen letzten Arten auch
durch die gemeinen terri-humicolen, in Wäldern vorkommenden
Arten gekennzeichnet (Dicranum scoparium, Pleurozium schre-
beri, Hylocomium splendens, Rhytidiadelphus triquetrus u.a.).
Die Sukzessionen beginnen von den Resten der epiphytischen
Bryozönosen, die eine gewisse Zeit auf den umgestürzten Stäm-
men verbleiben (Hypnum cupressiforme var. filiforme, Ortho-

dicranum montanum, Isothecium alopecuroides, Leucodon sciuroides u.a.), gehen dann zu den epixylischen und saprolignischen über, um schliesslich von den terri-humicolen gefolgt zu werden, die das Klimax-Stadium darstellen.

Die Bryozönosen von den umgestörzten Stämmen entwickeln sich auf dem charakteristischen Substrat in Abhängigkeit vom Helligkeitsgrad, wobei gewisse Arten sich auf der oberen, zenitalen Seite und andere, von der Bodenentfernung abhängigen Arten, auf den Seitenteilen an siedeln und die standortlichen ökologischen Faktoren in ihrer Gesamtheit bestimmend einwirken.

Die epiphytischen Bryozönosen von der Rinde getrockneter, stehender Bäume sterben ab und lösen sich allmählich, zusammen mit der sich freischälenden Rinde, ab. Auf dem getrockneten, senkrecht stehenden Stamm siedeln sich nur eine geringe Anzahl, mengenmässig schwach vertretener Bryophyten mit verringerter Lebenskraft an. Sind die Stämme einmal umgestürzt, so treten zusammen mit der fortschreitenden Anfeuchtung des Substrates auch die ersten Stadien der Holzvermoderung ein, wobei nun die normalerweise ökologisch aufeinanderfolgenden Bryozönosen mit den epixyéischen ihre Ansiedlung beginnen.

Die erste Sukzessionsphase der Entwicklungsstadien der Bryozönosen zeichnet sich durch eine Verringerung und ein Zurückweichen der epiphytischen Arten von den umgestürzten Baumstämmen aus, wobei sich aber einige von ihnen noch für längere Zeit behaupten.

In der zweiten, epixylischen Phase, siedelns sich auf dem harten Holzteil des sich allmählich entrindenden und mit Feuchtigleit getränkten Stammes, zenital zunächst die cormoiden Lebermoose, an wie Lophocolea heterophylla, Nowelia curvifolia, Cephaloziella rubella var. sullivantii u.a., die von Odontoschisma denudatum, Ptilidium pulcherrimum u.a. begleitet werden sowie auch die eutallischen Riccardia palmata und R. latifrons sowie von den Laubmoosen Herzogiella seligeri, Buxbaumia viridis und auch Ptilium crista-castrensis u.a., einschliesslich Myxomyceten-Arten. Hand in Hand mit der fortschreitenden Vermoderung des Holzes folgen vorherrschend die Lebermoose der Gattungen Riccardia, Calypogeia, Lophozia, Cepha-

lozia, Tritomaria, Scapania u.a., dem Stadium, in welchem
sich die Bryozönosen mit Tetraphis pellucida und Dicranodontium
denudatum und von den Flechten verschiedene Cladonia-Arten zu
entwickeln beginnen.

Die dritte Phase gehört den Arten mit üppiger Entfaltung
der Populationen von Lepidozia reptans mit Lophozia porphyro-
leuca, Jamesoniella autumnalis, Blepharostoma trychophyllum u.
a. dann einigen Flechten (Icmadophila ericetorum, Cladonia und
Peltigera div. spec.) und zahlreichen Myxomyceten an. Mit der
fortschreitenden Mazerierung des morschen Holzes findet die
massive und kompakte Heranbildung von monospezifischen Bryo-
zönosen mit Tetraphis pellucida statt, wobei in der gleichen
Phase Dicranodontium denudatum vorausging oder kodominiert.

Die vierte Phase ist in den Endstadien der Zersetzung des
vermoderten Holzes auch durch die dominierende Sukzession der
terri-humicolen Moose der Mooschicht des Waldes: Bazzania tri-
lobata, Dicranum scoparium, Leucobryum glaucum, Eurhyncium
striatum, Polytrichum formosum u.a. und von Mnium, Rhizomnium,
Plagiomnium-Arten, zwishen denen sich eine gewisse Zeit auch
die letzten Büschel von Tetraphis pellucida und Dicranodontium
denutatum noch behaupten, charakterisiert.

Es ist zu erwähnen, dass die epiphytischen Bryozönosen nur
selten und nur bei höherer Luftfeuchtigkeit die Aufenanderfolge
einer begrenzten Zahl von Kormophyten veranlassen können,
während die saprolignischen Bryozönosen in der Sukzession, be-
sonders in den fortgeschrittenen Stadien, eine grosse Zahl von
Farnen und zu den Gräsernzählende Angiospermen, etwas Nieder-
holz sowie Fichten- und Tannenjungpflanzen heranziehen, die
sich auf dem rohhumusreichen Waldboden reihenweise entwickeln.
Es sind Klimax-Stadien mit reichhaltiger Teilnahme erdbewohnen-
der Bryozönosen.

Was die Beständigkeit anbelangt, so sind die epiphytischen
Bryozönosen des Waldes, im Vergleich zur Vitalität und Leben
dauer der Bäume (ja selbst der jahrundertealten) über eine
längere Teitspanne hin lebensfähig und können eine unvergleich-
lich längere Periode überdauern, als die epixylischen und sap-
rolignischen Bryozönosen, die in verhältnismässig kürzeren

Zeiträumen - je nach den ökologischen Bedingungen des Standortes zwischen 25 - 30, höchstens 50 Jahre - aufeinanderfolgen und dies in direktem Zusammenhang mit dem Rhytmus der Zersetzung des Substrates.

Beziehen wir uns auf den geographisch begrenzten Karpatenraum, so stellen die beiden Moosgruppen (die epiphytische und die saprolignischen) im bryozönotaxonomischen System zönologisch-ökologisch differenzierte syndynamische sukzessionell evolutive Einheiten dar.

Ebenfalls charakteristisch sind auch ainige Ubergänge zwischen den (regressiven) epiphytischen Bryozönosen von den umgestürzten Baumstämmen und den progressiven (epixylischen, saprolignischen und terri-humicolen) saprolignischen Bryozönosen.

Unter den saprolignischen Bryozönosen trifft man häufig Arten an, die gleichzeitig auch felsbewohnend sind sowie auch auf Torf, Kieselsteinen lebende und zufälligerweise auch einige kalkliebende Arten an. So wachsen sowohl auf morschem Holz, als auch auf quarzitischem Gestein die Lebermoose: Cephalozia catenulata, Lophozia incisa, Odontoschisma denudatum, Scapania umbrosa, Mylia taylorii, u.a.

Ökologische Übergänge beobachtet man, geographisch gesehen, besonders bei polyedaphischen Arten (terri-saxi-turfi-saprolignicol u.s.w.). Von den Übergängen vom felsigen Substrat (Silikat-gesteine) der Atlantischen Küste Westeuropas zum (häufig) epixylisch-saprolignischen Substrat der Südkarpaten Rumäniens, führen wir als Beispiel in diesem Sinne die Art Mylia taylorii (Ştefureac 1969) an.

VI. ABGRENZUNG UND EINGLIEDERUNG EPIPHYTISCHER UND SAPRO-LIGNISCHER BRYOZÖNOSEN IN EIN NATÜRLICHES BRYOZÖNOTAXONOMISCHES SYSTEM

Wir erachten es, dass diese Beobachtungen und Präzisierungen genügende Beweise zur Natürlichen Abgrenzung und Eingliederung der epiphytischen and saprolignischen Bryozönosen in zwei zönologisch getrennte Gruppen liefern.

Auf Grund der dargelegten Beweise schlagen wir nun vor,
dass die für verschiedene Substrate und Standorte von Pflanzen-
formationen charakteristischen Moosgesellschaften nicht in vier
(Hübschmann 1973), sondern in fünf grosse bryozönotische Grup-
pen zusammengefasst werden sollen, wobei zur fünften Gruppe, die
der saprolignischen (einschliesslisch der epixylischen) Bryo-
zönosen mit ihren Sukzessionstadien wird, die von den physika-
lischen und biochemischen Zersetzungsprozessen des organischen
Substrates abhängig sind. Diese Stadien entwickeln sich von den
(regressiven) baumrindenbewohnenden epiphytischen Bryozönosen
beginnend zu den epixylischen und von diesen dann fortschreitend
zu den eigentlichen saprolignischen bis zum terri-humicolen-
Klimax (Stefureac 1941, 1969, 1977)(Schema):

An der basis von Stämmen

(am Wurzelansatz)

Epiphytische-corticole → Auf Stämmen
(auf der Rinde)
Europäischer Raum
(Fichtenwälder)

Auf Asten
(Baumkronen)

A. Auf lebenden Bäumen

Epiphylische-auf Blättern Tropen-regionen

Bryozönosen
(Moosgesellschaften)

Epixylische (Stadium I-II)

B. Auf abgestorbenen morschen Stämmen

Saprolignische (Stadium III-IV)

Terri-humicole (Klimax)

Schema: Ökologische Abgrenzung und syndynamische Eingliederung
der epiphytischen und saprolignischen Bryozönosen (T. I.
Ștefureac 1980).

Was nun die epiphytischen Moosassoziationen anbelangt, so
gliedert Barkman (1958) in die IV. Ord. Lophocoletalia hetero-
phyllae Bark. 1958 und zwar in die X. Al. Blepharostomion
(Stefureac) Bark. 1958 die Assoziationen ein, die nach ihren
charakteristischen Arten epixylisch und saprolignisch und nicht
epiphytisch sind: Leptoschyphetum taylorii Stefureac 1941, Hyp-
netum fertilis (Stefureac) Bark. 1958, Sphenolobetum hellerinae
Bark. 1958, Jamesonielletum autumnalis Bark. 1958, Nowellieto-
Lepidozietum pinnatae Bark. 1958 nov. ass. prov. u.a. und in
die XI. Al. Tetraphido-Aulacomnion (v. Kruss.) Bark. 1958 die
Assoziationen Leucobryeto-Tetraphidietum Bark. 1958, Ortho-
dicraneto-Plagiothecielletum Bark. 1958, Ptilidieto- Hypnetum
pallescentis (Herzog 1943) Bark. 1958 u.a., die auch nicht
epiphytisch sind, sondern den Sukzessionsstadien der epixylisch-
saprolignischen Bryozönosen angehören.

Die Benennungen VI. Ord. Lophocoletalia heterophyllae Bark.
1958, der X. Al. Blepharostomion (Stefureac) Bark. 1958 und
XI. Tetraphido-Aulacomnion (v. Kruss.) Bark. 1958 mit den nach
gewissen (nicht epiphytischen) Leit-Lebermoosen, wie Lophocolea
heterophylla, Blepharostoma trichophyllum, Mylia taylorii, u.a.
einschliesslich des Laubmooses Tetraphis pellucida bestimmten
Assoziationen, können ökologisch und zönologisch nicht zu den
epiphytischen Bryozönosen eingereiht werden, da sie epixylische
und saprolignische Bryozönosen des morschen Holzes darstellen.
Saprolignische Arten, wie Lophocolea heterophylla, Tetraphis
pellucida, u.a. treffen wir sekundär auch innerhalb der ter-
ricolen, saxicolen, turficolen und silicicolen Bryozönosen an
und nur vereinzelt innerhalb einiger Bryozönosen von der Basis
der Stämme einiger Bäume.

Lophocoletum heterophyllae Peciar 1965 von Mihai (1974)
in der Moldau (Birnova-Repedea, Wälder neben Jassy) analysiert,
stellt ebenfalls eine saprolignische Bryozönose dar. Bryolo-
gische Erforschungen über die saprolignischen Moosgesellscahften
der rumänischen Karpaten wurden auch von Lungu (1971) im Bis-
tritzer Gebirge (Cristişor) und von Plamada (1976) im Natur-
schutzgebiet des Retezat Gebirge vorgenommen.

Zwecks Verbesserung des natürlichen bryozönotaxonomischen allgemeinen Systems schlagen wir vor, dass die Moosgesellschaften des morschen Holzes in rechtfertigterweise getrennte Einheiten vom Range der Ordnungen darstellen sollen, wobei die epixylischen derselben in die Ord. Lophocoletalia heterophyllae (Bark. 1958) Stefureac 1977 nov. sens., die eigentlich saprolignischen in die Tetraphidetalia pellucidae (Bark. 1958) Stefureac 1977 nov. sens. einzureihen sind, da sie ökologisch, zönologisch und syndynamisch die Sukzession derselben bis zum Stadium der terri-humicolen Klimax anzeigen; die Sukzessionsphasen bilden hierbei Einheiten (Verbände) innerhalb derer die betreffenden Moosgesellschaften einzugliedern sind.

Diese natürliche Eingliederung wird zugleich auch die Abgrenzung einiger (zeitliche) Übergange von den epiphytischen Bryozönosen (nach dem Umsturz der Bäumme) zu den epixylischen ermöglichen, indem sie die stadiale Entwicklung der Bryozönosen des morschen Holzes bis zum terri-humicolen Klimax darstellen (Schema). Bryozönotische Übergänge fehlen auch innerhalb der epiphytischen Bryozönosen nicht, so wie es die Übergänge von den erdbewohnenden Moosgesellschaften zu denen der Basis (Wurzelansatz) der lebenden bäume und von diesen zu den eigentlichen epiphytischen Bryozönosen der Bäumstämme und Zweige darstellen.

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BRYOPHYTE VEGETATION AND ECOLOGY OF CALCAREOUS AREAS IN THE IBERIAN PENINSULA

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Since 1982 a program of bryological research has been
undertaken in four calcareous regions in the Iberian peninsula.
Exploration of the bryophyte vegetation of the western areas
was carried out in regions with altitudes up to 500 m and re-
lated to the bryophyte vegetation of the eastern areas up to
1400 m altitude, with particular reference to the different
types of habitats. 347 taxa were found. The ecology and bio-
geography of the species are treated here; the degree of flo-
ristic similarity among the four Iberian areas is presénted.

INTRODUCTION

The aim of the present work was to provide detailed in-
formation about the bryophytic flora of limestone regions of
different mediterranean areas of the Iberian Peninsula.

This type of study can provide important information
about the ecology and chorology of the Iberian bryoflora
and particularly the special and interesting calcareous com-
munities.

Four poorly known areas were selected, two in the western
part (Portugal) and two in the eastern part (Spain) (see Fig.
1). Precise locations, about 25 to 40 sites in each area, with
well-defined physiognomic vegetation types were selected, and
an annotated list of bryophytes from each zone was produced.

More detailed studies concerning the bryophyte vegetation
in each area have contributed to two published papers (Sérgio

et al. 1984, Casas et al. 1985), and two papers are in preparation (Casas et al. 1985, Sérgio et al. 1986).

The four selected areas are of Tertiary and secondary rocks mainly from the Triassic to upper Cretaceous periods, sometimes composed of compact or karstic limestones.

The areas covered by the present study are about 1000 km^2 each. Altitudes vary from 5 to 500 m in Portugal and to 1400 m in Spain.

The four regions studied have a typical Mediterranean climate in which the summer is the dry season, and the pattern of the driest months is characteristic (see the climate diagrams in Fig. 1).

Due to the heterogeneity of the Mediterranean climate, especially as regards precipitation and temperature (Quezel 1977), there are a very large number of bioclimatic types present in the areas studied.

Using the criteria for the delimitation of bioclimatological types in the Iberian Peninsula (Rivas-Martinez 1984), each region can be characterized:

The Portuguese northern area (Lu 1) with a sub-humid climate presents a climax vegetation in the more protected sites. It is included in the mesomediterranean basophilous series of the Quercus faginea subsp. broteroi the Arisaro-Quercetum faginea. In more exposed localities the Rhamno-cocciferetum is present.

In the Algarve (Lu 2), with a drier climate, species of the thermophilous series are also present (Oleo-ceratonion) and thermomediterranean semi-arid species such as Chameropsis humilis and Pistacea lentiscus. Our first Spanish region (Hs 1) has a dry climate with a climax vegetation in the highest areas included in the supramediterranean iberic basophilous series with Quercus faginea ssp. valentina. The mesomediterranean series is also present in the Alicante region (Hs 2) with Quercus rotundifolia and in more xeric lowland the thermomediterranean series, the Chameropo-Rhamnetum lycioides.

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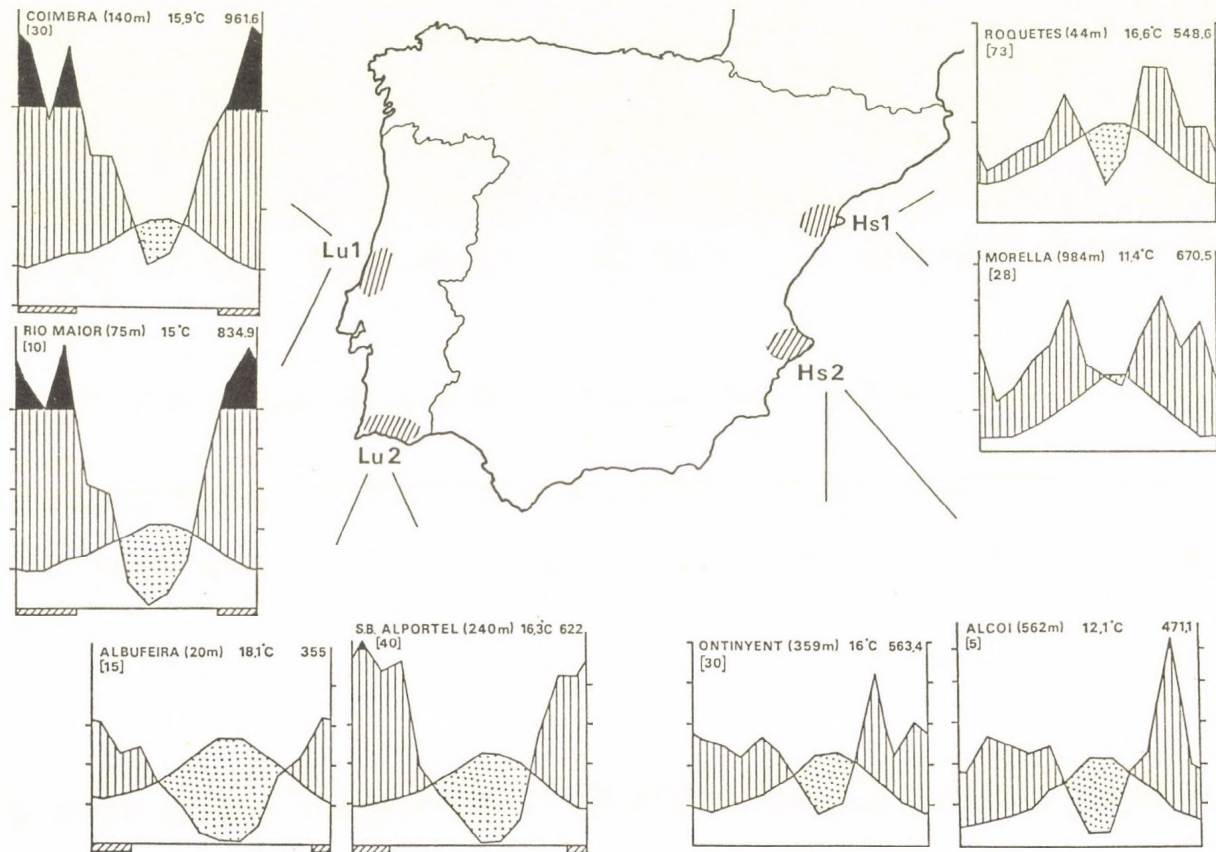
Fig. 1. Location of the areas studied in the Iberian Peninsula with two climatic diagrams for each area. Lu 1 Macico calcario central (1000 km^2), Lu 2 Barrocal algarvio (1000 km^2), Hs 1 Ports de Beseit (800 km^2), Hs 2 Comarcas Alicantinas (1000 km^2).

MAIN HABITAT TYPES

In general, the limestone areas support a very character-
istic assemblage of bryophytes. The different communities are
presented and treated separately in relation to environmental
factors.

AQUATIC COMMUNITIES

The bryophyte flora of calcareous rocks in or at the mar-
gins of streams and temporary lakes and slopes includes a dis-
tinctive assemblage of species, many of which are exclusive
to this habitat and some have characteristic horizontal zona-
tion pattern. Some, such as Fontinalis spp., Fissidens grandi-
frons, F. crassipes, Cinclidotus spp., and Cratoneuron spp.,
require a prolonged submersion. Several species, for example,
Dialytrichia mucronata and Didymodon tophaceus and other taxa
characteristic of stream borders, such as Pellia endiviifolia,
Gymnostomum calcareum, Eucladium verticillatum and Marchantia
paleacea are more markedly tolerant and can support some de-
siccation.

A facies of the communities of semi-innundated limestones
often has Bryum gemmiparum and Brachythecium rivulare and in
some localities the interesting Tortula solmsii.

TERRICOLOUS COMMUNITIES

The exposed terricolous communities offer some of the
richest habitat type and present a large number of ephemeral
elements, dominated by Riccia spp., Fossombronia spp., Oxymit-
ra paleacea, Corsinia coriandrina. Minute Pottiaceae (Acaulon
spp., Pottia spp., and Aschisma carniolicum) are also impor-
tant. However, in Spain, the hepatic species and Ephemerum
spp. are less frequent and some species of Didymodon, Barbula
and Tortula are more abundant. Some famous rarities of the Me-
diterranean basin, such as Grimmia pitardii as well as Acaulon
dertosensis n. sp. (Casas et al. 1985) are found in this
habitat.

On less exposed and more humic substrates the bryophyte communities are heterogeneous, generally rather poor in species and are a traditional condition in rock associations or epiphytic communities. The mosses are mainly pleurocarpic, including Hypnum cupressiforme, Scleropodium purum, Ctenidium molluscum, Homalothecium aureum, Anomodon viticulosus, as well as hepatics such as Plagiochila spp., Scapania spp. in the highest regions of the Spanish areas.

SAXICOLOUS COMMUNITIES

A diversity of ecological conditions is present in all limestone habitats due to differing altitudes.

The communities of exposed limestones have generally species-poor facies and are more or less restricted to Orthotrichum and Grimmia species. The latter genus is, however, less represented in the Portuguese flora and some Tortella spp. are more frequent.

The species of humus rock crevices have a very great diversity, but an interesting facies is present in Portugal, with Plagiochasma rupestre and Enthostodon curvisetus with Fissidens intralimbatus. On the other hand, in Spain some rare species such as Athalamia spathysii and Preissia quadrata were found in rock crevices.

Factors controlling the development of these communities enable some species of epiphytic substrates, such as Homalothecium sericeum, Eurhynchium meridionale and Scorpiurium circinatum to colonize this habitat.

Shaded rocks present a more rich community with interesting components such as Marckesinia mackaii (only in one locality of Spain), but frequently including species of Porella, Rhynchostegium, Neckera, Radula and also some Lejeuneaceae, as well as Metzgeria furcata and Leptodon smithii.

EPIPHYTIC COMMUNITIES

The epiphytic bryophytes develop a particular species assemblage in the Mediterranean climates, generally with a markedly xerophilous and thermophilous facies. However, in the four areas studied it is optimally developed in the more Atlantic region (Lu 1).

Here they are extremely complex and composed of an important lichen community with large foliose species of the Lobarion pulmonariae Oschsn. 1928 mixed with large patches of bryophytes of the Leucodontetalia (von Hübschmann 1952) emend. Lecointe 1975. The number of species is frequently more than 40 and the cover is sometimes 80 to 100%.

In Spain, these situations are rarer and some species-poor communities occur only in more shaded and protected sites. In these communities, however, some interesting epiphytic elements were found, such as Fabronia pusilla, Habrodon perpusillus, Zygodon forsteri and also Scorpiurium sendtneri, Pylaisia polyantha and Neckera webbiana.

It is important to mention that Cololejeunea minutissima, an aerohygrophilous species with a Mediterranean-Atlantic distribution, is present only in (Lu 1).

RESULTS AND CONCLUSIONS

Based on the percentage of occurrence of bryophyte species present in the four areas studied (Table 1) and also the values of the altitudinal gradient we can obtain a detailed treatment of this flora.

Many other ecological correlations among the species can be inferred but some should be considered preliminary.

The bryophyte vegetation of the four calcareous areas studied has a characteristic Mediterranean assemblage with a high diversity near 33% of the taxa of the Iberian Peninsula.

The major community type is in Portugal (Lu 1) with 203 taxa.

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Table 1. List of bryophyte species occurring in the four areas studied, in % with number of sites investigated.

