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Inga E. Bruteig

DISTRIBUTION, ECOLOGY AND BIOMONITORING STUDIES OF EPIPHYTIC LICHENS ON CONIFERS

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ABSTRACT

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This study presents the results of investigations of epiphytic lichens on conifers, mainly with a biomonitoring approach. The concentrations of nitrogen and sulphur measured in *Hypogymnia physodes* at 179 sites on a national grid net were related to estimates of the deposition of these two elements. The influence of climatic factors on lichen growth and nutrient status is discussed. Seven lichen species or groups of species growing on trunks of *Pinus sylvestris* have been mapped at 193 sites in the same monitoring network. A measuring tape technique was used for abundance estimates. Distributional patterns have been interpreted using multivariate techniques. Climatic parameters summarized in north-south, inland-coast and high-low altitude gradients are ascribed a major influence on variations in the epiphytic lichen vegetation. Lichens on *Picea abies* branches have been mapped in detail in coniferous forests in Høylandet, central Norway and Åmli and Gjerstad, southern Norway. Major differences have been found between these areas as regards species composition, lichen abundance and the proportion of thalli with visible morphological damage. Using direct gradient analysis along *P. abies* branches, epiphytic lichens have been classified as generalists and broad or narrow specialists. Indications of interspecific associations have been found. Whether there is competition for space is discussed. The problem of discriminating between the effects of air pollution and closely correlated climatic factors is considered. The validity of using space-for-time substitution as a biomonitoring technique when two climatically different areas are being compared is questioned. The importance of using objective methods to quantify abundance in biomonitoring studies is emphasized.

Key words: Acid precipitation, biomonitoring, conifers, epiphytic lichens, gradient analysis, *Hypogymnia physodes*, morphological damage, Norway.

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PREFACE

This work has been carried out at the Department of Botany, Faculty of Science, AVH, and the Department of Botany, Museum of Natural History and Archaeology, both at the University of Trondheim.

Besides those mentioned in the individual papers, I wish to thank some on a more general basis:

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CONTENTS

1 LIST OF PAPERS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I. Bruteig, I. E. 1993. The epiphytic lichen Hypogymnia physodes as a biomonitor of atmospheric nitrogen and sulphur deposition in Norway. *Environmental Monitoring and Assessment 26:* 27-47.

II. Bruteig, I. E. 1993. Large-scale survey of the distribution and ecology of common epiphytic lichens on Pinus sylvestris in Norway. *Annales Botanici Fennici 30:* 161-179.

III. Bruteig, I. E. Epiphytic lichens on Picea abies branches in two coniferous forest areas in Norway with different pollution loads. Manuscript.

IV. Bruteig, I. E. & Såstad, S. M. Distribution of epiphytic lichens along Picea abies branches in two coniferous forest areas in Norway. *Journal of Ecology* (submitted).

2 INTRODUCTION

2.1 LICHEN BIOMONITORING

Lichens have long been recognized as useful biomonitors of air quality (Hawksworth 1971, Ferry et al. 1973, Steubing & Jäger 1982, Burton 1986, Arndt et al. 1987, Nash & Wirth 1988, Bates & Farmer 1992). One of the classical lichen-air pollution studies was indeed from Norway (Haugsjå 1930). Documentation in this field of applied lichen research is comprehensive and updated lists of scientific works are published regularly (Henderson 1993). A review of recent North American air pollution monitoring studies using lichens showed that most studies monitored lichens on trees around a point source of air pollution (Will-Wolf 1988).

The usefulness of lichens as biomonitors is related to some physiological properties of the lichen thallus: its slow growth and its effectiveness in absorbing mineral nutrients from ambient air and precipitation with little subsequent loss. A main reason for choosing to study epiphytes rather than terrestrial lichens, is that tree bark is chemically and physically less complex than soil. The habitat can moreover, easily be standardized by choosing one species as the phorophyte to be studied.

