

Review

EPIPHYTIC BRYOPHYTES AND LICHENS IN BOREAL AND NORTHERN TEMPERATE FORESTS

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Epiphytic lichens and bryophytes are commonly used as indicators of forest biodiversity and continuity. The richness and abundance of epiphytic species depend on forest stand age, host tree age, size, and growth rate, and also on the chemical and physical properties of the bark. Epiphyte community composition changes with height on a tree, in relation to light intensity, relative humidity, and features of the bark of the host tree. Aspen trees are particularly important for biodiversity due to their unique epiphyte flora. The limiting factors for epiphyte development can be studied by transplanting and sowing experiments from, for example, their typical habitats in old growth forests to other areas such as young forests, forest edges, and clear-cuts. Such experiments have indicated that a broad range of forest age classes can provide suitable habitats for old growth species. Often, despite what might have been expected, microclimate has not been found to be the main factor determining the distributional patterns of the species studied, but rather, diaspore production, early fixation of diaspores, and poor dispersal ability. This implies that forest management needs to consider the following: retention of trees, groups of trees and patches, retention of deciduous trees in logged boreal forests, selective cutting, extension of rotation age, and transplantation of endangered epiphyte species. The literature review was used as a basis to make recommendations for future research in this direction in Latvia, regarding management for protection of biodiversity and research in epiphyte ecology and dynamics, both at local and at landscape scales.

Key words: forest, biodiversity, bryophyte, lichen, epiphyte.

INTRODUCTION

Much research has been conducted on the conservation of biological diversity in forests. Forests managed for wood harvest support fewer epiphytic lichen and bryophyte species than natural forests (in this paper, natural forests refer to forests that have been minimally disturbed by man and where stand development has been due largely to natural disturbances), and young forests have fewer species than old forests. Very old, natural forests have not only a larger number of species, but they support many species that do not exist elsewhere (Lesica *et al.*, 1991; Johansson and Gustafsson, 2001; Rolstad *et al.*, 2001). Epiphytic lichens and bryophytes are widely used for the evaluation of forest biological diversity. They are good bioindicators of forest continuity in terms of forest stand age, history, microclimate, and other parameters (Kuusinen and Siitonen, 1998; Boudreault *et al.*, 2000; Hedenås and Ericson, 2000).

Many epiphyte species have become very rare due to intensive forestry, and therefore they now require protection. Protection of a few epiphytes in their natural habitats will also ensure the protection of other species that require similar environmental conditions in forests. When we establish a

protected territory for a species, we may even lack knowledge of the full spectrum of species that also require protection in these habitats.

As stated in the Forestry Policy of Latvia (accepted by the Cabinet of Ministers, 1998), protection of biological diversity in forests is a goal of forest management in Latvia. However, knowledge is insufficient regarding the type of protection required, management actions for protection, and the expected consequences of the management regime.

Ecological studies on limiting factors and dispersal of epiphytes generally are lacking in Latvia. Publications on epiphytic bryophytes and lichens in Latvia have been mostly restricted to descriptions of flora (Āboliņa, 2000; Piterāns, 2000), regional patterns (Motiejūnaitė and Piterāns, 1998; Piterāns and Žeivīniece, 2000), and pollution studies. Epiphytic lichens and mosses have been used for mapping and evaluation of environmental pollution (Laiviņš *et al.*, 1993; Liepiņa un Nikodemus, 1990; Piterāns un Bērziņa, 1990).

The purpose of this review was to survey the literature that has been published during the past 10–15 years regarding the ecology of epiphytic lichens and bryophytes in boreal

and northern nemoral zones, to aid planning of future research in Latvia.

DESCRIPTIVE STUDIES: CHARACTERISTICS OF FOREST STANDS AND HOST TREES

Forest stand age. It has been well established that richness and abundance of epiphytic species increase with increasing forest stand age (Lesica *et al.*, 1991; Hyvärinen *et al.*, 1992; Kuusinen, 1996b; Kuusinen and Siitonen, 1998; Aude and Poulsen, 2000; Johansson and Gustafsson, 2001; Price and Hochachka, 2001). However, old stands are not required for all of the species. Many species are restricted to younger stands and each stand age class is associated with some specific species (Aude and Poulsen, 2000; Boudreault *et al.*, 2000). However, there are more generalist species in young forests. The number of rare and endangered species increases with increasing stand age (Kuusinen, 1996b; Hedenås and Ericson, 2000; Rolstad *et al.*, 2001), and the highest biodiversity can be found in old-growth forests. The higher number of species is due to both the older age of trees and to the higher structural diversity (variability in tree height and age, dead wood) that is missing in managed forests (Lesica *et al.*, 1991).

Tree age. Several authors have found a relationship between the age of individual trees and epiphyte diversity, which is independent of stand age. In general, the number of epiphytic species increases with host tree age, and some epiphyte species prefer very old trees (Kuusinen and Siitonen, 1998; Uliczka and Angelstam, 1999). The above can be explained by simple stochastic processes, as there has been a longer period of time for dispersal to and colonisation of old trees. Because of relatively slow growth and colonisation rates, it may take many decades for bryophytes and lichens to develop a substantial cover and species richness (Crites and Dale, 1998; Uliczka and Angelstam, 1999). Also, as old trees are bigger, they have larger trunks and branches, therefore, here is more surface area for colonisation (Lyons *et al.*, 2000). Other reasons for late colonisation relate to changes in the substrate for epiphytes. With aging of the tree, the bark structure becomes more suitable for epiphyte growth. The bark of young trees is thin and smooth, often scaly and peeling. A scaly bark surface hinders attachment of diaspores to the trunk. Old trees develop a thick, rough shield bark with sheltered microhabitats (cracks etc.) that are important for trapping lichen propagules prior to germination (Hyvärinen *et al.*, 1992).