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
HEPATICAE						
Aneura pinguis (L.) DUM.				4	3	350- 375
Athalamia spathysii (LINDENB.) HATT.				4	3	200-1050
Cephaloziella baumgartneri SCHIFFN.	28	30	25- 500	11	15	50-1200
Cephaloziella calyculata (DURIEU & MONT.) K. MULL.	13		100- 325			
Cephaloziella divaricata (SM.) SCHIFFN.	6		200- 300	4		300
Cephaloziella stellulifera (TAYL. ex SPRUCE) SCHIFFN.	13	4	150- 325			
Cololejeunea calcarea (LIBERT) SCHIFFN.				11		400-1150
Cololejeunea minutissima (SM.) SCHIFFN.	19		200- 500			
Cololejeunea rossettiana (MASS.) SCHIFFN.	3		275	4		600
Conocephalum conicum (L.) UNDERW.	3		75	7		300- 350
Corsinia coriandrina (SPRENC.) LINDB.	53	17	50- 550			
Exormotheca bullosa (LINK ex LINDENB.) K. MULL.	3		425			
Fossombronia angulosa (DICKS) RADDI		4	50			
Fossombronia caespitiformis DE NOT. ex RABENH.	13	43	125- 400		13	0- 600
Fossombronia crispa NEES	9	9	25- 300			
Fossombronia achinata MACV.	19	13	50- 400		3	500
Fossombronia husnotii CORB.	56	35	50- 550			
Fossombronia pusilla (L.) NESS		9	100- 175			
Fossombronia wondraczekii (CORDA) LINDB. var. loitlesbergeri (SCHIFFN.) CHAL.	3		150			

Table 1 (continued)

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Frullania dilatata (L.) DUM.	63	43	50- 500	21	3	900-1125
Frullania muscicola STEPH.				4		300
Frullania tamarisci (L.) DUM.	22	4	50- 400	7		1050-1150
Frullania tamarisci (L.) DUM. var. mediterranea DE NOT.	3		300			
Gongylanthus ericetorum (RADDI) NESS		4	50			
Jungermannia atrovirens DUM.				7		375- 900
Lejeunea cavifolia (EHRH.) LINDB.	16		200- 500	25		375-1150
Lophocolea bidentata (L.) DUM.	6		225- 300	4		1050
Lophocolea minor NEES				7		900-1050
Lophozia badensis (GOTT. in RABENH.) SCHIFFN.					3	650
Lophozia collaris (NEES) DUM.				4		1100
Lophozia turbinata (RADDI) STEPH.	9	13	50- 300	29	8	300-1150
Lunularia cruciata (L.) LINDB.	50	52	25- 500	4	28	200- 900
Mannia androgyna (L.) EVANS	6	9	50- 400			
Marchantia paleacea BERTOL.				14		300- 650
Marchesinia mackaii (HOOK.) S. GRAY.				4		375
Metzgeria furcata (L.) DUM.	13		250- 300	25		600-1150
Oxymitra paleacea BISCH.	50	22	50- 550		5	500- 525
Pellia endiviifolia (DICKS.) DUM.	3	4	50- 250	21	15	170- 700
Phaeoceros bulbiculosus (BROTERO) PROSK.	22	9	50- 550			
Phaeoceros laevis (L.) PROSK.		9	50- 100			
Plagiochasma rupestre (FORST.) STEPH.		22	50- 350			

Table 1 (continued)

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Plagiochila porelloides (TORREY ex NEES) LINDENB.				25		600-1150
Porella arboris-vitas (WITH.) GROLLE				18	3	600-1150
Porella canariensis (F. WEB.) BRYHN	3		325			
Porella obtusata (TAYL.) TREV.	6	4	250- 425			
Porella platyphylla (L.) PFEIFF.	9		300- 325	36	10	300-1200
Preissia quadrata (SCOP.) NEES				4		1000
Radula complanata (L.) DUM.	9		300- 400	46		300-1150
Radula lindenbergiana GOTT. ex HARTM.	38		200- 500	7		650- 900
Reboulia hemisphaerica (L.) RADDI	25	13	50- 400	14	18	375-1200
Riccia atromarginata LEVIER		17	50- 250	4		50
Riccia beyrichiana HAMPE ex LEHM.	3		125			
Riccia bicarinata LINDB.	25	39	25- 400			
Riccia bifurca HOFFM.		4	50			
Riccia ciliata HOFFM.	9		300- 375			
Riccia ciliifera LINK ex LINDENB.	6		250- 325			
Riccia crozalsii LEVIER	19	4	275- 550			
Riccia crystallina L. emend. RADDI		4	25			
Riccia gougetiana DURIEU MONT.	38	4	50- 550		5	500-1125
Riccia lamellosa RADDI	6	30	25- 375	4	8	175- 525
Riccia macrocarpa LEV.	22		100- 550			
Riccia michelii RADDI	3	4	50- 325			
Riccia nigrella DC.	13	22	25- 550		8	500
Riccia sommieri LEVIER	13	4	50- 375			

Table 1 (continued)

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Riccia sorocarpa BISCH.	19	43	25- 400	4	5	375- 575
Riccia subbifurca WARNST. ex CROZALS		9	25- 50			
Riccia trabutiana STEPH.	3	9	75- 125		3	200
Riccia trichocarpa HOWE	6		250- 500			
Riccia warnstorfii LIMPR. in WARNST.		4	150			
Scapania aspera M. & H. BERN.				11		1050-1150
Scapania nemorea (L.) QROLLE				4		1075
Southbya nigrella (DE NOT.) HENRIQUES	44	35	75- 500		3	400
Southbya tophacea (SPRUCE) SPRUCE	38	17	50- 550		13	300- 900
Sphaerocarpus sp.					3	400
Targionia hypophylla L.	13	17	50- 350		15	300-1200
Targionia lorbeeriana K. MULL.	28	48	25- 425		5	200- 500

MUSCI

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Abietinella abietina (HEDW.) FLEICH.				14		900-1100
Acaulon dertosensis CASAS et al.				4		50
Acaulon minus (HOOK. & TAYL.) JAEG.	3	4	50- 275			
Acaulon triquetrum (SPRUCE) C. MULL.		4	150	4	8	550- 650
Aloina aloides (K.F. SCHULTZ) KINDB.	22	35	100- 400	25	25	125- 900
Aloina ambigua (D. & S.) LIMPR.	6	39	25- 500	18	28	50-1200
Cinclidotus riparius (BRID.) ARNOTT	3		50			
Cirriphylum crassinervium (TAY.) LOESKE & FLEISCH.				4		900

Table 1 (continued)

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Cratoneuron commutatum (HEDW.) G. ROTH.				25	8	175-1000
Cratoneuron filicinum (HEDW.) SPRUCE				21	13	175- 900
Crossidium crassinerve (DE NOT.) JUR.				11	8	50- 650
Crossidium squamiferum (VIV.) JUR.	13	9	50- 200	14	35	125-1200
Cryphaea heteromalla (HEDW.) MOHR	19		200- 500	4		975
Ctenidium molluscum (HEDW.) MITT.	28		200- 500	39	5	300-1150
Cynodontium bruntonii (SM.) B., S. & Q.	6		250- 275			
Dialytrichia mucronata (BRID.) BROTH.	34	17	75- 400			
Dicranella howei REN. & CARD.	22	74	125- 375	11	30	50-1200
Dicranella varia (HEDW.) SCHIMP.	6		125- 200		3	650
Dicranoweisia cirrata (HEDW.) LINDB. ex MILDE	3		325			
Dicranum scoparium HEDW.				18		900-1150
Didymodon acutus (BRID.) K. SAITO	16	35	25- 550	7	23	550-1200
Didymodon cordatus JUR.					3	675
Didymodon fallax (HEDW.) ZANDER	22	17	100- 375	18	15	350-1100
Didymodon insulanus (DE NOT.) M. HILL	9	4	50- 300			
Didymodon luridus HORNSCH. ex SPRENQ.	41	26	75- 425			
Didymodon sinuous (MITT.) DELONQE					3	900
Didymodon tophaceus (BRID.) LISA	16	13	25- 225	11	30	200- 900
Didymodon trifarius (HEDW.) ROHL.				36	30	50-1200
Didymodon vinealis (BRID.) ZANDER	9	9	50- 425	7	10	175-1100
Distichium capillaceum (HEDW.) B., S. & Q.				4		1150
Ditrichum flexicaule (SCHWAEGR.) HAMPE				11	3	900-1150

Table 1 (continued)

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Ditrichum subulatum HAMPE	3	4	50- 425			
Depanocladus aduncus (HEDW.) WARNST.	3		200			
Encalypta streptocarpa HEDW.				18	8	500-1200
Encalypta vulgaris HEDW.	9		100- 350	14	18	400-1200
Entosthodon attenuatus (DICKS.) BRYHN	3		425			
Entosthodon curvisetus (SCHWAEGR.) C. MULL.	3	9	25- 400			
Entosthodon fascicularis (HEDW.) C. MULL.	3		325			
Entosthodon obtusus (HEDW.) LINDB.	3		150			
Ephemerum recurvifolium (DICKS.) BOUL.		17	75- 200			
Ephemerum serratum (HEDW.) HAMPE		4	150			
Ephemerum sessile (BRUCH) C. MULL.	3	4	150- 500			
Ephemerum stellatum PHILIB.	6		275- 500			
Epipteragium tozeri (GREV.) LINDB.	3	4	50- 425		5	700- 900
Eucladium verticillatum (BRID.) B., S. & Q.	6	9	125- 400	36	18	300-1100
Eurhynchium hians (HEDW.) LAC.					10	325- 400
Eurhynchium meridionale (B., S. & Q.) DE NOT.	41		125- 500	32	5	300-1150
Eurhynchium praelongum (HEDW.) B., S. & Q. var. stokesii (TURN.) DIX.	25	4	25- 425			
Eurhynchium pulchellum (HEDW.) JENN.					3	1125
Eurhynchium pumilum (WILS.) SCHIMP.	6	9	25- 275			
Eurhynchium schleicheri (HEDW.) J. LOR.				4		1100
Eurhynchium speciosum (BRID.) JUR.	3	4	75- 200	11	5	175- 750
Eurhynchium striatulum (SPRUCE) B., S. & Q.				11		600-1150

Table 1 (continued)

Species	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Fabronia pusilla RADDI	3	9	150	4		400
Fissidens algarvicus SOLMS	6	4	50- 375			
Fissidens crassipes WILS. ex B., S. & Q.	16	22	50- 250	7		200- 350
Fissidens crassipes WILS. ex B., S. & Q. var. philibertii BESCH.	6		125- 225		3	200
Fissidens crassipes WILS. ex. B., S.& G. var. rufipes SCHIMP.					13	350-1200
Fissidens cristatus WILS. ex MITT	66	4	100- 550	46	3	350-1150
Fissidens grandifrons BRID.				11		350- 600
Fissidens incurvus STARKE ex ROHL.	25	35	25- 550	4	5	375
Fissidens intralimbatus RUTHE		4	25			
Fissidens limbatus SULL	6	4	25- 500	4	8	200- 700
Fissidens taxifolius HEDW.	16		125- 300	4		900
Fissidens viridulus (SW.) WAHLENB.	41	48	200- 550	18	18	100-1200
Fontinalis antipyretica HEDW.				4		350
Fontinalis hypnoides HARTM.	9		50- 225			
Fontinalia squamosa HEDW. var. dixonii (CARD.) E.J. SMITH.		9	175- 250			
Funaria convexa SPRUCE	13	17	25- 400		3	200
Funaria hygrometrica HEDW.	34	17	50- 500	7	18	200- 900
Funaria muhlenbergii TURN.		4	100			
Funaria pulchella PHILIB.	6	22	25- 400		8	100- 675
Grimmia crinita BRID.					3	500
Grimmia decipiens (K.F. SCHULTZ) LINDB.					3	900

Table 1 (continued)

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Grimmia orbicularis BRUCH ex WILS.	9		100- 325	25	30	200-1200
Grimmia itardii CORB.	3		325	4	3	50- 200
Grimmia pulvinata (HEDW.) SM.	38	9	100- 500	32	8	400-1200
Grimmia pulvinata (HEDW.) SM. var. africana (HEDW.) HOOK.					10	425-1200
Grimmia tergestina TOMM. ex. B., S. & G.					3	500
Grimmia trichophylla GREV.	9	9	50- 550	4	10	550-1200
Gymnostomum calcareum NEES & HORNSCH.	47	26	50- 500	18	25	300-1200
Gymnostomum luisieri (SERGIO) SERGIO ex Crundw.	28	30	50- 550	25	23	50-1200
Gymnostomum recurvirostre HEDW.				11		350-1000
Gyroweisia tenuis (HEDW.) SCHIMP.					3	1200
Habrodon perpusillus (DE NOT.) LINDB.		4	150	11	5	400-1125
Homalothecium aureum (SPRUCE) ROBINS.	34		100- 550	4	3	575-1125
Homalothecium lutescens (HEDW.) ROBINS.				21		575-1150
Homalothecium philippeanum (SPRUCE) B., S. & G.	3	4	125- 300			
Homalothecium sericeum (HEDW.) B., S. & G.	66	22	50- 500	21	23	300-1200
Hygrohypnum luridum (HEDW.) JENN.				4		900
Hylocomium splendens (HEDW.) B., S. & G.				11		900-1100
Hypnum andoi A.J.E. SM.	6		300- 350	14		300-1100
Hypnum cupressiforme HEDW.	56		125-550	39	13	550-1200
Hypnum imponens HEDW.	6		400			
Hypnum jutlandicum HOLMEN & WARNCKE				4		700
Hypnum vauchari LESG.				4		1000

	Lu1 (%)	Lu2 (%)	Alt. gra-dient (M)	Hs1 (%)	Hs2 (%)	Alt. gra-dient (M)
Leptobarbula berica (DE NOT.) SCHIMP.		22	0- 350	4		375
Leptodon smithii (HEDW.) WEB. & MOHR	53	9	100- 550	32	3	400-1150
Leucodon sciuroides (HEDW.) SCHWAEGR.				4		1150
Leucodon sciuroides (HEDW.) SCHWAEGR. var. morensis (SCHWAEGR.) DE NOT.	66	17	100- 550		3	1125
Mnium marginatum (WITH.) P. BEAUV.				4		1150
Mnium stellare HEDW.				4		1050-1150
Neckera complanata (HEDW.) HUB.	34		200- 500	18	3	600-1150
Neckera crispa HEDW.				14		600-1150
Neckera webbiana (MONT.) DULL.				7		600- 900
Orthothecium rufescens (BRID.) B., S. G.				4		1000
Orthotrichum affine BRID.	25	13	50- 425	21	3	550-1125
Orthotrichum affine BRID. var. fastigiatum (BRID.) HUB.				4		975
Orthotrichum anomalum HEDW.	66	9	100- 550	21	13	300-1200
Orthotrichum anomalum HEDW. var. saxatile (BRID.) MILDE					4	375
Orthotrichum cupulatum BRID.	9	9	275- 550	11	8	400-1200
Orthotrichum cupulatum BRID. var. riparium HUB.				4		600
Orthotrichum cupulatum Brid. var. sardagnanum (VENT.) VENT.					3	1200
Orthotrichum diaphanum BRID.	9	26	50- 500	18	13	300-1125
Orthotrichum lyellii HOOK. & TAYL.	22		200- 500	7	3	1100-1125
Orthotrichum pallens BRUCH ex BRID.	16		100- 500	11		700-1100

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Orthotrichum pumilum SW.	3		400	11		600-1100
Orthotrichum rupestre SCHWAEGR. var. franzonianum (DE NOT.) VENT.					3	1125
Orthotrichum schimperi HAMMAR				4		1150
Orthotrichum speciousum NEES				4		650
Orthotrichum stramineum BRID.				4		575
Orthotrichum striatum HEDW.				14		575-1100
Orthotrichum tenellum BRUCH ex BRID.	6	9	125- 300			
Phascum curvicolle HEDW.				14		50- 650
Phascum cuspidatum HEDW.	3		200			
Phascum cuspidatum HEDW. var. piliferum (HEDW.) HOOK. & TAYL.	3	9	275		3	375
Phascum floerkeanum WEB. & MOHR.				7		50- 650
Philonotis marchica (HEDW.) BRID.				4		175
Plagiomnium affine (BLAND.) T. KOP.	3		200	4		1050
Plagiomnium undulatum (HEDW.) T. KOP.	9		200- 300	11		900-1150
Pleuridium acuminatum LINDB.	19	4	50- 550			
Pleuridium subulatum (HEDW.) RABENH.	6		150- 250			
Pleurochaete squarrosa (BRID.) LINDB.	69	22	50- 550	18	30	200-1200
Pogonatum aloides (HEDW.) P. BEAUV.	3		425			
Pohlia delicatula (HEDW.) GROUT		9	75- 250	14	18	175- 900
Pohlia wahlenbergii (WEB. & MOHR) ANDR.		9	25- 250			
Polytrichum juniperinum HEDW.	16		150- 500			
Pottia bryoides (DICKS.) MITT.				7		200- 650

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Pottia caespitosa (BRUCH ex BIRD.) C. MULL.	19	26	50- 425		8	0-1200
Pottia commutate LIMPR.	6	9	200- 300		5	500
Pottia davalliana (SM.) C. JENS.	3	17	25- 550	7	3	175- 700
Pottia intermedia (TURN.) FURN. var. littoralis DIXON	6		100- 300			
Pottia lanceolata (HEDW.) C. MULL.				4		650
Pottia recta (WITH.) MITT.	3		325			
Pottia starckeana (HEDW.) C. MULL.	3		275	14	13	50- 650
Pottia starckeana (HEDW.) C. MULL. ssp. starckeana		26	0- 150			
Pottia truncata (HEDW.) B. & S.	3	9	25- 425			
Pottia wilsonii (HOOK.) B. & S.	3		300		3	750
Pseudocrossidium hornschuchianum (K.F. SCHULTZ) ZANDER	9	22	50- 350	11	10	50-1125
Pseudocrossidium revolutum (BRID.) ZANDER		4	100	4	5	650-1200
Pterogonium gracile (HEDW.) SM.	50	13	50- 550		3	1125
Pterygoneurum ovatum (HEDW.) DIX.					15	125-1200
Pterygoneurum ovatum (HEDW.) DIX. var incanum JUR.					5	650-1200
Pylaisa polyantha (HEDW.) SCHIMP.	3		400			
Rhynchostegiella curviseta (BRID.) LIMPR.	13	9	100- 350	11	3	200-1100
Rhynchostegiella curviseta (BRID.) LIMPR. var. laeviseta BROTH.		4	50	4		375
Rhynchostegiella tenella (DICKS.) LIMPR.	22		200- 425	18	3	300- 900
Rhynchostegiella tenella (DICKS.) LIMPR. var. litorea (DE NOT.) MONK.	3	4	50- 200		5	375-1125

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Rhynchostegium confertum (DICKS.) B., S. & Q	6	4	100- 350	4		600
Rhynchostegium megapolitanum (WEB. & MOHR) B., S. Q.	25	35	125- 375	23		325-1200
Rhynchostegium riparioides (HEDW.) CARD.	6		75- 225	14	10	175- 700
Rhytidium rugosum (HEDW.) BROTH.				4		900
Schistidium apocarpum (HEDW.) B., S. & Q.	25		200- 425	29	10	400-1200
Scleropodium purum (HEDW.) LIMPR.	25		200- 500	32		550-1150
Scleropodium touretii (BRID.) L. KOCH	41	22	25- 400	4	3	900-1100
Scorpiurium circinatum (BRID.) FLEISCH. LOESKE	66	52	50- 500	18	20	200-1125
Scorpiurium deflexifolium (SOLMS) FLEISCH. LOESKE	9	22	25- 250			
Scorpiurium sendtneri (SCHIMP.) FLEISCH.	6	9	50- 400		3	900
Seligeria sp.					3	1125
Thamnobryum alopecurum (HEDW.) NIEUIL.				11		900-1150
Thuidum delicatulum (HEDW.) MITT.				4		600
Timmiella anomala (B., S., & Q.) LIMPR.					3	400
Timmiella barbuloides (BRID.) MONK.	28	30	50- 400			
Timmiella flexiseta (BRUNCH) LIMPR.	3	4	200- 375			
Tortella flavovirens (BRUNCH) BROTH.	41	9	50- 550	7	5	550- 900
Tortella humilis (HEDW.) JENN.		4	150	21	3	575-1150
Tortella inclinata (HEDW.) LIMPR.		13	25- 50	4		575
Tortella inflexa (BRUCH) BROTH.	6	26	150- 425	4	3	50- 900
Tortella nitida (LINDB.) BROTH.	50	48	50- 500	4	5	100-1200

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Tortella tortuosa (HEDW.) LIMPR.	19		125- 500	32	13	375-1200
Tortula atrovirens (SM.) LINDB.		4	350		8	425- 750
Tortula canescens MONT.	3		300	4		50
Tortula caninervis (MITT.) BROTH.					3	1200
Tortula inermis (BRID.) MONT.	3		200		15	400-1200
Tortula intermedia (BRID.) DE NOT.	47	9	200- 550	4	15	400-1200
Tortula laevipila (BRID.) SCHWAEGR.	53	26	75- 500			
Tortula marginata (B. & S.) SPRUCE	6	9	50- 100		3	200
Tortula muralis HEDW.	41	26	50- 500	29	20	175-1200
Tortula muralis HEDW. var. obcordata (SCHIMP.) LIMPR.				4	10	200-1125
Tortula pagorum (MILDE) DE NOT.					3	300
Tortula papillosa WILS.				4	3	400- 900
Tortula ruraliformis (BESCH.) INQH. var. subpapillosissima (BIZ. PIER) W. KRAMER					3	1200
Tortula ruralis (HEDW.) GAERTN., MEYER & SCHREB.	3		300	25	8	650-1150
Tortula solmsii (SCHIMP.) LIMPR.	3	4	50- 225	4		1075
Tortula subulata HEDW.	3		300	11		975-1150
Tortula subulata HEDW. var. subinermis (B., S. & Q.) MILS				7		1075-1100
Trichostomum brachydontium BRUCH	34	30	225- 500	7	10	400-1125
Trichostomum brachydontium BRUCH ssp. cuspidatum (BRAITHW.) GIAC.				4		375

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)
Trichostomum brachydontium BRUCH var. littorale (MITT.) C. JENS.	22	9	25- 425		3	500
Trichostomum brachydontium BRUCH var. unguiculatum (PHILIB.) CORB. & JAH.					3	200
Trichostomum crispulum BRUCH	56	61	25- 500	36	40	125-1100
Trichostomum crispulum BRUCH var. brevifolium SCHIMP.					3	350
Weissia brachycarpa (NEES & HORNSCH.) JUR.	19		300- 375		5	0- 100
Weissia condensa (VOIT) LINDB.	34	17	50- 550	11		600-1150
Weissia controversa HEDW.	31	13	100- 500		3	900
Weissia levieri (LIMPR.) KINDB.		4	100			
Weissia longifolia MITT.	13	9	50- 500	4		575
Weissia longifolia MITT. war. angustifolia (BAUMGR.) CRUNDW. & NYL.		4	150	7	5	500-1200
Weissia triumphans (DE NOT.) M. HILL	3	9	25- 350	4		50
Zygodon baumgartneri MALTA	50	30	50- 425	11	5	300-1125
Zygodon forsteri (WITT.) MITT. var. sendtneri (JUR.) DIX.				4		400
Zygodon viridissimus (DICKS.) BRID.	13		200- 400			

T O T A L   V A L U E S

HEPATICAE

Total number of species	49	40	33	24	75
Total number of infraspecific taxa	2	0	0	0	2
Total number of genera	22	17	22	15	33

Total number species

Lu1 — 203
Lu2 — 154
Hs1 — 180
Hs2 — 162

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)

MUSCI

Total number of species	149	111	141	129	242
Total number of infraspecific taxa	9	8	9	17	28
Total number of genera	62	47	62	52	85

Sørensen's Quotient
of Similarity (Q.S.)

Lu1			
68.3	Lu2		
51.2	43.7	Hs1	
57.5	56.3	54.4	Hs2

SPECIES AREA-RELATIONSHIPS (Km^2)

AREA TYPE SPECTRA IN %

Cosmopolitan (incl. Sub-cosm.)	14	13	17	17	13
Circumboreal (incl. Oroph.)	25	16	39	22	29
Atlantic (incl.Sub and euryatl.)	6	4	7	5	8
Atlantic-mediterranean	32	38	14	24	25
Mediterranean (incl.Sub and eurymed.)	24	29	22	31	24

WATER RELATIONS IN %

Hygrophilous (incl. Hydroph.)	12	7	18	13	16
Mesohygrophilous	9	9	9	6	9
Mesophilous	30	30	30	23	31
Mesoxerophilous	20	20	16	17	16
Xerophilous	29	34	27	40	27

	Lu1 (%)	Lu2 (%)	Alt. gradient (M)	Hs1 (%)	Hs2 (%)	Alt. gradient (M)

SUBSTRATE TYPE IN %

Terricolous	39	44	35	35	39
Terricole-saxicolous	29	32	21	28	26
Saxicolous	10	10	18	19	15
Saxicole-corticolous	12	9	15	9	11
Corticolous	7	3	7	4	6
Ubiquitous	3	3	4	5	3

CHEMICAL NATURE OF SUBSTRATE IN %

Calcicolous (incl. Basophilous)	14	19	22	19	19
Neutrophilous	23	25	26	28	24
Acidophilous	15	6	7	5	12
Indifferent	48	51	45	46	45

LIGHT RELATIONS IN %

Sciophilous	24	25	27	21	29
Photosciophilous	29	28	27	22	26
Photophilous	41	40	36	44	37
Photoheliophilous	5	7	7	10	7
Heliophilous	0	0	2	2	1

The highest values of Mediterranean species are present in the Alicante area and the Mediterranean-Atlantic elements are richly represented in Portugal (32-38%).

It is interesting to note that the circumboreal elements including orophytes are more poorly represented in Portugal than in Spain (22-39%), possibly due to the altitudinal distribution of some species.

Characteristic xerophilous components are best represented in Hs 2 corresponding to a more xeric amd thermophilous region.

There are very high values of 39-44% of terricolous species in Portugal, probably due to the predominance of "terra rossa" soils.

On the other hand, there appears to be a greater presence of acidophilous species in Portugal, possibly due to a high level of precipitation and leaching of the soils.

It is also interesting to note that the Marchantiales and Metzgeriales are present with high percentage of 40% in Portugal, whereas in Spain they represent only 28% of the total hepatic species.

In case of mosses it is the Pottiaceae that dominates with 33% of the total number of taxa.

The results of the analysis based on Sørensen's index of similarity are shown in Table 1 and we can conclude that the highest values were found in the Portuguese areas (68.3). The two Spanish zones are less similar (54.4). The two more southern areas have an important similarity (57.5).

These similarities correspond to the climatic conditions and in reality there is a high correlation between the environmental gradients and the bryophyte communities. The present study shows once more that bryophytes are effective indicators of environmental factors including the bioclimatological conditions.

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DIVERSITY AND DYNAMICS IN BRYOPHYTE COMMUNITIES ON EARTH BANKS IN A DUTCH FOREST

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In a Dutch forest on sandy soil, 16 permanent quadrats of 1/16 or 1/4 m^2, with 5-14 bryophyte and lichen species each, were more or less regularly micro-charted during four years. Superficially, most plots did not change much during these years, the same species remaining present in approximately the same amounts. By comparing successive charts of each plot, we estimated the dynamics of each species and of the stand as a whole. Generally, dynamics were rather higher than expected. Diversity of the plots showed a weak positive correlation with plot dynamics. Plots which were clearly in succession or had been disturbed showed higher dynamics and lower diversity. The results conform to Huston's (1979) diversity model.

INTRODUCTION

The causation of species diversity in communities has been a central theme in plant ecology for many years, especially since Whittaker (e.g., 1965, 1969) and McArthur & Wilson (1967). Co-existence of many plant species in one community may be explained partly by microhabitat differentiation and niche differentiation, especially when the 'regeneration niche' is taken into account (Grubb 1977); evidence is accumulating, however, that under certain circumstances a number of species may co-occur in the same niche ('niche-sharing", During & Willems 1984, Grubb 1984). For vascular epiphytes Benzing (1981) showed that the degree of population dynamics in relation to the rate

at which new micro-sites become available is crucial in this respect. Huston (1979) theoretically derived a more generalized relationship between diversity and the frequency of population reduction (related to population dynamics), with the rate of competitive exclusion (related to potential growth rate of plants and populations) as a second determinant axis. Independently such a relationship between diversity and frequency of disturbance was shown for algal vegetation on intertidal boulders by Sousa (1979).

The diversity of bryophyte communities has only recently received attention, mainly in relation to habitat- and niche-differentiation (e.g., Slack 1977, Lee & LaRoi 1979). However, since bryophytes do not possess roots and in many habitats do not show many phenological differences, the coexistence of many species on a very small scale can hardly be explained by such factors alone, as pointed out by, e.g., Slack (1977) and Watson (1980). As population and community dynamics in bryophytes can be rather high, both in successional situations (e.g., Clement & Touffet 1981, Gloaguen & Gautier 1981) and in more stable communities (Kimmel 1962, Orbán 1978), the equilibrium of local, small-scale disturbances and re-establishment might yield a potential explanation for the coexistence of several species.

A first indication of the value of this idea might be gained from a comparison of detailed charts made of permanent plots at regular intervals (cf. Austin 1981).