Lichens are known to be vulnerable to sulphur compounds, especially SO_2 (e.g. Hawksworth & Rose 1970, 1976, Nash 1973, Richardson & Nieboer 1983, Holopainen & Kärenlampi 1984, Richardson 1988). Decline of epiphytic lichens is therefore often related to increased levels of gaseous SO_2 in their environment (e.g. Rose 1973, de Wit 1976, Seaward & Hitch 1982, Wirth 1987a). Farmer et al. (1992) state in their review that there have been relatively few field observations of decline due to wet deposition of acidic pollutants. As regards the effects on epiphytes, most attention has been paid to effects on *Lobaria* species (e.g. Gilbert 1986, Hallingbäck 1986). Deposition of acidic pollutants may have deleterious effects on certain species and habitats, but floristic changes may also be attributed to the fertilizing effect of nitrate in precipitation (Farmer et al. 1992). Studies on the influence of nitrogen pollution on lichens show that several lichen species benefit from a moderate rise in ambient nitrogen (Nash 1976, Kauppi 1980, Holopainen & Kärenlampi 1985, von Arb 1987, de Bakker 1989).

Changes in air quality may cause changes at different organizational levels of lichens. Field and experimental studies have described several microstructural effects, including damage to cell membranes (Pearson & Henriksson 1981, Pearson & Rodgers 1982, Alebic-Juretic & Arko-Pijevac 1989), damage to the ultrastructures of algal cells (Holopainen 1984, Holopainen & Kärenlampi 1985) and chlorophyll degradation (Nash 1973, Will-Wolf 1980, Beekley & Hoffman 1981). Effects demonstrated on the level of the organism include visible morphological abnormalities (Scott & Hutchinson 1990) and physiological changes (Kärenlampi et al. 1989, von Arb et al. 1990). Populations may experience habitat niche restrictions (Wirth 1987b) and ultimately local extinction (e.g. van Dobben 1983). Changes may also occur on community level, including shifts in species dominance, interspecific associations, composition and growth forms, decreased lichen cover and diversity. The effects observed on different levels are not independent. Ultimately, alterations on all levels are in some way linked to processes on the cellular level. Relationships between the response of individual species and shifts in community composition are discussed by Will-Wolf (1980).

More needs to be known about the different organizational levels, to enable anthropogenous effects to be distinguished from natural structure and fluctuations. Recent studies by Esseen (1981), Oksanen (1988), Halonen et al. (1991), Hyvärinen et al. (1992) and Hilmo (1994) have contributed to our understanding of aspects of epiphyte ecology and environmental relationships in Nordic boreal forests. In dense spruce forests, the bulk of the lichen vegetation is found on branches, but knowledge of these epiphytic communities is limited (Degelius 1978, McCune 1990).

2.2 DEPOSITION OF ACIDIC POLLUTANTS

During the past few decades, there has been great interest in and awareness of "acid rain" in Norway. This is mainly due to the drastic effects of wet deposition of long-range transported acidic pollutants on surface waters in southern parts of the country, resulting in virtual extinction of fish populations from a large number of lakes and rivers (Overrein et al. 1981). During 1985-90, long-range transport of pollutants from heavily industrialized parts of Europe supplied Norway with approximately 140 000 tons of oxidized sulphur, 80 000 tons of oxidized nitrogen and 40 000 tons of reduced nitrogen per year (Iversen et al. 1991). This accounts for about 90 per cent of the total deposition of airborne acidifying components in Norway. The deposition of nitrogen and sulphur shows a distinct latitudinal gradient with five to ten times higher deposition in the south than in northern Norway (Pedersen et al. 1990). The deposition is also correlated to amounts of precipitation, so that the areas in southern Norway with high annual precipitation receive the highest pollution loads (Pedersen et al. 1990).

This wet deposition of acidic pollutants is characterized by high concentrations of H^+ ions, sulphate, nitrate and ammonium, as well as various heavy metals and other elements and organic micropollutants. Farmer et al. (1992) consider acidic pollutants, together with the low pH conditions that they can cause, to be an increasing threat to cryptogam communities.