Tree stem diameter. Epiphytic species richness and abundance generally increase with tree size. The number of species has been found to be positively correlated with tree stem diameter at breast height (DBH) in boreal forests in Finland (Kuusinen, 1996a). Gu *et al.* (2001) also found a clear relationship between tree size and the incidence of lichen *Lobaria pulmonaria* on both *Populus tremula* (European aspen) and *Salix caprea* (goat willow) in boreal forests in Finland. Hedenås and Ericson (2000) estimated that the mean DBH of *Populus* explained 30.2% of the variation in

species composition of boreal forest stands in central Sweden. The number of species in a stand, the number of signal species (species indicating forest habitats with conservation values), and the number of species restricted to *Populus* and *Salix* increased with the increase of mean DBH.

Species number and abundance are not linearly related to stem DBH. Several authors consider that there is a critical DBH that needs to be attained before the number or abundance of signal species starts to increase. On *Populus tremula* in central Sweden, the number of signal species begins to increase when stem DBH reaches somewhere between 13 and 24 cm (Hedenås and Ericson, 2000). Rolstad and Rolstad (1999) found that, in central Norway, the lichen *Usnea longissima* occurred more frequently on *Picea abies* (Norway spruce) stems that were over 10 cm DBH. The bryophyte *Ulota crispa* was observed in Norway to respond slowly to an early increase in the diameter of *Acer platanoides* (Norway maple), but showed a great increase in the number of cushions when a tree reached a diameter of about 20–30 cm. For *Salix caprea* and *Populus tremula*, this trend was more close to linear, and only a slightly greater rate of increase of cushion number was observed for *Populus tremula* 20–30 cm DBH and for *Salix caprea* with 15–20 cm DBH.

Since the relationship with stem diameter is not linear, several authors consider that tree size is a better predictor of epiphyte abundance and richness than tree age. It was observed that the occurrence of lichen thalli on *Picea abies* was not correlated with tree age in central Norway (Rolstad and Rolstad, 1999). Also, epiphyte cover can differ among *Tsuga heterophylla* (western hemlock) trees of different sizes, even though the trees have similar age (Lyons *et al.*, 2000).

Shade tolerance of different tree species may explain why epiphyte abundance is correlated with tree age for some tree species, and not for others. *Populus tremula* is a fast-growing early successional species (Bergeron, 2000). Therefore, the stem diameter of this species is linearly correlated with age, and hence diameter can be used as an estimate of relative age (Hedenås and Ericson, 2000). When the stem diameter is correlated with age, there is also a linear relationship between age, epiphyte richness, and abundance.

Picea abies is a shade-tolerant late successional species that can persist for several tens of years in the forest understorey, maintaining very slow growth. Seedlings and saplings rapidly invade the upper canopy when openings develop. As a result, neighbouring trees may have a similar diameter, but greatly different age (Örlander and Karlsson, 2000). Therefore, epiphyte richness and abundance in certain cases is much better related with tree diameter than with age.

The low species richness on small trees can be indirectly related to stand structure, as a low cover of epiphytes can often be explained by shading from other trees (Lyons *et al.*, 2000).

Growth rate. Individual trees which grow slowly are more valuable substrates for epiphytic lichens and bryophytes than faster-growing individuals of the same species. Uliczka and Angelstam (1999) in south-central Sweden found a negative correlation between the tree growth rate and the number of signal species. Hyvärinen *et al.* (1999) found a close negative correlation between the growth rate of *Pinus sylvestris* (Scots pine) saplings and the number of epiphyte species using this tree species as a substratum, which was presumed to be due to greater exfoliation of the bark of faster-growing saplings.

When a tree that has grown in the interior of a forest stand suddenly is subject to full sunlight in a clear-cut, many epiphytes usually die and fall from the tree stem. The death of epiphytes may be not only due to exposure to full sunlight, as hastened tree growth due to increased availability of resources can cause shedding of the bark substrate along with the epiphytes (Gauslaa *et al.*, 2001).

Physical properties of the bark substrate. Bark physical properties determine the preference of epiphytes for tree species and age classes, as the bark differs between species and changes with age, becoming rougher, thicker, and more stable. The rate of change of bark properties also varies between species. Bark sheds faster for faster growing trees, which are therefore less suitable for epiphytes.

Bark of *Pinus sylvestris* saplings is usually scaly and peeling, while the bark of young *Picea abies* is stable. As a result, the majority of lichens colonise the annual shoots of *Picea* faster than those of *Pinus*, suggesting that the peeling bark of young *Pinus* hinders lichen colonisation (Hyvärinen *et al.*, 1999). The scaly, peeling bark of young *Pinus* changes to a thick, rough shield bark on old trees (Uliczka and Angelstam, 1999) providing sheltered microhabitats (cracks etc.) that are important for trapping lichen propagules prior to germination (Hyvärinen *et al.*, 1999). The bark of *Picea* peels more easily and it does not change much with age, which can explain the more homogeneous epiphytic vegetation associated with this species (Hyvärinen *et al.*, 1992).

Lichens colonise *Betula* (both silver birch *Betula pendula* and downy birch *Betula pubescens*) more rapidly than conifers (Uliczka and Angelstam, 1999). The bark of *Picea abies* often becomes rough quickly, which makes it suitable for lichens, although it does not reach the roughness of old *Pinus sylvestris*.

