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Author Per-Anders Esseen			
Title Ecology of lichens in boreal coniferous forests with reference to spatial and temporal patterns			
Abstract <p>The thesis deals with the ecology of lichens in two contrasting types of forest, epiphytic lichens in old <i>Picea abies</i> forest of the fire-refugia type and epigeic as well as epixylic lichens in a successional sequence of fire-susceptible <i>Pinus sylvestris</i> forests. Results in five separate papers form the basis for a discussion of general patterns of dispersal, succession and life strategies in lichens. The study sites were located in Medelpad and Västertotten, in the central and northern part of Sweden, respectively.</p> <p>Special attention has been paid to the rare, pendulous, spruce-lichen <i>Usnea longissima</i> and the coexisting lichen species. <i>U. longissima</i> is largely restricted to north-facing hill slopes covered with old, mesic spruce forest that is characterized by a very long continuity not disturbed by fire. A marked decline in the number of sites with <i>U. longissima</i> was found. The decline was mainly due to the effect of different forestry practices as the species is very sensitive to environmental disturbances.</p> <p>The epiphytic lichen vegetation of six tree species occurring in the spruce forest is described. Clear successional trends with increasing tree size were obtained for <i>Alectoria sarmentosa</i>, <i>Bryoria fuscescens</i> coll., <i>B. nadvornikiana</i>, <i>Usnea filipendula</i> and <i>U. subfloridana</i>, to a lesser extent for <i>Bryoria capillaris</i> while <i>U. longissima</i> had no relationship to tree size or age.</p> <p>A study of the litterfall of macrofragments of epiphytic lichens showed that thallus fragments were dispersed throughout the year with late autumn, winter and early spring as the most critical periods. It is suggested that dispersal through thallus fragmentation is more important in fruticose than in foliose species and that <i>U. longissima</i> has a shorter range of propagule transport than the other species of <i>Alectoria</i>, <i>Bryoria</i> and <i>Usnea</i> studied. The latter proposition was supported through a study of the horizontal patterns of lichen occurrence in the spruce forest.</p> <p>It is shown that the diversity in ground vegetation, after an initial increase, declines with succession in the pine forests. A mechanism of succession in ground vegetation is presented which suggest that variations in habitat heterogeneity, i.e. the diversity of substrates caused by the initial disturbance and the stand development, largely determines diversity changes during succession. Trends of increasing thallus size, increasing size of asexual reproductive propagules and increased competitive ability with succession formed the basis for recognizing three types of strategies in <i>Cladonia</i>.</p> <p>It is concluded that lichens have features that are compatible with the r-K continuum and that they are variously adapted to both the stability of the substrates and that of the forest as a whole.</p>			
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ECOLOGY OF LICHENS IN BOREAL CONIFEROUS FORESTS WITH REFERENCE TO SPATIAL AND TEMPORAL PATTERNS

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- III. Esseen, P.-A. 1983. Dispersal and dynamics of epiphytic lichens in two boreal spruce forests measured by litterfall. In manuscript.
- IV. Esseen, P.-A. 1983. An analysis of horizontal distribution patterns of epiphytic lichens within three Picea abies forests. In manuscript.
- V. Esseen, P.-A. 1983. Species composition and diversity in a successional sequence of dry lichen-rich pine forests in northern Sweden. Manuscript submitted to *Holarctic Ecology*.

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B, Fysiologi-Botanik Hufo.

Examinator: Prof. Lars Ericson, Umeå.

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1 LIST OF PAPERS

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2 INTRODUCTION

Lichens are important constituents in many ecosystems, especially in boreal, alpine and arctic areas, in spite of an often low total biomass. In comparison with many other plant groups lichens have received rather little interest. However, during the last few decades there has been a rapid increase in the number of studies dealing with different aspects of lichen ecology; this is clearly reflected in two recent reviews (Brown et al. 1976, Seaward 1977). Despite the rapid increase in knowledge, many areas of lichen ecology are still very much at a nineteenth century stage (Bailey 1976). We are, for example, only just beginning to understand such vital processes in the life cycles of lichens as dispersal, establishment and competition. This is due partly to the scarcity of experimental work performed and partly to a number of methodological problems involved, which will be discussed in the next section.

3 METHODOLOGICAL PROBLEMS

There are several aspects of the biology of lichens that it is important to consider in ecological studies. Some of the most important of these aspects are listed and briefly discussed below.

