Restoration of endangered epiphytic lichens in fragmented forest landscapes: the importance of habitat quality and transplantation techniques

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The cover photo shows Ramalina dilacerata (Späd brosklav) at the clear-cut border site at Svartberget, eight years after transplantation.

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Abstract

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In a situation with increasingly rapid changes in landscape mosaics, driven by large-scale forestry and future climate change, a number of epiphytic lichens are now becoming threatened. Many of these species are limited either by dispersal or the subsequent processes of immobilisation on the substrate and germination. Overcoming the bottleneck of dispersal and/or reproduction may therefore constitute a key factor in species conservation. The main aim of this thesis is to evaluate different strategies to optimise efficiency in restoration of populations of endangered epiphytic lichens in fragmented forest landscapes, with a special emphasis on the importance of habitat quality and transplantation techniques. The thesis includes the development of a modeling tool for habitat evaluation in relation to photosynthetic performance of individual species (III); exploration of underlying causes for habitat restrictions in hydrophilic lichens (IV); and identification of habitat and substrate characteristics that 1) are associated with high vitality in natural populations of hydrophilic lichens (II), 2) are beneficial for establishment during active transplantation of thallus fragments (I) or isidia (V), and 3) are beneficial for photosynthetic activity in adult thalli (III, IV).

The occurrence of pronounced photosynthetic activation time lags among hydrophilic species, with full activity for some species being reached first 24 h after hydration, is reported for the first time in the present study and may be one of the physiological causes explaining habitat restrictions in rare hydrophilic lichens (IV). Using a dynamic water and activity model, we assessed the capacities of four hydrophilic (*Bryoria bicolor*, *Lobaria amplissima*, *Platismatia norvegica* and *Usnea longissima*) and a generalist species (*Platismatia glauca*) to rehydrate and activate photosynthesis by liquid water and humid air available in natural habitats (III). Simulations show that for three of the four studied hydrophilic species, species-specific PSII activation time lags can, in combination with microclimatic differences, control photosynthetic performance in a most dramatic manner (III, IV). The distribution patterns of hydrophilic lichens coincide very well with habitat features that generate high realised activity among the slowly activated species studied here (II, III, IV). Both close proximity to streams and the presence of turbulent water had a consistent strong positive impact on realised activity among the studied species (IV). The occurrence of activation time lags may explain both the higher abundances in oceanic core habitats, and the affinity for stream habitats and turbulent water displayed by marginal populations of suboceanic lichens such as *P. norvegica* (II).

Further, we have shown that transplantations of fragments (using *Evernia divaricata* and *Ramalina dilacerata*) or isidia (using *P. norvegica*) can constitute a valuable tool for restoration of endangered lichen populations, and that both habitat characteristics (I) and the mode of transplantation (I, V) is of vital importance to fragment vitality. In Paper V, where isidia of *P. norvegica* were transplanted into six sites in the regions of Jämtland and Trøndelag in Central Scandinavia, we have shown that preparation of transplant surfaces with an adhesive Ac-Di-Sol® solution may constitute a highly efficient tool for enhancing the outcome of restorative transplantations targeting epiphytic lichens (V). However, in order to enhance the possibilities for long-term viability and persistence of the population, it is essential that restoration efforts are concentrated to habitats and substrates that can be viewed as optimal for the species in question (I-V). The model developed in Paper III and used in Paper IV may provide a tool for identifying such suitable habitats. Further, this thesis highlights the importance of fringe populations for conservation of endangered suboceanic lichens in Scandinavia (II), and also underscores the importance of separating the processes of dispersal, immobilisation and establishment, when studying lichen distributional patterns (I, II, V).

Keywords: Conservation management, hydrophilic epiphytic lichens, habitat restrictions, photosynthetic activation time lags, water relations, modelling, restoration, transplantation, macroclimate, stream evaporation, substrate, isidia, Ac-Di-Sol®, *Bryoria bicolor*, *Evernia divaricata, Lobaria amplissima*, *Platismatia glauca*, *Platismatia norvegica, Ramalina dilacerata*, *Usnea longissima*.

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I en situation med allt snabbare förändringar i skogslandskapets sammansättning, orsakade av ett storskaligt skogsbruk och framtida klimatförändringar, så hotas nu ett antal epifytiska lavar. Många av dessa arter begränsas antingen av dålig spridningsförmåga eller de efterföljande processerna av vidhäftning på substratets yta och etablering. Att övervinna den flaskhals som utgörs av spridning och/eller reproduktion kan utgöra en nyckelfaktor i bevarandet av dessa arter. Denna avhandling syftar därför till att utvärdera olika strategier att effektivisera restaureringen av hotade lavpopulationer i fragmenterade skogslandskap, med ett speciellt fokus på betydelsen av habitatkvalitet och transplantationstekniker. Avhandlingen omfattar utvecklingen av ett modellverktyg för utvärdering av habitat i relation till den fotosyntetiska prestandan hos enskilda arter (III); utforskar bakomliggande orsaker till habitatkrav hos fuktighetskrävande lavar (IV); samt identifierar habitat- och substrategenskaper som 1) är associerade med hög vitalitet i naturliga populationer av fuktighetskrävande lavar (II), 2) är gynnsamma för etablering vid aktiv transplantation av lavfragment (I) eller isidier (V), och 3) är gynnsamma för fotosyntetisk aktivitet hos adulta lavar (III, IV).

Förekomsten av kraftiga fotosyntetiska aktiveringslaggar hos fuktighetskrävande lavar, där full aktivitet hos vissa arter nås först 24 timmar efter att laven återfuktats, rapporteras för första gången i denna avhandling och kan utgöra en av de fysiologiska orsakerna bakom de habitatkrav som finns hos sällsynta fuktighetskrävande lavar (IV). Med hjälp av en dynamisk modell för vatteninnehåll och aktivitet, så uppskattade vi kapaciteten hos fyra fuktighetskrävande lavar (*Bryoria bicolor*, *Lobaria amplissima*, *Platismatia norvegica* and *Usnea longissima*) och en generalist (*Platismatia glauca*) att återfuktas och aktivera sin fotosyntes med flytande vatten och fuktig luft i naturliga habitat (III). Simuleringar visar att för tre av de fyra studerade fuktighetskrävande arterna, så kan artspecifika aktiveringslaggar i PSII, i kombination med mikroklimatiska skillnader, kontrollera den fotosyntetiska prestandan på ett ytterst dramatiskt sätt (III, IV). Utbredningsmönstren hos fuktighetskrävande lavar stämmer väl överens med habitategenskaper som genererar hög realiserad aktivitet hos de långsamt aktiverade arter som studerats (II, III, IV). Både närhet till vattendrag och förekomsten av forsande vatten hade genomgående en starkt positiv inverkan på realiserad aktivitet hos de studerade arterna (IV). Förekomsten av aktiveringslaggar kan förklara både den högre abundansen i de oceaniska kärnområdena och den koncentration nära vattendrag och forsande vatten som observeras hos randpopulationer av suboceaniska lavar som *P. norvegica* (II).

Vi har även visat att transplantation av fragment (studerat på *Evernia divaricata* and *Ramalina dilacerata*) eller isidier (studerat på *P. norvegica*) kan utgöra ett värdefullt verktyg för att restaurera hotade epifytiska lavar, och att både habitategenskaper (I) och transplantationstekniker (I, V) är av avgörande betydelse för fragmentens vitalitet. I Paper V, där isidier av *P. norvegica* transplanterades i sex habitat i Jämtland och Trøndelag, har vi visat att behandling av transplantationsytorna med en vidhäftande vattenlösning av Ac-Di-Sol® kan utgöra ett höggradigt effektivt verktyg för att förbättra utfallet vid restaurering av epifytiska lavar (V). Men, för att öka möjligheterna att skapa långsiktigt livskraftiga populationer, så är det av avgörande betydelse att restaureringsinsatser koncentreras till habitat och substrat som kan anses optimala för arten i fråga (I-V). Den modell som utvecklades i Paper III och används i Paper IV kan utgöra ett verktyg för att identifiera sådana gynnsamma habitat. Denna avhandling visar även på randpopulationernas betydelse för bevarandet av hotade suboceaniska lavar i Skandinavien (II), och understryker vikten av att särskilja spridning, vidhäftning och etablering vid studier av utbredningsmönster hos lavar (I, II, V).