Alnus incana (grey alder) in central and southern Finland has been observed to support more epiphyte species than other tree species (Kuusinen, 1996b). The bark of *Alnus* is smooth and hardly exfoliating. The low level of disturbance by bark scaling may be a main factor explaining the high total cover of epiphytes on trunks of *Alnus*. However, Kuusinen (1996b) considered that the open, moist habitats on *Alnus* trees, rather than the lack of bark scaling, may better explain the high epiphyte cover.

Bark chemistry. Epiphyte community composition is influenced by bark pH which differs between tree species. Kuusinen (1996b) divided tree species into three distinct groups according to the acidity of the surface bark. *Picea abies* and *Pinus sylvestris* generally have bark pH well below 4, *Betula sp.* between 4 and 5, and *Alnus sp.*, *Salix caprea*, and *Populus tremula* slightly above 5. Bark of coniferous trees is more acidic than bark of deciduous trees. Hobohm (1998) examined the pH range of the bark of 12 tree and shrub species which were inhabited by 17 lichen species, and pH was found to be a more important factor than host tree species in lichen preference. Several species were restricted to acidic bark, regardless of the tree species.

Bark pH can change within a single tree and tends to increase with tree height (less acidic at the top). The pH of *Picea abies* bark can differ by ± 0.4 between a 2 m difference in height (Goward and Arsenault, 2000). However, the bark at the base of trunks is less acid because of the proximity of soil (Hyvärinen *et al.*, 1992). Kivistö and Kuusinen (2000) found that the bark pH of *Picea abies* was higher on trees growing at the forest margin than in the interior, probably because the basal trunks of trees at the forest edge receive more atmospheric deposition than those in the interior. Bark of *Picea abies* and *Pinus sylvestris* trees becomes more acidic with stand age (Hyvärinen *et al.*, 1992).

Acid rain can lower the bark pH. As cyanolichens (foliose nitrogen-fixing macrolichens) are usually associated with trunks of well-buffered trees having a pH greater than 5.0, they are especially endangered by air pollution (Goward and Arsenault, 2000; Kermit and Gauslaa, 2001). *Lobarion* forms a characteristic epiphytic community in broadleaved forests, but in central Norway it is found also on *Picea abies* twigs in old forest stands (Gauslaa and Holien, 1998). Presumably, this is due to the less acidic precipitation in this region. Also, the decline of *Lobarion* on *Picea* twigs in eastern parts of Scandinavia is thought to be due to airborne acidic deposition (Gauslaa and Holien, 1998).

In an area affected by calcium carbonate emissions from a lime manufacturing factory in Latvia, pollution raised the pH of the otherwise acidic bark. In consequence, mosses typical on dolomite substrates and lichen species on calcareous substrates, such as deciduous trees, boulders, and limestone, were found also on *Pinus sylvestris* stems (Laiviņš *et al.*, 1993).

Epiphytes can change the pH of their substrate. Gauslaa and Holien (1998) measured the pH of both lichen and their substrata and found that the thallus of the acidic substrate-sensitive *Lobarion* species was more basic than the substrate. In contrast, the thallus of the widespread *Pseudoevernion* species was more acidic than the substrate. It was suggested that *Lobarion* leaches out protons, while *Pseudoevernion* raises the pH of the substrate.

Smith (1982) divides trees into three groups on the basis of bark electrolyte content: eutrophic bark – *Acer spp.*, *Sambucus nigra*, *Prunus avium*; mesotrophic bark –

Quercus spp., *Fagus sylvatica*, *Fraxinus excelsior* and *Salix alba*, and oligotrophic bark – *Betula* sp., *Picea abies* and *Abies alba*. Presumably, bark chemistry is a major factor that also determines epiphyte community composition. Facultative epiphytes that occur on eutrophic bark occur also on basic rocks, and epiphytes of oligotrophic bark occur on siliceous rocks.

Populus—host of unique epiphyte flora. *Populus* (both European aspen *P. tremula* in Eurasia and trembling aspen *P. tremuloides* in North America) are particularly important tree species for maintaining and improving biological diversity in boreal forests. Old *Populus* trees are rich in species and have a unique flora and fauna (Goward and Arsenault; 2000, Ojala *et al.*, 2000). Just one old *P. tremula* tree can increase the total epiphyte species number in a wood by several (4–6) species (Kuusinen and Siitonen, 1998). In Sweden, Uliczka and Angelstam (1999) found that about half of the epiphyte species in a stand were exclusive for *P. tremula*. The distinctive epiphyte flora on *Populus* can be explained by low acidity of the bark (pH < 0.5) and the abundance of nutrients available on the bark surface (Kuusinen and Siitonen, 1998).

Usually, *Populus* does not become a dominant species in the canopy, but is scattered among other tree species. Ojala *et al.* (2000) studied epiphyte assemblages on *P. tremula* in areas where the species had a patchy distribution in boreal forests in Finland. The number of epiphyte species tended to be higher in areas where *Populus* had a higher relative abundance. At a local scale, the size of *Populus* stems and tree density around the trunk were correlated positively with the occurrence of some epiphyte species.

Since *Populus* is a pioneer species, it is much more abundant in younger stands, and its abundance declines in old stands where large gaps are not created by natural disturbances. Therefore, the loss of *Populus* in succession can lead to declining epiphyte diversity. In *Picea abies* forests, the frequency occurrence of several lichen species (*Lobaria pulmonaria*, *L. scrobiculata*, *Nephroma* ssp.) was observed to increase with increasing stand age, but this relationship was positive only until about 100–150 years of age, after which time a decline was seen (Rolstad *et al.*, 2001). This was explained by the preference of many epiphyte species for deciduous trees, including *P. tremula*, which were less abundant in late seral stages.