- (i) There is much uncertainty around the species concept in lichens (Thaler 1982) and major taxonomical problems remain to be solved, e.g. at the species-, genera- and family-level. This is due partly to the enormous phenotypic plasticity found in many lichen species (Weber 1977) and their great chemical variation (Hale 1974). It has been shown that the same fungus can form morphologically discernible lichens with different phycobionts (Brodo and Richardson 1978, James and Henssen 1976). This discovery contradicts the axiom that each lichen species is the product of a different fungus.
- (ii) Little is known about the mechanisms of gene exchange and evolution in lichens (Ahmadjian 1970, Scott 1973).
- (iii) The concept of the genetical individual (genet; Kays and Harper

1974) is unclear in lichens, since asexual reproduction through thallus fragmentation and specialized propagules is a very common feature (Bowler and Rundel 1975). Even the recognition of separate thalli in the field can be extremely difficult for some lichens. This restricts the possibility of performing population studies through counts of thalli and thallus parts, at least for a number of species.

- (iv) The small size and the slow growth-rate of most lichens (Hale 1974) as well as their longevity emphasize considerable methodological problems. This applies both to observations of lichen dynamics in the field and to experimental studies.

These features of lichens impose restrictions on both the methods and the lichen-habitat systems suitable for ecological studies. Furthermore, they have led to a prevalence of studies using the correlative (referred to as comparative by some authors) approach to plant ecology. This approach tries to explain variation in the composition of vegetation by comparison of the occurrence of species and plant communities with the environmental variation found in the field (cf. Grime 1979). This *a posteriori* approach is sometimes considered inferior to an experimental approach since there is always a danger of confusing causal and correlational statements (Townsend and Calow 1979, Stearns 1976). However, comparative studies could be a very useful tool for asserting main trends and framing hypotheses, and could also provide numerous suggestions for additional studies by an experimental approach. In many cases comparative studies are the only practically useful methods (Mayr 1982).

4 OBJECTIVES

This thesis describes and discusses some ecological features of selected lichen species and lichen communities in boreal coniferous forest that determine lichen occurrence in time and space. The main aim is to provide a basis for a discussion of general patterns of dispersal, succession and life strategies in lichens as well as to discuss some methodological problems involved in correlative studies.

The research was carried out in two contrasting types of lichen-rich forests. Papers I-IV deal with epiphytic lichens in long-term stable, mesic Picea abies forests that have not been disturbed by fire for a very long period of time (fire-refugia), in the central part of Sweden. Paper V deals with epigeic and epixylic lichens in a successional sequence of dry Pinus sylvestris forest, of a type frequently disturbed by forest-fire in the past, in the northern part of Sweden. The field work was carried out between 1978 and 1982.

5 SUMMARY OF PAPERS I-V

(I) OCCURRENCE AND ECOLOGY OF USNEA LONGISSIMA IN SWEDEN

The main features of the ecology of the pendulous lichen Usnea longissima and its habitat, old Picea abies forest, are outlined. The main findings are as follows: (i) U. longissima occurs in old, preferably mesic spruce forests which are mainly located on north-facing hill slopes. (ii) The sites are often located on the highest hill in the 'local area'. The vertical distribution of thirty sites ranged between 120 and 520 m a. s. l. The altitude showed a significant increase with increased distance from the Bothnian Sea coast. (iii) The sites have a slightly oceanic climate with a comparatively low mean temperature and a rather high and stable relative humidity (RH). (iv) A marked reduction in the number of sites with U. longissima, due mainly to the effect of forestry practices, was observed. (v) The spruce forests have a mainly natural structure despite signs of earlier felling operations observed in all localities. The forests represent a type with a very long continuity and could be characterized as fire-free refugia. (vi) U. longissima was confined to the lower part of the tree crowns. (vii) The population size, measured as the total length of all thalli per tree, had a very wide variation, both within and between the localities. The population size was not significantly correlated with tree height, diameter or age. (viii) The species had a very patchy occurrence, most likely depending on short-range dispersal from the 'mother-trees' to nearby trees. (ix) It is concluded that U. longissima has a preference for sites protected against wind and with a high RH, and that the species is very sensitive to

environmental disturbances.