Keywords: Conservation management, hydrophilic epiphytic lichens, habitat restrictions, photosynthetic activation time lags, water relations, modelling, restoration, transplantation, macroclimate, stream evaporation, substrate, isidia, Ac-Di-Sol®, *Bryoria bicolor*, *Evernia divaricata, Lobaria amplissima*, *Platismatia glauca*, *Platismatia norvegica, Ramalina dilacerata*, *Usnea longissima*.

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II. Lidén, M., Hilmo, O. 2005. Population characteristics of the suboceanic lichen *Platismatia norvegica* in core and fringe habitats: relations to macroclimate, substrate, and proximity to streams. The Bryologist 108(4), 506-517.

III. Jonsson Čabrajić, A., Lidén, M., Ottosson-Löfvenius, M., Lundmark, T., Palmqvist, K. 2009. Modelling hydration and PSII activation in relation to *in situ* rain and humidity patterns - a tool to compare performance of rare and generalist epiphytic lichens. Submitted.

IV. Lidén, M., Jonsson Čabrajić, A., Ottosson-Löfvenius, M., Palmqvist, K., Lundmark, T. 2009. Species-specific activation time lags can explain habitat restrictions in hydrophilic lichens. Submitted.

V. Lidén, M., Hilmo, O., Bergsten, U., Lundmark, T. 2009. Effects of substrate manipulation and microsite quality on immobilisation and establishment of isidia in restorative transplantations of *Platismatia norvegica*.

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The papers are referred to in the text by their roman numerals.

Introduction

In the boreal and hemiboreal forest landscapes of Fennoscandia, forestry has historically been of fundamental importance for economic development. During the 20th century, large-scale forestry has resulted in profound alterations of the forest landscape. These alterations, characterised by increasing fragmentation, loss of old-growth habitats and loss of natural disturbance regimes, are considered to constitute the major threats to biodiversity in the boreal forest (e.g. Järvinen and Väisänen 1978, Angelstam 1992, Hunter 1996, Esseen et al. 1997, Gauslaa and Ohlson 1997, Fries et al. 1998). Today, old growth forests are scarce and heavily fragmented, and the boreal forest landscape is dominated by managed even-aged coniferous forests with low structural diversity (Esseen et al. 1997, Gauslaa and Ohlson 1997). Since the rotation period of managed forests typically does not exceed 80-120 years, species adapted to late successional stages are confined to small patches of suitable habitat (Nilsson and Ericson 1997, Nitare 2000). Populations may thus become geographically and reproductively isolated from each other, which increases the risk of random extinctions (Harris 1984, Svensson 1996). Since longer distances between remaining habitat patches will impede dispersal, species that are lost from a remnant patch might not be able to recolonise from other areas (MacArthur and Wilson 1967, Harris 1984).

While previously being a concern mostly for ecologists and environmental non-governmental organisations (NGOs), these threats were during the 1990s also brought to the political agenda, both on the national and international level. One outcome of the UN Conference on Environment and Development in Rio de Janeiro in 1992 was the Convention on Biological Diversity, which to this date has been signed by Sweden and over 170 other countries (Anon. 1992a, Larsson 2001). Also, the Swedish Forestry Act was reformed in 1993 (government bill 1993:553). One of the novelties was the general principle of the first paragraph, which states that goals for production and conservation/environmental considerations should be considered as equal. In 1995, the National Board of Forestry produced an "Action Plan for Biodiversity and Sustainable Forestry", in which measures were proposed for the development of silvicultural practises that comprise both preservation of biological diversity and sustainable use of the forests resources (Wallin et al. 1995). The implementation of this action plan has resulted in a rapid development of modified silvicultural practises, a process which has been characterised by an emphasis on voluntary efforts and cooperation among forest companies and forest owner's associations, environmental NGOs, the Environmental Protection Agency, county boards, national and regional forestry boards, and researchers (Lämås and Fries 1995, Anon. 1997, de Jong et al. 1999, Anon. 2002a,b).

The Swedish Environmental Code states that "native species should survive under natural conditions and in viable populations" (e.g. government bill 2000/01:130). Of the forest dwelling species that currently are found on the Swedish red list, at least 1464 are considered by the Swedish Species Information Centre to be threatened mainly by modern forestry practises and removal of dead wood (500 species from invertebrate taxa yet have to be classified). This group includes 277 species that are listed as endangered (EN) or critically endangered

(CR) (Ulf Bjelke, pers. com.). In order to conserve these species, it is likely that a broad range of conservation management approaches will be needed (Reid et al. 1992, Primack 1993, Daily and Erlich 1995, Young 2000).

General theories in conservation biology

Although many species have remained unchanged for millions of years, all species can through mutation, genetic drift, or natural selection undergo evolutionary change. However, each species has its own evolutionary constraints, allowing evolution to occur only in certain directions (Carroll 1997). Although exposed to identical pressure from genetic drift and natural selection, different populations may evolve different “genetic solutions”, due to their unique evolutionary constraints (Cohan 1984, Carroll 1997). With the loss of genetic diversity, such constraints might be added, permanently reducing the evolutionary “emergency exits” available within the genome of a species (Frankel and Soulé 1981, Allendorf and Leary 1986, Carroll 1997). Fenster and Dudash (1994) argue that the preservation of the evolutionary potential of a species must be the goal of any conservation or restoration policy. Preserving this potential can be achieved either by maintaining genetic variation among individuals within threatened populations, or by maintaining populations that are genetically different from each other (Hufford and Mazer 2004). Thus, knowledge of genetic distinctiveness of endangered populations can aid the process of making priorities and directing restoration efforts (Brown 1994, Hufford and Mazer 2004). In absence of such knowledge, Fenster and Dudash (1994) suggest that “the preservation of ecotypes or populations representing the extremes of the range of a species should be paramount”.

For any population, survival and vitality will be influenced by a number of factors, biotic and abiotic, present at its site of occurrence. However, an ad hoc hypothesis could be that e.g. climatic conditions generally are more favourable within the core of a species’ distribution range, which would speak in favour of concentrating conservation measures to this core. Since peripheral populations often are smaller or more isolated, factors like inbreeding, genetic drift, or stochastic events can also cause these populations to be more vulnerable (Menges 1990, Murphy et al. 1990, Bowles and Whelan 1994, Caughley 1994, Young 2000). On the other hand, relatively isolated fringe populations may be better protected from diseases or parasitism. From an evolutionary perspective, relative isolation among populations also allows for local genetic modification (Shaffer 1981, Fenster and Dudash 1994). For this reason, many scientists argue that it is important to preserve local gene pools, since independent evolutionary lineages constitute the foundation for future evolution and speciation (e.g. Avise et al. 1987, Templeton 1989, Hufford and Mazer 2004).

In the general discussion of restoration ecology, it is often argued that conservation efforts must – for economical and other reasons – be concentrated where the chances of reaching the stipulated conservation goals are the best possible (e.g. Anon. 1992b). This position is also reflected in the increasingly more widespread use of the terms "responsibility species" and "responsibility environments". These terms are referring to species or ecosystems that to some extent are unique or typical for a certain region, and were originally introduced in the EU habitat directive (Anon. 1992b, Tønsberg et al. 1996). When focussing on lichen species, one responsibility environment undoubtedly is the boreal rain forest, which is characterised by a luxuriant and species-rich lichen assembly (Holien and Tønsberg 1996, Tønsberg et al. 1996, Holien 1997). In Europe, these forests have their main distribution in Central Norway (Holien and Tønsberg 1996), within the suboceanic (O2) and euoceanic (O3) vegetation zones, as defined by e.g. Moen (1987) and Moen and Odland (1993). The main characteristics for boreal rainforest environments are an annual precipitation exceeding 1200 mm, and that precipitation is relatively evenly distributed over the year, often with more than 200 rainy days (prec. ≥ 0.1 mm) per year (Holien and Tønsberg 1996). Among the suboceanic boreal lichens, referred to as part of "The Trøndelag element", many species have their main or total distribution in Europe restricted to the coastal parts of Central Norway (Jørgensen 1996, Tønsberg et al. 1996). During the last century, these environments have become increasingly rare, due to conversion to production forests and other forms of land use (Tønsberg et al. 1996, Rolstad et al. 2001). Although at the outer margin of the boreal rain forest, the mountainous forests in Sweden might thus be of importance for the conservation of threatened suboceanic lichens in Scandinavia.