Not only does *Populus* support a unique epiphyte flora, but it can also serve to improve the species richness of neighbouring trees. Cyanolichens were observed to be more frequent on *Picea abies* trees which were growing close to *P. tremuloides*, and were almost absent on *Picea* growing far from *Populus* stems (Goward and Arsenault, 2000). Since calcium concentrations were significantly higher on *Picea* branches within the throughfall drip zone of *Populus* than elsewhere, it was concluded that nutrient-rich leachates originating from the upper crowns of *Populus* enriched the lower branches of nearby *Picea* trees, allowing the colonisation of cyanolichens.

Similar to *Populus*, other deciduous tree species can increase the epiphyte diversity in conifer stands. In managed conifer stands, canopy gaps of a size 0.1 and 0.3 ha overgrowing with *Coryllus*, *Acer*, and other hardwood species significantly improved lichen diversity, even more so when the gap size was 1000 m² (Neitlich and McCune, 1997). The smallest gaps (e. g. 25 m²) had only a slight effect on lichen diversity.

Vertical distribution. Epiphyte species richness and abundance change with height in the tree. Trees present a wide variety of habitat types for bryophytes, which vary in light intensity, relative humidity, and in the physical and chemical nature of the bark of the host tree. Light intensity and relative humidity are inversely correlated, the former being at its maximum at the tree crown and the latter at the tree base (Smith, 1982).

McCune *et al.* (2000) estimated that 44% of the total variation of epiphyte community composition and abundance in tree crowns was related to the height on a stem. The second most important (28%) factor was related to size of stem, contrasting trunks with branches. Some species are associated with the tree trunk, some with branches, and others with treetops.

Regarding bryophytes, the tree base is colonised mostly by facultative epiphytes, including species from the surrounding ground; the trunk and larger branch species can be facultative or obligate epiphytes while those of the smaller branches and twigs are usually pioneer obligate epiphytes (Smith, 1982).

Lyons *et al.* (2000) described the vertical distribution of epiphyte functional groups on *Tsuga heterophylla* in an old-growth *Pseudotsuga menziesii* (Douglas fir) forest in the north-western USA. Alectorioids (pendulous lichens belonging to genera *Alectoria*, *Bryoria*, *Usnea*) increased in abundance from the ground up, while bryophytes decreased. Maximum abundance of cyanolichens was in the middle canopy, and total epiphyte abundance increased with tree height class.

The vertical distribution of epiphytes can change depending on the local microclimate. A higher humidity can result in the occurrence of typical tree trunk epiphytes higher on the stem (Peck *et al.*, 1995). The crustose lichen *Lecanactis abietina* is found significantly higher on *Picea abies* in a swamp-forest, where it may completely cover basal trunks of *Picea* up to 3 m height, compared to trees growing on dry mineral soil (Kuusinen, 1996c). *Lecanora circumborealis* frequents the lower crowns of conifers in drier forests, but is restricted to more exposed sites in an oceanic climate (McCune *et al.*, 2000).

Hedenås and Ericson (2000) observed that the generalist species *Xantoria parietina* occurred on *Populus tremula* up to a height of 2 m in young forests, while it was found higher up in the crown in old forests—probably because the light intensity was insufficient for this species at low

heights on the stem. This pattern is important to bear in mind, as studies dealing with lichen species composition on trees are, for practical reasons, mostly restricted to the basal parts of the trunk. The decline of observed early successional species in older stands may therefore be an artefact due to their “climbing up” stems.

Dispersal. Poor dispersal has been frequently postulated as limiting the development of populations of lichens associated with old-growth forest (Hedenås and Ericson, 2000). The vegetative diaspores of lichens are believed to disperse only in short distances.

Dettki (1998) found that most of fragments of the pendulous lichens *Alectoria sarmentosa* and *Bryoria ssp.* were deposited within 100 m from a source (forest edge) into a clear-cut. *A. sarmentosa* produced fewer but larger fragments than *Bryoria* species. Dettki *et al.* (2000) sampled seven lichen species in young forests (35–78 years old) at different distances from old-growth (122 y) forests in northern Sweden. The authors found only a few *A. sarmentosa* sites of colonisation in young forests, despite its abundance in several old nearby forests. The other species had a lower average number of thalli per branch, compared to old forests, and the maximum thallus size decreased with increasing distance from old forests.

Sillett and Goslin (1999) sampled lichen litterfall in a stand where a few scattered 200–600 year old stems of *Pseudotsuga menziesii* had survived multiple fires, but the rest of the trees had established after fire and were 100 year old. *Lobaria oregana* and *Sphaerophorus globosus* were still strongly correlated with remnant trees. Thus, the lichens had survived the fire, but in 100 years had not been able to colonise the surrounding forest. It was concluded that the slow dispersal solely, and not the microenvironment, was the limiting factor for the species.

On a small spatial scale where the spores of epiphytes are dispersed at short distances, the environmental conditions (substrate properties) are the limiting factors for successful colonisation and growth of moss *Ulota crispa*. However, on a broader scale, the major problem for this species is the dispersal between suitable habitats (Heegaard and Hangelbroek, 1999; Heegaard, 2000).

Edge effect. Forest fragmentation is the replacement of large areas of native forest by other ecosystems, leaving isolated forest patches. Organisms that remain in the fragment are exposed to the conditions of a different surrounding ecosystem (Murcia, 1995). An increased amount of edge habitat is presumed to have deleterious consequences on forest interior species that are sensitive to an altered microclimate.