A phytosociological study of bryophyte communities on earth banks in the Netherlands showed large variation in species diversity between the stands; in addition, we got the impression that the patterns in the stands were very constant. To test the idea, that this apparent constancy was in fact a steady-state with rapid internal changes, we laid out a number of small permanent plots in a forest near Utrecht, and made micro-charts of these plots more or less regularly. In this paper, we will present data on species turnover and vegetation dynamics in these plots and relate these to the species diversity of the plots.

MATERIAL AND METHODS

The study was done in the 'Kaapse Bossen' nature reserve near Doorn, SE of Utrecht, The Netherlands. The vegetation now-adays is forest - needle, birch, and oak stands, and parts of coppiced oak woods - but the presence of many earth walls indicates a former use as arable fields mingled with heathlands. The soil generally is coarse acid sand very poor in nutrients. Terrestrial bryophytes are mainly found on the earth walls and locally in coppiced oak woods (Dicrano-Quercetum) and along paths (Table 1).

Table 1. The terrestrial bryophytes and lichens of the Kaapse Bossen nature reserve, Doorn, The Netherlands. c: common, o: occasional, r: rare or very local.

Mosses		Hepatics	
Aulacomnium androgynum	c	Calypogeia fissa	r
Brachythecium rutabulum	r	Cephaloziella divaricata	o
Campylopus flexuosus	c	C. rubella	r
C. introflexus	r	Lepidozia reptans	o
C. pyriformis	o	Lophocolea bidentata	r
Ceratodon purpureus	r	L. heterophylla	c
Dicranella heteromalla	o	Ptilidium ciliare	r
Dicranum polysetum	r		
D. scoparium	c	Lichens (incomplete)	
Eurhynchium praelongum	r		
Hypnum cupressiforme	c	Cladonia arbuscula	r
Isopterygium elegans	o	C. chlorophaea s.l.	c
Leucobryum glaucum	o	C. coniocraea	c
Mnium hornum	c	C. glauca	o
Orthodicranum montanum	r	C. portentosa	o
Orthodontium lineare	c	C. squamosa	r
Plagiothecium curvifolium	o	C. uncialis	r
Pleurozium schreberi	c	Hypogymnia physodes	r
Pogonatum aloides	r	Lecidea granulosa	c
Pohlia nutans	c	L. uliginosa	o
Polytrichum formosum	c		
P. juniperinum	r		
P. longisetum	r		
P. piliferum	r		
Pseudoscleropodium purum	r		
Tetraphis pellucida	c		

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Table 2. Characteristics of the permanent plots in the Kaapse
Bossen reserve. S(Size): s=25x25 cm^2, l=50x50 cm^2. N: mean no.
of species.

no	S	exp	incl (o)	N	dominant sp.	Remarks
1	s	N	60	8.7	Lep r/Ca fl	Very sheltered below Pteridium
2	s	W	30	10.2	Ca py/Di sc	In oak wood, fairly open
3	s	W	60	6.9	Di he/Po nu	In oak wood
4	s	N	50	9.3	Ca fl/Po nu	Along path in oak wood
5	l	NW	5	7.4	Hy cu/Ca in	Grassy border of heath fragment
6	l	S	10	6.1	Po nu/Clad - Di sc	Oak wood, young Pinus plantation to the S.
7	l	S	20	4.9	Di sc/Pl sc	Open spot in Pinus stand
8	l	–	–	9.9	Ca fl/Di sc	Path in oak coppice wood
9	l	W	25	10.2	Ca fl/Di sc	Below Fagus in oak wood
10	l	–	–	12.8	Di sc/Le gl	Floor of Dicrano-Quercetum
11	s	N	80	6.9	Di he/Po al	Along path, slightly loamy sand
12	s	N	50	8.7	Cal f/Di sc	As 11
13	s	N	20	6.2	Po nu	As 11, more litter
14	s	E	70	8.0	Di he/Cep b	Sheltered below Fagus trees
15	s	W	40	8.6	Di sc/Ca py	Oak wood bordering wall to E
16	s	W	40	8.2	Di sc	coppiced in 1978

In these habitats 14 permanent plots of 25x25 cm^2 or 50x50
cm^2 (plot size depending on coarseness of vegetation pattern)
were established in May 1977, to which 2 were added in 1978
(Table 2). In all plots except plot 5 phanerogams were nearly
or completely absent. Lichens were included in the analysis,
if present. Using a wire grid of appropriate size with 10x10
subplots we charted the distribution in the plot of each
species on mm-paper as accurately as possible. The microchart-
ing was repeated in autumn 1978 and from then at more or less
regular half-year intervals until spring 1981. The charts
were then compared carefully to establish for each species in
each plot: 1. cover; 2. amount of change; 3. size and cir-
cumference of each 'grain'. From these data we calculated
rates of change per species and per plot using simple formulae
derived from Sørensen's index of similarity (cf. Londo 1971):
Species dynamics: SD = $(x+y)/(x+y+2z)$, where x, y, and z
are the surface on which the species disappeared, appeared as
new, or remained present, respectively.

Plot dynamics: PD = (Σx+ Σy)/(Σx+ Σy+2Σz).
For each recording data we calculated both a measure of 'fine-grainedness' for each species: F = total circumference/cover, and Shannon's diversity index using cover for importance values.

RESULTS

As may be expected in such small plots, there was some change in species composition, a few species appearing or disappearing now and then. No consistent or directional change was observed, except in plot 6. This S-exposed plot was bordered to the S by a young Pinus plantation that in this period increasingly shaded it. Consequently, the original open bryophyte layer with Cladonia spp. and Pohlia nutans as prominent species was fairly rapidly replaced by dominant Dicranum scoparium; most of the associated species changed as well. Heavy rabbit burrowing activities in early 1980 in plot 15 caused considerable changes in the species composition and turnover rates in this plot, too. Interestingly, the coppicing of the oak wood bordering the wall of plot 15 and 16 early in 1978 did no cause such a change in the bryophyte layer, although the microclimate locally certainly changed.

Internal changes with regard to exact position of the different species or, conversely, in the species occupying each spot in the plots, were surprisingly high (Fig. 1). For most plots the value of PD was 0.4 or higher for each half-year period. Only in plot 7, situated in an open spot in a stand of Pinus trees, was this value consistently lower. The exceptionally high values for plot 6 and partly for plot 15 are reflections of the more 'catastrophic' changes that took place in these plots.

Diversity of the plots, here measured as H', ranged from 0.23 to 2.03. The large plots did not show higher diversity values, indicating that the scale difference was not too large to prevent comparison. Consistently the highest values were found in plot 10, the floor of a Dicrano-Quercetum stand,
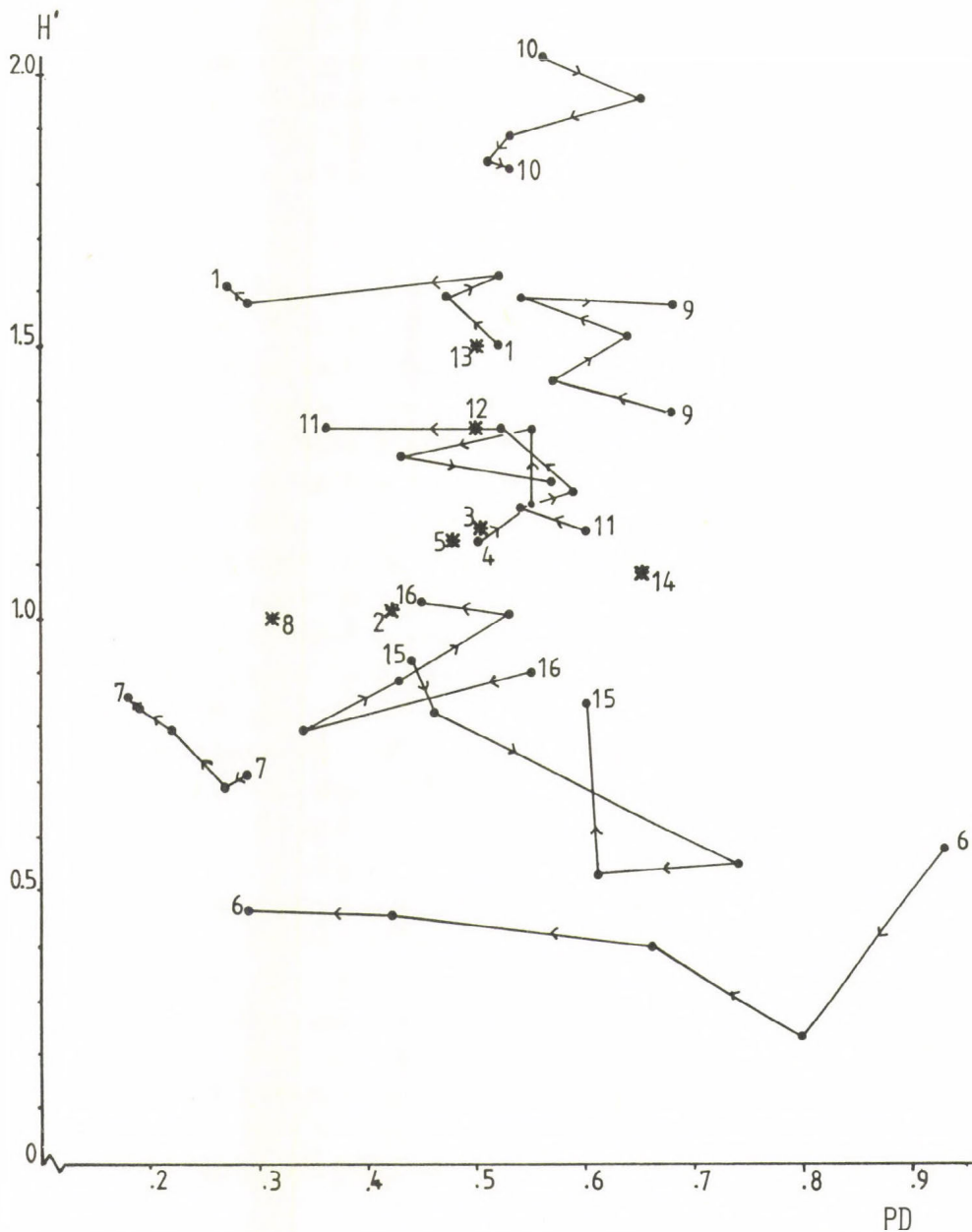
Fig. 1. Relationship between diversity (H') and plot dynamics (PD) in 5 periods for 9 permanent plots. For the other 7 plots the mean of the 5 positions is indicated.

whereas the lowest values were found in plots 6 and 7. Plots
15 and 16 beside the coppiced wood also were fairly low in
comparison to, e.g., plots 2 and 3 which were situated on the
same earth wall further on in an uncoppiced part of the wood.

Turning now to the relation between plot dynamics and diver-
sity, we see that H' tends to be higher with higher PD values,
although there is much variation both between plots and for
the same plot between periods. Again, plots 6 and 15 are
markedly outlying.

DISCUSSION

Most of the 16 plots had a fairly constant species compo-
sition during the study period, 1977-1981. In 1981-1985, the
species composition changed drastically - most of the plots
are now covered with the grass Deschampsia flexuosa. To what
extent this is caused by a larger nutrient input as a conse-
quence of air pollution, as has been suggested for a similar
take over by grasses in heathlands (Brunsting & Heil 1985),
we do not know. Despite this constancy of species composition
before 1981 we found surprisingly high dynamics within the
plots and for most of the species. Partly these are the result
of methodical differences - drawings are never completely ac-
curate. Checks by drawing a plot twice (by different persons)
on the same date yielded PD values of 0.1-0.2, and visual
inspection of the drawings did suggest that the changes were
for the greater part real; in each period a considerable num-
ber of clumps of each species appeared or disappeared. This is
probably due to many small-scale events: fallen leaves lying
on the bryophyte mat for some time, animal activities, and
many other mortality causes. The resulting small gaps are
filled rapidly, and the plots are more or less in a 'steady-
state". Larger-scale events, to the contrary, had much more
severe and longer-lasting effects, as is shown by plots 6 and
15.

As predicted by Huston (1979), there was some, though not
too clear, relationship between vegetation dynamics (his

'frequency of population reduction') and diversity. Deviations may partly be due to ecological differences between the plots, e.g., regarding impact of treading, exposure and inclination, exact type of litter falling on the plots, and soil type (influencing nutrient status and thus, rate of competitive exclusion). The roughly positive relation between PD and H' suggests that at low levels of disturbance still some competitive exclusion is involved. This will be analyzed further in the future by searching for regularities in sequence of species within the 100 subplots of each plot. An experimental proof by removal of bryophytes at small scale and different intensities (frequencies and amounts) would be worthwhile. The results of the 'natural experiments' of plots 6 and 15 do suggest that at higher levels of population reduction diversity is strongly lowered again.

The first analysis of the data suggests that indeed in a more or less homogeneous habitat a number of species can co-exist mostly without local niche differentiation, as was predicted by Slack (1977), Huston (1979), Watson (1980) and others. We hope to perform a more detailed analysis of the data to obtain more information about these matters.

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A COMPARISON OF THE LEVINS' AND FREEMAN-TUKEY NICHE WIDTH MEASURES FOR THE BRYOPHYTES IN AN ADIRONDACK STREAM

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Bryophyte niche width in Adirondack streams is obtained by the Levins equation and is compared to that using the Freeman-Tukey equation. The effect of an outlier has no effect on the Levins values but affects values for several species with the Freeman-Tukey equation. Percent cover and frequency are compared and demonstrate that frequency is adequate for the niche width measure.

INTRODUCTION

In 1985 we (Slack and Glime) used the niche width measure of Levins (1968) to describe the zonation patterns of plants (mostly bryophytes) in Adirondack streams. At the time that study was conducted, we had no way to determine a significance level for the niche width calculation. With few studies available, especially on bryophytes, in which the niche width parameter has been calculated, it is desirable to have some means by which to interpret these results.

In 1982, Smith published a different measure of niche width (Freeman-Tukey equation) in which Chi^2 could be used to calculate the statistical significance of a given niche parameter (resource) in determining the occurrence of a given species. The present study uses the data from four of the Adirondack streams in the Slide Mountain - Johns Brook area (Slack & Glime 1985, streams 4-7) as a means to evaluate the niche width parameter as it might apply to bryophytes.

Before one can evaluate any measure of a species within a community, such as the number obtained by a niche width equation, one needs an understanding of the effects of changing one or more related parameters, such as per cent cover or resource availability. To illustrate such effects, we have chosen two comparisons. In the first case, we will compare the effect of using percent cover to using frequency (presence/ absence) data. In the second case we will replace one rare species in the Garden brook (stream 4) with a hypothetical Species X that properly belongs to a different community (a high ground terrestrial community) and not to the stream community. We will compare the results of the analysis using the rare (in this study) species, Lophocolea heterophylla, with that of using the outlier, Species X.

Finally, we will demonstrate the relative sensitivity of the species to three resource (habitat) parameters.

METHODS

We collected field data in four streams near the Johns Brook Trail, near Keene, Essex County, District 4, New York (44°N, 74°W) at 425-685 m elevation (Slack & Glime 1985). We collected data from 10 1 m x 0.5 m plots in each stream. In order to fit the requirements of the new analysis (Smith 1982), we further subdivided the plots into 10-cm height increments from the water surface so that height above water could be used as a resource. This also permitted us to use greater resolution in describing rock size and aspect (position) in the stream.

We analyzed the data by the program COMMANAL, which uses the Levins equation:

$$\text{Niche Width}_j = \frac{1}{\sum\limits_{1}^{n} p_{ij}^2}$$

where   n = number of resource states

p$_{ij}$ = abundance of species j in resource state i

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divided by total abundance of all species in all resource states,

and the Freeman-Tukey equation:

$$FT = \sum_{1}^{R} (p_i q_i)^2$$

where

p_i = proportion of resource state i used

q_i = proportion of resource available for use at state i

R = total number of resource states.

To compare the effect of an outlier, we substituted the hypothetical Species X for the most infrequent species, Lophocolea heterophylla, in the Garden Brook. Species X occurs in a unique resource state for all three resources examined: height above water, rock size, and aspect in stream. Lophocolea heterophylla, on the other hand, does not occupy any unique resource states. Each of these two species occurs in only one quadrat.

We evaluated the specificity of a species for niche states using the Chi^2 method of Smith (1982).

RESULTS AND DISCUSSION

Comparison of the two measures

If one compares the niche width values in the Garden brook using Levins' equation with those using the Freeman-Tukey equation (Smith 1982), the values are quite dissimilar (Figs 1-3). The Levins' equation presents very narrow niches in this study, never exceeding 0.5, whereas the Freeman-Tukey equation presents rather broad niches that range from 0.31 to 1.00. (Both measures can range 0 to 1.0). Neither equation is linear; thus small changes in composition, especially for a small niche width, can result in large changes in the niche width value. Nevertheless, the trends with the two equations are quite similar for height above water and rock size, but often differ widely for aspect in stream (Figs 1-3).
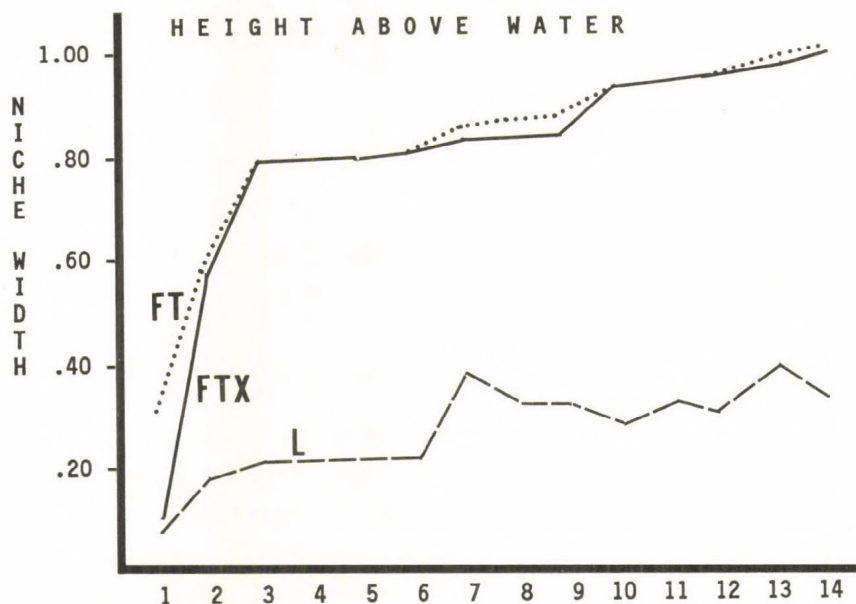
HEIGHT ABOVE WATER

<u>Fig. 1.</u> Comparison of niche width values for height above water from Levins (L), Freeman-Tukey (FT) and Freeman-Tukey with the substitution of Species X (FTX). Numbers represent species in order from smallest to largest Freeman-Tukey value.

The wide discrepancy in the magnitude of these niche width measurements lies in the definition of possible niches. Levins compares each species to every other species and his equation makes no use of the availability of each niche in the sampling area. The Freeman-Tukey equation includes the availability of the resource in the system being studied.

Both formulae suffer from the need for arbitrary decisions by the researcher. In each formula one must select the number of resource states to be considered (n in Levins, R in Freeman-Tukey) and the size of the range for each state. Therefore one could adjust the range of a state to encompass all of the oc-currences of a particular species, and depending on the number of states defined, this could result in a narrow or a wide niche width. In the Freeman-Tukey equation, lack of avail-ability of the resource state in a particular sample tends to broaden the niche width value because samples in which the resource state is lacking do not serve to make the species
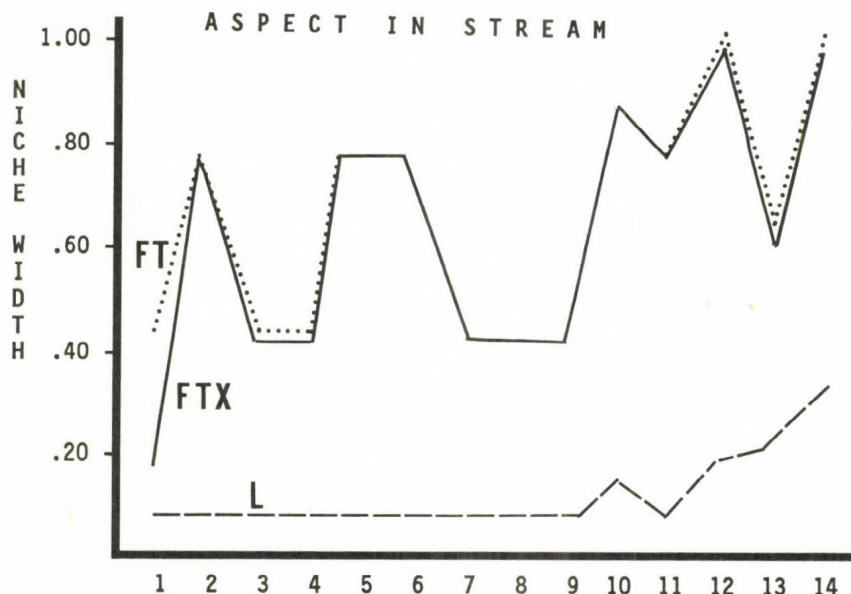
Fig. 2. Comparison of niche width values for aspect in stream from Levins (L), Freeman-Tukey (FT), and Freeman-Tukey with the substitution of Species X (FTX). Numbers represent species in order from smallest to largest Freeman-Tukey value for height above water.

seem rare. The Levins equation, on the other hand, can make the species seem rare when in fact it is the resource state that is rare. In both cases, given a continuous distribution of resource, the greater the number of divisions, the more accurate the measure.

Thus one might say that the Levins equation treats commonness and rarity with regard to the universe, whereas the Freeman-Tukey formula treats it with regard to the availability of a resource within a habitat. The result is that the Freeman-Tukey equation provides a consistently higher value than that of Levins, as shown by Figures 1-3.
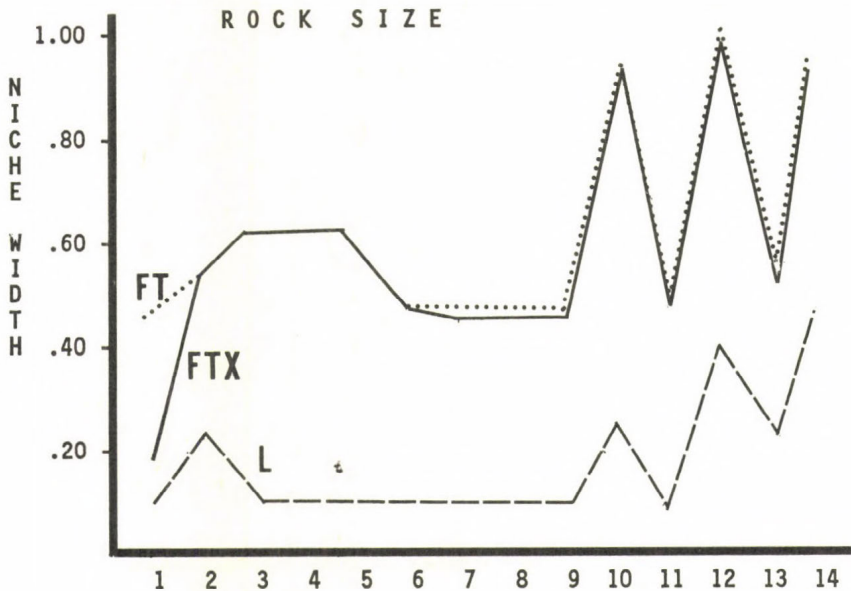
Fig. 3. Comparison of niche width values for rock size from
Levins (L), Freeman-Tukey (FT), and Freeman-Tukey with the
substitution of Species X (FTX). Numbers represent species
in order from smallest to largest Freeman-Tukey value for
height above water.

Effect of an outlier

When the species Lophocolea heterophylla was replaced by
Species X, the hypothetical species was assigned a height above
water surface that was higher than any of the other species in
the Garden brook (60-70 cm). It was likewise assigned a rock
size and an aspect not occupied by any other species.

The outlier effect had no impact on the Levins niche width
measure for any species; Lophocolea heterophylla and Species X
had identical niche widths for all three resources. But when
the community was analyzed using the Freeman-Tukey equation,
Species X had much more narrow niche than did Lophocolea hete-
rophylla (Figs 1-3). Furthermore, the niche width measures of
the other species in the stream likewise showed slight diffe-
rences.

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The reason for this seeming paradox is that the Freeman-
Tukey equation is sensitive to the fact that Species X occupied
only resource states that we had sampled elsewhere in the
stream.

Comparison of frequency and percent cover

Tables 1-3 show that little difference exists between
values obtained using frequency and values using percent cover.
Aspect in stream produced the most differences, with 6 species
out of 21 differing by 5% or more. Rock size had only 3 species
differing by 5% or more, and depth had only 2. Based on these
results, we feel that for the Freeman-Tukey niche width mea-
sure, presence is adequate to represent the effect of re-
sources on the species. It certainly suggest the accuracy
gained by obtaining very accurate percent measures (instead
of estimates) does not justify the time required.

Significant resource states

Tables 1-3 demonstrate the fact that most of the species
occurrences are significantly influenced by the resource
states, as we have chosen to subdivide them. (See Slack &
Glime 1985 for a discussion of these states.)

Only Hygrophypnum ochraceum appears to be insensitive to
height above water. Its lack of sensitivity is compensated
by the presence of two distinct growth forms, with falcate-
leaved plants growing at greater heights than straight-leaved
forms (Slack & Glime 1985). Hygroamblystegium tenax is in-
sensitive to aspect in stream, occurring both on the bank
and in the water midstream. (For further discussion on parti-
cular niche requirements of these species, see Glime & Slack
1985.)

It is interesting that if we examine only the Garden brook,
as done in Figures 1-3, Hygroamblystegium tenax and Rhizomnium
punctatum are insensitive to any of the three resources we
examined. Eurhynchium riparioides is only sensitive to aspect
in stream, avoiding the soil banks and occurring primarily
midstream. Both Eurhynchium pulchellum and Hygrohypnum molle
are insensitive to height above water. In fact, height above

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Table 1. Freeman-Tukey niche width values for height above water in streams on Slide Mountain on 16 July 1982, transect summary with 95% confidence intervals, standardized Freeman-Tukey niche width value, angle of distance between resource and species vectors, Chi square value for comparison of species and resource distribution, and probability level of Chi square. Column 1 is based on presence; column 2 is based on percent cover; other columns apply to column 2. (n=145; df=9).