2.3 MONITORING DESIGN

There are no older Norwegian investigations that are suitable for testing the hypothesis of a large-scale change in lichen abundance in recent decades as a result of increased levels of wet deposition of acidic pollutants. Eilif Dahl (in Aagaard & Framstad 1991) proposed applying the space-for-time substitution technique (Pickett 1987) in a monitoring context as an alternative to comparing the same sites over a long period of time. It was assumed that an area with low deposition rates represents an earlier stage in the process of ecosystem change than one with higher deposition, and that temporal variation can be replaced by spatial variation. This gave rise to several research projects where Trøndelag in central Norway and Agder in the south were compared to study the effects of air pollution on biological systems (e.g. Aune et al. 1989, Flatberg et al. 1991, Gulden et al. 1992, Såstad & Jenssen 1993).

As emphasized by Will-Wolf (1988), approaches to data analysis should be chosen as part of the original research design. She also pointed out that research related to monitoring the impact of regional air pollution such as acid precipitation is the most difficult to design. A combination of several different monitoring approaches is to be desired, as well as the choice of one habitat type found in a wide geographical range (Will-Wolf 1988). Oksanen (1988) also concluded that the type of habitat has a great bearing on variations in epiphytic vegetation. When the frequency and abundance of all species are recorded at a series of sites, the lichen distribution data collected can be treated mathematically (Herben & Liska 1986, Zobel 1988). In surveys involving several researchers and where long-term monitoring is the purpose of the study, it is especially important to have standardized abundance estimates which withstand personal and subjective evaluations.

2.4 ABOUT THE THESIS

This thesis follows the idea that various approaches are needed, especially when designing studies to monitor unknown future air qualities or pollution levels. Conifers were chosen as phorophytes, partly because of the great public and managerial interest in the effects of pollution on coniferous forests, and partly because of the existence of a national monitoring network for conifers (NIJOS 1991). At the onset of these studies, the following aims were important: 1) to gain knowledge about the ecology and present distribution patterns of epiphytic lichens on conifers; 2) to be able to relate any patterns observed to environmental factors, including pollution; 3) to generate hypotheses on causal relationships for future investigations and experimental studies; and 4) to try out methods using epiphytic lichens, suitable for monitoring the effects of future changes in air quality.

This thesis consists of four parts, all of which are of a descriptive nature. The first two refer to material sampled by non-specialist research teams at a large number of monitoring sites throughout Norway. Nitrogen and sulphur concentrations in lichens were related to deposition and environmental variables [I], and the national distribution of lichens on pine trunks was quantified [II]. The last two parts are based on in-depth investigations in two areas with different pollution loads. The epiphytic lichen vegetation on spruce branches was described and compared [III], and the community structure of lichens along spruce branches was studied [IV]. The results described in these four papers are summarized and discussed in the following review.

3 SUMMARY OF PAPERS

3.1 PAPER I

This paper presents the results of analyses of nitrogen and sulphur in *Hypogymnia physodes* sampled from *Pinus sylvestris* trunks at 179 sites regularly distributed throughout Norway. The concentrations of these two elements were closely related (correlation coefficient 0.90), and the nitrogen content was about 10 times that of sulphur. The ratio of nitrogen to sulphur decreased northwards and was five to 21 times higher in *H. physodes* than in estimated deposition. This shows that the lichen takes up nitrogen more efficiently than sulphur.

Nitrogen concentrations in *H. physodes* ranged from 0.42% to 1.96% of dry weight, sulphur concentrations from 0.046% to 0.183%. The highest concentrations of both elements were found along the south coast and at some inland sites in southern Norway. The content in lichen was significantly correlated to the estimated atmospheric deposition of nitrogen and sulphur. High pH values in bark, winter and summer temperatures, annual precipitation, evapotranspiration and ammonium deposition were all associated with lower nitrogen and/or sulphur concentrations than expected from deposition. These factors may promote lichen growth and thus cause the element concentrations to be diluted. On the other hand, higher concentrations were found at high altitude sites, possibly due to unfavourable growth conditions and accumulation of deposited elements in these areas.

