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Conservation Biology of Lichenised Fungi

Christoph Scheidegger
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Abstract:

Conservation Biology of Lichenised Fungi
The volume includes papers covering different aspects of conservation activities of mainly lichen-forming fungi. Replies to a questionnaire sent to lichenologists provide an overview of various threats to lichen-rich habitats in the world and confirm the need for a broad range of conservation programs. Papers on Red Lists from different parts of the world, their preparation and use, as well as practical approaches to survey and management for lichen diversity are presented. Other studies focus on factors influencing the diversity of lichens in old-growth forests, the distribution of rare species and the maintenance of populations by non-destructive in situ propagation. One paper summarises the distribution of non-lichenised fungal diversity and factors affecting it.

Keywords: Biodiversity, Conservation Biology, Lichenised Fungi, Red List, Restoration Biology

Artenschutz lichenisierter Pilze (Flechten)
Das vorliegende Heft umfasst Originalarbeiten zu unterschiedlichen Aspekten des Artenschutzes flechtenbildender Pilze. Eine unter Lichenologen durchgeführte Umfrage zeigt Bedrohungen flechtenreicher Habitate auf und bekräftigt die Notwendigkeit von Artenschutzprogrammen. Mehrere Arbeiten diskutieren «Rote Listen» aus verschiedenen Gebieten der Erde und beschreiben Ansätze zur Erhaltung einer hohen Flechtenvielfalt. Andere beschreiben Faktoren, welche die Flechtenvielfalt in Primärwäldern beeinflussen, untersuchen die Verbreitung seltener Arten oder beschreiben Methoden zur Erhaltung kleiner Populationen durch zerstörungsfreie in situ Vermehrung. Eine Arbeit fasst die Verbreitung der Vielfalt nicht-lichenisierter Pilze zusammen.

Keywords: Biodiversität, Artenschutz, Lichenisierte Pilze, Rote Liste, Restoration

Contents

Preface

Lichenised fungi are mutualistic symbioses between a fungus, often an ascomycete, and a phototrophic micro-organism such as a green alga or a cyanobacterium. The photobiont is encapsulated by the mycobiont and the morphology of the lichen thallus is mainly formed by the mycobiont. Growth forms of lichenized fungi include crustose, foliose and fruticose taxa and the vegetative organs formed by lichens are amongst the most complex structures found in fungi.

Lichenised fungi are widespread in natural and man-made environments, and are often the dominant organisms in extreme environments. Different growth rates, from considerably less than one millimeter to more than one centimeter per year, and various strategies of colonising available substrates, allow their use in chronicling environmental changes over short and long periods of time. Their sensitivity to atmospheric conditions has long been recognized, and the loss of species in industrialised regions of Europe and America, due to atmospheric pollutants, has continued throughout the 19th and 20th centuries. Past changes in agricultural and forestry management have led to further losses, especially of taxa with a narrow ecological range and complex reproductive strategies. The use of epiphytic lichens as indicators of ecological continuity has been developed in oceanic woodlands of Europe and the western seaboards of the USA and Canada. At a time when the use of lichens as indicators of environmental change is being extended to the Antarctic and the tropics, our knowledge of the rates of loss of lichen species and habitats in parts of the world outside Europe is also increasing.

During the second IAL symposium in Båstad (Sweden) in 1992, a Committee for the Conservation of Lichens (ICCL) of the International Association for Lichenology (IAL) was set up. An important part of this committee's work has been to prepare an action plan and questionnaire in order to establish contact with lichenologists and interested parties in as many countries as possible. The response to the questionnaire has amply demonstrated the need for a conservation programme that will accommodate and target species and habitats that are threatened. Since its formation, the committee has expanded to 10 members, they are as follows; Eva Barreno (Spain), Jacob Garty (Israel), Hiroyuki Kashiwadani (Japan), Christoph Scheidegger (Switzerland), Clifford Smith (USA, Hawaii), Nell Stevens (Australia), Göran Thor (Sweden; chairman), Dirk Wessels (South Africa), Clifford Wetmore (USA, Minnesota) and Pat Wolseley (Great Britain, secretary).

The symposium "Lichens – a strategy for Conservation"convened by G. Thor and Pat Wolseley at the Fifth International Mycological Congress in Vancouver 1994 was a direct outcome of this committee's work. From the outset it was planned to present the results of the questionnaire (Wolseley), and to include papers on Red Lists from different parts of the world, their preparation and use (Thor and Kashiwadani), as well as practical approaches to survey and management for lichen diversity (Rosentreter), ongoing research on the distribution of rare species (Goward) and the maintenance of populations by non-destructive in situ propagation (Scheidegger).

However, other contributors to the Congress produced evidence to show the urgent need for conservation of fungal and lichen biodiversity, and of developing appropriate techniques to describe it, in the face of rapidly increasing threats from present agricultural and silvicultural practices and an ever-expanding human population. With the involvement of Christoph Scheidegger and Ruth Landolt, this has led to an expanded volume of conservation papers from the Congress, with important additions concerning the distribution of fungal diversity and factors affecting it (Lodge), and of the relation of diversity of foliicolous lichens to environmental factors in a lowland Costa Rican rain forest (Lücking). Although much of the current debate on loss of biodiversity is centred on the tropics, these papers emphasise some of the things that we do not know, and help us to target areas of future research. The sparse distribution of lichenologists in tropical areas shown on the map of contributors to the questionnaire (Wolseley), further demonstrates that knowledge is still largely based on work in Europe, Japan, Australia, Antarctica and North America. Contributions from respondents to the questionnaire are included (Tschabanenko, Kondratyuk and Navrotskaya), and two papers about factors influencing the diversity of lichens in old growth forests in Finland (Kuusinen) and an experimental approach to growth and fragmentation of alectorioid lichens (Renhorn and Esseen) show that there is still much to be learned in Europe. All this must be seen against a background of increasing interest in conservation biology and political commitment to sustainable management, so that we have a responsibility to provide the information. We hope that this volume will stimulate lichenologists to further research, conservation activity and cooperation at a local and international level.

We would like to thank everyone who helped in the preparation of this volume, the referees, P.W. James and Teuvo Ahti for linguistic editing of the manuscripts, and especially the managing editor Dr. Ruth Landolt for the skilful editing of the volume. We acknowledge financial support from the Swedish University of Agricultural Sciences; the Natural History Museum, London and the Royal Society; and the Swiss Federal Institute of Forest, Snow and Landscape Research.

Göran Thor
Patricia Anne Wolseley
Christoph Scheidegger

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A Global Perspective on the Status of Lichens and their Conservation

Patricia Anne Wolseley
Botany Dept., The Natural History Museum, Cromwell Rd, London SW7 5BD, UK

Abstract

Information from replies to a worldwide questionnaire is used to identify and locate current lichen information, including areas where at present there is little information or interest in lichens. The distribution of lichen-rich environments across the globe, their conservation status in regional, national and international terms and the threats identified by respondents in a range of climatic, environmental and human population conditions are discussed. Lichenological evidence for environmental change at global and regional levels is illustrated by current literature and research projects identified by respondents. These will also be used to illustrate the importance of lichens as monitors of changing conditions in a wide range of ecosystems.

Keywords: lichens, conservation, protected areas, biodiversity

1 Introduction

The formation of the International Committee for the Conservation of Lichens (ICCL) in Båstad (Sweden) in 1992, highlighted our lack of information on lichen conservation even within the countries represented in the membership of the International Association for Lichenology (IAL). As a preliminary means of identifying current practices and problems, a questionnaire was devised (Appendix I) and distributed to IAL members in 57 countries in December 1993. The questionnaire was devised to be equally applicable for site or regional information and to identify threats on a specific or general level.

2 Results

77 replies from 33 countries were received (Appendix II) containing information on 267 sites (Fig. 1). This paper is based on replies, literature and projects that we have received, from which examples have been chosen in as many fields as possible.

The data are at present on a relational database (Paradox 4.1) at the Natural History Museum, in files on: site and country data, contributor, research projects and bibliography. The last is hardly started yet, but the rest are completed for all answers contributed. Maps of sites and threats have been kindly contributed by World Conservation Monitoring Centre (WCMC) in Cambridge, using the same format as their International Union for the Conservation of Nature (IUCN) publications.

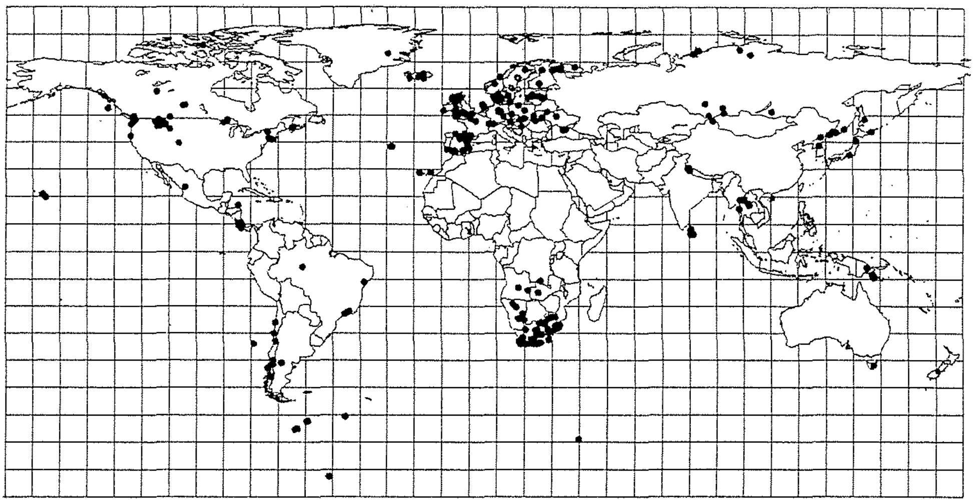

Fig. 1. Distribution of lichen sites or regions • included in replies to the questionnaire.

2.1 Distribution of replies

The distribution of sites or regions identified by respondents as being of conservation interest for lichens (Fig 1.) indicates that there are large areas where no information has been contributed. This is due to several factors:

1) absence of IAL members in e.g. African and Asian countries
2) existence of independent conservation networks which makes abstraction of information at the level of the questionnaire difficult e.g. Australia
3) absence or restriction of information on lichens or conservation e.g. Asian countries, African and many South American countries.

The majority of lichen sites identified are in temperate and boreal zones, and few are in the wet and seasonally dry tropics, where there are extensive areas of forest forming a major component of the planet's vegetation (see BAILEY 1989). Is this because lichens are the dominant life-form in extreme environments where they are a conspicuous component of the vegetation or are these biomes undescribed lichenologically? Biodiversity is frequently assessed in numbers of taxa identified. Figures in Global Biodiversity (GALLOWAY in GROOMBRIDGE 1992) suggest that lichen diversity is lowest in tropical countries, but recent assessments of the lichen flora of Papua New Guinea indicate that the low number may be due to inadequate sampling of tropical regions. In 1956 the lichen flora of Papua New Guinea was less than 250 (SZATALA 1956), in 1986, 145 genera and 500 taxa were known (STREIMANN 1986), and by 1992 the species number has been doubled again (APTROOT and SIPMAN, manuscript). Many of these additions are undescribed species. In the seasonally dry tropics in Thailand 226 taxa have been found in published records

(Aguirre-Hudson and Wolseley: A checklist of lichenised fungi recorded from Thailand. In prep.), and this has now been increased to c. 400 corticolous taxa found in limited areas of the north of Thailand. New records include conspicuous macrolichen genera of *Cetrelia, Menegazzia, Platismatia, Pseudocyphellaria* as well as many crustose genera (WOLSELEY and AGUIRRE-HUDSON 1995a, 1995b, in press). Many more are crusts which may remain undescribed and unidentified for many years to come. Distinguishing areas of high diversity, and protecting these areas is a priority, especially in remote regions where species distribution is not known or new species may yet to be described.

2.2 Selection of sites

The inclusion of sites or regions in the answers to the questionnaire was based on lichen interest, and not on the existence of national or international recognition of Protected Areas. Although many of the sites coincide with existing Protected Areas in practice this is largely coincidental as criteria for selection of these may not coincide with lichen interests. There is also a confusing number of different names describing protected areas in different countries. The International Union for the Conservation of Nature (IUCN) proposed a system of ten categories classified according to site interest and objectives for management (IUCN 1994b), and ranging from strict nature reserves where access was restricted, national parks, to sustainably managed resource areas. The present list of sites of International importance or Protected Areas (IUCN 1994a) is based on a combination of the United Nations list of National Parks and Reserves, Ramsar sites and World Heritage Sites (where countries are signatories to the conventions), and the Biosphere Reserves which were selected to represent global biotopes and species diversity as part of the international scientific Man and the Biosphere programme. Criteria for inclusion in this list state that areas should be >1000 ha, that management objectives are clearly defined and that the authority for management is at government level. Lichen-rich sites may or may not be defined by respondents within the larger area of an international Protected Area, but respondents sometimes targetted smaller lichen-rich sites within the larger reserve as in Nanda Devi Biosphere reserve (Upreti, India). Smaller high-priority lichen sites, where relict or rare species may be restricted to small areas or atypical vegetation, may be excluded from protected status (KUUSINEN 1995, same vol.; COPPINS and O'DARE 1992). Within the European Community the Corine programme (Commission of the European Community 1991) is compiling an inventory of all sites of conservation interest in member countries, irrespective of their size, conservation status or legislation. However this does not ensure that specialist groups get included in site-evaluation, especially where lichen-rich sites fall within a non prioritised vegetation type as in the atlantic facies of *Quercus petraea* woodlands. There is a vast difference when it comes to site evaluation in tropical areas where information is only available on a few groups (frequently faunal) (MACKINNON *et al.* 1986). In Tasmania the existence of World Heritage Areas has encouraged the making of inventories, and this has been achieved for a limited number of sites within existing World Heritage Areas (Kantvilas, Tasmania).

If existing protected areas are the basis for investigation, what proportion of the lichen flora is included within the protected areas? In the Ukraine, KONDRATYUK and NAVROTSKAYA (1995, this vol.) have looked at proportions of lichens in protected areas and shown that it is highest in the Steppe zone of the plains and in the mountainous regions of the Carpathians and lowest in the Forest-Steppe zone on the plains. Their information is drawn from published (3 lists) and unpublished lists (3 for national parks and 7 for reserves) for what is still only a small proportion of the protected areas. The mountainous regions also support 29 Red Data Book species as compared to 10 on the plains of the Ukraine. Chile is rich in National parks and protected areas, many of which are in remote little populated areas only reached with difficulty. The 66 National Parks and protected areas occupy 13,725,125 ha (IUCN 1994a), and of these Galloway distinguishes 8 as having an exceptionally rich lichen flora. These include areas of great remoteness with rich lichen floras such as the glacial wilderness of Laguna San Rafael (GALLOWAY 1992), and a further site at Chuschenco in Valdivia that has been known for the richness of its lichen communities since the early 1940's but which is not included in the IUCN list. This is a type locality for many lichens and without protection is threatened by increasing logging (Galloway, New Zealand).

2.3 Lichen-rich habitats falling outside usual conservation categories

It has long been recognised that ancient forests of temperate and boreal regions have a particular structure and associated lichen flora that includes genera that may be rare but widespread in these conditions such as species of *Lobaria, Pannaria, Nephroma, Sticta, Lecanactis, Schismatomma* and *Calicium* (ROSE 1976, 1988, 1992; CIESLINSKI *et al.* 1992).

These forests were formerly associated with much higher populations of herbivores that maintained open and gladed situations within the forest structure where lichen diversity was high. Such communities are now largely restricted to ancient man-made parks and hunting reserves where conditions have not changed over long periods of time (HARDING and ROSE 1986), or to areas where the traditional management of forest as wood-pasture has continued (e.g. parklands and Royal forests in Britain, dehesas in Spain). This has allowed the survival of epiphytic species long after their natural open forest habitat has disappeared. However because these sites were to some extent managed and not 'natural' they are frequently left out of conservation lists, and in Britain have only recently been accepted as candidates for Sites of Special Scientific Importance (HARDING and ROSE 1986). Species associated with scattered ancient trees regularly appear in lists of disappearing or endangered species across the world. A similar situation is found in India, Madagascar and many Asian countries, including Japan (KASHIWADANI and KUROKAWA 1995, this vol.), where religious taboos have allowed the survival of undisturbed and relict forest in sacred groves. There are many countries where a change in ancient agricultural practices, such as removal of grazing may endanger terricolous lichen species that are characteristic of an open community (e.g. Spain; Tasmania, BROWN *et al.* [1994]; Britain).

Man-made sites may also provide sites for rare or restricted lichen species, such as mining spoil heaps, which may be the habitat for rare metal-tolerant lichens (PURVIS 1985, 1993; WIRTH 1972; THOR 1993; Huneck, Germany), or undisturbed ancient edifices such as churches and tombstones which in Britain support c. 300 species or 18% of the British lichen flora (Chester, pers comm.), and this applies to many other areas of Europe especially in such areas where prehistoric man has left large monuments as at Carnac in

Brittany or Stonehenge in Britain. We do not know how many of our lichen species are associated with human settlements or long-established management patterns, but this pattern may also be found in the tropics. In a Karen-managed forest in Doi Inthanon National Park, Thailand (IUCN category II) at c. 900 m altitude management ensured the retention of the largest trees as seed stock, and continuity of moist environmental conditions within the forest to allow regeneration. Lichens were abundant on slender saplings and on old trees and included several rare species of macro-lichen new to Thailand (WOLSELEY and AGUIRRE-HUDSON 1995a, 1995b, in press).

3 Threats

Although threats identified by respondents varied with country and habitat, most of the threats are directly or indirectly associated with the rapid increase in human population and its requirements. HOLDGATE (1994) points out that the world population was 5.3 billion in 1990 and is expected to be 10–12 billion within the next century, with growth focused on South and East Asia and Africa. This is reflected in the replies, e.g. 23% of the protected sites in South Africa are threatened by urbanisation (Fig. 5, Wessels, South Africa). Increase in industrialisation in Asia has resulted in potential rapid increase in air pollution about which we have as yet little environmental evidence. The threat from agricultural production has increased with the expansion of cash aid to projects in marginal land areas. This has recently happened in Spain since joining the EC, as CAP agricultural policy encourages grant-aided reclamation and conversion of formerly marginal land. This now includes drainage of lowland heaths and intensive afforestation programmes.

3.1 Air pollution

Industrialisation has followed the increase in population, and air pollution has become an increasing threat, so that 24% of respondents identified it as a threat to lichen communities. Although this is still concentrated in Europe and America, the pattern is changing with increasing pressure on the third world countries to industrialise, as shown by the prediction of future problem areas (RODHE and HERRERA 1988) (Fig. 2).

The use of lichens as indicators of atmospheric pollution associated with production of oxides of sulphur and wet deposition of the acids has been widely developed in Europe and the American continent where industrialisation has been occuring over the last 150 years (e.g. FARKAS *et al.* 1985, in Hungary; FARMER *et al.* 1992). This questionnaire has highlighted the continuing affect of atmospheric pollution in areas of the globe where information is now becoming available. The literature in Poland is extensive, and charts the loss of sensitive species from reserves that are affected by long range air pollution. Bialowietsca biosphere reserve (47.5 km^2) is situated within an extensive area of forest reserve (1250 km^2) and has been protected by law since 1921 and is the largest strict forest reserve in Europe. A comparison of selected species shows the extinction of sensitive species between 1953/5 and 1982/9. 75% of the genus *Bryoria* are extinct within the park and 60% of *Usnea* species (CIESLINSKI *et al.* 1992). The decline in health of *Lobaria pulmonaria* is observed, and can typically be illustrated by material in Britain in the Lake

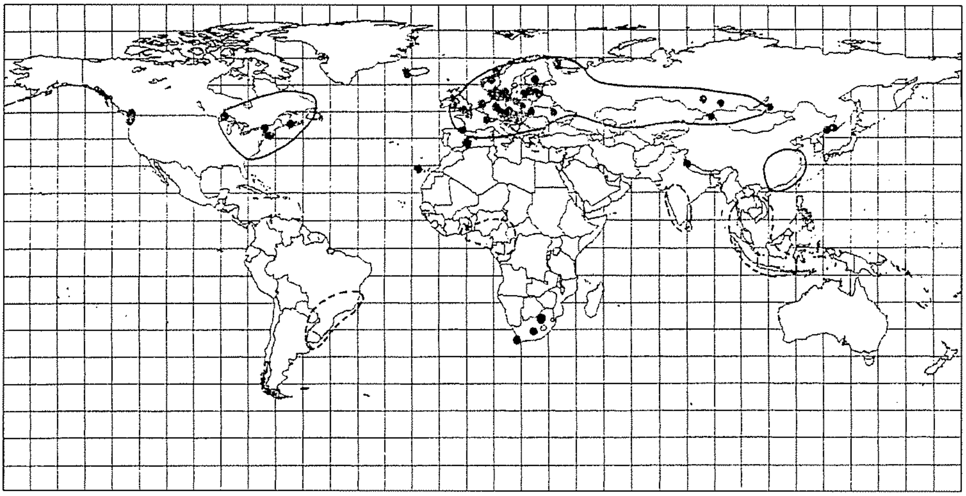

Fig. 2. Lichen sites affected by air pollution (from replies to questionnaire), showing present areas and predicted areas with acidification problems (after RODHE and HERRERA 1988).

District where thallii are reduced to fragmented sterile lobes on bare bark or amongst mosses.

The distribution of sites affected by air pollution (Fig. 2) also shows the distribution of areas where population and industrial growth are taking place at the moment. Long range pollution, or events such as the release of radioactive compounds into the atmosphere, have now produced international concern over the control of pollutants, and initiated lichen monitoring projects in many other countries such as Turkey (BARTH and DUTHWEILER 1988). Present studies on accumulation of radioactive compounds in lichens in Turkey provide evidence of the environmental effects of radioactive pollution (TOPCUOGLU *et al.* 1992).

3.2 Habitat destruction

Habitat destruction may occur in any environment, and was identified as a threat in 90 (34%) sites. Of these, destruction of old or natural forests accounted for 57 or 63% of the sites (Fig. 3). In many places we cannot even estimate this loss, but it is certain that it has been accelerating rapidly in this century (GRADSTEIN 1992; MACKINNON *et al.* 1986). Removal of forest cover in all regions of the world has caused the loss or near extinction of many epiphytic lichens. At the same time the use of lichens as indicators of ecological continuity to identify relict forest communities has been developed; indicator species being dependent on the presence of ancient native trees and uneven-aged forests (ROSE 1976, 1992; KUUSINEN 1995, this vol.; GOWARD 1994). Recent developments in the USA towards Forest Ecosystem Management (ROSENTRETER 1995, this vol.), and in Canada termed New Forestry (Land Management Reports 71 and 72, 1991) have stressed the importance of the use of lichens as monitors of the healthy conditions of the forest en-

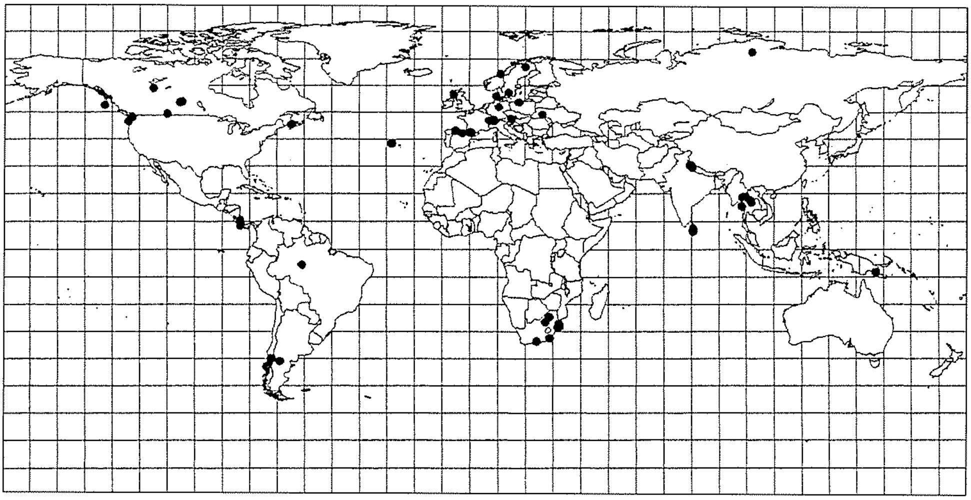

Fig. 3. Lichen sites threatened by loss of old growth forest (from replies to questionnaire).

vironment. Loss of old forest is well documented as a threat in Europe and North America, but in the tropics the loss of large areas of lowland forest has already occurred, with little or no documentation of lichens. Thailand is a typical example where forest cover was estimated at 60% of the land area in 1950 and in 1988 was estimated to be between 12.2–26.4% of the land area (BELCHER and GENNINO 1993). This includes large areas where the former species-rich evergreen forest has been replaced by a species-poor fire-tolerant deciduous forest, and where lichens can be used to indicate the time scale on which this has been happening (WOLSELEY and AGUIRRE-HUDSON 1995a, 1995b, in press). Recently the most rapid loss in Thailand has been occurring in the fagaceous montane forest above 1000 m, where already many new records for epiphytic lichens for the country, now exist in isolated pockets of undisturbed forest. The montane forest, if undisturbed, has been found to be one of the most lichen-rich and diverse forests throughout the tropics (SIPMAN 1989; WOLFE 1993; WOLSELEY *et al.* 1994). In these unexplored areas, where information is scarce or absent, we need to develop techniques of rapid survey using indicator taxa that can be used to identify and locate species-rich areas. Rapid assessment techniques using flowering plants have been developed in Australia and New Zealand, but at present these methods do not include lichens (BROWN *et al.* 1994).

3.3 Fire

Fire occurs naturally wherever seasonally dry climates occur, and where there is fuel in the form of dry vegetation. In many habitats such as boreal heaths and monsoon tropical forest these may be associated with a rich lichen flora (Fig. 4). In some situations lichen-rich heaths may be maintained by fire and exclusion of fire favours the invasion of phanerogamic vegetation and the loss of the lichen community (James and Rose, pers.

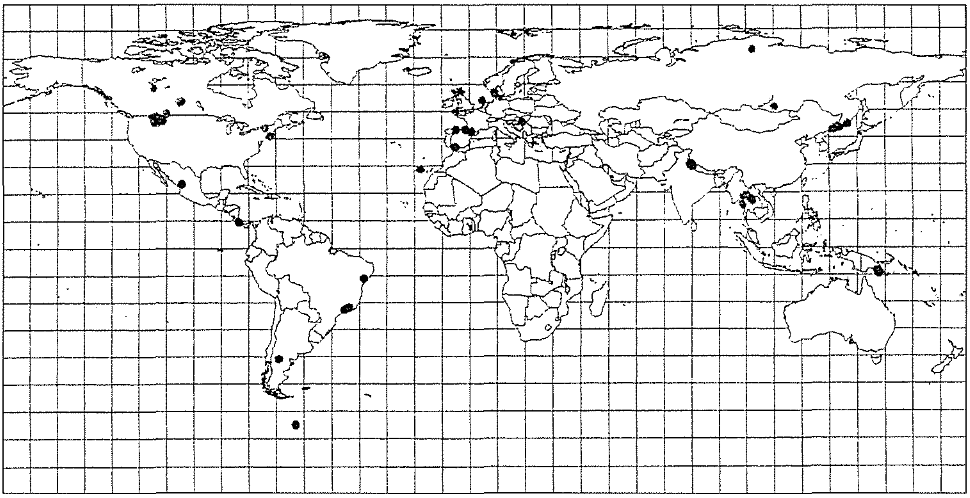

Fig. 4. Lichen sites threatened by fire (from replies to questionnaire).

comm.). Continual use of fire as a management tool may result in a shift in environmental conditions towards a drier climate (CHRISTENSEN 1993) and a loss of diversity (WOLSELEY and AGUIRRE-HUDSON 1995a, 1995b, in press). In a recent report on threats to Australian lichens fire was identified as a major threat to lichens (STEVENS 1995). Fires are most destructive to vegetation that is not fire-adapted, as in temperate heaths e.g. Isle of Man, and moist montane vegetation in the tropics or southern temperate regions e.g. Tasmania. Where lichens are strongly associated with a forest type, loss of the forest will also result in loss of associated lichens and their replacement with lichens characteristic of disturbance (WOLSELEY and AGUIRRE-HUDSON 1995a, 1995b, in press).

Fires may also be associated with increased tourist pressure in areas where the dry season coincides with the tourist season. In 26% of the sites threatened by fire, tourism was also a threat, especially in *Cladonia* heath and coastal communities where trampling and/or fire in the growing season may do considerable damage to terricolous lichens. In Europe coastal heaths are at risk e.g. Isle of Man, Spain, in the tropics evergreen forest in seasonal monsoon areas where fires coincide with tourist pressure e.g. Thailand, and in boreal zones e.g. Canada, Russia.

3.4 Tourism

Tourism is identified as a threat in 25% of sites, an increasing number of these occurring in formerly innaccessible areas such as the former USSR. This reflects the increasing demand for access to unspoilt areas and the corresponding pressure on fragile lichen communities, where growth is slow and maximum damage occurs during the growing season. Lichen communities are often rich in exposed areas above the tree line on mountains, and these areas may experience increased pressure during warm and cold seasons where ski stations have been developed. This problem is identified in many countries in Europe and America and also includes such places as Puyehue National Park in Chile where the loss of major areas of lichen diversity and type sites has occurred with the development of ski-fields (Galloway, New Zealand).

Coastal areas also come under threat through tourist development, and this is often concentrated in areas where lichen diversity is high such as the European coasts (Barreno, Spain), where a combination of tidal regime and rock type have allowed the development of rich lichen communities.

3.5 Climate change

Global warming was only mentioned in two countries, probably because national conservation groups can do little about this large scale international problem. However climate change associated with the movement of the El Nino currents has been observed in Chile where the unusually rich coastal fog communities of cacti and lichens are disappearing (FOLLMANN 1994). In the antarctic where lichens represent a large proportion of the flora and where the ozone hole is largest, lichens are being used as long term monitors of these changes (Kashiwadani, Japan; Lewis-Smith, UK).

Other habitats that may suffer from the effects of global warming include montane communities, especially those containing rare species that are relicts of colder climates. Furthermore rising sea levels will obliterate those areas of coast with rich lichen communities, as in Europe. The European rocky coast supports a great diversity of lichen communities that are also relicts of warmer climates. These would be endangered with a rise in sea level.

3.6 Agriculture

Agriculture is identified as a threat in a wide range of situations, in 26 sites or 9.7% of all sites. Threats ranged from eutrophication caused by inorganic fertilisers, to reclamation, and changes in management which may also include changes in grazing routine leading to scrub invasion or coarse grasses and loss of terricolous species (BROWN *et al.* 1994). Overgrazing is a threat to terricolous species in boreal zones and in South Africa. In densely populated areas of Europe the affects of agricultural chemicals on lichen species and communities are being investigated (VAN DOBBEN 1993).

The demands of developed nations for timber and agricultural products have had far reaching effects especially where grant-aid has made it possible to reclaim areas of land that were formerly considered marginal. This is becoming obvious in Spain where recent entry to the EC and the Common Agricultural Policy is causing threats from both intensive agriculture and forestry in formerly unspoilt areas where low grazing routines and diverse land management supported species-rich lichen communities. This is associated with other damaging activities such as dam building and irrigation schemes. Change in long-standing agricultural practices such as removal of grazing may alter the habitat to coarse grasses and scrub which is detrimental to terricolous lichen communities as happened in Britain with the loss of the rabbit population.

3.7 Multiple threats

One of the striking results of this questionnaire is the number of sites where multiple threats are occurring, this being characteristic of densely populated areas or where rapid increases in population are occurring. South Africa provides a good example of this (Fig. 5) (Wessels, South Africa), where loss of habitat from deforestation or urbanisation may be combined with air pollution over a large area, resulting in species extinction.

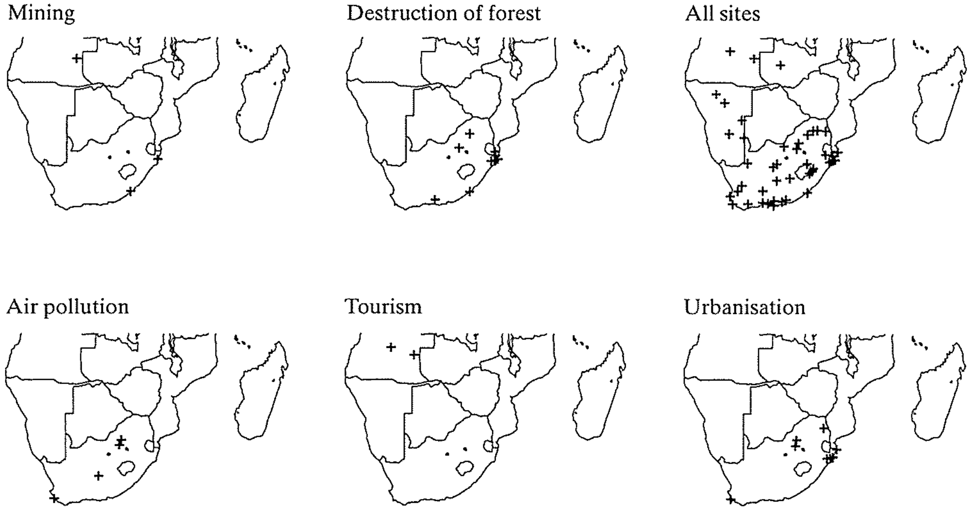

Fig. 5. Multiple threats – a changing situation in South Africa (from replies to questionnaire).

4 Species protection

Red Lists (THOR 1995, same vol.) are frequently not available in countries where rapid changes are occurring. The preparation of Red Lists is dependent on information on the distribution of species in a country. Lichens are only specifically protected in 13% of sites identified by respondents, mainly in European countries, Russia and Japan where there is already a considerable body of knowledge in existence (e.g. WIRTH and OBERHOLLENZER 1990). In 30% of sites respondents asked for help either as surveys, literature or funds and these are widely distributed throughout the world.

5 Conclusion

The large number of responses to the questionnaire, together with literature and site information reflects the urgency of the situation, particularly in countries where there is little available information on lichens, even at the macro level, and where sites are being lost before they are documented. The evidence shows that there are lichen-rich sites that do not fall within the usual conservation categories, and that threats to these sites are mainly associated with human activities or recent changes in established management patterns.

Following the Rio Summit in 1992, the Convention on Biological Diversity was signed by 153 countries. A significant result of this is the recognition of the need to identify diversity in all groups at a national and international level. A recent publication on Biodiversity Challenge (WYNNE *et al.* 1995) has stressed the targetting of both rare species and habitats under threat, especially where there is insufficient knowledge on the distribution of rare taxa. Lichens are frequently in this category in many parts of the world, and we need to develop techniques of rapid survey, combined with the targetting of identification of indicator taxa to be used in assessing new areas. The production of keys and literature, that can be used by local people to estimate lichen diversity, will facilitate the location of species-rich areas before they are lost. The importance of establishing regional and international information sources towards more effective lichen conservation is emphasised by SMITH (Manuscript). The database set up as a result of the questionnaire provides a basic list of researchers and conservationists interested in lichens, together with literature and research projects, and the beginning of site dossiers for lichen-rich sites. An expansion of this information base will enable us to target priorities at the regional and international level, to collaborate in research projects, and to produce a bibliography of available literature and research projects that can be used to protect lichen interests.

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Appendix I

Information concerning lichens and lichen-rich habitats

Questionnaire
In order to facilitate compilation of a data base please answer all questions even where negative or unknown.
If you respond on separate sheets please specify question number and letter.

1. Are there any sites of conservation status in your region/country where lichens form a major component of the site?
   a) Country
   b) State or Province
   c) Name of site
   d) Geographic locality, give Lat/Long as near as possible + projection if possible.
   e) Conservation status of the area (e.g. national park, wildlife sanctuary or other).
   f) major lichen habitats present (e.g. rainforest, montane, desert etc).

2. Are any of these sites of internationally designated? Please specify.
   (e.g., world heritage site, Biosphere Reserve, Ramsar site etc.).

3. Are any of these sites threatened?
   if so by what? (e.g., air pollution, habitat destruction, fire, agriculture/fertilisers, over collecting, tourism).

4. Do you need help to.
   a) investigate the sites?
   b) prepare a conservation plan?

5. Is there a marked decline of lichens in a region of your country that you know about?
   If so, which species (or groups) and/or ecological groups have decreased?

6. Is there a Red Data List for lichens in your country, or one being prepared, or in the region where you have studied lichens?
   If it is not published please send us a copy.
   If it is published please give full reference.
   If neither exist are there any lists of rare species?

7. Can you identify the major threats to lichens in
   a) these regions?
   b) your country?

8. Is there anything written (besides Red Data Lists) about changes in the lichen flora in the regions listed above, or in your country?
   Please include full references.

9. Is there any research going on at your institute, in NGOs or societies about changes in lichen flora caused directly or indirectly by man?
   If so please give name of researcher, affiliation, title of project, brief descriptions.

Measures for protection of lichens

10. Are lichens in general or any lichen species protected by law in your country?
If yes, please provide references to laws.

11. Are lichens explicitly protected in nature reserves and/or national parks in your country?
a) by general management policy e.g., collecting prohibited or by permit.
b) by specific species management policy.

12. Is there any research carried out in connection with protective measures for lichens?

13. Do you know of any other persons involved with nature conservation who should receive this questionnaire?

Please return completed questionnaires to: Pat Wolseley, Botany Department, The Natural History Museum, Cromwell Rd, London SW7 5BD, U.K. as soon as possible, and at least by Jan 30th to allow time for data processing.
Tel no: 071.938.9351
Fax no. 071.938.9260

Please give your name and address, phone no. fax no and e-mail address if possible.

Appendix II

List of contributors

Aptroot A., Centraal Bureau Voor Schimmelcultures , Netherlands
Baltzo, D. E., California, USA
Barreno, E., Universitat de Valencia, Spain
Bielczyk, U., Polish Academy of Science, Krakow, Poland
Boom van den, P., Netherlands
Brenneman, W. S., Wyoming, U.S.A.
Brodo, I., Canadian Museum of Nature, Ontario, Canada
Burgaz, A., Universidad Complutense, Madrid, Spain
Chabanenko, S., Sakhalin Botanical Garden, Russia
Chung, C., Taiwan, Republic of China
Clauzade, G., France
Clerc, P., Conservatoire et Jardin Botaniques, Geneva, Switzerland
Dirig, R., Cornell University, New York, USA
Doell, J., California Lichen Society, California, USA
Douglas, G. W., British Columbia Conservation Data Centre, Canada
Dudoreva, T., Polar Alpine Botanical Garden, Murmansk, Estonia
Dza, R. J., Botanical Institute, Academy of Sciences, North Korea, D.P.R.K
Etayo, J., Pamplona, Spain
Eversman, S., Montana State University, Montana, USA
Farkas, E. , Hungarian Academy of Sci., Hungary
Fletcher, A., Leicester Museum, U.K.
Gadgil, M., Indian Institute of Sciences, Bangalore, , India
Galloway, D., New Zealand
Gerrad, L. S., The Manx Museum & National Trust, Isle of Man, U.K.
Goward, T., British Columbia, Canada
Guzman, G., Instituto de Ecologia, Veracruz, Mexico
Hansen, E. S., Botanical Museum, University of Copenhagen, Denmark
Hill, D. J., University of Bristol, U.K.
Horakov, RNDr Jana, Mycological Dept, Natural History Museum, Czech Republic
Huneck, S., Institut fur Pflanzenbiochemie, Halle, Germany
Ikoma, Y., Japan
Inoue, M., Akita University, Akita-shi, Japan
Kantvilas, G., Tasmanian Herbarium, Tasmania, Australia
Kashiwadani, H., National Science Museum, Japan
Kirschbaum, U., FH Giessen-Frieslberg, Giessen, Germany
Kondratyuk, S., Institute of Botany, Kiev, Ukraine
Kristiansson, H., The Akureyri Museum of Natuaral History, Iceland
Kudratov, I., Botanical Institute of Tajikstan, Russia
Kuusinen, M., Department of Botany, University of Helsinki, Finland
Ladd, D., The Nature Conservancy, Missouri, USA
Lambley, P., English Nature, U.K.
Lerond, M., France
Lewis-Smith, Dr R.I., British Antarctic Survey, Cambridge, U.K.
Lipnicki, L., Lab of Biology & Nature,Protec Inst Physical Educcation, Poland
Liska, J., Institute of Botany, Academy of Sciences, Czech Republic
Lucking, R., Universitat Ulm, Germany

Maass, W., Dalhousie University, Nova Scotia, Canada
Marcelli, M. P., Instituto de Botanica, San Paulo, Brazil
McCune, B., Oregon State University, USA
Mikcelin, A, Far Eastern Research Centre, Vladivostok, Russia
Nelson, W., Museum of New Zealand, Wellington, New Zealand
Pisut, I., Institute of Botany, Slovak Acad of Sciences, Bratislava, Slovakia
Piterans, A., University of Latvia, Latvia
Pittam, S. K., Oregon, USA
Purvis, O. W., The Natural History Museum, UK
Randlane, T., Tartu Univeristy, Estonia
Rhoades, F., Biology Department, WWU, USA
Ruoss, E., Natur Museum Luzern, Switzerland
Scholz, P., Markkleeberg, Germany
Sedelnikova, N. V., Central Siberian Botanical Garden, Novosibirsk, Russia
Skirina, I.F., Far Eastern Branch, Russian Academy of Sciences, Vladivostock, Russia
Smith, C. W., University of Hawaii, USA
Sochting, U., University of Copenhagen, Denmark
Stevens, N., Brisbane, Queensland, Australia
Suwaris, M., Surrey, UK
Thor, G., Swedish University of Agricultural Science, Uppsala, Sweden
Tonsberg, T., University of Bergen, Norway
Tschermak-Woess, E. University of Vienna, Austria
Upreti, D. K., National Botanical Research Institute, Lucknow, India
Urbanavichene, I., Buryatia, Russia
Vries de, B., University of Regina, Saskatchewan, Canada
Vobis, G., Universidad Nacional del Comahue, Rio Negro, Argentina
Weber, W. A., University of Colorado, USA
Wessels, D., University of the North, South Africa
Wetmore, C., University of Minnesota, USA
Wolseley, P., The Natural History Museum, London, UK
Zhurbenko, M., Komarov Botanical Institute, St Petersburg, Russia

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Red Lists – Aspects of their Compilation and Use in Lichen Conservation

Göran Thor
Swedish Threatened Species Unit, Swedish University of Agricultural Sciences, PO Box 7072, S-750 07 Uppsala, Sweden.
Present address: Department of Botany, National Science Museum, 1–1 Amakubo-4, Tsukuba, Ibaraki 305, Japan.

Abstract

Lichen-rich habitats all over the world are being continuosly destroyed and many species have become rarer or even extinct, leading to further loss of biological diversity. An invaluable tool for promoting lichen conservation as well as stimulating research are Red Lists. Information from replies to a worldwide questionnaire is summarized and discussed. The need for lichen Red Lists, both regional (e.g. countries or continents) and world-wide, is emphasised. The present number of Red Lists covering different regions is presented. The need for cooperation between lichenologists in different countries for compilation of lists covering continents and a global Red List is encouraged. The criteria for selecting species for Red Lists are discussed and different problems are emphasised.

Keywords: Red Lists, lichens, biological diversity, threatened species, conservation biology

1 Introduction

The interest in conservation biology is rapidly increasing. The conservation of organisms, such as large mammals and birds, has been considered important for a long time. However, it is evident that also lichen-rich habitats around the world are being continuously destroyed (e.g. by forestry, agriculture, air pollution, the rapid increase in human population, and tourism), and that many lichens have become rarer or even extinct without attracting the same attention. Nevertheless, their extinction means a loss of biological diversity, and from an ethical point-of-view, each species has an intrinsic value which the IAL Committee for Conservation of Lichens (ICCL) believe cannot be disputed (see also e.g. NORTON 1986, MCNEELY *et al.* 1990, SÖDERSTRÖM *et al.* 1992). Significant developments are now occurring, both at national and international levels, and greater attention is now being focused also on other organisms, such as lichens. This broadened perspective is consistent with an internationally increasing awareness by scientific and government agencies of the importance of other organisms, such as lichens; their contribution to biodiversity, the critical functional role they play in natural ecosystems, the threats they face, and the urgent need to implement effective conservation strategies (e.g. BROWN *et al.* 1994, HEDENÄS *et al.* 1992, SYNGE 1981). Habitats rich in threatened organisms of e.g. mammals, birds or vascular plants are not necessarily also rich in threatened lichens. Nor are management techniques and conservation programmes for these organisms always appropriate for lichens and can even be contradictory (see e.g. BROWN *et al.* 1994).

The IAL Committee for Conservation of Lichens (ICCL) was set up during the second IAL (International Association for Lichenology) symposium in Båstad, Sweden in 1992. The Committee became a Specialist Group under the umbrella of the Species Survival Commission (SSC) at IUCN in 1994. It now includes ten members from Australia, Israel, Japan, South Africa, Spain, Sweden, Switzerland, United Kingdom and USA (2 members). The Committee started with drawing up a constitution and policy document which was distributed to all IAL members in 57 countries in December 1993 together with a questionnaire (the questionnaire is included in WOLSELEY 1995, this vol. appendix 1). The questionnaire included questions to find out the status of lichens and their habitats on a global scale. The response from lichenologists from all over the world was overwhelming with 76 replies from 40 countries. The information from the questionnaires was evaluated by G. Thor and P. Wolseley and presented at the Fifth Mycological Congress in Vancouver 1994 at a contributed Symposium, "Lichens – a strategy for Conservation". In this paper the information from question no. 6 in the questionnaire is summarized and discussed. Information concerning the other questions is covered by WOLSELEY (1995).

2 Conservation process

The conservation process for threatened species involves four main steps (slightly modified from SÖDERSTRÖM *et al.* 1992):

1) Recording the systematics, distribution, biology and threats for the species;
2) Listing extinct and threatened species in Red Lists;
3) Proposing conservation programmes;
4) Implementation of these programmes to insure the maintenance and recovery of the species.

This conservation process has reached different stages for different groups of organisms and in different parts of the world. Most work has been done for some mammals, where conservation programmes have been started. No global conservation programmes are proposed for any lichen species.

3 Aim with Red Lists

An invaluable tool in conservation biology are lists of extinct and threatened species, usually called Red Lists. The objective of Red Lists is to secure the survival of the threatened species by:

1) Summarize the knowledge about extinct and threatened species (how many species are extinct or threatened and which Red List category do they have);
2) Assist authorities, land owners and planners in determining which species are in need of conservation within their given management jurisdictions (the Red Lists are an important reference point between scientists and administrators);

3) Help focus the attention of professional and amateur botanists on taxa in need of field searches and data collection;
4) Contribute to the international work on threatened species;
5) Use these species as indicator species or as monitors. Many threatened lichens are good indicators of threatened habitats, e.g. forests with a long continuity in the tree layer.

4 Present Red Lists

In July 1994, 14 countries have published Red Lists on lichens (Tab. 1), most of them also including an outline of the threats to the species.