SPECIES	NICHE WIDTH		95 % CONF INT		STAND FT	ANG	CHISQ	P
Atrichum undulatum	0.77	0.77	0.72	0.82	1.77	0.69	262.68	.001
Brachythecium curtum	0.68	0.68	0.61	0.73	1.48	0.83	376.64	.001
Brachythecium plumosum	0.91	0.86	0.81	0.90	2.06	0.54	164.59	.001
Brachythecium rivulare	0.90	0.91	0.88	0.94	2.31	0.42	99.51	.001
Eurhynchium pulchellum	0.89	0.89	0.85	0.92	2.19	0.47	127.83	.001
Eurhynchium riparioides	0.92	0.93	0.90	0.96	2.38	0.38	82.83	.001
Fissidens bryoides	0.68	0.68	0.61	0.73	1.48	0.83	376.64	.001
Fontinalis antipyretica	0.68	0.68	0.61	0.73	1.48	0.83	376.64	.001
Fontinalis dalecarlica	0.78	0.78	0.73	0.83	1.80	0.67	250.03	.001
Grimmia alpicola	0.35	0.35	0.28	0.43	0.72	1.21	750.49	.001
Hygroamblystegium tenax	0.87	0.84	0.79	0.88	1.99	0.57	186.00	.001
Hygrohypnum eugyrium	0.98	0.94	0.91	0.96	2.45	0.35	69.18	.001
Hygrohypnum molle	0.97	0.97	0.94	0.98	2.62	0.26	39.78	.001
Hygrohypnum ochraceum	0.99	0.98	0.96	0.99	2.75	0.20	22.72	NS
Lophocolea bidentata	0.77	0.77	0.72	0.82	1.77	0.69	262.68	.001
Lophocolea heterophylla	0.36	0.36	0.28	0.43	0.73	1.21	745.92	.001
Plagiochila porelloides	0.91	0.91	0.87	0.94	2.27	0.44	108.73	.001
Racomitrium aciculare	0.92	0.87	0.83	0.91	2.12	0.51	147.11	.001
Rhizomnium punctatum	0.93	0.88	0.84	0.92	2.16	0.49	137.91	.001
Scapania undulata	0.82	0.82	0.77	0.86	1.93	0.61	207.53	.001
Thuidium delicatulum	0.82	0.82	0.77	0.86	1.92	0.61	210.28	.001

water results in wide niches for most species, even though it is still a discriminatory resource, as indicated by the significant Chi^2 value.

It may be somewhat misleading that rock size results in the smallest niche width values overall. This may be due to the fact that rock size really represents several resource parameters. Large rocks by definition provide greater heights and therefore small rocks will not be occupied by species that occur only at greater heights. Likewise, large rocks are more stable and therefore more easily colonized by mosses. Finally, we defined rock size to include soil, so aspect in

Table 2. Freeman-Tukey niche width values for aspect in streams
on Slide Mountain on 16 July 1982, transect summary with 95%
confidence intervals, standardized Freeman-Tukey niche width
value, angle of distance between resource and species vectors,
Chi square value for comparison of species and resource dis-
tribution, and probability level of Chi square. Column 1 is
based on presence; column 2 is based on percent cover; other
columns apply to column 2. (n = 145; df. = 8).

SPECIES	NICHE WIDTH		95 % CONF INT		STAND FT	ANG	CHISQ	P
Atrichum undulatum	0.19	0.19	0.11	0.26	0.37	1.38	944.59	.001
Brachythecium curtum	0.74	0.74	0.68	0.79	1.66	0.74	303.78	.001
Brachythecium plumosum	0.87	0.80	0.75	0.84	1.85	0.65	233.50	.001
Brachythecium rivulare	0.93	0.87	0.82	0.90	2.09	0.53	156.47	.001
Eurhynchium pulchellum	0.65	0.65	0.59	0.71	1.42	0.86	402.24	.001
Eurhynchium riparioides	0.99	0.90	0.86	0.93	2.23	0.45	117.63	.001
Fissidens bryoides	0.74	0.74	0.68	0.79	1.66	0.74	303.78	.001
Fontinalis antipyretica	0.63	0.63	0.56	0.69	1.36	0.89	432.70	.001
Fontinalis dalecarlica	0.63	0.63	0.56	0.69	1.36	0.89	432.70	.001
Grimmia alpicola	0.74	0.74	0.68	0.79	1.66	0.74	303.78	.001
Hygroamblystegium tenax	0.96	0.99	0.97	1.00	2.80	0.17	17.05	NS
Hygrohypnum eugyrium	0.95	0.97	0.94	0.99	2.64	0.25	36.64	.001
Hygrohypnum molle	0.95	0.85	0.81	0.89	2.04	0.55	172.40	.001
Hygrohypnum ochraceum	0.92	0.88	0.84	0.91	2.14	0.50	142.65	.001
Lophocolea bidentata	0.19	0.19	0.11	0.26	0.37	1.38	944.59	.001
Lophocolea heterophylla	0.74	0.74	0.68	0.79	1.66	0.74	303.78	.001
Plagiochila porelloides	0.74	0.74	0.68	0.79	1.66	0.74	303.78	.001
Racomitrium aciculare	0.96	0.91	0.88	0.94	2.31	0.42	99.33	.001
Rhizomnium punctatum	0.94	0.89	0.85	0.93	2.21	0.47	124.04	.001
Scapania undulata	0.87	0.87	0.82	0.90	2.10	0.52	155.15	.001
Thuidium delicatulum	0.19	0.19	0.11	0.26	0.37	1.38	944.59	.001

stream becomes a part of this parameter, including differences
between soil of streambank and rocks of midstream.

Because this paper includes only one a small geographic
area, we prefer not to emphasize the nature of the niche of
any of these species. Instead, we wish to conclude that the
Freeman-Tukey niche width measure provides a sophisticated
tool for assessing the sensitivity of a species to the states
of a particular resource, and that this tool does not require
the time-consuming task of precise cover measurements. On the
other hand, we caution its users that comparisons can only be

Table 3. Freeman-Tukey niche width values for rock size in streams on Slide Mountain on 16 July 1982, transect summary with 95% confidence intervals, standardized Freeman-Tukey niche width value, angle of distance between resource and species vectors, Chi square value for comparison of species and resource distribution, and probability level of Chi square. Column 1 is based on presence; column 2 is based on percent cover; other columns apply to column 2. (n = 145, df. = 8).

SPECIES	NICHE WIDTH		95 % CONF INT		STAND FT	ANG	CHISQ	P
Atrichum undulatum	0.20	0.20	0.12	0.28	0.41	1.37	924.03	.001
Brachythecium curtum	0.35	0.35	0.28	0.43	0.72	1.21	751.29	.001
Brachythecium plumosum	0.88	0.84	0.80	0.88	2.01	0.57	181.90	.001
Brachythecium rivulare	0.73	0.73	0.68	0.79	1.65	0.75	308.06	.001
Eurhynchium pulchellum	0.25	0.25	0.17	0.32	0.50	1.32	875.16	.001
Eurhynchium riparioides	0.93	0.86	0.81	0.90	2.05	0.54	167.17	.001
Fissidens bryoides	0.35	0.35	0.28	0.43	0.72	1.21	751.29	.001
Fontinalis antipyretica	0.35	0.35	0.28	0.43	0.72	1.21	751.29	.001
Fontinalis dalecarlica	0.73	0.73	0.68	0.79	1.65	0.75	308.06	.001
Grimmia alpicola	0.48	0.48	0.41	0.55	1.01	1.07	598.29	.001
Hygroamblystegium tenax	0.77	0.74	0.68	0.79	1.67	0.74	299.91	.001
Hygrohypnum eugyrium	0.93	0.89	0.85	0.93	2.20	0.47	125.60	.001
Hygrohypnum molle	0.93	0.86	0.82	0.90	2.07	0.54	162.49	.001
Hygrohypnum ochraceum	0.94	0.89	0.85	0.93	2.20	0.47	125.50	.001
Lophocolea bidentata	0.20	0.20	0.12	0.28	0.41	1.37	924.03	.001
Lophocolea heterophylla	0.20	0.20	0.12	0.28	0.41	1.37	924.03	.001
Plagiochila porelloides	0.71	0.71	0.65	0.76	1.57	0.79	340.77	.001
Racomitrium aciculare	0.88	0.88	0.84	0.92	2.15	0.49	138.87	.001
Rhizomnium punctatum	0.97	0.95	0.92	0.97	2.49	0.33	61.54	.001
Scapania undulata	0.92	0.92	0.88	0.95	2.34	0.40	93.05	.001
Thuidium delicatulum	0.20	0.20	0.12	0.28	0.41	1.37	924.03	.001

made validly between samples in which niche state partitioning has been done in the same way.

Persons interested in the program COMMANAL for analyzing stream bryophyte data should contact the senior author.

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LONG-TERM RESULTS OF CUTTING ON THE BRYOPHYTES OF THE SEQUOIA SEMPERVIRENS FOREST IN NORTHERN CALIFORNIA

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A large portion of the Sequoia sempervirens forest of
Humboldt Co., California, was clear-cut in 1860-1900. Despite
the highly destructive nature of cutting all the trees on a
large tract of land, the forest has regenerated. Many tracts,
cut 100 years ago (old second-growth forests), now closely
resemble the undisturbed (virgin) forest, both in size of trees
and in the vascular flora. The bryophyte flora, however,
shows significant differences when compared to the virgin
forest. Of the 128 species of bryophytes which characterize
the virgin forest, nine have not yet been found even in the
richest of the old second-growth forest; twenty-two species
are reduced in abundance; and twenty-eight show increased
abundance in old second-growth forest types. All of the bryo-
phyte species restricted to the virgin forest are at their
southernmost station in coastal California. Apparently, a
single event of cutting in this forest may have a longer term
of influence upon the bryophytes than upon the vascular plants.

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The Sequoia sempervirens forest is restricted to a belt
never more than 40 kilometers wide in coastal California
(Zinke 1977). It is adapted to high winter rainfall, and to
very high frequency of fog during the largely rain-free sum-
mer. It is found mainly on sandstone-, siltstone- and cong-
lomerate-derived acid soils, and ranges from about 35°N

latitude in California to about 42°N in extreme southern Oregon. In the south, it is confined to moist, narrow canyons of river valleys. In the north, it may occupy broad alluvial flats as well as slopes and ridges up to about 400 m elevation. Its abrupt disappearance near the Oregon border is correlated with a broad band of diorites and serpentines which there extend to the coast (Baldwin 1981).

From about 40°N to its extreme northern limit, the sequoia forest is especially moist with a greater diversity of trees, shrubs and herbs. With the sequoia in this more northern portion of its range are such trees as _Picea_ _sitchensis_, _Tsuga_ _heterophylla_, _Abies_ _grandis_, _Thuja_ _plicata_, and _Pseudotsuga_ _menziesii_. Only the latter tree commonly extends into the drier, more depauperate southern expression of the sequoia forest, and, here in the south, deciduous trees such as _Arbutus_ _menziesii_ and _Lithocarpus_ _densiflorus_ are its more common associates.

This forest contains some of the largest trees in the world, and, because of their size and shallow root system, clear-cutting is the only effective means of lumber harvest. Large areas of this forest have been cut, beginning about 1860 and continuing to the present. In the early history of the cutting, it was customary to lay a narrow gauge railroad track up a single river valley, and to cut all of the available timber in that valley. This resulted in continuous blocks of clear-cut forest, some of which may have exceeded several hundred square kilometers.

The impact of clear-cutting is especially noticeable in the sequoia forest. Precipitation in this region is almost restricted to the months of October through May. The heavy fog of the summer months is a major source of water because it condenses on the taller trees and drips from the branches to the soil. Deforested areas, in contrast, do not have the fog receptors, and they become very dry in the summer.

Most of the remaining uncut sequoia forests are now preserved in parks, but those tracts of land which were cut a centrury ago now support luxuriant closed stands of second-

growth forests. These forests rival the uncut forests in height,
density of canopy, humidity patterns in the understory, and in
variety of understory vascular plants.

Are there clear-cutting effects of such long duration that
the old second-growth forests retain differences in their bryo-
phyte floras relative to that of the uncut land? Can these dif-
ferences be attributed to an event of cutting over a century
ago? I wish here to present some preliminary discussion. My
comments are not based upon comparative measurement of the
environment of the two forest types. Micro-topographic envi-
ronmental variation within a single forest is so great that
the relevancy of such comparison is dubious. My comments are
necessarily based upon negative data - the species absent
(or present) in a particular forest type. I believe my obser-
vations have value because I have lived in the region for
eighteen years. Over much of this time I have vigorously
searched for and collected bryophytes in both the uncut and
the second-growth sequoia forests.

For the purpose of this paper, I have pulled together data
from forests dominated by Sequoia sempervirens in the more
humid portion of its range - from Eureka, California (40^ON
latitude) to the Oregon border (42^ON). I have considered
only those forests with a closed canopy at least 60 m tall
with an undisturbed shrub and herb layer, and with an abundance
of large logs densely covered with bryophytes. Recent man-made
openings such as trail and road-banks in such forests were not
included in the study, but openings which result from wind-
fallen trees, and from river erosion were included. The cor-
ridor of deciduous trees, primarily Acer macrophyllum, which
follows the streams was considered a part of this study.

The above restrictions result in a rather small list of
128 species of bryophytes. Many of the most common plants
of recently cut forest such as Pleuridium subulatum and Didy-
modon rigidulus are altogether absent from my records of this
forest, while most of the other species of open soil are
restricted to river banks or the soil on the base of fallen
trees. The low level of diversity in this forest may appear

surprising to European or eastern North American bryologists. However, in the forest of the Pacific Coast of North America, there is high biomass of bryophytes but low diversity.

About ten years ago, I began to notice a difference in the abundance of some bryophytes in the uncut forest as compared with the second-growth forest. Since noticing this phenomenon, I have carefully attempted to document the comparative abundance.

Of the nine species restricted to the uncut forest (Table 1), the only moss is Fontinalis howellii which occupies a shallow pond in one of the richest of the uncut sequoia forests. Its absence from the second-growth forest may be simply a lack of appropriate aquatic habitat rather than a reflection of the effects of disturbance.

The effect of cutting on hepatics obviously is greater than the effect on mosses. This may be explained by the generally lower level of desiccation tolerance in hepatics. Especially notable in Table 1 are Geocalyx graveolens, Bazzania tricrenata, and Kurzia makinoana which are moderately common in the uncut forest but absent elsewhere in California. These are common plants of the very moist forests farther north. They reach the southern extremity of their western North American range in northern California. It is not surprising that such plants would show curtailment of their distribution as a result of

Table 1. Bryophytes found in the uncut sequoia forest but absent from the old second-growth forest.

Fontinalis howellii Ren. & Card.
Blasia pusilla L.
Geocalyx graveolens (Schrad.) Nees
Cephalozia connivens (Dicks.) Lindb.
Douinia ovata (Dicks.) Buch
Lophozia incisa (Schrad.) Dum.
Tritomaria exsectiformis (Breidl.) Schiffn.
Kurzia makinoana (Steph.) Grolle
Bazzania tricrenata (Wahlenb.) Trevis

Table 2. Bryophytes found more abundantly in the uncut sequoia forest than in the old second-growth forest

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Tetraphis pellucida Hedw.
Dichodontium pellucidum (Hedw.) Schimp.
Dicranum fuscescens Turn.
Dicranum scoparium Hedw.
Orthodontium gracile Schwaegr. ex B.S.G.
Plagiomnium insigne (Mitt.) T. Kop.
Antitrichia curtipendula (Hedw.) Brid.
Bestia vancouveriensis (Kindb.) Wijk & Marg.
Hookeria lucens (Hedw.) Sm.
Claopodium crispifolium (Hook.) Ren. & Card.
Heterocladium macounii Best
Brachythecium frigidum (C. Muell.) Besch.
Eurhynchium riparioides (Hedw.) P. Rich.
Kindbergia brittoniae (Grout) Ochyra
Kindbergia praelonga (Hedw.) Ochyra
Plagiothecium laetum B.S.G.
Rhytidiadelphus loreus (Hedw.) Warnst.
Rhytidiadelphus triquetrus (Hedw.) Warnst.
Conocephalum conicum (L.) Dum.
Pellia neesiana (Gottsche) Limpr.
Metzgeria conjugata Lindb.
Diplophyllum obtusifolium (Hook.) Dum.

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the drying effects of forest cutting.

The other five hepatics in Table 1 are found in other parts of California, primariliy in the more humid montane forests.

Table 2 contrasts with Table 1 in that a large proportion of the plants are mosses. Some of these probably persist in small quantities after the forest is cut, and they may require many hundreds of years to return to previous levels of abundance. For example, Antitrichia curtipendula, in California, primarily appears as scattered stems on deciduous trees in narrow river canyons. However, in the uncut sequoia forest, it may grow as large spherical clones similar to its growth form in the very humid Olympic Peninsula (600 kilometers north).

Table 3. Bryophytes found more abundantly in the old second-growth sequoia forest than in the uncut type.

Atrichum selwynii Aust.
Pogonatum contortum (Menz. ex Brid.)Lesq.
Polytrichum juniperinum Hedw.
Fissidens pauperculus Howe
Ceratodon purpureus (Hedw.) Brid.
Ditrichum schimperi (Lesq.) O Kuntze
Campylopus introflexus (Hedw.) Brid.
Dicranella schreberiana (Hedw.) Dicks.
Dicranoweisia cirrata (Hedw.) Lindb. in Milde
Orthodicranum strictum (Mohr) Broth.
Timmiella crassinervis (Hampe) L. Koch
Weissia controversa Hedw.
Discelium nudum (Dicks.) Brid.
Funaria hygrometrica Hedw.
Funaria muhlenbergii Hedw.f. ex Lam. & DC.
Bryum argenteum Hedw.
Bryum bicolor Dicks.
Epipterygium tozeri (Grev.) Lindb.
Aulacomnium androgynum (Hedw.) Schwaegr.
Zygodon rupestris Schimp. ex Lor.
Claopodium whippleanum (Sull.) Ren. & Card.
Lunularia cruciata (L.) Dum.
Fossombronia pusilla L.
Gyrothyra underwoodiana Howe
Jungermannia rubra Gott. ex Underw.
Cephaloziella turneri (Hook.) K. Muell.
Scapania umbrosa (Schrad.) Dum.
Anthoceros fusiformis Aust.

Similar persistence along river corridors, on rock outcrops, or on coastal bluffs probably applies to most, or all, of the species in Table 2. Especially notable here is Rhytidiadelphus triquetrus which seems not to produce sexual or asexual propagules in California.

Dispersal to the second-growth forest is a further possibility that cannot be ruled out for some of the plants in Table 2. I have not yet seen Hookeria lucens or Metzgeria conjugata in sites which could have acted as effective refugia during the unfavourable times immediately after cutting.

Most of the plants in Table 3 are normally found on the vertical soil banks which are formed in great abundance by logging activities. They apparently persist on this soil long after the forest has regenerated. Most of them are also com-

mon on the soil on the roots of wind-fallen trees.

It is notable that the rather restricted endemics, Fissi-
dens pauperculus and Gyrothyra underwoodiana, show markedly
increased abundance as a result of disturbance. Campylopus
introflexus is, as in Europe, a rather recently introduced
plant which is rapidly spreading in disturbed areas.

Clear-cutting of large blocks of the sequoia forest has
had diverse effects. Its impact must be evaluated for indivi-
dual species of plants rather than for the community as a
whole. It is striking that so large a percentage of the bryo-
phyte flora can return after the regrowth of the forest.

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DISPERSAL AS A LIMITING FACTOR FOR DISTRIBUTION AMONG EPIXYLIC BRYOPHYTES

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Earlier studies of microhabitat occupation have shown
that competition is insufficient to explain the distribution
patterns for species growing on decaying wood in old forests,
a patchy, temporary substrate. It is suggested that competi-
tion is low because of failure to fully saturate the sub-
strate due to insufficient dispersal. If dispersal between
sites is limiting, the species should be absent from some
sites, while occupying the majority of the available logs,
and also suboptimal substrates, in other sites. This hypo-
thesis was tested for 19 species growing on decaying logs in
10 geographically separated forest sites in northern Sweden.
The species showed two distinct groups, those occupying almost
all sites (core species) and those occupying few of the avail-
able sites (satellite species). The core species were generally
locally frequent and often also occurred on other substrates
such as boulders, stumps, litter, etc. The satellite species
were separated into two groups; 1) species that were locally
infrequent and only occasionally occurred on substrates other
than logs, and 2) locally more frequent species, which also
frequently occurred on other, suboptimal substrates. Therefore,
it is suggested that effective dispersal is a major limiting
factor for the distribution of many log-inhabiting species.

1. INTRODUCTION

Earlier studies of microhabitat occupation have been con-
tradictory. Kunkel (1975) found that competition was important

on north-facing cliffs and Rydin (1985) showed competitive re-
lations between Sphagnum species in a bog. However, Watson
(1980a,b, 1981a) and Söderström (in prep.) have shown that
competition is insufficient to explain the distribution pat-
terns for Polytrichum species on forest floors and species on
decaying logs, respectively. The lifetime of the substrates
differs between the investigations. The two first mentioned
are stable compared with the growth rate of inhabiting species
while thw two last are more unstable. Competition may be low
on substrates with a short lifetime because of failure of the
species to fully saturate the substrate. This may be due to
insufficient growth rate or a limited ability to disperse. If
dispersal is ineffective, the species will be absent even from
parts of the optimal substrate. On the other hand, if disper-
sal is effective the species will occur also on other, less
suitable (suboptimal) substrates where they can establish but
not develop such a large population that they can serve as
dispersal cores. The aim of this investigation is to see if
epixylic bryophyte species show any of these distribution
patterns.

2. MATERIAL AND METHODS

    This study is confined to ten old spruce forests in north-
ern Sweden (Alsberget, Alsträsket, Altarliden, Blaikfjället,
Mörrösjöliden, Oxberget, Oxfjället, Tallberget, Vallsjöskogen,
and Vändåtberget, Fig. 1). These forests are now isolated
sites ("islands") in a landscape of young managed forests. They
are characterized by a patchiness with a large amount of fallen
trees in different degrees of decay. The area belongs to the
northern boreal zone (Ahti et al. 1968).
     e epixylic bryophytes selected for this study are
listed in Table 2. All grow mainly on decaying wood but they
can sometimes be found on other substrates, e.g., wood litter,
stumps, tree bases and moist boulders. These species can be
divided into two groups (Table 2); core species which are
found on almost all available sites and satellite species
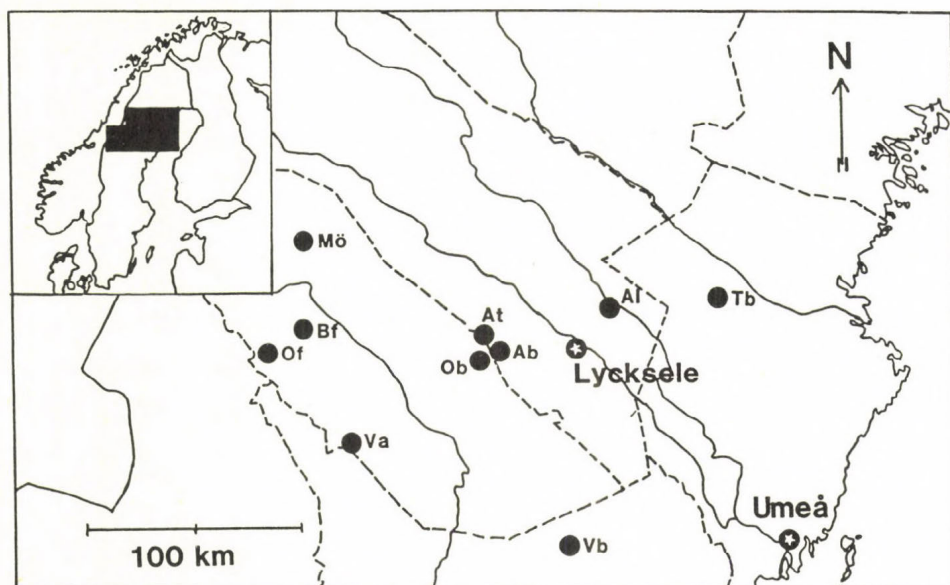which are found only on some sites (Hanski 1982).

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Fig. 1. The location of investigated sites in northern Sweden.
Ab = Alsberget, Al = Altarliden, At = Alsträsket, Bf = Blaik-
fjället, Mö = Mörrösjöliden, Ob = Oxberget, Of = Oxfjället,
Tb = Tallberget, Va = Vallsjöskogen, Vb = Vändåtberget.

Sites varied in size from 3 to 100 ha. Depending on the
size of the site and on the amount of investigated substrates,
between 3 and 5 parallel transects, 10 by 50 m, were analysed.
All logs, boulders and wood litter (including stumps) were re-
corded. For each log, all epixylic species present were noted
together with the following niche variables: decay stage,
greatest and smallest diameter (in cm), highest height above
ground (in cm), wood softness (in cm), percent of bark still
remaining in situ and wood texture type.

Decay was divided into 8 classes modified from McCullough
(1948) in the following manner: 1. Wood hard, bark remaining
intact. 2. Wood hard, bark broken up in patches but remaining
to more than 50%. 3. Wood hard, less than 50% bark remaining.
4. Wood starting to soften, without bark, texture smooth. 5.
Wood soft, with small crevices and small pieces lost. 6. Wood
fragments lost so that the outline of the trunk is deformed.
7. The outer surface of the log is hard to define, possibly

Table 1. Niche boundaries used to determine available logs for each species. De = decay stage, Ba = percentage bark, So = softness in cm, Te = wood texture, Md = maximum diameter in cm, He = highest height above ground in cm.

Species	De	Ba	So	Te	Md	He
Anastrophyllum hellerianum	2-8	0-99	0-10	1-7	11-99	<140
Barbilophozia attenuata	4-8	0-40	0-10	3-7	20-60	<70
Blepharostoma trichophyllum	4-7	0-30	0-10	2-6	21-59	<42
Calypogeia integrestipula	3-8	0-60	0-10	3-7	12-60	<50
Calypogeia suecica	6-7	0	0-10	5-6	17-32	<21
Cephalozia leucantha	5-8	0-30	0-10	2-7	22-59	<31
Cephalozia lunulifolia	2-8	0-90	0-10	1-7	8-71	<90
Lepidozia reptans	3-8	0-60	0-10	3-7	20-60	<50
Lophocolea heterophylla	2-8	0-90	0-10	1-6	11-60	<55
Lophozia ascendens	2-8	0-99	0-10	1-6	8-71	<110
Lophozia incisa	2-8	0-99	0-10	1-7	21-61	<110
Lophozia longidens	1-8	0-100	0-10	0-7	5-99	<110
Lophozia longiflora	2-8	0-100	0-10	0-7	8-71	<100
Lophozia silvicola	2-8	0-99	0-10	1-7	5-99	<70
Ptilidium pulcherrimum	1-8	0-100	0-10	0-7	3-99	<185
Riccardia latifrons	2-6	0-95	0-5	1-6	24-61	<55
Riccardia palmata	2-6	0-95	0-10	1-6	8-61	<185
Tetraphis pellucida	1-8	0-100	0-10	0-7	21-71	<90

with a core of harder wood. 8. Completely soft without evidence of hard wood, outline undeterminable.

Softness was measured as how deep, in 1 cm classes, it was possible for a knife to penetrate with moderate hand power. Values over 10 cm were considered as well-decayed and registered as 10 cm.

Wood texture was divided into 8 classes: 0. completely covered by bark (i.e., when the wood is completely unreach-

able by the plants), 1. smooth, 2. small crevices present, 3. large crevices present, 4. small wood pieces lost, 5. large wood pieces lost, 6. outline partly gone (hard to determine), 7. outline completely lost (impossible to determine).

For other substrates only frequencies of the investigated species were recorded.

Every log which had the niche variables within the highest and lowest measured value for a species (Table 1) was regarded as available (optimal) to that species, whether it occurred or not.