Metapopulation theory and artificial dispersal

Species endangered by human activity often are so due to the severely fragmented landscape resulting from modern land use, in which their sites of occurrence are scattered like islands in a sea of unsuitable habitat (Harris 1984, Quammen 1996, Laurance and Bierregard 1997, Schwartz 1997, Radford and Bennett 2004, Suorsa et al. 2004). Metapopulation theory describes the dynamics of populations that are to some extent, but not completely, isolated from each other (den Boer 1981, Gilpin 1987, Goodman 1987, Gilpin and Hanski 1991). In such populations, local genetic change - beneficial or harmful - may occur, but is moderated by low-intensity gene flow (i.e. dispersal of individuals, larvae or seeds) among the populations (Hanski 1999). On a regional level, the species survives in a balance between loss of local populations and establishments of new populations in suitable habitats. Rare occasions of long-distance dispersal among isolated sites both counteract losses of different sub-populations, and provide opportunities for recolonisation in cases of local extinction (Pulliam 1988). Thus, as long as some degree of connectivity remains, the risk of regional extinction at the metapopulation level might be rather low, while relatively high at each local site of occurrence of a species (Menges 1990, Murphy et al. 1990, Bowles and Whelan 1994).

Since the degree of connectivity among populations is dependent on the dispersal ability of the individual species, this factor is of outmost importance for a species' chances of survival in a fragmented landscape. Therefore, different methods to mitigate dispersal among remnant habitat patches stands out as a most valuable tool in order to counteract losses of species with poor dispersal abilities (Shaffer 1981, Gilpin and Soulé 1986, Murphy et al. 1990, Gilpin and Hanski 1991, Andrén 1997). When evaluating to what degree certain habitats might function as corridors for dispersal between populations, it is important to identify which qualitative aspects that are needed, in order for habitats to be functional for certain species (Simberloff et al. 1992, Bowles and Whelan 1994, Forman 1995, Bengtsson et al. 2003, Douglas Shields et al. 2003). The degree of connectivity is essential for whether naturally occurring processes will suffice to maintain viability, or whether there will be a need for human intervention to aid gene flow among endangered populations (Bowles and Whelan 1994). Such forms of human intervention include creation of substrates to which boreal forest species have adapted by evolution, such as e.g. burnt wood or snags, or creation of habitat corridors on wet forest sites (Jäghagen and Sandström 1996, Gustafsson and Hansson 1997).

Today, old-growth forests in Fennoscandia are typically much more distantly separated than they were in the naturally dynamic landscape in which they evolved (Pennanen and Kuuluvainen 2002). As a consequence, isolated populations of severely threatened species may not survive in a long-term perspective, unless new methods are developed to facilitate their colonisation of other suitable habitats. One option for these species is to use *artificial dispersal* as a conservation management tool to ensure sufficient gene flow among isolated populations (Griffith et al. 1989, Bowles and Whelan 1994, Pavlovic 1994). Artificial dispersal of organisms can involve e.g. seeds, lichen thalli fragments, or wild or captive animals (Griffith et al. 1989, Scheidegger et al. 1995), and can also be used to establish new populations in suitable habitats that are inaccessible to the species by natural dispersal (Pavlovic 1994). In recent years, a number of transplant experiments have been performed on epiphytic lichens in order to study e.g. the importance of dispersal limitation versus habitat quality on epiphyte distribution (Hilmo 2002, Keon and Muir 2002), or the influence of different environmental factors on e.g. metabolic activity or growth responses (Boucher and Nash 1990, Sillett 1994, Renhorn and Esseen 1995, Muir et al. 1997, Renhorn et al. 1997, Hazell and Gustafsson 1999, Palmqvist and Sundberg 2000). However, few studies of lichen transplantation have been carried out with the explicit purpose of evaluating artificial dispersal as a tool for restoration of endangered populations (but see Scheidegger et al. 1995, Gilbert 1991, 2002).

Artificial dispersal from an evolutionary and ethical perspective

In view of recent progress e.g. in the fields of population genetics and metapopulation theory, there is also increasing awareness that many threatened species will need targeted efforts in order to persist in viable populations (Young 2000). Brown (1994) observes that we may assess the naturalness of an ecosystem based on either its species assembly, or whether ecosystem processes are functional without human intervention. He points out that if we want ecosystems to maintain themselves, we might have to accept that these systems degrade in species richness, or change over time. In cases when the naturalness of species richness trades off with the systems naturalness of function, there are two ways to deal with conservation: either by deciding to use conservation management techniques, which means accepting human intervention, or by increasing the area devoted to conservation (Brown 1994, Römermann et al. 2004).

When translocating plants or animals into new regions, a common criticism is that by introducing alien genotypes, local gene pool characteristics - resulting from adaptations to the local environment - are being jeopardized (Templeton 1986, Bowles and Whelan 1994, Fenster and Dudash 1994, Hufford and Mazer 2004).

This argument can also be used against projects aiming at altering the degree of isolation among subdivided populations, a method often advocated in order to counteract random losses of local populations (Cf. Brown 1994). In other words, there is a conflict between the need to maximise genetic diversity, and the need to preserve coadapted gene complexes (Avise 1992, Ellstrand 1992, Bowles and Whelan 1994).

On the other hand, there are scientists who argue that hybridization, resulting from rare events of contact between populations or subspecies that have been isolated from each other for a long time, is likely to have been an important phenomenon in the evolutionary history of species (Anderson 1949, Ainouche et al. 2004, Hoot et al. 2004, McFadden and Hutchinson 2004, Schon and Martens 2004, Verkaar et al. 2004). These events of contact may occur through rare occasions of long-distance dispersal, or through slow-moving waves of range expansions and contractions during the history of a species (Fenster and Dudash 1994). Since the gene pools present today may be the result of a dynamic process of isolation and mixing, Fenster and Dudash (1994) conclude that "...[the] preservation of genetic integrity of a species may be an ideal with no natural basis...", and that it therefore should not be used, *a priori*, as an argument against allowing genetic contact among gene pools.

Conservation management and restoration in the boreal forest

During the 20th century, conservation efforts have mainly been focused on establishment of reserves (Hunter 1996, Jäghagen and Sandström 1996). However, many reserves are too small to contain a continuum of successional stages. Therefore, there is a risk that the continuity of suitable substrates in a long-term perspective will be broken for many species, causing loss of species from their current habitats (Esseen et al. 1997, Fries and Lämås 2000). In the last 15 years, development within the field of ecology has been characterised by an increasing focus on populations, patch dynamics, and fragmentation (Fielder et al. 1997, Young 2000). As a result of this process, landscape planning and restoration of habitats have become urgent topics in the discourse of species conservation (Reid et al. 1992, Primack 1993, Daily and Erlich 1995, Young 2000). In both North America and Europe, it has been suggested that silvicultural practises should mimic the natural dynamics of forest ecosystems, in order to achieve patterns and processes at the level of landscape, habitat, and individual structural elements which can allow for conservation and restoration of forest biodiversity (Remmert 1991, Peterken 1996, Angelstam 1998, Fries et al. 1998, Bergeron et al. 2002, Franklin et al. 2002, Kuuluvainen 2002).

Most likely due both to the economical importance of the forestry sector and the low proportion of remaining old-growth forests, a "Swedish Model" for conservation of forest biodiversity has developed, where a lot of emphasis is placed on preservation and recreation of natural forest components within the matrix subjected to forestry (Lämås and Fries 1995, Angelstam and Pettersson 1997, de Jong et al. 1999, Angelstam and Andersson 2001). In this process, one central issue has been the reconstruction of underrepresented key substrates (Berg et al. 1994, Jäghagen and Sandström 1996, Fries et al. 1997). Also, leaving habitat corridors along watercourses and groups of trees in regeneration units has been proposed to facilitate dispersal among isolated habitats (Gustafsson and Hansson 1997, Hazell and Gustafsson 1999). As a consequence of public debate and the implementation of the FSC and PEFC certification systems, silvicultural practises adopted in Swedish forestry today include a range of conservation management techniques, including creation of logs, snags, and high stumps, prescribed burnings, and retention of deciduous trees and "eternity trees" (Fries et al. 1997, Anon. 1997, Anon. 2002b).