In Europe there are published Red Lists from Austria (TÜRK and WITTMANN 1986), Denmark (Anonymous 1991c), Estonia (TRASS and RANDLANE 1986, with some additions by TRASS and RANDLANE 1987), Finland (RASSI *et al.* 1992), Latvia (Anonymous 1991a), Lithuania (Anonymous 1992b), Netherlands (APTROOT and VAN DOBBEN 1992), Norway (STØRKERSEN 1992), Poland (CIEŚLIŃSKI *et al.* 1992), Slovakia (Pišút 1993), Slovenia (BATIČ 1990), Sweden (Anonymous 1991b), and Switzerland (CLERC *et al.* 1992). There is also one Red List for the former Soviet Union (BORODIN *et al.* 1984) and one for Russia (GOLOVANOV *et al.* 1988). In other countries lists are under preparation, e.g. Germany (WIRTH 1984 published a Red List for the former West Germany), Great Britain, Hungary and Ireland. In Iceland, there is no official Red List but an unofficial draft including 53 species (Kristinsson in litt.). Outside Europe and the Asiatic parts of the former Soviet Union, only Japan has published a Red List (KUROKAWA and KASHIWADANI 1993; a new version in same vol.). This means that national Red Lists are lacking from the whole tropical and subtropical world, Antarctica, Australasia as well as all countries in North, Central and South America.

Besides Red Lists covering countries, there are also several more local lists, covering different administrative regions, e.g. three states in the U.S.A. (Idaho, MOSELEY and GROVES 1990; Maryland, SKOREPA and NORDEN 1984; Missouri, Anonymous 1992a), some Bundesländer in Germany (see JACOBSEN *et al.* 1992 and SCHOLZ 1992 for summaries), some plant communities of the Spanish Mediterranean area (BURGAZ *et al.* 1994), as well as even municipalities or rural districts. These Red Lists will not be further discussed here.

Europe has for a very long time been heavily populated and cultivated and a large number of lichens are threatened and some probably even extinct today. Among the published Red Lists, the percentage and number of extinct and threatened species differ drastically between different countries (Tab. 1). Denmark, with 70%, has the highest number of extinct and threatened lichens, while only 9% are regarded as extinct or threatened in Finland (Tab. 1). The explanation for this is for the most part that the number of evaluated species differs in different countries but also that the type and degree of threats differ. Sometimes only a limited number of macrolichens have been evaluated (e.g. Russia), and sometimes almost all species (e.g. Denmark). Usually, macrolichens have been more intensely studied than crustose species and accordingly Red Lists include proportionally more such species.

Most species are rare in parts of their range, especially at the periphery. Such species are included in the Red Lists (e.g. *Arthonia cinnabarina* in Sweden and *Nephroma arc-*

Tab. 1. Countries with published Red Lists. For each country the year of publication is given as well as if the lists include only macrolichens (m) or macrolichens (m) and crustose (c) species, the number of extinct and threatened species and the percentage of extinct and threatened species. For some countries, the total number of reported species are not known and the percentage of extinct and threatened species are not given. * = percentage of macrolichens in these countries (the Red Lists in these countries only include macrolichens).

Country	Year of publication	Lists include macrolichens (m), crustose lichens (c)	Number of extinct and threatened lichens	% extinct and threatened lichens
Within Europe				
Austria	1986	m + c	223	–
Denmark	1991	m + c	634	70
Estonia	1986, 1987	m + c	131	–
Finland	1992	m + c	138	9
Latvia	1991	m + c	16	–
Lithuania	1992	m	13	–
Netherlands	1992	m + c	367	58
Norway	1992	m	62	16*
Poland	1992	m + c	602	38
Russia	1988	m	29	–
Slovakia	1993	m + c	578	41
Slovenia	1990	m + c	81	–
Sweden	1991	m + c	212	11
Switzerland	1992	m	152	37*
Outside Europe				
Japan	1993	m + c	74	–

ticum in Denmark) but it is striking that the same species are threatened in many or almost all European countries where there are Red Lists. Examples of such species are *Bactrospora corticola, B. dryina, Bryoria smithii, Cetrelia olivetorum, Chaenotheca cinerea, C. laevigata, Collema* spp., *Cybebe gracilenta, Evernia divaricata, Opegrapha illecebrosa, Ramalina obtusata, R. roesleri, R. thrausta, Sticta fuliginosa, S. sylvatica* and *Usnea longissima.* There is also a difference between north and south Europe. Some lichens which are still more or less common in north Europe are now threatened in south and central Europe, e.g. *Cetraria sepincola, Lobaria pulmonaria, Nephroma bellum* and *Peltigera venosa.*

The publication of Red Lists often initiates considerable activity at all levels of government, non-governmental organizations (NGO's), researchers and amateurs in order to find new information and to facilitate the survival and recovery of threatened species. This can be illustrated by events in the USA after the Endangered Species Act was published in 1973 (even though this list did not include lichens). Red Lists often induce a rapid increase of knowledge of lichens, and especially threatened species, in a region. New editions of Red Lists have been published after only a few years in Finland, Poland and Slovakia, and in other countries new lists are under preparation. In Finland the Red List from 1986 (English summary by RASSI and VÄISÄNEN 1987) included 79 species (5% of the total number) while the list from 1992 includes 138 species (RASSI *et al.* 1992). In Poland, the Red List from 1986 (CIEŚLIŃSKI *et al.* 1986) included 480 species (29% of the total number) while the list from 1992 (CIEŚLIŃSKI *et al.* 1992) includes 602 species. In Slovakia, the Red List from 1985 (PIŠÚT 1985) included 568 species (41% of the total number) while the list from 1993 (PIŠÚT 1993) includes 578 species. As more information has emerged, the new editions thus include more species than the earlier ones. This indicates that lichenologists tend to be very careful about including species and that the numbers of threatened lichens in many Red Lists are underestimated. Another less likely explanation is that the threat have increased rapidly during a few years.

5 Preparation of existing Red Lists

The following principles have been followed when preparing Red Lists for the countries listed in Table 1.

1) Only species threatened in a country as a whole have been listed. Species threatened only in limited parts of a country have been excluded.
2) For the extinct and most threatened species the IUCN categories (Anonymous 1980) have mainly been followed even though occasionally the definitions have been slightly changed. For species with decreasing populations but which still are rather widely distributed, local categories have sometimes been established.
3) The Red List has usually been officially sanctioned by a nature conservation authority in the country.
4) Besides Red List category and scientific name, some additional information is often provided for the species, e.g. information on main habitat and location within the adminstrative regions of the country. Sometimes, notes about the need for research to confirm their actual state is included as well as vernacular names (if existing).
5) Most Red Lists have been prepared by a group of lichenologists, coordinated by some university or authority involved in nature conservation.
6) In some countries Red Lists are followed by Red Data Books with data sheets or short summaries and drawings or photographs of the species.

6 Recommendations for elaboration of National Red Lists

There is an urgent need for Red Lists from those countries where such lists are not yet present, especially for tropical and subtropical countries, as an invaluable tool for future conservation strategies.

Red Lists should at least include information on the scientific names of the threatened and extinct species and their Red List category. It is also recommended that at least information on the main habitat and location within the adminstrative regions of the country is included. The lists should preferably be officially sanctioned by a nature conservation authority in the country. This is important to make the Red List official as well as stressing the importance of the list. Within each country, there is also a need for one place where collection, storage and evaluation of information on the threatened species can be made. The storage is preferably made in a database. High quality, effective and successful conservation work must be based on competent specialists, active research programmes and reliable, accurate, up-to-date information based in well-established and maintained databases (see also BROWN *et al.* 1994).

6.1 Selecting species

In a Red List, the species are listed depending upon the type and degree of threat. If possible, changes in size of populations over as long a time as possible and expected changes with regard to existing and probable threats should be included. To summarize the knowledge from all parts of a country, as well as from different taxonomic groups, it can be necessary to include experts from different fields of research. We still have incomplete or meagre knowledge of the lichens in many parts of the world and it is therefore only rarely that we have information about the distribution, habitat requirements and documentation of changes in population sizes. Many species are also only known from a few scattered findings or only from the type-material. In these cases it is difficult to estimate if a species is threatened or not. The following criteria must be fulfilled for all species in Red Lists:

1) the taxonomy and ecology of the species must be clearly understood,
2) there must be considerable documentation showing that the species is threatened,
3) the species should be threatened in all parts of the country,
4) the species must not be much over-looked. Even though all localities are rarely known for a species, it must be possible to approximate the total number of localities from the known localities and, for example, by estimates of areas covered with suitable habitats.

It is also recommended that if a Red Data Book does not exist, the criteria for including each species should be shortly justified in a few sentences including information about the morphology, habitat, distribution within the country, number of localities (present and earlier) and threats.

These criteria are most important for the credibility of Red Lists. In a field as contentious as conservation biology, the scientific ethic can suffer at the expense of political expediency if data are unreliable or even incorrect (BROWN *et al.* 1994).

We often have meagre or unreliable data on the earlier status of the species and it is therefore difficult to estimate changes in status. A way of estimating change in status of a species is to compare the number of collections and their locations in the herbaria for different dates and/or literature records. For species not observed for some time, it must, however, be clear how much effort has been made to refind the species and how much we know about in which habitat the species occurs. Also, the reliability of data only from the literature sources must be assessed.

The elaboration of Red Lists must start with floristic data collection and a first step towards this objective can be a checklist. Even checklists for specific regions, habitats or for particular taxonomic groupings are most valuable. If it is known that a species is only found within a special habitat, and it is also known that this habitat is now rapidly disappearing or very rare, it can be assumed that the species is threatened. This more "ecological" indication can be used particularly if we lack other kinds of information. Many threatened lichens are confined to restricted habitats (naturally restricted or restricted by human activities) or rare substrates. An approach to rapidly identify such habitats is to select a few threatened, easily recognized indicator species (probably mainly macrolichens) for each habitat. These indicator species can be used to identify habitats with high conservation values, and it is highly probably that many species of which we now have limited information (e.g. some crustose species), will be added once these habitats are protected and further studied as a result. This approach is perhaps often the only possible in areas where information is only available on a few, frequently macrolichen, groups (e.g. most tropical areas and the Antarctic). However, this is an effective, cheap and reliable method which can be performed also by knowledgeable non-lichenologists all over the world. It has recently been evaluated and found most useful to discern areas with high conservation values in coniferous forests in the northern part of Sweden (OLSSON and GRANSBERG 1993). Lichen species which can be used as indicators of ancient broad-leaved deciduous forests in United Kingdom have been presented by ROSE (1976). It is, however, important to emphasise that all areas with threatened species and all threatened habitats will not be found by this method. Thus, it is important to target both conservation programmes for individual species and different methods to discern habitats under threat (see also WOLSELEY 1995).

6.2 Red List categories

The IUCN categories of threat have been under revision and a new system based on the classification of species according to their extinction risk has recently been adopted (IUCN 1994). The new categories have until now only been applied to primates and birds respectively but ICCL will adopt these categories in the global Red List for lichens. An absolute condition for international cooperation as well as comparing different national Red Lists in the future is that all countries will follow the same categories. The IUCN categories are established to be applied to all organisms and are strongly recommended.

6.3 Revising lists

Red Lists should not be seen as a single event. They are dynamic and are, of course, based on the knowledge we have today and must be regularly revised, preferably every 3 to 10 years or when new information is available. New findings can be made and better protection can increase the existing known populations. Also, new threats can emerge and others intensify, resulting in species disappearing from many localities or the deterioration in the health of populations. The status for the species must therefore be followed continuously.

6.4 Priorities

It is also very important to keep in mind that the Red Lists only indicate how threatened the species are. It does not include how to assess priorities between species. If possible, all species should be maintained over all their distribution area as well as in all countries where they occur. Each country must have a responsibility for all species occurring in that country, e.g. in order to protect the genetic variability of the species. If there is a shortage of financial support in the conservation work, it might be necessary to give priority to one species over another. A system for assessing priorities for conservation action will include numerous factors such as costs, logistics, chances of success, and even perhaps the taxonomic distinctiveness of the subject (IUCN 1994). It is very important to keep in mind that all priorities inevitably mean a loss of unique genetic material.

6.5 Research proposals

Compared with some other organisms, there is a considerable body of data available on the lichens and in many cases we have information on how and where to act to retain or restore threatened lichen populations and/or prevent further negative influence. In spite of this, there are still large gaps of knowledge and the processes causing threats must be further studied and clarified and if possible assessed and removed. No effective Red List or system of species conservation can be established without sufficient information on the taxonomy, distribution and ecology of the species concerned and research in these fields is paramount. The knowledge about lichens varies considerably in different parts of the world. Even though lichens are most well-known in Europe, new species are still continuously being described. It seems likely that several of the still undescribed species are threatened. It is of course difficult to protect lichens about which nothing is known, though protection of important habitats may ensure their future conservation.

An effective conservation work is impossible without coherent, up-to-date knowledge of the taxonomy of the species. Only a few countries have recently published floras and/or checklists with notes on the biology and distribution. There is an urgent need for scientific floras and checklists covering all regions of the world. A major problem is the small number of lichenologists world-wide and the great inbalance between numbers of lichenologists in Northern and Southern Hemispheres (GALLOWAY 1992). We urgently need more trained lichenologists, who can describe the species and clarify their phylogeny. The IAL Committee for Conservation of Lichens (ICCL) fully supports "Systematics Agenda 2000" (CLARIDGE 1995, and other papers in the same volume of Biodiversity and Conservation) which states that basic systematic research on species diversity is urgently needed. Systematic information is of immediate relevance in choosing and designating sites for preservation. Within ecology we need better understanding on, for example, population structure of different species, information on which edaphic factors determine lichen distributions, and the relation between different vascular plant habitats and lichen occurrences (cf. BROWN *et al.* 1994).

7 International Red Lists

A classification in national Red Lists of a species in a Red List category is of course only a judgement of the situation in that country. A species can be extinct or severely threatened within one country but common and unthreatened in an adjacent country. Examples are *Acrocordia conoidea, Arthonia leucopellea, Massalongia carnosa, Nephroma arcticum, Peltigera aphthosa, Psoroma hypnorum* and *Racodium rupestre* which all are extinct in Denmark (Anonymous 1991c) while still not threatened in e.g. Norway (STØRKERSEN 1992), Finland (RASSI *et al.* 1992) or Sweden (Anonymous 1991b). Even though national Red Lists provide important information for those working with threatened lichens in other countries, even on other continents, there is an urgent need to establish Red Lists covering larger geographical areas, e.g. continents or all the world. Such lists are essential to evaluate differences between local threat and threat to the whole gene pool of the species. International Red Lists therefore contribute with very important information towards a more effective lichen conservation. Until now, all lichen Red Lists are national except one covering the macrolichens in the countries in the European Community (EC) by SÉRESIAUX (1989). The IAL Committee for Conservation of Lichens (ICCL) therefore intends to initiate the work by compiling a global Red List.

8 Conclusions

At the United Nations Conference on Environment and Development in Rio de Janeiro in 1992, the world community recognized the need for continued economic growth while maintaining the integrity of the biosphere. Achieving these dual activities will entail complex political and economic decisions – which must be informed by accurate scientific information about the earth's biodiversity. In their global action plan, the world's nations underscored this need by calling for increased knowledge about the Earth's species (Systematics Agenda 2000).

Red Lists are an invaluable tool for promoting lichen conservation as well as for stimulating research. Compilation of international Red Lists are important as well as international and national cooperation among lichenologists working with threatened lichens. Extinction of species is irreversible, but we can influence this process.

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Transplantation of Symbiotic Propagules and Thallus Fragments: Methods for the Conservation of Threatened Epiphytic Lichen Populations

Christoph Scheidegger, Beat Frey, Stefan Zoller
Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland

Abstract

Transplantation of vegetative diaspores and adult thalli of various threatened foliose lichens such as *Sticta sylvatica, Lobaria pulmonaria*, and *Parmotrema crinitum* was found to be a successful approach for *in situ* conservation and the successful establishment of additional populations of these species. Immobilization of diaspores on artificial and natural substrates appears to be a major limiting factor in this reproductive process. Only when isidia of *P. crinitum* were carefully placed between the fibres of surgical gauze was there a substantial degree of immobilization of the diaspores which eventually produced anchoring hyphae from the apices of the isidial cilia to improve their attachment to the substrate. Our experiments with *L. pulmonaria* show that either adult thalli or vegetative diaspores could be used for re-establishment of endangered lichen populations. However, where possible, the non-destructive method of transplanting natural, vegetative diaspores should take priority. In *S. sylvatica* the duration of the juvenile development from the transplantation of the isidia until the first development of elongate lobules of up to 0.2 mm was found to be 24 months; this is the longest period so far reported for lichens. In *S. sylvatica* this very slow rate of growth seems to also continue after the development of stratified thalli and even after 4 years the thalli only measured about 3 mm in length. Analysis of permanent plots with juvenile thalli further demonstrated that slow growth seems to be typical for this life stage, making this species very vulnerable to competition, e.g. from bryophytes.

Keywords: conservation biology; epiphytes; lichenized ascomycetes; low-temperature scanning electron microscopy; permanent plots; transplantation; vegetative diaspores

1 Introduction

Although acidic air pollution and ozone are important causes of local and regional decline and extinction of numerous lichen species (WIRTH 1976, NASH and GRIES 1991) it seems likely that also for lichens, especially epiphytic species, habitat loss constitutes the most immediate threat in many parts of the world (WOLSELEY 1995, this volume). Thus protection of the habitat from anthropogenic destruction is a priority in every conservation schedule (PRIMACK 1993).

However, for many rare species, protection and conservation of the original habitat are not sufficient to maintain a natural epiphytic population in the face of increasing human disturbance. Especially when a small population with a high extinction probability (SOULÉ 1987, WISSEL *et al.* 1994) is restricted to a very small number of phorophytes with a limited remaining lifespan, long-term maintenance of small populations could probably be most successfully achieved by increasing the metapopulation in terms of numbers of individuals (GOODMAN 1987) and populations (LANDE and BARROWCLOUGH 1987, GILPIN 1987) which, in very scattered epiphytic lichens, can be expressed as the number of phorophytes colonized.

Two main conservation strategies for ecological continuity of endangered populations are outlined (see PRIMACK 1993). If a remnant population is too small to persist, or if all the remaining individuals are found outside protected areas, the only way a species can be prevented from becoming extinct is to maintain individuals under artificial conditions under human supervision (SEAL 1988). This strategy is known as *ex situ*. For lichens *ex situ* conservation can include cryopreservation, a method which is widely used to store lichen specimens over many years for physiological experiments (FEIGE and JENSEN 1987). Such captive colonies could be used later to re-establish species in nature. Further, protected areas such as parks or botanical gardens in the tropics and elsewhere are considered to be interesting sites for the conservation of rare lichen species (ARVIDSSON 1991). However, an *ex situ* conservation outside the original site is the last chance for the conservation of critically threatened populations. The best strategy for long-term protection of biological diversity is the preservation of natural communities and populations, known as *in situ* preservation. *In situ* conservation activities include protection and special management of the habitat, and sometimes also direct restoration of the endangered population (BOWLES and WHELAN 1994), are urgently needed to conserve also lichen biodiversity.

In the past, most intensive activities have been developed in the conservation of lichen-rich habitats (see WOLSELEY 1995). However, the literature reports only few examples where lichen populations have actively been restored for conservation reasons (HALLINGBÄCK 1990, SCHEIDEGGER 1995b), mainly by transplantation. Various techniques for transplantation of thallus fragments, which may also be applied for various rare species, have been reviewed by HALLINGBÄCK (1990). Unfortunately, many endangered populations are very small, often consisting of a few individuals on a few trees. Transplantation of individuals on previously non-colonized trees may increase the number of populations but could cause a dangerous fragmentation of the natural populations. A non-destructive alternative for conservation purposes where vegetative propagules of *Lobaria pulmonaria* were transplanted has recently been described by SCHEIDEGGER (1995b). The major difficulties relating to this technique included the following two aspects: a high percentage of diaspores from *L. pulmonaria* were lost during the first months after transplantation and, secondly, that the first lobules were only observed after 12 months, which seems to be an extraordinarily long period for a fast-growing species reaching relative annual growth rates of adult lobes up to 0.35 (LOONEY and JAMES 1990).

In the present paper particular attention was paid to the discovery of suitable methods which encouraged better physical immobilization of diaspores and also the use of adult thallus fragments as an alternative to diaspores as a viable method for transplanting lichens. We report on *in situ* conservation experiments with lichens where small populations of *Parmotrema crinitum*, *Sticta sylvatica* and *L. pulmonaria* were transplanted to previously uncolonized trees in the original habitat. In the past years these species have obtained special attention in our research projects on lichen conservation. Focus was on three types of problems relating to the transplanting of vegetative diaspores based on the previous work with *L. pulmonaria* (Scheidegger 1995b). 1) during the first months after transplantation and before the propagules developed hyphae for attachment, a very high loss of diaspores was observed. The aim of the present research was to determine whether fixation of diaspores can be at all enhanced by entrapment of the diaspores within the substrate. *Parmotrema crinitum* was selected because of the relatively large size of its ciliate isidia which are easily entangled within the experimental gauze. 2) it was not known whether propagules could develop on every site where adult thalli of *L. pulmonaria*, natural or transplanted, were able to grow. The aim of this last experiment was to compare and contrast the ecological amplitude of the two stages of development of this species. 3) a relatively long period was needed for the development of stratified lichen thalli. Our interest was whether the slow juvenile development was also found in another threatened species with a similar ecology. Therefore diaspores and adult thalli of *S. sylvatica* were selected as an example of a threatened, foliose species which usually grows in competition with mat-forming bryophytes. *S. sylvatica* is considered an even more specific indicator species for a high ecological continuity than *L. pulmonaria* (Rose 1976, 1992).

2 Materials and methods

2.1 Species and localities

Parmotrema crinitum (Ach.) M. Choisy is a common saxicolous or epiphytic species in oldgrowth fir forests in the commune of Bondo, Canton of Graubünden, where the experiments were initiated on the 24th of November 1992. In other areas of Switzerland, especially north of the Alps, the species is rare and threatened (Clerc *et al.* 1992). Transplanted thalli and diaspores were collected in the same area, the transplantation experiments were established on the different sized boles of fir trees (*Abies alba* Mill.) in very steep, open forests (Coord.762.9/133.4, 850–960 m a.s.l.).

Five study sites belonging to different bioclimatic regions were selected for the transplantation experiments of *Lobaria pulmonaria* (L.) Hoffm.:

Canton of Schwyz; commune of Muotathal, “Fläschenwald” on *Acer pseudoplatanus* L. coordinates 706.2/204.9, 1360 m a.s.l; the experiment was established on 12th of September 1990, transplanted thalli and diaspores were collected at the same site.

Canton of Zug; Steinhausen, “Steinhuser Wald” on *Fraxinus excelsior* L. coordinates 680.0/229.0, 480 m a.s.l; the experiment was established on 12th of April 1991, transplanted thalli and diaspores were collected in the Canton of St. Gallen, Toggenburg, Alt St. Johann; between Sellamatt and Iltios, Tarentobel; coordinates 741.5/227.4 1260 m a.s.l.

Canton of Aargau; Rothrist, “Langholz” on *F. excelsior*, *A. pseudoplatanus* and *Abies alba*; coordinates 633.0/237.5, 460 m a.s.l; the experiment was established on 8th of October 1990, transplanted thalli and diaspores were collected from the same site.

Canton of Bern; Mühleberg, “Schwarzenbrünnen” on *Fagus sylvativa* L. and *F. excelsior*; coordinates 589.0/196.9, 605 m a.s.l; the experiment was established on 9th of April 1991, transplanted thalli and diaspores were collected in the same area.

Canton of Zürich; Affoltern, “Jonenbachtal” on *F. excelsior*; coordinates 677.6/235.7, 510 m a.s.l; the experiment was established on 22th of March 1991, transplanted thalli and diaspores were collected from the above mentioned locality in Alt St. Johann.

Sticta sylvatica (Huds.) Ach. is an endangered species in Switzerland (CLERC *et al.* 1992); in the Bödmerenwald it has only been found on two trees (GRONER and CLERC 1988). The propagules of *S. sylvatica* are minute isidia which are usually less than 100 µm long. The Bödmerenwald is located in the Canton of Schwyz, commune of Muotathal. Two experimental sites were selected. "Eigeliswald" is one of the sites with a natural population (coordinates 705.9/203.8, 1400 m a.s.l.). At the other locality at "Fläschenwald" (coordinates 706.2/204.9, 1360 m a.s.l.) *S. sylvativca* did not occur before our experimental transplants. These experiments commenced on 11th of April 1991. Transplanted thalli and diaspores were collected from "Eigeliswald", the substrate was *A. pseudoplatanus* on both sites.

2.2 Methods of transplantation

For the transplantation of adult thalli either actively growing lobes with non-sorediate or non-isidiate margins were collected or, especially in the case of threatened populations of *L. pulmonaria,* freshly detached thalli through natural causes were directly attached by staples (see below) directly to the bark of the phorophyte (SCHEIDEGGER 1995b) or over mats of epiphytic bryophytes, mainly *Hypnum cupressiforme* Hedw. Thalli were tightly fixed to the substrate and care was taken to place growing lobes close to the substrate. The vegetative diaspores of the species investigated were harvested from the thallus with a moist paintbrush, transferred to a petri dish containing distilled water, and transplanted onto the discs within 30 minutes.

Discs (8 mm in diameter) of two layers of surgical gauze (Flawa, Schaffhausen, CH) were mounted with staples STCR 2115–1/4" Alum (Stanley Bostich, F) on the bark or on mats of epiphytic bryophytes of trees (Fig. 1). Adult thalli were mounted by the same method.

Receiver trees were selected according to our field knowledge of potential habitats of the species studied. Up to 30 discs were mounted on homogeneous parts of the bole, directly on the bark (Fig. 1) or on the upper limits of thin mats of pleurocarpous bryophytes. Diaspores were transferred onto the fixed artificial substrates, either with a pipette in a droplet of water, or with a moist paintbrush. In *P. crinitum* and *L. pulmonaria*, single diaspores were individually placed within the mesh of the surgical gauze. The diaspores of *S. sylvatica* were too small to be treated thus and were therefore passively dispersed by oozing water through the gauze. After 2, 4 and 12 (24 for *S. sylvatica* only) months one or two randomly selected discs were harvested for further investigation by low-temperature scanning electron microscopy (LTSEM); the other discs were photographed with a macro-lens equipped with a ring flash at the same intervals and later irregularly over 4 years. Annual growth rates of the length of lobes were measured from slides and relative growth rates calculated.

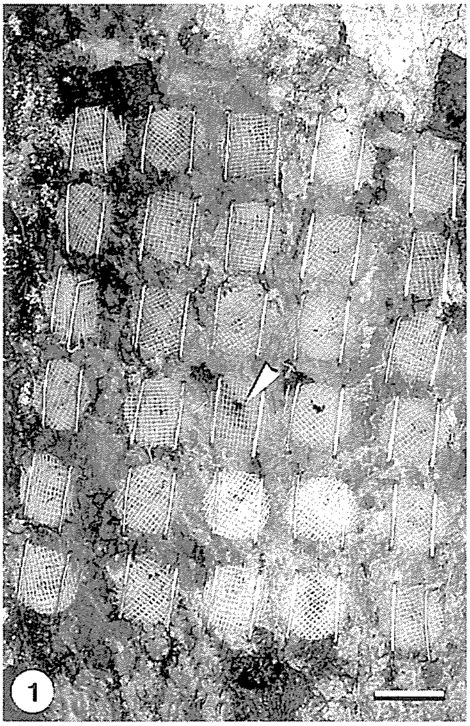


Fig. 1. Experimental set-up for the transplantation of vegetative diaspores of *Sticta sylvatica* on a partially moss-covered trunk of *Acer pseudoplatanus*. Discs of surgical gauze are fixed to the bark with aluminium staples. Arrowhead indicates the disc shown in Figs. 19 and 20. Bar ~ 1 cm.

2.3 Methods of microscopical studies

For investigations of fine structure in the LTSEM (see ECHLIN 1992, SCHEIDEGGER 1994), discs were hydrated in the laboratory with distilled water for 10 minutes, then carefully blotted to remove surface water and mounted with double-sided self-adhesive paper (Fotofix, Herma Germany) on aluminium stubs. Specimens on the aluminium stubs were then immediately frozen in liquid nitrogen (LN_2) and stored in LN_2 until further treatments. The specimens were transferred to the cold stage in the preparation chamber of a SCU 020 scanning cryopreparation unit (Bal-Tec, FL) (MÜLLER *et al.* 1991, SCHEIDEGGER *et al.* 1991) and partially freeze-dried for 10 minutes at –80 °C in a high vacuum ($P< 2 \times 10^{-4}$ Pa). Platinum sputter coating was then carried out after raising the pressure to 2.2 Pa. The coating thickness was 15 nm, measured by a quartz thin film monitor. After coating, the specimens were transferred with a manipulator through the sliding vacuum valve onto the SEM cold stage of a SEM 515 (Philips, NL).

3 Results

3.1 Attachment of transplanted vegetative diaspores of *P. crinitum*

On the thalli of *P. crinitum* the isidia were first cylindrical but later continuously developed into 1mm long branched, sometimes spathulate isidia (Fig. 4). Isotropic ramifications were found equally from the base to the apex of the isidia. Furthermore, simple cilia were formed subapically and continuous growth of both the isidia and the cilia led to intercalary cilia rising above the isidial tip. Such branched isidia were very fragile and were easily broken, either at the base or near ramifications (ZOLLER 1995).

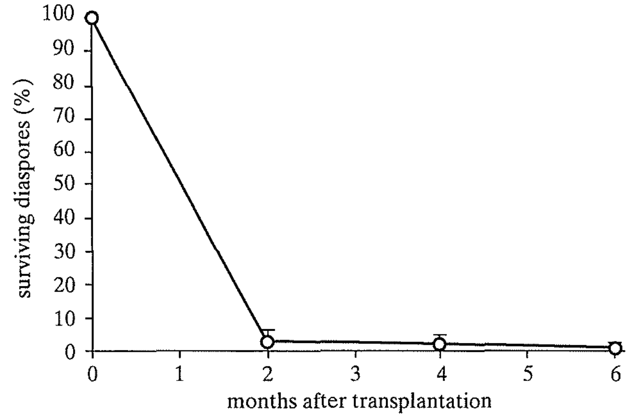


Fig. 2. Percentage of surviving diaspores of *Parmotrema crinitum* on surgical gauze. Diaspores simply transferred onto the surface of the substrate.

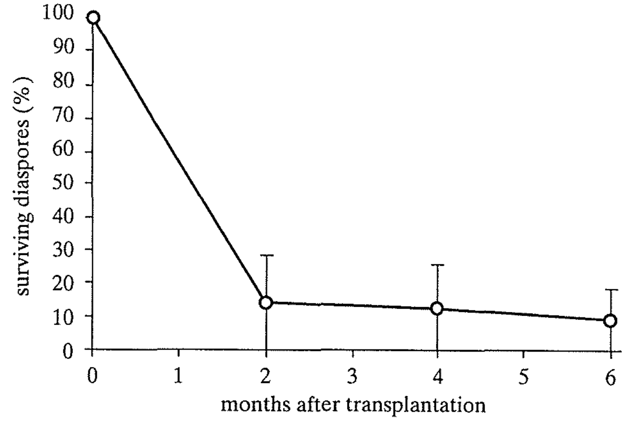


Fig. 3. Percentage of surviving diaspores of *Parmotrema crinitum* on surgical gauze. Diaspores individually placed between the fibres of the substrate.

If ciliate isidia or their fragments were transferred onto the surgical gauze without further manipulation, more than 97% of the diaspores disappeared during the first 2 months of the experiment and, after 6 months, only 1.3% of the original inoculation of diaspores survived (Fig. 2). However, if diaspores were carefully placed between the meshes of the surgical gauze, about 14 and 9% remained on the substrate after 2 and 6 months respectively (Fig. 3).

LTSEM micrographs showed that the cilia of diaspores placed between the meshes of the surgical gauze became generally entangled with the cotton fibres of the artificial substrate (Fig. 5). Besides this physical immobilization, the active attachment of the diaspore was usually achieved within 2 months. At the tips of cilia bundles of outgrowing prosoplectenchymatous hyphae established a fan-shaped contact zone with the cotton fibres of the artificial substrate. Such hyphae produced large amounts of extracellular matrix which was spread over the substrate (Fig. 6). No attachment hyphae were formed by outgrowing cortical or medullary cells.

After transplantation the isidia or their fragments often showed a single or very few pseudomeristematic growth zones (Fig. 5) and 6 months later additional growth zones were formed which further developed into about 0.1 mm broad spathuliform lobules (Fig. 7). Accelerated growth of these lobules led to broadly obovate lobes which reached about 0.6 mm in diameter after 16 months (Fig. 8). At this stage the cortex of the isidia had often begun to disintegrate.

3.2 Transplantation of adult lobes and vegetative diaspores of *L. pulmonaria*

Transplanted thallus fragments survived in all localities selected (Tab. 1). However, about 50% of the inoculated lobes were lost during the experiment, mainly due to browsing of invertebrates, especially of slugs and arthropods, but also as a result of strong competition from bryophytes. Transplants with lobes with non-sorediate margins reached a considerable average longitudinal growth rate of 11 mm/year. Figure 9 shows a thallus fragment originally oriented downwards but transplanted in upward direction. Before transplantation lobes were slightly spoon-shaped and adscending from the substrate. After 26 months lobes growing upwards were typically canaliculate and remained adpressed to the substrate. Lobes growing downwards became spoon-shaped and the lobes became adscendent and grew away from the substrate (Fig. 10).

Tab. 1. Transplantation of thallus lobes and vegetative diaspores of *Lobaria pulmonaria* at different localities in Switzerland.
*natural dispersal and development of diaspores observed

Locality	Natural occurence	Substrate	Adult thallus	Diaspores
Vordemwald	yes	*Fraxinus*	growth	develop into lobes
Mühleberg	yes	*Fraxinus*	growth	develop into lobes
Muotathal	yes	*Acer pseudoplatanus*	growth	degenerate
Affoltern	no	*Fraxinus*	growth	degenerate
Steinhausen	no	*Fraxinus*	growth*	degenerate

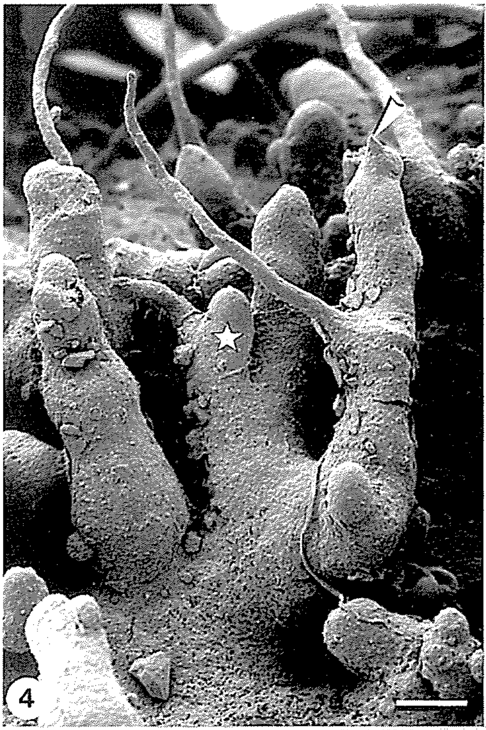
Isidioid soredia transplanted on surgical gauze (Fig. 11) developed into single-lobed thalli after about 12 to 15 months (Fig. 12) (see SCHEIDEGGER 1995b). However, only at two localities was successful regeneration of the vegetative diaspores obtained (Tab. 1). At the other sites, the propagules were either destroyed by invertebrates or the transplants were overgrown by pleurocarpous bryophytes. No successful development was obtained if diaspores were directly placed over *Hypnum cupressiforme* or if they were put into deep bark crevices. Although the transplanted isidioid soredia degenerated at the experimental site "Steinhausen", vegetative propagules which dispersed from a transplanted adult thallus successfully fixed to the bark a few centimeters below the adult thalli and developed into small lobules of about 0.3 mm in size 30 months after the experiments were begun.

3.3 Very slow development of vegetative diaspores and juvenile thalli of *S. sylvatica*

The annual growth rate and the relative growth of a natural population of juvenile *S. sylvatica* thalli at "Eigeliswald" were measured from macrophotographs taken at regular intervals (Figs. 13–16). The annual growth rate of the juvenile thalli measured was highly dependent on the relative sizes of the thalli. For the smallest thalli the annual growth rate was as low as about 0.6 mm increasing to about 1.2 mm in the 2 mm size category (Fig. 17). However, the annual relative growth rate was highest for the smallest size decreasing from 295% to 56% for 0.25 and 3.0 mm long thalli (Fig. 18). By comparison on the same site, the annual growth of *Peltigera praetextata* (Flörke ex Sommerf.) Zopf was about 10.6 ± 2.5 mm/year, and the latter species was able to overgrow about 50% of the permanent plot of the developing colony of *S. sylvatica* during the 4-year observation period (Figs. 13–16).

The minute coralloid isidia of *S. sylvatica* were clustered on the thallus surface (Fig. 21) and individually measured around 50 µm. When broken from the thallus, scars in their upper, paraplectenchymatous cortices remained visible. The minute diaspores were best transferred onto the artificial substrate within a droplet of water. Because of their small shape it was impossible to manipulate them further between the fibre mesh of the artificial substrate. However, they spontaneously stuck to the fibres of this substrate (Fig. 19, 22) and, except for a few discs where slugs removed all the diaspores, numerous diaspores were still present after 4 months.

Figs. 4–6: LTSEM-micrographs of *Parmotrema crinitum*
Fig. 4. Mature isidia on the thallus. Isidia are sparsely isotropically branched (asterisk). Cilia are formed subapically (arrowhead) but later rise above the isidial tip. Bar ~ 100 µm.
Fig. 5. Diaspores 4 months after transplantation: Cilia (c) are entangled with the fibres of the surgical gauze. One apical pseudomeristematic growth zone is present. Note scar where the diaspore has broken from the basal part of the isidium. Bar ~ 100 µm.
Fig. 6. Diaspore 14 months after transplantation: Tip of a growing cilia (c) form outgrowing prosoplectenchymatous hyphae (double arrowheads) which establish a fan-shaped contact (asterisk) zone with the cotton fibres of the artificial substrate. The outgrowing hyphae produce large amounts of extracellular matrix (arrowhead). Bar ~ 50 µm.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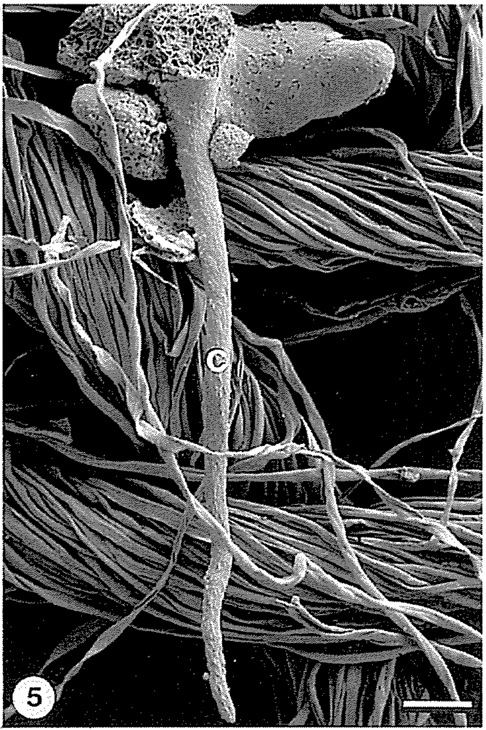
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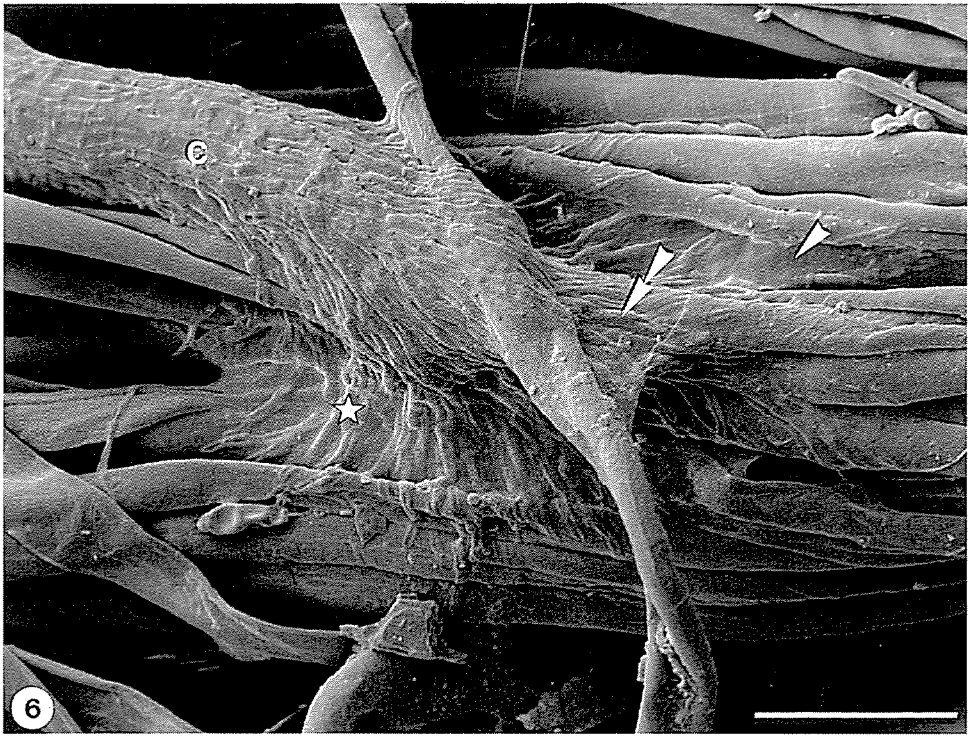
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After 2 months the scar where the isidium had formerly been fixed to the parent thallus was still visible, although the coralloid protuberances of the isidium continued to grow (Fig. 22). Within 4 months the propagules developed into ramifying granular clusters, probably derived from the aggregation of isidia (Fig. 23); only after 24 months did the coralloid outgrowths of the isidium develop into spathulate lobules less than 0.2 mm long which further developed into longer, 1–3 mm long lobes after 42 months (Fig. 20). No extracellular matrix was produced during the development of the juvenile thalli and it is still uncertain whether the hyphae visible on Figure 23 were formed by the propagules or not. No attachment hyphae were found in most of the developing diaspores studied so far (Fig. 24).

Interestingly, on both experimental sites "Eigeliswald" and "Fläschenwald" transplanted diaspores developed in a similar fashion, irrespective of the presence or absence of a natural population of *S. sylvatica*. At "Fläschenwald", the site without a natural population of *S. sylvatica*, also adult thalli transplanted did grow further. Numerous marginal lobes developed from their margins, which considerably increased the number of individually developing thalli.

On both experimental sites, successful development of the diaspores of *S. sylvatica* was only obtained if the artificial substrates were directly mounted on bryophyte-free patches of the bark. If they were transplanted on *Hypnum cupressiforme* or on surgical gauze fixed over the same moss species, the cultures were completely overgrown by the bryophyte and no successful development of *S. sylvatica* from diaspores occurred.

Figs. 7–8: *Parmotrema crinitum*
Fig. 7. Diaspores 11 months after transplantation: No attachment hyphae have been formed by outgrowing cortical or medullary hyphae. Two lateral pseudomeristematic growth zones developed into 0.1 mm long spathuliform lobules. Several marginal cilia (arrowheads) are formed. Bar ~ 100 µm.
Fig. 8. Diaspores 16 months after transplantation: Two lobes have been formed by an isidial fragment. The isidium is disintegrating. Bar ~ 100 µm.


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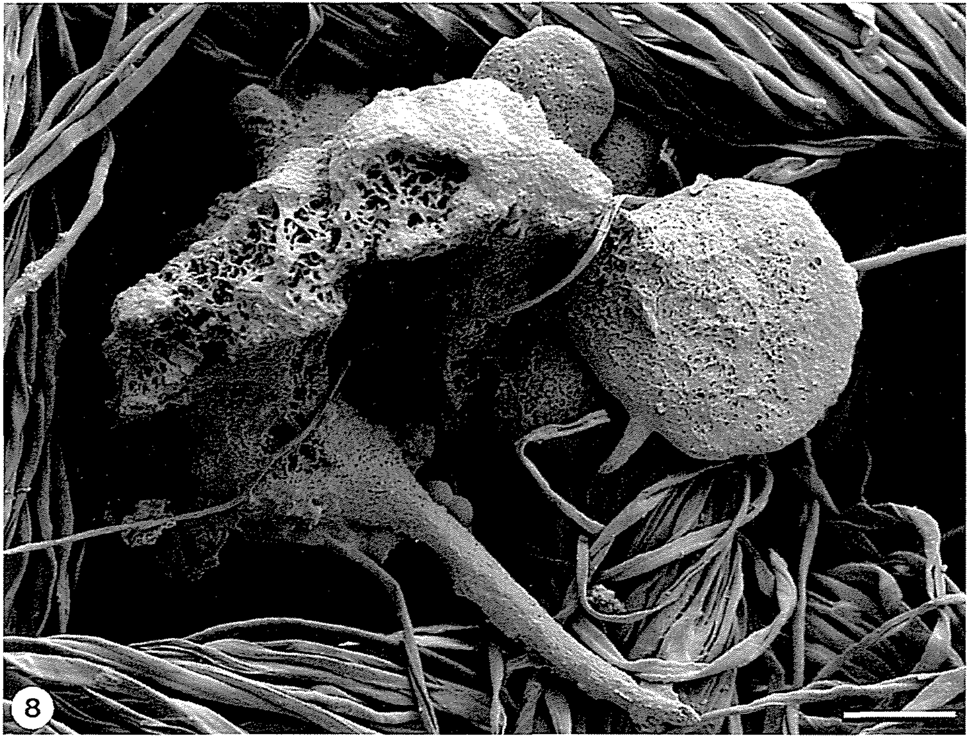
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Figs. 9–12: *Lobaria pulmonaria*. Corresponding points of figures 9–10 and 11–12 are marked with arrowheads.

Fig. 9. Adult thallus transplanted on the trunk of *Fraxinus excelsior*. The thallus fragment was transplanted in inverse geotropical position. Growing lobes are spoon-shaped or convex. Bar ~ 1 cm.

Fig. 10. Same thallus 26 months after transplantation. Canaliculate lobes are growing upwards. Bar ~ 1 cm.

Fig. 11. Diaspores transplanted on surgical gauze, immediately after transplantation. Bar ~ 1 mm.

Fig. 12. Same disc as in Fig. 11, 22 months after transplantation. Many diaspores had dropped but a few had regenerated into small lobes. Note bryophytes growing through the artificial substrate. Bar ~ 1 mm.

Fig. 13. Site with numerous small thalli of *Sticta sylvatica* (arrowheads). *Peltigera praetextata* (asterisk) is outside the area of the permanent plot (9. 1990). Bar ~ 1 cm.