3.2 PAPER II

The distribution of epiphytic lichens on *Pinus sylvestris* was surveyed at 193 sites in the same monitoring network as was used when sampling *Hypogymnia physodes* [I]. The field work was carried out by research teams from the Norwegian Institute of Land Inventory (NIJOS). All epiphytic lichens occurring along measuring tapes around *P. sylvestris* trunks were mapped and classified to the following seven lichen species or groups of species: *H. physodes*, *Pseudevernia furfuracea*, *Parmeliopsis* spp., *Bryoria* spp., *Usnea* spp., "other foliose species" and "crustose species".

The lichen cover was highest along the coast of southern Norway, considerably lower inland, in mountainous areas and in the north. The highest registration of lichen cover (mean of four trees per site) was 56.7%. Fairly distinct distribution patterns were found even though some species were lumped in heterogeneous groups. *Bryoria* and *Parmeliopsis* species had a continental and somewhat northerly distribution. *Usnea* species were sparse both in the north and in the most polluted areas in the south. *H. physodes* and *P. furfuracea* were most abundant in the southern, warmer parts of the country. "Other foliose species" and "crustose species" were most abundant along the west and south coasts. The lichen occurrences seemed to be mainly related to environmental parameters associated with moisture and temperature, summarized in north-south, inland-coast and high-low altitude gradients. The interpretations were mainly based on multivariate techniques (Gauch 1982, Jongman et al. 1987): ordination of species data by detrended correspondence analysis (DCA) and principal component analysis (PCA) of environmental variables.

3.3 PAPER III

This paper describes and compares the epiphytic lichen vegetation on *Picea abies* branches in the boreal coniferous forests at Høylandet in central Norway and Åmli and Gjerstad in southern Norway. Høylandet is little affected by atmospheric pollution, whereas Åmli and Gjerstad are within the area in Norway that is most heavily loaded with long-range transported acid precipitation. The lichen vegetation of the two areas differed in several major respects: species composition, abundance, growth form relations and abundance of thalli with visible signs of damage.

Of the fifty lichen taxa recorded, 21 were common to the two areas, 15 were only found in Høylandet and 14 only in Åmli-Gjerstad. Lichen abundance, recorded as percentage cover of branch lengths, was significantly lower in Åmli-Gjerstad than in Høylandet in the case of all growth forms: crustose, foliose and pendant taxa. The floristic gradients in both areas seemed to primarily reflect local humidity differences, secondly to height above the ground (based on DCA ordinations and their correlations to environmental variables). Due to less dominance and more species relative to lichen abundance, the log series index (a) of diversity (Magurran 1988) was highest at the sites in Åmli-Gjerstad. The "index of atmospheric purity" (IAP) based on lichen species abundance and occurrence (LeBlanc & De Sloover 1970) was calculated to be more than twice as high in Høylandet (1.41) as in Åmli-Gjerstad (0.59). The proportion of recorded visible signs of damage in Åmli-Gjerstad by far exceeded that in Høylandet. For example, nearly half the *Platismatia glauca* were morphologically damaged in Åmli-Gjerstad, compared to less than 5% in Høylandet. This difference may be related to variations in air pollution.

3.4 PAPER IV

This paper examines the frequencies of lichen taxa on different parts of *Picea abies* branches, based on the same material as [III]. The original abundance data were transformed to presence-absence data scored in 30 equally long segments from the base of a branch to its tip. Species-specific habitat niche differentiation along branches was found, and the species were classified as generalists and broad or narrow specialists with regard to the branch gradient. The epiphytic lichen communities in both Høylandet and Åmli-Gjerstad included base and tip specialists as well as randomly distributed species.

The lowest diversity was found at the branch tip. The diversity increased from the tip to about a third of the way along the branch. In Høylandet, the diversity then decreased towards the base, but there was no such tendency in Åmli-Gjerstad. A species association analysis indicated commensalism between *Bryoria* species and several foliose species. There was also a tendency for growth forms to occur separately, as crustose and foliose species intermingled more rarely than chance should dictate. The bases of the branches were more similar than the tips when the two areas were compared. This pattern was found for total lichen frequency, species composition and species diversity.