(II) HOST SPECIFICITY AND ECOLOGY OF EPIPHYTIC MACROLICHENS IN SOME CENTRAL SWEDISH SPRUCE FORESTS

This study describes the epiphytic lichen vegetation in ten Picea abies forests of the type studied in paper I. The main findings are as follows: (i) A total of 35 macrolichens were found on the six tree species studied, viz. Betula spp., Picea abies, Pinus sylvestris, Populus tremula, Salix caprea and Sorbus aucuparia. (ii) The largest number of species occurred on Picea abies, the dominating tree species. (iii) Each tree species had a characteristic lichen vegetation. (iv) It is suggested that the dominance of spruce, with its characteristic lichen vegetation, influences the epiphytic lichen vegetation of the other tree species present. (v) Tree morphology seems to be important in determining lichen abundance since it is related to the number of sites available for lichen colonization. (vi) For five of six fruticose lichens investigated, maximum thallus length per tree increased significantly with tree height, indicating clear successional trends. (vii) The slope of linear regression curves between maximum thallus length and tree height was related to the maximum attainable thallus lengths of the species. Possible reasons for these patterns are briefly discussed.

(III) DISPERSAL AND DYNAMICS OF EPIPHYTIC LICHENS IN TWO BOREAL SPRUCE FORESTS MEASURED BY LITTERFALL

This paper and the next one (IV) describe two indirect methods of studying the process of lichen dispersal. The seasonal variation in litterfall of lichens and tree litter was measured at two sites with traps, and for one species, Usnea longissima, by a collection of all specimens on the ground. The main findings are as follows: (i) Litterfall showed a large spatial and temporal variation. (ii) Total lichen litterfall was 116 and 162 kg ha⁻¹ yr⁻¹ which is equivalent to 4.6 and 5.7 % of the total litterfall at the two sites. (iii) Lichen litterfall was highest during the period late autumn to early spring, due mainly to snow

accumulation on the spruce twigs. (iv) No marked difference in species composition and biomass proportions of the lichen litter was observed between the different periods in the year. (v) The size of the lichen fragments was related to the 'robustness' of the species; small fragments were much more abundant for small and fragile species than for more robust species. (vi) Data for U. longissima showed that the annual litter-fall constituted 6.9 and 9.7 % of the amount present on the standing trees at the two sites. (vii) The size distribution of the collected thalli of U. longissima was highly skewed in preference for short thalli, i.e. over 90 % of the thalli were shorter than 30 cm. (viii) It is concluded that wind dispersal of whole thalli and thallus fragments are likely to occur throughout the year with late autumn, winter and spring as the most important periods. (ix) Dispersal through thallus fragmentation appears to be more important in fruticose species than in foliose species. The fruticose species Alectoria sarmentosa, Bryoria spp., Usnea longissima and perhaps also the other Usnea spp. are apparently adapted to dispersal by means of thallus fragmentation. (x) It is suggested that U. longissima has a shorter range of dispersal than the other species studied.

(IV) AN ANALYSIS OF HORIZONTAL DISTRIBUTION PATTERNS OF EPIPHYTIC LICHENS WITHIN THREE PICEA ABIES FORESTS

A method for studying the effect of tree spacing on the distribution patterns of epiphytic lichens by using nearest-neighbour technique is presented. Tree positions were mapped in three 30x30 m plots and the occurrence of seven species of fruticose lichens was recorded on each tree. The results showed that: (i) The distribution patterns were aggregated for low spruce trees and had a clear tendency towards a regular pattern for tall trees. (ii) Tests performed with a simulation technique gave no significant deviations from random distributions on the spruce trees for the seven lichen species, except in three out of the twenty-one tests performed. No species gave significance for a regular pattern. Usnea longissima showed the strongest tendency towards an aggregated pattern with low values of the dispersion index used at two of the three sites. (iii) It is suggested that an aggregated distribution pattern is

likely to be caused by an inefficient mechanism of dispersal of lichen propagules within a forest. A regular pattern could arise in cases where a lichen exhibits a strong preference for the more regularly spaced, large-sized trees. (iv) The results thus indicate that U. longissima has a less efficient mechanism of propagule dispersal than the other six species investigated, viz. Alectoria sarmentosa, Bryoria capillaris, B. fuscescens coll., B. nadvornikiana, Usnea filipendula and U. subfloridana. (v) It is concluded that further development of both sampling and analytical methods is necessary before it is possible to use the degree of aggregation within forest stands as a relative measure of dispersal efficiency in lichens. A consideration of special importance is lichen abundance per tree.