Three levels of frequency were calculated: 1. Regional frequency (F_r) is defined as $F_r = S_o/S_a$ where S_a is the number of sites with available logs and S_o is the number of sites occupied. Mean local frequency (F_l) is defined as $F_l = F_o/F_a$ where F_a is the number of available logs on occupied sites and F_o is the number of logs occupied. 3. Frequency on suboptimal substrates (F_s) is defined as $F_s = S_s/S_o$ where S_o is the number of occupied sites where it also occurred on suboptimal substrates.

The nomenclature follows Corley et al. (1981) for mosses and Grolle (1983) for hepatics, except that _Lophozia_ _silvicola_ Buch is used instead of _L._ _ventricosa_.

3. RESULTS

The results are summarised in Table 2. Five of the eight core species were locally frequent (F_l between 30 and 70%). Four of these also occurred with between 50 and 100% frequency on suboptimal substrates. However, four species showed a deviating pattern. _Cephalozia_ _lunulifolia_ occurred with F_l value of only 15% but with F_s value of 55%. _Anastrophyllum_ _hellerianum_ occurred with F_l value of only 18% and F_s value of 29%. _Lophozia_ _longidens_ and _L._ _ascendens_ were also found with rather low F_l values (24 and 35%, respectively) and with F_s less than 30%.

The satellite species showed two different patterns. _Riccardia_ _latifrons_, _R._ _palmata_, _Lophocolea_ _heterophylla_, and _Cephalozia_ _leucantha_ had F_l values between 12 and 24% and were absent or very rare on suboptimal substrates (F_s values between

Table 2. Regional frequency, mean local frequency, and frequency on suboptimal substrates for each of the 19 investigated species. * = found on only one log; niche boundaries and therefore also frequency measurements are not possible.

Species	Regional frequency	Mean local frequency on logs	Frequency on suboptimal substrates
Core species			
Ptilidium pulcherrimum	100	70	70
Lophozia longiflora	100	51	50
Lophozia silvicola	100	45	100
Lophozia ascendens	100	35	29
Lophozia longidens	100	24	30
Anastrophyllum hellerianum	100	18	29
Tetraphis pellucida	90	30	88
Cephalozia lunulifolia	90	15	55
Satellite species			
Lophozia incisa	60	13	50
Blepharostoma trichophyllum	50	30	100
Barbilophozia attenuata	50	29	60
Calypogeia integrestipula	40	30	50
Lepidozia reptans	40	10	50
Cephalozia leucantha	40	17	25
Riccardia palmata	40	24	0
Lophocolea heterophylla	40	12	0
Riccardia latifrons	30	24	0
Calypogeia suecica	22	67	0
Geocalyx graveolens *)	?	?	0

O and 25%). Lophozia incisa, Barbilophozia attenuata, Blepha-
rostoma trichophyllum, Calypogeia integrestipula, Lepidozia
reptans, and Calypogeia suecica had F_1 values over 30% and/or
F_s values of 50% or more.

One species, Geocalyx graveolens was only found on one
site, and there only on one log.

4. DISCUSSION

Decaying logs in old spruce forests are patchy substrates
at two levels, the logs within a stand and the stands within
a sylvicultural landscape. Hanski (1982) has predicted two
distribution patterns for species on patchy substrates, core
species that are regionally frequent and locally common, and
satellite species that are regionally and locally rare. Bryo-
phytes on decaying logs show these patterns clearly (cf.
Söderström in prep.). If the dispersal is effective, large
local populations can serve as dispersal centres wherefrom
the majority of the available sites nearby are colonized.
Near larger dispersal centres some propagules will disperse
to suboptimal substrates, too, where the species can establish
but not develop enough to contribute to dispersal. The major-
ity of the core species in this investigation occur with a
high local frequency and also frequently on suboptimal sub-
strates. Ther dispersal abilities are probably effective or
they have so many dispersal centres that it is impossible to
detect any restrictions with the sample method used in this
investigation.

Anastrophyllum hellerianum, Lophozia longidens, and L.
ascendens are core species but locally only occupy 35% of the
sites or less. There are two possible explanations for this.
One or more of the niche variables may be measured on an
extreme, suboptimal, log. Too many logs are then regarded as
available and the local frequency will be too low. Another ex-
planation is that they have a rather ineffective dispersal
mechanism even over shorter distances. Their occurrence on so
many sites may be an effect of earlier periods with more effec-
tive dispersal or more extensive and continuous areas with

suitable habitats. Today, old spruce forests are decreasing due to logging activity and some forest species are decreasing heavily and at least A. hellerianum and L. ascendens are commonly regarded as threatened by forestry in Sweden (Söderström 1983, Ingelög et al. 1984).

Species with small populations may develop too few propagules to disperse and establish on many sites. Those satellite species that are neither regionally nor locally frequent can be restricted by an extremely ineffective dispersal ability even on the local level. But other factors can equally well be invoked, especially for species near the limits for their distribution. Lophocolea heterophylla and Calypogeia suecica are such species which have some of their most nothern localities among the investigated sites (Söderström 1981, 1983).

Satellite species which are locally frequent and also occur frequently on suboptimal substrates must be able to disperse and establish effectively over the shorter distances within sites. But over long distances, dispersal seems not to be effective enough to transport viable propagules between sites in sufficient number for the establishment rate to exceed the extinction rate. Therefore, a patchy pattern of a few dispersal centres with dense populations may develop.

Three species, Cephalozia lunulifolia, Lophozia incisa and Lepidozia reptans occur frequently on substrates such as e.g., boulders and stumps, but not so frequently on logs. As for the three deviating core species mentioned above, their extreme niche values for one or more variables may be so measured so that many of the logs will be suboptimal and therefore the local frequency too low. Another explanation is that these species are not true epixylics and only occur suboptimally on logs.

In conclusion, this investigation shows that dispersal, both between and within stands, may be a major limiting factor for many species to increase their distributions.

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BRYOPHYTE AND LICHEN SUCCESSION ON FALLEN LOGS
AND SEEDLING ESTABLISHMENT IN TSUGA-ABIES FORESTS
OF CENTRAL JAPAN

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In order to clarify the pattern and process of the suc-
cession on logs, 314 plots were sampled on trunks, fallen
logs and the ground in the subalpine forests dominated by Tsu-
ga diversifolia, Abies veitchii and Picea jezoensis spp. hon-
doensis in central Japan.

The bryophyte and lichen communities were divided into eight
types characterized by dominant component. Based on the thick-
ness of the rotted materials of logs, the succession from the
community on fresh logs to the terricolous community was es-
timated as following order: Parmelia-Dicranum community, Hete-
rophyllium-Parmelia community, (bark lost), Heterophyllium-
Blepharostoma community, Heterophyllium community, Scapania
community, Hylocomium-Pleurozium community on logs, and the
same community on the ground.

The establishment of seedlings of Picea and Tsuga was re-
stricted to the Heterophyllium and Scapania communities, while
that of Abies was successful on most communities.

INTRODUCTION

The death or fall of large tree of a forest results in a
gap where the development of a new series of plant communities
occurs (Borman & Likens 1971). On the other hand, the fallen
logs offer new habitats to small plants such as bryophytes and
lichens, and thus another development of plant communities
begins on the surface.

In the bryophyte and lichen communities there are seedlings including those of tree species dominating the forest. The establishment of some seedlings is influenced by bryophyte and lichen communities (Larsen 1980).

The pattern and process of bryophyte and lichen succession on logs were studied in subalpine coniferous forests of Japan, in relation to establishment of seedlings of tree species.

STUDY AREA

Field work was carried out in the subalpine forests ranging from 1700 m to 2300 m in elevation at three locations in central Japan, i.e., Mt. Fuji, Mugikusa Pass in Yatsugatake mountains and Odarumi Pass in Chichibu mountains.

According to Franklin et al. (1979), Ohsawa (1981) and Nakamura (1984), Tsuga diversifolia is the most dominant species in the mature forests, and Abies veitchii, A. mariesii and Picea jezoensis var. hondoensis are also important species there. The forest floors are mostly full-covered with moss communities dominated by Hylocomium splendens and Pleurozium schreberi.

METHODS

Data were collected from plant communities on trunks, fallen logs and the ground during the summer of 1984. The total number of plots sampled was 314.

Epiphyte communities were sampled only on Abies veitchii and Tsuga diversifolia. The sample portion of the trunks was the cylinder surface at the heights between 1.3 and 1.8 m. The sizes of plots on logs and the ground were 0.5 m x 0.15 m to 0.4 m corresponding to the diameter of the log, and 0.5 m x 0.5 m, respectively.

In each plot, cover of each species or species group and the total cover were estimated, The densities of seedlings of the major tree components were obtained from the plots on logs and the ground, and the height of every seedling was measured.

The thickness of rotted materials of every log was meas-
ured at the center of each plot in order to estimate the degree
of the decay of logs.

RESULTS

Heterophyllum foliolatum was the most abundant species on
logs. The communities dominated by this species were divided
into three types according to the associate species and also
the aspect of log surface. The first type was characterized by
the remains of bark in plots, the second type by the appear-
ance of wood because of the slipping off of the bark. The
plots of third type were fully covered by the moss community
dominated by H. foliolatum.

Scapania bolanderi was second most abundant on logs. Hylo-
comium splendens and Pleurozium schreberi were always more or
less mixed with each other on logs as in the case of the ter-
ricolous moss communities in the forest dominated by Tsuga
diversifolia and Abies spp. (Nakamura 1984). Parmelia squarrosa
frequently occurred on fresh-fallen logs of both Abies and
Tsuga.

The terricolous communities of all locations were occupied
by Hylocomium and Pleurozium. The epiphyte communities were
different from those on logs and the ground in species compo-
sition and structure.

The plots sampled in this study were divided into eight
community types from the dominant species and the aspect of
logs.

Successional pattern

The composition of the eight community types in the subalpine
forests is shown in Table 1. Mean coverages of lichens, hepa-
tics and mosses and mean thickness of rotted materials of logs
in each community type are given in Fig. 1.

The successional pattern from the epiphyte community of
Abies or Tsuga, through the communities on fallen logs, to the
terricolous community was estimated as follows:

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Table 1. Composition of the plant communities on trunks, logs and the ground in the subalpine coniferous forests of central Japan

Habitat	Trunk (Abies)	(Tsuga)				Log			Ground
Community	Parmelia	Dicranum-Frullania	Parmelia-Dicranum	Hetero-phyllium-Parmelia	Hetero-phyllium Blepharostoma	Hetero-phyllium	Scapania	Hylocomium-Pleurozium	
Number of plots	community 30	community 27	community 22	community 21	community 19	community 40	community 46	community 55	54
Species									
l Menegazzia asahinae	I	+							
l M. terebrata	II	+	+						
l Platismatia interrupta	II	+		+					
l Sphaerophorus melanocarpus	I			+					
l Hypogymnia vittata	II	II	+		+				
h Nippololejeunea subalpina	II		+	+					
l Cetraria ornata	II	I	I	+					
l Lecidia spp.	II	I	+	+					
l Parmelia laevior	III	II	II	I					
h Frullania tamarisci ssp. obscura	II	II	+	+	+				
l Alectoria lata	III	II	II	I					
l A. americana	II	I	I	+					
m Habrodon leucotrichus	I	+	+	I					
h Nipponolejeunea pilifera	II	II	I	+	+				
l Parmelia squarrosa	III	II	III	I					

		30	27	22	21	19	40	46	55	54
l	Pertusaria spp.	III	II	II	II		+			
l	Sphaerophorus meiphorus	+	II	II	I	+				
l	Cladonia coniocraea	+	II	I	I		+	+		
m	Dicranum viride var.hakkodense	II	I	II	+	+		+	+	
h	Ptilidium pulcherrimum	+	+	I	I	+		+		
m	Dicranum hamlosum	I	III	III	III	+	I	II	+	
h	Bazzania denudata	+	II	+	+	+	I	II	+	
h	Diplophyllum plicatum	+	II	+	+		+	+	I	
h	Cephaloziella microphylla					I				
h	Scapania ampliata		+		+	II		+		
h	Blepharostoma trichophyllum					III				
h	Nowellia curvifolia					II				
h	Plagiochila satoi		+	+	I		I	I	+	
l	Cladonia cornuta		+	II	I		+	I		
m	Heterophyllium foliolatum		+	III	III	III	III	II	+	
m	Hypnum oldhamii		+	I	I	I	+	+		
h	Scapania bolanderi			I	III	I	III	III		
h	Mylia verrucosa			+	I	I	I	II	+	
h	Lepidozia reptans			+	I	I	+	I	+	
m	Hypnum plicatulum	+		+	I		+	+	+	+
T	Picea jezoensis var.hondoensis						I	I	+	

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		30	27	22	21	19	40	46	55	54
m	Pseudobryum speciosum			+	I	+		+	+	I
T	Tsuga diversifolia			II	III	+	III	III	III	I
m	Pleurozium schreberi			+	II		II	III	III	III
m	Hylocomium splendens			+	II	+	II	II	III	III
T	Abies veitchii			+	I	I	+	I	III	III
l	Cladonia gracilis ssp. turbinata							II	I	+
h	Lepidozia subtransversa							I	+	+
T	Sorbus commixta						+	+	+	I
H	Oxalis acetosella						+	+	+	I
H	Pyrola renifolia								+	I
H	Maianthemmum dilatatum								+	I

T: tree, H: herb, m: moss, h: hepatic, l: lichen. Frequency Class, +: -25%, I: 25-50%, II: 50-75%, III: 75-100%.
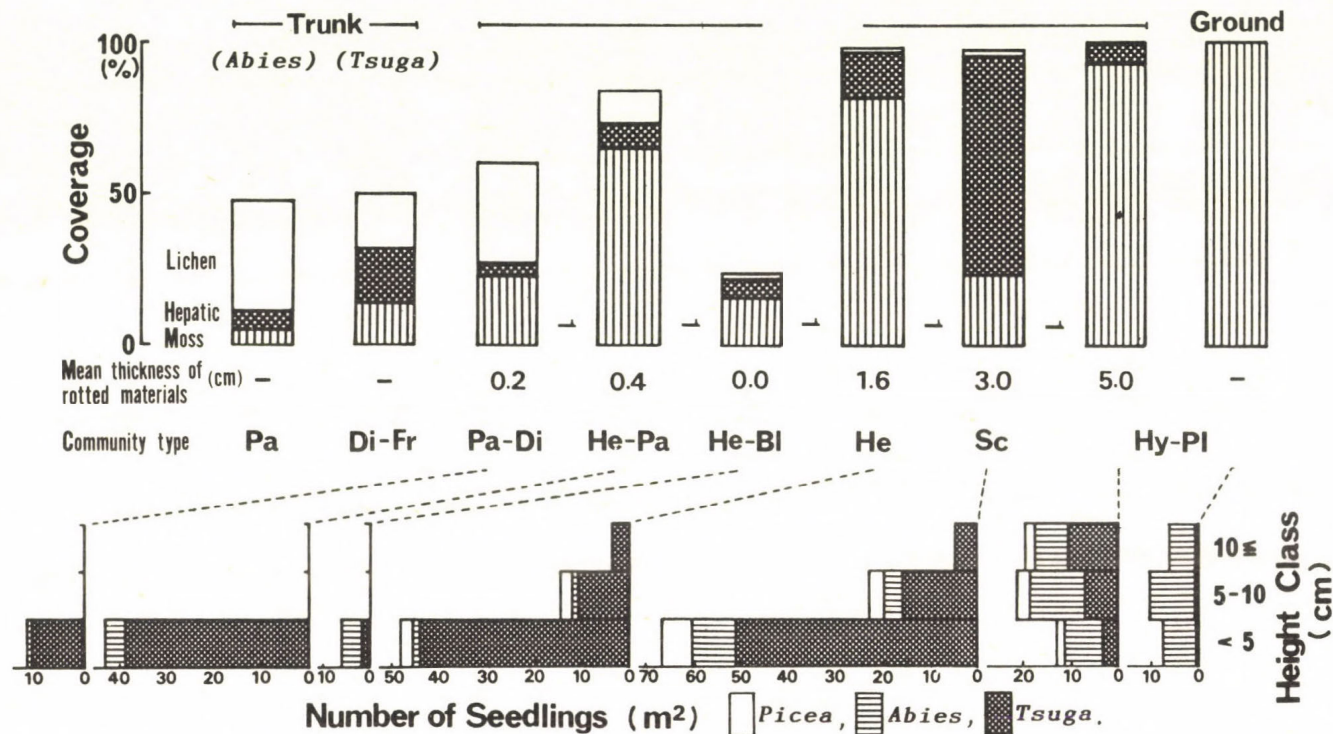
Fig. 1. Changes in the coverages of lichens, hepatics and mosses, the mean thickness of rotted materials of logs, and the number of tree seedlings during succession. Pa: _Parmelia_ community, Di-Fr: _Dicranum-Frullania_ community, Pa-Di: _Parmelia-Dicranum_ community, He-Pa: _Heterophyllium - Parmelia_ community, He-Bl: _Heterophyllium-Blepharostoma_ community, He: _Heterophyllium_ community, Sc: _Scapania_ community, Hy-Pl: _Hylocomium - Pleurozium_ community.

The epiphyte communities had some similarities in composition between Abies and Tsuga, and the coverages were about 50%. But they were different in the dominant component. The community of Abies was dominated by lichens such as Parmelia laevior and P. squarrosa while that of Tsuga was dominated by mosses and hepatics such as Dicranum hamlosum and Frullania tamarisci ssp. obscura.

On fresh logs of both Abies and Tsuga, the Parmelia-Dicranum community occurs. With decay of barks, the coverage of mosses increases. Especially the increase of Heterophyllium foliolatum is remarkable. As a result, the Heterophyllium-Parmelia community is formed on logs. With this community most bark seems to peel off.

On the logs whose wood was exposed, H. foliolatum and other miscellaneous hepatics occur; thus the Heterophyllium-Blepharostoma community is formed there. With increasing coverage of H. foliolatum, the community eventually fully covers the logs. It seems that this Heterophyllium community directly follows the Heterophyllium-Parmelia community when the bark of logs remains.

In accordance with decay of logs, Scapania bolanderi occurs and its dominance increases, and the Heterophyllium community gradually gives way to the Scapania community. Then the rotted materials of logs become 3 cm in thickness. The Scapania community is also replaced by the Hylocomium-Pleurozium community gradually.

The Hylocomium-Pleurozium community occupied the ground as well as decayed logs. The community involves some differences in species composition between two substrates. The community on logs usually contains some hepatics common to the Scapania community while that on the ground scarcely has the other species.

Establishment of tree seedlings during bryophyte and lichen succession

Changes in seedling densities of the major tree components during the bryophyte and lichen succession on logs and the

ground are shown in Fig. 1.

During the early stages of the succession many small seedlings less than 5 cm in height were found. In the middle stages, when the Heterophyllium community and the Scapania community occur, not only small-size seedlings but also large-size ones were found. In the late stage on logs, on which the Hylocomium-Pleurozium community is formed, small-size seedlings decreased, especially Tsuga seedlings of small size were few. But the densities of large-size seedlings of both Abies and Tsuga became higher at this stage than at the earlier stages. In the terricolous community of Hylocomium and Pleurozium, no Picea seedlings were found and there were few Tsuga seedlings, while Abies seedlings were abundant.

DISCUSSION

It is reported that lichens are dominant in the early stages of plant succession on logs, but with increasing porosity and breakdown of the logs they are replaced by mosses which are finally accompanied by herbs and tree seedlings (McCullough 1948, Muhle & LeBlance 1975). A similar pattern was observed during the succession on logs in the subalpine forests of central Japan.

Katsurayama (1972) distinguished four successional stages on logs in a Picea forest of Japan, and these were characterized by the following components, i.e., Lepidozia at the pioneer stage, Heterophyllium and/or Pleurozium at the middle stage, Bazzania at the late stage, and Hylocomium, Pogonatum, and/or Polytrichum at the final stage. The Lepidozia community and the Bazzania community seem to correspond to the Heterophyllium-Blepharostoma community and to the Scapania community in the subalpine forests, respectively.

Nakamura (1984) studied development of terricolous moss communities in subalpine coniferous forests of Mt. Fuji. As a result, four stages were distinguished there. The lichen community in the earliest stage was replaced by moss communities, and in the final stage the mixed community of Hylocomium and Pleurozium occurred as in the case of the succession on logs.

The courses of the succession from trunk, through logs, to the ground converged in a moss community dominated by Hylocomium and Pleurozium.

It is recognized that the growth of bryophytes and lichens and the development of their communities are largely influenced by the canopy through light interception and litter fall. On the other hand, bryophytes and lichens also influence the other plants including major tree species especially in the seedling establishment in boreal forests (Larsen 1980).

According to Okada & Ohsawa (1984), seedlings of Cryptomeria japonica establish on the substrates with mosses better than on those without moss. Cross (1981) reported that seedlings of Rhododendron ponticum were closely associated with bryophyte communities and the germination was only successful in a bryophyte mat.

Nakamura & Obata (1985) showed the differences of seedling density in bryophyte communities in a coniferous forest. The seedling density of Tsuga diversifolia is high in Heterophyllium and Scapania communities on logs, but there are few Tsuga seedlings in the Hylocomium-Pleurozium community on both logs and the ground. The density of Abies seedlings scarcely differs in types of bryophyte communities.

Hustich (1954) indicated that many Picea seeds germinate in heavy moss but the roots fail to reach mineral soil through the thick moss and humus. The same cause seems to apply to the difficulty of establishment of both Picea and Tsuga seedlings in the Hylocomium-Pleurozium community.

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THE MOSS PLANT COMMUNITIES IN THE QINLING RANGE OF CHINA

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This paper deals with the moss vegetation of the Qinling Range, China. Four main categories, Hydrophytia, Petrophytia (including a moss-animal community), Geophytia, and Epixylophytia are recognized. Detailed phytosociological characterization of each category is presented.

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On the basis of the taxonomic system put forward by Chen Pan-Chich (1958) and our investigations in the field, the moss vegetation in the Qinling Range can be divided into 4 types, namely: Hydrophytia, Petrophytia (inlcuding a moss-animal community Eurohypnum leptothallum (C. Muell.) Ando + Kaburagia rhusicola Takag. which is important for man), Geophytia, and Epixylophytia.

1. HYDROPHYTIA

Moss communites growing on the sides of canals, by streams, around falls, and in moist places are included.

(1) *Natantia*

The representatives of liverwort communities in the area are Ricciocarpus natans and Riccia fluitans communities which occur in rice field and in the depressions of Yang Hsien County, Shaanxi Prov. They usually occur singly.

Calliergonetum. Its main element is Calliergonella cuspidata which forms a pure community on the rock cliff by the stream of Yuquanyuan Temple at the foot of Huashan Mountain at 460 m. It is firmly attached to rocks, and floats on the stream. In streams at the elevation of 1200 m occur the pure communities of Platyhypnidium riparioides. On the top of eastern Taipaishan Mountains, in the depressions among the Poaceae weeds occur Calliergon stramineum communities.

Hygrohypnietum. On rocks and in the big gravel of ravine streams at an elevation of 700 to 1200 m in the Huogoukau of the Haopingsi of eastern Taipashan, in Changan Hsien, and on western Taipaishan grow great patches of Hygrohypnum smithii communities mixed with small plants of Rosaceae. floating on the water of the slow streams (Fig. 1). In the stream of Ning-shaan Hsien occurs a small patch of a community of H. eugyrium.

Drepanocladetum. The main elements of this community are many different kinds of Drepanocladus, such as D. fluitans, D. revolvens, D. lycopodioides, and D. sendtneri which mostly occur in the depressions at elevations between 2500 and 3600 m. It spreads in the eastern and western Taipaishan, Hu Hsien, and Ningshaan Hsien.

(2) *Nareidia*

Fissidentetum. At the lower elevation of Yang Hsien and Ningshaan Hsien (Shaanxi Prov.) and Wei Hsien (Kansu Prov.) on the wet calcareous rocky walls of streams and on limestone rock or rocky walls beside waterfalls grows Fissidens grandifrons, forming a pure plant community. This species is frequently submerged, causing the water to appear dark green. In the ponds of Yuchenshan Mountain, Peijing, and Jinci Temple (Shaanxi Prov.), this moss community is also found.

Sphagnetum. A small patch of marsh on the peak of Taipaishan is reported in the literature, but Prof. Zhu Zianmo in 1963 could not confirm the existence of the Sphagnum moor, although a patch of Sphagnum occurs there. In the Larix chinensis forests of Fangyangshi on the northern slope of
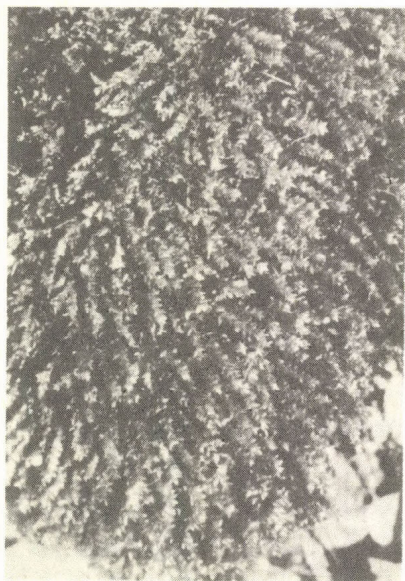
Fig. 1. Hygrohypnietum on   Fig. 2. Sphagnetum   on moist
rocks of ravine streams.   rock in Larix forest.

Taipaishan and of Yaowangchi and on the southern slope of
Taipaishan especially on moist rock and on sand and earth se-
diments occur patches of Sphagnum teres (Fig. 2) mixed with
Aulacomnium palustre, forming a community. There is only a
single species of Sphagnum in the Qinling Range and its area
of distribution is very narrow.

   Climacietum. In the wet places of the forests where streams
flow over the ground grow communities of Climacium dendroides
and C. americanum ssp. japonicum. They are distributed in
Yang Hsien, Ningshaan Hsien, Sichuan Hsien, Fuping Hsien, Mei
Hsien, Huo Hsien, Taipai Hsien, Feng Hsien, on eastern and
western Taipaishan, and on Huashan of Shaanxi Prov.; in the
Tiensu of Kansu Prov., they are found in the broad-leaf for-
ests and in the forests of Betula sp.

   Amblystegietum. Chief species of Amblystegietum are Am-
blystegium serpens and Cratoneuron filicinum, which occur in
the communities of Cyperus sp. and Phragmites sp. in moist
places, and in depressions at altitudes of 800 to 2700 m all
over the Qinling Range.

2. PETROPHYTIA

These communities grow on the rock substrata and on the
rock face. In accordance with moisture, light, and various
physical-chemical features of the rocks, the group may be
divided as follows:

(1) *Xero-petrophytia*

These are communities growing on sunny, dry, and bare
exposed rocks.

Grimmietum. On the bare exposed rocks of the high moun-
tains eastern and western Taipaishan and Huashan, and the
plains of Changan Hsien, Shichchuan Hsien, Ningshaan Hsien,
etc., commonly grow Grimmia ovalis communities. At elevations
from 700 to 2300 m, they are accompanied with G. elatior and
G. hartmannii communities. On granite rocks and rock walls at
altitudes from 1700 to 3500 m occur G. unicolor communities.
In the lower mountains grow firm communities of Hedwigia cilia-
ta, mixed with Sedum species.