4 DISCUSSION

4.1 ECOLOGY AND DISTRIBUTION

The geographical distribution of lichens in Norway is relatively well known through extensive herbarium collections and several major studies (e.g. Degelius 1935, Ahlner 1948, Almborn 1948, Krog èt al. 1980, Tønsberg 1992, Santesson 1993). The distribution of species described in paper [II] confirms known patterns. This study, however, introduces quantitative measurements of lichens at objectively selected sites and on one specific habitat. Hence, the data can be handled statistically and numerically, and the lichens studied reveal regional and ecological preferences that were not quantified earlier. As an example, the ubiquitous species *Hypogymnia physodes* was found at 191 of 193 sites investigated, but its mean cover on trunks of *Pinus sylvestris* varied from 0.1% to 24.3% per site [II]. Moreover, its highest abundance was in the southern parts of the country, and the abundance was positively correlated with evapotranspiration, temperature sum and forest density and growth ('site index') [II]. This also agrees with the results from the studies on *Picea abies* branches [III]; *H. physodes* differed from all other abundant species (mean cover > 2%) present in both areas by being more abundant in Åmli-Gjerstad in the south, than in Høylandet in central Norway.

The total lichen cover on *Pinus sylvestris* trunks was generally lower than on *Picea abies* branches [II, III]. In coniferous forests in central Finland, Halonen et al. (1991) found that most macrolichens had higher cover values on *P. sylvestris* trunks than *P. abies* trunks. This was partly ascribed to the low light intensity on trunks of *P. abies*. *P. sylvestris* has a somewhat unstable, flaking bark, and its lichen communities are therefore often rather fragmentary and temporary assemblages (Ahti 1977). Bark acidity is within the same range for the two substrates [II, III], but *P. sylvestris* bark is known to represent a drier substrate, due to low water-holding capacity (Barkman 1958). The importance of humidity for lichen growth is well documented (e.g. Kershaw 1985), and it is likely that the differences between Høylandet and Åmli-Gjerstad can partly be ascribed to different humidity [III]. The species distribution curves along *P. abies* branches may also be related to humidity [IV], but how the humidity conditions vary from branch tip to base has not been studied.

There seems to be a negative relationship between crustose and foliose lichen species on *Picea abies* branches. This is apparent from both the association analyses in [IV] and the ordination analyses in [III]. Pairs of crustose species more frequently occurred together on the same branch segment and mixed pairs (crustose + foliose) less frequently than predicted [IV]. Species with similar growth form were also located close to each other in the ordination space, and crustose and foliose species dominated at opposite ends of the first ordination axis [III]. The ordination analyses in [III] also suggests that the most diverse lichen communities have a large proportion of crustose species.

4.2 POLLUTION AND ENVIRONMENTAL EFFECTS

In Norway, gross climatic parameters like temperature and precipitation, vary along south-north, low-high altitude and coast-inland gradients. Since deposition of pollutants in Norway follows similar gradients (Pedersen et al. 1990), discriminating between pollution and climatic factors is a statistical problem. Consequently, the high abundance of *Hypogymnia physodes* and *Pseudevernia furfuracea* in southern parts of the country [II] may be a response to favourable climatic conditions, or the species may have benefited from deposition of nitrogen in those areas. The assumption that temporal variation can be replaced by spatial variation, as applied in the comparisons between Høylandet and Åmli-Gjerstad, is questionable. The large distance separating the two areas and the climatic differences per se would imply differences in the epiphytic lichen vegetation. When only two areas are being compared, all the environmental differences between them may explain the observed variation in the epiphytic vegetation.