Tree crowns at the forest edges (mostly, edges of clear-cuts) are more exposed to sunlight and wind than those of the forest interior. Wind penetrates easily in the forest. Epiphytes in these trees may dry more rapidly as a consequence of higher vapour pressure deficits (Sillett, 1994), which may be detrimental to some species, while being at the same time favourable to others (Kivistö and Kuusinen, 2000).

While the “edge effect” is a well known term, there are few well documented studies on its influence on vulnerable epiphytic species. The threatened foliose lichen *Erioderma pedicellatum* vanished from its single location in Sweden apparently because of an altered microclimate following cutting of the surrounding forest (Essen and Renhorn, 1998).

Studies of the edge effect on endangered old growth forest species are complicated because of the patchy environment of these forests (Kruys and Jonsson, 1997) and because individuals are scattered, distributed on few of the potential substrate trees (Kuusinen and Penttinen, 1999). Therefore, studies on the edge effect are usually conducted in homogeneous forests and are focused on species that are wide-spread in these forests.

Essen and Renhorn (1998) studied the lichen *Alectoria sarmentosa* at south-faced clear-cut edges in boreal *Picea abies* forests in northwestern Sweden. Lichen mass and length was markedly lower at the edge. The major factor reducing lichen abundance was physical damage by strong wind. The authors suggested that epiphytic lichens may have been strongly affected by the edge effect during the first year after cutting, but that lichen abundance recovered after about a decade at some intermediate distance from the edge.

Sillett (1995) examined crowns of four 700-year-old *Pseudotsuga menziesii* trees in Oregon (USA): two trees growing in the forest interior and two on the edge of a 20-year-old clear-cut. Lichen biomass and species richness was similar on all of the trees studied. However, there were differences in the vertical distribution of epiphytes. Branches in the exposed portion had a relatively high cover of alectoroid lichens and cyanolichens, and a relatively low cover of bryophytes. Branches in the sheltered portion had a very high cover of bryophytes, and no alectoroid lichens. Species that in the forest interior were distributed more in tree tops (the most sunny and windy microhabitat), in forest edges were slightly more distributed in whole crowns. After two decades of exposure on a clear-cut edge, no epiphyte species in this forest appeared to be lost or seriously declining. The author explained the results by thick moss mats that can regulate moisture regimes of epiphytic microsites, thus benefiting desiccation-sensitive species.

Some authors have described gradients of epiphyte communities around large clear-cuts. At the edges of large clear-cuts in old-growth boreal forest fragments in central Finland, the diversity of epiphytic lichens was lower at the forest margin than in the forest interior (Kivistö and Kuusinen, 2000). However, that was found only for sunny south-facing edges, while the species diversity in north-exposed edges was independent of the distance from the forest margin. In that study, only the most common boreal epiphytic lichen species were studied, but the authors suggested that rarer species might be more sensitive.

Hilmo and Holien (2002) studied edge effects on lichens living on lower branches in an old *Picea* forest. The mean

number of species per branch was lower at the forest edge; generally because there were a few crustose lichen species that did not occur at the edge. The number of foliose and pendulous species did not change significantly along the gradient. Impact of the forest edge on species was most evident for those growing on the branch tips, for example, *Cavernularia hulthenii* and *Hypogymnia tubulosa*. The authors suggested that these small pioneer species are sensitive because of the higher light exposure and wind speed; such species might be indicators of the edge effect in humid boreal spruce forests.

In some studies (Kivistö and Kuusinen, 2000; Essen and Renhorn, 1998), the edge effect was observed to extend in a 25–50 m wide forest zone. Surprisingly, at an intermediate distance from the forest edge (20–30 m), lichen abundance was higher than in the forest interior, indicating that the changed microclimate was beneficial to the studied species.

EXPERIMENTAL STUDIES

Transplantation and sowing. Reciprocal transplant experiments can aid to understand the main limiting factors for successful colonisation and growth of epiphytes. They present a direct means of examining the relationships between environmental factors and biological response.

Such experiments are usually conducted using cyanolichens, which are well documented as old-growth associated epiphytes. These lichens have large thalli that allow to easily estimate growth. To a lesser extent, also moss or less sensitive lichen species are transplanted.

One of the first lichen transplant studies was conducted by Gilbert (1991) who transplanted cyanolichen *Lobaria amplissima* from ash tree (*Fraxinus excelsior*) onto other trees: *Quercus petraea* (mossy oak), *Acer pseudoplatanum* (sycamore), and *Fraxinus* in Cumbria (UK). After ten years, six of the ten transplants were still in place and the lobes had extended by up to 25 mm. This was considered to be unexpected, as *L. amplissima* is a rare lichen thought to have demanding habitat requirements.

Edge effect. The cyanolichen *Lobaria oregana* and was reciprocally transplanted between the interior and edge of a Douglas fir forest. Thalli that were transported from the edge to interior grew well. Thalli that were transplanted from the interior to edge decreased in mass but continued to survive (Sillett, 1994). The results suggested a higher desiccation tolerance of lichens at the clear-cut edges.

Renhorn *et al.* (1997) removed the foliose lichens *Lobaria pulmonaria* and *Platismatia glauca* from a *Picea abies* forest interior, and transplanted them into lower canopies at various distances from the forest edge. As there was no significant growth reduction in relation to distance from edge in either of the species, the authors considered that the east-facing edge to interior gradient in microclimate was too small to significantly influence lichen growth. It was hypothesised that the edge effect is more apparent in warmer

climates with more intense solar radiation than in boreal climates.