Fig. 14. Same site as in Fig. 13, after 1 year. Bar ~ 1 cm.

Fig. 15. Same site as in Fig. 13, after 2 years. Bar ~ 1 cm.

Fig. 16. Same site after 4 years. *Peltigera praetextata* has overgrown about 50% of the permanent plot. Bar ~ 1 cm.

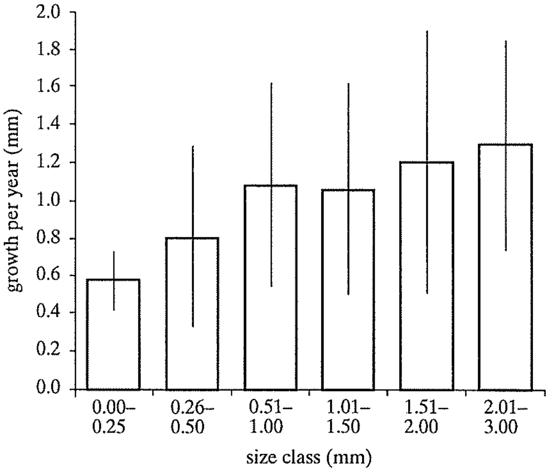

Fig. 17. Annual growth rate [mm year^{-1}] of different size classes of juvenile thalli of *Sticta sylvatica* as calculated from Figs. 13–16.

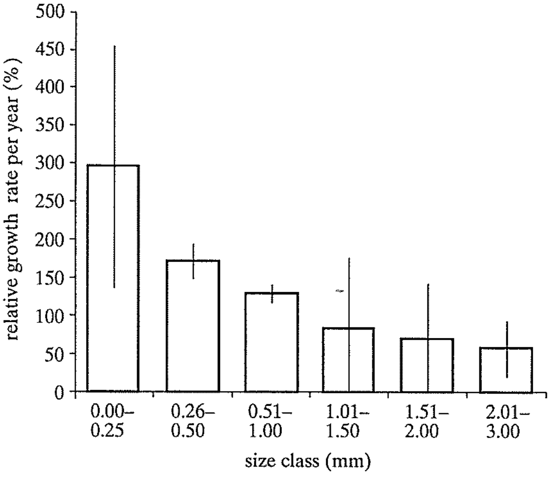

Fig. 18. Relative annual growth rates [year^{-1}] of different size classes of juvenile thalli of *Sticta sylvatica* as calculated from Figs. 13–16.


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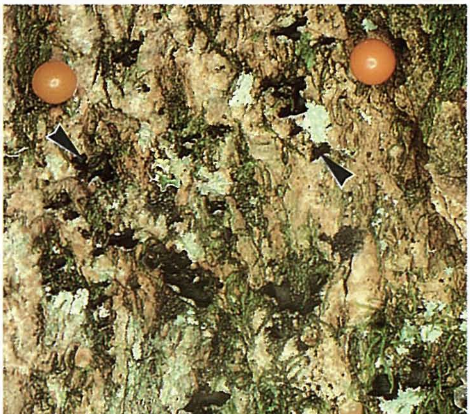
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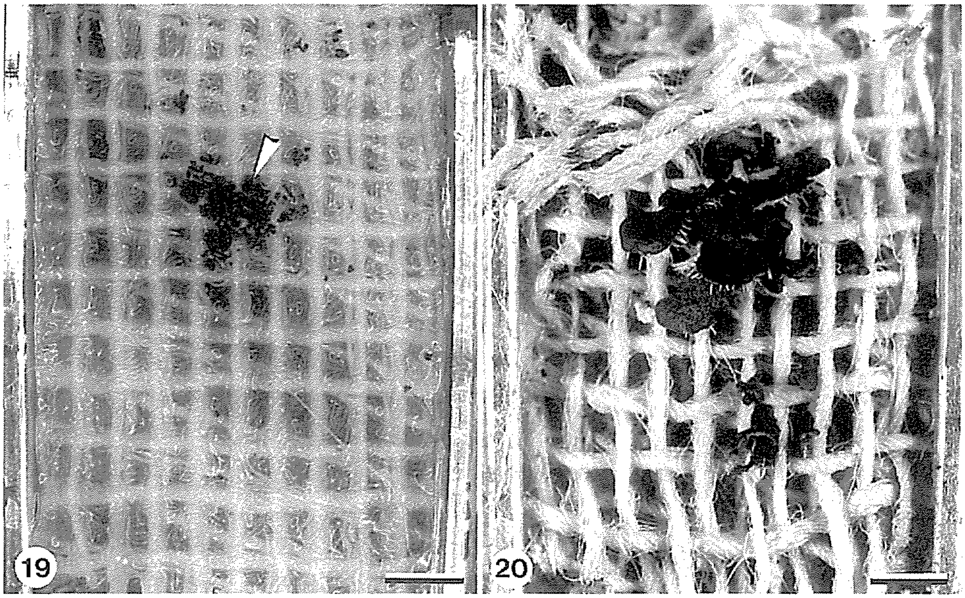


Figs. 19–20: *Sticta sylvatica*: macro-photographs of early development of transplanted vegetative diaspores.

Fig. 19. Disc of surgical gauze inoculated with isidia (arrowhead) of *Sticta sylvatica*. Isidia are predominantly between the fibres of the artificial substrate. Bar ~ 1 mm.

Fig. 20. Same disc as in Fig. 19, 42 months after transplantation. Numerous juvenile thalli developed. Note well developed tomentum on the lower cortex. Bar ~ 1 mm.

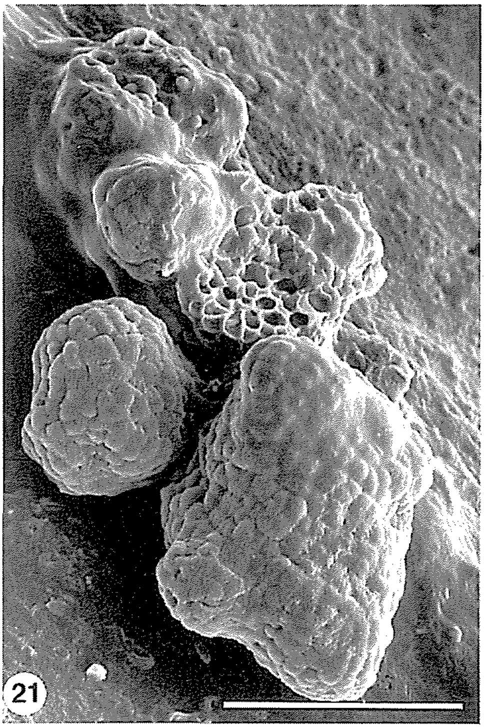
Figs. 21–24: *Sticta sylvatica*: LTSEM- micrographs of early development of transplanted vegetative diaspores.

Fig. 21. Thallus surface with granular and coralloid isidia. Note scar with paraplectenchymatous cortical hyphae where an isidium has broken. Bar ~ 50 μm.

Fig. 22. Coralloid diaspore on surgical gauze, 2 months after transplantation. Note scar where isidium was attached to the upper cortex of the thallus. Bar ~ 50 μm.

Fig. 23. Coralloid diaspores on surgical gauze, 4 months after transplantation. No attachment organs have been formed. Bar ~ 100 μm.

Fig. 24. Diaspore on surgical gauze, 24 months after transplantation. Spathulate lobules have developed out of the coralloid isidium. Bar ~ 100 μm.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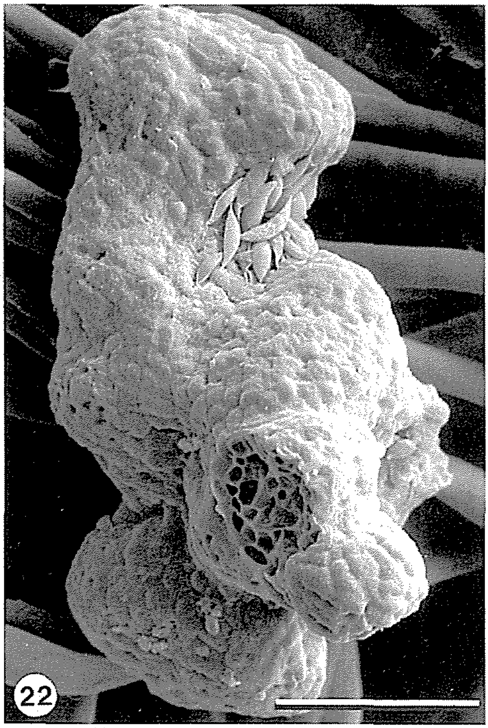
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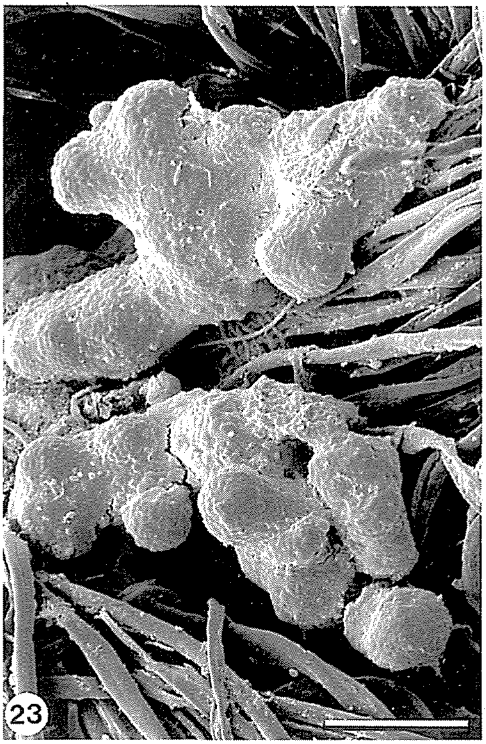
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4 Discussion

Transplantation of vegetative diaspores and adult thalli of various threatened foliose lichens such as *Sticta sylvatica, Lobaria pulmonaria,* and *Parmotrema crinitum* was found to be a successful approach for *in situ* conservation and enabled the establishment of additional populations.

Immobilization of diaspores on artificial and natural substrates seems to be a major limiting factor in the reproductive process, as has recently been shown for *L. pulmonaria* (SCHEIDEGGER 1995b) where vegetative propagules have no structures which could cause the immobilization of the diaspores. In this study we found that the isidia of *P. crinitum* were also not easily immobilized, even on a rough surface such as the cotton gauze. A substantial loss occurred if diaspores were put on the rough surface of the natural bark substrate. If the diaspores were placed onto the artificial substrate most of them fell off within the first months after transplantation. This was a somewhat unexpected result, as diaspores of *P. cinitum* have long subapical cilia (HALE 1965, OTT *et al.* 1993) which were expected to function as effective anchors of the diaspores on a rough surface. Only if isidia were carefully placed between the fibres of surgical gauze were a substantial percentage of the diaspores immobilized and producing anchoring hyphae from the tips of the isidial cilia thus improving their attachment to the substrate. Comparison of the mode of fixation and early development revealed important differences between the species: *P. crinitum* developed fascicles of anchoring hyphae only at the tips of the isidial cilia, whereas *S. sylvatica* never produced anchoring hyphae unless at first a tomentum was formed at the lower cortex of stratified juvenile thalli. Alternatively, isidioid soredia of *L. pulmonaria* developed anchoring hyphae derived from cortical cells at different parts of the propagule, forming broad, fan-shaped contact zones with the substrate as previously recorded by SCHEIDEGGER (1995b). A similar strategy of propagule attachment has been reported for *Hypogymnia physodes* (L.) Nyl. (SCHUSTER *et al.* 1985, OTT 1987a) where anchoring hyphae spread over the substrate and large amounts of an amorphous, cartilaginous, extracellular matrix were produced. In contrast to the rhizinate species, *Physcia tenella* (Scop.) DC., where rhizines formed very early in the thallus development are responsible for the elevation of the differentiating lobe, (OTT 1987a) the marginal cilia in *P. crinitum* did not function as stilts and developing lobes often remained adpressed to the substrate. The isidial cilia of *P. crinitum* have recently been described in detail (OTT *et al.* 1993). It is also interesting to note that in developing, spathuliform isidia, cilia were regularly formed next to growing pseudomeristems. In small lobes this coordinate development of a thallus lobe next to a marginal cilia regularly led to considerably asymmetric growth.

The development of stratified lobules was usually confined to a single pseudomeristematic zone in *L. pulmonaria* whereas in *S. sylvatica* and especially in *P. crinitum* several pseudomeristematic growth zones were initially developed leading to the initiation of several lobes. This formation of multiple lobes from propagules had been previously reported from studies of the soredial development, of, for instance, the foliose species *Hypogymnia physodes, Parmelia sulcata* Taylor, (OTT 1987a) and *Peltigera didactyla* (With.) Laundon (STOCKER-WÖRGÖTTER and TÜRK 1990), as well as in the fruticose species *Usnea filipendula* Stirton (SCHUSTER 1985). Furthermore, the development of multiple lobes seems to be typical for morphogenesis in *Xanthoria parietina* (L.) Th. Fr.

after sexual reproduction of (OTT 1987c), as well as mycobiont-photobiont resynthesis in *Cladonia furcata* (Schrader) Hudson (STOCKER-WÖRGÖTTER and TÜRK 1993) and *Peltigera praetextata* (Flörke ex Sommerf.) Zopf (STOCKER-WÖRGÖTTER and TÜRK 1991). The primary formation of single lobes which later rapidly divide has been reported from the isidioid *Parmelina pastillifera* (Harm.) Hale (HONEGGER 1987) and from the isidial development of *Peltigera praetextata* (Scheidegger unpubl.).

Parallel experiments with adult thalli and isidioid soredia of *L. pulmonaria* showed that adult thalli were able to grow at all localities selected, whereas vegetative diaspores only formed new lobes at two of the localities. This could indicate a broader ecological amplitude for the adult thalli as at the sun-exposed experimental site at "Fläschenwald" where surprisingly all the diaspores degenerated within a big population of mature *L. pulmonaria*. A possible explanation for this unsuccessful development was the altered light regime at the experimental site due to a recent wind-throw where some of the neighbouring shading trees were suddenly overturned.

Further, the observations at "Steinhuserwald" showed that even if the transplanted diaspores degenerated, a successful development of naturally dispersed propagules from a transplanted adult thallus, acting as a diaspore donor was possible within the next three years. Although we have no direct evidence from microclimate measurements, we believe that periods of unfavourable weather conditions were responsible for the degeneration of the transplanted diaspores. Some propagules which were continuously dispersed from a transplanted adult thallus, however, were able successfully to attach themselves to the natural substrate during a favourable weather conditions which allowed successful development into stratified thalli. Therefore a repeated transplantation of vegetative diaspores would probably be needed to promote the successful development into fully differentiated thalli and to establish new populations from diaspores artificially.

Our experiments demonstrated that the small population size of *S. sylvatica* was not primarily due to unfavourable microclimatic factors for juvenile development. The distribution of this species was clearly restricted by an inadequate reproductive potential and a low frequency of suitable habitats. By transplantation of vegetative diaspores it was therefore possible to increase the number of populations as expressed as number of trees colonized by the endangered lichen species. Increasing the number of populations in such small metapopulations is a promising approach for decreasing the probability of extinction and therefore improving the conservation status (MACE and LANDE 1991) of such species.

Either adult thalli or vegetative diaspores could be used for restorating endangered lichen populations. However, whenever possible the non-destructive method of transplanting vegetative diaspores should be first taken into account. Especially in small populations transplantation of adult thalli carries the risk of endangering natural populations further by fragmentation and should therefore only be used if insufficient numbers of diaspores are available. If adult thalli are to be transplanted, young lobes with intact growth zones should be selected in preference. Only in these cases transplants of *L. pulmonaria* were able to develop the faster growing lobes enabling them to colonize the new habitat. Lobes with sorediate margins were usually not able to develop satisfactorily and only in a few cases did marginal isidioid soredia develop into lobes which remained attached to the parent thallus.

In *S. sylvatica* the duration of the juvenile development from the transplantation of the isidia until the development of the first lobules of 0.2 mm length was 24 months. This is the longest period reported so far for lichens, although, apart from species with a ruderal ecological strategy (ROGERS 1990, SCHEIDEGGER 1995a), most lichenized ascomycetes have probably a relatively long juvenile phase within a typical period range from 8 to 15 months (SCHUSTER 1985, OTT 1987a, SCHEIDEGGER 1995b) until stratified thalli regenerate from vegetative propagules. In *S. sylvatica* this very slow growth seems to continue also after the development of stratified thalli and after 4 years only thalli about 3 mm large were present. The analysis of permanent plots with juvenile thalli further demonstrated that slow growth seems to be typical for this life stage, making it very vulnerable to competition and predation. Besides ecological parameters (OTT 1987b), competition seems to be a crucial factor in the establishment and development of lichens in general and especially of slow-growing species such as *S. sylvatica*. For reasons of bark acidity, *S. sylvatica* is restricted to *Acer pseudoplatanus* in the study area. Older trees usually have their trunks covered with mats of pleurocarpous bryophytes which make new colonization by *S. sylvatica* impossible. Only in gaps of this bryophyte cover, where bryophyte mats had fallen away due to disturbance, fluctuation or periodicity (VAN DER MAAREL 1988) or where scaley bark of the phorophyte had been shed, is a successful fixation possible, with the development into stratified thalli, and subsequent growth of this slow-growing species.

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Experiments with *P. crinitum* were established by Susanne Geissbühler (Bern). Stimulating discussions with Sieglinde Ott and Martin Jahns (Düsseldorf), and Pat Wolseley (London and elsewhere) are thankfully acknowledged.

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Biodiversity and Conservation of Foliicolous Lichens in Costa Rica

Robert Lücking
Abteilung Spezielle Botanik (Biologie V)
Universität Ulm, D-89069 Ulm, Germany

Abstract

The high species diversity of foliicolous lichens in Costa Rica is demonstrated at the regional, site, microsite, and sample level. Some 334 species are known from that region. Species diversity is affected by altitude, seasonality, and anthropogenic influence. In contrast, "form" diversity, measured as heterogeneity diversity of morpho-biologically different genera, is more affected by natural gradients, such as altitude and seasonality, than by anthropogenic influence. 213 species are found at a single site type (primary lowland wet forest), 177 at a single site ("Botarrama" trail), 84 at a single microsite type (margin of light gaps, phorophyte species *Ocotea atirrensis*), 65 at a single microsite (one phorophyte), and 39 (–68) on a single sample (leaf). These figures show that ecological equivalence of species contributes more to biodiversity than environmental heterogeneity and habitat adaptation. The principal mechanisms allowing co-existence of high numbers of ecologically equivalent species are discussed, such as reduction of population size, microhabitat fragmentation, and leaf renewal as an intermediate disturbance. If site biodiversity and uniqueness, together with ecological amplitudes of the species, are taken into consideration, lowland areas are more important for the conservation of foliicolous lichens than montane areas. The presence of the genus *Badimia* correlates with high foliicolous lichen biodiversity, so that this genus can be used to indicate sites of particular conservation potential with respect to foliicolous lichens and other organisms.

Keywords: *Badimia*, biodiversity, conservation, Costa Rica, foliicolous lichens, tropics

1 Introduction

Protection and conservation of organisms in nature can take place either at the species or site level. Although Red Lists of endangered species are widely used especially in Europe and North America (IUCN 1978; Blab *et al.* 1984; Sérusiaux 1989 a), these are often not more than status lists (Röser 1990; Eser *et al.* 1992; Munro 1993). Direct protection of a single taxon "*in situ*" is restricted to particular key species and more convenient for animals than for plants. This is mainly due to the lack of detailed knowledge of the biology of a species, especially population dynamics, which is necessary for its effective conservation (Eser *et al.* 1992).

In spite of the direct connection between the conservation of a particular species and the protection of its respective habitat, site protection on its own involves completely different strategies of selection and management. Therefore, quite different information is required with respect to site characteristics. Rather than the presence of key species, the overall importance of a site in terms of ecological significance, biodiversity, biological resources, and uniqueness, should be considered as a satisfactory criterion for site conservation (RÖSER 1990; ESER *et al.* 1992).

In areas where the ecological significance, resources, or the uniqueness of a site in question is unknown, its biodiversity becomes the most important parameter in relation to conservation procedures (GOLDSMITH 1987; PIELOU 1993). Biodiversity is thereby not only to be seen as species diversity, but also as the diversity of landscapes, ecosystems, and communities, as well as the diversity of populations and individuals (both at phenotype and genotype level), and the character diversity of a single individual (MUHLE 1978; SALWASSER 1993). However, species diversity is the most obvious and most objective index of biodiversity, and perhaps the most appropriate at hand with regard to conservation (PIELOU 1993).

Biodiversity, as a parameter for conservation purposes, is especially important in tropical regions, where our knowledge of biological backgrounds is still fragmentary, even though the influence of tropical ecosystems on the global climate is continuously discussed (ROTMANS and SWART 1991; DIXON *et al.* 1993, 1994). Site protection is also a question of availability of space, money, and politics, especially in the tropics, where virgin forests are converted at a high speed into cultivated land by a rapidly increasing human population (GROOMBRIDGE 1992; DAVIS 1993). Not all sites worthy of protection can really be preserved. Abundance of biological resources, and the probability that potentially important, but at present unknown, organisms are protected within a given site, are directly correlated with biodiversity. Thus, biodiversity becomes an important argument when discussing spatial and financial necessities and possibilities of conservation.

For conservation purposes in the tropics it is therefore a fundamental necessity to produce reliable data on site biodiversity, particularly species diversity. This aim is not easy to achieve because of the large number of still unknown or poorly understood taxa, especially among cryptogams and non-lichenized fungi (HAWKSWORTH 1991; GALLOWAY 1992a; GRADSTEIN 1992), and the scattered, sometimes inaccessible literature. Taxonomists are therefore urged to provide the preconditions for reliable species identifications in form of monographic or floristic work and adequate preservation of reference material (NEVLING 1967; WILSON 1988; GALLOWAY 1992a; GRADSTEIN 1992).

In order to protect sites of high biodiversity, it is also necessary to understand the underlying natural mechanisms on which their maintainance depends. These mechanisms are still the subject of further discussion (HUSTON 1979; BOURGERON 1983; STOCKER *et al.* 1985; KUBITZKI 1985; LINSENMAIR 1990). In spite of, or rather because of, the contradictory experimental evidence, it seems clear that high biodiversity cannot be explained by a single hypothesis, but is itself dependent on a variety of diverse mechanisms. These mechanisms, in turn, might be influenced by particular circumstances, such as the kind of community or taxonomic group observed (SHMIDA and WILSON 1985). As to the selection and management of sites worth of protection, biodiversity must be considered more than a static parameter. Factors responsible for high biodiversity, and conditions necessary for their function, must also be considered.

The present paper documents the high biodiversity of foliicolous lichens in Costa Rica at the regional, site, microsite, and sample level, and analyses the factors contributing to that biodiversity. Although no experimental evidence is available on mechanisms contributing to the maintenance of biodiversity in foliicolous lichens, the factors which are probably important are discussed here, and an attempt is made to point out the implications for effective conservation of foliicolous lichen diversity in the tropics. The genus *Badimia* is used as an example how the protection of single taxa and the conservation of sites of high biodiversity can go hand in hand.

2 Material and methods

2.1 Investigated area

Costa Rica is located in the southern part of Central America, between 8° 01' and 11° 13' N, and 82° 33' and 85° 58' W. It covers an area of about 51,100 km^2 (GÓMEZ 1986). A range of four mountain ridges, with the highest point (Cerro "Chirripó") reaching 3819 m above sea level, divides the country into an Atlantic and a Pacific side (Fig. 1).

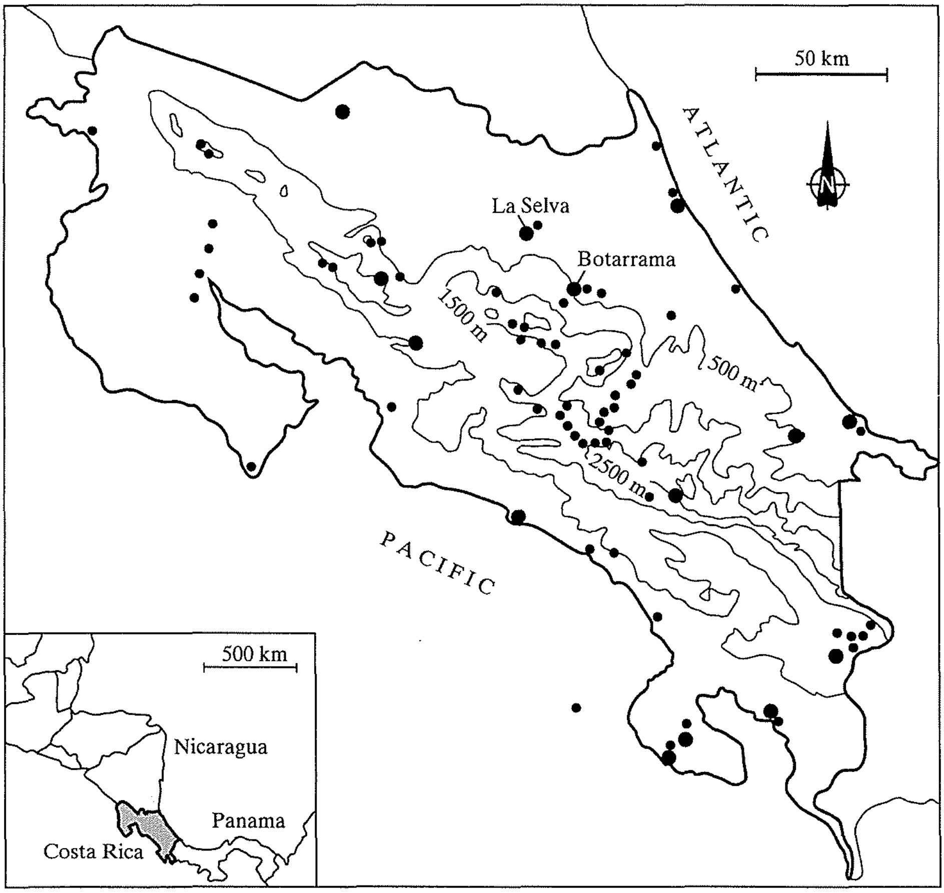


Fig. 1. Geographical situation of Costa Rica, and location of the studied sites. The larger circles represent localities with more than one site type included.

The climate is distinctly oceanic (HERRERA 1985; COEN 1991). Annual precipitation in the Atlantic lowlands amounts to 2500–5500 mm, without a distinct dry season. The southern Pacific lowlands receive 3000–6000 mm, with a distinct dry season between January and March. In the northern Pacific lowlands the precipitation is relatively low, 1300–2000 mm, with a marked dry season extending from December to April. Very high precipitation 5000–7700 mm and absence of any dry season is characteristic of the premontane and lower montane ranges of the Atlantic slopes, especially in the area of the Cordillera Central. A more distinct dry season is found on the southern Pacific slopes, which receive 3000–4500 mm precipitation. In the upper montane ranges, above 2500 m, the annual precipitation is between 2000–2500 mm. The mean annual temperature at sea level is 26 °C on the Atlantic side, and 27.5 °C on the Pacific side. Mean temperature decreases at 0.52 °C each 100 m altitude on the Atlantic slope, and at 0.57 °C on the Pacific slope (HERRERA 1985; COEN 1991).

According to HOLDRIDGE *et al.* (1971) and HARTSHORN (1991), Costa Rica includes twelve of the world life zones defined by HOLDRIDGE (1947, 1967), which are primarily delimited according to annual precipitation and temperature regime. Life zones in Costa Rica comprise tropical dry forest, tropical moist forest, tropical wet forest, tropical rain forest, with the respective altitudinal divisions (lowland, premontane, lower montane, montane), and the subalpine rain paramo (HARTSHORN 1991). Life zones change approximately each 500 or 1000 m of the altitudinal gradient (TOSI 1969). Most of the primary vegetation has already been converted into cultivated land or exhibits at least signs of anthropogenic influence (FOURNIER 1985; PORRAS and VILLARREAL 1985).

2.2 Collection sites and treatment of data

An earlier study of foliicolous lichens of Costa Rica was based on samples from 36 sites (LÜCKING 1992a, b, c). For this study, data from a further 93 sites, obtained during a second visit of the author in Costa Rica in 1991–1992, has been added (Fig. 1). A detailed taxonomic treatment of these collections is in progress (LÜCKING 1995a; LÜCKING and MATZER 1995; Lücking, in prep.). Species number ("richness diversity"; WHITTAKER 1972, 1977) was used as the principal biodiversity parameter. Four hierarchical levels, viz. regional diversity, site diversity, microsite diversity, and sample diversity, were considered. Different gradients were established to detect which components contribute the most to species diversity on a given level.

Regional diversity was estimated using the Atlantic/Pacific subdivision, altitudinal gradients, seasonality, and vegetation (anthropogenic influence) were considered. Altitudinal limits were set at each 500 m, where 0–500 m corresponds to the lowland, 500–1500 m to the premontane, 1500–2500 m to the lower montane, and 2500–3500 m to the montane belt of Holdridge's life zone system (TOSI 1969; HARTSHORN 1991). Seasonality was determined relative to the distinctness of the dry season, and six humidity provinces were distinguished (HERRERA 1985): No dry season (corresponding to rain forest in Holdridge's life zone system), slight dry season (wet forest), distinct dry season (transition between wet and moist forest), marked dry season, but vegetation evergreen (moist forest), marked dry season, vegetation evergreen along gallery forests, and marked dry season, vegetation deciduous (dry forest). The vegetation was assigned to five different types: Primary forest (HARTSHORN 1980), remnant forest (usually present in narrow stripes along flowing waters), secondary forest (Hartshorn 1980), forest margin, and anthropogenic vegetation (mainly plantations and fruit trees). Each of the 129 study sites was thus characterized by a combination of altitude, seasonality, and vegetation. Based on the species found at each locality, species number and species composition were computed for each type of altitude, seasonality, and vegetation.

For each species, geographical and ecological distribution type was determined. Five types of geographical distribution were distinguished: pantropical, neotropical-asian, neotropical-african, neotropical, and Costa Rican. Data were principally taken from Farkas and Sipman (1993), supplemented by the author's unpublished observations. The ecological distribution type was calculated by the formula $c = r_{alt.} \text{ x } r_{season.} \text{ x } r_{veget.}$, with c = coefficient of ecological distribution type, $r_{alt.}$ = altitudinal range of the species (number of 500 m-steps), $r_{season.}$ = seasonality range, and $r_{veget.}$ = vegetational range. In this way c can take values between 1 and 210 (7 x 6 x 5). Ecological distribution types were assigned to six classes: very rare, respectively strongly restricted (c = 1–3), rare (c = 4–15), moderately rare (c = 16–42), moderately common (c = 43–91), common (c = 92–165), and very common, respectively widely distributed (166–210). The value 210 refers also to the maximum number of possible site type combinations.

As a measurement for uniqueness, the percentage of geographical and ecological distribution types was calculated for each altitudinal step. Furthermore, of all species occurring in primary forests, the percentage of species occurring in both primary forests and at forest margins was computed. The ß-diversity ("dissimilarity"; Whittaker 1960; MacArthur 1965), between adjacent altitudinal steps was calculated using the formula $d = 1 - 2\, n_{a+b}/(n_a + n_b)$, with d = dissimilarity, n_a = species number at the first step, n_b = species number at the next step, and n_{a+b} = species number which both steps have in common. This formula represents the complement of the community coefficient of Sørensen (1948).

Data on site diversity, microsite diversity, and sample diversity were mainly obtained from Lücking (1994). Site biodiversity was estimated using: relative light intensity regime, relative air humidity regime, and phorophyte species. Five types of light and humidity regime were distinguished: very shady (0–1% average relative light intensity), shady (1–2%), moderately shady (2–4%), moderately light (4–8%), and light (8–16[–30]%), respectively very humid (94–95% average relative humidity), humid (92–93%), moderately humid (89–91%), moderately dry (86–88%), and dry (82–85%). 39 phorophyte species were analysed.

In addition to species diversity, "form" diversity was estimated using the heterogeneity diversity of selected genera, which represent different types of thallus (colour/smooth – farinose – verrucose) and ascocarp structure (unorganized – organized/apothecioid – perithecioid – hysterothecioid), reproduction (sexual – asexual – vegetative/types of diaspores), and photobiont *(Trebouxia – Phycopeltis – Trentepohlia – Cephaleuros)*. The following 30 genera (of 54 occuring in Costa Rica) were selected: *Arthonia, Aspidothelium, Asterothyrium, Aulaxina, Bacidina, Bapalmuia, Badimia, Byssolecania, Byssoloma, Calenia, Chroodiscus, Coccocarpia, Cryptothecia, Dimerella, Echinoplaca, Enterographa, Fellhanera, Lasioloma, Linhartia, Loflammia, Mazosia, Opegrapha, Phyllophiale, Phyllobathelium, Porina, Sporopodium, Strigula, Tapellaria, Tricharia*, and *Trichothelium* (Fig. 2, 3). "Form" diversity was calculated by the following formula: $div_f = -1 \sum p_i \log(p_i)$, with div_f = form diversity, and p_i = percentage of the genus i, expressed by its relative spe-

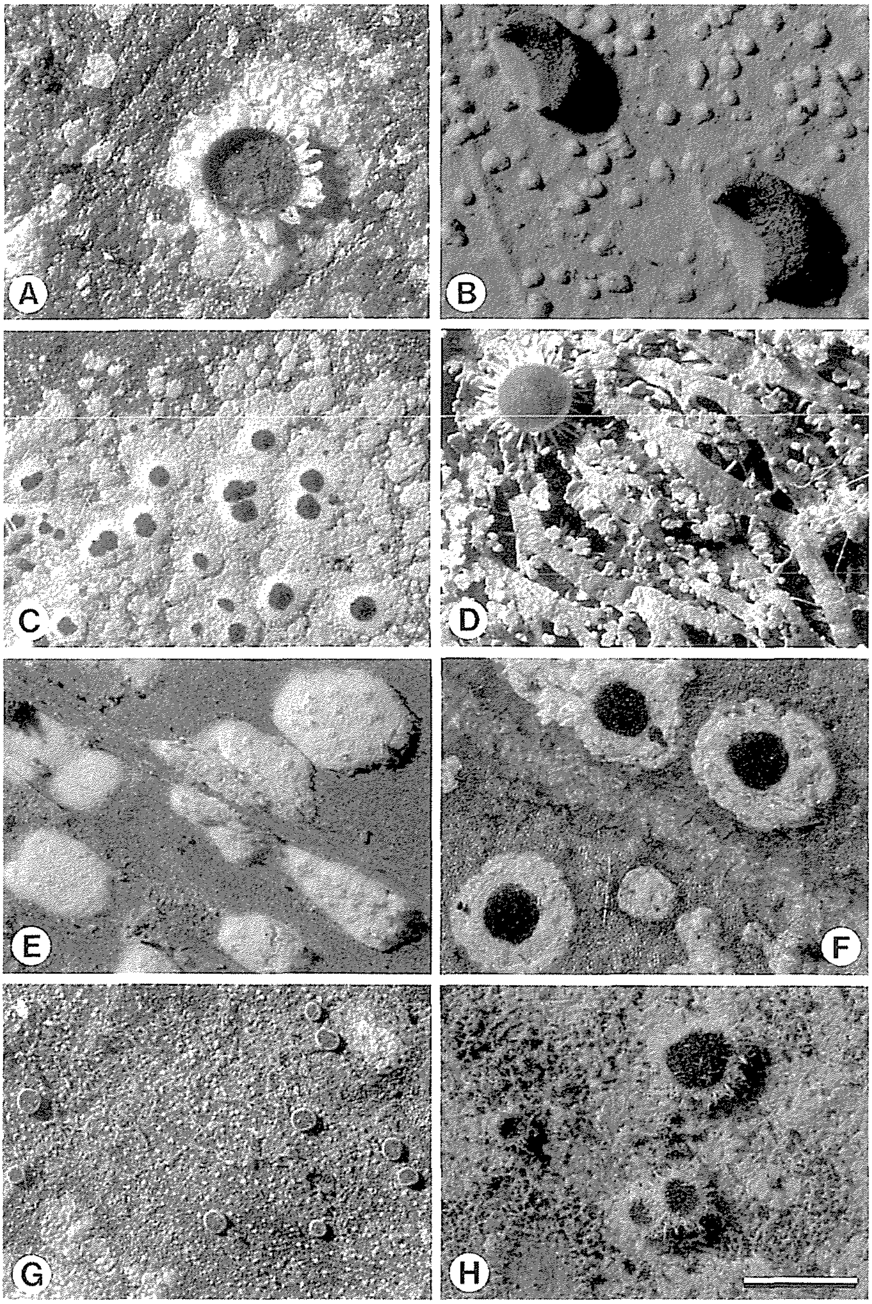


Fig. 2. "Form" diversity of foliicolous lichens in Costa Rica. (A) *Asterothyrium pittieri* Müll. Arg. (B) *Badimia galbinea* (Kremp.) Vězda. C) *Byssoloma subdiscordans* (Nyl.) P. James. (D) *Coccocarpia domingensis* Vain. (E) *Cryptothecia candida* (Kremp.) R. Sant. (F) *Echinoplaca atrofusca* R. Sant. (G) *Fellhanera verrucifera* R. Lücking. (H) *Lasioloma arachnoideum* (Kremp.) R. Sant. Bar ~ 1 mm.

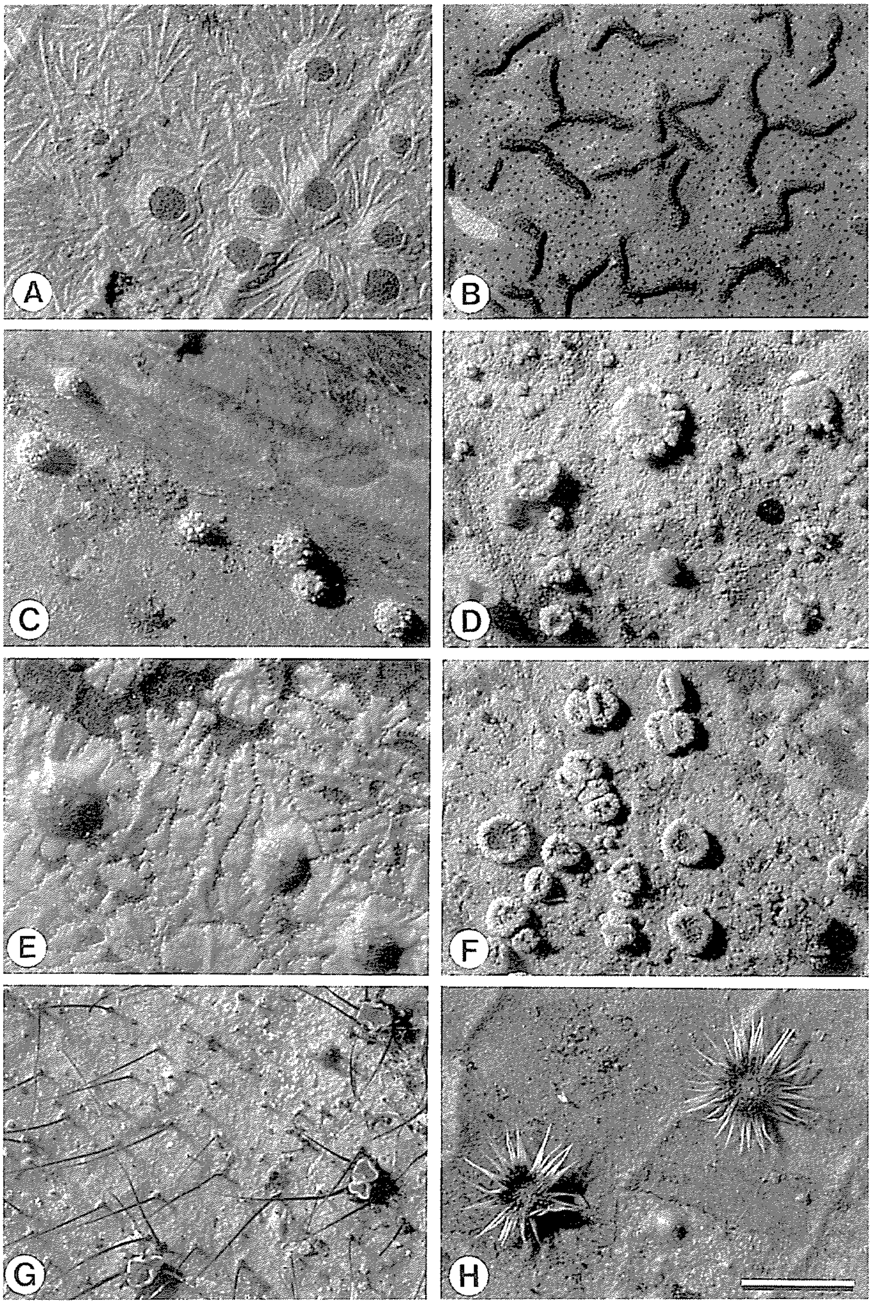


Fig. 3. "Form" diversity of foliicolous lichens in Costa Rica (cont.). (A) *Mazosia rotula* (Mont.) Massal. (B) *Opegrapha filicina* Mont. (C) *Porina papillifera* (Stirt.) F. Schill. (D) *Sporopodium xantholeucum* (Müll. Arg.) Zahlbr. (E) *Strigula nemathora* Mont. (F) *Tapellaria nana* (Fée) R. Sant. (G) *Tricharia urceolata* (Müll. Arg.) R. Sant. (H) *Trichothelium argenteum* R. Lücking & Ferraro. Bar ~ 1 mm.

cies number. This formula is equivalent to the Shannon-Weaver-Index (SHANNON 1948), often used to calculate heterogeneity diversity (LLOYD and GHELARDI 1964; PEET 1974; MUHLE 1978). "Form" diversity is the highest if as many genera of different morpho-biological types as possible occur, and if the distribution of species among different genera is as homogeneous as possible. As morpho-biological characters could be regarded as adaptations (LÜCKING 1992b, 1994), "form" diversity might depend on the available site or microsite types. The selection of genera in this case seems appropriate as the species belonging to one and the same genus are remarkably uniform as to their morpho-biological characters and their ecology (LÜCKING 1992a, b, 1994).

3 Results

3.1 Regional diversity

Of the 334 foliicolous lichen species presently known to occur in Costa Rica, 35% are pantropically distributed, whereas 26% are actually reported from Costa Rica only (Lücking, in prep.). The smallest group, neotropical-asian species, is represented by 5% (Fig. 4 A). Within the ecological distribution types, the very rare and rare species amount to 62.5%, whereas the common and very common species make up only 3.3% (Fig. 4 B). The Atlantic side is richer in species (308) than the Pacific side (243), and includes as much as 92% of Costa Rica's species diversity. 91 species are exclusive to the Atlantic side, whereas 26 species are confined to the Pacific side only, mainly restricted to the southern Pacific lowlands. 65% of all species occur on both the Atlantic and Pacific side.

Species number is the highest at low altitudes and decreases with altitude (Fig. 5). 252 species, i.e. 75% of the overall species diversity, are found at 0–500 m above sea level. If species numbers are summarized in order of increasing altitude, 307 species (92%) are already found between 0–1000 m above sea level, and 330 species (99%) between

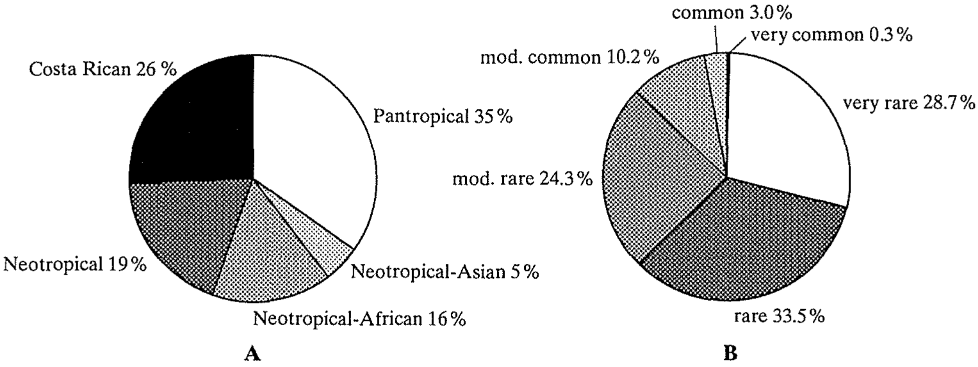


Fig. 4. (A) Percentage of geographical distribution types, and (B) percentage of ecological distribution types among the foliicolous lichens in Costa Rica.

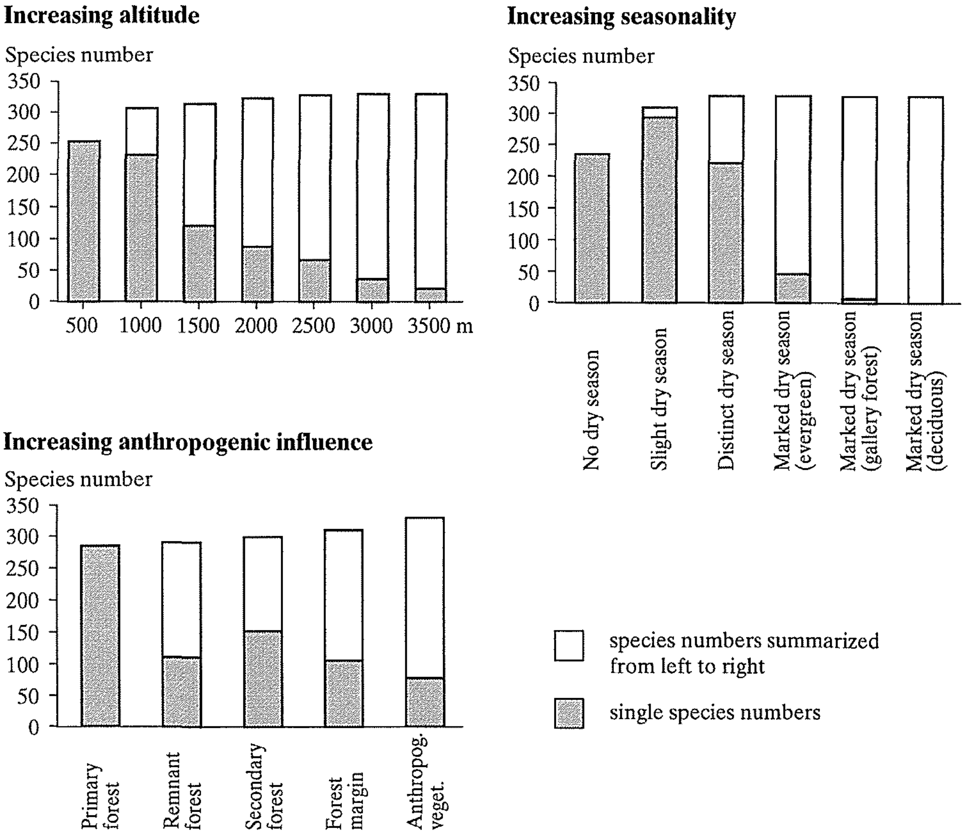


Fig. 5. Species diversity of foliicolous lichens in Costa Rica along altitudinal, seasonal, and vegetational gradients.