Epiphytic lichens in boreal forests

Industrial forestry has resulted in a severe decline in the abundance of many species of epiphytic lichens (Lesica et al. 1991, Hyvärinen 1992, McCune 1993, Esseen et al. 1996, Dettki and Esseen 1998). In Sweden, 164 of the total of 1464 species that currently are redlisted as predominantly threatened by forestry or removal of dead wood are lichens are lichens. A total of 64 of these are classified as endangered (EN) or critically endangered (CR), and 23 of these 64 occur in boreal forests (Ulf Bjelke, pers. com.). According to Esseen et al. (1996), old-growth stands may have up to six times higher lichen (*Alectoria* and *Bryoria* spp.) mass per spruce branch, or two times higher per unit of branch mass, than mature managed stands. Also, old-growth forests usually have higher numbers of species compared to young even-aged forests (Lesica et al. 1991, Tibell 1992, Holien 1997, Kuusinen and Siitonen 1998). The confinement of many lichen species to old-growth forest environments has been attributed to microclimatic characteristics created by the structure of old forests (Lesica et al. 1991, Kuusinen 1996). However, transplantation experiments have shown that the abiotic environment in a young forest plantation is not necessarily unfavourable neither to diaspore establishment (Hilmo and Såstad 2001) nor growth (Sillett et al. 2000a, Hilmo 2002). Instead, it has been shown that thalli fragments transported by wind often disperse no more than 100 m, and sometimes only up to 10 m, making the colonisation of fruticose filamentous lichens in a fragmented landscape a very slow process (Tapper 1976, Esseen et al. 1981, Gauslaa and Ohlson 1997, Dettki 1998, Dettki et al. 2000). These findings show that certain epiphytic lichens might be more limited by dispersal ability than by demands on habitat quality. Several recent papers support the view that poor dispersal is an important limiting factor for many epiphytic lichens (e.g. Samuelsson et al. 1994, Nilsson and Ericson 1997, Sillett and McCune 1998, Sillett et al. 2000a, b, Keon and Muir 2002). Hilmo (2001) suggests three factors that could be important for the confinement of many species to old-forest environments: 1) limited dispersal ability, 2) high loss of diaspores and slow juvenile development, and 3) shortage of suitable substrates in young forests.

Taken together, these factors may have the effect that most old-forest species are unable to complete their reproductive cycle within the rotation time of modern even-aged forestry, possibly colonising only the fringes of previously clear-cut areas. Thus, many species may be dependent on old-growth environments mainly due to their dependence on substrate continuity (Ohlson et al. 1997). For many species that exist in isolated remnant populations, habitat corridors are unlikely to be functional to increase connectivity among the different sites of occurrence. In these cases, artificial dispersal could have a potential as a resource-efficient conservation management tool, in order to circumvent the effects of dispersal limitation for endangered epiphytic lichens.

Growth and reproduction in epiphytic lichens

Lichens are symbiotic organisms, composed of a fungal partner and one or more photosyntetic partners, which may be either a green alga (in chlorolichens) or a cyanobacterium (in cyanolichens) (Nash 1996). Lichen reproduction is either sexual or asexual. In boreal spruce forests, foliose and fruticose epiphytic lichens predominantly reproduce asexually by simultaneous dispersal of both bionts (Ahti 1977), either by vegetative diaspores such as soredia and isidia, or by thallus fragments (Nash 1996). Apart from dispersal, there are indications that the process of germination constitutes a critical phase in the vegetative reproduction of lichens. With establishment rates of 1.3-9% and 4.4-5.2%, respectively, Scheidegger et al. (1995) and Hilmo and Såstad (2001) have shown that immobility of the diaspores on the substrate appears to be a limiting factor in the reproduction process of several old-forest lichen species. During germination of sexual or vegetative propagules, and the juvenile stages of development, it is also likely that the lichen is particularly sensitive to unfavourable levels of irradiation and humidity (Ott 1987, Scheidegger et al. 1995, Hilmo and Holien 2002). Many authors have emphasised the importance of substrate quality for the distribution of epiphytic lichens. Some of the qualities that have been found to be of great importance are bark pH and mineral content (e.g. Bates 1992, Gustafsson and Eriksson 1995, Gauslaa et al. 1998, Wolseley and James 2000) and bark roughness, which is thought to 1) facilitate immobilisation of diaspores and fragments and 2) be correlated to the water-holding capacity of the substrate (Armstrong 1990, Scheidegger 1995, Holien 1996, Holien 1997).

Metabolic activity in lichens is restricted to the periods when the thallus is both hydrated and receiving sufficient irradiation (Nash 1996, Palmqvist and Sundberg 2000, Gaio-Oliveira et al. 2003). Since lichens are poikilohydric organisms, with no mechanisms for regulating uptake and loss of water, they are dependent on rainfall, dew or high atmospheric humidity to achieve a satisfactory level of thallus hydration (Kershaw 1985). Palmqvist and Sundberg (2000) have shown that lichen growth is strongly correlated to the light dose received by presumably active thalli, termed I-wet (mol m^{-2}). Although threshold levels vary, many species require a thallus water content of 70-150% of dry weight to maintain metabolic activity (Nash 1996). For cyanolichens, which require liquid water to activate their photosynthesis (Lange et al. 1986), high relative air humidity will slow down the process of desiccation after each rainfall (Gaio-Oliveira et al. 2003). Undoubtedly, this implies that growth of many lichens is likely to be hampered in a more continental environment (Boucher and Nash 1990, Halonen et al. 1991, Nash 1996, Muir et al. 1997, Palmqvist and Sundberg 2000). However, since chlorolichens can activate their photosynthesis after desiccation only with high levels of air humidity (Lange et al. 1986, Lange et al. 1988, Friedl and Büdel 1996), elevated levels of humidity due to e.g. stream evaporation have a large potential to influence I-wet.

Still, there is limited knowledge of how differences in macro- and microclimate affect vitality, growth, and reproductive ability in peripheral populations of suboceanic lichens. When working with conservation of endangered lichens, it is important to know in what respects a species' habitat and substrate requirements differ in marginal environments. If habitat, substrate, and climate characteristics associated with high vitality in peripheral populations were better known, this would greatly enhance the potential for performing efficient conservation or restoration measures in fringe habitats.

Objectives of the thesis

The main aim of this thesis is to evaluate different strategies to optimise efficiency in restoration of endangered epiphytic lichens in fragmented forest landscapes, with a special emphasis on the importance of habitat quality and transplantation techniques. The thesis discusses epiphytic lichen response, in transplanted (I, V) and naturally established (II) populations, to macroclimatic (II, V), microclimatic (I-V), and substrate-related (I, II, V) environmental constraints, aiming at identification of habitat and substrate characteristics that can enhance the outcome of site selection for restoration purposes (II-V). The thesis also addresses the issue of how priorities in conservation management could be made on a landscape scale, in order to obtain an optimal outcome of performed measures (II, V). Moreover, development of transplantation techniques in order to achieve optimal resource efficiency in the use of rare biological material is stressed (I, V). The more specific aims of the thesis have been:

1. To evaluate the possibilities for using transplantation as a resource-efficient method for novel establishment of rare species into new habitats and/or for enlarging existing populations, we studied how resource efficiency in terms of lichen material can be optimised using different modes of transplantation (I, V). For *Evernia divaricata* (L.) Ach. and *Ramalina dilacerata* (Hoffm.) Hoffm., the effects on fragment vitality of (i) transplantation on north- or south-facing branches on the trees, (ii) the presence of an artificial shield, and (iii) habitat quality were quantified. In addition, (iv) the effect of thalli fragment area on survival and vitality was studied on *R. dilacerata*. For *Platismatia norvegica* (Lynge) W. Culb. & C. Culb.), we tested if application of an adhesive agent, the hydrogel Ac-Di-Sol® (Pamuk 2004, Anon. 1998), on the transplant surfaces may improve diaspore *immobilisation* (as assessed by per cent diaspore cover) and *establishment* (as assessed by numbers of microthalli per transplant surface). Further, the effects of varying tree and twig properties on immobilisation and establishment were also tested.