Influence of forest microclimate. Several field experiments have been conducted to investigate the effect of changed forest microclimate on the growth of lichens restricted to old-growth forests. Hazell and Gustafsson (1999) transplanted the bryophyte *Anthriscia curtispindula* and lichen *Lobaria amplissima* on *Populus tremula* trees in central Sweden, between three environments: trees in a forest interior, isolated trees in a clear-cut, and clustered trees in a clear-cut. Although it is considered that both of the transplanted species demand shaded environments and are sensitive to forest operations, both species successfully acclimated in all of the environments. The bryophyte grew better in the forest than in the clear-cut; the lichen grew better on the clustered trees in the clear-cut. In the above experiment, samples were transplanted both to the north and south sides of tree stems. The vitality for lichen was higher on south side of trees in the forest interior, and for both species, on the north side in the clear-felled sites. The observations showed that the mature forest environment was not optimal for *L. amplissima* and that factors other than microclimate limit the distribution of this species.

In experiments on *Antitrichia curtispindula* (Rosso *et al.*, 2001), the transplants grew well in a young stand and in old-growth *Pseudotsuga menziesii* dominated forests in western Oregon (USA). It was found that the association of *Antitrichia* with old growth is not due to limited ability to grow in young stands, but rather by dispersal or establishment.

Sillett and McCune (1998) transplanted the old-growth associated lichen *Lobaria oregana* and bryophyte *Pseudocyphellaria rainarensis* into the crowns of Douglas fir trees of four age classes: old-growth (400–700 years), mature (140–150 years), young (35–40 years), and a recent clear-cut, in Oregon (USA). After one year, both species grew at least as well in younger forests as they did in old-growth forests. The growth rates were significantly lower in clear-cuts; mortality rates were low in all forest age classes. The results indicated that a broad range of forest age classes can provide suitable habitats for epiphytic cyanolichens.

Sillett *et al.* (2000a) transplanted thalli of the lichens *Lobaria oregana* and *L. pulmonaria* (old growth species) into forests of different ages and in a clear-cut. After one year, *L. oregana* grew better in old forests and did not grow in clear-cuts; but the survival and growth of *L. pulmonaria* did not differ significantly between forest age classes. Thus, it was suggested that the specific substrates and microenvironments found only in old growth forests are not essential for *Lobaria* establishment, and that the development of *L. oregana* is limited by poor dispersal and establishment.

Gauslaa *et al.* (2001) transplanted the lichens *Lobaria pulmonaria* and *Parmelia sulcata* in an open site at six defined aspects (north, south, west, and east, perpendicular to

the sun and shade) and assessed damage from high-irradiance. All transplants survived. *P. sulcata* was less sensitive to increased irradiation than *L. pulmonaria*. Relatively low damage in lichens was observed even on the south sides of stems, which was attributed to the unusual wet conditions during the experiments.

Compared to indirect methods where data on community composition and environmental factors are estimated in survey plots, and later the relationships are examined, field transplant experiments are more time-consuming, there can be failures (transplants can fail to grow), and only a few species can be examined simultaneously. Indirect survey methods can identify the most probable relationships, and the direct transplant methods can be used for direct tests of presumed relationships. The use of transplants is recommended, as the results of these experiments have frequently shown false assumptions suggested from survey studies.

Establishment and dispersal. The experimental sowing of vegetative lichen propagules is both a method for the study of lichen ecology and a tool for the conservation of threatened epiphyte species that have poor natural dispersal ability. Scheidegger (1995) sowed vegetative diaspores of lichen *Lobaria pulmonaria* on previously uncolonised trees in Switzerland. The development of lichens was monitored by scanning electron micrographs of lichen propagules. During the first two months, 80% of the diaspores were lost. After two months, the remaining diaspores began to develop anchoring hyphae, fixing them to the substratum, and after four months the additional loss of propagules was only minor. The high loss during the first period was due to the smooth surface of the diaspores of *L. pulmonaria*, which lacks viscous material as is present in some other species. It was concluded that the early fixation of diaspores was a very crucial period for propagation for this species.

Zoller *et al.* (2000) sowed vegetative diaspores of threatened epiphytic lichens *Menegazzia terebrata*, *Sticta fuliginosa*, and *Leptogium saturnum* on cotton gauze discs fixed onto the bark of *Acer pseudoplatanus* (sycamore maple) trees in Switzerland. After one month, the diaspores of all species had developed anchoring hyphae, fixing them to the substratum. The first lobes resembling adult thalli were observed after 8 to 12 months in *S. fuliginosa* and *L. saturnum*, but only after 16 months in *M. terebrata*. The low frequency of occurrence of the former two species was explained by a low ability of lichen thalli to compete in growth with bryophytes. In comparison, *M. terebrata* grows on smooth bark with no or few bryophytes. Therefore, it can survive with a lower growth rate and has no need to raise lobes above the substratum as for the former species.

Hilmo and S st ad (2001) sowed vegetative diaspores of the lichens *Lobaria scrobiculata*, *Platismatia glauca*, and *Platismatia norvegica* on *Picea abies* twigs and then transplanted these twigs in young and old *Picea* forests (in central Norway). The lichens developed in both habitats and were even found on twigs placed in extreme light exposure. However, the growth was better in old natural forest com-

pared to young forest. The results indicated that the environmental conditions in young forests were not necessarily unfavourable for diaspores of old-forest species such as *L. scrobiculata* and *P. norvegica*, and that diaspore production and dispersal ability probably determine the distributional patterns of these species.