(V) SPECIES COMPOSITION AND DIVERSITY IN A SUCCESSIONAL SEQUENCE OF DRY LICHEN-RICH PINE FORESTS IN NORTHERN SWEDEN

The succession of ground vegetation in a spatial sequence of six Cladonia-dominated Pinus sylvestris forests of different ages has been studied. The objectives were to investigate differences between post-fire and post-felling successions, reproductive strategies in the species, diversity changes and mechanisms of succession. Data on forest structure were obtained in one 50x50 m plot per stand. The relative cover of the species in ground vegetation and of four habitat components recognized was estimated in fifty 0.5x0.5 m quadrats per plot. The main results are as follows: (i) Stand age ranged from 14 to 150-160 years after the initial disturbance, viz. clear-felling in the three youngest stands and forest-fire in the three oldest stands. (ii) The total material comprised 57 species of which 6 were vascular plants, 34 lichens and 17 bryophytes. Nearly half of the total number of species occurred in all stands. (iii) Species abundance patterns in ground vegetation followed lognormal distributions in all stands with gradually steeper slopes as succession proceeded. (iv) Both species richness and diversity, assessed with the Shannon-Wiener index (H') and the mid-range statistic (Q), declined with succession. This was mainly due to a reduction in the number of medium-abundant lichen species, predominantly species in Cladonia subgenus

Cladonia. (v) Accompanying this decline there was a decline in habitat diversity, measured as the diversity (H') of tree litter and other habitat components. It is suggested that variations in habitat diversity largely determine patterns of species diversity. (vi) A possible mechanism of succession in pine forests is proposed, suggesting that the species composition in ground vegetation is governed by both the amount and the quality of tree litter, which may be regarded as extrinsic factors, in combination with competitive interactions between the species, i.e. intrinsic factors. (vii) Post-fire and post-felling development have many features in common although the former is characterized by a more severe initial disturbance as well as by a higher frequency of disturbance. (viii) The reproductive strategies of the bryophytes and lichens with their maximum of abundance in early-, mid- and late-successional stages are discussed on the basis of a comparison of characteristics of the species with their position along the time gradient. A preliminary system of three types of strategies in Cladonia is also presented. (ix) It is concluded that in order to detect general patterns and mechanisms of succession it is necessary to consider the type, severity and frequency of disturbance as well as to have a basic knowledge of the autecology of the species.

6 DISCUSSION

6.1 Dispersal

The data in paper III provide indirect evidence for the importance of vegetative dispersal through thallus fragmentation in epiphytic lichens. Judged by their morphology most species of Alectoria, Bryoria and Usnea studied are apparently adapted, at least in a functional sense, to dispersal by thallus fragments, and in some species, also by specialized propagules (soredia). Sexual reproduction through ascospore propagation is probably of little importance in the Picea abies forests investigated as the majority of the species does not produce apothecia (III). Bowler and Rundel (1975) suggested that the advantages of asexual reproduction in lichens are the possibility of a rapid invasion to new habitats and a greater survival for propagules. However, no experimental evidence

has yet been presented.

It is shown that dispersal through thallus fragmentation occurs throughout the year with the late autumn, winter and early spring as the most critical periods (III). The lichens are liberated and transported passively through the action of wind, rain, snow and ice. Although wind transport of numerous macrofragments seems to be of large importance in the dispersal from tree to tree within the forest stand, it is probably not as effective as soredia in long-range dispersal.

Both paper III and IV support the hypothesis that Usnea longissima has a much shorter range of dispersal within forest stands than the other fruticose lichens investigated. An inefficient mechanism of propagule transport over greater distances than a few metres (I, III) may explain why no significant correlation was obtained between the abundance of U. longissima and the height, diameter and age of the host trees (I). Further, U. longissima seems to a very great extent to rely on dispersal by comparatively large thallus fragments, which provides an efficient means of attaining successful establishment on nearby trees. Similarly, the high and significant correlations between maximum thallus length and tree height obtained for Alectoria sarmentosa, Bryoria fuscescens coll., B. nadvornikiana, Usnea filipendula and U. subfloridana (II) could only be obtained under the assumption that the dispersal of lichen propagules is more or less efficient and occurs at random.