2. To examine the underlying physiological reasons for habitat restrictions in rare hydrophilic epiphytic lichens, by determining the extent to which 1) activation time lags and 2) air temperature and humidity conditions in stream habitats affect realised photosynthetic activity (IV). To achieve this, species-specific patterns in photosystem II (PSII) activation after hydration, and inactivation during desiccation, were characterised by laboratory analysis of chlorophyll fluorescence for *Bryoria bicolor* (Ehrh.) Brodo & D.Hawksw, *Lobaria amplissima* (Scop.) Forssell, *P. norvegica*, *Usnea longissima* Ach., and the generalist epiphyte species *P. glauca* (L.) W. Culb. & C. Culb.

3. To simulate and quantify the effects of species-specific activation time lags and fluctuating water sources on hydration and subsequent realized activity for hydrophilic lichens (III). Using data obtained in Paper IV, we developed the models presented by Jonsson et al. (2008) by including species- and water source-dependent variations in photosynthetic (PSII) activation kinetics, and performed simulations for *B. bicolor*, *L. amplissima*, *P. norvegica*, *U. longissima*, and the generalist epiphyte species *P. glauca*, in three (Paper III) or twelve (Paper IV) contrasting microclimatic scenarios.

4. To identify habitat and substrate characteristics associated with high vitality in hydrophilic epiphytic lichens, in order to optimise the possibilities for successful restoration and selection of conservation areas for these species (II, IV). In paper II, populations of *P. norvegica* in oceanic (core distribution) and more continental (fringe) habitats were compared, quantifying and describing how (i) proximity to streams and (ii) substrate quality affect abundance, vitality, and morphological characteristics of the species, and (iii) investigating whether possible effects of proximity to streams and/or substrate quality differ between oceanic and more continental habitats. In paper IV, habitat simulations of hydration and activity were performed by integrating laboratory analyses together with field data on the microclimatic characteristics of stream habitats, using the model developed in Paper III. Further, analysis of variance (ANOVA) was applied on the simulation results to quantify and describe the effects of (i) species; (ii) distance to the watercourse; and (iii) stream characteristics on wet time and potential and realised photosynthetic activity in the studied epiphytic lichens.

Study areas

Paper I: The first study was performed in two different regions in northern Sweden. The northernmost study area is situated 30 kilometres north-west of Jokkmokk in the county of Norrbotten (Fig. 1), and has a growing season (mean temperature >5°C) of 133 days/year (Wastenson et al. 1995). Since the area was harbouring two of the richest sites of occurrence in Sweden for the two studied lichen species, these sites were chosen as both the sample sites for the collection of lichen material, and used as *"near-optimal"* transplantation sites for the respective species. Both sites consist of open, multi-layered old-growth forests dominated by Norvay spruce, where close proximity to rushing water (both species) and an adjacent inlet (*E. divaricata*) creates a humid microclimate. The southern study area is situated about 270 kilometres south of the sample sites adjacent to Vindeln in the county of Västerbotten, with a growing season of 145 days/year (Degermark 1980-2002). Here, both species were transplanted into the *"old-growth"* and *"clear-cut border"* sites, located at the experimental forests Kulbäcksliden and Svartberget, respectively (Fig. 1). Although both southern transplantation sites consist of old (>160 years) stands, the old-growth transplantation site has an open, multi-layered old-growth forest character, while the forest stand at the clear-cut transplantation site is dense, single-layered, and exposed to the ENE towards a clear-cut that had a regeneration height of 50 cm when the study was performed.

Paper II and V: The studies were performed in two different regions in central Scandinavia, characterised by an oceanic and a slightly more continental climate (Holien and Tønsberg 1996). The *"oceanic"* study region comprises the counties of Sør-Trøndelag and Nord-Trøndelag in central Norway, belongs to the middle-boreal vegetation zone (Ahti et al. 1968), and has more than 200 rainy days (prec. ≥ 0.1 mm) per year (Holien and Tønsberg 1996). At the chosen study sites, annual wet precipitation ranges from 513-956 mm/year (II). In the region, growing season is 140-160 days/year (Anon. 1984), and pH of precipitation ca. 5.2 (Tørseth 1996). The *"continental"* study region is situated on the Swedish side of the Scandic mountain range in the county of Jämtland, approximately 100-150 kilometres east of the oceanic survey sites (Fig. 1), and belongs to the northern boreal vegetation zone (Ahti et al. 1968). Growing season in the region is around 135 days/year (Wastensson et al. 1995), and pH of precipitation is 4.6-4.8 (Wastensson et al. 1992). Annual wet precipitation at the chosen study sites ranges from 387-489 mm/year (II). Since this region is one of the centres of distribution in Sweden for suboceanic species, and it corresponds latitudinally to the Trøndelag region, it was chosen as the survey region for the more continental *P. norvegica* habitats. For paper II, four survey sites were selected in the oceanic region and five in the continental region (Fig. 1), which had rich populations of *Platismatia norvegica*, indications of long forest continuity, and presence of a stream running through the habitat. At Nævra, Strukstadmyra, and the five continental sites, the tree canopy has a multi-layered and relatively open old-growth forest character, while Gresja and Dølelva are more single-layered and dense. Rushing water is present at Gulån, Storbekken, and Styggdalen, while the other sites have streams with calm water flow. For paper V, the Kjolån, Gulån, Storbekken, Nævra, and Dølelva sites were used, complemented with Gartland (RN 1335130, 7162304).

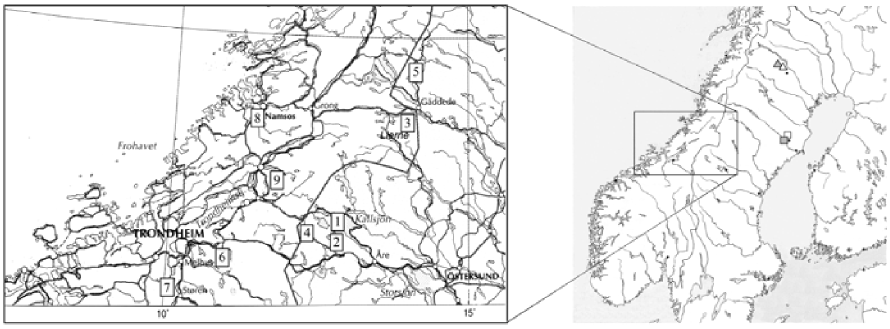

Figure 1. In Paper I, the sample sites and near-optimal transplantation sites were Nautijaureälven (for *R. dilacerata*, grey triangle) and Gräsviken (for *E. divaricata*, white triangle). The old-growth transplantation sites for both species were situated at Kulbäcksliden (grey square), and the clear-cut border transplantation sites for both species were situated at Svartberget (white square). In paper II, the study sites were: Kjolån (1), Gulån (2), Storbekken (3), Styggdalen (4), Vallåsa (5), Nævra (6), Gresja (7), Dølelva (8), and Strukstadmyra (9). Sites 1-5 constitute the continental region, while sites 6-9 constitute the oceanic region. I paper V, the Kjolån, Gulån, Storbekken, Nævra, Dølelva, and Gartland (not shown, RN 1335130, 7162304) sites were used for transplantation.

Paper III and IV: Field microclimatic monitoring of air temperature and humidity was performed in 2005 and involved three measurement campaigns, carried out at three stream sites in the county of Västerbotten in northern Sweden:

Kulbäcken, (1687684, 7123715, 11-22 July), Stenträskbäcken (1666480, 7150566, 27 July to 9 August) and Lögdeälven (1675543, 7058436, 14 to 24 September). The region has a fairly continental climate, with 450 to 600 mm annual precipitation (including snow) and a growing season (period with daily temperature > 5 °C) of 140-160 days/year (Wastensson *et al.* 1995). The stream sites were selected to have both calm and turbulent water within 200 m of each other, so that any steep topography would not consistently covary with turbulent water flow, and so that other abiotic and habitat-related factors would be as similar as possible. At both Lögdeälven and Kulbäcken, the chosen sites are dominated by Downy Birch (*Betula pubescens* Ehrh.) and Grey Alder (*Alnus incana* (L.) Moench) with limited Norway Spruce (*Picea abies* (L.) H. Karst), while the Stenträskbäcken stream site was dominated by Norway Spruce (≥ 95% of standing volume), with limited Downy Birch.