Sillett *et al.* (2000a) tested the hypothesis that rough bark with cracks is better than smooth bark for trapping lichen propagules prior to germination. Propagules of the lichen *Lobaria oregana* were sown on *Pseudotsuga menziesii* branch fragments both with smooth bark and with rough bark. These branches were transplanted into forests of different ages—in clear-cuts, young stands, and old-growth forests. After one year, the establishment of sown *Lobaria oregana* propagules on young, smooth-barked branches, as compared with old, rough-barked branches, depended on the location. In clear-cuts and in young forests, the establishment was better on smooth bark than on rough bark, on lower surfaces of the branches in the dripline. In old forests, rough bark was a more suitable substrate. On rough bark, the propagules were trapped in fissures on the upper surface of the branch. In the open stands, therefore, they remained fully exposed to direct sunlight where they quickly died.

The same twigs of the above study were assessed again after three years (Sillett *et al.*, 2000b). By that time, a total of six genera, including six moss species and four cyanolichens, had colonised the twigs. For most of the lichen genera, colonisation was generally most rapid in the exposed environment of clear-cuts. Alectorioid lichens rapidly colonised both clear-cut and old-growth forest, but were infrequent in young stands. Similar colonisation patterns were seen for *Cladonia* and *Sphaerophorus globosus*. In contrast to the lichens, bryophyte colonisation was most rapid in the old forest. *Cladonia* colonised rough bark much more than smooth bark. This indicates the danger of extrapolating the experimental results of one species (*L. oregana*) to other epiphytes. Overall, however, epiphytes colonised smooth bark just as quickly as rough bark, implying that few genera require deep bark fissures for successful establishment.

In cases when it is not known whether dispersal or environmental conditions limit successful establishment, sowing experiments can be used. Further, by sowing in a broad range of environmental conditions, inferences can be made regarding the specific environmental factors limiting establishment.

IMPLICATIONS FOR FOREST MANAGEMENT

The results of investigations of epiphyte ecology have been used to recommend the best means of forest management to support epiphyte diversity. The importance of leaving individual living trees in clear-cuts has become a common practice in many countries, including Latvia. However, further recommendations are required regarding the choice of trees to protect, to obtain the best effect for biological diversity.

The retention of groups of trees has been suggested to be more beneficial to forest epiphytes than retention of single isolated trees (Sillett and McCune, 1998; Hazell and Gustafsson, 1999; Sillett and Goslin, 1999). Retaining groups of live trees rather than scattered, isolated trees may improve the chances for cyanolichen persistence in the remaining tree crown because of a more favourable canopy microclimate within the tree patches (Sillett and Goslin, 1999). Retaining large, live trees for the duration of stand rotation would permit inoculation of the regenerating forest canopy by populations persisting on remnant trees (Sillett and McCune, 1998; Hilmo and S astad, 2001). Moreover, leaving groups of trees is more convenient than leaving single trees because machine harvesting is facilitated (Hazell and Gustafsson, 1999).

Several studies summarise more detailed recommendations on retaining tree groups after logging. In the managed forest landscape, a continuum of patches with old deciduous trees should be maintained (Kuusinen, 1996a). The location of the remnant clump of trees within a cutting unit is also important. Dettki and Essen (2000) suggest that the tree patches should be left on the upwind side of a clear-cut to increase the potential dispersal area for alectorioid lichen (*Alectoria sarmentosa*) propagules. Rolstad *et al.* (2001) recommended protection of the riparian zone with buffers because the epiphytic cyanolichen biomass was highest near streams and other humid sites.

The effect of the size of retained tree groups is less studied. A larger size of a remnant group of trees is also considered to be better, since edge effects reduce the effective reserve area (Essen and Renhorn, 1998). However, Sillett and Goslin (1999) and Sillett *et al.* (2000a) recommend that, for some species, retention of single trees can be more beneficial than retention of tree groups, as particular substrates and microenvironments found only in old-growth did not appear to be essential for establishment of the cyanolichen *Lobaria oregana*. Dispersal, not microclimate, was the major factor found to be limiting development of *L. oregana* in *Pseudotsuga menziesii* forests. Therefore, scattered, isolated trees conserved in a clear-cut may lead to more effective dispersal of this species over a broader area.

It has been recommended to maintain several deciduous tree stems in commercial coniferous forests (Rolstad *et al.*, 2001). *Populus tremula* is a particularly important species which must be conserved, both in old-growth stands and young stands (Ojala *et al.*, 2000; Heden as and Ericson, 2000). Sillett and McCune (1998) recommend maintaining of hardwood trees in the understorey, as this will speed the recovery of epiphytic cyanolichens.

In the Norwegian coastal *Picea abies* forests, a habitat for many threatened epiphyte species, some of the lichen species were so rare and patchily distributed within the studied forest stands that selective logging which removes 30–50% of the trees could exterminate the species locally just by chance (Rolstad *et al.*, 2001). Therefore, the lichen flora in old forests should be thoroughly surveyed prior to cutting,

lichen-rich trees should be left undisturbed, and at least 30% of trees in each 0.1 ha should be conserved.

Sillett and McCune (1998) recommended to reduce the size of clear-cuts, which would facilitate cyanolichen dispersal from the edges of old forests. In managed *Fagus sylvatica* (European beech) forests, monocultures over large areas were too dark for many epiphytic species (Aude and Poulsen, 2000). In that case, regular forest cutting was essential for the epiphytic community in these forests.

Extending rotation ages would significantly improve the chances for successful cyanolichen colonisation in managed forests (Sillett and McCune, 1998). Kuusinen and Siitonen (1998) consider that the rotation period in part of the managed stands of Finland should be extended to 120 years. Rolstad and Rolstad (1999) recommend lengthening of rotation ages of *Picea abies* forests in Norway from 60–100 to over 100 years, and Price and Hochachka (2001) suggest a forest rotation period in nature reserves of the Coastal Western Hemlock zone (USA) of 200 years.