0– 2500 m. The pattern regarding seasonality and vegetation is slightly different (Fig. 5). The highest species number is found at sites with a slight dry season. As to the vegetation, the highest diversity must be attributed to primary forests with 283 species, whereas secondary forests support only slightly more than half of that number. Even so 78 species are found within anthropogenic vegetation. Whereas sites of high altitude (above 2500 m) and sites with a marked dry season hardly contribute to overall diversity, the opposite is the case with anthropogenic vegetation, where 20 species not found in other vegetation types are present.

The ß-diversity ("dissimilarity") between each of the seven altitudinal steps shows two distinct peaks at 1000 m and at 2500 m altitude (Fig. 6). Species turnover is largest at the step from below to above 1000 m, and at the step from below to above 2500 m. The percentage of geographical distribution types exhibits no distinct pattern along the altitudinal gradient (Fig. 7), except for the pantropical type, which increases above 2500 m

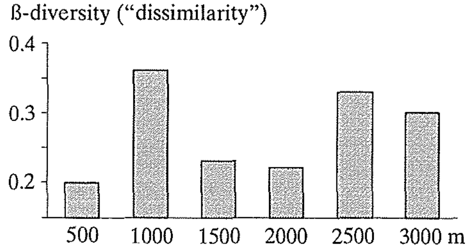


Fig. 6. ß-diversity (“dissimilarity”) between adjacent steps of the altitudinal gradient.

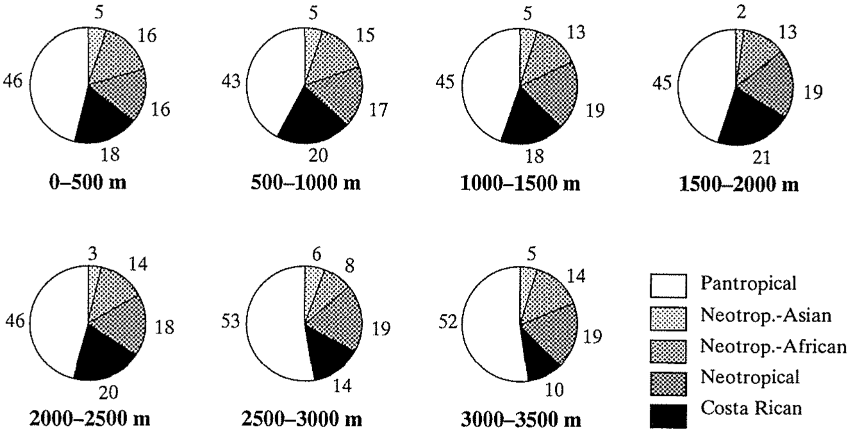


Fig. 7. Percentage of geographical distribution types along the altitudinal gradient.

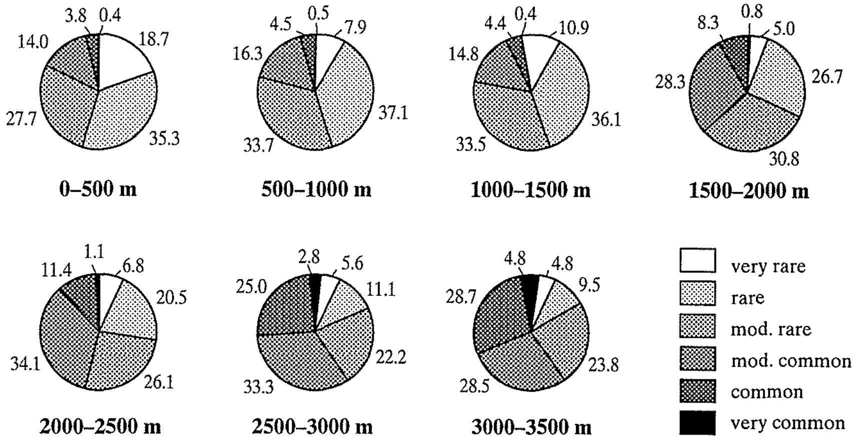


Fig. 8. Percentage of ecological distribution types along the altitudinal gradient.

($r = 0.80$, $p < 0.05$), and the Costa Rican type, which decreases above 2500 m. In contrast, the relative presence of ecological distribution types varies clearly with altitude (Fig. 8). Whereas the percentage of moderately to very common species increases with altitude ($r = 0.96$, $p < 0.001$), amounting to 18.2% at 0–500 m versus 62% at 3000–3500 m, the percentage of moderately to very rare species decreases in the same way. Very rare species are the best represented at 0–500 m. The percentage of species that occur both within the understory of primary forests and at forest margins increases with altitude, forming a saturation curve (Fig. 9).

"Form" diversity reaches maximum values of $div_f = 1.34$ both on the Atlantic and the Pacific side, with all 30 selected genera present on both sides. "Form" diversity and genus number decrease with altitude (Fig. 10). Both "form" diversity and genus number are almost identical at sites with absent to distinct dry season, but drastically decrease at sites with marked dry season. With regard to vegetation, "form" diversity and genus number are high in primary forests, but even higher in secondary forests and at forest margins, and only slightly lower in remnant forests and in anthropogenic vegetation (Fig. 10).

If altitude, seasonality, and vegetation are combined, the species number is highest at the site combination 0–500 m altitude, slight dry season, and primary forest, which corresponds to primary lowland wet forest. 213 species, i.e. 64% of Costa Rica's overall diversity, occur in this site type. Seven localities can be assigned to this site combination, with an average species number of 97, and a maximum number found at "La Selva" of 128 species. The species number at a single site thus amounts to only half of the total species number if all sites of the same type are combined, indicating a relatively high ß-diversity ("dissimilarity") between ecologically equivalent sites.

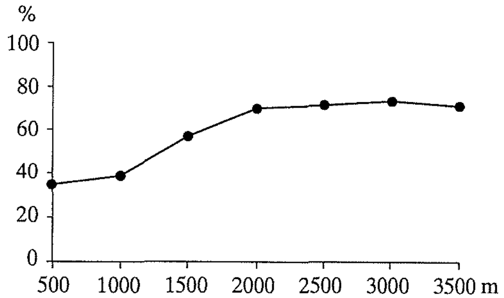


Fig. 9. Percentage of foliicolous lichen species in Costa Rica occurring both within the primary forest interior and at forest margins, relative to the total number of species occuring within the primary forest interior, along the altitudinal gradient.

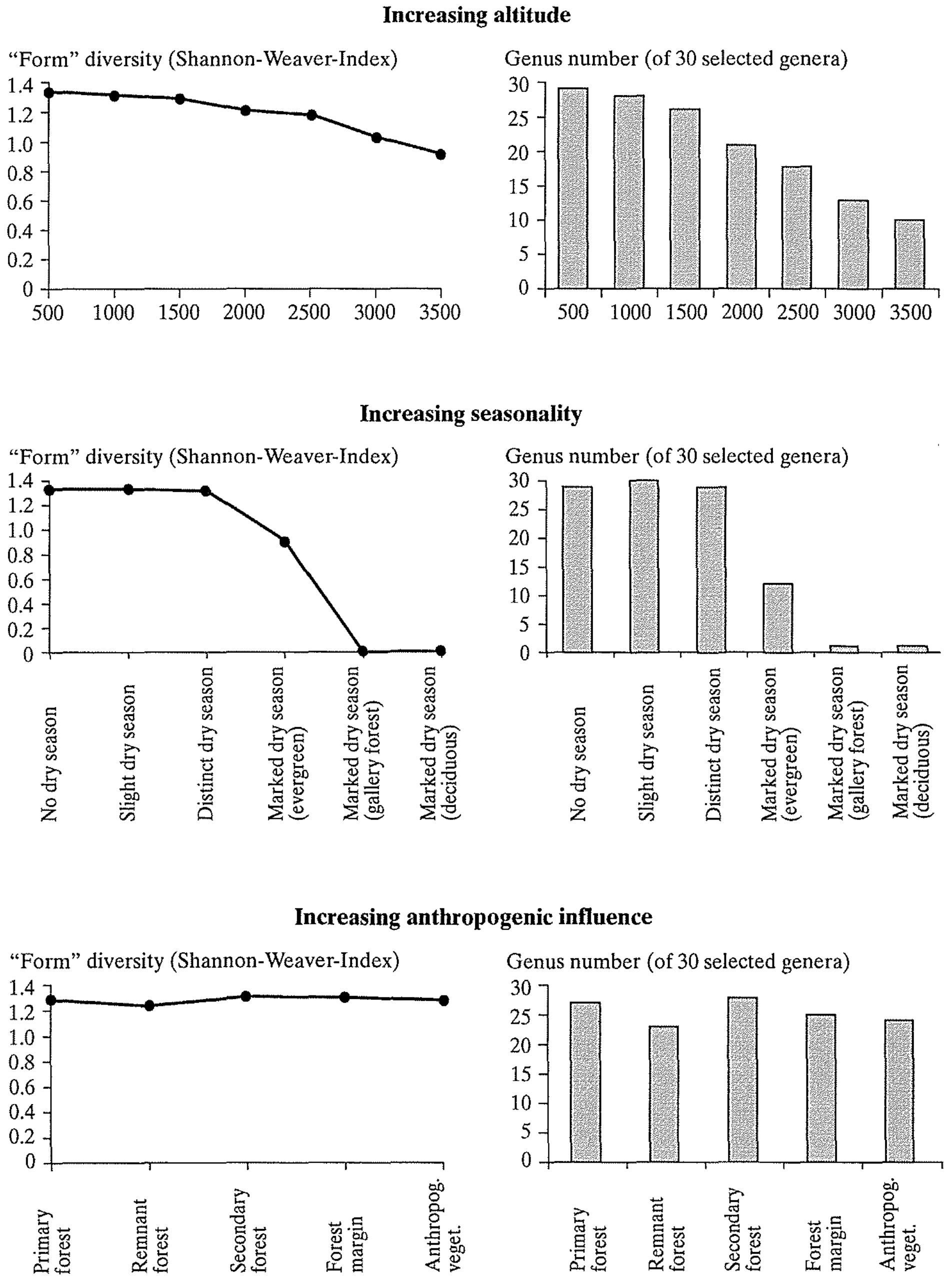


Fig. 10. "Form" diversity and genus number of selected genera of foliicolous lichens in Costa Rica along altitudinal, seasonal, and vegetational gradients.

3.2 Site diversity

The “Botarrama” trail, belonging to the site combination: 0–500 m altitude, no dry season, and primary forest, was selected because this site has been investigated more systematically than other sites, such as “La Selva”, and species numbers are thus more representative (LÜCKING 1994).

The total number of species found at the “Botarrama” trail is 177 (LÜCKING 1994), thus distinctly higher than at “La Selva”. About half of these 177 species must be considered as rare or very rare, as they occur on 10 or less of the 343 phorophytes investigated (Fig. 11 A). If the area covered by each foliicolous lichen species is related to the area covered by all individuals together (308,126 mm^2; Lücking, in prep.), this relation is even more pronounced (Fig. 11 B). 141 species are below the average area cover of 1740 mm^2, and 124 species are below half of the average area cover.

With respect to relative light intensity, the highest species diversity with 136–141 species (77–80%) is found under moderately shady to moderately light conditions (Fig. 12). A similar pattern is found with regard to relative humidity. Here, the highest

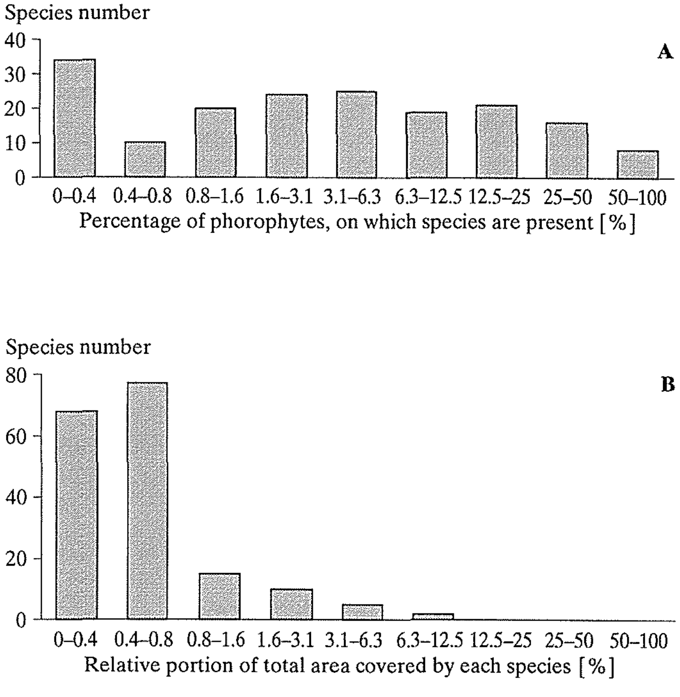


Fig. 11. Frequency (A) and relative area cover distribution (B) of foliicolous lichens occurring on the “Botarrama” trail (after LÜCKING 1994, and in prep.).

species numbers, with 141–143 species (80–81%), occur under moderately humid to moderately dry conditions (Fig. 12). Whereas shady and humid conditions are typical of the closed understory, light and dry conditions correspond to natural light gaps. Thus, species diversity is the highest at the transition between the closed understory and light gaps, open light gap conditions contributing more to the overall diversity than shady understory conditions. Of the 39 phorophyte species studied (Lücking 1994), *Ocotea atirrensis* clearly shows the highest diversity with 130 species (73%), 13 species being exclusive to that phorophyte, whereas the next species *Calyptrogyne condensata* has 45 species less (Fig. 13).

Of 975 (5 x 5 x 39) possible microsite combinations of relative light intensity, relative humidity, and phorophyte species, the highest diversity with 84 species is found under moderately light and moderately dry conditions, and with *Ocotea atirrensis* as phorophyte species. This is nearly half (47%) of the overall site diversity. Two phorophytes can be assigned to this combination, one with 65, and the other with 59 species, thus with an average number of 62 species, which corresponds to 74% of the single microsite combination diversity.

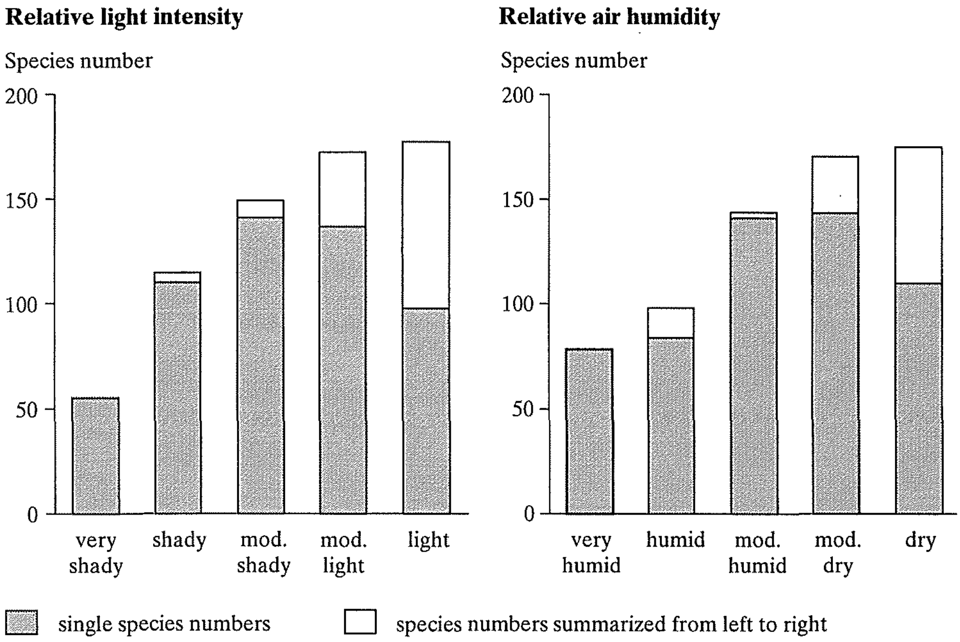


Fig. 12. Species diversity of foliicolous lichens on the "Botarrama" trail along a gradient of relative light intensity and a gradient of relative humidity (after Lücking 1994).

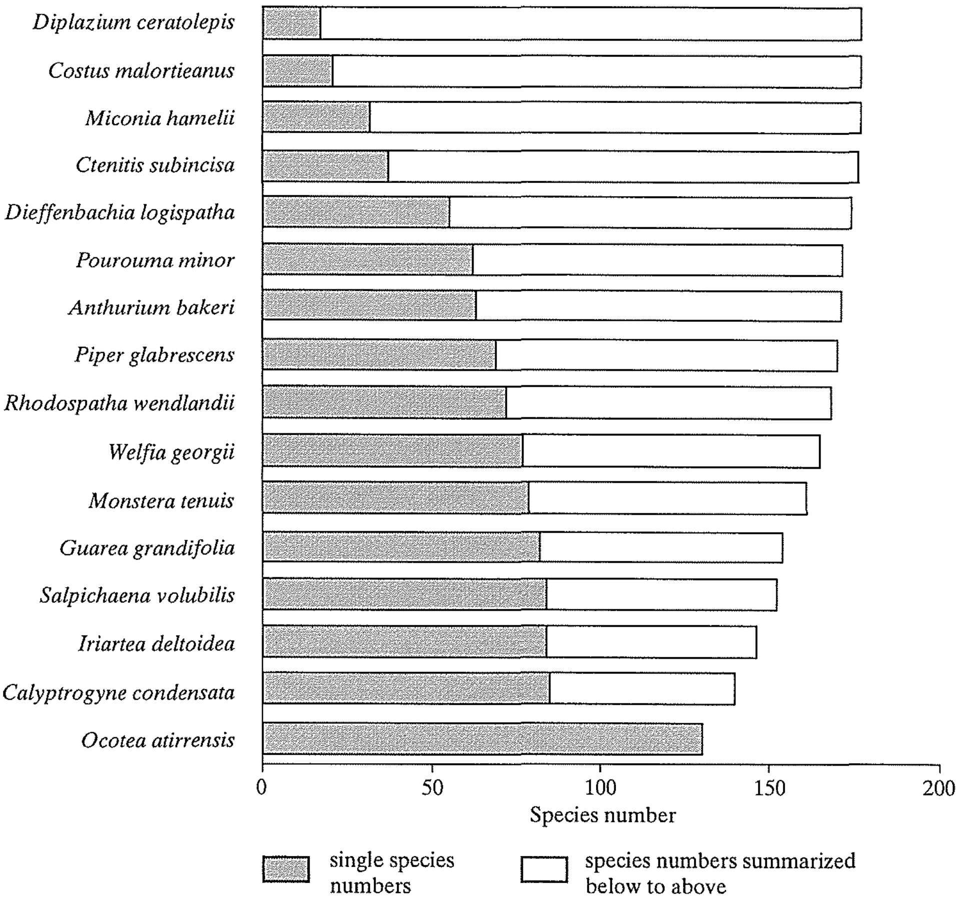


Fig. 13. Species diversity of foliicolous lichens on the "Botarrama" trail on 16 selected phorophyte species (of 39 investigated), beginning with the phorophyte species with lowest diversity (after LÜCKING 1994).

3.3 Microsite and sample diversity

Ocotea atirrensis, supporting 65 foliicolous lichen species, is now considered as one microsite of definite microsite conditions. On this phorophyte 25 subsequent leaves of a single shoot were investigated, with one leaf representing one sample (Lücking, in prep.). The highest species number found on a single leaf of that shoot was 38, which at the same time was the highest diversity found on any leaf of the 343 phorophytes studied (Tab. 1). However, 68 species were found on a leaf of *Carludovica palmata*, collected on the "Botarrama" trail, independently of the other studies. Furthermore a 0.7 dm^2 large leaflet of the climbing fern *Salpichlaena volubilis* showed a species density of 42 species/dm^2 (Tab. 1).

With some limitations, the subsequent leaves of a shoot, the so-called chronosquence, reflects the succession occurring on a single leaf over time (Rogers *et al.* 1994). The change in species number from the youngest to the oldest leaf is shown for the shoot of the phorophyte mentioned above (Fig. 14). A high variance is found between subsequent leaves, which might be due to spatial patterns or historical events occurring during succession. A smoothed curve, computed with CSS: STATISTICA™, using the Daniell-transformation (Bloomfield 1976), shows that species number increases with leaf age, but then slowly decreases, after a maximum diversity stage is passed, and shortly before leaves are shed. Other phorophytes display a similar diversity curve, whereas in some phorophytes, leaves are obviously shed before the maximum diversity stage is reached (Fig. 15). The age of the leaves with maximum diversity depends on the phorophyte species, but is usually between 24 and 32 months (Fig. 15).

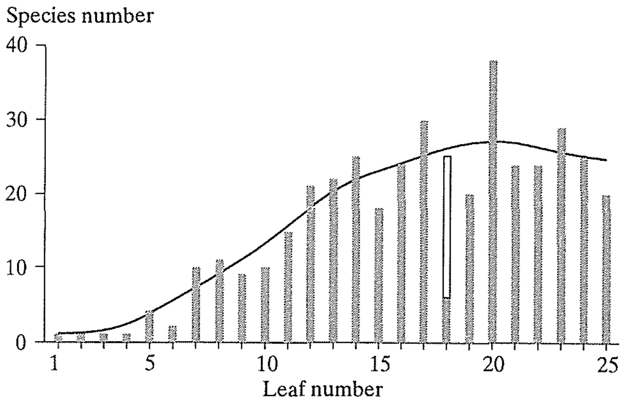
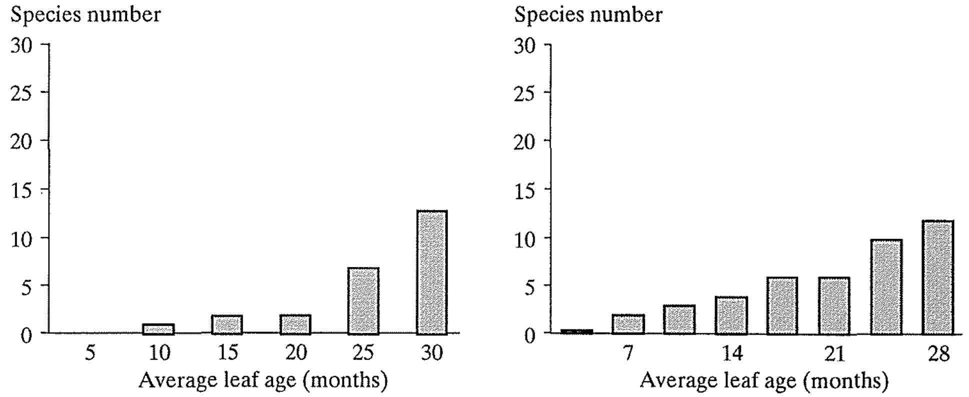
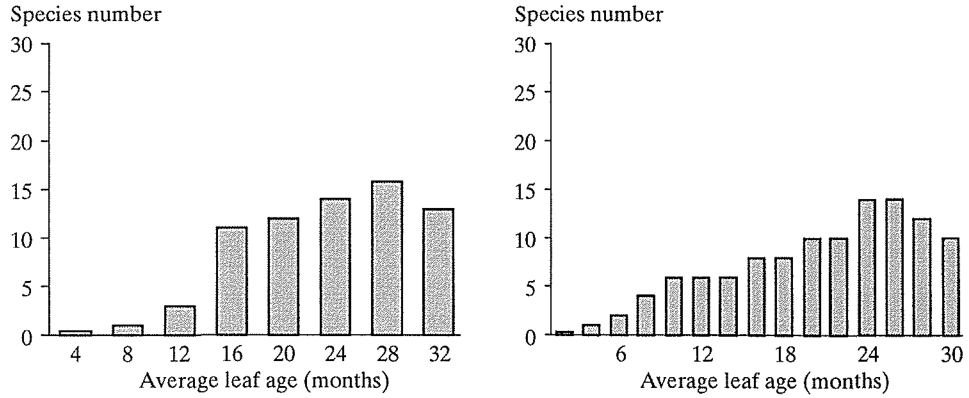


Fig. 14. Species diversity of subsequent leaves of a single shoot of *Ocotea atirrensis*, with a total species number of 65. The smoothed curve was computed with CSS: STATISTICA™, using the Daniell-transformation (Blomfield 1976; after Lücking, in prep.).



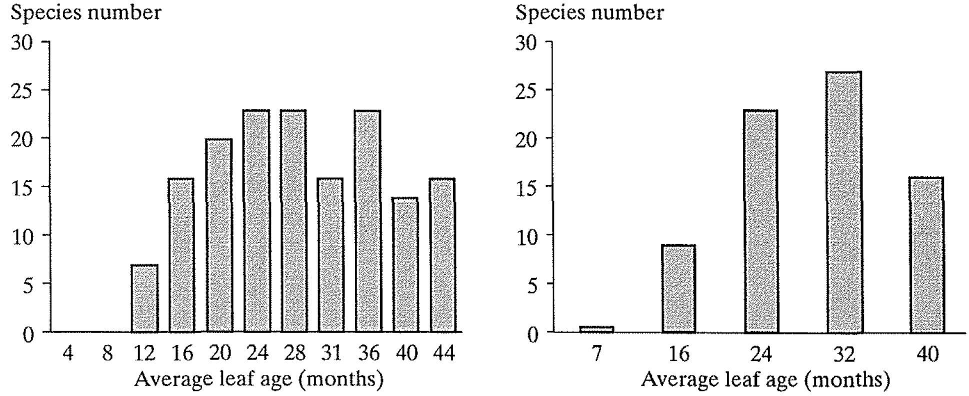
Dieffenbachia longispatha **(Araceae)**

Thelypteris gigantea **(Pteridophyta)**



Guarea kunthiana **(Meliaceae)**

Rhodospatha wendlandii **(Araceae)**



Guarea grandifolia **(Meliaceae)**

Welfia georgii **(Arecaceae)**

Fig. 15. Average species diversity of subsequent leaves of selected phorophyte species on the "Botarrama" trail, combined from 2–5 phorophytes per species occurring under shady understory conditions. Average leaf age is based on weekly observations of leaf exchange (after Lücking, in prep.).

Tab. 1. Single leaves with highest numbers of foliicolous lichens on the "Botarrama" trail, arranged by species diversity. The leaf with the highest species density (42 species/dm^2) is underlined

Phorophyte species	Family	Leaf type	Species number	Investigated leaf area [dm^2]	Species density [species/dm^2]
Carludovica palmata	Cyclanthaceae	palm	68	18.7	4
Ocotea atirrensis	Lauraceae	dicot	38	1.9	21
Monstera tenuis	Araceae	Aracean	37	6.6	6
Welfia georgii	Arecaceae	palm	37	7.2	5
Calyptrogyne condensata	Arecaceae	palm	35	1.8	32
Welfia georgii	Arecaceae	palm	35	4.5	8
Calyptrogyne condensata	Arecaceae	palm	34	3.2	11
Salpichlaena volubilis	Blechnaceae	fern	33	0.9	38
Salpichlaena volubilis	Blechnaceae	fern	33	1.0	33
Salpichlaena volubilis	Blechnaceae	fern	33	1.3	26
Guarea grandifolia	Meliaceae	dicot	33	1.5	23
Guarea grandifolia	Meliaceae	dicot	33	6.4	5
Guarea grandifolia	Meliaceae	dicot	32	1.2	27
Guarea kunthiana	Meliaceae	dicot	32	1.9	17
Ocotea atirrensis	Lauraceae	dicot	32	2.7	12
Guarea grandifolia	Meliaceae	dicot	31	1.5	21
Guarea kunthiana	Meliaceae	dicot	31	1.6	19
Guarea grandifolia	Meliaceae	dicot	31	6.9	4
Salpichlaena volubilis	Blechnaceae	fern	30	0.7	42
Guarea grandifolia	Meliaceae	dicot	30	1.5	20
Calyptrogyne condensata	Arecaceae	palm	30	1.9	16
Calyptrogyne condensata	Arecaceae	palm	30	2.6	12
Ocotea atirrensis	Lauraceae	dicot	30	3.5	8

3.4 *Badimia* – a case study of a possibly endangered taxon

The genus *Badimia* comprises eleven species, the majority being foliicolous taxa. The genus has a world-wide distribution, with two distinct diversification centres in the neotropics and tropical Australasia, whereas in tropical Africa it is scarcely represented. The most important species are *B. pallidula* (Kremp.) Vězda, *B. polillensis* (Vain.) Vězda, *B. dimidiata* (Babingt. ex Leight.) Vězda, *B. montoyana* R. Lücking, *B. viellardii* (Müll. Arg.) Vězda, *B. galbinea* (Kremp.) Vězda, *B. elegans* (Vain.) Vězda, and *B. tuckermanii* (R. Sant.) R. Lücking, Lumbsch & Elix. Of these, five species occur in Costa Rica or have been reported from there, viz. *B. pallidula, B. dimidiata, B. montoyana, B. galbinea*, and *B. tuckermanii* (SANTESSON 1952; SÉRUSIAUX 1986; VĚZDA 1986; LÜCKING 1992c; FARKAS and SIPMAN 1993; LÜCKING *et al.* 1994; LÜCKING and LÜCKING 1995; VĚZDA and LÜCKING 1995).

In Costa Rica, *Badimia* is confined to primary forests of low elevations (0–500 m, exceptionally up to 850 m), with the dry season absent or indistinct, as found in the Atlantic and southern Pacific lowlands (Fig. 16). In the lowland areas, this type of vegetation is practically confined to strictly protected areas, that means national parks, biological reserves, and wildlife refuges. However, if conditions are appropriate, members of *Badimia* are particularly common and often determine the foliicolous lichen flora of entire leaves in the understory, as in "La Selva" or the national parks of "Tortuguero" and "Corcovado". Similar observations have been made in foliicolous lichen collections from tropical Asia, especially New Caledonia (Kalb and Lücking, unpubl.).

Badimia dimidiata is the most common representative of the genus in Costa Rica (Fig. 16). *B. galbinea* is mainly found on the Atlantic side, whereas *B. pallidula* seems to be restricted to the southern Pacific lowlands. *B. montoyana* is hitherto only known from

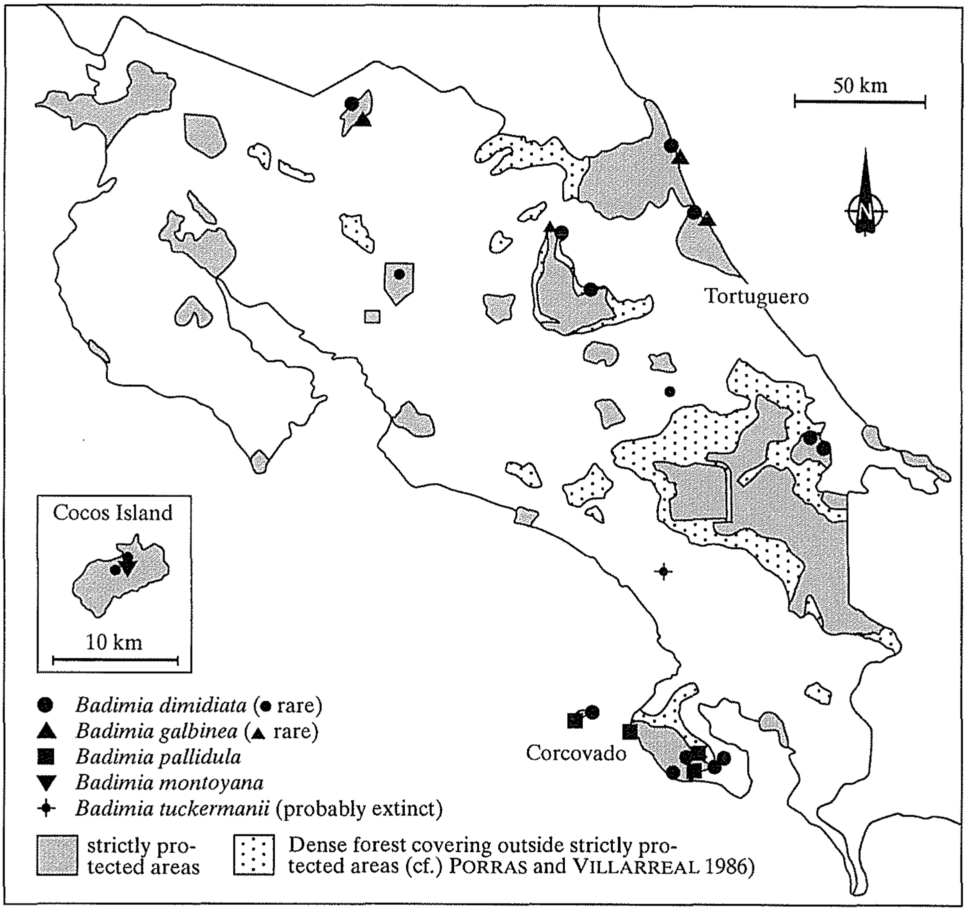


Fig. 16. Distribution of *Badimia* species in Costa Rica, relative to the location of strictly protected nature reserves and areas of dense forest covering. The locality of *B. tuckermanii* dates from 1894 (Pittier and Tonduz n. 6062, G) and is roughly approximated.

Cocos Island, an extracontinental possession of Costa Rica (LÜCKING and LÜCKING 1995). *B. tuckermanii* has been reported from Costa Rica only once (SANTESSON 1952) and is most probably extinct. *B. dimidiata* is a widespread and common species in the Neotropics and is also reported from Africa. *B. pallidula* and *B. galbinea* are mainly found in tropical Asia (Malesia), and *B. tuckermanii* occurs in Cuba (SANTESSON 1952; VĚZDA 1984), and is very common in New Caledonia (Kalb and Lücking, unpubl.). Most of the species are probably not directly endangered in terms of global abundance, but the restriction to primary forests in strictly protected areas in Costa Rica indicates that the genus is at least regionally threatened.

The site type at which *Badimia* is most common in Costa Rica is primary lowland (rain to) wet forest, and corresponds to the type with the highest species diversity of foliicolous lichens. The average species number of sites at which *Badimia* is abundant is 88. This figure comes very close to the 97 species representing the average of the site combination with the highest biodiversity. There is a high probability that the occurrence of *Badimia*, whose species are easily recognized in the field, indicates the sites of the highest foliicolous lichen biodiversity.

4 Discussion

4.1 Global importance of the foliicolous lichen biodiversity of Costa Rica

Estimations of known foliicolous lichen taxa include between 500–700 currently accepted species (FARKAS and SIPMAN 1993; Lücking, unpubl.). At present the foliicolous lichen flora of Costa Rica includes 334 species, representing c. 60% of the known taxa of the world. Costa Rica, covering only 0.03% of the earth's land surface, and 0.5% of the area usually referred to the tropics, supports about 50% of the global diversity of foliicolous lichens. This phenomenon is also known, to a lesser extent, from other organisms, for example flowering plants (BURGER 1980).

In contrast to higher plants or animals, a large percentage of foliicolous lichens reported from Costa Rica has a pantropical or at least a wide geographical distribution, whereas perhaps only a small part is really endemic, although many species are hitherto only known from Costa Rica. Costa Rica's contribution to global biodiversity of foliicolous lichens is thus smaller than indicated by the high species number, although its importance increases at the regional level. On the other hand, local populations of widely distributed species, although phenotypically similar, may differ genetically. With its high species number, Costa Rica gives a unique contribution to the global genetic diversity of foliicolous lichens, which might even be more important than simple species diversity (LEDIG 1993).

Another aspect of global importance is the fact that Costa Rica is perhaps one of the regions with the highest density of foliicolous lichen species worldwide. This provides an unique opportunity to demonstrate and investigate the biology and high biodiversity of foliicolous lichens on a very small scale.

4.2 Factors that contribute to biodiversity

Unfortunately, in spite of the pioneering work of DODGE (1933) and a modern, local treatment of KAPPELLE and SIPMAN (1992), who report 94 foliose and fruticose species from the Talamanca region, no comparable data exists on non-foliicolous lichens from Costa Rica. For bryophytes, annotated check-lists of mosses (BOWERS 1974; see also GRIFFIN and MORALES 1983) and hepatics (MORALES 1991; GRADSTEIN *et al.* 1995) are available, with more than 1000 taxa reported so far, but data on the distribution and ecology of single species is rather scarce.

However, the more detailed investigations of MONTFOORT and EK (1990), SIPMAN (1989, 1991, 1992a, 1992b), SIPMAN and APTROOT (1992), and WOLF (1993a–c) in South America (particularly Colombia, The Guianas, and Venezuela) allow at least some general conclusions with regard to non-foliicolous lichens. Allowing that the foliicolous lichen flora in the treatments cited above is 20–25% of the whole, and that foliicolous lichens could be determined to species level in 70% of all cases (SIPMAN 1991), but non-foliicolous lichens in only 50% (SIPMAN 1992a), then the total species number of a single country, such as Colombia or Costa Rica, might be estimated to be 6–8 times as high as the number of foliicolous lichens alone, that is 2000–3000 taxa. This figure seems not to be exaggerated, as for example the well-known British lichen flora contains some 1730 species (GALLOWAY 1992a), and tropical regions, especially if they include both lowland and higher montane areas, are generally believed to be more rich in lichen species than temperate zones (SIPMAN and HARRIS 1989).

In non-foliicolous lichens, the highest species numbers seem to occur in mid-elevation ranges from above 1000 m to below 3000 m, and single vegetation types may shelter several hundred species. Although the lichen flora is usually most conspicuous in montane areas, the highest percentage of specialized taxa (i. e. those taxa which occur only within one altitudinal belt) is found in the lowland rain forests, with up to 70% in comparison to some 20% in the páramo region (SIPMAN 1991). This means that also in non-foliicolous lichens the lowland zone contributes most to the overall diversity. The ecological differentiation, and thus the contribution of habitat preferences to the overall diversity, seems to be more pronounced in non-foliicolous than in foliicolous taxa (SIPMAN 1991), perhaps due to the higher competition with bryophytes and the more close relationship with the substrate.

As factors important for the maintainance of biodiversity are highly dependent on the taxon in question, it seems appropriate to compare the present data with those of other systematical groups, such as higher plants and animals. For example, the Atlantic/Pacific subdivision is one of the factors which account for the high biodiversity of organisms in Costa Rica. Of the 362 species of amphibians and reptiles known from Costa Rica, 45–50% are exclusive to either the Atlantic or the Pacific side (SAVAGE and VILLA 1986). As to foliicolous lichens, this effect is much less pronounced, with only 35% of the species being exclusive to either side. This percentage will be even reduced when more floristic data are available. The lower species diversity on the Pacific side coincides with the low diversity found at sites with marked dry season, as this site type is more pronounced on the Pacific side.

A large part of Costa Rica's foliicolous lichen diversity is already conserved within a single site type, the lowland wet primary forest, suggesting that the altitude, seasonal, and vegetational gradients are obviously not important factors for foliicolous lichen diversity. More than half of the regional diversity is found at a single site, within an area of only 1 ha. Almost 50% of the site diversity is concentrated at a single microsite type, more than 35% on a single phorophyte, and more than 20(–40!)% on a single leaf. The leaf area hearby amounts to only 0.0002% of the site area, and to much less if the leaf area index (LAI) is taken into consideration. In spite of its comparably small area, a single leaf may shelter up to 10% of the estimated global diversity of foliicolous lichens. This means an enormous increase of species density with decreasing area, much more pronounced than in other plant groups, as for example orchids, one of the largest families of flowering plants (LÜCKING 1994).

From these figures it becomes obvious that environmental heterogeneity and microhabitat adaptations can only explain a part of the diversity. This is especially interesting as environmental heterogeneity is often claimed to explain the high biodiversity of Costa Rica's phanerogam flora (BURGER 1980). The reduced effect of altitudinal zonation for the biodiversity of foliicolous lichens indicates that the evolution of these organisms mainly took place in lowland areas, a fact also confirmed by the high diversity of the Amazonian region (SANTESSON 1952; KALB and VĚZDA 1988a, b, 1990; Lücking and Kalb, in prep.), which is probably one of the centres of foliicolous lichen evolution.

Ecological equivalency must be considered as an important component of foliicolous lichen diversity in Costa Rica. According to SHMIDA and WILSON (1985), this accounts for diversity at a large scale, whereas at the small scale the niche relations are more important. However, the coexistence of that many species of foliicolous lichens on a single leaf, with no apparent niche differentiation (except for some specialists growing at the leaf margins or along major vains; cf. SÉRUSIAUX 1977, 1989b), shows that here the ecological equivalence is important also at the small scale. The global importance of ecological equivalence, as postulated by SHMIDA and WILSON (1985), is mainly due to geographical separation of similar habitats and convergent adaptations of non-related organisms.

The problem of biodiversity maintainance at the small scale is equivalent to the question of species survival. The latter depends on population size, as the probability that a species becomes extinct increases in reduced populations (WILCOX 1980). Besides intraspecific interactions, population size is regulated by the abundance of resources and by competition for these resources. Extinction of a population due to competitive exclusion can be avoided by specifically different resource exploitation, by means of different habitat preferences and niche adaptation (MACARTHUR 1965; WHITTAKER *et al.* 1973), by increased reproduction efficiency that allows reduction of population size ("escape in space and time"), and by mechanisms that avoid competitive exclusion of ecologically equivalent species.

Whereas niche differentiation is necessarily deterministic, the mechanisms that avoid exclusion of equivalent species are of stochastic nature. These mechanisms are for example niche or microhabitat fragmentation, in combination with diaspore dispersal, which allows the random establishment of different species in different fragments of the same niche or microhabitat (WHITTAKER and LEVIN 1977; SHMIDA and WILSON 1985). Intermediate disturbances, which prevent a community of ecologically equivalent species from being finally dominated by the strongest competitor, but do not exterminate the latter, are also important (CONNELL 1978). A further component of biodiversity is the so-called "mass effect", the phenomenon that species establish in habitats where they cannot be self-supporting (SHMIDA and WILSON 1985). These species cannot become extinct because re-establishment from outside the habitat is always possible.

In the case of foliicolous lichens, the discontinuous distribution of phorophytes and leaves which present more or less similar conditions might be considered as microhabitat fragmentation. Due to this discontinuity, the development and succession of potential microhabitat colonizers is independent within each microhabitat fragment, i.e. phorophyte or leaf, and thus different species have the same chance to establish themselves within different fragments. This effect is amplified by random dispersal of diaspores, which allows the species arriving first to establish themselves earlier than strong competitors. In this way disadvantages in competition capacity are compensated. The time course of succession along a single shoot indicates that leaf renewal forms an important intermediate disturbance, as leaves are usually shed shortly after the diversity maximum (CONRAN and ROGERS 1983; cf., however, ROGERS *et al.* 1994). A subsequent decrease of diversity, due to the growth of larger bryophytes and facultatively foliicolous lichens, is thus avoided. Furthermore, a large percentage of species, both on the site and regional level, are rare or very rare. Microhabitat fragmentation due to spatial isolation, random diaspore dispersal, continuous leaf renewal, co-occurrence of leaves of different age classes, and reduction of population size in many species, must therefore be considered as the main mechanisms of biodiversity maintainance in ecologically equivalent foliicolous lichens (LÜCKING 1994).

The site types of highest "form" diversity are not identical with those of highest species diversity. This shows that different parameters for biodiversity do not necessarily give the same information. "Form" diversity is obviously much less affected by anthropogenic influence than species diversity. The higher "form" diversity in secondary forests and at forest margins, in comparison to primary forests, is due to the fact that these figures are based on the understory level only. Preliminary investigations have shown that the canopy of primary forests shelters a foliicolous lichen flora very different from that of the understory, but in turn quite similar to that of open areas, such as plantations (SIPMAN and HARRIS 1989; LÜCKING 1995b). This is also the case for other organisms, for example grasshoppers (K. Riede, Freiburg, pers. comm. 1993). In secondary forests and forest margins there is a much more pronounced mosaic of microclimatic conditions reflecting both the understory and the canopy, so that understory and canopy species can live together within very small distances. The increase of diversity often observed in secondary forests and disturbed areas, especially with regard to lichens (GALLOWAY 1992a), might be due to an increase of "form" diversity, whereas the actual species diversity in fact decreases. As "form" diversity is correlated to site adaptations, the strong decrease of species diversity, in comparison to "form" diversity, in secondary habitats indicates a reduced capacity of co-existence of ecologically equivalent species in these areas.

The percentage of species with both restricted geographical and restricted ecological distribution decreases with altitude, in favour of species with wide geographical and ecological amplitude. Therefore, in terms of uniqueness, lowland areas are more exclusive than montane areas. Apparently, there is no higher rate of speciation among foliicolous lichens of ecogeographically isolated montane areas, as often observed in other organisms. This coincides with the high number of pantropically distributed taxa, showing that many species retained their habit during long time of geographical isolation. This is a general phenomenon in lichens (SIPMAN 1991, 1992a; GALLOWAY 1992a) and perhaps other cryptogams, and is also confirmed by the low rate of endemism in remote areas, such as Cocos island (LÜCKING and LÜCKING 1995). Presumed endemism of foliicolous lichens in montane areas, as reported for the Costa Rican *Porina umbilicata* (Müll. Arg.) F. Schill. and *P. barvica* R. Lücking (SANTESSON 1952; LÜCKING 1991, 1992c), must often be corrected, due to subsequent detection of the species in other parts of the world. This is also the case with the two species mentioned above, which have recently been found in Colombia (Lücking and Henssen, in prep.).

4.3 Implications for foliicolous lichen conservation

For both biodiversity and uniqueness lowland primary forests are the most important sites for the conservation of foliicolous lichens, at regional and global level. In this category in Costa Rica the highest species diversity is conserved, and the highest percentage of species with restricted geographical and ecological distribution found. This is especially significant as lowland forests are destroyed on a much larger scale than montane forests, where forest destruction often leaves a dense mosaic of forest remnants, especially along flowing waters.

Furthermore, montane areas support a distinctly higher percentage of species which occur both in the primary forest and at forest margins. This is probably due to the less pronounced climatic differences between the forest interior, the canopy level, and the forest margin at higher altitudes. In lowland areas, microclimatic gradients are more distinct because of the longer lasting direct radiation and higher temperatures. Hours of direct solar radiation in Costa Rica amount to 4–5.5 per day in the lowland areas, but only 3–4 in the higher montane areas (HERRERA 1985; COEN 1991). As deforestation increases the relative proportion of forest margin vs. forest interior, species diversity and composition change more dramatically in lowland than in montane areas, even if deforestation rates are similar. Foliicolous lichens of the interior of lowland primary forests are therefore particularly threatened, whereas in montane areas a relative diverse foliicolous lichen flora is maintained within small, semi-exposed forest remnants.

In spite of the importance of lowland forests for the protection of foliicolous lichens, it should be emphasized that the altitudinal gradient contributes at least partly to the overall species diversity. If the canopy flora of the primary forest is taken into consideration, the altitudinal gradient is definitely more important than the vegetational gradient. According to the ß-diversity along the altitudinal gradient, sites at 0–500 m, 1500–2000 m, and 2500–3000 m, together should shelter a maximum of species diversity.