Experimental studies are needed on the processes of liberation, transport, deposition and establishment of lichen propagules in order to achieve a more complete understanding of the mechanism of dispersal in lichens (cf. Bailey 1976).

6.2 Succession

In some aspects succession in lichen communities differs from that in phanerogam communities. Yarranton (1972) concluded that epiphytic succession cannot be considered a true succession as defined by Clements because lichens generally seem to have little power to influence their host trees. Any site on a tree will experience directional change with time but changes in the substrate are mainly caused by the growth and

development of the host trees and only to a minor extent by the influence of the lichens (Topham 1977).

The close coupling between lichens and their substrates is also an important consideration in terrestrial successions as shown in paper V. The available evidence suggests that there is a more or less direct relationship between the species diversity and the diversity of the substrates in the pine forests investigated (V). This leads to the conclusion that a considerable part of the change in abundance of the lichen species during succession is governed by both the type and the quality of the substrates present, which themselves are related to the dynamics and the development of the forest stand. It therefore appears that this type of succession cannot be considered wholly autogenic if viewed from the species concerned. This would also apply to epiphytic lichen successions.

6.3 Life strategies in lichens

The concept of life strategies (tactics) emerged as a consequence of modern theory of evolution and has proved to be very useful in a number of organisms including animals and phanerogams (cf. Grime 1979, Southwood 1981 and Stearns 1976, 1977 for reviews). Recently, the life strategies of bryophytes were covered in the paper by During (1979). The strategy concept has received little attention in lichen ecology although Bowler and Rundel (1975) and Topham (1977) made some general statements.

Below I will try to distinguish a few general patterns about the life strategies in lichens with the papers I-V as a basis. However, since the data are of a correlational nature the conclusions made should be considered as tentative until confirmed by appropriate experimental work.

A major factor that all lichen species have to face is the stability of the substrate (habitat), i.e. its permanence and predictability. For example, epiphytic lichens obviously must reproduce within the life-span of the host trees (Barkman 1958, Topham 1977), as also epixylic lichens must before the wood disintegrates. This suggests that selection in lichens occurring in forests might operate at two levels, i.e. they have to contend with both the stability of the substrate and that of the forest as a whole. The importance of these levels could be illustrated

by two cases with a different hazard of burning. In a forest where the recurrence of fire on average occurs before the substrate disintegrates or becomes unfavourable for lichen growth, the fire-frequency will be the dominating selective force and species with opportunistic features will be favoured. On the other hand, with a very low recurrence or absence of fire, adaptations to the stability of the substrates would be operating. In this type both opportunistic and equilibrium species would be able to coexist in proportion to the variations in the permanence and predictability of suitable substrates. The first case described might well apply to the pine forests, frequently disturbed by fire in the past, studied in paper V. The second case might apply to the spruce forests of the fire-refugia type investigated in papers I-IV.

The strategy of a species is largely determined by the stability of the environment (Southwood et al. 1974). It is therefore suggested that the different lichen species found in both the pine and the spruce forest investigated have evolved various strategies that are coupled to the variations in the stability of both the substrates and the forest as a whole. Unfortunately, very little experimental evidence is available in the literature on the relative importance of different life history traits in lichens. For example, the experimental demonstration of differences in competitive ability was not made until very recently (Armstrong 1982). This makes it difficult to discuss the importance of such traits as e.g. the size and number of propagules, reproductive effort, the balance between asexual and sexual reproduction, and longevity in relation to the characteristics of the substrate. The trends obtained from the comparison between the successional position and the characteristics of the species (V) provide some tentative ideas. These trends include an increased thallus size, an increased size of asexual reproductive propagules and increased competitive ability, in the sequence from early- to late-successional species. It seems also probable that there is an increase in longevity and a decrease in the proportion of resources that are devoted to reproductive structures, although no relevant data were presented.

The trends presented above lead to the conclusion that lichens have features that are compatible with the well-known theory of r- and K-selection (MacArthur and Wilson 1967) and the continuum between the two extremes (Pianka 1970). In analogy with this theory the crustose lichens

and the Cladonia-species with cups or needle-like podetia (V) clearly emphasize r-selection (cf. Ahti 1982 for Cladonia). The richly branched reindeer lichens in Cladonia subgenus Cladonia (V) as well as the fruticose species of Alectoria, Bryoria and Usnea (I-IV), on the other hand, emphasize K-selection with Usnea longissima at the extremity.

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