For more detailed descriptions of the study areas and study sites, please see Papers I - V.

Materials and methods

Study species

Figure 2. Evernia divaricata. Photo: Marlene Lidén.

Figure 3. Ramalina dilacerata. Photo: Svante Hultengren.

Figure 4. Platismatia norvegica. Photo: Marlene Lidén.

In the present thesis, there has been a recurrent focus on the hydrophilic epiphytic lichens of the boreal forests that display a suboceanic pattern of distribution, which in continental Scandinavia (i.e. Sweden) results in a predominantly western distribution (Ahlner 1948, Jørgensen 1996, Holien and Tønsberg 1996) and smaller populations compared to the oceanic distributional core (i.e. coastal Norway). These species are favoured by habitats with high air humidity e.g. adjacent to rushing waters or in swamp forests, but can in oceanic regions be found in more diverse environments (Hultengren et al. 1991, Hilmo 1994, Holien 1996, Nitare 2000). All studied species have green algal photobionts, except for the tripartite *Lobaria amplissima* which also has cyanobacteria (Purvis et al. 1992). Transplantations have been performed on three species categorised as Vulnerable (VU) in the Swedish red list (Thor and Arvidsson 1999): using fragments from the up to 0.3 m fruticose *Evernia divaricata* and the 1-2 cm shrubby fruticose *Ramalina dilacerata* (I, Figures 2 and 3), and using the 0.2-2 mm large and abundant isidia from the up to 10x25 cm foliose *Platismatia norvegica* (Lynge) W. L. Culb. & C. F. Culb. (V, Figure 4). *P. norvegica* was assigned by Holien and Tønsberg (1996) to the Boreal coastal species group, the group most strictly associated with the suboceanic Trøndelag element, and has also been used for the survey in Paper II, for the field monitoring performed in Papers III and IV, and for the laboratory test series performed in Paper IV. This laboratory work also included the 3-4 cm fruticose *Bryoria bicolor* (Ehrh.) Brodo & D.Hawksw. (VU), the thick up to Ø 1 m foliose *Lobaria amplissima* (Scop.) Forssell. (EN), the 0.3-10 m fruticose *Usnea longissima* Ach. (VU), and the up to Ø 10 cm thinly foliose common generalist species *Platismatia glauca* (L.) W. Culb. & C. Culb (Thor and Arvidsson 1999, Brodo *et al*. 2001, Gärdenfors 2005). *E. divaricata, P. norvegica, P. glauca, U. longissima, B. bicolor, and R.. dilacerata* most commonly, but not exclusively, grows on branches of old Norway spruce trees (Ahlner 1948, Hultengren et al. 1991, Holien 1997). *R. dilacerata* is also found on grey alder (*Alnus incana* (L.) Moench), aspen (*Populus tremula* L.), and goat willow (*Salix caprea* L.), and *L. amplissima* mainly occurs on different broadleaf trees.

Transplantation of epiphytic lichens (Papers I and V)

For Paper I, field work was carried out in August 2001. After collecting the lichen material, fragments were transplanted into the near-optimal sites within two hours, and within three days at the old-growth and clear-cut border sites. The design of the experiment was factorial, including the factors site (three levels, cf. above), lichen exposition on branches (two levels), and presence of an artificial shield (two levels). For each species, a total of 120 fragments were used, with 40 fragments being distributed on 10 randomly selected trees at each transplantation site. The effect of exposition was tested for by transplanting fragments using nylon thread at either north- (50%) or south- (50%) facing branches on the tree, and with or without a sheltering cocoon of cultivation fabric. The effect of size variation in the range between 35-340 mm^{2}was tested for on *R. dilacerata*.

Following observations by e.g. Hultengren et al. 1991, Gries 1996, Sillett et al. 2000a, and Hedenås and Ericson 2003, fragment vitality was assessed using a visual method of classification according to a vitality scale ranging from 5 to 0. Fragments were monitored on four occasions: 2 December 2001 (only the two old-growth sites), 27-29 March 2002, 25 June-1 July 2002, and 19-23 August 2002. In addition, notes were made on the probable causes of mortality and disease in the fragments, and occurrences of new growth were registered for *E. divaricata*. This assessment was founded on the presence of newly grown shoots on the fragments, which appear as having a distinctly more greenish hue than older lichen tissue.

In Paper V, transplantations of *P. norvegica* isidia (N = 240) were performed in September and October 2003 at six sites in the regions of Jämtland and Trøndelag in Central Scandinavia, with 50% of the 150 mm^2 standardised twig surfaces being treated with a 20% adhesive solution of the hydrogel Ac-Di-Sol® and water. Subsequently, *P. norvegica* isidia were applied on both transplantation microsites, covering a 35 mm^2 area. For covariate analyses, tree diameter at breast height (cm), twig height from the forest floor (cm), twig slope (deviation in from a horizontal plane, in degrees), and twig exposition (degrees) were noted for each transplant microsite. Further, crown cover photographs were taken immediately over (<10 cm) each pair of transplant microsites (treated with Ac-Di-Sol®/untreated), to estimate microsite exposure assessed as *per cent canopy openness* using Gap Light Analyser 2.0.

One year after transplantation, the twigs included in the experiment were harvested. After harvest, the transplant surfaces were photographed at 5.8x magnification, and transformed to dichotomous black and white using Adobe Photoshop CS2 and ImageJ 1.36b. After this, per cent cover of remaining isidia (=black) was calculated for each transplant surface in ImageJ, to provide an estimate of the *immobilisation*[1] of isidia in *P. norvegica*. Further, in order to provide an estimate of the number of successful *establishments*, in which transplanted diaspores de facto had managed to germinate, the occurrence of microthalli[2] one year after transplantation was assessed numerically.

Identifying factors associated with good growth prerequisites for hydrophilic species in natural habitats (Papers II and IV)

To identify factors associated with high lichen abundance and vitality in naturally established populations, field work for Paper II was carried out from June to September 2003. At each site, one 20-30 metre wide transect was placed in the centre of distribution of *P. norvegica* population, directed at a 90º angle running 0-50 metres from the watercourse. Along each transect, fifteen to twenty Norway spruce trees surveyed, the higher number chosen in the continental area due to an expected rarity of the species. At each transect, aspect, altitude, direction of the watercourse, ground floor vegetation, and average basal area of the stand were recorded. The two latter parameters were noted every tenth metre along the transect. For each tree included in the survey, distance to the watercourse (dm), diameter at breast height (cm), lower starting point of the survey segment (cm), number of branches, and proportion of living branches within the survey segment were recorded. The survey segment was set as the lowest 150 cm of the canopy, measured from the lowest lichen-carrying branch >40 cm in length.

Within this segment, all thalli of *P. norvegica* were registered and measured for a number of lichen variables: 1) height within the survey segment (cm); 2) exposition (degrees); 3) distance from the trunk (cm); 4) substrate (dead or living wood); 5) number of hyperepiphytes (c.f. Barkman 1958); 6) parasite infection (number of nodules); 7) thalli area (mm^2); 8) necrotic tissue (mm^2); 9) cover of diaspores (classes 1-5); and 10) pigmented thalli area (mm^2). Cover of diaspores was assessed visually in classes corresponding to an average surface cover of ≤ 1% (class 1); >1%-≤ 5% (2); >5%-≤ 15% (3); >15%-≤ 35% (4); >35% (5). Thallus area was measured as maximum length multiplied with the maximum width, measured perpendicularly to the length axis. Necrotic tissue and pigmented thalli area were measured in the same manner for each spot, thereby adding the areas for

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[1] Natural immobilisation, i.e. adhesion to the substrate surface, is achieved by growth of hyphae from the lichen diaspore. In the present study, however, the term 'immobilisation' is also used for diaspore adhesion to the surface by the use of an adhesive agent.