Besides heterogeneity, area is often quoted as an important parameter for the selection of sites appropriate for conservation. The advantages and disadvantages of large, continuous areas, against a number of similar small, but discontinuous areas, are thereby discussed (ESER *et al.* 1992). Based on the theory of island biogeography (MACARTHUR and WILSON 1967), species diversity should be a function of area, an assumption which has often been claimed for the design of nature reserves (ZIMMERMAN and BIERREGAARD 1986; BOND *et al.* 1988; RÖSER 1990; ESER *et al.* 1992). With the data available at present, it is not possible to state whether at the scale at which sites are usually protected, area is an important factor for foliicolous lichen diversity. The example of the "Botarrama" trail shows that already above the scale of 1 ha there is possibly no substantial increase of diversity if site conditions are homogeneous (LÜCKING 1994). On the other hand, the distinctly reduced species number in narrow remnant forests along rivers and creeks indicates that area might affect species diversity under certain circumstances. Perhaps more important than area alone is the presence of a buffer zone between the interior and exterior of a reserve. Such a buffer zone does not usually exist in remnant forests. The relatively low average species number found at the sites representing primary lowland wet forest, in comparison to the total species number found at that site combination, is probably due to insufficient sampling, rather than to real differences in species composition. At least in the case of foliicolous lichens, protection of ecologically different sites might thus be more efficient than preservation of a single, large site, or of several small, ecologically similar sites.

Although area in general is undoubtedly an important consideration when establishing the boundaries of nature reserves, it is now more accepted that species diversity is not a simple function of area, but ecological factors must also be taken into consideration (ZIMMERMAN and BIERREGAARD 1986; BOND *et al.* 1988). If ecological equivalence contributes substantially to biodiversity, nature reserves must be selected and managed to allow the mechanisms responsible for the maintainance of high diversity to operate. The low species diversity in disturbed areas, in comparison to the high "form" diversity, shows that here the mechanisms in question fail to function.

Protection of single taxa in the tropics is usually not appropriate, except for larger mammals, but the example of *Badimia* shows that key species can help with the selection of sites of high biodiversity appropriate for conservation. The importance of lichens as indicators for environmental changes in the tropics and subtropics has already been shown (KANTVILAS and MINCHIN 1989; WOLSELEY 1991; WOLSELEY and AGUIRRE-HUDSON 1991; GALLOWAY 1992b). Members of *Badimia* share an important feature of bioindicators in general, as they are obviously common when conditions favour high biodiversity of foliicolous lichens, but disappear with smallest signs of anthropogenic influence. In Costa Rica, the occurence of *Badimia* proves "Tortuguero" on the Atlantic side and "Corcovado" on the Pacific side to be important sites, worthy of protection. These two areas, especially "Corcovado", are often cited as belonging to the most important, still intact lowland rain forest areas in Central America (BOZA and MENDOZA 1981; HARTSHORN 1991). This demonstrates the possible importance of *Badimia* as a key taxon, not only for foliicolous lichens, but perhaps for lowland regions in general. The inclusion of already protected areas as worth of conservation might be criticized as being superfluous, but the still uncontrolled and illegal logging in marginal parts of these nature reserves proves the opposite.

It is clear that the preceeding statements are based on data obtained from foliicolous lichens only. Although general conclusions can be drawn from the data, if other organisms are considered, the detailed picture might be different. For example, macrolichens growing on bark are much more frequent and diverse in montane areas between 1500 and 2500 m, and are often more richly developed in the canopy than in the understory (POELT 1973; SIPMAN 1989; SIPMAN and HARRIS 1989; WOLSELEY 1991). When discussing priorities for conservation, taxonomists, such as the author, tend to point out the particular importance of their respective groups (HAWKSWORTH 1991; GALLOWAY 1992a; GRADSTEIN 1992; GRADSTEIN and SALAZAR 1992). This is quite important, as no one else would do that for us. Nevertheless, it should be emphasized that this kind of detailed information can be only a small contribution, and that effective site conservation must consider the ecosystem as a whole, because the requirements important for the protection of a group of organisms might be different from that important for another group.

5 Conclusions

To conclude, it seems clear that biodiversity is an important argument for conservation purposes in the tropics, not only in the case of foliicolous lichens, but also in general. For effective protection, a detailed analysis of single components contributing to overall diversity, supplemented by an analysis of geographical and ecological distribution types, can already reveal important information. Depending on the sample method, this information can be taken from simple presence/absence data of species at the regional, site, microsite, and sample level. However, to produce these "simple" data for tropical regions, much more floristic or faunistic, as well as monographic treatments are needed.

The calculation of "form" diversity, based on the relative abundance of morphologically or biologically similar taxa, represents an important complement to the determination of species diversity, and is feasible even with presence/absence data. The use of key species, correlated with high biodiversity and readily distinguished in the field, to identify sites that should be protected, is especially important in the tropics, when rapid decisions are required, and where primary vegetation is disappearing at a great rate.

Co-existence of ecologically equivalent species on a small scale is an important component of biodiversity, especially in foliicolous lichens, but probably in many other organisms, too. The mechanisms that allow co-existence of high numbers of ecologically equivalent species are still largely unknown, although plausible explanations are at hand in various cases. The fact that effective mechanisms creating and maintaining high biodiversity have evolved in primary systems, and that most of these primary systems support higher biodiversity than any anthropogenic habitat, should be reason enough to protect primary vegetation in its original state as far as possible.

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Nephroma occultum and the Maintenance of Lichen Diversity in British Columbia

Trevor Goward
Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 2B1, Canada[1]

[1] Mailing address: Edgewood Blue, Box 131, Clearwater, British Columbia V0E 1N0, Canada

Abstract

Based on field studies conducted in British Columbia in 145 forested sites of different ages, the distributional ecology of *Nephroma occultum* is described. Three macroclimatic "range classes" are recognized for this species: 1) a primary range, in which it is restricted to the upper and middle canopies of oldgrowth forests; 2) a secondary range, in which it colonizes the middle and lower canopies of oldgrowth and seral forests alike; and 3) a tertiary range in which it is confined to the lower canopy of oldgrowth forests. In British Columbia, *N. occultum* is judged to have its widest ecological amplitude in its secondary range, which may therefore be termed this species' "effective ecological epicentre".

Any viable conservation strategy intended to maintain *N. occultum* throughout its current distribution area must effectively treat this species as a separate ecological entity within each of its range classes. It is concluded that the range class model may prove useful for expressing the distributional ecologies – and hence the conservation requirements – of other oldgrowth-dependent lichens.

Keywords: British Columbia, Canada, lichens, ecology, oldgrowth, conservation, *Nephroma occultum*

1 Introduction

Oldgrowth dependency among lichens has been documented in the deciduous woodlands of Great Britain (Rose 1976) and Luxembourg (Diederich 1991), as well as in the coniferous forests of Sweden (Tibell 1992), New Brunswick (Selva 1989, 1990) and British Columbia (Goward 1993, 1994a). The authors of all these studies have called attention to the usefulness of lichens as indicators of environmental continuity.

Goward (1994a) has further discussed the phenomenon of oldgrowth dependency *per se,* suggesting that certain species are restricted to oldgrowth forests by reason of: 1) the unique microclimatic conditions associated with such forests; 2) their relative environmental stability; and/or 3) their great age. Goward also distinguished between "Type A" lichens, which can be defined as having a broad ecological amplitude within a given region, and "Type B" lichens – including oldgrowth-dependent species – which have a much narrower ecology within the same region. He noted that a lichen may behave as a Type A species in one portion of its range, and a Type B species in another. Finally, he proposed that old oldgrowth (= "antique") forests may have greater conservation value for Type B lichens than younger oldgrowth forests.

In British Columbia, oldgrowth-dependent lichens are highly vulnerable to habitat disruption associated with current forestry practice. They are, indeed, probably more at risk of local or regional extirpation than any other single group of organisms (GOWARD 1994b). Notwithstanding these observations, conservation strategies aimed specifically at the maintenance of lichen diversity in forested ecosystems in British Columbia have yet to be developed. In the light, however, of recent modifications to forestry practices in adjacent portions of the American Northwest (ROSENTRETER, 1995 this vol.), there is reason to believe that a Canadian conservation strategy for lichens may not be far off.

In this paper I discuss certain aspects of lichen distribution and ecology which warrant special consideration in the development of such a strategy. I base my discussion on field observations on *Nephroma occultum* Wetm.: a recently described western North American epiphyte (WETMORE 1980) that provides a rare opportunity to examine the distributional ecology of a lichen throughout its presumed historic range.

Nephroma occultum is a conspicuous and distinctive species whose main diagnostic features include the foliose habit, proportionately broad lobes (to 1.5 cm across), bluish grey colour, reticulate upper surface, sorediate ridges and glabrous lower surface. As the only North American representative of the *N. cellulosum* group – an assemblage of four species otherwise endemic to the southern hemisphere, especially southern Chile and Argentina (WHITE and JAMES 1988) – *N. occultum* is phylogenetically isolated on this continent.

2 Materials and methods

Field studies for this report were carried out in various humid regions of coastal and inland British Columbia during the summers of 1991 and 1992 (Goward, in prep.). In total, 145 localities were investigated for the presence of *N. occultum.* Approximately half of the localities supported oldgrowth forests (as defined below), whereas the other half contained younger forests types. At each locality an attempt was made to assess epiphytic macrolichen diversity as thoroughly as possible, usually by means of comprehensive collections. In total, nearly 3,000 lichen specimens were assembled in connection with these studies.

For localities found to support *N. occultum,* detailed relevés were performed. These yielded data on canopy structure, canopy closure, height of the dominant trees, spacing, and size class distribution of standing stems. In an effort to determine the relative degree of environmental continuity at these sites, I also documented the presence, size and state of decomposition of large logs, and assessed the age of representative standing trees using an increment borer.

Most observations were made within two to three metres of the ground. However, in order to assess the vertical distribution of *N. occultum* in the forest canopy, the branches of recently wind-thrown trees were also closely examined; such trees are almost invariably present along the perimeters of recent clear-cuts. With the assistance of professional climbers, I also sampled the crowns of standing trees at three localities.

In general, ecologists prefer to define oldgrowth with reference to various ecosystem attributes, including structural diversity, canopy heterogeneity, numbers of standing dead trees, and presence of large woody debris (FRANKLIN *et al.* 1981). For practical purposes, however, the British Columbia Ministry of Forests has recently proposed minimum age criteria for the recognition of oldgrowth in British Columbia (Old Growth Strategy Project 1992). The ages recommended vary from 120 years to 200 years. In this study the term oldgrowth will be applied to forests older than about 150 years. Forests younger than 150 years will be referred to here as "seral" forests, though this is not meant to imply that forests older than 150 years are thought to represent climax forest types.

3 Study area

Within the biogeoclimatic system of the British Columbia Ministry of Forests (MEIDINGER and POJAR 1991), most of the localities visited may be classified as belonging in the Coastal Western Hemlock Zone (CWH) or the Interior Cedar-Hemlock Zone (ICH). These are the only vegetation zones in which *N. occultum* has been found to date, and the only zones in which it is expected to occur.

The CWH encompasses the most humid and highly oceanic region of North America. On the mainland this zone hugs the western edge of the continent in a broad band stretching eastward to the crest of the coast ranges. Mean annual precipitation ranges from 1000 to 4,400 mm, roughly 75% of which occurs during the winter half year, and most of which falls as rain. Mean temperatures average between 13 °C and 18.5 °C during the warmest month, and between -6.5 °C and 4.5 °C during the coldest month. Extreme maximum temperatures are between 23 °C and 40.5 °C, and extreme minimum temperatures between –10 °C and –30 °C. Continentality is between 5 and 20 according to the Conrad Index of Continentality (CONRAD 1946). By comparison, continentality in the ICH registers between 20 and 35 on the same index, and the Great Plains (east of the Rocky Mountains) register between 50 and 65.

The ICH is comprised of two geographically distinct forest regions (see MEIDINGER and POJAR 1991). The larger of these occupies the south-east corner of the province, extending north in a 200 km-wide band from the Canada-U.S.A. border (at 49° N) to roughly 54° N. Precipitation varies from 500 mm to 1400 mm per annum, and is rather uniformly distributed through the year, with a slight peak, in most areas, in early summer. One-quarter to one-half of this precipitation falls as snow, and snow packs of between 0.5 m and 1.5 m are typical. Mean temperatures during the warmest month average between 16 °C and 21 °C, and during the coldest month between –3 °C and –10 °C. Extreme maximum and minimum temperatures are 43 °C and –46 °C respectively.

The second, more north-westerly portion of the ICH was earlier included in the CWH (KRAJINA 1973). Located roughly between 55° N and 57° N, this region occupies the leeward slopes and adjacent lowlands of the coast ranges, and is therefore thermally much more oceanic than its south-eastern counterpart. It is also much more continental than the CWH, and in fact combines the climatic features of both zones.

Both the CWH and the ICH are of broad climatic amplitude, and are comprised of ten and eleven subzones respectively. Within the Bioclimatic System of AHTI *et al.* (1968) and TUHKANEN (1984), they embrace the humid and perhumid expressions of four subzones, i.e., the North Temperate Subzone, the Orohemiboreal Subzone, the Lower Oroboreal Subzone, the Lower Oroboreal Subzone and the Middle Oroboreal Subzone. The comparative positioning of these subzones in Europe and other regions of the world is discussed by AHTI *et al.* (1968), HÄMET-AHTI *et al.* (1974), HÄMET-AHTI (1986) and TUHKANEN (1984, 1987, 1992). See also GOWARD and AHTI (1992).

4 Results

In Washington and Oregon, *N. occultum* has been reported from a total of five localities (NEITLICH *et al.* 1994) spanning five degrees of latitude and one degree of longitude. In British Columbia, by contrast, it has been detected at 21 localities (Goward, in prep.) spanning ten degrees of latitude and eight degrees of longitude. Based on current data, therefore, British Columbia comprises roughly 75% of this species' global distribution area. Yet even here, *N. occultum* occurs in only two of 14 biogeoclimatic zones, i.e., the CWH and the ICH. Within the CWH, moreover, it is further restricted to subzones of intermediate humidity, whereas in the ICH it is confined to the wettest and/or coolest subzones.

Though *N. occultum* can be broadly characterized as oldgrowth-dependent, its ecological behaviour is by no means uniform throughout its range. In inland regions (Range III

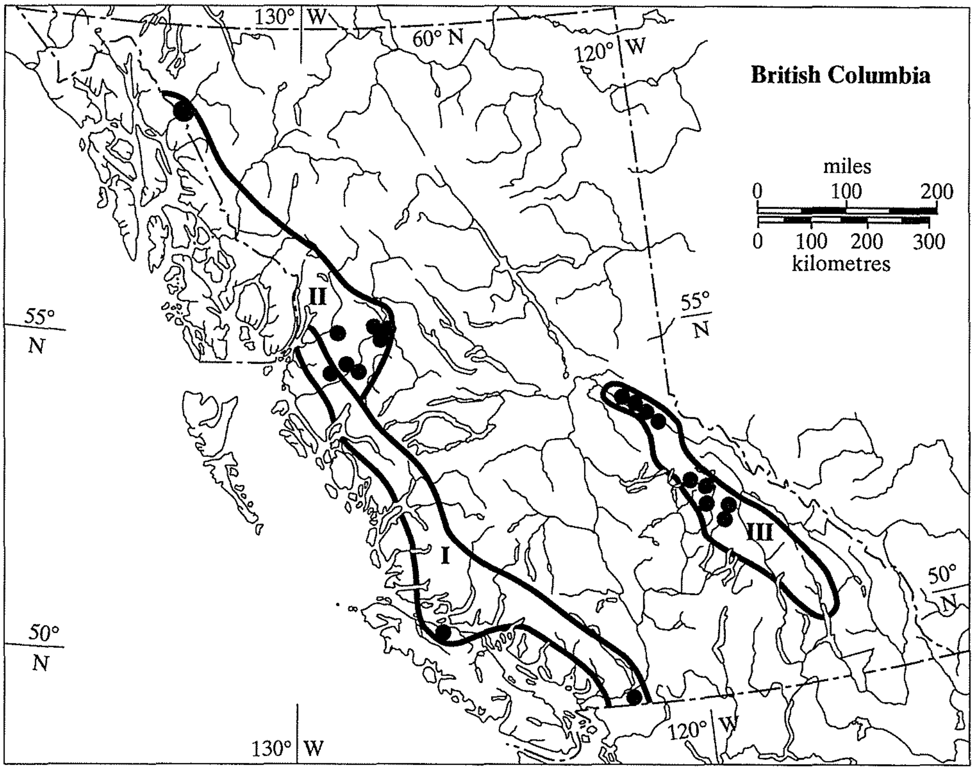

Fig. 1. The range classes of *Nephroma occultum* in British Columbia. Dots represent known localities.

of Fig. 1), for example, it is essentially restricted to oldgrowth forests in valley-bottom situations, whereas in coastal and near-coastal localities (Ranges I and II), it inhabits oldgrowth forests in valley bottoms and on valley slopes alike. What is more, in the northwest portion of the ICH (Range II), it appears to occupy both oldgrowth forests *and* seral forests (as young as 40 years), again in a variety of topographic positions.

These habitat differences closely parallel regional differences in *N. occultum's* vertical distribution in the forest canopy. Originally, WETMORE (1980) characterized this species as occurring "high up in old trees on moderate-sized branches, and never lower on the trunks". In fact this comment would apply in British Columbia only to coastal localities (Range I), where *N. occultum* is indeed usually located in the upper and middle portions of the canopy, often as high as 30 m above the ground. In somewhat more inland localities (Range II), by contrast, it occurs in the middle and lower canopy. Farther inland again (Range III), it seems to be entirely restricted to the lower canopy, usually within two to three metres of the ground. Exceptions, however, do occur. In well-illuminated, well-ventilated coastal localities, for example along the margins of streams, the lower trunks and branches of trees are also on occasion colonized. Conversely, *N. occultum* has been found to occur in inland localities as high as 10 m in the spray zones of waterfalls.

5 Discussion

Based on the above regional differences in ecological expression, it is possible to distinguish three range classes for *N. occultum* (see Fig. 2). These range classes are broadly defined by this species' response to regional climatic conditions. In the first category, i.e., its "primary range" (= Range I in Fig. 1), *N. occultum* appears to be well adapted to regional climate. This is suggested both by its occurrence in the upper forest canopy (where regional climate is presumably most fully expressed), and by its broad topographic distribution in valley-bottom and valley-slope forests alike. Given that *N. occultum* is likewise reported to be restricted to the middle and upper canopy in the holotype locality in Oregon (WETMORE 1980), this area, too, could possibly be classified as belonging within *N. occultum*'s primary range.

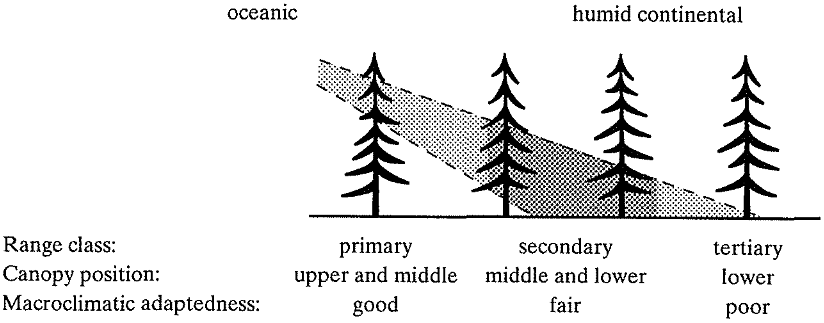

Fig. 2. The range class model as applied to *Nephroma occultum* in British Columbia. Darker shading indicates the effective ecological epicentre of the species (see text).

Interestingly, *N. occultum* does not achieve maximum ecological amplitude within its primary range. In the first place it appears to be essentially absent here from the lower canopy. And in the second place it usually does not occur in younger forest types. Its absence from the lower canopy can perhaps be explained by an inability: 1) to withstand the continuously high humidity associated with this portion of the forest (FRANKLIN *et al.* 1981); and/or 2) to compete for space with epiphytic bryophytes such as *Isothecium stoloniferum* Brid., which are ubiquitous in the lower canopy.

Nephroma occultum's absence from seral forests within its primary range probably reflects the relative environmental instability associated with such forests. Here vertical canopy growth rates may exceed 75 cm per year (Goward, unpublished data), resulting in rapidly changing microclimatic conditions unsuited to the physiological requirements of most lichen species. Only after growth rates decline – usually after the forests attain 100 years of age – do epiphytic lichens encounter the relative environmental stability for which many species, including *N. occultum,* appear to have evolved (see also GOWARD 1994a).

In its secondary range (Range II), *N. occultum* displays a somewhat broader ecological amplitude. Here it: 1) colonizes both oldgrowth forests and (to a lesser extent) seral forests; 2) occurs in the lower and middle canopies; and 3) occupies valley-bottom sites and valley-slope sites alike. This relative breadth of ecological tolerance can be interpreted as suggesting at least partial physiological adaptedness to macroclimatic conditions. However, *N. occultum*'s absence from the upper forest canopy indicates that it is less well macroclimatically adapted here than in its primary range.

In its tertiary range (Range III) *N. occultum* is again ecologically more restricted, and is, indeed, entirely confined to within two or three metres of the ground in oldgrowth forests in sheltered, humid, valley-bottom localities. Here this species appears to be supported entirely by the localized microclimatic conditions associated with the lower canopies of such forests (see MCCUNE 1993). Certainly it could not persist in this portion of its range in the absence of oldgrowth forests.

As defined above, the primary, secondary and tertiary ranges of *N. occultum* can be viewed as nodes along an east-west macroclimatic continuum. At one end of the continuum, near the Pacific coast, conditions are thermally oceanic; and at the other end, near the British Columbia–Alberta border, conditions are thermally much more continental. It is possible to record *N. occultum*'s varying degrees of adaptedness to these regional climates by observing its vertical distribution in the forest canopy: higher in regions of greater oceanity, versus lower in regions of greater continentality.

It is intriguing that, as already mentioned, *N. occultum* displays a much broader ecological amplitude in its secondary range than in its primary range. This suggests that the primary range of a species, in which it is at macroclimatic optimum, need not always coincide with what may be termed its "effective ecological epicentre", i.e., that portion of its range in which it occupies the greatest number of ecological niches. This concept will be more fully discussed in a future paper.

6 Conclusions

That *N. occultum* behaves differently in different portions of its range is by no means unexpected. For those who study the distributional ecology of lichens, such behaviour is known to be the rule rather than the exception. Perhaps the best documented instance of this phenomenon is that of "substrate switches" (BRODO 1974), in which a lichen may colonize one substrate in one portion of its range, and a strikingly different substrate elsewhere. No less unusual, however, are regional discrepancies of other kinds, including zonal amplitude (e.g., AHTI 1977), microniche (e.g., KARSTRÖM and THOR 1991), frequency status, and – as documented here – oldgrowth dependency. In some instances such behavioural differences presumably reflect genetic variation within the species (e.g., CULBERSON *et al.* 1990), though in other instances genetic factors are probably less important than environmental factors.

These observations are intended to serve as a caveat for land managers charged with designing conservation strategies in which maintenance of lichen diversity has priority. As I have attempted to demonstrate, the global ecology – and therefore the global conservation requirements – of a given lichen cannot be deduced from its behaviour in any one portion of its range. In those instances in which a range class (i.e., primary or secondary or tertiary) exceeds a conservation unit (i.e., township or county or province or country) in areal extent, a single conservation strategy may perhaps suffice. But in those cases where the reverse obtains, i.e., where the political unit is larger than the functional ecological unit, two or more different strategies may be required. Indeed, the species in question must then be treated as a separate ecological entity in each of its range classes.

Island biogeography theory (MACARTHUR and WILSON 1967) suggests that any attempt to preserve species within small, isolated "islands" of appropriate habitat is doomed from the outset. If we wish to maintain *N. occultum* throughout its full historic range, we must be prepared to set aside considerable tracts of oldgrowth forest. How large, how closely spaced and how topographically specific these tracts need be must depend on the range class under consideration. Though considerable work remains to be done on these difficult questions, a few preliminary recommendations can be given.

Within *N. occultum*'s primary range (Range I), oldgrowth forests in valley bottom localities and on the adjacent valley walls are probably of equal value for conservation purposes. Set-asides need not be extensive. In the secondary range (Range II), by contrast, valley bottom forests, especially oldgrowth forests, should probably be selected over hillside forests. Again the set-asides need not be extensive; and there is evidence that some level of selective logging may be tolerated within them (Goward, unpublished). In the tertiary range (Range III), the set-asides should be much larger and much more intimately connected, and should also be confined to valley bottom localities.

It is of course unlikely that any broad-scale conservation plan will be designed specifically around the ecological requirements of a single lichen species. However, on the basis of the field studies on which this report is based, there are strong indications that the distributional ecologies of most, if not all, oldgrowth-dependent lichens may be reducible to three or four general patterns of the kind observed for *N. occultum*. There is also reason to believe that the range class model outlined above will be useful not only in articulating these patterns, but also in helping to formulate the most effective lichen conservation strategies possible.

7 Summary

1) Though *N. occultum* is typically described as oldgrowth-dependent, this characterization is less apt in some portions of its range than in others. In a small portion of its distribution area, *N. occultum* may occur in oldgrowth forests and seral forests alike.
2) A close examination of the distributional ecology of this species permits recognition of three range classes: 1) a primary range, in which it is well adapted to regional climatic conditions, but in which, in British Columbia at least, it is essentially restricted to the upper canopy of oldgrowth forests; 2) a secondary range, in which it is moderately adapted to regional climate, and in which it colonizes oldgrowth and seral forests alike; and 3) a tertiary range, in which it is supported entirely by special microclimatic conditions associated with the lower canopy of oldgrowth forests.
3) The existence of oldgrowth forests has enabled *N. occultum* to occupy a distribution area much larger than it would otherwise occupy in the absence of such forests. From the perspective of the macrodistribution of this species, oldgrowth forests may be viewed as an important vehicle of range extension.
4) For the purposes of lichen conservation, *N. occultum* must be treated as a different ecological entity in different portions of its range. No single management strategy is likely to allow it to persist throughout its current range. Conservation efforts must be tailored to the differing ecological requirements of this lichen in its primary, secondary and tertiary ranges.

Acknowledgements
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Lichen Diversity in Managed Forests of the Pacific Northwest, USA

Roger Rosentreter
Bureau of Land Management, U.S. Department of the Interior, 3380 Americana Terrace, Boise, Idaho, 83706, USA

Abstract
Forest management practices in the Pacific Northwest have recently come under intense scrutiny and changing attitudes. In an effort to improve management of the plant and animal diversity of these forests, an ecosystem-based plan known as FEMAT (Forest Ecosystem Management Assessment Team) was developed. The plan analyses the effect of nine management options on lichen species by placing the species into functional groups. The preferred option requires that lichen diversity be maintained, and recommends management guidelines to reach this goal. Some of these guidelines include: 1) the retention and buffering of key populations of rare species, 2) the limited use of piling and slash burning after harvesting, 3) no herbicide use, and 4) the retention of trees containing high lichen and moss biomass. Extensive surveys for rare lichen species are needed to locate high priority sites for appropriate management. The retention of mature green trees on ridgelines is recommended to optimise lichen dispersal and fog interception. To moderate climatic conditions, 15% of the trees in each cutting unit will be retained in 0.2 to 1 ha clumps over several harvest rotations. Hardwoods will be encouraged in addition to conifer regeneration.

Keywords: diversity, forestry, lichens, indicator, managed forests, mitigation, rare species

1 Introduction

Controversy over the decline of the threatened northern spotted owl (*Strix occidentalis* ssp. *caurina*) and rapid harvest of its required old-growth forest habitat in the Pacific Northwest has continued since the 1970's. Five federal laws in the United States applicable to land management in this area include the National Environmental Policy Act (NEPA), the Endangered Species Act (ESA), the National Forest Management Act (NFMA), the Federal Land Policy and Management Act (FLPMA), and the Oregon and California Lands Act (O&C Act). In keeping with the federal land management agencies' responsibility of preventing additional species from becoming endangered (thereby necessitating their listing under the ESA), the viability of all species of plants and animals is of management concern. At a 1993 National Forest Conference, U.S. President Clinton directed the federal agencies to craft a balanced, comprehensive land use plan for the management of over 10 million hectares in the Pacific Northwest. Maintaining diversity in managed forests, including lichen diversity, became a goal and legal mandate of this regional plan known as FEMAT (Forest Ecosystem Management Assessment Team). The President set forth five principles to guide the agencies in the development of this plan to protect old-growth related species and produce a sustainable level of timber:

1. The human and economic dimensions of these problems should not be forgotten. Where sound management policies can preserve the health of forest lands, timber sales should go forward.
2. Protect the long-term health of our forests, our wildlife, and our waterways.
3. Our efforts must be, insofar as we are wise enough to know it, scientifically sound, ecologically credible, and legally responsible.
4. The plan should produce a predictable and sustainable level of timber sales and non-timber resources that will not degrade or destroy the environment.
5. To achieve these goals, the federal agencies will work together in collaboration, not confrontation.

A team of agency scientists was formed, including the author, to produce the ecosystem-based FEMAT plan (THOMAS *et al.* 1993). It was the first time the two largest federal land management agencies, the Bureau of Land Management and the U.S. Forest Service, developed and adopted a common management approach throughout an entire ecological region. The final management direction of FEMAT consists of extensive standards and guidelines, including land allocations, that comprise a comprehensive ecosystem management strategy. The conservation measures included in this strategy are based upon available scientific information. They attempt to anticipate and forestall future environmental problems, and avoid severe economic dislocation and legal gridlock that occur when environmental problems are ignored.

The geographic area addressed by FEMAT is the range of the northern spotted owl, since this species was the focus of controversy. This area includes the states of California, Oregon and Washington (Fig. 1). The area is divided into 12 physiographic provinces based on differences in vegetation, soils, geologic history, climate, and political boundaries (Fig. 2). The dominant tree species include *Pseudotsuga menziesii, Tsuga heterophylla, Picea sitchensis, Thuja plicata* and *Abies grandis,* which in various associations may be referred to as temperate rainforests.

In the plan, the term late-successional forest includes all forests in which the dominant overstory trees are at least 80 years old, including old-growth forests. An old-growth forest is defined as a forest stand at least 180–220 years old with moderate to high canopy closure, a multilayered, multispecies canopy dominated by large overstory trees, a high incidence of large trees, some with broken tops and other indications of old decaying wood (decadence), numerous large snags, and accumulation of wood, including large logs, on the ground.

Lichens are well documented components of old-growth forests both in the Pacific Northwest and other parts of the world (DENISON 1973, ROSE and WOLSELEY 1984, BROAD 1989, GOWARD 1992, ESSEN *et al.* 1992, MCCUNE 1993). The rich lichen flora of the Pacific Northwest is documented by PIKE (1978) and PIKE *et al.* (1975). The functional role of these lichens, especially the nitrogen-fixing species, is a concern in maintaining the integrity of the Pacific Northwest forests (DENISON 1973, PIKE 1978). The management plan (MASER and TRAPPE 1984, HAYWARD and ROSENTRETER 1994) treats lichens as functional groups or "guilds" rather than as individual species including their role in the food chain. Managing for each plant and animal species individually is an impossible task. However, biodiversity can be promoted by maintaining the habitats and structural diversity in which the various lichen guilds occur.

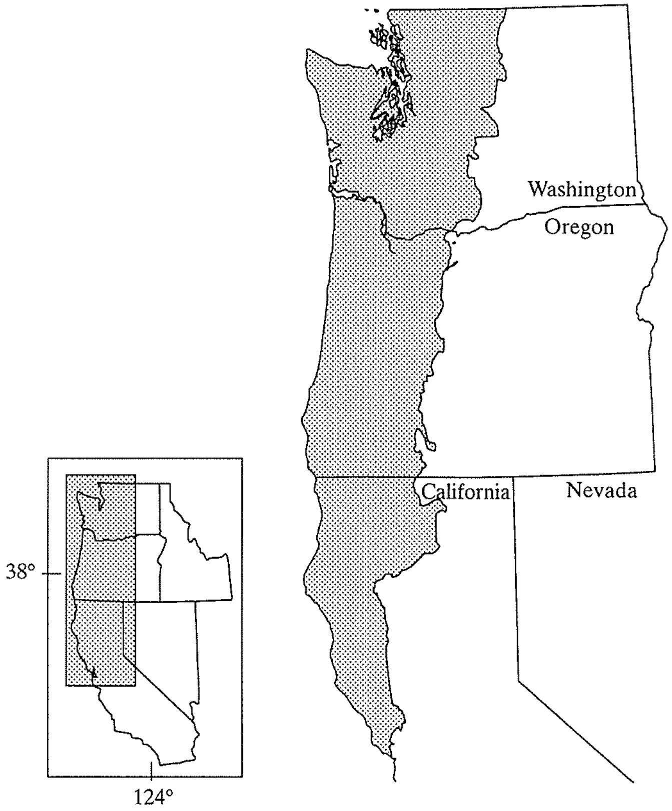

Fig. 1. The geographic area addressed by the Forest Ecosystem Management Team (FEMAT) plan.

Many of the lichen species addressed here are cosmopolitan, yet have experienced marked declines or extirpation in many parts of Europe and eastern North America (Rose and Wolseley 1984, Rose 1988, Olsen and Gauslaa 1991). The extirpation and drastic decline of these species has been attributed to both forestry practices and air quality degradation (Alstrup and Søchting 1989, Broad 1989). Old-growth forest fragmentation in the Pacific Northwest is a problem for lichens and many other organisms (Harris 1984). Some lichens, particularly the nitrogen-fixing species, do not become established until forest stands are several hundred years old (Goward 1992, McCune 1993). Many species have limited dispersal capabilities and are unable to move far from the parent plant. Old-growth stands that are widely distributed geographically may be critical to the survival and persistence of these species in the ecosystem. Landscape-level rather than stand-level planning is necessary to conserve lichen diversity in the temperate rainforest ecosystem. The preferred option of the FEMAT plan requires that lichen diversity be maintained and recommends forest management guidelines to achieve this goal.

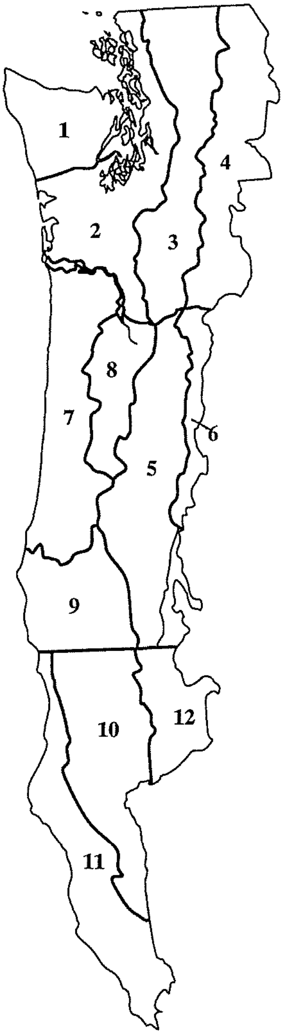

Fig. 2. The physiographic provinces within the Forest Ecosystem Management Team (FEMAT) study area. 1 Olympic Peninsula, 2 Western Lowlands, 3 Western Cascades, 4 Eastern Cascades, 5 Oregon Western Cascades, 6 Oregon Eastern Cascades, 7 Oregon Coast Range, 8 Willamette Valley, 9 Oregon Klamath, 10 California Klamath, 11 California Coast Range, 12 California Cascades.

2 Methods

The following methods were used to evaluate the forest planning options for this geographic area. The first step in the development of the ecosystem plan for lichens was the identification of species closely associated with late-successional Pacific Northwest forests. To identify these species, publications and lichen experts from the region were consulted. Once the list was produced the effect of ten proposed management options or alternatives on species habitat and viability could be rated. The outcome ratings were an assessment of the likelihood of maintaining species viability, defined as the "continued persistence of the species population widely distributed throughout its historical range on federal lands within the geographic range of the northern spotted owl over the next 100 years." One hundred and fifty-seven lichen species were included in the assessment (see list) (THOMAS *et al.* 1993). Nomenclature follows EGAN (1987).

Experts were selected from universities, the private sector, and agency management and research branches based on their technical expertise with the taxa, ecological understanding of habitat requirements, and availability to attend meetings. The experts advised the team, which made the final judgement about viability effects.

Lichen species were divided into 12 functional groups based on ecological relationships; some groups were further subdivided by rarity to produce 16 groups. Seven species were not rated because of uncertainty about their biology or distribution. The effect of each management option on each functional lichen group was rated by the experts. The use of functional groups helped to focus and simplify the task of rating and managing for so many species.

An outcome-based scale was used to assess the likelihood that a habitat would support a given functional group. The scale developed represents the range of possible trends and future condition of habitat on federal lands.

Description of the outcomes used for rating the level of habitat support for populations in the Forest Ecosystem Management Team (FEMAT) plan.

Outcome A. Habitat is of sufficient quality, distribution, and abundance to allow the species population to stabilize; it is widely distributed across federal lands. (Note that the concept of adequate distribution must be based on knowledge of the species distribution, range, and life history.)

Outcome B. Habitat is of sufficient quality, distribution, and abundance to allow the species population to stabilize, but with significant gaps in the species' historic distribution on federal land. These gaps cause some limitation in interactions among local populations. (Note that the significance of gaps must be judged relative to the species distribution, range, and life history, and the concept of metapopulations.)

Outcome C. Habitat only allows continued species existence in refugia, with strong limitations on interactions among local populations.

Outcome D. Habitat conditions result in species extirpation from federal land.

Experts assigned 100 "likelihood votes" (or points) across the four outcomes in the scale. Maps of the ten options, overlays of key watersheds, and summary tables comparing the options were referred to as the experts predicted the likely outcomes. Figure 3 illustrates the factors that were considered to affect a functional group's (species') population trend and distribution. Higher ratings (or more points) imply higher viability outcomes for the functional species group. This method worked well but only as a relative scale among the different options.

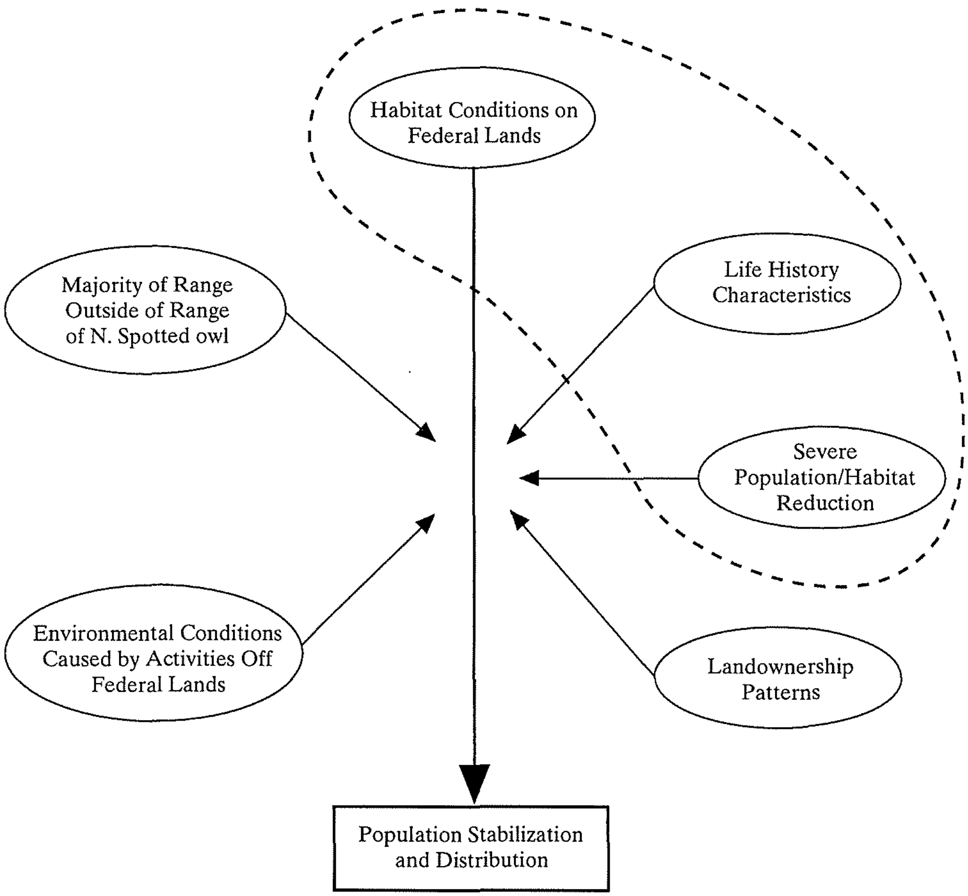

Fig. 3. Factors that affect a species' population trend and distribution. Factors encircled with the dashed line were the focus of the species' habitat assessments in the Forest Ecosystem Management Team (FEMAT) plan.

2.1 Lichen functional groups

Members of a functional group are similar in their ecological functions and requirements, may be similar morphologically, and are often taxonomically related (see list). The eleven functional groups are:

Forage lichens (Alectoroid): Pendant lichens on limbs and boles of trees or snags, including *Alectoria, Bryoria, Usnea,* and allied genera. These lichens are an important forage source for small forest mammals and ungulates, especially during the winter (Maser and

TRAPPE 1984, HAYWARD and ROSENTRETER 1994). Many of these species are more common and abundant in well-lit montane forests (BRODO and HAWKSWORTH 1977).

Arboreal leafy lichens: Short, tufted or flat, leaf-like species found on tree boles, small branches, and twigs, including the genera *Cetraria (Tuckermannopsis), Hypogymnia, Parmelia,* and *Platismatia.* Some related species are common on forest trees at any successional stage and some are pollution tolerant. Air quality can be determined by evaluating the species present.

Nitrogen-fixing lichens (Cyanolichens): Medium to large, lettuce-shaped lichens, including the genera *Nephroma, Pannaria, Peltigera, Pseudocyphellaria,* and *Sticta.* These lichens contain cyanobacteria (blue-green algae), which fix atmospheric nitrogen. Their addition of nitrogen to the forest ecosystem is significant (DENISON 1973, PIKE 1978). They are also critical components in the food-chain for many invertebrates. Many of these lichens do not enter forest stands until late successional stages, and become more frequent or abundant in old-growth conifer forests only after 200 years (MCCUNE 1993).

Pin lichens (Caliciales): These diminutive lichens resemble small pins arising from a bed of green algae. They are inconspicuous but their association with late-successional and old-growth forests is well documented (ROSE 1992). Many different genera comprise this group *(Calicium, Chaenotheca, Cyphelium, Stenocybe),* which occur in sheltered high humidity microsites, often on the side of large leaning trees (TIBELL 1980). Pin lichens are substrate specific.

Decaying wood lichens: This group includes eight species found only on decaying wood in various decay classes. This group includes species in the genus *Cladonia, Icmadophila,* and *Xylographa.*

Tree bole lichens: This diverse group of lichens includes 14 species that occur on the base and boles of trees or snags, including some crustose species. Several genera are represented, including *Buellia, Mycoblastus, Ochrolechia,* and *Parmeliopsis.*

Soil occurring lichens: This group of lichens includes eight species that are restricted to growing on soil, protecting the forest floor from surface erosion. The relatively fast-growing genus *Peltigera* makes up the bulk of this group.

Rock lichens: This group of six macrolichens occur on rocks in shaded, ameliorated climatic conditions maintained by old-growth forest canopies. Genera include *Leptogium, Pilophorus, Psoroma,* and *Sticta.*

Riparian lichens: This group includes nine species from trees associated with lake edges or streambanks. The increased humidity and hardwood component within riparian areas appear critical to the distribution of these species. This group includes medium to large pendant lichens, some gelatinous, and some flat, leaf-like lichens that become locally abundant and are usually conspicuous.

Aquatic lichens: The three species in this group are truly aquatic and, unlike most other lichens, will die if desiccated. They are found on rocks in streams and create conditions that enhance aquatic invertebrate populations. These species are good indicators of water quality and constancy of flow levels.

Oceanic influenced lichens: This morphologically diverse and unique group includes 16 species that occur on mature trees within one kilometer of the Pacific Ocean. Frequent fog along the coast, combined with moderate temperatures, create a unique environment for these species.

Lichen species closely associated with late-successional forests within the range of the northern spotted owl, arranged by functional ecological groups.
*endemic to the Pacific Northwest or North America.

Rare forage lichen (arboreal)
**Bryoria tortuosa*

Forage lichens (arboreal) (10 species)
Alectoria lata
Alectoria sarmentosa
**Alectoria vancouverensis*
Bryoria capillaris
Bryoria friabilis
Bryoria glabra
**Bryoria pikei*
**Bryoria pseudofuscescens*
Usnea filipendula
Usnea scabrata

Rare leafy (arboreal) lichens (2 species)
**Hypogymnia duplicata*
Tholurna dissimilis

Arboreal leafy lichens (17 species)
**Ahtiana sphaerosporella*
Cavernularia hultenii
Cavernularia lophyrea
**Cetraria subalpina*
**Hypogymnia metaphysodes*
**Hypogymnia rugosa*
Melanelia subelegantula
Parmelia kerguelensis
Parmelia squarrosa
Parmotrema arnoldii
Parmotrema chinense
Parmotrema crinitum
**Platismatia herrei*
Platismatia norvegica
**Platismatia stenophylla*
Sphaerophorus globosus
**Tuckermannopsis pallidula*

Rare nitrogen-fixing lichens (6 species)
Dendriscocaulon intricatulum
Lobaria hallii
Lobaria linita
**Nephroma occultum*
Pannaria rubiginosa
**Pseudocyphellaria rainierensis*

Nitrogen-fixing lichens (20 species)
**Lobaria oregana*
Lobaria pulmonaria
Lobaria scrobiculata
Nephroma bellum
Nephroma helveticum
Nephroma laevigatum
Nephroma parile
Nephroma resupinatum
Pannaria leucostictoides
Pannaria mediterranea
Pannaria saubinetii
Peltigera collina
Peltigera neckeri
**Peltigera pacifica*
**Pseudocyphellaria anomala*
**Pseudocyphellaria anthraspis*
Pseudocyphellaria crocata
**Sticta beauvoisii*
Sticta fuliginosa
Sticta limbata

Pin lichens (16 species)
Calicium abietinum

Calicium adaequatum
Calicium adspersum
Calicium glaucellum
Calicium viride
Chaenotheca brunneola
Chaenotheca chrysocephala
Chaenotheca ferruginea
Chaenotheca furfuracea
Chaenotheca subroscida
Chaenothecopis pusilla
Cyphelium inquinans
Microcalicium arenarium
Mycocalicium subtile
**Stenocybe clavata*
Stenocybe major

Decaying wood lichens (8 species)
Cladonia bacillaris
Cladonia bellidiflora
Cladonia cenotea
Cladonia macilenta
Cladonia umbricola
Icmadophila ericetorum
Xylographa abietina
Xylographa vitiligo

Tree bole lichens (14 species)
Buellia penichra
Dimerella lutea
Dimerella pineti
Hypocenomyce friesii
Lecanactis megaspora
Lopadium pezizoideum
Mycoblastus alpinus
Mycoblastus sanguinarius
Ochrolechia androgyna
Ochrolechia oregonensis
Parmeliopsis hyperopta
Pertusaria amara
Protoparmelia ochrococca
Thelotrema lepadinum

Soil occurring lichens (8 species)
Baeomyces rufus
Epilichen scabrosus
**Pannaria cyanolepra*
Pannaria pezizoides
Peltigera horizontalis
Peltigera leucophlebia
Peltigera neopolydactyla
Peltigera venosa

Rare rock lichens (2 species)
Pilophorus nigricaulis
Sticta arctica

Rock lichens (4 species)
Leptogium gelatinosum
Pilophorus acicularis
Pilophorus clavatus
Psoroma hypnorum

Riparian lichens (9 species)
Cetrelia cetrarioides
Collema nigrescens
Leptogium burnetiae var. hirsutum
Leptogium cyanescens
Leptogium saturninum
Leptogium teretiusculum
Platismatia lacunosa
Ramalina thrausta
Usnea longissima

Aquatic lichens (3 species)
Dermatocarpon luridum
**Hydrothyria venosa*
Leptogium rivale

Rare oceanic influenced lichens (12 species)
**Bryoria pseudocapillaris*
**Bryoria spiralifera*
Bryoria subcana
**Buellia oidalea*
Erioderma sorediatum
**Hypogymnia oceanica*
Leioderma sorediatum
**Niebla cephalota*
Pseudocyphellaria mougeotiana
Teloschistes flavicans
Usnea hesperina

Oceanic influenced lichens (4 species)
**Cetraria californica*
Heterodermia leucomelos
**Loxospora* sp nov. (Brodo in edit)
Pyrrhospora quernea

Species not rated (7 species)
Cladonia norvegica
**Heterodermia sitchensis*
Hyptogymnia vittata
Hypotrachyna revoluta
**Nephroma isidiosum*
Ramalina pollinaria
**Sulcaria badia*

3 Results

The following strategies and recommendations for dealing with the various functional groups have been approved by the federal land management agencies and are being implemented in the Northwestern U.S.A.