Andreaea-Barbuletum. On the bare rocks at elevations from
3200 to 3660 m is found a community of Andreaea mamillosula,
the main species of moss in the area, mixed with Barbula nig-
rescens and many different kinds of lichens.

Ptychomitrietum and Meteorietum. A pure community of
Ptychomitrium dentatum occupies rock surfaces at elevations from
from 500 to 2000 m. In the sunshine on open rock surfaces in
the broad-leaf forests at elevation from 1100 to 1300 m on the
eastern Taipaishan and in Shihchuan Hsien hang pure individual
communities of Chrysocladium retrorsum. On the dry rocks at
various places in the Qinling Range at altitudes from 900 to
2000 m widely spread Meteorium helminthocladium communities
are found.

Racomitriietum. On dry rocks in various parts of the
Qinling Range at altitudes from 1600 to 3600 m are commonly
encountered the communities of Racomitrium canescens, R. fas-
ciculare, R. heterostichum, R. aquaticum, and others.

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On the sunny   dry rock surfaces along the valleys of the
Xieyugnankou of Mei Hsien grow the communities of Pterogonium
gracile var. tsinlingense, mixed with Pteridophyta such as
Pyrrosia petiolosa (Fig. 3).

(2) *Hygro-petrophytia*

In the middle section of the Qinling Range are distributed
communities composed of moss-petrophytes and their associated
insects, namely the community of Europhypnum leptothallum and
Kaburagia rhusicola. E. leptothallum is an exclusive winter
host of K. rhusicola. When autumn comes, K. rhusicola flies to
the E. leptothallum community, where it absorbs nutrients
from the moss stems and leaf cells, surviving the severe winter
cold. When spring arrives, K. rhusicola flies from the moss
mats to the leaves of Rhus potaninii, to absorb nutrients from
the plants. Finally, it forms nutgalls which have many uses
for mankind on the leaves of R. potaninii. From nutgalls may
be obtained forest chemical products such as gallic acid and
tannic acid, which find wide use in light industry, the che-
mical industry, medicine, petroleum exploration, and the aero-
nautical industry. If no E. leptothallum existed in that re-
gion, K. rhusicola would not accomplish its life cycle, causing
nutgall to have a poor harvest. E. leptothallum is widely dis-
tributed in Ningshaan Hsien, Taipai Hsien, Mei Hsien, Zhouzhi
Hsien, Ankong Hsien, Nanzheng Hsien, Pingli Hsien, Xixiang
Hsien, Hiashan, eastern and western Taipaishan. It is also
distributed in southern and northern Prov. of China. Abroad
it is found in the cold temperate zone of Asia, and is also
reported from Japan and the far eastern part of the Soviet
Union. It is commonly seen in the broad-leaf forests at an al-
titude of 400 to 1300 m on the roadsides, and on rock cliffs,
growing obliquely in patches. Its main shoots and lateral
shoots alternately grow and form layers. The new layer formed
every year is larger than in the past year. Moreover, it is
easily separated from the substratum. The mosses growing at
this altitude represent one of the communities in the temperate
zone, covering the rock cliffs. Vital water can be maintained
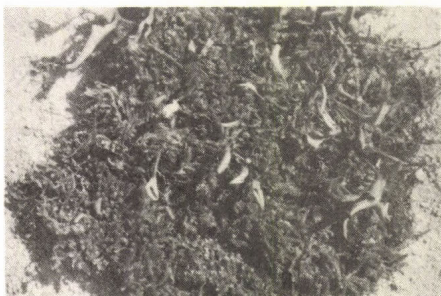by capillarity. Lush growing E. leptothallum is well-developed

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Fig. 3. Pterogonietum on the   Fig. 4. Bartramietum on rocky soils
sunny dry rock.   in Betula or Rhododendron forests.

in this region. Sporophytes are easily seen. The main peak of
the Qinling Range is located in Shaanxi Prov., which is the
chief region for the production of Kaburagia.

Bartramietum. It occurs in Taipaishan, Hiashan, Hu Hsien,
Ningshan Hsien and elsewhere. It is mainly composed of Bartra-
mia pomiformis, associated with some Hypnum sp. and Thuidium
sp. This community os found on the rocky soils in the conife-
rous - broad-leaf   forests, coniferous forest or in the
Rhododendron forests. It is also common in forest districts
of northeastern China and in the eastern part of Inner Mongolia.
In rocky soils or on shady rocks in the Betula forests or in
the Rhododendron forests at 1800 to 3100 m grows a pure com-
munity of B. halleriana, which also spreads on the mountains
to the south of Yangtze River and in Taiwan, mixed with Thui-
dium sp., Hypnum sp. and Lobaria sp. (Fig. 4). In the region
at elevations between 2000 and 3200 m a pure community of B.
ithyphylla is found. It is widely distributed in China and is
common in the northern temperate zone.

Bryoxiphium norvegicum spp. japonicum community. On the
dripping rocks in the forest at 1200 to 1800 m in Ningshaan

Hsien, Yang Hsien of Shaanxi Prov. grows a pure community of
Bryoxiphium norvegicum ssp. japonicum.

By newly dug canals or in the sites with direct sunshine
exists a community of Philonotis-Bryetum usually with the
grasses of Poaceae. Various species of Bryum also appear among
them.

Plagiomnietum. On the south sides of rock grooves, near
water, occurs the community of hygrophilous and sciophilous
plants and Plagiomnium, the main species of which are P. cus-
pidatum, P. integrum, P. maximowiczii, P. succulentum, and P.
arbuscula. On the dripping rock walls in the Betula forests
grow large patches of a community of Rhizomnium punctatum var.
elatum associated with Caryophyllaceae.

Thuidietum. This community is composed of Thuidium cymbi-
folium, T. philibertii, mixed with Hypnum sp. and Lobaria sp.
It is seen in the broad-leaf forests or in the coniferous -
broad-leaf forests in various places of the Qinling Range.

Trichocolea-Conocephaletum. This community is mainly
composed of Trichocolea tomentella, mixed with Conocephalum
conicum and some Plagiochila. It is generally found on the rock
surfaces in the broad-leaf forests. It is distributed in
Ningshaan Hsien, Zhouzhi Hsien, and eastern and western Tai-
paishan.

Porelletum. The dominant element of this community is
Porella caespitans mixed with Ascidiota blepharophylla which
is only seen from the Pingansi Temple to the Fangyansi Temple
in Taipaishan at an elevation of about 3000 m. P. ceaspitans
always forms a firm community mixed with P. densifolia on the
northern slope of Dabashan mountain. On the rock cliffs in the
Bishnakou of Wei Hsien, Kansu Prov. at an altitude of ca. 600
m grows a pure community of Macvicaria ulophylla.

3. GEOPHYTIA

This community refers to the mosses growing in soil, on
ground walls or on the rocky soil. In accordance with moisture
and soil types, it may be divided into the following communi-
ties:

(1) *Ephemero-geophytia*

Most of these are geophytic ephemeral small mosses showing
seasonal luxuriance and decline. As soon as the sporophyte is
produced from the gametophyte, the gametophyte dies. This
group usually contains mosses on open mineral soil.

Riccia spp. community. On the Han River basin, by the side
of banks, on rice field is usually found a single community of
Riccia spp. However, on the Wei River basin it is rarely en-
countered.

Funaria-Bryuetum. This community consists of Funaria hyg-
rometrica and Bryum argenteum, which are found in the lower
mountains and plains of the Qinling Range, around houses in wet
situations. In the greenhouses they may be seen at all seasons;
even at -8°C they still grow vigorously. In September and
October, the rainy season, they appear extremely luxuriant.
The sporophytes of F. hygrometrica are standing upright and
Bryum argenteum spreads its silvery light. In the following
spring spores are germinating again, growing into new shoots.

Funaria-Physcomitrietum. This community consists of Funa-
ria hygrometrica and Physcomitrium sphaericum which occur in
the moist, sandy soil on the shores of the Han River basin and
on the stone bricks and wet fertile soil of Heihuguan Temple
of eastern Taipaishan. The pure community of Funaria hygro-
metrica is found on burnt areas, roadsides and abandoned
fields.

On the alkaline soil wall at an altitude of 2000 m of
temple Luotuosi on the Taipaishan occurs a single small com-
munity of Aloina rigida.

(2) *Hygro-geophytia*

There are the following communities on the forest edges,
on the roadsides and on moist sloping ground walls in the
Qinling region.

Conocephaletum. This community is mainly composed of
Conocephalus conicus mixed with a few Plagiochila sp. and
Thuidium sp. forming a layered community (Fig. 5). It is

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Fig. 5. _Conocephaletum_ on the wet ground walls in forests.

usually found in the broad-leaf forests of the lower mountains
and on the wet ground walls. The _Marchantia_ _polymorpha_ com-
munity is abundant on the southern slope of the Qinling Range.

Atrichetum. This community is found on the ground walls
by roadsides. It is composed of _Atrichum_ _undulatum_, _A_. _crispum_,
and _A_. _henryi_ forming large patches.   It is distributed in
the Ningshaan Hsien mountains of Shaanxi Prov. and the Zhechuan
of Honan Prov. In the Taipaishan, the main peak of the Qinling
Range, it is widespread, _A_. _undulatum_ var. _gracilisetum_ and
_A_. _obtusulum_ forming a pure community. This usually grows on
roadsides along forest edges.

Pogonatetum. This community is composed of _Pogonatum_ _in-_
flexum or _P_. _spurio-cirratum_, distributed in the mountainous
region of the southern slope of the Qinling Range. In the
Quercus sp. forest of the northern slope of the Qinling range
is found a pure community of _P_. _urnigerum_ (Fig. 6).

Mnietum. On the moist ground wall in the forest grow
Mnium _laevinerve_, _M_. _lycopodioides_, _M_. _thomsonii_, _M_. _spinosum_,
Trachycystis _ussuriensis_, and _Plagiomnium_ _undulatum_, forming
a pure community. It is encountered in the broad-leaf forests
of Taipaishan, in the Huashan, and Hui Hsien, Kansu Prov.

Fig. 6. Pogonatetum in Quercus forest.

(3) *Alpino-geophytia*

The alpine steppe is characterized by its poor soil and accumulation of bare rocky fragments and gravely mats. In the wind shadow and thickets of this area the following communities are commonly found.

Distichium-Myurellosetum. This community is composed of Distichium capillaceum mixed with a little Myurella sibirica, generally found in alpine meadows. Myurella sibirica associated with Ditrichum flexicaule also forms a community growing in the larch forests or in the coniferous broad-leaf forests. The community, mainly composed of Distichum capillaceum with occasional Encalypta ciliata or E. alpina is frequently seen on the top of Taipaishan.

Dicranetum. A pure community consisting of Dicranum bonjeani, D. delavayi, D. elongatum, D. nipponense, which is distributed in alpine meadows at 3400 to 3600 m, such as in the Paomaliang, Baxiantai, Wengong-miao, Dayeha of the Taipaishan.

Paraleucobryetum. Its main component is Paraleucobryum
enerve mixed with Cladonia stellaris or Thamnolia subuliformis,
forming moss-lichen communities. These are typical boreal
alpine communities.

The main species of Bryetum are several species of Bryum,
e.g., B. caespiticium, B. capillare, B. lonchocaulon, B. schle-
icheri, and B. argenteum. It is a moss community which is often
seen in alpine meadows. On the summit of the Taipaishan, on
the exposed rocks of the Baxiantai, and in the rocky crevices
also grow Grimmietum and Rhacomitrietum and Tetraplodon mnio-
ides communities, in dense cushions.

(4) *Hylo-geophytia*

The woodland is an especially sutiable environment for
most bryophytes. The species and genera which form communities
vary according to the moisture, temperature, and soils of
forests. We analyze them as follows:

In the very moist woodlands of Larix chinensis on the
northern slope of the Taipaishan grows Hylocomium splendens
(Fig. 7) mixed with a little Thuidium cymbifolium, which form
a thick spongy moss floor. This usually occurs in large
patches on the southern slopes of the Taipaishan Woodlands of
Larix chinensis, at 2900 m to 3100 m and are covered with
Actinothuidium hookeri mixed with many different kinds of
Hylocomium splendens and Brachythecium ssp., together forming
a community. The chief species of the moss floors in the
Rhododendron elementinae forests located on the northern slope
of Taipaishan is Hylocomium splendens which forms a thick
spongy moss floor. Walking through the Rhododendron elemetinae
forest from Nantianmen on the south slope of Taipaishan takes
4 hours. As one proceeds, the community becomes inlaid with
Plagiomnium tezukae. In the mixed coniferous and broad-leaf
forests grow large patches of a pure community of Rhytidia-
delphus triquetrus. In the sunshine and drier sites at forest
edges frequently grows a community of Rhytidium rugosum (Fig.
8) and Abietinella abietina. A Pleurozium schreberi community
is often seen in coniferous forest portions. Plagiobryetum is a
moss community which is also often seen in the alpine. In the

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Fig. 7. Hylocomium splendens
phytocoenosis in the very moist
woodlands of Larix.

Fig. 8. Rhytidietum in forest.

Rhododendron forest in the Fangyangsi of the Taipaishan grows
a large patch of Plagiobryum giraldii community, while in the
Larix forests grows a P. demissum community which is in dense
cushions.

In the places of the Rhododendron and Betula forests in
which the humus accumulates thickly is found a small patch of
a community of Lyellia platycarpa. Moreover, on the grassland
in the forests is often encountered a community of Oreas mar-
tiana and Plagiopus oederi on cushions.

Entodonetum. This is one of the communities of the
Qinling Range which is often seen in Betula and Quercus for-
ests. It is composed of many species of Entodon such as E. ca-
liginosus, E. nanocarpus and E. cladorrhizans which form a
large pure community. It usually occurs at elevations between
1300 and 2700 m.

In the Quercus forest of the lower mountains another rep-
resentative community often seen in Plagiomnietum which is

composed of many species of Plagiomnium such as P. cuspidatum, P. venustum, P. japonicum, P. drummondii, P. maximowiczii, P. arbuscula and Mnium heterophyllum, etc. which occur everywhere in the Qinling Range. Secondly, there is a community of Fissidenetum, composed of Fissidens cristatus and F. bryoides forming a pure community.

Barbuletum. There are representatives of this community from the plain to the high mountain of the Qinling Range. In the plain is encountered a pure community of Barbula unguiculata, B. reflexa and B. tectorum. In the mountainous area occurs a single community composed of B. fallax, B. vinealis, B. constricta, B. preobtusa, and B. ditrichoides. In the alpine and cold zone grows a community composed of B. nigrescens and B. asperifolia, rather large, reddish-brown Barbula species.

Tortuletum. In the alpine and cold zone are found communities of Tortula princeps and T. sinensis. which appear on the top of the main peak of the Qinling Range such as in the Baxiantai and Eryehai and in some other places. Another community of the alpine zone is Bryoerhytrophylletum which is composed of several species of Bryoerythrophyllum such as B. gymnostomum, B. recurvirostrum, and B. atrorubens which mostly occur above 3000 m. Otherwise B. alpigenum and B. yunnanense communities are distributed in the Tatien located on the Taipaishan and in the Betula forests of the western Taipaishan.

4. EPIXYLOPHYTIA

The trees themselves are a complex living environment for the bryophytes. The absorption of the light is different in various parts of trees. Apart from typical tropical rain forests and the moister temperate evergreen forests, the distribution of moisture in a tree is not uniform. Therefore, the species of bryophytes covering the tree, and the epiphytic forms of bryophytes in the trees are very varied. We describe them as follows:

(1) *Compacrae epixylophyta*

Pylaisietum. On the tree trunks or branches of Sorbus and Acer in deciduous broad-leaf forests at elevations of 1700 to 1800 m is often seen a small patch of a pure community of Pylaisia brotheri and P. polyantha. Corticolous mosses frequently encountered on the plain and the lower mountains are Venturiella sinensis, Fabronia matsumutae as well as crustose lichens forming a firm community. They closely attach to the trunks of Ligustrum, Diospyros, Syringa, Juglans, and Acer. In the forest district of the middle section of the Qinling Range often occurs a small community of Orthotrichum anomalum, Schwetschkea courtoisii, Schwetschkeopsis japonica and S. denticulata.

A liverwort community which consists of Frullania chinlingensis growing on the trunks of Betula is most evident. On the trunks of Betula albosinensis or B. platyphylla, a F. tamarisci community also grows. The communities mentioned above are mostly encountered in the woodlands at 2700 to 3200 m in the eastern and western Taipaishan.

(2) *Laxae epixylophytia*

Leucodontetum. The most remarkable large patch of moss community, growing on the trunks of Betula albo-sinensis and B. platyphylla and some secondary forest trees is the pure community of Leucodon exaltatus (Fig. 9). It wraps trunks and grows very lush. It is found at 2100 to 2740 m in various places of the Qinling Range.

Neckeretum. This community is mainly composed of Neckera pennata and N. complanata, which grow in the broad-leaf forest zones and in the Betula forest zone, forming a large patch of a pure community. The Forsstroemietum also appears there. On the trunks of Quercus grow large pure patches of a community of Forsstroemia lasioides (Fig. 10) and F. kusnezovii, which were incorrectly identified as Leucodon by C. Mueller.

Fig. 9. Leucodontetum on the trunks of Betula.

Fig. 10. Forsstroemietum on the trunks of Quercus.

(3) *Demigratae*

Leucodonetum. This is composed of Leucodon, a large pure
community. It winds around branches and grows lush. It is
mostly found on the trunks and tree bases of Abies or on the
trunks of Betula and Quercus at 1800 to 3100 m in the Ning-
shaan Hsien, Hu Hsien of Shaanzi Prov. and in the eastern

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and western Taipaiashan. On the trunks of Abies and Sorbus grow small patches of L. angustiretis or L. mollis. The latter two are very scarce and are rarely seen.

Barbelletum. The main element of this community is Barbella pendula forming a large patch hanging on branches. It is found in Taipai Hsien, Feng Hsien, and western Taipaishan.

(4) *Basae Epixylophytia*

On the bses of tree trunks in the broad-leaf forest edges and forest clearings grow a community of Radula complanata. A community composed of Myurocladia maximowiczii and Neckera pennata also occurs here. Basae epixylophytia communities also consist of many species of Entodon, such as E. obtusatus, E. caliginosus, E. angustifolius, and E. luridus mostly growing on the broad-leaf forest land less than 2000 m forming extensive mats, and there is a pure community of Dicranoweisia crispula growing on the tree trunk bases. In the Betula and Quercus forests occurs a community of Hypnum cupressiforme growing on the tree trunk bases, while in the Larix forest is found a community of H. hamulosum.

(5) *Putridae epixylophytia*

On decayed bark or on decayed logs in the Larix-Abies forest grows a small community composed of Buxbaumia punctata and Brachythecium spp. Buxbaumia punctata is a small annual moss, which is only found in the Fangyangshi and Mingxiangshi of the Taipaishan. Another moss community growing on decayed wood in the coniferous forests is Tetraphietum. Its main element is Tetraphis pellucida mixed with community of Oncophorus wahlenbergii, Pohlia elongata or P. nutans. On decayed logs is often encountered the Lepidozia robusta community growing extensively associated with the Metzgeria pubescens community found in the coniferous forests.

On decayed logs or the fallen trees of broad-leaf forests grow large patches of a community composed of Brothera leana and Campylopus japonicus, which is found on the southern and

northern slopes of Taipaishan. On the decayed logs of broad-leaf forests in the Hoditang, Ningshaan Hsien, occurs a community of Hypopterygium japonicum mixed with Brachythecium sp. On the decayed trees is also encountered Lophozietum composed of Lophozia chinensis and L. muelleri. They are widespread in the broad-leaf forests of eastern Taipaishan.

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HEPATIC FLORA OF THE DECIDUOUS FOREST OF PURANDHAR AND NEIGHBOURING HILLS, MAHARASHTRA, INDIA

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Purandhar hill fort (18°17'N, 74°2'E, alt. 85o-1390 m) shows deciduous type of forest. The chief difficulty in study- ing the ecofloristics of a deciduous forest is the disconti- nuity of communities in time and space. It was, therefore, thought worthwhile to make a critical survey of the liver- worts from taxonomic as well as ecological viewpoints; accord- ingly extensive collections were made during last three to four years.

An analysis of the hepatic flora from the locality revealed a wide range of ecological diversity and the presence of phytogeographically miscellaneous elements. It further showed the occurrence of a monotypic endemic Indian genus, viz., Sewardiella tuberifera Kash. and several Himalayan genera, such as Petalophyllum, Exormotheca, and Cyathodium.

Moreover, a number of habitats on which bryophytes tend to grow, showing various growth forms, along with certain biolo- gical features that are associated with their way of life, are discussed. The information given in the paper represents the first extensive account of the liverwort flora of Purandhar along with interesting ecological observations.

INTRODUCTION

The last two decades have witnessed a remarkable progress in the study of bryophyte systematics in many parts of the world, providing us with useful and significant data on their ecology,

migration, and distribution. However, there are areas in India which have not yet been seriously studied bryologically. An example is the State of Maharashtra, which is extensive and appears to be potentially rich in hepatics. The suggestion by Pande (1958) of the importance of studies on hepatic vegetation stimulated the author to undertake the present work.

The Western Ghats of India are still mostly unexplored bryologically, although casual references to them are found in the literature, e.g., in the work of Mahabale (1941) and Bapna (1958). Mahabale drew attention to the occurrence of the long-lost Aspiromitus St., a rare member of the Anthocerotae, and the epiphyllous liverwort Leptocolea lanciloba St. in Khandala. Bapna (1958) recorded a species of Petalophyllum Kash. from Purandhar, but he did not collect mature plants. It was therefore thought worthwile to make a general survey of liverwort flora from ecological as well as taxonomic viewpoints; accordingly extensive collections were made during the last three years from Purandhar and the surrounding hilly tracts of Maharashtra State.

I. TOPOGRAPHY AND CLIMATE

Purandhar is a hill fort situated about 40 km southwest of Poona. The approximate bearings of the hill are $70^{\circ}2'E$ and $18^{\circ}17'N$. It rises suddenly from the Deccan Plains, although on the Poona side it has many lesser hills. The highest point of Purandharm according to the geological survey of India is at 1,387 m (4564 ft) a.s.l., about 750 m above the surrounding plains.

Temperature

It is agreeably cool and pleasant during the greater part of the year, the maximum reaching 37.8°C and the minimum 10°C.

Humidity

It can be about 90 to 95% throughout the monsoons, when the fort is often masked with dense clouds of mist. During dry

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months, in the early hours of the morning, the humidity may
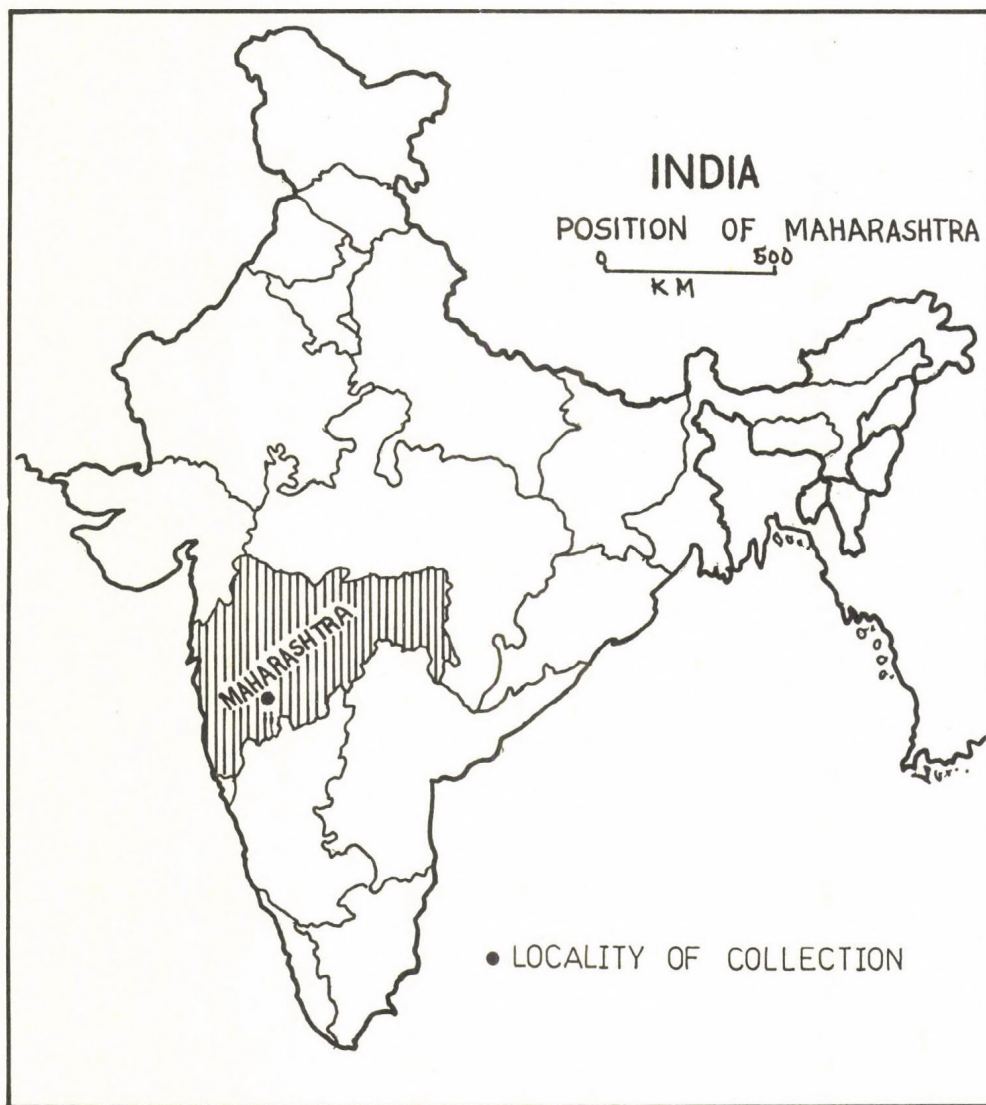reach 60 to 70%, but it falls to about 25% for the afternoon.

Fig. 1. Map showing the position of Maharashtra State and
the study area in India.

As Purandhar is on the leeward side of the Western Ghats, its rainfall is rather low. The maximum rainfall recorded is 1721 mm, and the minimum 1020 mm. Since most of the rains occur from June to September   the vegetation is of the deciduous type.

In the following account, three 'life-forms' of liverworts are described according to the patterns given by Giesenhagen (1910) and Herzog (1916).

a) Annuals: Gametophytic growth stops after production of gametangia, and death follows as soon as the sporangium has ripened, e.g., Riccia.

b) Mats: Most of the plagiotropic bryophytes belong to this category, their main and lateral shoots lying close to the substrate to which they are attached by rhizoids. They grow on rocks and the bark of trees, e.g., Lejeunea, Asterella, Targionia, Cyathodium, and Anthoceros.

c) Short turfs: The short shoots, rarely more than 1 cm high, stand close together, often forming spreading turfs which do not last for more than a year. They often grow on mineral-rich soil and on rocks, e.g., Fossombronia himalayensis Kash.