When natural dispersal is unsuccessful for a species, transplanting of propagating lichens to previously uncolonised trees may be a solution, as it is a promising means for the *in situ* conservation and augmentation of small populations of threatened and endangered lichen species (Scheidegger, 1995; Zoller *et al.*, 2000).

Neitlich and McCune (1997) note that old-growth forests are not the only reservoirs of lichen diversity, as they are more clearly distinguished from young forests by their alectorioid lichens than by cyanolichens, and several rare species can be conserved by the creation of overgrowing hardwood patches within managed conifer forests.

IMPLICATIONS FOR FURTHER INVESTIGATIONS

Several authors have commented on the general lack of knowledge on the ecology of epiphytic lichens and bryophytes, both at landscape scale and at the scale of forest stands and single trees. Gu *et al.* (2001) notes the necessity for further studies on temporal processes, especially regarding colonisation. Experiments are needed to clarify the relative importance of local versus regional dispersal of different types of lichen propagules (Dettki and Essen, 2000). More study is also needed on the interactions between epiphyte species (Ojala *et al.*, 2000).

Price and Hochachka (2001) recommend future studies in which epiphytic lichens are sampled in large patches of mature forest with varying levels of structural elements (e. g., large trees, snags, and deciduous patches), to determine the relative effects of stand age, stand structure, and the surrounding landscape. Lyons *et al.* (2000) suggest further study regarding direct comparisons of epiphyte abundance on trees of known ages in young versus old stands; coupled measurements of canopy microclimate and epiphyte abundance; and experiments that include placing transplants in different positions within a single forest and measuring their

growth and mortality. The above types of studies are required to provide information on the interactions between stand and tree age, canopy position, and microclimate and their effects on epiphyte abundance and distribution. To determine whether the population density of a threatened species is already too low to persist in an area, such as *Neckera pennata* in Finland (Kuusinen and Penttinen, 1999), more detailed knowledge of the temporal and spatial dynamics of the species is required. Also edge effects should be studied at all levels in the trees, including canopies, as well under varying microclimatic conditions, in humid and continental areas.

While the positive effect of remnant trees left after logging operations is known, further knowledge on the consequences for the flora and fauna is required, including long-term effects caused by dense regeneration, and by cleaning and thinning operations (Hazell and Gustafsson, 1999). Specific recommendations are desirable on the spatial pattern and density of remnant trees, to increase their potential as a source of lichen propagules (Sillett *et al.*, 2000a). Since the epiphytes of remnant trees are subject to high-irradiance stress, more information is required regarding acclimation (Gauslaa *et al.*, 2001). For example, will *Lobaria pulmonaria* be able to survive in the remaining patches until the host trees die (Gu *et al.*, 2001)?

Old *Populus* stands should be conserved, but it is not known how these old and young *Populus* stands should be patterned in the landscape to improve conservation of lichen diversity (Hedenäs and Ericson, 2000). Additional studies should be undertaken also to evaluate the consequences of the isolation of *Populus* stands and of microclimatic changes in managed forests on colonisation, survival and growth of lichens and bryophytes (Boudreault *et al.*, 2000).

Rolstad (2001) recommend retrospective dendroecological studies as an important scientific tool to clarify the development of late-successional species that has been affected by human activity, which can aid in assessment of future management options.

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EPIFĪTISKĀS SŪNAS UN ĶĒRPJI BOREĀLAJOS UN ZIEMEĻU MĒRENĀS JOSLAS MEŽOS

Epifītiskās sūnas un ķērpji bieži ir lietoti kā mežu bioloģiskās daudzveidības un kontinuitātes indikatori. Epifītu sugu skaits un segums ir atkarīgs gan no mežaudzes vecuma, gan no atsevišķu koku vecuma un lieluma un augšanas ātruma, kā arī no koka mizas ķīmiskajām un fizikālajām īpašībām. Epifītu sugu sastāvs mainās arī atkarībā no novietojuma koka vainagā – mainoties gaismas intensitātei, relatīvajam mitrumam un koka mizas īpašībām. Īpaši nozīmīgi koki bioloģiskās daudzveidības uzturēšanai ir apses, kurām raksturīga unikāla epifītu flora. Epifītu attīstību limitējošos faktoros var pētīt ar pārstādīšanas un sēšanas eksperimentiem, piemēram, pārstādot tos no tipiskās dzīvotnes vecā dabiskā mežā uz jauniem mežiem, mežu robežjoslām un kailcirtēm. Šie eksperimenti liecina, ka dažāda vecuma meži var būt piemēroti vecajos mežos sastopamo sugu augšanai. Nereti epifītu izplatību nosaka nevis mikroklimats, bet gan diasporu veidošanās, diasporu agra piesaiste substrātam, kā arī vāja izplatīšanās spēja. Lai mežu apsaimniekošanā saglabātos retās epifītu sugas, ieteicams pēc mežu ciršanas atstāt cirmās atsevišķus kokus un koku grupas, saglabāt lapu kokus, veikt izlases cirtes un palielināt cirtmetu. Ieteicams arī pārstādīt apdraudēto epifītu sugu īpatņus. Turpmāk ieteicams pētīt epifītu sugu ekoloģiju un dinamiku Latvijā, gan vietējā, gan ainavas mērogā, lai sekmētu tādu mežu apsaimniekošanu, kas saglabātu bioloģisko daudzveidību.