3.1 General land allocations

The predicted species viability outcomes for lichens was correlated with: the amount of hectares in late-successional reserves, the stand treatments within the matrix (managed forest), and the hectares protected in riparian reserve corridors. Species viability ratings were higher in the management options with more hectares in late-successional reserves (THOMAS *et al.* 1993). The sizing, spacing, and silvicultural activities allowed in reserves varied among the ten options. The size of the reserves varied from 1.7 to 4.6 million hectares. Some rare lichen species have narrow geographic ranges and occur only in specialized habitats. Groups dominated by these rarer species rated much lower than the other groups. The management options did not specifically address the concerns of species occurring in special habitats, which include geologic sites, refugia from fire, oceanic dune deflation plains, waterfalls, and river gorges. Many of these special habitats occur as rare combinations of abiotic and biotic conditions such as specific tree species in the fog zone of a waterfall at low elevations. These special habitats need to be addressed at the local level and were not mapped for the large scale assessment. Additional specific standards and guidelines will address the conservation of special habitats.

Of the 10 million hectares of federal land in the planning area, approximately 30% has previously been set aside by congress as national parks or wilderness areas. The prefered alternative (option #9), which encompasses the remaining 70% of the area, includes a large number of late-successional reserves (30%), matrix (managed) forests (16%), riparian reserve corridors (11%), administratively withdrawn areas (6%), adaptive management areas (experimental managed forest) (6%), and managed late-successional areas (1%). Standards and guidelines for each land allocation provide a coordinated ecosystem management approach. Although certain thinning and salvage activities are allowed in the reserves, programmed timber harvest only occurs on land designated as matrix or adaptive management areas (total of 22%), and only in compliance with standards and guidelines designed to achieve conservation objectives.

3.2 Survey and management strategies

The need for protection and conservation of lichens and other forest species in reserves is obvious. The protection or maintenance of lichens in the timber harvesting areas is more complex and multi-staged. Within the timber harvest areas, survey and management strategies were identified requiring land managers to take certain protective actions for rare organisms, particularly amphibians, bryophytes, lichens, mollusks, vascular plants, fungi, and arthropods (Anonymous 1994a). These include: 1) managing known sites of rare organisms; 2) surveying for the presence of rare organisms prior to ground-disturbing activities; 3) conducting surveys to identify locations and habitats of rare species; and 4) conducting general regional surveys for rare and some common but critical species. The survey and management strategies, described below (also see Tab. 1), allow an implementation time for completing the necessary survey work (Anonymous 1994b).

Strategy #1 – Manage known sites. Management of known rare species' sites will receive the highest priority of these four categories. All known sites of rare species will be protected and managed. This standard will be implemented within one year for those species so marked in Table 1. Harvest activities implemented in 1995 and later must include provisions for these species. In most cases, the appropriate action will be protection of relatively small sites, on the order of tens of hectares.

Strategy #2 – Survey prior to ground-disturbing activities. This strategy is only required for three of the species (Table 1). Measures to survey for species and manage newly discovered sites will be phased-in over a somewhat longer timescale than the measures specified for currently known sites.

Strategy #3 – Extensive surveys. Extensive surveys will be conducted to find high priority sites for protection of the species. Specific surveys prior to ground-disturbing activities are not a requirement. Rather, surveys will be done according to a schedule that is most efficient, and protection sites will be identified at that time. This strategy is primarily for rare species whose characteristics make site and time-specific surveys difficult. Broad surveys for these species will most efficiently be done during times of appropriate conditions rather than attempting more narrow site-specific surveys. Surveys under this strategy will be underway by 1996.

Strategy #4 – General regional surveys. The objective is to survey for these species to acquire additional information and to determine necessary levels of protection. Species intended to benefit from this strategy are those that are poorly known. Only general information is presently available on their abundance and distribution. These general regional surveys will be initiated by 1996 and will be completed by 2006.

Annual status reports summarizing the results of the four strategies will be submitted to the Regional Ecosystem Office beginning in 1995. As information on species is accumulated, the transition from one strategy to another, or removal from the list if the status is more secure than originally projected, can be proposed. The Regional Ecosystem Office reviews such proposals and makes recommendations to the Regional Interagency Executive Committee for appropriate action.

Table 1. Species to be protected through survey and manage standards and guidelines in option #9 of the Forest Ecosystem Management Team (FEMAT) plan. Each of the four survey strategies is described in the text. Survey strategies: 1 = manage known sites by providing protection for these sites; 2 = survey prior to ground disturbing activities for rare species and protect and manage sites where rare species are found; 3 = conduct extensive surveys for specific rare species and manage sites; 4 = conduct general regional surveys for more common and some poorly known but functionally critical species to determine how to manage these species.

Species	Survey strategies			
	1	2	3	4
Rare forage lichen				
Bryoria tortuosa	X		X	
Rare leafy (arboreal) lichens				
Hypogymnia duplicata	X	X	X	
Tholurna dissimilis	X		X	
Rare nitrogen-fixing lichens				
Dendriscocaulon intricatulum	X		X	
Lobaria hallii	X		X	
Lobaria linita	X	X	X	
Nephroma occultum	X		X	
Pannaria rubiginosa	X		X	
Pseudocyphellaria rainierensis	X	X	X	
Nitrogen-fixing lichens				
Lobaria oregana				X
Lobaria pulmonaria				X
Lobaria scrobiculata				X
Nephroma bellum				X
Nephroma helveticum				X
Nephroma laevigatum				X
Nephroma parile				X
Nephroma resupinatum				X
Pannaria leucostictoides				X
Pannaria mediterranea				X
Pannaria saubinetii				X
Peltigera collina				X
Peltigera neckeri				X
Peltigera pacifica				X
Pseudocyphellaria anomala				X
Pseudocyphellaria anthraspis				X
Pseudocyphellaria crocata				X
Sticta beauvoisii				X
Sticta fuliginosa				X
Sticta limbata				X

Table 1. Continued.

Species	Survey strategies			
	1	2	3	4
Pin lichens				
Calicium abietinum				X
Calicium adaequatum				X
Calicium adspersum				X
Calicium glaucellum				X
Calicium viride				X
Chaenotheca brunneola				X
Chaenotheca chrysocephala				X
Chaenotheca ferruginea				X
Chaenotheca furfuracea				X
Chaenotheca subroscida				X
Chaenothecopis pusilla				X
Cyphelium inquinans				X
Microcalicium arenarium				X
Mycocalicium subtile				X
Stenocybe clavata				X
Stenocybe major				X
Rare rock lichens				
Pilophorus nigricaulis	X		X	
Sticta arctica	X		X	
Riparian lichens				
Cetrelia cetrarioides				X
Collema nigrescens				X
Leptogium burnetiae var. hirsutum				X
Leptogium cyanescens				X
Leptogium saturninum				X
Leptogium teretiusculum				X
Platismatia lacunosa				X
Ramalina thrausta				X
Usnea longissima				X
Aquatic lichens				
Dermatocarpon luridum	X		X	
Hydrothyria venosa	X		X	
Leptogium rivale	X		X	
Rare oceanic influenced lichens				
Bryoria pseudocapillaris	X		X	
Bryoria spiralifera	X		X	
Bryoria subcana	X		X	
Buellia oidalea	X		X	
Erioderma sorediatum	X		X	

Table 1. Continued.

Species	Survey strategies			
	1	2	3	4
Hypogymnia oceanica	X		X	
Leioderma sorediatum	X		X	
Leptogium brebissonii	X		X	
Niebla cephalota	X		X	
Pseudocyphellaria mougeotiana	X		X	
Teloschistes flavicans	X		X	
Usnea hesperina	X		X	
Oceanic influenced lichens				
Cetraria californica	X		X	
Heterodermia leucomelos	X		X	
Loxospora sp nov. *"corallifera"* (Brodo in edit)	X		X	
Pyrrhospora quernea	X		X	
Additional lichen species				
Cladonia norvegica			X	
Heterodermia sitchensis			X	
Hygomnia vittiata			X	
Hypotrachyna revoluta			X	
Ramalina pollinaria			X	
Nephroma isidiosum			X	

3.3 General standards and guidelines for timber harvesting

In addition to the survey and management strategies, the following seven standards and guidelines have been identified for timber harvest areas to ensure long-term protection and maintenance of lichens and other organisms.

3.3.1 Retention of fifteen percent old-growth fragments

The distribution of old-growth stands is an important component of ecosystem diversity that plays a significant role in providing biological and structural diversity across the landscape. Isolated remnant old-growth patches are ecologically significant as refugia for a host of old-growth associated lichens, particularly those with limited dispersal capabilities. For example, *Lobaria oregana* normally reproduces by large fragments (lobulate margins); reproduction by spores appears to be less common. Forest remnants function as refugia where old-growth associated species can persist until conditions become suitable for their dispersal into adjacent stands. It is prudent to retain this old age class within landscapes where it is currently very limited. This will ensure future options for management and enhancement of the diversity within developing stands.

Landscapes where few late-successional forests persist should be managed to retain late-successional patches. This standard and guideline will be applied in "fifth field watersheds" (8–80 square hectares) (USGS 1975, SEABER *et al.* 1987). "Fifth field" describes a hydrologic unit. This guideline applies if federal forest lands are comprised of 15 percent or less late-successional forest.

3.3.2 Retention trees

For all lands within the matrix, retain uncut at least 15 percent of the area associated with each cutting unit (stand) except within the Oregon Coast Range and Olympic Peninsula Provinces (Fig. 2). Exceptions are made for these provinces because extensive riparian protection corridors provide substantial retention. This limitation does not apply to intermediate harvests (thinnings) in even-age young stands because leaving untreated portions of young stands would retard stand development and be detrimental to the objective of creating late-successional patches. This level of retention (15 percent plus the riparian corridor reserve) was reached as a compromise between the maximum harvest of timber and the minimum stand legacy needed to sustain ecosystem functions (FRANKLIN 1992). It is based on the professional judgement and field experince among the FEMAT team members.

For many organisms, including lichens, the benefits will be greatest if trees are retained in clumps rather than singly (CHEN *et al.* 1993, SILLETT 1994). Clumps should generally be larger than one hectare (CHEN *et al.* 1993), as small clumps or single isolated trees do not provide suitable microclimates for many of these organisms. While there is little scientific evidence to support the concept that tree clump retention benefits forest epiphytes, both field observations and the known physiological requirements of the epiphytes support it (FRANKLIN 1992). Although many lichen species will benefit from tree clump retention, other biota such as terrestrial woodpeckers may be favored by single tree retention. As a compromise between the two spacial methods of retention, a general guide was accepted that 70 percent of the total retention area should be clumps of 0.2 to 1 hectare or more with the remainder as dispersed individual trees (FRANKLIN 1992). Larger clumps may be particularly important where adjacent areas have little late-successional habitat. To the extent possible, clumped and dispersed retention should include the largest, oldest live trees, decadent or leaning trees, and the hardest snags in the cutting unit. Retention clumps should be protected for multiple rotations to provide habitat for species requiring very old forests. Retention of mature green trees on ridgelines is recommended to optimize lichen dispersal and fog interception.

3.3.3 Snags

Snags are dead or partially dead trees at least 240 cm in diameter at breast height and two meters tall. As a minimum, snags will be retained within the harvest unit at levels sufficient to support species of cavity-nesting birds at 40 percent of potential population levels based on published guidelines and models (BULL *et al.* 1986). To the extent possible, snag management within harvest units should occur within the areas of green-tree retention. Snags within the green-tree retention clumps will provide conditions suitable for the continued existence of arboreal lichens and will protect these snags from blowdown.

3.4 Coarse woody debris

Retaining coarse woody debris within a forest patch will ensure that the appropriate microclimate for lichens, bryophytes, fungi, and forest animals dependent on this substrate is available. The objective is to provide a renewable supply of large logs well distributed across the landscape. In general, 30 linear meters of logs per hectare greater than or equal to 50 centimeters in diameter should be left (MASER and TRAPPE 1984). Logs less than 6 meters in length cannot be credited toward this total. Decay class 1 and 2 logs can be counted towards these totals (MASER and TRAPPE 1984). Logs should reflect the species mix of the original stand. Coarse woody debris already on the ground should be retained and protected from disturbance during harvesting (e.g. slash burning and yarding which is the movement of logs from the stump to a central area), which might otherwise destroy the integrity of the substrate. Logs should be left within forest clumps under green-tree retention guidelines to provide the appropriate microclimate for organisms that use this substrate, such as decaying wood lichens and bryophytes.

3.5 Riparian reserves

Riparian reserves are protected riparian corridors along streams. Riparian reserve widths were determined based on the benefits afforded by coarse woody debris (CWD) entering the stream and enhancing streambank stability. They were not based specifically on forest epiphyte needs. These corridors primarily benefit hardwood-occurring epiphytic lichen and moss species. The initial riparian reserves and their corridor widths are: 1) fish-bearing streams, lakes and natural ponds – the areas on each side of the stream equal to the height of two site potential trees, or 91 meters slope distance, whichever is greater; 2) permanently flowing nonfish-bearing streams, and reservoirs – one site potential tree, or 46 meters slope distance, whichever is greater; and 3) seasonally flowing or intermittent streams – one site potential tree or 30 meters slope distance, whichever is greater. These widths may be modified following a watershed analysis (THOMAS *et al.* 1993).

3.6 Promote hardwoods

Hardwoods are promoted at the same species mix and abundance as before harvest, rather than favoring only conifer regeneration, as in the past. Hardwoods support certain epiphytic lichens and mosses better than conifers (ESSEEN *et al.* 1992, KUUSINEN 1994). Hardwoods also enhance epiphyte growth on surrounding trees by increasing moisture and light (NEITLICH 1993).

3.7 Site treatment modification

Many species of soil- and litter-dwelling organisms are sensitive to soil disturbance. Site treatments will be prescribed which minimize intensive burning, unless appropriate for certain habitats, communities or stand conditions. Prescribed fires should minimize the consumption of litter and coarse woody debris, and yarding of logs and heavy equipment operation should minimize soil and litter disturbance. The intensity and frequency of soil and litter disturbance in a stand will be minimized to avoid soil compaction and removal of humus layers and coarse woody debris.

4 Discussion

In the past, most federal lands included in the FEMAT plan were managed for multiple uses, often leading to management conflicts and declining biological diversity. FEMAT attempts to distinguish the type of management and goals for a given parcel of land while it increases the amount of land managed for late-successional forest cover. The plan recognizes the ecological role of many lichen species in the forest and addresses their needs by identifying specific survey strategies and management standards and guidelines.

The slow growth rates and long periods required for some old-growth associated lichens to colonize stands, emphasizes the considerable importance of existing old-growth fragments and old trees within younger stands of trees. The "late-successional" forests are not adequate for the continued existence of old-growth associated lichen species if stands are to be harvested at 80 year intervals (McCune 1993). Without the "legacy" provided by old-growth trees supporting a rich epiphytic lichen flora, regenerating forests will not support many lichen species even as they mature into stands suitable for the growth of these species. Lichen diaspores must disperse into the regenerating stands for initial establishment. Without some lichen legacy (ecological continuity), the old-growth associated lichen species will not be maintained in a forest stand (Rose and Wolseley 1984).

Lichen diversity in managed forests is dependent on the timber harvest methods used. Harvest methods include clear-cutting, unit area control, gap cutting, partial cutting, thinning, and single tree selection. Partial cutting would be the preferred method for maintaining lichen diversity since the lichen legacy along with climatic conditions would be retained in the stand (Fig. 4). Maintaining a lichen-rich clump of old-growth forest to serve as lichen "seed trees" is another method of maintaining lichen biodiversity and is much preferred over the traditional clear-cutting and general lack of consideration for the epiphytic lichen flora.

The primary mitigation measures in the FEMAT plan that benefit lichens in managed forests are the green-tree retention prescriptions and the provision for a well-distributed network of old-growth forests throughout the landscape. Clumping retention trees in managed forests will moderate climatic factors and provide a variety of microclimates to enhance the survival of many lichen species. The retention of clumps within small modified clear-cuts allows for economic harvesting, natural regeneration of a stand, and the retention of many plant and animal species within a given stand.

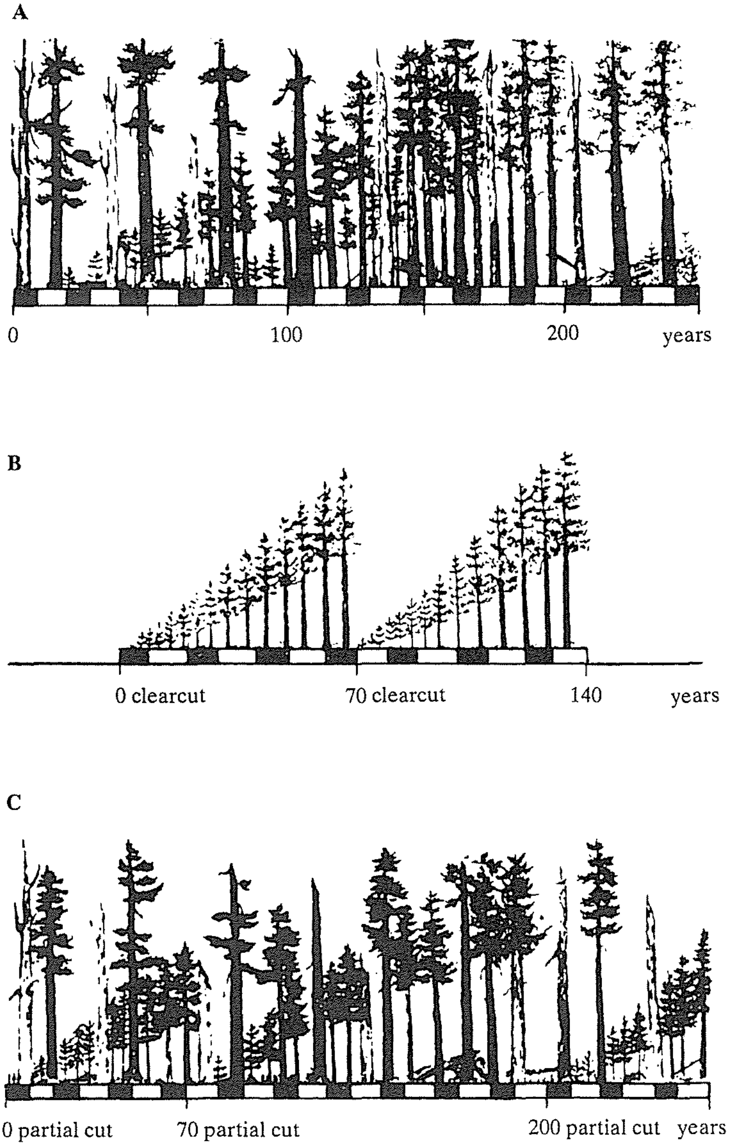

Fig. 4. Forest structure following different harvest techniques: (A) natural recovery following a moderate intensity disturbance such as wildfire or windstorm; (B) with intensive management for timber production, the early seral stages are shortened, and the late-seral stages with their associated structural features are eliminated; (C) a partial cut thins the forests and changes the structural features similar to natural, moderate intensity disturbances.

These clumps may need some measure of protection from edge-related mortality. Topography, natural breaks, ridges and aspects will play a role in the prescription. If high risk of mortality from wind or other sources is anticipated, the prescription should address minimizing losses from the clump by extending a feathering or partial cutting outside the core retention zone. The goal is to slow or deflect wind as it hits the edge created by harvesting.

Retention trees should be the big, old trees with large lateral branches and trees with emergent crowns. Maintaining the same leave trees over several harvest rotations is important. What we leave, not what we take, is important for the ecological continuity of a forest. Traditionally, foresters marked the trees for cutting in a stand. The FEMAT guidelines direct foresters to mark individual trees and clumps of trees for retention within the harvest unit.

To maintain populations of nitrogen-fixing lichens, clumps rather than single retention trees are required. Unpublished data suggests that from 10–20% of single retention trees may blow down. NEITLICH (1993) found that nitrogen-fixing lichens are sparse on old-growth trees whose neighbors have been removed. For some species of *Lobaria* and *Pseudocyphellaria,* studies have demonstrated that lichens transplanted from interior forests to the forest edge lose weight after one year (SILLETT 1994). This suggests that exposure of unacclimated lichens to the harsher conditions of an edge environment results in poor growth and high mortality.

Pin lichens require special considerations to maintain them in managed forests. Selecting retention trees that are asymmetrical, leaning or irregular in their growth form, is critical for the pin lichens. Leaning trees can only be retained safely by clumping the retention trees. Leaning trees and exposed but sheltered root masses are also suitable substrate for these species. Retention of large coarse woody material will also benefit the pin lichens.

The FEMAT plan requires the protection of special habitats such as rock talus, monoliths, and rock piles containing rare lichen species. These special habitats are considered the "core area" and a zone of influence should also be determined. The size, shape and management actions in the zone of influence will dictate the prescription for a buffer, if necessary. Generally, buffering special habitats with a "halo" of trees at least one tree height in width maintains the appropriate shade and microclimate for mosses and lichens. Any greater width may enhance the climatic conditions but would not directly shade the core area. Similar to retention tree clumps, the edges may need to be feathered to prevent blowdown.

The riparian reserves provide greatly improved habitat conditions for both aquatic and riparian lichen species. Water quality in forested streams is important to maintain healthy populations of these species. Aquatic lichens are negatively affected by any type of water pollution. For example, *Hydrothria venosa* is very sensitive to stream sediment. Reintroduction of *Hydrothyria* to restored stream courses where it historically existed could be attempted by transplanting colonized rocks. The riparian reserves serve as dispersal corridors for many animal species and as centers of dispersal for lichen species. These reserves will greatly enhance populations of the riparian lichen species.

Hardwoods often have a different textural and chemical composition than conifers, and are preferred substrates for some lichen species (KUUSINEN 1994). Hardwoods provide shade in the hot dry summers and allow frequent wetting and drying in the cool moist winter climate of the Pacific Northwest (McCune and Antos 1981).

A diversity of tree species should be selected for green tree retention and regeneration. Limiting the use of herbicides after timber harvesting will help stabilize and enrich the soil surface and prevent the destruction of soil- and decaying wood-occurring lichens. Herbicides may also deplete the remaining epiphytic lichens on the retention trees.

In addition to timber harvesting, commercial moss and lichen harvesting, also referred to as secondary forest products, has become a significant industry in the Pacific Northwest and may represent a serious threat to epiphytes, especially in coastal and riparian areas. This industry must be monitored and regulated to preserve riparian and other lichen species. Studies should address the effect of harvesting on mosses and riparian and nitrogen-fixing lichen species before continuing to allow their harvest.

5 Conclusion and summary

The conservation of Pacific Northwest lichens is part of a landscape level plan to conserve all forest associated species. Conservation management plans developed at this level must insure that landscape level biological and functional processes are addressed in addition to the local or site level preservation of special habitats and rare species. Some conservation measures that benefit one group of species also benefit other unrelated groups (or guilds) of plants or animals. In forest ecosystems, retention of species and structure provides the legacy that benefits many groups of species.

Some of the major conservation actions required by the FEMAT plan are to:
1) Manage and survey for rare species.
2) Retain 15% old-growth forests within each watershed.
3) Retain 15% of the trees within each cutting unit.
4) Retain green trees in clumps.
5) Retain the largest and oldest trees.
6) Retain snags.
7) Retain coarse woody debris.
8) Promote hardwoods.
9) Retain extensive riparian corridor reserves.

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Epiphytic Lichen Diversity on *Salix caprea* and *Populus tremula* in Old-growth Forests of Finland

Mikko Kuusinen
Department of Ecology and Systematics, P.O. Box 47, FIN-00014, University of Helsinki, Finland

Abstract

The epiphytic lichen flora on basal trunks of old *Salix caprea* and *Populus tremula* trees was surveyed in eight old-growth stands in the southern and middle boreal forests of Finland. Both the total species number and average species number per tree were higher on *S. caprea* than on *P. tremula*. The epiphyte flora on *S. caprea* was dominated by widespread generalist foliose lichens, but some rarer specialists were also found. The flora of *P. tremula* was quite unique, and was dominated by crustose lichens and bryophytes, foliose and fruticose lichens being only sparsely represented. Cyanobacterial lichens, such as *Lobaria* spp., *Nephroma* spp. and *Peltigera* spp., were frequent on both tree species. Structure and acidity of the bark, as well as the availability of different microhabitats, are suggested to be the most important factors contributing to floristic differences and diversity. The bark of *S. caprea* and *P. tremula* is one of the key habitats for conservation of epiphyte diversity in the boreal forests of Finland.

Keywords: biodiversity, boreal forests, conservation, lichens, old-growth, *Populus tremula, Salix caprea*

1 Introduction

The conservation of important keystone components is essential for maintaining the natural species richness of old-growth forests. Good examples of such components in boreal forests of Fennoscandia are old deciduous trees, particularly goat willow *(Salix caprea)* and aspen (*Populus tremula*; Esseen *et al.* 1992). These tree species, having only minor commercial value, have extensively been removed by forestry. Moreover, the present scarcity of forest fires and the dense moose populations largely prevent the establishment of these essentially pioneer trees in the forests of northern Europe.

Salix caprea and *Populus tremula* usually grow as scattered individuals in mesic to moist stands dominated by *Picea abies*. *Populus* typically occurs in groups of 10–50 trees formed by one or a few clonal individuals. The largest trunks may reach a diameter at breast height (DBH) of 75 cm and an height of 35 m. *Salix* tends to grow more solitary than *Populus* and prefers particularly moist depressions, mire edges and spring-sides. *Salix* trunks are smaller than *Populus* trunks and only rarely reach a DBH of 40 cm and an height of 25 m. In old-growth stands both tree species reach the age of well over 100 years and the oldest living trunks may even be over 200 years old.

The aims of this study were 1) to describe the composition and species diversity of the epiphytic lichen flora of old *Salix caprea* and *Populus tremula* trees in fragments of old-growth forests in Finland and 2) to evaluate the major ecological factors controlling the flora and diversity. The study is part of a project dealing with the diversity of epiphytes in old-growth boreal forests in southern and central Finland. The results presented here are a synopsis of two already published papers (KUUSINEN 1994a, b) with some additional unpublished data.

2 Study areas

Eight study areas were selected from patches of old-growth forests on state-owned land in southern and middle boreal Finland (Fig. 1). Five sites (1, 4, 5, 6 and 8) are of primeval nature with no or only slight human impact. In three sites (2, 3 and 7) minor human

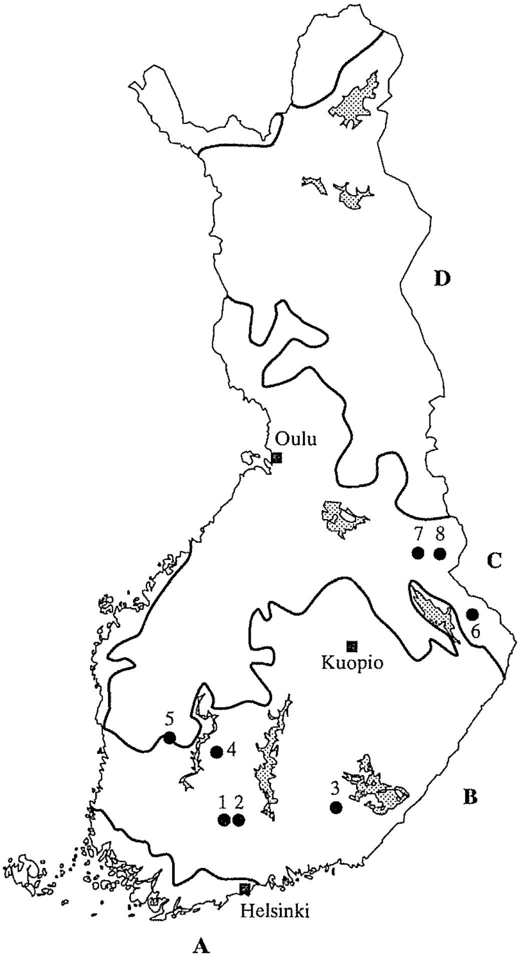

Fig. 1. Study areas: 1 – Lammi, Kotinen, 2 – Lammi, Sudenpesäkangas, 3 – Mäntyharju, Kolmikanta, 4 – Ruovesi, Susimäki, 5 – Parkano, Rengassalo, 6 – Lieksa, Patvinsuo, 7 – Kuhmo, Teeri-Losonsuo, 8 – Kuhmo, Honkavaara. The thick lines show the borders between vegetation zones (AHTI *et al.* 1968): A – hemiboreal, B – southern boreal, C – middle boreal, D – northern boreal.

impact, such as selective logging of larger trees, is evident, but the overall structure of these forests has remained more or less intact.

Picea abies is the dominant tree species in all stands. Other common trees are *Pinus sylvestris, Betula pendula, B. pubescens, Populus tremula* and *Salix caprea.* The most significant climatic difference between the southern and middle boreal areas is the higher humidity, measured as the difference between precipitation and evaporation, in the latter (ALALAMMI 1987). For more details on the study areas see KUUSINEN (1994a, b).

3 Methods

A total of 125 *Salix* and 190 *Populus* trees were sampled. The number of sampled *Salix* trees was 9 in area 1, 9 in area 2, 5 in area 3, 16 in area 4, 26 in area 5, 30 in area 7 and 30 in area 8. No data on *Salix* was collected on site 6. Random sampling of living trees having a DBH of at least 10 cm was used (KUUSINEN 1994a). The number of sampled *Populus* trees was 40 in area 1, 20 in area 2, 30 in area 3, 10 in area 4, 20 in area 5, 20 in area 6, 20 in area 7 and 30 in area 8. *Populus* trees were sampled as random groups of 10 living trees having DBH at least 20 cm (KUUSINEN 1994b).

The occurrence of each lichen species was recorded on the basal trunk below 2 m height on each tree. To obtain cover estimates, 10 x 50 cm^2 sample plots on *Salix* and 20 x 50 cm^2 on *Populus* were marked out with a transparent plastic sheet at 80 cm height above ground, on the south and north sides of the trunk. The cover estimates were obtained with a point frequency method (KUUSINEN 1994a, b). DBH and inclination of the trunk, bark pH, canopy cover, basal area of the stand and distance from the sample tree to the three closest living trees were measured.

Nomenclature of lichens follows SANTESSON (1993).

4 Results and discussion

4.1 Species composition

The epiphyte flora of *Salix caprea* is dominated by common and widespread, mainly foliose, lichens, such as *Hypogymnia physodes, Parmelia sulcata* and *Platismatia glauca,* which may be classified as habitat generalists in boreal forests of Fennoscandia (Figs. 2, 3). Some rare habitat specialists, such as *Arthonia incarnata, Biatora fallax* and *Rinodina cinereovirens,* can also be found. Bryophytes, especially *Ptilidium pulcherrimum,* have quite a high cover on *Salix.*

The epiphyte flora of *Populus tremula* is quite unique if compared to other forest trees in eastern Fennoscandia. It is dominated by the crustose lichens *Biatora* spp. and *Phlyctis argena* and bryophytes, whereas foliose lichens are sparse and fruticose lichens almost absent (Figs. 2, 3). The proportion of habitat specialists is higher on *Populus* than on any other forest tree in eastern Fennoscandia. The total cover of epiphytes is generally lower on *Populus* than on *Salix* (Fig. 3).

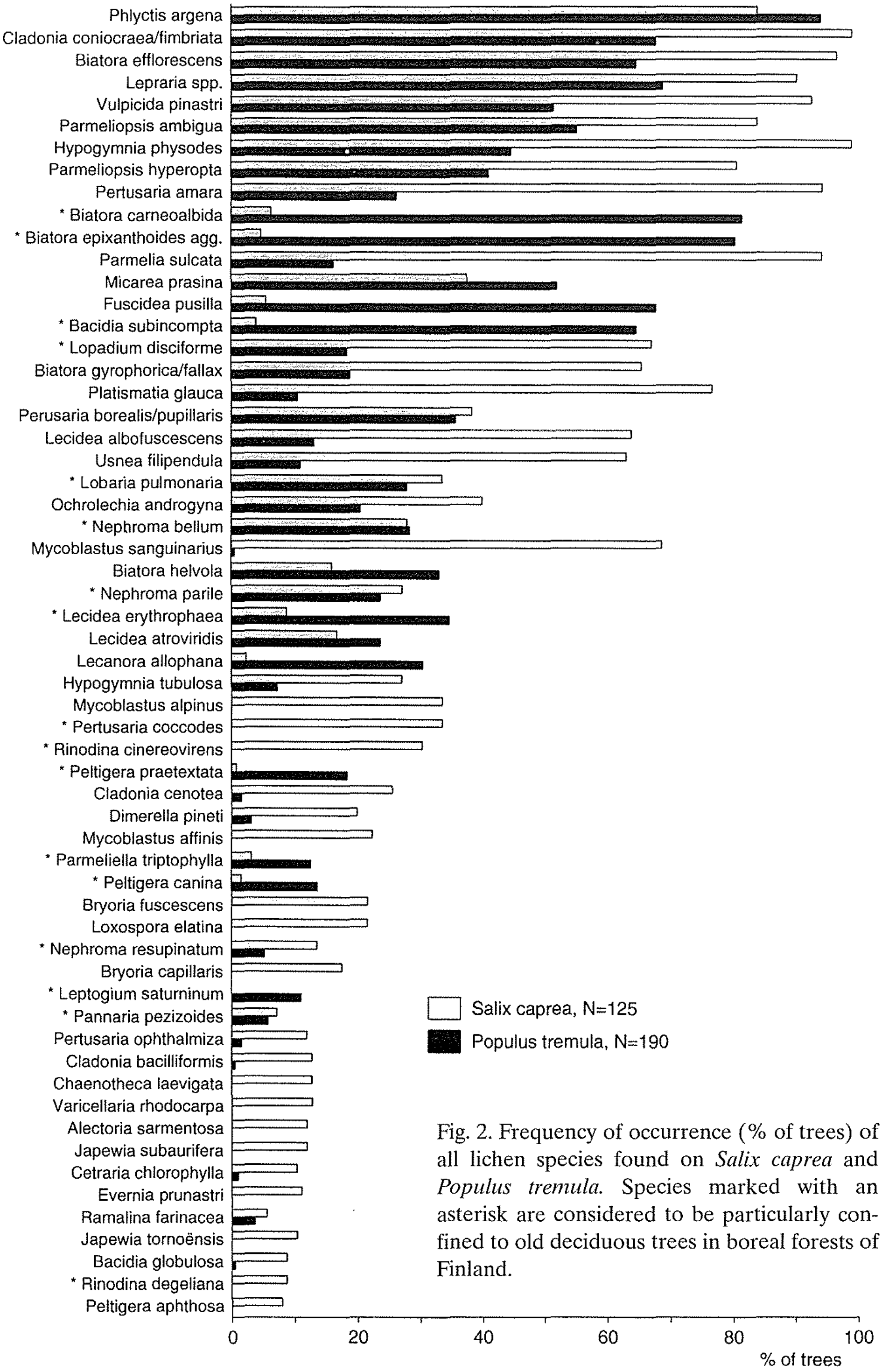

Fig. 2. Frequency of occurrence (% of trees) of all lichen species found on *Salix caprea* and *Populus tremula*. Species marked with an asterisk are considered to be particularly confined to old deciduous trees in boreal forests of Finland.

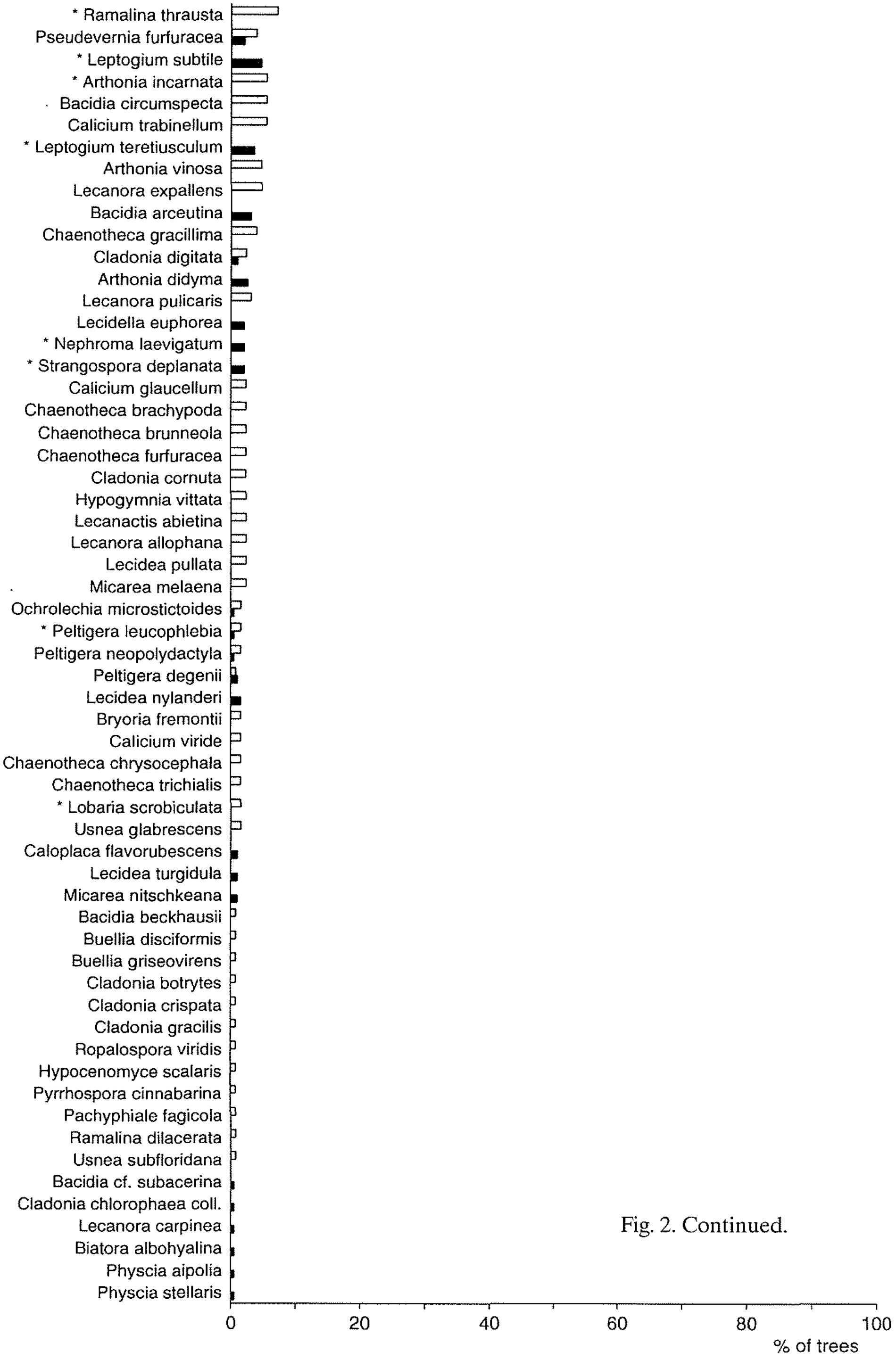

Fig. 2. Continued.

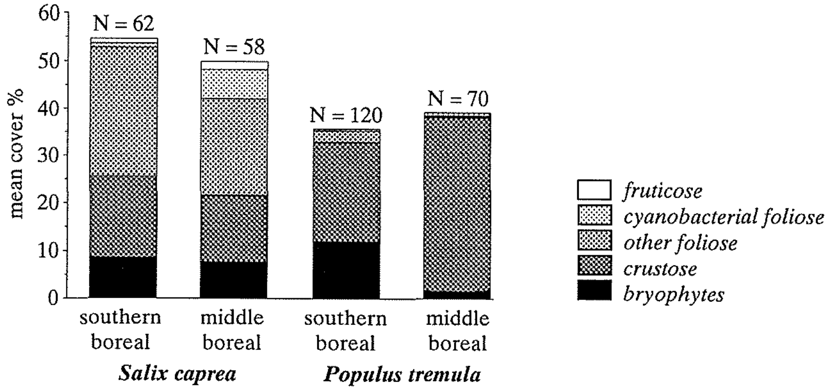

Fig. 3. Mean cover of bryophytes and different morphological groups of lichens on the study trees in the southern (1–5, Fig. 1) and middle boreal areas (6–8). Combined data of sample plots on the south and north sides of trunks.

The quite frequent occurrence of cyanobacterial lichen species, such as *Lobaria* spp., *Nephroma* spp. and *Peltigera* spp., is characteristic of the epiphyte flora of both trees. These lichens are very rare on the dominant forest trees, *Pinus sylvestris, Picea abies* and *Betula* spp., in eastern Fennoscandia. Several, overlooked crustose lichens, such as *Fuscidea pusilla, Pertusaria pupillaris, Biatora gyrophorica, Lecidea albofuscescens* and *Japewia subaurifera,* appear to be fairly common on both tree species.

4.2 Species diversity

Species richness is higher on *Salix* than on *Populus:* a total of 100 lichen species were found on the 125 *Salix* trees, but only 70 species on the 190 *Populus* trees (Fig. 2). Mean species number per tree is also higher on *Salix* than on *Populus* (Table 1). The number of species on *Salix* is, especially in the middle boreal areas, higher than on the dominant forest trees, whereas on *Populus* it is lower (Kuusinen, unpubl.).

It is suggested that the high lichen diversity on *Salix caprea* is best explained by high micro-habitat heterogeneity on the trunks. Often the basal trunk is twisted or inclined and the bark cracked and fissured, providing a variety of niches for lichen colonization

Table 1. Mean and ± one standard deviation of the number of lichen species per tree on the study trees in the southern (1–5, Fig. 1) and middle boreal areas (6–8).

Tree species	Southern boreal Mean ± S.D.	Middle boreal Mean ± S.D.
Salix caprea	19.0 ± 3.5	25.0 ± 4.6
Populus tremula	14.0 ± 4.8	12.1 ± 5.9

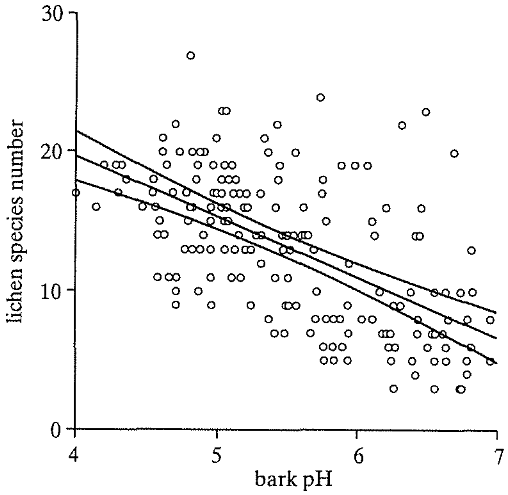

Fig. 4. Linear correlation between lichen species number and bark acidity (pH value) on *Populus tremula* trees (Pearson correlation: $r = -0.549$, $p = 0.000$; $N = 190$). The upper and lower lines represent 95% confidence limits for correlation.

and growth. The relatively high bark pH (mean = 4.8) is favourable to several species that avoid extremely acidic bark. Finally, the moist microclimate of the typical habitats of *Salix* trees – mire edges and paludified depressions – is also favourable to certain epiphytes, e. g. the cyanobacterial lichens.

The low number of lichen species on *Populus* may partly be explained by the abundance of epiphytic bryophytes. There is also a much smaller variation in the microhabitat structure on basal trunks of *Populus* than on *Salix*. There is a considerable variation in the bark pH of *Populus* from pH 4 up to pH 7 (Fig. 4). Trunks with high bark pH (>6) have especially few lichens. Species such as *Biatora carneoalbida* and *B. epixanthoides* that are adapted to high bark pH conditions on shaded forest trees strongly dominate the vegetation on trees with high bark pH. Preliminary results using generalized linear models have shown that most lichen species on *Populus* either prefer low bark pH or are indifferent to it.

The study shows that old *Salix caprea* and *Populus tremula* trees are important components for conserving epiphytic lichen diversity in the boreal forests of eastern Fennoscandia: *Salix* especially because of high species diversity, *Populus* because of the high number of specialist species.

Acknowledgements

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Biomass Growth in Five Alectorioid Lichen Epiphytes

Karl-Erik Renhorn, Per-Anders Esseen
Department of Ecological Botany, Umeå University, S-901 87 Umeå, Sweden

Abstract

Biomass growth in alectorioid lichens was measured during one year by repeated weighing technique. Five pendent lichens were transplanted to a mature *Picea abies* forest and suspended in netting cages. The change in biomass with time was substantially affected by thallus fragmentation in all species except *Usnea filipendula*. The highest annual growth rate for unfragmented thalli was found in *U. filipendula* (16.3%), followed by *Alectoria sarmentosa* (11.5%), *U. longissima* (9.2%), *Bryoria fuscescens* (8.6%) and *B. fremontii* (6.3%). Maximum growth of individual thalli ranged from 11% in *B. fremontii* to 40% in *Alectoria sarmentosa*. The study shows that lichen transplants can be used to measure biomass growth in alectorioid species. The results suggest that some alectorioid lichens possess a considerable growth potential and that the extent of thallus fragmentation strongly influences the pattern of biomass accumulation. The method should have wide application in ecological and biomonitoring studies, for example, to follow the vigour of transplants of threatened lichen species.