BRYOPHYTIC HABITATS

The following habitats were recognised at Purandhar hill fort.

a) Rock surfaces and crevices. With a summer wet season and a winter dry season that lasts for seven to nine months, a rich flora of Marchantiales occurs in the clefts in rock outcrops. Included are species of Exormotheca, Asterella, Plagiochasma, Targionia, and Riccia. An interesting member of the Marchantiales, viz., Cyathodium tuberosum Kash., with a yellow luminescence, was found flourishing in dark, moist rock crevices.

b) Seepage areas and ponds: Where moisture is more presistent, the bryophyte flora becomes more conspicuous with, for example,

species of <u>Riccia</u> and <u>Anthoceros</u>. These are confined to clay soils that stay moist, as around the edges of temporary lakes or on river flood plains. These plants may have to survive for a long time without receiving water. The spores, therefore, remain viable in the dry soil, but for how long, no one knows.

c) Epiphytes and commensals: <u>Lejeunea</u> <u>flava</u> (Swartz) Nees. occurs on the bark of trees up to a height of two meters above soil level. It is not uncommon to find, at least in small patches, a mixture of different species of <u>Lejeunea</u> and allied genera at the base of the trunks where there is shade from the canopy and a concentration of water from the occasional rains by rain tracts down the trunks. The epiphytes thus receive an enhanced share of the occasional rains. Besides this, a very interesting species of <u>Cyathodium</u> was found on the bark of a tree, which I tentatively refer to in this paper as <u>C</u>. <u>epiphytum</u> sp. nov.

In addition to the different habitats, life forms, and physiological characteristics, certain biological features were noted. Such features allow hepatics to cope with semi-arid conditions, at least in the region at the foot of Purandhar fort.

Like mosses, thallose liverworts roll up on desiccation into a tubular form so that the dorsal photosynthetic surface is hidden, so that the ventral surface and/or ventral scales, which may be intensely pigmented with anthocyanin, are the only parts exposed. The pigmentation is usually dense enough to appear black. This is typical of <u>Exormotheca</u> <u>tuberifera</u> Kash., <u>Asterella</u> <u>angusta</u> St., <u>Targionia</u> <u>hypophylla</u> (Mich.) L., and various species of <u>Plagiochasma</u> and <u>Riccia</u>.

To my surprise, in <u>Fossombronia</u> <u>himalayensis</u> Kash., the whole of the uppermost surface of the fronds is tinted with anthocyanin, although never as heavily as the ventral surface and scales in the majority of the <u>Marchantiales</u>.

Although the normal vegetative method of reproduction of thallose liverworts is by growth of the persistent shoot apex which can withstand a great deal of desiccation, tubers are also important and of frequent occurrence in <u>Sewardiella</u>

tuberifera Kash., Petalophyllum indicum Kash., Exormotheca
tuberifera Kash., and Cyathodium tuberosum Kash.

TAXONOMIC ACCOUNT

Systematic enumeration of the species following Evans
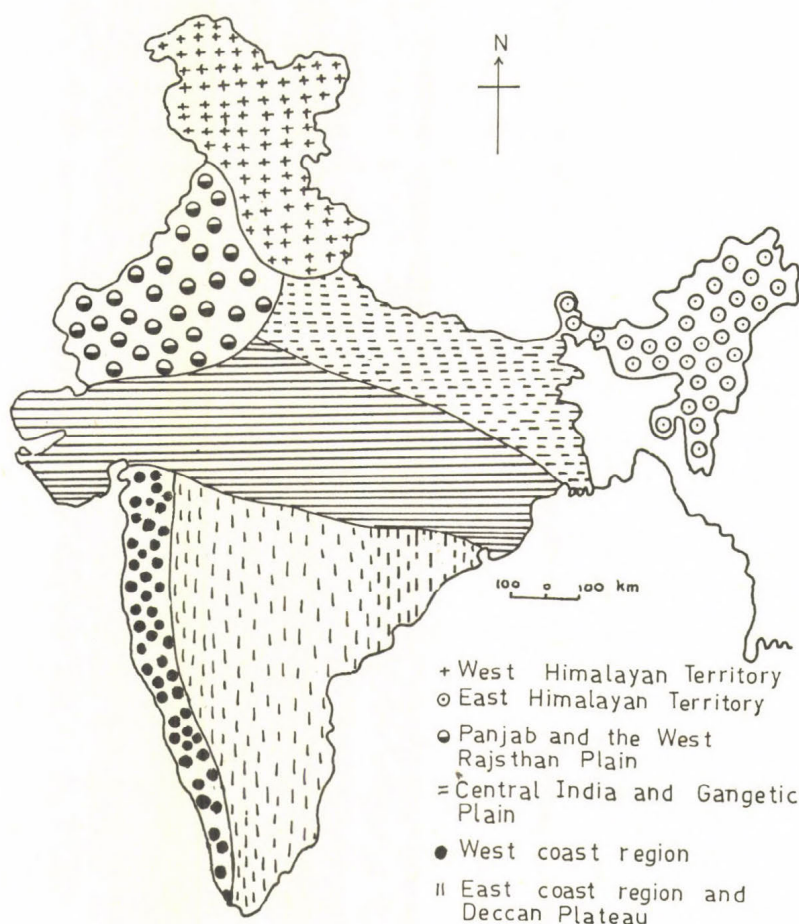(1939), except that Anthocerotae, have been placed first.

+ West Himalayan Territory
⊙ East Himalayan Territory
⊖ Panjab and the West
   Rajsthan Plain
= Central India and Gangetic
   Plain
● West coast region
‖ East coast region and
   Deccan Plateau

Fig. 2. Bryogeographical units of the flora of India. After
Pandey (1958).

ANTHOCEROTALES - Anthocerotae

1. <u>Anthoceros</u> <u>erectus</u> Kash. Collection made on clayey cuts and a rocky cliff in semi-shaded, damp sites along the path. Common.

2. <u>Phaeoceros</u> <u>himalayensis</u> (Kash.) Prosk. In small clusters on shady slopes. Less common.

3. <u>Folioceros</u> sp. On soft lumps of moist soil near streams. Less common. Probably a new species.

4. <u>Notothylas</u> <u>indica</u> Kash. In small patches on moist soil, sometimes associated with mosses. Common. Also collected at the Poona University Campus.

5. <u>Notothylas</u> sp. Monoecious, occurring on moist soil in thick shade of Banyan trees at Poona University Campus, commonly forming a rosette. Non-columellate. Elaters rudimentary. Probably a new species.

JUNGERMANNIALES - Lejeuneaceae

6. <u>Lejeunea</u> <u>flava</u> (Swartz) Nees. On decayed bark of fallen logs and on tree trunks, mostly in damp, shady sites in forest. Common.

7. <u>Fossombronia</u> <u>himalayensis</u> Kash. On moist soil and exposed ground or in green isolated patches on rocks, especially during later part of the rainy season. Generally associated with mosses and grass. Fairly common.

8. <u>Petalophyllum</u> <u>indicum</u> Kash. In moist clefts of rocky surfaces and on soft lumps of damp soil on slopes in dense patches. Always associated with <u>Sewardiella</u> <u>tuberifera</u> Kash., <u>Fossombronia</u> <u>himalayensis</u> Kash., and with mosses. Rare.

9. <u>Sewardiella</u> <u>tuberifera</u> Kash. As stray patches on moist soil in shady places among mosses and grass. Rare.

Riccardiaceae

10. <u>Riccardia</u> <u>indica</u> St. On moist rocks near streams and on moist earth among grasses in the plains at Poona. Rare.

MARCHANTIALES - Marchantiaceae

11. <u>Exormotheca</u> <u>tuberifera</u> Kash. In patches on moist exposed rocks, always associated with mosses and with <u>Riccia</u> during early season only. Rare.

Rebouliaceae

12. <u>Asterella</u> <u>angusta</u> St. On old moist exposed walls, almost covering the whole surface. Common.

13. <u>Plagiochasma</u> <u>appendiculatum</u> L. et L. On moist ground and rocks, exposed walls of the old buildings forming large thick patches, associated with mosses and species of <u>Asterella</u> and <u>Plagiochasma</u>. Fairly common.

14. <u>P</u>. <u>articulatum</u> Kash. On moist exposed walls near military camp area, associated with mosses and other species of <u>Plagio-</u> <u>chasma</u>. Fairly common.

15. <u>P</u>. <u>simlensis</u> Kash. In small patches on moist walls and rocky surface, associated with mosses. Common.

16. <u>P</u>. sp. On moist walls near military camp area. Monoecious. Thallus long, linear. Antheridial cushions knob-like and circular, never horseshoe-shaped. Rare. Probably a new species.

Targioniaceae

17. <u>Targionia</u> <u>hypophylla</u> (Mich.) L. On damp exposed rocks, associated with mosses. Fairly common.

18. <u>T</u>. <u>hypophylla</u> var. <u>Lodwickii</u>. Thallus considerably long as compared to <u>T</u>. <u>hypophylla</u>. Less common.

19. Cyathodium tuberosum Kash. In dark shady corners and caves in large thick patches, shining green. Fairly common.

20. C. sp. Epiphytic. On moist bark of the trees on the way to Kedareshwar temple at Purandhar. Less common. Probably a new species.

Ricciaceae

21. Riccia melanospora Kash. On moist soil and rocks. Common.

22. R. discolor L. et L. On moist soil forming patches. Common.

23. R. cruciata Kash. On moist walls and damp soil in association with mosses. Common.

24. R. crystallina L. On wet ground. Less common.

DISCUSSION AND SUMMARY

Unlike most higher plants, bryophytes are rarely found as single individuals, normally occurring as groups of individuals. The assemblage of individuals and their various growth forms, modified by external factors, together provide the characteristics which can be termed 'life-form'. A considerable variety of life-forms have been described from tropical forests. Nonetheless, the deciduous forest of Purandhar shows some of them, e.g., annuals, mats, short turfs, etc.

The chief difficulty in studying the ecology of deciduous forests is the discontinuity of communities in time and space. Under the pressure of desiccation, communities (especially of thalloid liverworts) can disappear, only to appear again days later after a rain shower. Such characteristic biological features were noticed at Purandhar.

Moreover, from year to year, the communities that develop are as unpredictable as the rains that cause them to reappear. Although there are usually favourable and unfavourable locations, the richest communities shift in response to trivial and unpredictable events. The cover of bryophytes is never extensive over large areas.

With these points in mind, it seems that the atmospheric conditions of Purandhar on the Deccan plateau are conducive to the luxuriant growth of liverworts. For example, in the rock crevices, on moist tree bark, and near streams where there is enough shade and moisture, a rather large number of species occur, particularly during the monsoons. By way of contrast, only a few xeromorphic forms, such as species of Asterella, Plagiochasma, and Riccia grow on the plains, which remain dry for a longer part of the year.

Pande (1958) characterized the West Himalayan Territory as one of the bryogeographical units of India (Fig. 2) with monotypic endemic genera such as Sewardiella, Stephansoniella, and Aitchisoniella. However, the author has collected Sewardiella tubifera Kash. from the sierra of the present locality indicating another site for such genera in India. The same is true of the species of Petalophyllum indicum and Exormotheca tuberifera, which are supposed to be of rare occurrence on other parts of India, but commonly occur at Purandhar. Moreover, it has been brought to the author's attention that the genus Exormotheca Mitt. is on the verge of extinction in the Western Himalayas, which is supposed to be the richest Indian region for liverworts. Further, it may be stated that even though Purandhar exhibits a deciduous forest type of vegetation, some of the genera like Sewardiella and Petalophyllum occur prominently, although typical of the high mountain ranges of the Himalayas.

The findings presented above constitute the first extensive account of the hepatic ecoflora of Purandhar. In view of the short time available to the author in the field, additional collection should be made, since a thorough search of comparable localities elsewhere in Maharashtra State will probably reveal many more species of liverworts. On the basis of the present collection, it may be stated that 24 species of liverworts belonging to 15 genera occur in the Purandhar area. Many of these species are really interesting in that they are believed to be rare throughout India, while three of the species appear to be new taxa awaiting description.

ACKNOWLEDGEMENT

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SPECIES ASSOCIATIONS AMONG CORTICOLOUS CRYPTOGAMS.
A COMPARATIVE STUDY OF TWO SAMPLING METHODS

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105 plots of 5 dm^2 were randomly selected in epiphytic
cryptogamic vegetation belonging to the Physcietalia ascen-
dentis and the Leucodontetalia. Species performance was es-
timated using two methods: a relevé method with cover estimates
and a plotless sampling method based on 9341 systematic
sample points taken from the same plots. Relative species
frequencies and species associations (χ^2 criterion) were
compared taking into account all species with at least 1%
frequency. Interspecific relations found with data based on
cover estimates (analysed with TWINSPAN and DCA) and on fre-
quencies (χ^2 criterion) revealed largely similar patterns. DCA
ordination diagrams based on cover estimates and presence/ab-
sence data respectively gave comparable results.

The relevé method gives more positive species associations
than the plotless method, mainly because of the smaller number
of species under consideration in the latter (e.g., most of
the erect, acrocarpous mosses are omitted); there are more ne-
gative associations in the plotless sampling method.

The associations found with both approaches are mostly in
the same direction, although in some cases they are opposite.
In the unfolded matrix of the plotless sampling method not less
than 39% of the positive and 33% of the negative associations
are unidirectional; in some cases species i as hit species is
positively associated with species j as contact species,
while vice-versa they are negatively associated.

INTRODUCTION

Many different sampling methods have been used in the study of cryptogamic vegetation, yielding results that are rather difficult to compare. A method that has been used by many European investigators (e.g., Barkman 1958, Philippi 1965, Lecointe 1975) is the relevé method described by Braun-Blaquet. A more recent approach, the plotless sample method, was applied by, e.g., Yarranton (1966, 1967).

When studying these different approaches one questions to what degree the obtained results are comparable. Therefore, we applied these two sampling methods on the same material (chosen randomly and not subjectively as in the Braun-Blanquet approach) to be able to compare the results.

MATERIAL

The samples were collected on elm trees (Ulmus minor) which were dead or dying because of the notorious elm disease. The study area is the Boulonnais (Department Pas-de-Calais, NW France) where we set up this study initially to describe the epiphytic vegetation before it vanished with its phorophyte. The samples were taken randomly over the area (Fig. 1) in various habitats: trees from roadsides, meadows, small spinneys, gardens and forest.

Although a detailed vegetation analysis will be published elsewhere we will give a brief description of the syntaxonomical affinities of the studied communities:

The lichen communities all belong to the Physcietalia ascendentis with affinities to either the Buellion canescentis (Ramalinetum duriaei (Duvign.) Barkm. 1958 and Buellietum punctiformis Barkm. 1958) or to the Xanthorion parietinae (Physcietum ascendentis Frey & Ochsner 1926, Physcietum elaeinae buelliosum canescentis Barkm. 1958 and Parmelietum acetabulae Ochsner 1928). Especially in the last 3 mentioned communities several bryophytes regularly appear. They occur optimally in the Tortulion laevipilae (Leucodontetalia) with
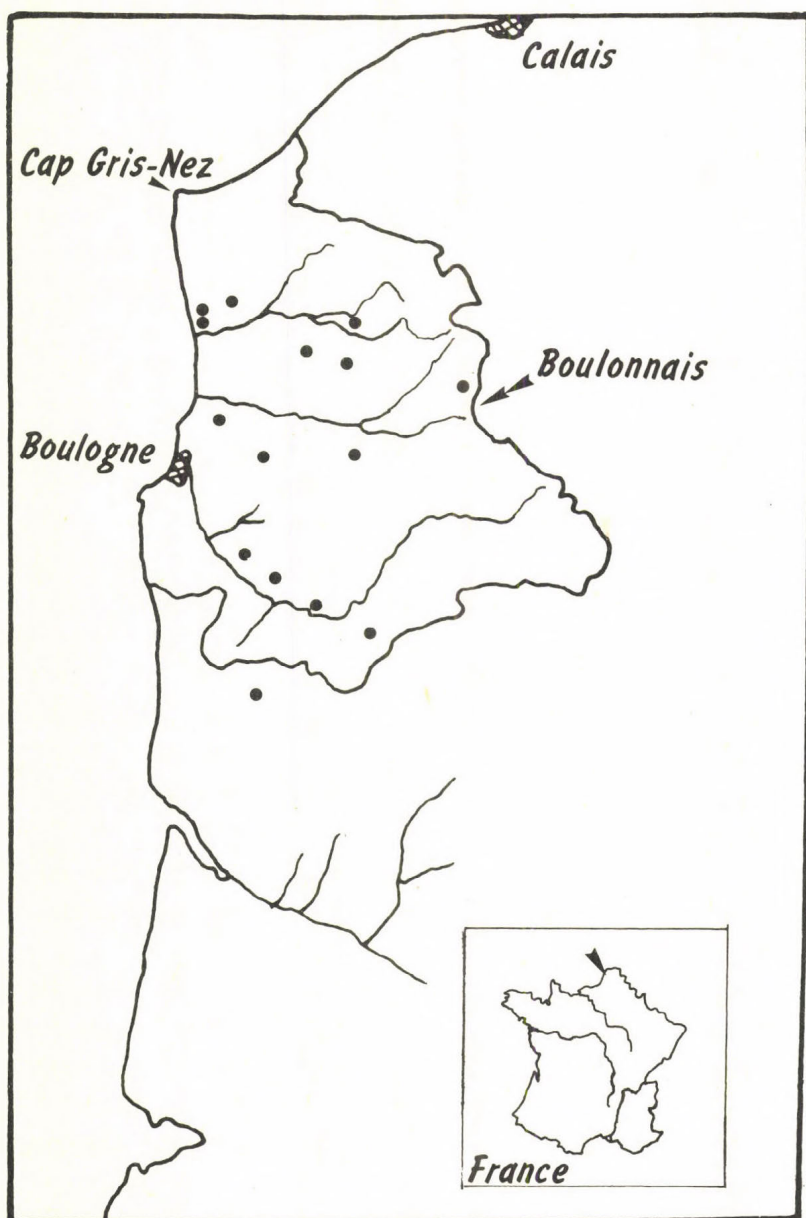
Fig. 1. Study area; the Boulonnais (Department Pas-de-Calais, NW France). The sample sites are indicated by a point.

as most common bryophyte community the <u>Tortuletum</u> <u>laevipilae</u>
(Allorge 1922) Duvign. 1941. <u>Leptodon</u> <u>smithii</u>, an element of
the mediterranean <u>Fabronietum</u> <u>pusillae</u> Ochsner 1936, is often
found in this community. The other bryophyte communities show
some resemblance to the <u>Anomodonteto-Isothecietum</u> Lippmaa
1935 (<u>Leucodontetalia</u>, <u>Anomodontion</u> <u>europaeum</u>).

METHODS

At different sites 105 pieces of bark of definite size
(± 0.25 m high and ± 0.20 m wide) were randomly sampled from
dead elm trees. Samples were taken from the base up to 13 m
high, with inclinations varying between 80° and 94° (excep-
tionally 100°) and with various exposures.

Of these samples the floristic composition and the cover
degree of the species (using the decimal scale of Londo 1984)
were recorded. These quantitative data were analysed using
TWINSPAN (Two-Way INdicator SPecies ANalysis; Hill 1979,
Hermy 1984) which results in a two-way table, and DECORANA
(DEtrended CORrespondence ANAlysis; Hill & Gauch 1980, Hermy
1984) resulting in ordination diagrams for relevés and spe-
cies.

The two sampling methods that were compared for relative
frequencies and species associations can be described as fol-
lows:
- The relevé method takes into account the species composition
of every sample, the total frequency of every species and the
number of times the different species occur in the same samples.
χ^2 (with Yates correction), its significance level and φ
($\sqrt{\chi^2/N}$) were calculated for all possible combinations of
two species. Only the species occurring in at least 1% of the
samples were considered. In this way positive and negative as-
sociations between species can be computed.
- The plotless sample method was applied to the same samples.
Therefore, a 2-cm grid was spanned over the samples and at
every point of intersection a point sample was taken, in
which the species hit by the point and the species contacting
the first one nearest to the sample point were recorded, with

the restriction that the contact species should appear within a radius of 1 cm around the sample point. In this way we made 9341 point samples. χ^2, its significance level and φ were calculated for all possible combinations, leaving out all point samples with no species hit, all those without a contact species and all species occurring in less than 1% of the point samples.

RESULTS

A. *The relevé method*

The species associations found with the relevé method are given in Fig. 2. On the circle the species occurring in at least 1% of the relevés are given (56 species of the 66 occurring in total). There are more significantly positive associations (174, Fig. 2.a) than negative ones (73, Fig. 2.b). The sequence of the species obtained with TWINSPAN, as it was used in Fig. 2, is largely confirmed by the positive associations. The species can be divided into 3 groups. A first group starting with Opegrapha vulgata and ending with Parmelia acetabulum, a second from Xanthoria parietina to Physconia grisea and a third group from Rhynchostegium confertum to Opegrapha atra can be distinguished. Some species show intermediate positions and can be regarded as linking species between the groups. The species from Buellia punctata to Caloplaca cerina form a link between group 1 and 2; Zygodon viridisssimus, Leptodon smithii and Homalothecium sericeum form a link between group 2 and 3, while Hypnum cupressiforme can be regarded as link between 1 and 3.

Some species seem to be less favorably placed, e.g., Pylaisia polyantha is only positively associated with Homalothecium sericeum and should therefore be placed in its neighbourhood. Physcia tenella shows strong positive association with group 2 and none with group 1 and should be placed nearer to the species of group 2; the place of Physconia grisea is somewhat doubtful, too. There are some species (Lecanora conizaeoides, L. symmicta, Physcia clementei and Pyrenula laevigata)

which are not positively associated with any other species. They cannot be placed in any of the distinguished groups.

The similarity between the species associations found on the basis of frequency and cover estimates respectively is best positioned in the ordination diagram based on the latter data (Fig. 5.a). The lines connect species with significantly positive association. This results in 3 groups with some intermediate species: Buellia punctata, Hypnum cupressiforme, Opegrapha vulgata, Tortula laevipila and Zygodon viridissimus.

Fig. 2. Significant species associations found with the relevé method (——: p<0.005; ---: p<0.05). Species sequence based on TWINSPAN starting with Opeg vulg and ending with Pyre laev. Space is left open where TWINSPAN distinguishes groups of species. a) Positive associations, b) negative associations. Only species occurring in at least 1% of the samples are given. *Opeg vulg = Opegrapha vulgata; Hymn cupr = Hypnum cupressiforme s.l.; Dipl cane = Diploicia canescens; Rama fari = Ramlina farinacea; Parm glab = Parmelia glabratula; Parm borr = Parmelia borreri; Parm cape = Parmelia caperata; Lera chla = Lecanora chlarotera; Rama fast = Ramalina fastigiata; Lera coni = Lecanora conizaeoides; Parm sulc = Parmelia sulcata; Parm eleg = Parmelia elegantula; Rama duri = Ramalina duriaei; Phys aipo = Physcia aipolia; Parm acet = Parmelia acetabulum; Lera symm = Lecanora symmicta; Pyla poly = Pylaisia polyantha; Phys tene = Physcia tenella; Buel punct = Buellia punctata; Parm subr = Parmelia subrudecta; Pert al co = Pertusaria albescens var. corallina; Leci euph = Lecidella euphorea; Calo ceri = Caloplaca cerina; Xant pari = Xanthoria parietina; Leia cyrt = Lecania cyrtella; Phys adsc = Physcia adscendens; Gyal trun = Gyalecta truncigena; Phae orbi = Phaeophyscia orbicularis; Phys clem = Physcia clementei; Coll cong = Collema conglomeratum; Phis adgl = Physciopsis adglutinata; Coll furf = Collema furfuraceum; Orth pumi = Orthotrichum pumilum; Phyo pulv = Physconia pulverulacea; Anap cili = Anaptychia ciliaris; Orth lyel = Orthotrichum lyellii; Orth affi = Orthotrichum affine; Frul dila = Frullania dilatata; Tort papi = Tortula papillosa; Cand conc = Candelaria concolor; Orth diap = Orthotrichum diaphanum; Leuc sciu = Leucodon sciuroides; Tort laev = Tortula laevipila; Phyo gris = Physconia grisea; Zygo viri = Zygodon viridissimus; Lept smit = Leptodon smithii; Homa seri = Homalothecium sericeum; Rhyn conf = Rhynchostegium confertum; Neck comp = Neckera complanata; Tham alop = Thamnobryum alopecurum; Homa tric = Homalia trichomanoides; Hede heli = Hedera helix; Metz furc = Metzgeria furcata; Lepr inca = Lepraria incana; Opeg atra = Opegrapha atra; Pyre laev = Pyrenula laevigata.*

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a

b
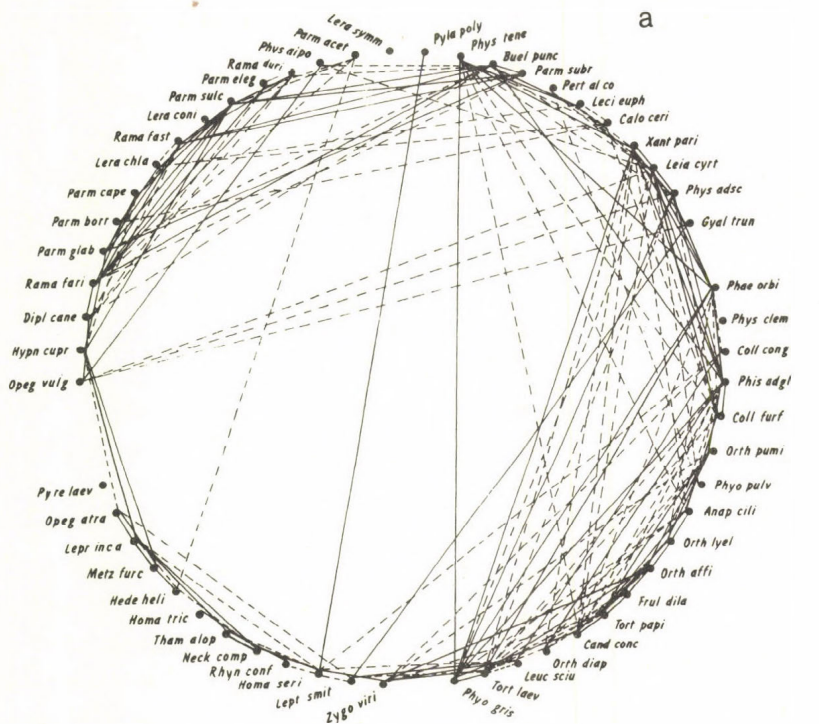
The first group is situated on the left side of the diagram, the second in the middle and the third on the right side. The species of group 3 are more scattered because in most of the cases one of them is dominant over the others.

The number of linking species indicated on Fig. 2.a are diminished to the 5 last mentioned species. Parmelia subrudecta now clearly belongs to the first group, Physcia tenella, Pertusaria albescens var. corallina, Lecidella euphorea and Caloplaca cerina belong to the second and Homalothecium sericeum and Leptodon smithii belong to the third group.

The question is whether estimating the cover degree of the species, which is very time-consuming, gives much more information than just the floristic composition of the samples. Therefore, we ordinated the presence/absence data with DECORANA (Fig. 6) and compared the result with Fig. 5.a. The correlation between the first four axes of the two ordinations was calculated. At first sight there seems to be little similarity between the two ordination diagrams, but when we indicate the positive associations (based on the χ^2 criterion) and when we outline the groups as distinguished before (see Fig. 5.a), we see that practically the same groups can be distinguished in Fig. 6. Their general positions, however, are different.