[2] This term refers in the present study to the tiny (< 1 mm) earliest stages of juvenile thalli visible subsequent to germination, which appeared as small, often three-lobed, white cushions bursting out from the dark isidia (Figure 2).

each thallus. During the survey, one dry, dead, bark-covered twig (∅ 4-7 mm) was collected from each survey tree, and then stored in paper envelopes awaiting analysis. Measurements of bark pH were performed in January 2004, using a method following Gauslaa and Holien (1998), but slightly modified so that a fixed bark area of 3 cm^2 was obtained.

To identify factors associated with good prerequisites for wet time, potential and realised photosynthetic activity in hydrophilic lichens, meteorological measurements were in Paper IV collected on the basis of a factorial design involving a) three different stream sites, including at each site the effects of b) proximity to streams (0.5 *vs*. 20 m), and c) stream flow quality (calm *vs*. turbulent, aerosol-producing water flow), resulting in a total of 12 microhabitats. In Paper III, only the three 0.5 m calm habitats were used for simulations. In each microhabitat, seven fragments of *P. norvegica* were transplanted 50 cm apart on nylon nets with a mesh size of 10 mm. Thallus water content (*WC*) in the fragments was monitored by the impedance technique (Coxson 1991, Jonsson *et al*. 2008) using two silver-plated crocodile clips. During each measurement campaign, in each of the four microhabitats selected at each stream site, a data logger (CR10X with an AM416 relay scanner, Campbell Sci, UT, USA) recorded the thallus WC, the air temperature and relative air humidity. All measurements were recorded at 1-min intervals and 10-min averages were stored. The same set of instrumentation was used in the different campaigns. All microhabitats were visited at least weekly to collect the data, check for broken sensors, and to adjust the WC-clips if necessary.

Determination of species-specific PSII activation and inactivation patterns in response to fluctuating hydration levels (Paper IV).

After fragment preparation, laboratory experiments were performed in three sets to quantify species-specific traits with respect to 1) photosynthetic (PSII) activation by liquid water; 2) deactivation of photosynthesis during subsequent desiccation; and 3) PSII activation by humid air. The water-related environmental conditions were based on the water potential of the air (Ψ_{air}) (Eqn. 1):

$$\Psi_{air} = \frac{RT_{air}}{V}\ln\left(\frac{RH}{100}\right)$$

Cuvette experiments were performed at 10°C and 15°C, in accordance with e.g. Green *et al*. (2002), and using a flow-through gas-exchange system (Compact Minicuvette System 400, gas mixing unit GMA1 and cuvette GK-022, H. Waltz, Effeltrich, Germany), with temperature regulation controlled by a built-in Peltier element, and an illumination of 200 µmol $m^{-2}s^{-1}$ during all experiments. Different levels of humidity were obtained by transferring 20.5°C water vapour saturated air through a cooling trap unit. Photosynthetic activity in all three sets of experiments was indicated by the maximum capacity (variable chlorophyll *a* fluorescence) of photosystem II (PSII) (Fv/Fm), measured by a PAM-2000 fluorometer (H. Walz, Effeltrich, Germany) on dark-adapted thalli (5 min, sufficient duration tested before measurements) (Roháček and Barták 1999, Schlensog and Schroeter 2001).

For all series, Fv/Fm was measured and fragment WC monitored gravimetrically at fixed intervals, on 4-6 fragments per species, with the initial measurement after 10 min followed by measurements every hour. To monitor PSII activation patterns for the different species, Fv/Fm was recorded following thallus rehydration by liquid water (Fig. 1). Wetted thalli were placed in water vapour saturated air at 10 °C and exposed to an irradiance of 200 µmol $m^{-2}s^{-1}$, in accordance with Palmqvist and Sundberg (2000). In the second series, development of Fv/Fm was followed in fully activated thalli fragments during desiccation at eight different Ψ_{air} levels, in order to monitor the process of desiccation and inactivation in the species. At a temperature of 10°C, desiccation was monitored under 200 µmol $m^{-2}s^{-1}$ and at Ψ_{air} values of -2.1 MPa (corresponding to relative humidity, rh 98.4%), -5.5 MPa (rh 95.9%), -11.0 MPa (rh 91.9%), -22,9MPa (rh 83.9%), and -68.3MPa (rh 59.3%). At a temperature of 15°C and 200 µmol $m^{-2}s^{-1}$, desiccation was monitored at Ψ_{air} values of -1.6MPa (rh 98.9%), -8.2MPa (rh 94%), and -46.5 MPa (rh 70.5%). Measurements were repeated at 1 h intervals (as described above) until measured Fv/Fm rates levelled out below a threshold value of 0.1. Examples of species-specific desiccation time-series with Ψ_{air} = -68.3MPa at 10ºC are presented in Paper IV.

Simulating the effect of activation time lags on lichen photosynthetic output (Papers III and IV):

In Paper III, in order to develop a simulation tool to predict the effect of activation time lags on lichen photosynthetic output, laboratory results from Paper IV were used as the raw material to parameterise species-specific model constants representing water balances and activity patterns. The constants were used in the construction of a dynamic model that continuously alternates between rehydration and desiccation and discriminates between rain and humid air as sources of hydration (III). The lichen water content was simulated assuming time-dependent hydration and subsequent desiccation, according to Eqn. (2):

$$\frac{\partial WC}{\partial t} = -k(WC - WC_{eq}) \qquad (2)$$

where WC_{eq} (%) is the measured *in situ WC* for *P. norvegica* interpolated to obtain a continuous function, and k (min^{-1}) is the species-specific rate constant for desiccation (k_{des}) or rehydration (k_{reh}), depending on the direction of the process. Realised activity, A_{real}, which incorporates species-specific activation time-lags, was simulated using the following expression:

$$\frac{dA_{real}}{dt} = -k_a(A_{real} - A_{pot}) \qquad (3)$$

where A_{real} (%) is the realised activity, A_{pot} (%) is the maximum potential activity at a given ambient *WC*, i.e. that which would be achieved if PSII activation occurred instantaneously following lichen hydration, and k_a (min^{-1}) is the species-specific activation rate. The integrated functions for A_{real} or A_{pot} over time, i.e. the area below the simulated curves for the respective activity, indicates the amount of photosynthetic activity that can potentially be achieved by A_{real} and A_{pot}, respectively. Hence, A_{real} will result in a lower amount of estimated photosynthetic activity than $A_{pot,}$ the difference depending on the magnitude of activation time lags in the species under consideration. Further, the ratio (quota = *q-value*) A_{real}/A_{pot} was used to describe the efficiency of each species' utilization of water resources¸ and thus to illustrate the impact of activation time lags on resultant photosynthetic activity. In Paper IV, the model was used to generate simulation data for use in a factorial habitat analysis, where species, distance to the stream and stream type were included as independent variables.

Statistical analysis

In Papers I, II, IV and V, ANOVA tests were performed (Minitab General Linear Model). In Paper I, vitality scores recorded in August 2002 were used as the experimental unit, the effects of site, exposition, and shield were included as fixed factors, and the effect of the host trees as a random factor nested under 'site'. For *R. dilacerata*, fragment size was added as a covariate.

In Paper II, the surveyed trees were used as the experimental unit, in a model including the fixed effect of region, the random effect of site as a factor nested under region, and distance to the watercourse and bark pH as covariates. The test was also repeated for each region separately, excluding the fixed effect of region. In order to investigate other possible correlations between tree and lichen variables, Pearson correlation tests ($p \leq 0.05$) were performed on a lichen level data matrix for each region separately. To evaluate the effect of "occurrence on dead wood" on other lichen variables, and to examine whether mean values of lichen and tree variables differed between the two regions, 2-sample T-tests were performed ($p \leq 0.05$). In performing the latter tests, a lichen thalli matrix was used for the lichen variables, and a tree matrix was used for the tree variables.

In Paper IV, statistical analyses were performed on the dependent variables wet time, potential photosynthetic activity, and realised photosynthetic activity from the habitat simulation results, in combination with the parameters characterising the 12 monitored microhabitats on which simulations were performed. Tests were performed using 1) the total data set from the simulations, 2) using only time periods induced by humid air, and 3) using only time periods induced by rain, resulting in a total of nine dependent variable combinations. The simulated results for each lichen fragment from all species tested in the laboratory experiments were used as the experimental units, in a model including the random effect of habitat (three stream sites), the fixed effects of distance from the stream (two levels) and stream type (two levels), two-way interactions among the variables mentioned above, and crown cower (%) as a covariate.