Keywords: lichen growth, thallus fragmentation, fruticose lichens, *Alectoria, Bryoria, Usnea*

1 Introduction

The existing literature on lichen growth rates mainly concerns foliose and crustose species (reviewed by AHMADJIAN 1993). Change in thallus size measured as increase in radius or area dominates the available information, while data on biomass accumulation is more scarce, no doubt because of the methodological problems involved. Information on biomass growth is necessary to evaluate the contribution of lichens to ecosystem functions, such as mineral cycling (PIKE 1978; KNOPS *et al.* 1991) and food and shelter for animals (RICHARDSON and YOUNG 1977).

For a long time the notion of lichens as slow growers has prevailed (HALE 1974; TOPHAM 1977). Recent transplant studies, however, have shown that some foliose and fruticose lichens have a considerable potential for biomass accumulation. DENISON (1988) presented a transplant method for culturing foliose lichens and reported a biomass growth of 16% per year in *Lobaria oregana* and 8% in *L. pulmonaria* in western Oregon. Only a few attempts have been made to measure directly biomass accumulation in fruticose lichen epiphytes. However, STONE (1986) used the same transplant technique as DENISON (1988) and found a relative growth of 10% during a four-month period in *Usnea subfloridana*. In *Ramalina menziesii*, BOUCHER and NASH (1990) reported an annual biomass growth as high as 24% at a coastal site in California. In this study we evaluate a transplant method to determine biomass growth in alectorioid lichens and compare annual growth in five pendent species.

2 Materials and methods

2.1 Study site and lichen species

The site was a mature (c. 100 year) mesic conifer forest at Svartberget Experimental Forest (64° 14' N, 19° 46' E; 230 m a.s.l.) in the county of Västerbotten, northern Sweden. Tree species composition was dominated by Norway spruce *(Picea abies)*, but scattered, large individuals of Scots pine *(Pinus sylvestris)* also occurred. The lichen flora at the study site was representative for mature stands of mesic conifer forest in middle boreal Sweden. The most common macrolichens were: *Alectoria sarmentosa, Bryoria capillaris, B. fremontii, B. fuscescens, Hypogymnia physodes, Platismatia glauca* and *Usnea filipendula*. Other frequent species were *B. furcellata, H. tubulosa, Imshaugia aleurites, Parmelia sulcata, Parmeliopsis ambigua, P. hyperopta,* and *Vulpicida pinastri*. Abundant growth of *A. sarmentosa* and *Bryoria* spp. occurred on large conifers.

Total precipitation during the study period (July 31, 1992 to August 3, 1993) amounted to 710 mm. This was 24% higher compared to mean annual precipitation during the period 1970–1993. Average temperature between 1970 and 1993 was 12.8 °C during the warmest month (June) and –14 °C during the coldest month (January). The corresponding values for 1993 were 13.6 °C and –11.0 °C, respectively.

We measured growth in five alectorioid species: *Alectoria sarmentosa, Bryoria fuscescens, B. fremontii, Usnea filipendula* and *U. longissima*. The first four species were collected from lower branches in conifer stands within Svartberget Experimental Forest while *U. longissima* was taken from a semi-natural *Picea abies* forest 90 km southwest of the study site. *Usnea longissima* is classified as endangered in Sweden and has disappeared from about 90% of old sites (including those closer to our study area), mainly because of forest cutting operations (ESSEEN *et al.* 1992). However, a number of sites have been discovered during recent years and the species is currently known to occur on c. 100 localities in Sweden. *Usnea longissima* was recently found in a *Picea abies* forest 220 km north of our study site (ANDERSSON and WILLIAMSON 1993).

2.2 Growth determination

Lichen growth was determined in netting cages by using a method modified after Susan K. Stevenson (personal communication) and BOUCHER and NASH (1990). Netting cages are necessary for quantification of thallus fragments that are lost through the action of wind and heavy rain. Ten cages measuring 60 x 30 x 20 cm were constructed of wood and nylon netting (5 mm mesh size). The netting allowed the passage of more than 95% of the incident light (photosynthetically active radiation, µmol m^{-2} s^{-1}), as measured with a quantum sensor (Li-189-A; Lambda Instrument Co., Lincoln, Nebraska, USA). Each cage contained five lichen thalli (one of each species), 15–20 cm long and positioned at successively alternating locations. Each lichen thallus was suspended from a group of five wooden pins (60 mm long, 2 mm in diameter) fastened in a frame screwed to the roof of the cage. The frame consisted of two 5 x 60 cm plexiglas plates spaced 5 cm apart by long screws. One plexiglas plate was removable and a flap at one side of the cage allowed access to the lichens. This method permitted removal and repeated weighing of the lichens without using any adhesives. For comparison, we also measured lichen growth without the netting but with the same plexiglas frame as described above. This procedure was used for ten thalli of *A. sarmentosa* (two frames) and five thalli of *U. longissima* (one frame).

The lichens were brought into the field on July 31, 1992. Thirteen large *Picea abies* trees were selected for the lichen transplants (one for each set of five thalli). All trees were within 200 m of the laboratory to minimise the risk of damage to lichens during transportation. The cages and frames were suspended horizontally from branches 3–4 m above the ground and at a distance of 20–50 cm from the trunk. On four occasions up to August 3, 1993, lichen transplants were brought indoors, air-dried for 24 hours, and the thalli weighed to the nearest 0.0001 g. Several thalli were fragmented during the course of the experiment and we recorded the weight of all fragments captured by the netting. Relative air humidity (RH) in the laboratory was measured using an aspirated psychrometer (Assman, type 761, Wilhelm Lambrecht GmbH, Göttingen, Germany).

Thallus weights were affected by variation in relative humidity (32–50%) between weighing occasions. To control for this we suspended five, freshly collected, thalli of each species inside 2000 ml glass containers. Constant relative humidities were created by varying the concentration of a 400 ml sulphuric acid solution. Four levels of RH at 20 °C were used and curves of thallus weight change with RH were constructed for each species (Fig. 1). All lichen biomass data were then adjusted to weight at 40% relative humidity by linear regression within the 20–70% interval. Recalculating all data to 40% RH increased lichen weights obtained at 32% RH by 1.2–1.3% while weights obtained at 50% RH were lowered by 1.4–1.6%.

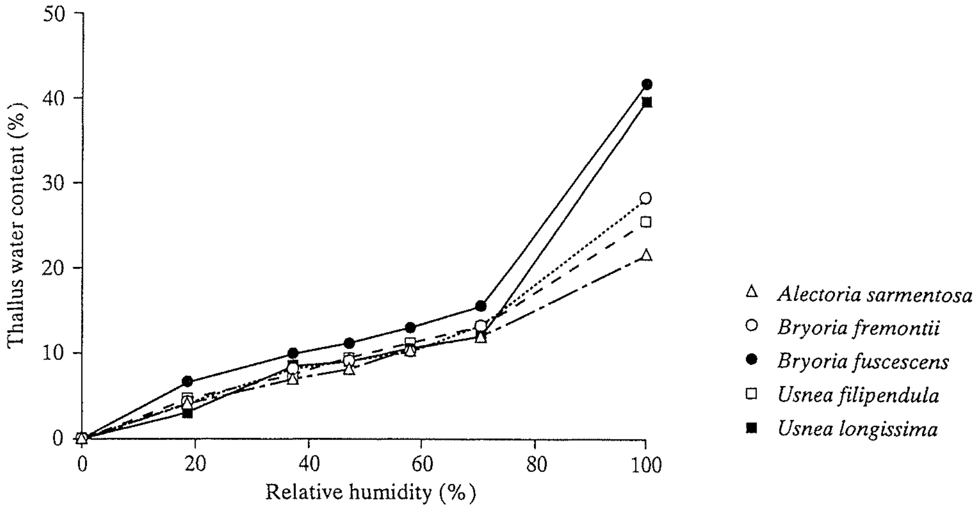

Fig. 1. Uptake of atmospheric water in five alectorioid lichens. Measurements were made at 20 °C on thalli enclosed in glass containers with different relative humidities (RH).

3 Results

The change in lichen mass with time was substantially influenced by thallus fragmentation. Two thalli, one *Bryoria fuscescens* and one *Alectoria sarmentosa,* were entirely lost and hence excluded from all calculations. Data for all remaining thalli (both intact and fragmented) show that three species, *A. sarmentosa, B. fuscescens* and *Usnea filipendula,* increased in biomass in the netting cages, while two species, *B. fremontii* and *U. longissima,* lost weight (Tab. 1). Fragments large enough to be captured by the netting (>1 cm) were observed in all species, except in *U. filipendula.* The largest fragments were found in *U. longissima* (mean of 0.31 g, n = 2) and resulted in 71% loss of initial mass in one thallus. The fragments were considerably smaller in *A. sarmentosa* (mean of 0.056 g, n = 4), *B. fremontii* (mean of 0.055 g, n = 6) and *B. fuscescens* (mean of 0.009 g, n = 8).

Table 1. Mean annual weight change (percent) and initial weights (g) in five alectorioid lichens. Data adjusted to weights at 40% RH. [1] all thalli except two that were lost, [2] fragmented and lost thalli excluded.

	All Thalli[1]			Intact Thalli[2]			Initial weight (g)
	Weight change (%) Mean ± SE	Weight change (%) Min – max	Number of Thalli	Weight change (%) Mean ± SE	Weight change (%) Min – max	Number of Thalli	Min – max
Alectoria sarmentosa							
with netting	7.0±4.9	-33.9–21.0	10	11.5±1.9	2.9–18.7	7	0.40–1.25
without netting	7.2±8.9	-42.8–40.3	9				0.08–0.30
Bryoria fremontii	-2.1±7.2	-65.8–10.8	10	6.3±1.5	0.6–10.8	6	0.23–0.80
Bryoria fuscescens	8.2±2.4	-3.4–20.9	9	8.6±2.7	3.8–13.5	3	0.16–0.52
Usnea filipendula	16.3±1.8	3.6–25.1	10	16.3±1.8	3.6–25.1	10	0.25–1.04
Usnea longissima							
with netting	-3.8±9.1	-70.7–18.0	10	9.2±1.7	2.9–18.0	8	0.26–0.59
without netting	5.5±2.7	3.9–11.5	5				0.18–0.53

The relative biomass growth rate of intact (unfragmented) thalli showed a large variation, both within and between species. Maximum annual growth of individual thalli ranged from 11% in *B. fremontii* to 40% in *A. sarmentosa* (Tab. 1). Mean growth rate of the five species varied between 6.3 and 16.3% in the netting cages and differed significantly among species as revealed by non-parametric ANOVA (Kruskal-Wallis H = 12.7, p = 0.013). The most rapidly growing species was *U. filipendula,* followed by *A. sarmentosa, U. longissima, B. fuscescens,* and *B. fremontii.* All species increased in biomass during all four sampling periods, with the exception of *B. fremontii* and *B. fuscescens* in July 1993 (Fig. 2). Overall, the highest growth rates were found during summer and autumn, coinciding with high rainfall. The summer of 1993 was unusually rainy with 228 mm rainfall during June/July (Fig. 3). Most precipitation fell as snow between October 1992 and April 1993.

Comparing all thalli with the intact ones shows that fragmentation had a great impact on growth in three of the five species. Thallus fragmentation decreased growth rates in *A. sarmentosa* from 11.5 to 7% and caused weight loss in both *B. fremontii* and *U. lon-*

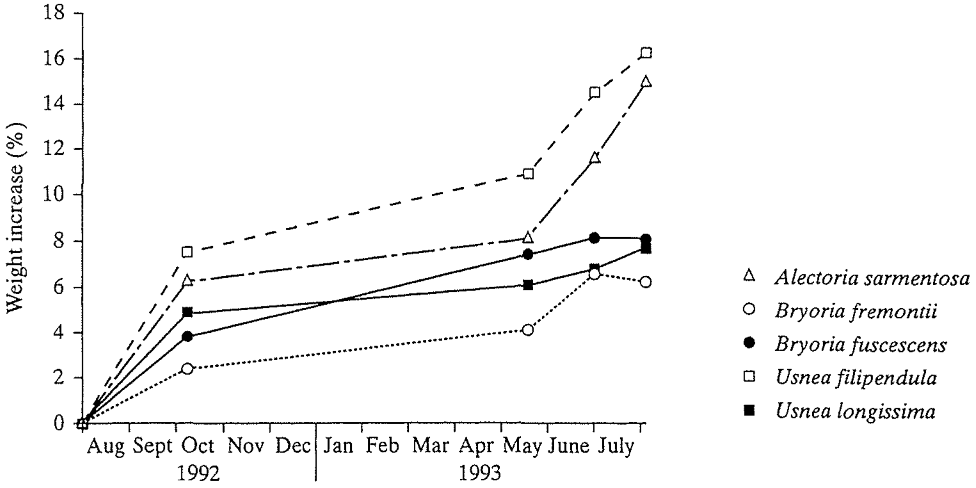

Fig. 2. Mean relative weight change during one year in five alectorioid lichen species in a boreal conifer forest. All data are from intact (unfragmented) thalli except for *Bryoria fuscescens*. Data adjusted to weights at 40% RH.

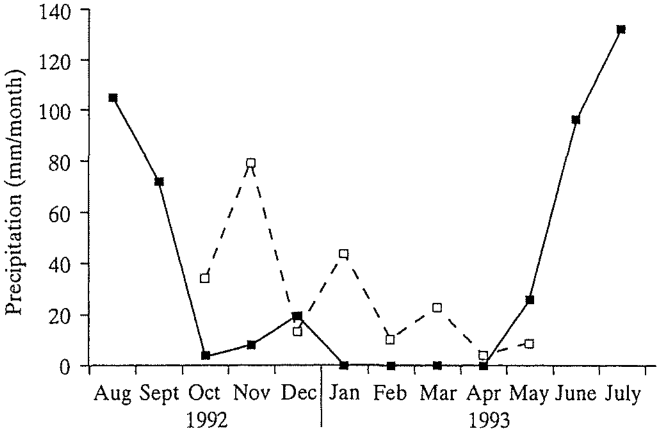

Fig. 3. Rainfall (solid line) and snowfall (broken line) in mm per month at Svartberget Experimental Forest between August 1992 and August 1993.

gissima. Fragmentation occurred in six out of nine thalli of *B. fuscescens* but mass loss was not great enough to cause any significant decrease in growth rate. The relative growth of *A. sarmentosa* was only marginally affected by the netting (Tab. 1). *Usnea longissima*, however, lost weight in the cages, but this was due to the fact that large thallus fragments were lost from two of the thalli. Excluding these thalli we found a higher growth rate (9.2%) in the netting cages than in thalli transplanted without netting (5.5%).

4 Discussion

The study shows that transplants can be used to determine biomass growth rates in alectorioid lichen epiphytes. However, to determine the maximum growth potential of epiphytic lichens it is necessary to enclose them. Netting cages protect the transplants from disturbance by animals and make it possible to quantify the extent of thallus fragmentation. A potential drawback of the method is that cages probably change the microclimate around the lichens to some degree. Our study was not specifically designed to evaluate the influence of the cages on microclimate. However, we found only minor effects of the netting on the amount of incident light. The similar growth rate in caged and uncaged thalli of *A. sarmentosa* suggests that the microclimate in the cages did not substantially differ compared to the conditions outside.

Our study included a relatively small number of thalli (10–20) of each lichen species resulting in large standard errors in some of the species (Tab. 1). However, the mean growth rates found for unfragmented thalli of *A. sarmentosa* (11.5%) and *U. filipendula* (16.3%) suggest that some alectorioid lichen epiphytes have a potential for relatively rapid growth. Growth rates up to 10–25% have been found for some *Alectoria* and *Bryoria* spp. in Canada (S.K. Stevenson, personal communication) and for *U. longissima* in USA (B. McCune, personal communication). The rather low growth rate found for *U. longissima* and *B. fremontii* in the present study might be due to the fact that the site was not an optimal habitat for these species.

The significance of microclimate, particularly rainfall, for lichen growth has been demonstrated by many workers (e.g., HALE 1967; KÄRENLAMPI 1971; ARMSTRONG 1973; BOUCHER and NASH 1990). In the present study, high growth coincided fairly well with high rainfall, but measurements were not frequent enough to allow assessment of the influence of temperature. Growth of epiphytic lichens is likely to vary considerably between different positions in the canopy due to variation in microclimate. For example, STONE (1986) found higher growth rates in both *Parmelia sulcata* and *Usnea subfloridana* transplanted to the outer part of branches than in the canopy interior (near the trunk). Our lichen transplants were positioned close to the trunk and probably received less light and precipitation compared to the outer part of the branches. We may therefore have underestimated the growth potential of alectorioid lichens in the present study.

The high degree of fragmentation in our lichen transplants supports the view that liberation and transport of thallus fragments is an important dispersal method in alectorioid lichen epiphytes (BAILEY 1976; ESSEEN 1985; STEVENSON 1988). The sensitivity to fragmentation appears to be related to thallus morphology. Unfortunately, we could not fully evaluate the role of morphology because of the small sample size and the absence of data on very small fragments that may have passed through the rather coarse netting (5 mm mesh). However, *Usnea longissima*, a relatively robust species with a strong central cord, mainly releases large fragments (ESSEEN 1985) that can have a major impact on pattern of biomass accumulation (cf. Tab. 1). In contrast, we did not observe any fragments large enough to be captured by the netting in the related but more richly branched species *U. filipendula*. It has been suggested that long-distance dispersal through thallus fragmentation may be more important in *A. sarmentosa* and *Bryoria* spp., due to their finely dissected morphology, than in *Usnea* spp. (ESSEEN 1985). Small, c. 2–20 mm long, fragments of *A. sarmentosa* and *B. fuscescens*, in particular, were more numerous in litterfall traps than for *Usnea* spp. In the present study we found considerably smaller fragments in *B. fuscescens* than in *A. sarmentosa*. This supports the view that some *Bryoria* spp. seem to be less limited by dispersal than *A. sarmentosa* (S.K. Stevenson, personal communication). Carefully designed experiments involving a large number of replicates are required to understand the importance of morphology for the degree of thallus fragmentation, dispersal efficiency and patterns of biomass accumulation in lichens.

It has previously been shown that transplants may be used to establish lichen populations on sites where the species have vanished (e.g. HAWKSWORTH 1971). For example, thalli of *U. longissima* continued to grow after being transplanted to branches of *Picea abies* trees in middle boreal Sweden (ESSEEN and ERICSON 1982). On the assumption that growth rate is related to the well-being of the lichen, transplant experiments may be mployed to assess the sensitivity of epiphytic lichens to different kinds of habitat disturbance. In this context, however, it is necessary to gain further information on the significance of microclimate and position in the canopy for lichen growth. The method for measasuring biomass growth of lichens used in this paper is suitable for monitoring the vigour of transplants of threatened lichens such as *U. longissima* and other pendent species. It should also have wide application in studies monitoring the effects of air pollutants and forest management practices on epiphytic lichen communities.

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Threatened Lichens in Japan

Hiroyuki Kashiwadani[1], Syo Kurokawa[2]
[1] Department of Botany, National Science Museum, 1-1 Amakubo-4, Tsukuba, Ibaraki 305, Japan
[2] Botanic Gardens of Toyama, Kamikutsuwada 42, Fuchu, Nei-gun, Toyama 939-27, Japan

Abstract
As in other areas of the world, some lichens are extinct, endangered, vulnerable or rare in Japan. The threatened species for this country were nominated a Red List by KUROKAWA and KASHIWADANI (1993) and include 75 species. In this paper a revised list including 82 threatened species is presented. Those found in high mountains are least threatened while temperate and subtropical species in well populated areas are at risk from factors such as air pollution, urbanization, quarrying, and from forestry practices, especially *Cryptomeria* plantations.

Keywords: threatened lichens, Japan, Red List

1 Introduction

A little more than one thousand lichen species have been recorded from Japan. While foliose and fruticose lichens have been studied resonably well, our knowledge of the crustose lichens is still very limited. Although representatives of *Graphis, Lecanora, Lecidea, Pertusaria, Verrucaria* and allied genera in the local flora have been studied by some authors, most of the species in these genera have not been throughly compared with possibly related species outside of Japan and including a large number of crustose species in other genera often referred to only once in the literature by for example, W. Nylander, J. Müller Aargau and E.A. Vainio.

Four major vegetational zones have been recognized in Japan; there are the boreal or alpine, the cool temperate, the temperate, and the subtropical zones. These zones are distinguished by their higher plant vegetation and by climatic conditions. In addition the ancient groves of *Cryptomeria japonica* in the precincts of old shrines or temples should be mentioned, as oldgrowth *Cryptomeria* trees may support unusual lichens.

Japan has 28 national parks and 55 quasi-national parks (ca 8.9% of the area of the country), where natural vegetation is conserved. These are mainly located in the regions of high mountains, where boreal and alpine species are not threatened by changing conditions. However, a rapid deterioration of habitats in the temperate and subtropical areas is occurring due to several factors such as, urbanization, air pollution (with increase of SO_2 and NO_x concentration), and forestry practices, e.g. resulting in even aged plantations of *Cryptomeria japonica.*

2 Methods

The commonly used IUCN categories are here slightly modified from their current use. **Extinct** species refer to lichens, which have not been collected within the last 20 years, though they are quite well documented. **Endangered** species are those with a restricted distribution, and vulnerable to extinction by environmental changes including air pollution, forestry or urbanization. **Vulnerable** species are those which have seldom been reported from Japan and their distribution is still in need of detailed study. **Rare** species include species rarely found in Japan and the distribution has been monitored quite well.

3 Results

Our knowledge of Japanese lichens is limited and the threatened lichens enumerated here are mostly foliose and fruticose species, and, due to lack of knowledge, crustose species are incompletely considered. The first lichen Red List was published by KUROKAWA and KASHIWADANI (1993). In the authors revised version, *Cetrariella delisei, Dermatocarpon moulinsii, D. tuzibei, Flavocetraria cucullata, F. nivalis, Lethariella togashii, Phaeographina pseudomontagnearum,* and *Stereocaulon tomentosum* are added and included in the rare species. Cladonia caperatica is excluded from the list. The new version includes 3 as extinct *(Anaptychia angustiloba, A. leucomelos, Erioderma asahinae),* 7 as endangered (*Gymnoderma insulare, Umbilicaria muehlenbergii* and 5 others), 23 as vulnerable (*Cladonia koyaensis, Gymnoderma coccocarpum, Thyrea latissima, Toninia tristis* ssp. *fujikawae* and 19 others), and 49 as rare (*Acroscyphus sphaerophoroides, Flavopunctelia soredica, Hypotrachyna sinuosa* and 46 others).

4 Threatened lichens in different vegetational zones

4.1 Lichens of boreal and alpine vegetation

Boreal and alpine vegetation is characterized by *Pinus pumila,* and species of *Picea* or *Abies.* Although many circumpolar lichens are as common in montane areas of Hokkaido and alpine areas of Honshu, as in mountains in Europe or North America, some are quite rare in Japan. For instance, *Cetrariella delisei, Flavocetraria nivalis,* and *Stereocaulon tomentosum* are only known from higher elevations in Hokkaido and *Flavocetraria cucullata* from high elevations in Hokkaido and a single locality in Honshu. *Acroscyphus sphaerophoroides* grows on rocks in summit areas of central Hokkaido (Prov. Iburi: Mt. Tomuraushi. Prov. Ishikari: Mt. Aka-dake, Mt. Chubetsu, Mt. Keigetsu-dake) and central Honshu (Prov. Etchu [Pref. Toyama]: Mt. Yakushi. Prov. Shinano [Pref. Nagano]: Mt. Tengu and Mt. Kinpu. Prov. Hida [Pref. Gifu]: Mt. Ontake). This species shows a unique circum-Pacific distribution, being known also from Canada, Mexico, Peru and the Himalayan regions.

4.2 Lichens of cool temperate vegetation

Cool temperate vegetation is characterized by deciduous broad-leaved trees such as *Fagus crenata* and *Quercus mongolica* var. *grosseserrata.* Although many of the cool temperate lichens are still common, others such as *Gymnoderma insulare, G. coccocarpum, Lethariella togashii, Toninia tristis* ssp. *fujikawae* are endangered or vulnerable. *Gymnoderma insulare* grows on bark of very old *Cryptomeria japonica* trees in Yakushima Island, Mt. Hiko-san in Kyushu, and Mt. Koya in Honshu. *G. coccocarpum* is restricted to Yakushima Island. Yakushima Island is protected as a National Park, and the *Cryptomeria* forest on Mt. Koya is in the precinct of an old Buddhist temple. Although deforestation will not occur in these areas in the near future, lichens face other threats such as changes in humidity, air pollution and visitor pressure in the forests. *Lethariella togashii* grows on twigs or bark of *Picea torano* at the base of Mt. Fuji and on *Abies sachalinensis* in Hokkaido. On Mt. Fuji, shrubs and small trees in the forest have been gathered as wood for fuel or charcoal for centuries. Following the designation of this forest as a natural monument by the Cultural Properties Protection Committee, wood-gathering has been prohibited and the increased growth of small trees and shrubs has resulted in an increase of humidity and a decrease in air circulation with unfavourable effects on the micro-habitat and growth of *L. togashii. Umbilicaria muehlenbergii* has a disjunct distribution in eastern Asia and eastern North America. While it is rather common in northern United States, it has been recorded only from two localities in Japan (Prov. Ishikari: Mt. Ashibetsu. Prov. Mutsu [Pref. Aomori]: Mt. Nuidoiwa) and is endangered. The cliffs of Mt. Nuidoiwa were formerly used as a training area for rock climbing, causing considerable disturbance to the vegetation. However, rock climbing is now prohibited there, and the vegetation seems to be recovering.

4.3 Lichens of temperate vegetation

Temperate vegetation is characterized by having evergreen broad-leaved trees such as *Castanopsis cuspidata* var. *sieboldii, Quercus glauca, Persea thunbergii,* and the coniferous tree *Tsuga diversifolia.* Among lichens found in this vegetation are some species which are apparently very rare or vulnerable in Japan. For example, *Parmelia erumpens, Phaeographina pseudomontagnearum, Ramalodium japonicum,* and *Relicina sydneyensis* are known only from one or two localities in lower elevations in middle Honshu and Shikoku. Although the localities are located in or close to tourist resorts, little consideration has been paid to the protection of these species. In west and middle Honshu and in Kyushu calcareous rock sites are threatened by quarrying of rocks for cement production and by road constructions and the following species are now very rare; *Collema latzelii* (Prov. Shinano: Todai, Prov. Awa [Pref. Ehime]: Mt. Ken-zan), *C. nipponicum* (Prov. Tosa [Pref. Kochi]: Tosayama-mura), *C. polycarpon* var. *corcyrense* (Prov. Higo [Pref. Kumamoto]: Itsuki-mura) *Leptogium corniculatum* (Prov. Musashi: Mt. Ryogami, Prov. Aki [Pref. Hiroshima]: Taishaku-kyo Gorge), *Paulia japonica* (Prov. Tosa: Mt. Yokokura), and *Thyrea latissima* (Prov. Musashi [Pref. Saitama]: Chichibu, Prov. Bitchu [Pref. Okayama]: Niimi, Prov. Awa [Pref. Tokushima]: Sawatani-mura).

4.4 Lichens of subtropical vegetation

Subtropical vegetation in Japan is largely characterized by evergreen broad-leaved forest mixed with tree ferns and/or palms. It is developed south of Yakushima island to the Yaeyama Islands through the Amami and Okinawa Islands. The Bonin Islands are also covered with subtropical vegetation. Although these islands have a rather rich lichen flora, including species belonging to the subtropical or tropical element, some of these are now extinct, rare or vulnerable. For example, *Anaptychia angustifolia* and *A. leucomelos* must now be considered extinct in Japan, as these have not been recorded in the last 20 years. Rare corticolous species reported from islands with subtropical vegetation include: *Coccocarpia pellita, Mazosia melanophthalma, Parmotrema paraphypotropum, Pertusaria boninensis, Porina nitidella, Pseudocyphellaria argyracea, Pyrenula gigas, Pyxine cocoes, P. philippina, Strigula nitidula, Trypetheliopsis boninensis,* and *Trypethelium boninense.* The major threat to these species has been the loss of natural forests. However, during recent field work in the Amami, Ishigaki and Iriomote Islands in 1995, H. Kashiwadani and G. Thor found *Mazosia melanophthalma* and *Pyrenula gigas* to be rather common.

List of threatened lichen species in Japan

* generic position unclear.

Extinct

Anaptychia angustiloba (Müll. Arg.) Kurok. (Physciaceae)
Anaptychia leucomelos (L.) Mass. (Physciaceae)
Erioderma asahinae Zahlbr. (Pannariaceae)

Endangered

Brigantiaea nipponica (Sato) Hafellner (Brigantiaceae)
Gymnoderma insulare Yoshim. (Cladoniaceae)
Lobothallia alphoplaca (Wahlenb. in Ach.) Haffellner (Lecanoraceae)
Pyrgillus boninensis Asah. (Pyrenulaceae)
Solorina saccata (L.) Ach. (Peltigeraceae)
Solorina saccata (L.) Ach. var. *spongiosa* Nyl. (Peltigeraceae)
Umbilicaria muehlenbergii (Ach.) Tuck. (Umbilicariaceae)

Vulnerable

Bacidia palmularis Zahlbr. (Bacidiaceae)
Baeomyces sanguineus Asah. (Baeomycetaceae)
Cladonia acuminata (Ach.) Norrl. (Cladoniaceae)
Cladonia brevis (Sandst.) Sandst. (Cladoniaceae)
Cladonia koyaensis Asah. (Cladoniaceae)
Coniocybe lutea Asah. (Coniocybaceae)*
Gymnoderma coccocarpum Nyl. (Cladoniaceae)
Lecanora muralis (Schreb.) Rabenh. (Lecanoraceae)
Leptogium corniculatum (Hoffm.) Minks (Collemataceae)
Letrouitia bifera (Nyl.) Hafellner (Lopadiaceae)
Pannaria mariana (Th. Fr.) Müll. Arg. (Pannariaceae)
Pannaria stylophora Vainio (Pannariaceae)

Parmelia erumpens Kurok. (Parmeliaceae)
Paulia japonica Asah. (Lichinaceae)
Physma radians Vainio (Collemataceae)
Psoroma boninense Kurok. (Pannariaceae)
Pyxine asiatica Vainio (Physciaceae)
Pyxine meissnerina Nyl. (Physciaceae)
Ramalodium japonicum (Asah.) Henssen (Collemataceae)
Relicina echinocarpa (Kurok.) Hale (Parmeliaceae)
Relicina sydneyensis (Gyelnik) Hale (Parmeliaceae)
Thyrea latissima Asah. (Lichinaceae)
Toninia tristis (Th. Fr.) Th. Fr. ssp. *fujikawae* (Sato) Timdal (Catillariaceae)

Rare
Acroscyphus sphaerophoroides Lév. (Caliciaceae)
Cetraria aculeata (Schreb.) Fr. (Parmeliaceae)
Cetraria kurokawae Shib. & Yoshida (Parmeliaceae)*
Cetrariella delisei (Bory ex Shaer.) Kärnef. & Thell (Parmeliaceae)
Cladonia hidakana Kurok. (Cladoniaceae)
Coccocarpia pellita (Ach.) Müll. Arg. (Coccocarpiaceae)
Collema callopismum A. Massal. (Collemataceae)
Collema coccophyllum Nyl. (Collemataceae)
Collema kiushianum Asah. (Collemataceae)
Collema latzelii Zahlbr. (Collemataceae)
Collema nipponicum Degel. (Collemataceae)
Collema polycarpon Hoffm. var. *corcyrense* (Arn.) Degel. (Collemataceae)
Collema substipitatum Zahlbr. (Collemataceae)
Collema undulatum Flot. (Collemataceae)
Dermatocarpon moulinsii (Mont.) Zahlbr. (Dermatocarpaceae)
Dermatocarpon tuzibei Sato (Dermatocarpaceae)
Flavocetraria cucullata (Bellardi) Kärnef. (Parmeliaceae)
Flavocetraria nivalis (L.) Kärnef. (Parmeliaceae)
Flavopunctelia soredica (Nyl.) Hale (Parmeliaceae)
Haematomma fuliginosum Asah. (Haematommataceae)
Hyperphyscia adglutinata (Flörke) H. Mayrhofer & Poelt (Physciaceae)
Hypotrachyna crenata (Kurok.) Hale (Parmeliaceae)
Hypotrachyna sinuosa (Sm.) Hale (Parmeliaceae)
Lethariella togashii Krog (Parmeliaceae)
Lobaria angustifolia (Asah.) Yoshim. (Lobariaceae)
Lobaria kazawaensis (Asah.) Yoshim. (Lobariaceae)
Mazosia melanophthalma (Müll. Arg.) Sant. (Opegraphaceae)
Orphniospora moriopsis (A. Massal.) D. Hawksw. (Fuscideaceae)
Parmotrema parahypotropum (Carb.) Hale (Parmeliaceae)
Parmotrema rampoddense (Nyl.) Hale (Parmeliaceae)
Peltigera lepidophora (Vainio) Bitter (Peltigeraceae)
Pertusaria boninensis Shib. (Pertusariaceae)
Phaeographina pseudomontagnearum M. Nak. (Graphidaceae)
Phaeographis flavicans Kashiw. (Graphidaceae)
Phaeographis fujisanensis Kashiw. & M. Nakan. (Graphidaceae)
Porina nitidella Müll. Arg. (Trichotheliaceae)
Pseudocyphellaria argyracea (Del.) Vainio (Lobariaceae)

Pyrenula gigas Zahlbr. (Pyrenulaceae)
Pyxine cocoes (Sw.) Nyl. (Physciaceae)
Pyxine philippina Vainio (Physciaceae)
Solorina crocea (L.) Ach. (Peltigeraceae)
Solorina platycarpa Hue (Peltigeraceae)
Stereocaulon incrustatum Flörke (Stereocaulaceae)
Stereocaulon tomentosum Fr. (Stereocaulaceae)
Sticta limbata (Sm.) Ach. (Lobariaceae)
Strigula nitidula Mont. (Strigulaceae)
Trypetheliopsis boninensis Asah. (Trypetheliaceae)
Trypethelium boninense Kurok. (Trypetheliaceae)
Umbilicaria deusta (L.) Baumg. (Umbilicariaceae)

5 Future activities

Most Japanese lichenologists will unite in a co-operative study on threatened lichens. Future activities of the Lichenological Society of Japan in cooperation with the National Science Museum are summarized here: 1) the compilation of a revised Red List, 2) a survey of all the nominated species with regard to their present state and circumstances in the field, including an evaluation of the factors causing a threat to the species. The results of this programme will be compiled in the National Science Museum, Tokyo (TNS) and published as a Red Data Book in Japan by the Environmental Agency in 1997. Along with studies in the field, consideration will be given to the preparation of distribution maps of lichens in Japan similar in format to those presently being produced by the British Lichen Society.

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Rare and Vulnerable Species of Lichens in the Southern Part of the Russian Far East – Primorye and Sakhalin Regions

Svetlana I. Tschabanenko
Sakhalin Botanical Garden, Yuzhno-Sakhalinsk, Gorky Street 25, 693013 Russia.

Abstract
29 species of lichens are included in the Russian Federation Red Data Book. They are all protected by law, 15 of them are found in the Primorye territory, 10 on Sakhalin Island and 6 in the Kuril Islands.

Keywords: Russia, Far East, lichens, conservation

The growing clash between the demands of a rapidly changing society and the maintenance and protection of natural resources has made the task of defining the use and conservation of such resources a national priority. The maintenance of natural undisturbed landscapes with their particular flora and fauna are often at variance with the human interest and thus pose a difficult problem. These sites must be considered to be a mutual and natural scientific laboratory for solving theoretical and practical biological problems.

There are two Red Data Books for our country, the Red Data Book of the USSR (1984), and the Red Data Book of the Russian Federation (1988). These list 29 lichen species with a status of R (rare) or V (vulnerable). All species in the Red Data Books are protected by law. The status of protection may be within a Reserve, a national park or a natural monument. However, only reserves are functionally protected in Russia.

The study of lichens in the Primorye Territory was started in the 1920s, but as yet there is no published checklist of the lichens of this region. According to the author's data there are 593 recorded species, of which 15 (2.5%) are Red Data Book species. *Lobaria amplissima* is considered to be erroneously recorded and is omitted from the list.

There are no reserves in the Primorye Territory or Sakhalin Region that were originally designated for lichen protection, and the study of cryptogams, such as fungi and lichens, in these reserves has begun only in the last ten years. At the present time 4 of the 6 reserves (Fig. 1) have lichen checklists, the exceptions being the Far-Eastern Marine Reserve and the recently created Khanka Reserve.

The well-studied Sikhote-Alin Reserve (SA) is situated in the middle part of Sikhote-Alin mountain ridge, in the northern part of Primorye where the northern variant of Far Eastern coniferous forest, broad-leaved forests and alpine tundra are well represented, with many rare and interesting lichens which are restricted to this region. 234 species of lichen are recorded (KNYAZHEVA and SKIRINA 1982; SKIRINA and KNYAZHEVA 1985; SKIRINA 1987, 1992; DOMBROVSKAJA 1987; INSAROV and PTCHELKIN 1988; GUSEVA *et al.* 1993). 12 Red Data Book species have been recorded here, but only 3 are given protected status in this reserve: *Omphalina hudsoniana (Phytoconis viridis), Asahinea scholanderi* and *Stereocaulon exutum.* Interesting species of far eastern distributed *Stereo-*

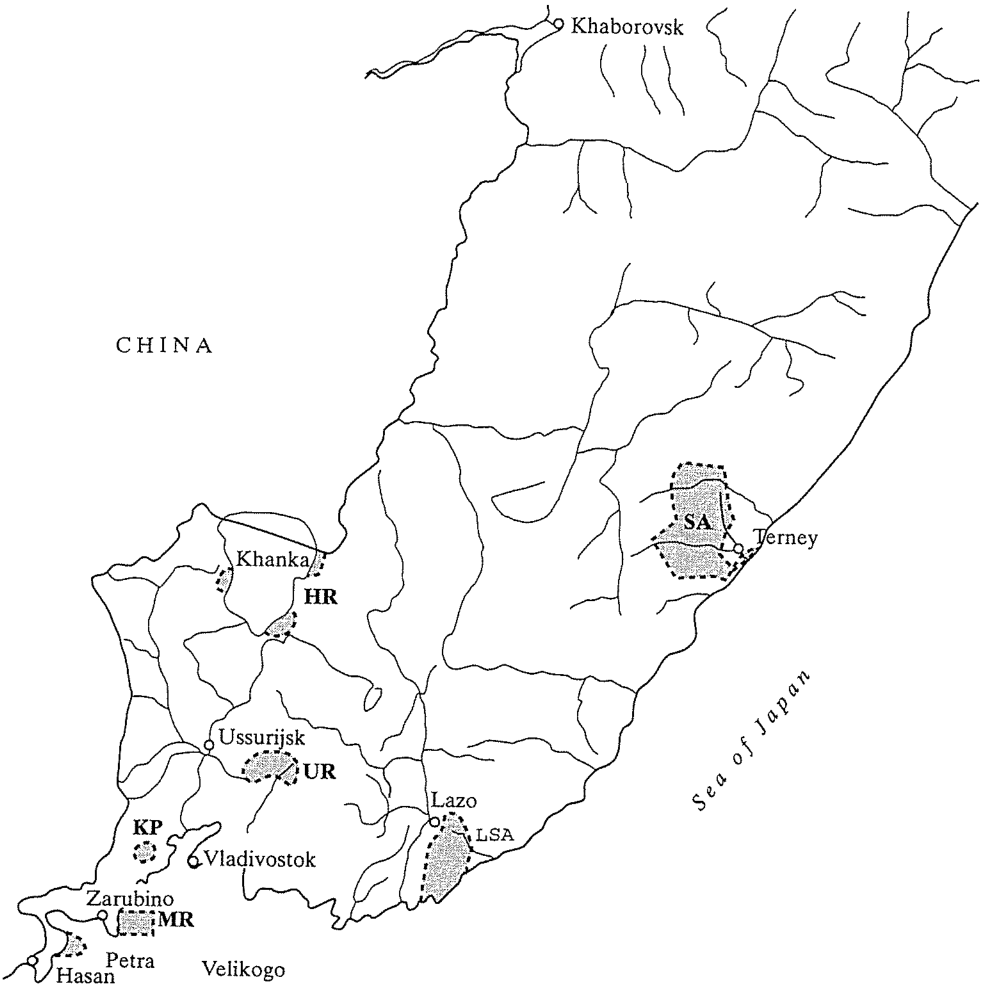

Fig. 1. Reserves (dashed line) in the Primorye and Sakhalin regions, SA (Sikhote-Alin), UR (Ussuri), KP (Kedrovaya Pad), MR (Far Eastern Marine), HR (Khanka), LSA (Lazovsky).

caulon are found (DOMBROVSKAJA 1987), as well as other species that are rare in the Primorye Region, such as *Glossodium japonicum, Sticta limbata, Hypogymnia farinacea (= H. bitteriana), H. fragillima, H. mundata* and *Brodoa intestiniformis.*

In the southern part of Primorye the Ussuriysky and Kedrovaya Pad, Far Eastern Marine and Khanka Reserves are situated (Fig. 1). There are 118 species of lichens recorded from the Ussuri Reserve, including 4 Red Data Book species, and 25 species belonging to the Eastern Asian component which is restricted to the low and high zones of southern and south-east Primorye. Kedrovaja Pad has been little studied, but of the 82 lichen species so far recorded, 7 have Red Data Book status. On the limestone areas of this reserve

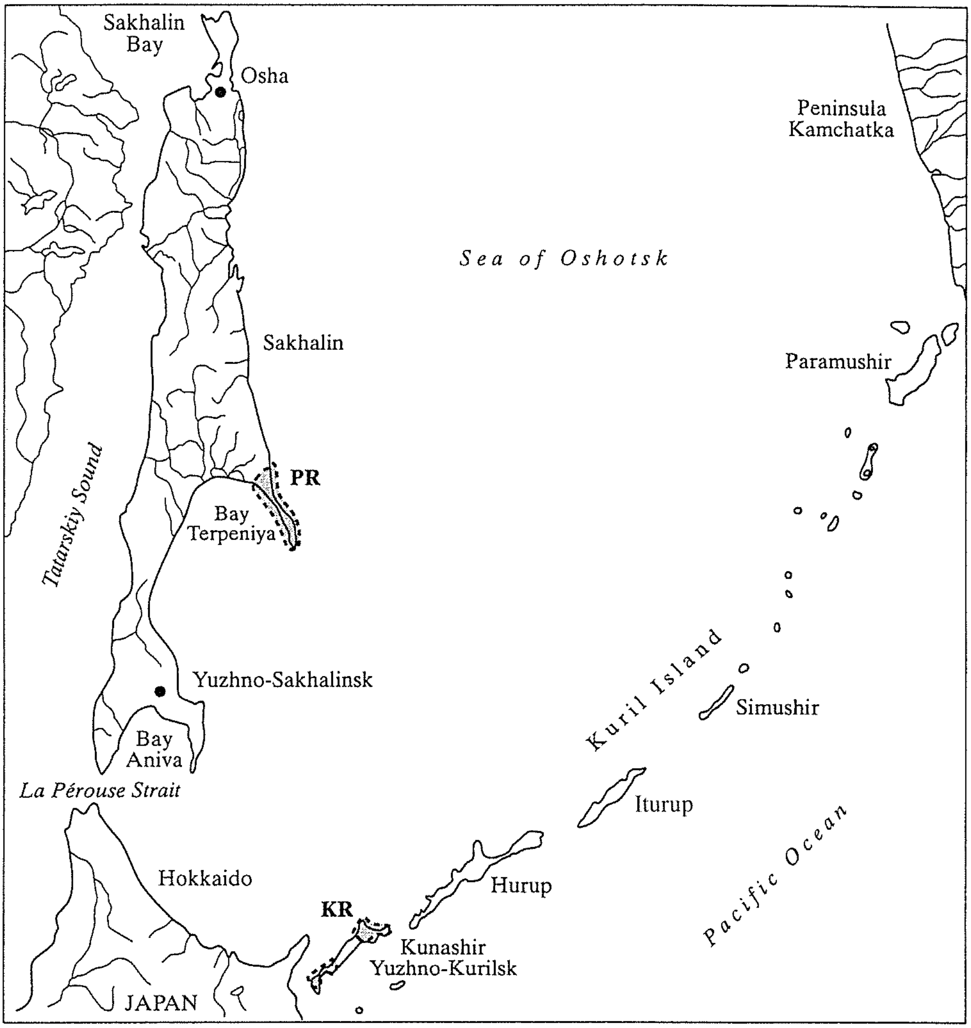

Fig. 2. Reserves (dashed line) on Sakhalin and Kuril islands, KR (Kurilsky), PR (Poronaysky).

(also found in Ussuri Reserve) there are rare and interesting species of *Collema* and *Endocarpon*, and an *Usnea* species with a red-pigmented cortex occurs in the *Pinus koraiensis* forests.

The south-eastern part of the Primorye Region is better studied, and has a rich and varried lichen flora, owing to the extensive areas of natural vegetation and the absence of large industrial enterprises. It includes 78.1% of the lichens known to the region with 66.9% being found in the Lazovsky Reserve, including 9 Red Data Book species. It is, therefore, a highly representative reserve, containing elements of many distribution types: 6 species endemic to the Primorye Region, 3 endemic to the Far East, 77 distributed along the Pacific coast of Eastern Asia. These last include *Usnea rubescens, U. pseudorubescens,* the genus *Anzia, Cetraria (Nephromopsis) asahinae, Parmelia (Hypotrachyna) laevigata, P. (Rimelia) reticulata, P. (Parmotrema) arnoldii,* together with rare species of *Lobaria, Sticta,* etc. (TSCHABANENKO 1990a, b).

The lichens of Sakhalin and Kuril Islands (Fig. 2) have been less well studied, but preliminary investigations have shown that they support a range of interesting species of the Eastern Asian component, some only recently recorded from Russia for the first time, e.g. *Stereocaulon* sect. *Botryoideum* with a centre of distribution in Japan (DOMBROVSKAJA 1987). Some species are known from only one or two sites. There are 228 species recorded within the Sakhalin region, of which 10 have Red Data Book status (SATO 1933, 1935, 1936; OXNER 1938; RASSADINA 1967; ROMS 1967; BLUM 1970; KASHIWADANI 1975, 1984; INSAROV and PTCHELKIN 1988; DOMBROVSKAJA 1987; TSCHABANENKO 1993). The northern Kurils and northern Sakhalin are little known, but due to extensive development in oil and gas prospecting there is an urgent need to study threatened terricolous species. The epiphytic communities are threatened by the use of fire. However, as there is no checklist for this region it is difficult at the present time to say which species are vulnerable. Only two reserves have been created in this region: the Kurilsky Reserve on Kunashir Island and Poronaysky in the east of Sakhalin (Fig. 2). The latter has not been explored for lichens, but the Kurilsky Reserve has 150 species, including 6 Red Data Book species. Our exploration in this reserve has revealed a great diversity of lichen species occurring in a range of complex lichen communities (TSCHABANENKO 1993).