Nevertheless, there are some dissimilarities, e.g., the linking species are far less obvious (Hypnum cupressiforme as well as Buellia punctata now clearly belong to group 1, Opegrapha vulgata and Tortula laevipila are included in group 2, while on the other hand Diploicia canescens and Caloplaca cerina appear as links between the first and the second group. Another difference is that group 1 and 3 are placed much closer to one another.

If we look at the correlation between the different axes (Table 1) we can conclude that:
- The first four axes of one ordination are never significantly correlated.
- The first axis based on cover estimates (A1) is significantly correlated (p 0.005) with the first (B1) and particularly with the second axis (B2) based on presence/absence data.

<u>Table 1.</u> Product moment correlation between the first four
axes of a DCA ordination based on cover estimates (axes A1 -
A4) and a DCA ordination based on presence/absence data (axes
B1 - B4). Significant (p< 0.005) correlations in italics.

A1	1							
A2	-0.001	1						
A3	-0.016	-0.103	1					
A4	0.001	-0.147	0.087	1				
B1	*-0.414*	-0.194	0.206	0.153	1			
B2	*-0.744*	*0.382*	0.089	-0.280	0.084	1		
B3	-0.126	*0.477*	*-0.471*	0.269	0.034	0.194	1	
B4	-0.202	-0.263	-0.065	0.154	-0.035	-0.188	0.072	1
	A1	A2	A3	A4	B1	B2	B3	B4

It seems that the variation expressed on A1 is distributed
over B1 and B2. In this respect it is important to notice
that in the first ordination most of the variation is ex-
pressed by A1 while it is practically equally spread over
B1 and B2 in the second ordination.
- The second axis (A2) is significantly correlated with B2
  and B3, while A3 is only significantly correlated with B3.
- A4 nor B4 shows any significant correlation on the 0.005
  level.

The most obvious negative associations (Fig. 2.b) appear
between most of the more abundant lichens of group 2 (e.g.,
<u>Xanthoria</u> <u>parietina</u>, <u>Physcia</u> <u>tenella</u>, <u>P.</u> <u>adscendens</u> and <u>Leca-</u>
<u>nia</u> <u>cyrtella</u>) and on the other hand the species of group 3
most of which are mosses. <u>Tortula</u> <u>laevipila</u> is negatively as-
sociated with the species of group 1, while these show some
negative association with most of the lichens of group 2. The
less frequent species show hardly any negative associations,
while it is rather surprising that there are only a few nega-
tive associations between species of group 1 and 3 although
they are spaced much more in the results of TWINSPAN and

DECORANA.

B. *The plotless sample method*

9341 point samples were taken of which no less than 3197
(34.3%) were "no contact" samples, i.e., no species was hit by
the sample point; a strong correlation exists with the mean
non-coverage (38.7%) of the sample plots.   Other 1132 point
samples had a species hit by the point but no species in con-
tact with it.

So 5012 point sample remain that can be used to calculate
species associations (Fig. 4). Only 32 of the 66 species occur-
ring in total are considered because only these appeared either
as hit species or as contact species in more than 1% of the
samples.

There are 74 significantly positive (Fig. 3.a) and 107
negative associations (Fig. 3.b). The sequence of the species
based on TWINSPAN can hardly be confirmed because of the small
number of species. We can, however, distinguish two groups of
species. Group 1 contains practically all lichens (including
Physconia grisea but with the exception of Lepraria incana and
Candelaria concolor) and Frullania dilatata, while the second
group contains practically all mosses. Hypnum cupressiforme
and Tortula laevipila can be considered as linking species.
The distinction of two groups confirmed in Fig. 5.b, in which
the positive associations are drawn in the DECORANA ordination
diagram based on cover estimates. The intermediate position of
Hypnum cupressiforme and Tortula laevipila is clearly shown.

Fig. 3.b indicates that most lichens are negatively asso-
ciated with the majority of the mosses and vice versa. Dominat-
ing mosses like Homalothecium sericeum, Leptodon smithii, Leu-
codon sciuroides and even Tortula laevipila show many negative
associations, even with some other often less prominent moss
species.

So far we considered that chance of a species to be hit by
the sample point equal to the chance of the same species   to
appear as contact species and Fig. 3 is based on a "folded
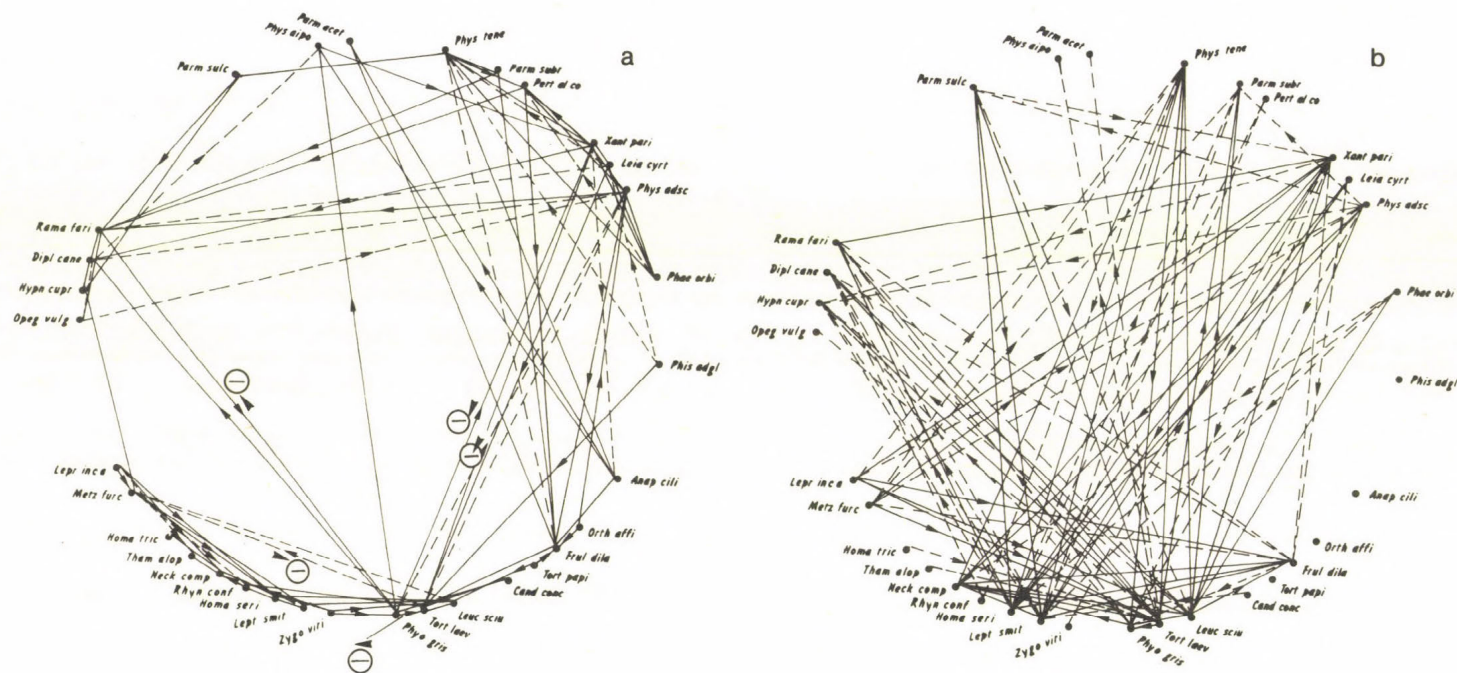matrix" in which the frequency of a species acting as hit species

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Fig. 3. Significant species associations found with the plotless sample method on the basis of a folded data matrix (——: p < 0.005; ---: p < 0.05); species sequence and names as in Fig. 2. a) positive associations, b) negative associations. Only the species occurring in at least 1% of the sample points are given.

Fig. 4. Significant species associations found with the plotless sample method on the basis of an unfolded data matrix (——: p < 0.005; ---: p < 0.05); ➤: unidirectional association; species sequence and names as in Fig. 2. a) positive associations (➤⊖ : negative associa- tion in the opposite direction); b) negative associations. Only the species occurring in at least 1% of the samples are given.
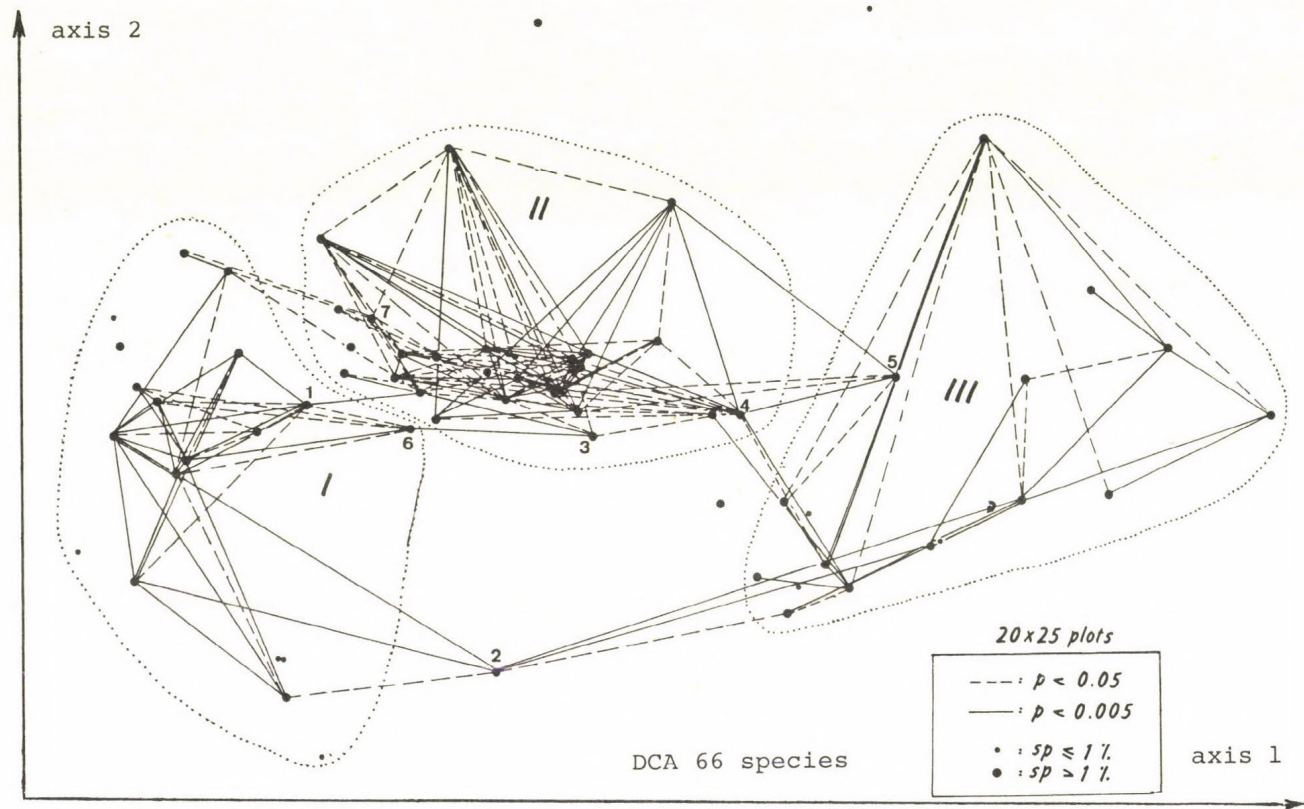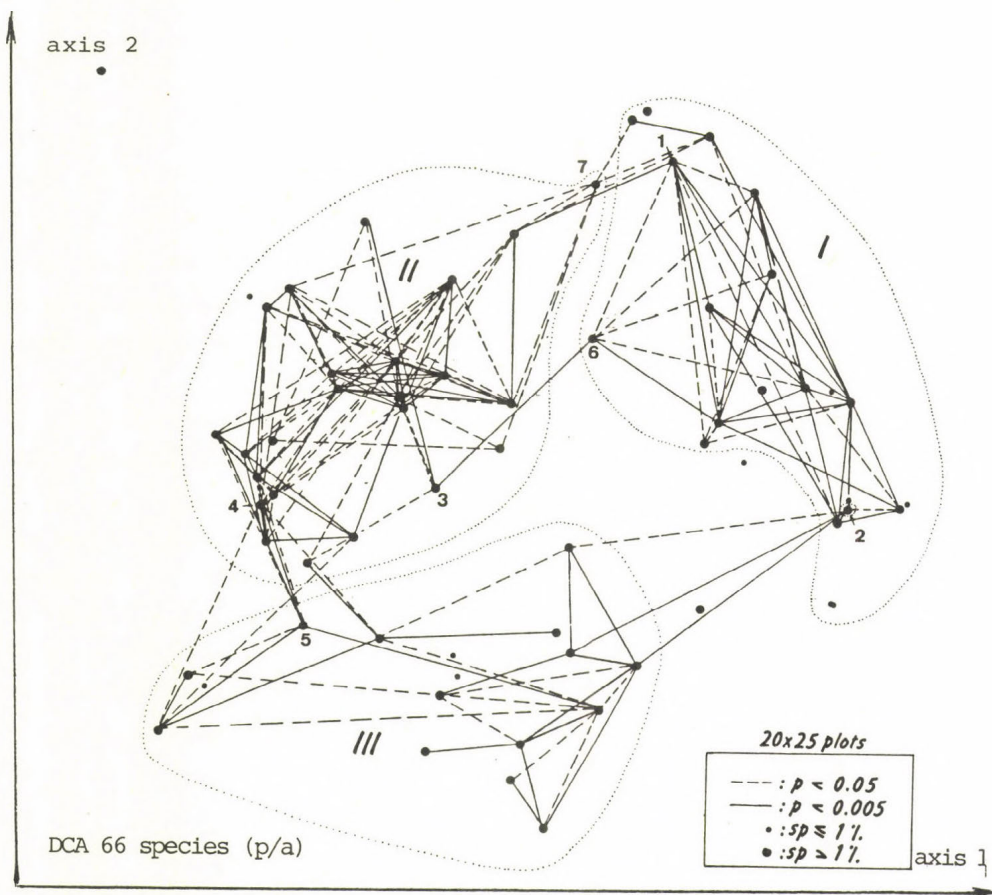
Fig. 5.a. Ordination diagram based on DECORANA (cover estimate data) with lines indicating significantly positive associations found with the relevé method. 1 = <u>Buellia</u> <u>punctata</u>, 2 = <u>Hypnum</u> <u>cupressiforme</u>, 3 = <u>Opegrapha</u> <u>vulgata</u>, 4 = <u>Tortula</u> <u>laevipila</u>, 5 = <u>Zygodon</u> <u>viridissimus</u>, 6 = <u>Diploicia</u> <u>canescens</u>, 7 = <u>Caloplaca</u> <u>cerina</u>. I,II,III = group 1, 2 and 3 (see text).
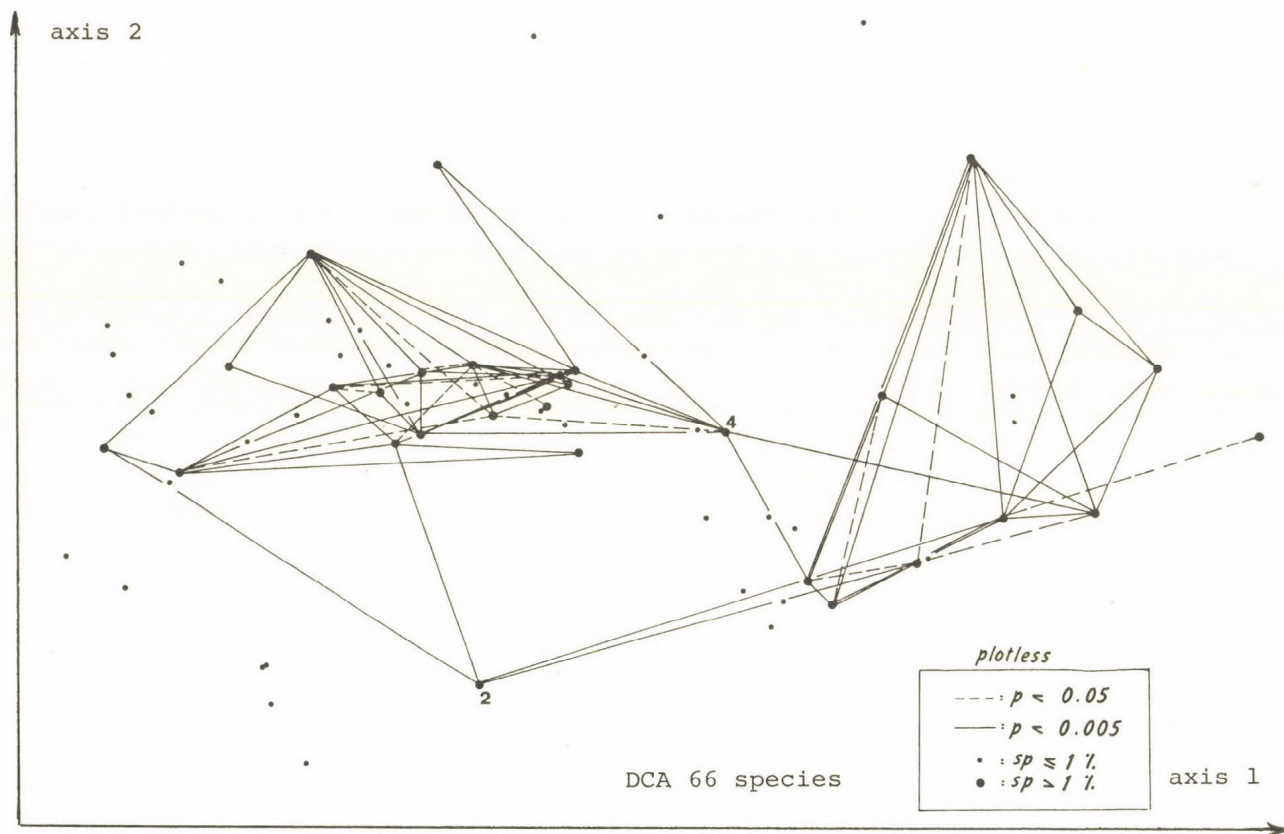
Fig. 5.b. Ordination diagram based on DECORANA (cover estimate data) with lines indicating significantly positive associations found with the plotless sample method (folded matrix) based on χ^2 criterion. See Fig. 5.a for explanation of numbers.

is added to the frequency of the same species acting as contact species.

However, it is known (De Jong et al. 1983) to be preferable to tabulate and analyse the data with an unfolded matrix where the combination (i,j) is distinguished from (j,i). With the unfolded matrix we find 111 significantly positive and 119 negative associations (Fig. 4), of which, however, no less than

Fig. 6. Ordination diagram based on DECORANA (presence/absence data) with lines indicating significantly positive associations found with the relevé method (χ^2 criterion). See Fig. 5.a for explanation of numbers.

Table 2. Frequency of species associations based on the plotless sample method found with a folded (F) and an unfolded (UF) data matrix.

F \ UF	+ twodir.	+ unidir.	O	- unidir.	- twodir.	+-
+	33	29	10	-	1	3
O	1	14		2	2	1
-	-	-	33	37	37	1

43 (39%) and 39 (33%) respectively are only unidirectional, i.e., for (i,j) a significant association is found but not so for (j,i). So there are only 34 (i.e., 34 x (i,j) + 34 x (j,i)) positive and 40 negative two-directional significant associations. There are even 5 cases in which (i,j) shows significantly positive association while (j,i) shows significantly negative association.

A comparison of the frequencies of species associations found on the basis of a folded and an unfolded matrix is given in Table 2.

Generally, the results are quite similar although there are several cases in which the associations found with the folded matrix only give unidirectional associations with the unfolded matrix. Particularly, the large number of cases with non-significant association in the unfolded matrix and significantly negative association in the folded matrix is remarkable. There is even a case where associations are opposite.

Comparison

The relative frequencies of the species found with both methods are significantly correlated (r = 0.72, p < 0.0001). Nevertheless, they are systematically lower in the plotless sample method through which far fewer species can be considered.

Taking the number of species into account, we can compare the number of significant associations found with both methods

Table 3. Possible associations and significant associations found (percentage of the possible associations in parentheses).

	Relevé method (56 species)	Plotless sample method (32 species)	
		folded $(i,j=j,i)$	unfolded $(i,j\neq j,i)$
Possible associations	1540 (100%)	496 (100%)	992 (100%)
Significant associations	247 (16%)	184 (37%)	240 (24%)
Positive	174 (11%)	76 (15%)	116 (12%)
Negative	73 (5%)	108 (22%)	124 (12%)
Non-significant associations	1293 (84%)	312 (63%)	752 (76%)

and relate them to the total number of possible associations (Table 3).

The absolute numbers show a larger number of associations with the relevé method. This is, however, entirely due to the fact that the species with a low cover degree are rarely hit by the sample point, while in spite of their low cover degree they are still recorded in the relevé method. Particularly acrocarpous, erect mosses (e.g., Orthotrichum spp. and Tortula papillosa), crustaceous (e.g., Lecanora spp., Buellia punctata and Lecidella euphorea) and foliaceous lichens (e.g., Collema spp.) with scattered distribution and relatively small size are rarely found in the point samples. However, proportionally the plotless sample method yields more significant associations (positive as well as negative) than the relevé method.

When we compare the frequencies of the significant associations (see Table 4) we find that the direction is largely the same. Nevertheless, in a large number of cases significant associations are found with the one and non-significant associations with the other method and, in one case, the

PS \ R	+	O	−	
+	38	37	1	x first figure : non significant asso-ciation in the PS method between spe-cies that occurred in at least 1% of the point samples.
O	29/106 x		15/22 x	Second figure : non significant asso-ciation in the PS method between spe-cies of which at least one appeared in less than 1% of the point samples.
−	−	72	36	

associations found are opposite.

Fig. 7 shows the relations between φ ($\sqrt{x^2/N}$), found with both methods. Only the combinations with at least significant species association in one of the methods are indicated. φ was given a negative sign if the association was negative. The figure shows that there are no less than 30 cases in which the associations are opposite (although 29 of them are non-significant in either the relevé method or the plotless sample method). Nevertheless, there is a strong correlation ($r = 0.63$, $p < 0.001$) for φ found with both methods.

Important to note is that φ must be at about ten times higher in the relevé method than in the plotless sample method to have significant association because of φ's dependence on $\sqrt{1/N}$.

To conclude, we can summarize the following resemblances and differences between the results of both methods:
- Relative frequencies are strongly correlated although sys-tematically lower in the plotless sample method.
- Because of this far fewer species can be considered in the plotless sample method; therefore, less abundant species (also those that are relatively rare even under optimal conditions, e.g., Orthotrichum spp.) cannot be considered
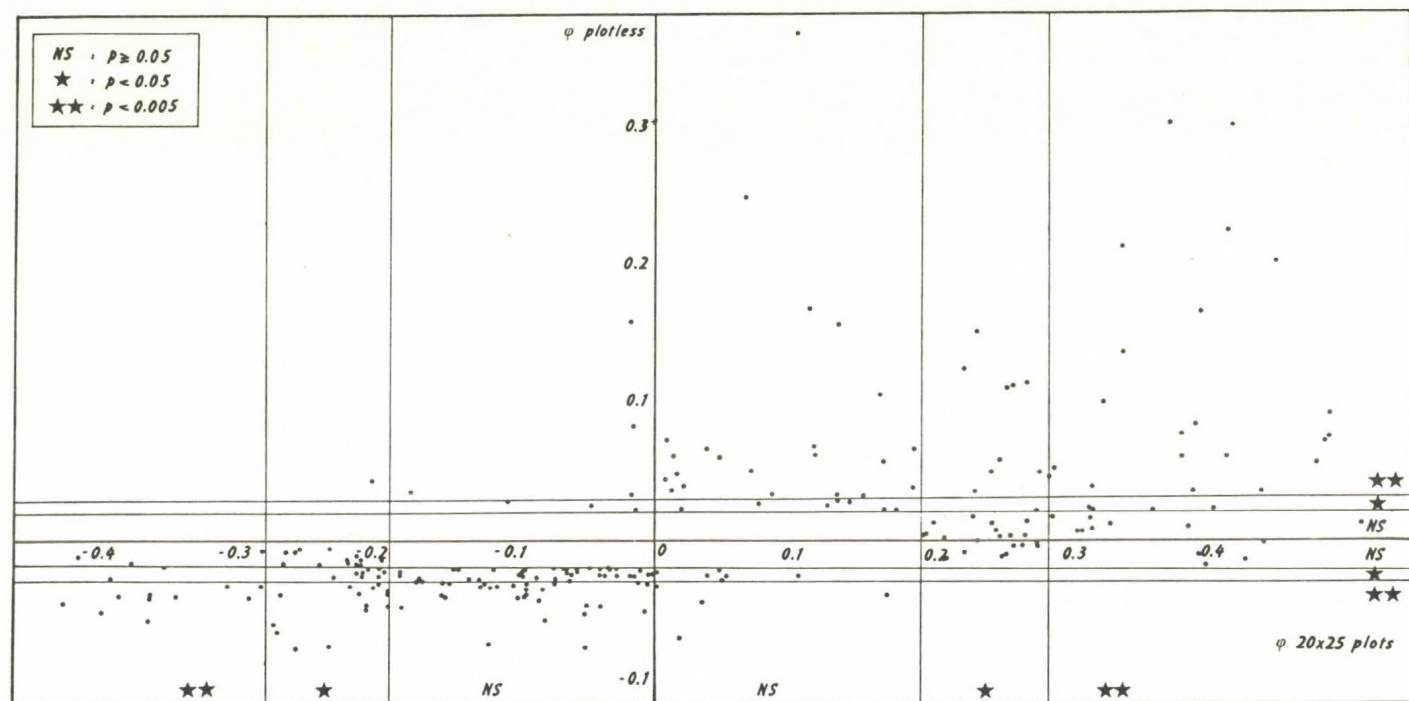
Fig. 7. Relation between φ found in the relevé method and the plotless sample method (folded matrix). Only the cases with the species occurring in at least 1% of the point samples are given. The significance level with N = 105 and N = 5012 (x2) respectively and 1 degree of freedom are indicated.

with the plotless sample method. One may not conclude that these species are not associated with other species, nor that they have no ecological affinities with other species. However, these cannot be detected with the plotless sample method. On the other hand, the releve method gives more satisfaction in this respect, but it is difficult to find a criterion for objective plot size delimitation and homogeneity within a sample plot of any size can hardly be ascertained.

- The correlation coefficients (φ) found with both approaches are strongly correlated.
- The time needed for the relevé method (105 samples) is practically equal to that needed for 9341 systematic point samples. However, when cover estimates have to be made the relevé method takes at least twice as much time.

The results above indicate that not much information is gained by estimating the cover of the species when one is concerned with species grouping (species association) in epiphytic vegetation. Nothing can be said, however, about competitive relations between species when cover estimates are not available. In this respect, the plotless sample method could be used when one takes the sample points with a hit species and no contact species into consideration.

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