The lichen communities on *Picea abies* branches are more luxuriant in Høylandet than in Åmli-Gjerstad [III, IV], but it cannot be ascertained that air pollution is the main reason that the lichen vegetation in the latter area is impoverished. It seems likely, however, that some of the lichen communities studied in the Åmli-Gjerstad area are in an unstable and changing phase, as judged by the high frequency of visibly damaged thalli [III]. Communities with a smaller proportion of damaged lichens may for example 1) be at a younger developmental stage where visible damage has not become obvious, 2) be sheltered from or less susceptible to the present level of environmental stress, or 3) have been through a phase with more extensive damage and have developed impoverished or altered lichen communities with a less sensitive species composition.

The lichen community may also be influenced by the indirect effects of acid precipitation. Interactions between the phorophyte and the epiphytic lichens are complex (Lawrey 1984). The pH of the *Picea abies* bark was about 0.5 pH units lower in Åmli-Gjerstad than in Høylandet [III]. The pH of *P. abies* is naturally low, however, and its epiphytic flora may be considered acidophilous. According to Farmer et al. (1992), acidophilous taxa are expected to possess natural resistance to low pH, and will therefore be less susceptible to acidification of the substrate. In the large-scale survey [II], no clear relationship between the pH of *Pinus sylvestris* bark and the epiphytic lichen vegetation was found. This does not exclude bark acidity as an important factor in the case of epiphytes on *Picea abies* branches, however.

The climatic data used in [I] and [II] were interpolated to the actual latitudes and longitudes of the sampling sites while the deposition estimates were calculated on a 50 x 50 km grid basis. Sulphate deriving from sea salt was not included in the deposition model. Actual deposition measurements or a finer deposition model may have improved the results, as indicated in the subset analysis in [I, Fig. 7]. The ordination analyses in [II] and [III] also show that the available environmental parameters could only explain a small part of the variation in the species data. It seems especially important to be able to include direct measurements of humidity at investigated sites.

Various indices of community health or integrity are often used in air pollution studies (Will-Wolf 1988). In the present studies, such indices have limited value. In the large-scale survey [II], the lichen data were not suitable for calculating either IAP (index of atmospheric purity; De Sloover 1964, LeBlanc & De Sloover 1970) nor diversity indices. More specific data on species as in [III, IV] are needed. The IAP and diversity values differed in Høylandet and Åmli-Gjerstad [III], but this did not aid the ecological interpretation much. Use of the Shannon Wiener diversity index (Krebs 1989) in the direct gradient analysis along *Picea abies* branches [IV], on the other hand, helped to visualize features of the lichen community structure and dynamics.

4.3 UNSOLVED QUESTIONS AND NEW HYPOTHESES

Descriptive studies commonly raise new questions and generate hypotheses that only further studies can answer. Some of the main questions arising from the present work are briefly discussed below.

How does lichen growth rate influence uptake and accumulation of elements?

The regression analyses on estimates of the deposition and concentrations of nitrogen and sulphur in *Hypogymnia physodes* [I], suggests that this species is a suitable biomonitor for the deposition of these elements. It is, however, important to consider other factors that may affect the nutrient status, such as element leaching, uptake mechanisms and growth rate. Lichens have been found to absorb ammonium-nitrogen from rain and release organic nitrogen (Millbank 1985). Although lichens grow slowly, their growth rate is influenced by environmental factors, especially humidity, and dilution of elements may occur when growth conditions are favourable [I]. Growth rate measurements at selected sites would improve the biomonitoring capacity of *H. physodes*.

Have species benefited from the deposition of nitrogen in southern Norway?

Trunks of *Pinus sylvestris* had relatively high lichen cover in the parts of the country most heavily affected by deposition of acidic pollutants [II]. This was mainly due to the abundance of *Hypogymnia physodes* and *Pseudevernia furfuracea*, species which were also abundant on *Picea abies* branches in Åmli-Gjerstad [III]. It is desirable to carry out experiments exposing branch epiphytes to different solutions of acidic pollutants. *H. physodes*. *P. furfuracea*. *Platismatia glauca* and *Parmelia sulcata* may be suitable study objects since these species differ significantly in the degree to which they show visible damage in areas affected by wet deposition of acidic pollutants [III]. Most experiments with simulated acid precipitation have studied the effects on *Cladonia* or other terricolous species (e.g. Hutchinson et al. 1986, Lechowicz 1987, Scott et al. 1989). These studies have shown that not only pH but also the relationship between sulphur and nitrogen is important.