It is apparent that the reserves in the Russian Far East are still rich in lichen species, and that deterioration of lichen communities is confined to areas of urban and industrial development.

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Lichens of Protected Areas in Ukraine

Sergey K. Kondratyuk, Irina L. Navrotskaya
N.G. Kholodny Institute of Botany, Kiev, Ukraine

Abstract
Ukraine includes two major mountain areas, the Carpathians and Crimea, as well as three distinct vegetation zones in the remaining lowland areas; Forest, Forest-Steppe and Steppe. The Country has 12 reserves and 4 national parks. A total of 1239 lichens have been recorded for the country. The Steppe zone is the most favoured area, where 205 species are present in protected areas (representing 87.6% of lichens recorded in this zone). In the reserves and national parks of the Carpathian mountains 715 species (79.4%), and in the Crimean reserves 340 species (59.8%) are found. In the reserves and national parks of the Forest zone 171 species (55%) are found while in the reserves of the Forest-Steppe zone only 179 species (37.6%) are found. The conservation status of 29 species of lichens in the Red Data Book of the USSR and the Red Data Book of Ukraine is discussed. Twenty-three of them are known only from mountainous regions of the state and 10 occur in the plain part of the Ukraine.

Keywords: lichens, national parks, reserves, Ukraine

1 Introduction

By 1993 Ukraine had designated 12 natural reserves of which two were biosphere reserves, 4 national nature parks, and 5732 additional sites with some degree of environmental protection. In total these represent 2.14% of the overall territory of Ukraine (SHELYAG-SOSONKO and ZIZIN 1985; Perspektyvnaya setj zapovednykh ob'ektov Ukrainy 1987; YAZENKO *et al.* 1988). The study of lichens in Ukraine began in the middle of the last century, but data on lichens of Ukraine was not summarized until the preparation of "Flora of the lichens of Ukraine" (OXNER 1956, 1968, 1993), and publication of some regional papers (MAKAREVICH *et al.* 1982; KOPACHEVSKA 1986); to date there is no published checklist of Ukrainian lichens. According to the authors' data (recently prepared checklist of lichens of Ukraine – Kondratyuk, Navrotskaya and Solonina, in prep.) there are 1239 species of lichens within Ukraine, and of these 29 species (2.3%) are Red Data Book species. No reserves in Ukraine have been created specially for lichen protection. Although the study of lichens in Ukrainian reserves began in the 1930s, lichens of protected areas are only now being studied in detail.

2 Results and discussion

At the present time only 3 of the 12 reserves have published lichen checklists (MASLOVA 1977 for Polesian Reserve; KONDRATYUK 1983 for Kaniv Reserve; KONDRATYUK 1995 for Reserve Medobory). However unpublished lists of lichens have been prepared for 3 of the 4 national parks and a further 7 of the reserves. The lichen floras of the recently created Asov-Sivash National Park and Dnieper-Orel and Danube plavny Reserves remain to be explored. Twenty-nine species of Ukrainian lichens are included in Red Data Books; 10 species in the Red Data Book of the USSR (1984), and 27 species in the Red Data Book of Ukraine (1995). Two species (*Pyxine endochrysoides* [Nyl.] Degel. and *Letharia vulpina* [L.] Hue) which were in the Red Data Book of the USSR are omitted in the Red Data Book of Ukraine (ZAVERUKHA 1992). The 29 species included in the Red Data Book have a status of R (rare) or V (vulnerable). All species in the Red Data Books are protected by law. The status of protection may be within a reserve, a national park or a nature monument. However, only national parks and reserves are functionally protected in Ukraine. There are two national parks (Carpathian and Synevir) and one reserve in the Carpathian mountain region. The lichen flora of the Carpathian Biosphere Reserve contains 450 species (Navrotskaya, unpublished data). In total there are 715 species of lichens (79.4%) in the territories of the reserves and national parks of the Carpathian mountains (NAVROTSKAYA 1979, 1985, 1990; NAVROTSKAYA and PARTYKA 1990; NAVROTSKAYA *et al.* 1991). There are three reserves in the Crimean mountains region. In the Yalta Mountain Forest Reserve 154 species of lichens belonging to 72 genera (KOPACHEVSKA 1962), and in the Karadag State Reserve 78 species of 27 genera (BEZNIS and KOPACHEVSKAYA 1982) have been recorded. In total, 340 species (59.8%) of the Crimean lichens have been recorded from the reserves (KONDRATYUK and NAVROTSKAYA 1994). Lichens of protected territories of the plain part of Ukraine have not been studied to the same extent, and an inventory of lichen species is very incomplete for most of the reserves (KONDRATYUK and SOLONINA 1990). Lichen species have been recorded in the following reserves (Tab. 1).

The most favourable situation is in the Steppe zone, where 205 species (87.6%) are found in protected areas. There are 171 lichens species (55%) on territories of reserves and

Table 1. Number of lichen species and genera recorded in selected reserves.

Reserve	Species	Genera	References
Polesian	134	41	MASLOVA 1977
Kaniv	170	47	KOPACHEVSKA and LYUBCHENKO 1979; SOLOMAKHINA 1979; KONDRATYUK 1982, 1983, 1984, 1989
Ukrainian Steppe	145	45	NAVROTSKAYA 1995
Mykhajliv Moor	43	22	BAIRAK 1987
Khomutov Steppe	45	19	NAVROTSKAYA 1995
Rock Mogyly	78	27	NAVROTSKAYA 1995
Black Sea	83	33	BACHURINA and BOIKO 1978; BOIKO 1980; KONDRATYUK and NAVROTSKAYA 1992; KHODOSOVTSEV 1995
Askania Nova	59	32	BACHURINA *et al.* 1977; KHODOSOVTSEV 1994
Roztochya	65	31	unpublished data, Navrotskaya
Medobory	68	27	KONDRATYUK 1994
Provalsky Steppe	25	?	MASLOVA 1979

national parks of the Forest zone, and only 179 lichen species (37.6%) known from Forest-Steppe zone reserves (KONDRATYUK and NAVROTSKAYA 1994). The Red Data Book species *Xanthoparmelia camtschadalis* (Ach.) Hale, *Neofuscelia ryssolea* (Ach.) Essl. and *Coelocaulon steppae* (Savicz) Barreno et Vazquez are protected in all reserves of the Steppe zone (almost all departments of Ukrainian Steppe Reserve, Askania Nova and Black Sea Reserve). *Teloschistes lacunosus* (Rupr.) Savicz and *Toninia massata* (Tuck.) Herre grow only in protected territories of Askania Nova and Black Sea Reserves. *Umbilicaria subpolyphylla* Oxner is known only in a single location in the Rock Mogyly of the Ukrainian Steppe Reserve. The Red Data Book species *Aspicilia fruticulosa* (Eversm.) Flag., *A. hispida* Mereschk. and *Letharia vulpina* are known from several locations of Steppe zones of Ukraine and mountain part of the Crimea, mainly outside of protected areas, and their conservation should be discussed separately.

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A Survey of Patterns of Diversity in Non-Lichenized Fungi

D. Jean Lodge[1], I. Chapela, G. Samuels, F. A. Uecker, D. Desjardin, E. Horak,
O. K. Miller, Jr., G. L. Hennebert, C. A. Decock, J. Ammirati, H. H. Burdsall. Jr.,
P. M. Kirk, D. W. Minter, R. Halling, T. Laessøe, G. Mueller, Sabine Huhndorf,
F. Oberwinkler, D. N. Pegler, B. Spooner, R. H. Petersen, J. D. Rogers, L. Ryvarden,
R. Watling, Evelyn Turnbull, A. J. S. Whalley.

[1]Center for Forest Mycology Research, Forest Products Lab, USDA-Forest Service, Luquillo, PR 00773-1377, USA
Addresses of the co-authors see page 173

Abstract
This paper summarizes the opinions of 26 mycologists who have worked in more than one hemisphere or continent regarding the locations, correlates, and potential causes of centers of fungal endemism and diversity in non-lichenized fungi. These views were initially obtained via a survey and then summarized by the lead author. Most authors working on basidiomycetes thought that fungal diversity was more strongly correlated with host and habitat diversity than with resource abundance, whereas most of those working on ascomycetes and Hyphomycetes indicated that all three factors were very important. Overall diversity was highest in the tropics, at intermediate to high rainfall, and at middle to low elevations. Certain fungal groups, however, such as the Cortinariaceae (Agaricales), and some members of the Heterobasidiomycetes are more diverse at middle to high latitudes and elevations. There was no apparent variation in Gasteromycete diversity with latitude. The Neotropics were ranked as having a greater diversity of fungi than Africa by three of the four authors with experience in both. Although this pattern might be related to historical factors or to a higher diversity of host plants in the Neotropics, collections of fungi from Africa and the Asian tropics have been too limited to make confident comparisons between continents. Except for the Gasteromycetes and certain plant parasites, Europe was always ranked lowest in fungal diversity when it was included in comparisons, even though collecting has been most intense there.

The types of areas most frequently mentioned as having many species that are unknown elsewhere were humid forests on islands, tropical mountaintops, and large tropical river basins. For example, Australia, New Zealand, New Guinea, Sulawesi, the Andes, and parts of Africa and South America, especially the Congo and Amazon river basins were thought to have many unique species. These areas encompass many wet to moist centers of endemism for plants. The concordance suggests that despite differences in the mechanisms of dispersal and sexual incompatibility, there may be similar forces governing the isolation and speciation of plants and fungi growing in humid areas. Some plant parasitic Heterobasidiomycetes that are host-restricted occur in all regions and habitats, including dry ones. Species with limited ranges also appear to be common in the Agaricales regardless of the region. Unfortunately, there is currently too little knowledge of fungal mating systems and dispersal barriers with regard to their roles in fungal evolution and distribution. The various gaps, hypotheses, and global patterns of fungal diversity identified in this paper are worthy of pursuit through experiments and comparable surveys.

Keywords: fungi, diversity, endemism, dispersal, reproductive isolation, speciation

1 Introduction

There is a growing consensus that there are at least one million, and perhaps 1.5 million or more species of fungi in the world (HAWKSWORTH 1991, 1993; HAMMOND 1992; ROSSMAN 1994). Mycology has been represented in recent forums on global biodiversity (e.g., HAMMOND 1992), but the types of information commonly available for plants and animals is unfortunately often lacking or fragmentary for fungi. Because relatively few mycotas are thoroughly known, it is difficult to know which species have truly restricted geographic ranges, where centers of high diversity lie, and what factors are related to fungal diversity. Such issues are crucial to the conservation of fungal diversity. In the absence of complete knowledge, the expert opinions of mycologists with broad geographical experience are valuable for suggesting where our conservation efforts might be directed with greatest effect in the short term, and for suggesting hypotheses about fungal diversity and evolution that may be worthy of further pursuit and testing. This paper summarizes the opinions of the 26 authors who have studied fungi in more than one hemisphere regarding the locations, correlates, and potential causes of centers of fungal endemism and diversity.

2 Methods

A survey was sent to 22 mycologists who were known to have worked with various basidiomycetes, ascomycetes, or anamorphic stages (asexual states) of non-lichenized fungi on more than one hemisphere or continent. Nineteen of the authors came from this group, and an additional seven came from colleagues of the 22 who were contacted initially. Some authors combined their responses to the survey for a particular group, while others supplied separate information for two different groups. In all, 29 surveys are summarized below, representing 17 for basidiomycetes, one for macrofungi (mostly large basidiomycetes), seven for ascomycetes, and four for fungi that are primarily asexual or vegetative states of ascomycetes (Hyphomycetes and plant endophytic fungi) (Tab. 1). Two responses were for a given genus, seven for families, seven for orders, six for higher taxonomic groupings, two for Hyphomycetes, and four for ecological or other groups (Gasteromycetes, ant-fungus gardens, plant endophytes, and macromycetes). These views were then summarized by the lead author.

The classification of geographical regions into areas of high, intermediate or low rainfall depends on the degree to which moisture losses from evapotranspiration are balanced or exceeded by inputs from precipitation, so it varies with temperature regimes, latitude, and altitude (HOLDRIDGE 1947). The amount of annual precipitation associated with the Rain Forest and Rain Tundra life zones, as defined by HOLDRIDGE (1947), (high rainfall in this survey) is 500–1000 mm in Alpine elevational belts at Subpolar latitudes, 2000–4000 mm in Boreal Subalpine and Cool Temperate Montane areas, 4000–8000 mm in Lower Montane and Premontane elevational belts at Warm Temperate and Subtropical latitudes, and greater than 8000 mm in lowlands at tropical latitudes. Intermediate rainfall, associated with Wet and Moist Forests and Tundra plant formations, occurs with an annual precipitation of 125–500 mm in Alpine elevational belts at Subpolar latitudes, 250–1000 mm in Subalpine elevational belts at Boreal latitudes, 500–2000 mm in Montane elevational belts at Cool Temperate latitudes, 1000–4000 mm at Lower Montane and Premontane elevational belts at Warm Temperate and Subtropical latitudes, and 2000–8000 mm in tropical lowlands (HOLDRIDGE 1947).

Tab. 1. A list of authors, the fungal groups for which they supplied responses, and the geographic regions in which they have studied them.

Author	Fungal group	Regions
J. Ammirati	Cortinariaceae (Agaricales)	Pacific NW USA
H.H. Burdsall, Jr.	Aphyllophorales (Basidiomycotina)	USA, Caribbean
I. Chapela	Endophytic fungi	Britain, Europe, Japan, Mexico
I. Chapela	Fungi of ant-gardens (Agaricales)	Western hemisphere
C.A. Decock and G.L. Hennebert	Aphyllophorales (Basidiomycotina)	Amazon basin, tropical Nepal, S. India, Zimbabwe, Europe
D. Desjardin	Agaricales	Hawaiian islands
D. Desjardin	Marasmioid fungi (Agaricales)	World-wide
R. Halling	Agaricales and Boletales	Western hemisphere
G.L. Hennebert	Hyphomycetes	Amazon basin, tropical Africa, Canaries, E. USA, Canada, Europe
E. Horak	Cortinariaceae (Agaricales)	S. South America, Australia, NZ
E. Horak	Entolomataceae (Agaricales)	N. & S. America, Europe, Australia, NZ, New Guinea
S. Huhndorf	Melanommatales (Ascomycotina)	Fr. Guiana, Venezuela, Puerto Rico, and E. USA
P.M. Kirk	Hyphomycetes	S.E. Asia, E. Africa
T. Laessøe	Xylariaceae (Ascomycotina)	S. America, Caribbean, Africa
D.J. Lodge	Tricholomataceae (Agaricales)	C. and S. America, Caribbean
O.K. Miller	Boletales (Basidiomycotina)	Korea, Japan, Nepal, USA, W. Australia, S. Africa, Namibia
O.K. Miller	Gasteromycetes	USA, Canada, Australia, deserts in Africa and Namibia
D.W. Minter	Rytismatales	World-wide database
G. Mueller	Agaricales of temperate forest	Western hemisphere
F. Oberwinkler	Heterobasidiomycetes and Corticiaceae (Basidiomycotina)	World-wide
D.N. Pegler	Homobasidiomycotina	E. and W. Africa, India, Sri Lanka, Malaysia, S. Brazil, Caribbean (L. Antilles), Australia, Europe
R.H. Petersen	Hymenomycetes (Basidiomycotina)	Neotropics, N. America, Europe, E. Russia, New Zealand
J.D. Rogers	Xylariaceae (Ascomycotina)	Mexico, N. America, Asia, New Zealand, Caribbean
L. Ryvarden	Polyporaceae (Basidiomycotina)	Zimbabwe, Ethiopia, Norway
G. Samuels	Pyrenomycetes (Ascomycotina)	Neotropics, E. USA, NZ, N. Sulawesi
B. Spooner	Discomycetes	Britain, NZ, New Guinea, Brunei
R. Watling and Evelyn Turnbull	Macromycetes (Basidiomycotina)	W. Africa, Peninsular Malaysia Philippines, India, Britain
A.J.S. Whalley	Xylariaceae (Ascomycotina)	Britain, Mediterranean, Malaysia
F.A. Uecker	Phomopsis (Ascomycotina)	

3 Results

3.1 Latitude

Overall diversity is higher at low latitudes in the Hymenomycetes (Homo- and Heterobasidiomycetes, excluding rusts and smuts), and macrofungi (primarily basidiomycetes), but there are mixed patterns of diversity with latitude at lower taxonomic levels (Tab. 2). For example, diversity is greatest at middle latitudes in the Homobasidiomycetes, increases or decreases with latitude among the Heterobasidiomycetes and related corticiaceous Homobasidiomycetes depending on the family or genus (OBERWINKLER 1993), and follows no pattern among the Gasteromycetes as a whole, though certain families or orders, such as the Phallales, are more diverse in the tropics and subtropics (DRING 1980, MILLER and MILLER 1988). The Gasteromycetes are a polyphyletic, ecological group (MALENÇON 1931, REIJNDERS 1963, SMITH and SINGER 1958, HORAK and MOSER 1965, HEIM 1971, BAS 1975, WATLING 1982, MILLER and WATLING 1987, MILLER and MILLER 1988). Among the Aphyllophorales (Cantharellales, Hericiales, Poriales, Ganodermales, Bondarzewiales, Fistulinales, Lachnocladiales, Stereales, and Thelephorales) there was a consensus that diversity was higher at middle and low latitudes than at high latitudes. Within the Aphyllophorales, there are more species of polypore fungi in tropical Africa than in temperate Europe, despite the comparatively light collecting in Africa (Polyporaceae; RYVARDEN 1993). A similar pattern of higher diversity in the New World tropics may occur in the Agaricales. The diversity of agarics associated with ant fungus-gardens, however, is highest in subtropical South America and decreases as one goes north through Central America into temperate North America. Strong latitudinal gradients in diversity were more apparent among some basidiomycete families, but the direction of the change differed among groups or hemispheres. For example, within the Agaricales, the Cortinariaceae is more diverse at middle to high latitudes in both the northern and southern hemispheres (HORAK 1979, MOSER and HORAK 1975), while the Tricholomataceae and Agaricaceae appear to be more diverse in the tropics (DENNIS 1970). In the New World, the diversity of Boletales decreases as one approaches the equator, but there is no corresponding increase in diversity at higher latitudes in the southern hemisphere. The New World Boletales are mostly ectomycorrhizal symbionts of trees in the Pinaceae, Fagaceae and Salicaceae, and their diversity follows the distribution of their host plants. The high diversity of Boletales associated with trees in the Leguminoseae and Dipterocarpaceae in Central Africa (WATLING 1993), and with Dipterocarpaceae in Malaysia (CORNER 1972, HAWKSWORTH 1993) also suggests that the low diversity in tropical New World Boletales is anomalous.

Within the Ascomycotina, species diversity is greater at tropical latitudes among the pyrenomycetes *sensu lato* and the Xylariaceae, and possibly also at middle to low latitudes in the Melanommatales (Loculoascomycetes; Tab. 2). Previous work by DENNIS (1970) indicates that several epiphytic and parasitic leaf ascomycete groups are much more diverse at tropical than at temperate latitudes, including the Parmulariaceae, Asterinaceae, Perisporiaopsidaceae, Schizothyriaceae, Atichiaceae, Dimeriaceae, Capnodiaceae, Meliolaceae, Polytigmataceae, and the Myrangiales. Speciation and diversity among discomycetes appears to be greater in temperate than in tropical areas, perhaps because of the more rapid decomposition of substrates in tropical climates. More species in the

Rhytismatales have been recorded in the temperate zone, but this may reflect the overwhelming number of collections from Eurasia and North America. A higher ratio of species to number of collections shows up in the Rhytismatales between 10 and 20 degrees N and S latitude, which suggests a need for greater collecting in this zone. Among hyphomycetes and plant-endophytic fungi (primarily asexual and vegetative states of ascomycetes, respectively), species diversity is generally higher at low latitudes (Tab. 2). Certain plant parasitic fungi are distinctly more diverse in the northern hemisphere than in the southern hemisphere, such as the Mastigomycotina (e.g., *Synchytrium* and *Physoderma* spp.), the downy mildews (Peronosporales: *Peronospora* spp.) and the Taphrinales (Ascomycotina) suggesting a possibly recent northern center of origin (WALKER 1983).

3.2 Altitude

Overall macrofungal and macrobasidiomycete diversity seem to be higher at middle or low elevations. Within this group, the Cortinariaceae (Agaricales) and the Boletales are most diverse at high and middle elevations (especially at tropical latitudes), whereas diversity is apparently greater at middle or low elevations in the Gasteromycetes, the Aphyllophorales (including the Polyporaceae), Neotropical Tricholomataceae (DENNIS 1970), and the Homobasidiomycetes in general (Tab. 2). There was no consensus on the relationship of elevation with overall mushroom diversity (Agaricales) in this survey, but a previous workshop on biodiversity and conservation of Neotropical montane forests concluded that the diversity of Agaricales was greater at higher elevations than at lower elevations (MUELLER and HALLING 1995). The diversity of most fungi, including the Agaricales, drops dramatically above the tree-line in the Neotropics (DENNIS 1970). No elevational patterns were noted for the Heterobasidiomycetes and related Corticiaceae.

There was a tendency for ascomycete diversity to be higher at middle to low elevations in the Melanommatales, Xylariaceae, Rhytismatales, and the broader grouping of Pyrenomycetes (Tab. 2), but the collections of Rhytismatales are biased toward countries with little topographic relief. Discomycete diversity tends to be greater at higher elevations than lower elevations in the tropics. Hyphomycetes are most diverse at low elevation. The relationship of species diversity to altitude is dependent on latitude in the Xylariaceae and plant endophytes, and probably in other fungal groups as well.

3.3 Rainfall

Diversity in almost all basidiomycete groups (except marasmioid agarics, many of which are adapted to fluctuating humidity), was related to total annual rainfall, although seasonality of rainfall may also be important. Overall diversity in basidiomycetes, Homobasidiomycetes, polypores, and macrofungi in general is apparently highest in areas of high rainfall (Tab. 2). However, certain groups such as the Aphyllophorales *sensu lato,* Boletales, Agaricales, Cortinariaceae (Agaricales), ant-garden fungi, Agaricales in the Hawaiian islands, and Tricholomataceae in the Neotropics appear to be more diverse at intermediate to high rainfall. A few groups of fungi are adapted to dry conditions and are

Tab. 2. Survey responses to questions concerning the correlates of fungal diversity (n/a means no answer or not applicable).

Taxonomic or ecological group	Fungal spp. diversity and latitude	Fungal spp. diversity and altitude	Fungal spp. diversity and rainfall	Fungal diversity and abundance	Fungal diversity and habitat diversity	Host diversity and fungal spp. diversity	Fungal diversity and resource abundance
Pyrenomycetes (Ascomycotina)	greater at low latitudes	greater at middle and low elevations	greater with constant, intermediate rainfall	family, genus and species diversity increases with abundance	strongly related	somewhat related	strongly related
Xylariaceae (Ascomycotina)	greater at low latitudes	response of diversity to elevation depends on the latitude	greater with intermediate to high rain, except for some genera	no consensus: genus and spp. diversity may increase with abundance	strongly related	strongly related	strongly related
Melanommatales (Loculoascomycetes)	greater at middle to low latitudes	greater at middle and low elevations	greater at intermediate to high rainfall	family, genus and species diversity increases with abundance	somewhat to strongly related	strongly related	strongly related
Discomycetes (Ascomycotina)	higher at middle to high latitudes	greater at high elevations	greater at high rainfall	genus and species diversity increases with abundance	strongly related	strongly related	somewhat to strongly related
Rhytismatales (Ascomycotina)	possibly greater between 10 and 20 degrees	greater at middle and low elevations	greater at high rainfall	genus and species diversity increases with abundance	somewhat related	host generic div. strongly related to fungal species diversity	n/a
Hyphomycetes (mostly asexual stages of ascomycetes)	higher at low latitudes	greater at low elevations	greater at intermediate to high rainfall	genus and species diversity increases with abundance	somewhat to strongly related	strongly related	1 response of strongly related; other n/a
Agaricales (Basidiomycotina)	somewhat greater at low latitudes	no consensus	greater at intermediate to high rainfall	no relationships at any level	greatly related overall, but less strongly in Marasmius	strongly related overall	somewhat related
Entolomataceae (Agaricales)	greater at high and low latitudes	greater at high and low elevations	n/a	no relationships at any level	strongly related	strongly related	strongly related
Tricholomataceae (Agaricales)	greater at low latitudes	greater at middle and low elevations	greater at intermediate to high rainfall	species diversity is related to abundance	strongly related	somewhat related	somewhat related
Cortinariaceae (Agaricales)	greater at middle to high latitudes	greater at high to middle elevations	greater at intermediate rainfall	species diversity increases with abundance, but no consensus	strongly related	strongly related	somewhat to strongly relted

Tab. 2. Continued.

Boletales (Basidiomycotina)	no consistent pattern among continents	higher at middle and low elevations	greater at intermediate rainfall	family, genus and species diversity increases with abundance	strongly related	strongly related	somewhat related
Heterobasidiomycetes and Corticiaceae (Basidiomycotina)	mixed	no pattern	greater at intermediate to low rainfall	n/a	somewhat related	strongly related	n/a
Endophytic fungi	greater at low latitudes	dependent on latitude	greater at intermediate rainfall	species diversity and abundance	strongly related	strongly related	n/a
Ant-garden fungi (Basidiomycotina)	greatest in subtropics	greater at intermediate elevation	greater at intermediate rainfall	n/a	strongly related	strongly related	strongly related
Macromycetes (Basidiomycotina)	greater at low latitudes	greater at low elevations	greater at high rainfall	species richness increases with abundance	strongly related	strongly related	strongly related
Hymenomycetes (Basidiomycotina except rusts and smuts)	greater at low latitudes	greater at middle elevations	greater at high rainfall	species richness increases with abundance	strongly related	somewhat related	strongly related
Homobasidiomycetes	higher at middle latitudes	greater at low elevations	greater at high rainfall	not related for spp.; is related for genera and families	somewhat related	somewhat related	n/a
Gasteromycetes (Basidiomycotina)	no pattern overall	greater at middle and low elevations	greater at intermediate to low rainfall	not related	little to somewhat related	somewhat correlated	somewhat related
Phallales (from lit.) (Gasteromycetes)	higher at low latitudes	n/a	greater at high rainfall	n/a	n/a	n/a	n/a
Aphyllophorales (Basidiomycotina)	higher at middle to low latitudes	greater at middle and low elevations	greater at intermediate to high rainfall	family, genus and species diversity increases with abundance	strongly related	somewhat to greatly related	somewhat related
Polyporaceae (Aphyllophorales)	higher at low latitudes	greater with decreasing elevation	greater at high rainfall	generic diversity increases with abundance	strongly related	strongly related	somewhat related

more diverse in areas with low to intermediate rainfall, such as the Gasteromycetes (excluding most stinkhorns: Phallales)(MILLER 1982), and rust and smut fungi (plant-parasitic Heterobasidiomycetes).

Among the Ascomycotina, species diversity in the Melanommatales and discomycetes is greater in areas of intermediate to high rainfall. Hyphomycetes and endophytic fungi are mostly asexual and vegetative states of ascomycetes, and follow a similar pattern (Tab. 2). In the Rhytismatales, there is a strong positive correlation of diversity with total annual rainfall in the United Kingdom. The Xylariaceae is also most diverse in areas of intermediate (2–4 m per annum in the tropics; Laessøe) to high rainfall (Rogers), but constant availability of moisture without inundation may be better than total rainfall for defining areas of high pyrenomycete diversity in general (Samuels). Some genera in the Xylariaceae are especially diverse in wet forests, such as *Xylaria* and *Camillea* (Laessøe), but other genera such as *Hypoxylon* (Whalley) and *Daldinia* (Rogers) have species that are adapted to dryer conditions.

3.4 Relationship of fungal abundance and diversity

Species diversity is not related to the abundance of fruiting bodies across all taxonomic groups, taxonomic levels, ecological groups, and geographical regions (Tab. 2). For example, positive correlations of abundance and species diversity were observed for tropical macrofungi and Hyphomycete microfungi, various orders of ascomycetes (Melanommatales, Rhytismatales, pyrenomycetes, discomycetes, and Xylariaceae) and Hymenomycetes in general, but not among tropical Homobasidiomycetes (Pegler). Abundance and species diversity were thought to be related in the Aphyllophorales *sensu lato*, but not the Polyporaceae which is included in this group. Unpublished data from tropical wet forests show that species richness is positively correlated with the number of fructifications among Agaricales growing on leaf litter in Puerto Rico and Ecuador (Lodge and Cantrell), but not among polypore fungi on wood in Puerto Rico (Lodge, Camilo and Corbin). Certain orders and families usually show an increase in species richness with abundance, such as the Boletales and the Cortinariaceae (Agaricales), but such relationships may not hold up in all regions (e.g., Agaricales in western North America), or in certain families that fruit abundantly everywhere (e.g., Xylariaceae).

Positive correlations have been observed between abundance and diversity of basidiomycete genera in the Aphyllophorales including the Polyporaceae, the Boletales, Homobasidiomycetes, macrofungi in the Paleotropics, and hyphomycetous microfungi (Tab. 2). A positive relationship of abundance and diversity also appears at the family level for these groups, except the polypores. In contrast, no relationships were noted between abundance and diversity at the genus or family level in the Agaricales or the Gasteromycetes. Among the Ascomycotina, abundance is related to generic diversity in the Melanommatales, Rhytismatales, and the pyrenomycetes in general. There was no consensus on the Xylariaceae. Family diversity appears to be higher in areas of high abundance in the Melanommatales and pyrenomycetes.

3.5 Relationship of species diversity with habitat and host diversity

Species diversity of fungi in a particular geographical area appears to be strongly related to the diversity of habitats and ecosystems (13 of 17 responses for basidiomycetes and macromycetes, and seven of nine responses for ascomycetes and Hyphomycetes). However in certain groups that are adapted to dry conditions, such as the Gasteromycetes, or periodic desiccation, such as the marasmioid agarics, species diversity is less strongly related to habitat or ecosystem diversity (Tab. 2).

Species diversity among basidiomycetes and ascomycetes is also strongly related to host diversity (12 out of 15, and 10 out of 11 responses, respectively). Species richness is apparently less strongly related to host diversity in large, inclusive groups that contain many decomposers, such as the Hymenomycetes, Homobasidiomycetes in general, the Aphyllophorales *s.l.*, and the Gasteromycetes (Tab. 2). However, even in genera composed primarily of decomposers, such as *Marasmius*, species diversity can be strongly related to the diversity of hosts. Similarly, species diversity in discomycetes (Ascomycotina) and Hyphomycetes is a strongly related to host diversity (Tab. 2) although these groups are dominated by decomposers. Specificity of decomposer *Xylaria* spp. for particular host genera or families also occurs (LAESSØE and LODGE 1994). Species richness is more closely related to host plant diversity at the genus rather than the species level in the parasitic Rhytismatales and probably in other fungal groups as well.

3.6 Species diversity and resource abundance

Only five of the responses for basidiomycetes indicated that resource abundance was greatly related to species diversity (Tab. 2). Resource abundance may be relatively more important for fungal diversity in groups that include many decomposers, such as the Agaricales, Entolomataceae, Hymenomycetes and macrofungi in general, but only one author (Petersen) felt it was more important than host diversity. The relationship between species richness and abundance of resources may be generally stronger among ascomycete and hyphomycete groups that are dominated by decomposers.

3.7 Areas with high diversity

Five of the six authors with experience in both the Neo- and Paleotropics ranked the Neotropics, especially the Amazon basin, as having the greatest diversity of Aphyllophorales, pyrenomycetes, Xylariaceae, and hyphomycetes. The exception was Homobasidiomycetes in the Lesser Antilles, a chain of small islands in the southern Caribbean (Pegler). The Neotropics have a higher diversity than Africa of hyphomycetes and xylariaceous ascomycetes (WHALLEY 1993). Subtropical and temperate South America were ranked higher in diversity of Cortinariaceae than New Zealand, Australia and New Guinea, but lower than those countries in diversity of Entolomataceae (Agaricales; HORAK 1976, 1979, 1980, 1982; MOSER and HORAK 1975). Subtropical São Paulo State in Brazil was also thought to have a lower diversity of Homobasidiomycetes than Africa, India, Sri Lanka, or Malaysia. Africa has a high diversity of macromycetes in general (WATLING

1993), polypores (RYVARDEN 1993), and hyphomycetes. India, tropical Nepal, and the Chinese and Asian tropics may also have high diversities of fungi, but our knowledge of these areas is limited. Except for the Gasteromycetes, Europe always had the lowest diversity of fungi when it was included in the rankings (six responses). However, a previous survey by WALKER (1983) indicates that the downy mildews (Peronosporales) are most diverse in Europe.

3.8 Species with restricted distributions

Two geographically isolated areas that were most frequently noted as having species restricted to the region were Australia (especially Queensland; Boletales, Gasteromycetes, Cortinariaceae, Entolomataceae, and Xylariaceae), and New Zealand (Hymenomycetes, Cortinariaceae, pyrenomycetes, Rhytismatales and discomycetes). New Guinea was also mentioned as having species of Entolomataceae (HORAK 1980) and discomycetes that have not as yet been found elsewhere. Species in the Gasteromycetes that are dispersed by flies (DRING 1980) or rodents (FOGEL 1994) often have very restricted distributions. Although gasteromycete species with airborne spores generally have very wide distributions, 56% of 183 species of Gasteromycetes that have been reported from Australia and New Zealand are endemic. Various parts of Africa were noted to have apparently unique species, e.g., species of Xylariaceae in parts of Ethiopia and the Congo basin (WHALLEY 1993), Polyporaceae in Miombo forest in South-Central Africa, and more generally, Heterobasidiomycetes (OBERWINKLER 1993) and Homobasidiomycetes in various parts of Africa. In the Western Hemisphere, unique species of Xylariaceae and Tricholomataceae are frequent in the western Amazon basin. Although species with restricted ranges appear to be the rule rather than the exception in the Agaricales, they may be especially prevalent in temperate habitats on mountaintops at tropical latitudes such as in Central America and the Andes of South America, and on islands such as those in the Caribbean and the Pacific. The knowledge of agaric mycotas in the Caribbean and Hawaiian islands and their neighboring regions is currently too fragmentary to draw conclusions about endemism, however. In addition to Australia, the South-Eastern United States has a high number of endemic Boletales. Some species of Rhytismatales are restricted to mountaintops in Greece, but this group and other parasitic fungi including many Heterobasidiomycetes (WALKER 1983, OBERWINKLER 1993) have species with restricted ranges in many parts of the world. Some species of the primarily saprotrophic Melanommatales are known to have widespread distributions. Similarly, no centers of endemism were noted for hyphomycetes.

4 Discussion

As in higher plants and many animal groups, the diversity of fungi in the Hymenomycetes (Basidiomycotina, excluding rusts and smuts) and the Ascomycotina overall appears to be greatest in the tropics and subtropics. This pattern may not be directly related to the climatic correlates of latitude. For example, fungi may be most diverse in the tropics because the diversity of host plants and invertebrates is greatest in the tropics. The tropics might also represent refugia for many taxa, including fungi. Total land area is greater at low than at high latitudes (TERBORGH 1977), a pattern that is likely to contribute to greater species richness in the tropics. Furthermore, the distances between continents are greater at tropical latitudes than at Cool-Temperate and Boreal latitudes, and this isolation may contribute to greater speciation in the tropics.

Most groups of fungi included in this survey reach their maximum diversity at intermediate to low elevation, suggesting a relationship with climate, but species/area relationships may contribute to this pattern. Area on the tops of mountains is very limited, and this may restrict the number of species that are adapted to temperate forests and paramos on the tops of mountains at tropical latitudes (TERBORGH 1977). Host diversity may also contribute to elevational gradients in fungal diversity because potential host plants and invertebrates reach their highest diversities at middle to low elevation. The ranges of taxonomic groups that are more diverse at high elevations, such as the Cortinariaceae (Agaricales), and the ranges of groups that are more diverse at lower elevations overlap at intermediate altitudes, possibly contributing to the high diversity in this zone. There was no consensus on the relationship of elevation with mushroom diversity (Agaricales). This may reflect a weak pattern, mixed patterns for different groups or an insufficiency of data. For example, some of the most speciose genera in the Agaricales (e.g., *Inocybe, Russula,* and *Cortinarius* with more than 2,000 spp. alone) are ectomycorrhizal associates of trees in certain plant families, and their diversity follows the abundance and diversity of their hosts. Consequently, there is a great diversity of ectomycorrhizal fungi in *Quercus* forests at intermediate to high elevations in Central America and Colombia and in association with Pinaceae in Mexico and northern Central America (MUELLER and HALLING 1995), as well as at low elevations in association with Leguminoseae and Myrtaceae in Africa (WATLING 1983), and at various elevations in association with Dipterocarpaceae in Malaysia.

Almost all of the published literature on endangered species of non-lichenized fungi relates to the diversity of macrofungi in Europe, especially mycorrhizal symbionts (e.g. FELLNER 1983, 1988, 1989, 1993; ARNOLDS 1988, 1991; DERBSCH and SCHMITT 1987; JAKUCS 1988; NAUTA and VELLINGA 1993). On a global scale, however, Europe has the lowest diversity of ectomycorrhizal basidiomycetes and many other fungal groups, so efforts to conserve global biodiversity will have to include many areas in the tropics that have a much higher fungal diversity, but have been poorly surveyed in the past. The rates of tropical deforestation are high, so rapid inventory and classification techniques are needed to identify areas having the highest diversity and greatest numbers of unique fungal species, genera and families for conservation (HAWKSWORTH 1993). For example, if a positive relationship exists between the abundance of fructifications and the diversity of fungi, then initial surveying of regions for areas of high diversity could be done by trained technicians rather than fungal taxonomists. Although positive correlations occur, such an approach is not likely to work across all taxonomic groups, ecological groups, or biomes, and in some cases may not be strong enough to be useful. For example, some genera that are tolerant of dryer conditions, such as *Hypoxylon*, fruit abundantly more or less everywhere and this may weaken the relationship of fruiting abundance and species diversity in the Xylariaceae. Most of the genera and families in the Agaricales are widely distributed, which may explain the absence of a relationship between abundance and diversity above the species level in this order.

In a recent book on biodiversity, an ecologist (HUSTON 1994) hypothesized that detrital and decomposer communities would reach their highest diversity where plant productivity was highest, independent of plant diversity. The results of this survey suggest that HUSTON'S (1994) hypothesis may not be correct. Only five authors felt that resource abundance was greatly related to species diversity in their basidiomycete group as compared to 12 authors who felt there was a strong relationship with host diversity. The relationship between species richness and abundance of resources may be somewhat stronger in groups such as the ascomycetes that are dominated by decomposers, but many decomposers are also host-specific to some degree. It is important for mycologists to test ecological hypotheses such as the one by HUSTON (1994) because they are likely to influence conservation policies in the absence of quantitative data on fungal diversity.

The Neotropics have a very high fungal diversity, and the Amazon basin may have a higher diversity of Xylariaceae and hyphomycetes than Africa. One possible explanation is that diversity in these fungal groups is apparently related to host diversity, and the diversity of higher plants is greater in the Neotropics than in Africa. Some genera, such as *Camillea* (Xylariaceae; LAESSØE *et al.* 1989; WHALLEY 1993) are found almost exclusively in the New World, which might indicate a diversification of this group after the continents parted, but almost nothing is known about vicariance biogeography in fungi. Alternatively, the limited extent of wet forests, and the waves of drought that have historically passed through Africa and are thought to have limited plant diversity (GARTLAN 1974) may have also reduced fungal diversity. The authors familiar with Africa and Asia suggest, however, that these areas are undersampled and in need of more collecting, so comparisons between continents are premature. Comparable surveys of fungi (using the same observers, methods, and sampling areas) in forest ecosystems on different continents, in which the study areas have been carefully paired for climate, would be more useful for addressing broad geographical patterns in fungal diversity than the ad hoc comparisons presented here.

There is some evidence cited in the ecological literature for long-distance dispersal of viable spores in the jet-stream (CARLQUIST 1965) that has led to a misconception that fungi are able to disperse everywhere. Although some species of polypores (RYVARDEN 1993) and Heterobasidiomycetes (OBERWINKLER 1993), and probably most species of Gasteromycetes, hyphomycetes, and Loculoascomycetes are widely distributed, other species and groups of fungi apparently have restricted geographic ranges. The ranges of some tropical species may not be as restricted as they appear because of the lack of adequate surveys; some species of ascomycetes and basidiomycetes that were once thought to be very restricted have later been found on other continents (OBERWINKLER 1993; WATLING 1993; WHALLEY 1993). The limited ranges of some fungal species (e.g., parasitic Heterobasidiomycetes and ascomycetes, and agaric fungi of ant-gardens) may be explained by the limited ranges of their hosts, while the distribution of others may indicate a recent origin. The common and widespread occurrence of species with limited ranges among the Agaricales, however, suggests that other factors such as intersterility or limited colonization potentials may be involved. For example, incompatibility between certain closely related mushroom taxa within continents and between Europe and North America indicates the presence of sibling species with geographically restricted ranges rather then one widely distributed species (PETERSEN 1995). There is little overlap of *Laccaria* species among regions (MUELLER 1992) and intersterility among related species is common in the *L. laccata* and *L. bicolor* complexes (FRIES and MUELLER 1984; MUELLER 1991, 1992). Other examples of incompatibility among sympatric or allopatric populations of Agaricales include species of *Marasmius*, *Oudemansiella*, and possibly *Armillaria*, and *Marasmiellus praeacutus*. Incompatibility is also found among some polypore fungi, such as *Fomitopsis pinicola* and the more ephemeral species of *Pleurotus* and *Polyporus (sensu stricto)*, and among ascomycetes in *Nectria* and *Gibberella*.

Taxonomic groups can exhibit different degrees of reduced diversity on islands with increasing geographic isolation (disharmony; CARLQUIST 1965) because of differences in their means of dispersal, sensitivity to environmental stress, or reproductive biology. For example, successful dispersal might be limited in agarics that have thin-walled spores because of their susceptibility to desiccation. This could help explain the disparity between the limited distributions that are prevalent in the Agaricales, and the widespread distributions of species of Gasteromycetes that are adapted to dry conditions (e.g. *Podaxis* spp.). Regional diversity in lineages with good disperal is sometimes less than in lineages with poorer dispersal because lack of reproductive isolation among populations can reduce speciation (RICKLEFS and COX 1972), but little is known about the relationship of dispersal and speciation in fungi.

Monokaryotic and dikaryotic mycelia of basidiomycetes frequently have different growth characteristics (GUILLAUMIN *et al.* 1991; MUELLER 1991; PETERSEN and BERMUDES 1992; LARSEN *et al.* 1994; PETERSEN 1995) but the significance of this to colonization and competitive abilities is unknown. However, in the Agaricales, the low probability of landing near enough to an opposite mating type to result in dikaryotization and subsequent sexual reproduction may favor colonization of islands or habitat islands by vegetative structures (fungi of ant-gardens) or asexual, homokaryotic or otherwise self-fertile spores (Homobasidiomycetes). This might lead to increased founder effects, reproductive isolation, and speciation of basidiomycetes on islands or in habitat islands in Agaricales, but dikaryon matings with monokaryons via the Buller phenomenon may provide gene flow among some populations (EGGER 1995). For example, DEACON and FLEMING (1992) suggest that while colonizing (ruderal) species of mycorrhizal fungi are more likely to become established as monokaryons, late stage species require substances produced by an established mycelium in order to break spore dormancy. If this pattern occurs among basidiomycetes in general, it could help explain differences between widespread and geographically restricted species.

5 Conclusions

Although the data on fungal diversity and distributions are limited and fragmentary, the consensus of opinions suggests that certain patterns are robust and are worthy of further pursuit and testing. Diversity in many fungal groups is apparently greatest at low or middle to low latitudes, intermediate to low altitude (except Agaricales and Heterobasidiomycetes), and intermediate to high rainfall. Species with restricted ranges are frequently more abundant on islands or in habitat islands, temperate habitats on top of tropical mountains, and in large expanses of tropical rain forest. Such patterns of limited distribution in fungi coincide with those of many plant and animal groups. Groups that have widespread species are often adapted to harsh conditions, and consist mainly of decomposers. Fungal diversity seems to be related most strongly to habitat and host diversity (especially among parasites and mutualists, but also among some decomposers), although the abundance of resources might also be important in certain groups. In addition to parasitic fungi, species with limited ranges are common among the Agaricales. Certain mating and incompatibility systems and the susceptibility of spores to desiccation in some genera may contribute to this pattern.

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Addresses of the co-authors

I. Chapela, G. Samuels, F.A. Uecker
USDA-Agricultural Research Service, Systematic Botany and Mycology Lab, Rm. 304, B-001A, BARC-West, 10300 Baltimore Ave., Beltsville, MD 20705-1523, USA

D. Desjardin
Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132-2401, USA

E. Horak
Geobotanisches Institut ETH, Herbarium ZT, Zollikerstrasse 107, CH-8008 Zürich, Switzerland

O.K. Miller, Jr.
Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0406, USA

G.L Hennebert, C.A. Decock
Mycothèque de l'Université Catholique de Louvain, Faculté de Sciences Agronomiques, Place Croix du Sud 3, B - 1348 Louvain - La Neuve, Belgium

J. Ammirati
Department of Botany, University of Washington, Seattle, WA 98195, USA

H.H. Burdsall, Jr.
Center for Forest Mycology Research, Forest Products Lab, USDA-Forest Service, One Gifford Pinchot Dr., Madison, WI 53705-2398, USA

P.M. Kirk, D.W. Minter
International Mycological Institute, Bakeham Lane, Egham, Surrey, TW20 9TY, U.K.

R. Halling
New York Botanical Garden, Bronx, New York 10458-5126, USA

T. Laessøe
Botanical Institute, Dept. of Phycology and Mycology, Øster Farimagsgade 2D, DK-1123 Copenhagen K, Denmark

G. Mueller, Sabine Huhndorf
Field Museum of Natural History, Roosevelt Rd. at Lakeshore Drive, Chicago, IL 60605-2496, USA

F. Oberwinkler
Botanisches Institut, Spezielle Botanik/Mykologie und Botanischer Garten, Eberhard-Karls-Universitat Tübingen, Auf der Morgenstelle 1, D-72076 Tübingen, Germany

D.N. Pegler, B. Spooner
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, U.K.

R.H. Petersen
Department of Botany, University of Tennessee, Knoxville, TN 37996-1100, USA

J.D. Rogers
Dept. of Plant Pathology, Washington State University, Pullman, WA 99164-6430, USA

L. Ryvarden
Department of Botany, Box 1045 Blindern, N-0316 Oslo, Norway

R. Watling, Evelyn Turnbull
Royal Botanic Gardens - Edinburgh, Inverleith Row, Edinburgh EH3 5LR, UK

A.J.S. Whalley
School of Biomolecular Sciences, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, U.K.

Eidgenössische
Forschungsanstalt
für Wald, Schnee
und Landschaft

Institut fédéral de
recherches sur
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et le paysage

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di ricerca per
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Landscape Research

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CH-8903 Birmensdorf
Schweiz/Suisse/Svizzera/Switzerland

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