Is interspecific competition partially responsible for the observed lichen distribution patterns on Picea abies branches, or are environmental factors solely responsible?

There are more species on *Picea abies* branches in Høylandet than in Åmli-Gjerstad [III], the total lichen cover is higher [III], the number of negative species associations is higher [IV] and the diversity declines towards the base of the branch [IV]. If competition for space is a factor regulating these lichen communities, these results suggests that the interspecific competition is stronger in Høylandet than in Åmli-Gjerstad. Competition for space may also be more important on branches with high lichen cover, dominated by large, foliose species. The cover and the number of species per branch showed opposite distributional trends in the DCA ordination plots in [III]. Experimental manipulations, including the removal of species, are needed to examine the dynamics and processes within the lichen communities on *Picea abies* branches.

Can morphological signs of visible damage to epiphytic lichens be classified and causally interpreted?

The volume of recorded thallus damage in Åmli-Gjerstad by far exceeded that at Høylandet [III]. Differences in deposition of acidic pollutants seems a plausible explanation. However, several factors influence the health and appearance of lichen individuals. Morphological aberrations may be caused by natural senescence and degeneration processes, arthropod grazing or parasite infections on the bark and deleterious levels of pollutants or other environmental factors such as drought. Fungal infections and insect attacks may also be secondary effects of reduced vitality due to environmental stress. It is not known whether the above factors cause similar or distinguishable morphological changes, and further studies are required.

4.4 EVALUATION OF METHODS

The measuring tape method represents an objective, but time-consuming, way of obtaining abundance estimates. Because reduced subjectivity in estimations reduces sampling error and the presence of systematic errors, the time consumption seems worthwhile. Data collected on line transects around tree trunks may also be used to study species exposure and height preferences, as in the investigation by Halonen et al. (1991); these aspects were not included in the present study. The spatial dependence of the measuring tape method may cause some variation in the observations, especially in investigations on tree trunks [II]. The least frequent species will be most susceptible to this drawback in the method.

The measuring tape method may be recommended for studying epiphytes on branches. The median line on a branch is more easily defined than a specific height on a tree trunk, and can easily be refound and analysed over time. McCune (1990) found significant correlations between subjectively scored cover classes and biomass measurements for several species of branch epiphytes, and recommended this method for rapid estimation of abundance on branches. However, cover class estimates may be too rough for monitoring purposes. The measuring tape method may be more suitable for detecting small spatial and temporal changes in the lichen vegetation, due to the accuracy of the abundance estimations.

Frequency in branch segments used in [IV] is comparable to frequency in subplots used in analyses of ground vegetation, strongly recommended by Økland (1990). A methodological problem in the case of branch segments, however, is the different lengths of branches and thus of branch segments. A standard number of segments was chosen instead of a standard segment length [IV]. Thus changes in physical properties from the base to the tip of the branch were attributed relatively greater importance for lichen distribution than differences in branch lengths. Sampling restrictions regarding branch lengths would decrease the problem. Additional studies using destructive sampling and age determination of branches may also provide valuable information on lichen succession on branches.

Analysis of the data and interpretation of the results were hampered by the lumping of species into groups involving species with different ecological demands. Effort should be made to include more detailed species determination, especially when the large-scale survey [II] is repeated and in the case of *Bryoria* species in detailed investigations [III, IV]. It is important to standardize methods for evaluating vitality and damage in various lichen species. Vitality characteristics need to be specified to reduce sampling error when comparisons are being made between sites analysed by different persons or at different times.

Long-term monitoring may reveal the rate and direction of changes in epiphytic lichen vegetation and may also establish more causal relationships. Such monitoring should preferably be combined with direct measurements of microclimatic factors and deposition of elements at the sites investigated and on different parts of branches.

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