In Paper V, the effects of site (6 levels), substrate manipulation (2 levels), microsite exposure, tree diameter, twig slope, and twig height, were determined on 1) immobilisation, assessed by per cent diaspore cover, and 2) establishment, assessed by the number of microthalli, in *P. norvegica* after 12 months. When testing these effects, the transplant microsites (50 mm^2) (N=240, r=20) were used as the experimental unit, in a model which for both the studied variables included the fixed effect of substrate manipulation, the random effect of site, and microsite exposure, tree diameter, twig height, and twig slope as covariates.

In Paper III, mean values of A_{pot}, A_{real} and total wet time ($WC>0$, induced by either humidity or rain) were calculated using the activity and *WC* simulations for each species and stream site. In Paper V, mean values of diaspore cover and numbers of microthalli for Ac-Di-Sol®-treated *vs*. untreated sites and microsites were calculated. In Papers I - V, the Tukey post hoc test was used in order to determine whether the significant effects found in the analyses were positive or negative ($p \leq 0.05$), and in Papers I, II, IV and V data were tested for homogeneity of variances using Levene's statistic. In Paper III, all regressions were fitted using SigmaPlot 8.0 (Systat Software Inc, Richmond, California, USA).

Results and discussion

Restoration by transplantation of fragments and isidia: general levels of survival and vitality

Using fragment transplantation as a tool for restoration, levels of survival were high in all habitats one year after performing the transplantations (I). At the near-optimal transplantation sites, survival (i.e. classes 1-5) was 95% for *R. dilacerata* (Rd) and 90% for *E. divaricata* (Ed), with 87.5% and 82.5% vital fragments (classes 3-5), respectively. At the old-growth sites, survival was 85% (Rd) and 97.5% (Ed), while the proportion of vital fragments was markedly lower than at the original sites of occurrence, with 70% (Rd) and 57.5% (Ed). At the clear-cut border sites, survival was 85% (Rd) and 87.5% (Ed), and frequencies of high vitality being similar to those noted at the old-growth site. Using transplantation of isidia, the main factor enhancing immobilisation was substrate manipulation with Ac-Di-Sol® (p 0.004), complemented with an interaction effect with site for transplantation surfaces without Ac-Di-Sol® ($p<0.001$) (ANOVA, adj. $r^2 = 55.46\%$). Ac-Di-Sol® improved immobilisation significantly on all sites, on average by a factor of 13 (23.8% diaspore cover, compared to 1.81% without Ac-Di-Sol®). For establishment, there was a significant interaction effect between substrate manipulation and site. On five of six sites Ac-Di-Sol® significantly increased the occurrence of microthalli. The increase was by a factor of 41 (37.2 thalli compared to 0.90 per transplant surface), i.e., Ac-Di-Sol® improved establishment to an even higher degree than immobilisation. The covariates microsite exposure, tree diameter, twig height, or twig slope had no significant effect neither on diaspore cover nor on immobilisation.

The very high levels of survival obtained for fragments of *E. divaricata* and *R. dilacerata* (I), and the high rates of immobilisation and establishment achieved for *P. norvegica* isidia transplanted using Ac-Di-Sol® (V), suggest that transplantation of fragments as well as isidia can constitute a valuable tool for restoration of endangered lichen populations if beneficial modes of transplantation are identified (cf. also Scheidegger et al. 1995). This indication is strengthened by the high frequency of new growth in *E. divaricata*, the apparent stability of the vitality scores for both *E. divaricata* and *R. dilacerata* especially at the optimal transplantation sites (I), and by the numerous observations of successful establishments in transplanted *P. norvegica* isidia (V).

The present thesis has shown that the choice of transplantation technique is of importance for fragment vitality (I, V). For transplanted isidia, we can see that Ac-Di-Sol® application enhances both immobilisation and establishment by several orders of magnitude compared to untreated surfaces. We conclude that preparation of transplant surfaces with Ac-Di-Sol® solution may constitute a highly efficient tool for enhancing the outcome of restorative transplantations targeting epiphytic lichens. For transplanted fragments, it was found that the mode of transplantation affects survival and vitality in the fragments, both in terms of how the fragments are attached to the branches, and, in certain environments, whether they are placed on north- or south-facing branches (I). Covering the fragments with an artificial shield can improve fragment vitality at wind-exposed sites (cf. Esseen and Renhorn 1998, Hilmo and Holien 2002, Keon and Muir 2002), but may also increase the risk of infection by lichenicolous fungi (I). This underscores that the mode of transplantation might need modification, depending on the characteristics of the habitat. Here, it must be taken into account that responses to applied modes of transplantation can differ among species depending on their ecological prerequisites.

The high levels of survival and vitality *E. divaricata* and *R. dilacerata* in the old-growth and clear-cut border habitats indicate that it is possible to perform inter-regional transplantations with good possibilities for establishment of the transplanted populations at their new locations (I). Depending on the characteristics of the transplantation site, the transplanted fragments showed different causes of reduced vitality and mortality (I). These observations, in combination with the highest levels of survival and vitality being obtained at the species original sites of occurrence, indicates that identification of beneficial microclimatic and substrate characteristics, both at habitat and microsite level, are likely to be of outmost importance for identification of suitable transplantation sites (I, II). This conclusion is also well supported by results obtained in Papers II-IV.

Optimisation of resource efficiency in transplantations

Although transplantations have been performed to study various aspects of lichen ecology and physiology (e.g. Renhorn et al. 1997, Hazell and Gustafsson 1999, Palmqvist and Sundberg 2000, Hilmo 2002, Keon and Muir 2002), few studies of lichen transplantation have been carried out in order to evaluate transplantation as a tool for restoration of endangered species, which is the focus of the present thesis. To achieve this purpose, one focus has been to evaluate to what extent resource efficiency in terms of lichen material can be optimised from the perspective of minimising the size of transplantation units.

In a population consisting of a small number of individuals, each individual holds a relatively high value for the survival of the population. Therefore, it is crucial that harvest of lichen material for transplantation purposes will cause minimal damage to the original lichen population (Scheidegger et al. 1995). If one argues according to a principle of resource efficiency, the success of a given transplantation method depends on two variables. The first is the amount of biomass that has been harvested from the existing population. The second is to what degree the transplanted fragments manage to germinate or grow in the new environment, measured in numbers of successful establishments per unit of lichen tissue removed from the original site.

For species that attach to their substratum, one elegant method of transplantation is to use small, intact thalli that remain attached to their natural substrates. This method was used by Hilmo (2002) on *Lobaria scrobiculata* (Scop.) DC., *P. glauca*, and *P. norvegica* in central Norway, resulting in the very high overall survival rate of 96% 14 months after transplantation. However, if intended for conservation purposes, one severe limitation is that this method only has the potential to give rise to one new establishment per harvested lichen thallus. In the present thesis, only 20 specimens of *R. dilacerata* and three specimens of *E. divaricata* were needed to produce the 120 fragments used for each species. For *R. dilacerata*, on which size variation was tested, results showed that smaller fragments had equal levels of vitality as larger fragments, at least within the studied size range of 35-340 mm^2 (I). Thus, it seems as if there are good reasons to choose to transplant relatively small fragments, since these can be considered as giving a higher degree of resource efficiency in the use of lichen material. Although many species rarely or never form soredia or isidia, it is, as pointed out by Scheidegger et al. (1995), of course preferable when possible to use the less destructive option to transplant vegetative diaspores, as was done in Paper V.

Estimating long-term viability in restored populations

One inherent problem when establishing new populations of a species is how to determine whether the new populations can be considered as viable (Pavlik 1994, Bain et al. 2000, Kentula 2000). One basic criterion for viability ought to be that individuals are able to reproduce (vegetatively or sexually) at their new site of occurrence, giving rise to offspring that in their turn can become reproductive. When transplantation has been used to circumvent critical life history stages, the ideal would be to be able to observe reproduction within the new habitat. Since this often is not possible within the time-frame of a scientific experiment, evaluation of many species-focussed restoration projects will have to suffice with predictions of the possibilities for future reproduction (Fahselt 1988). The only study that has provided long-term results on lichen transplant survival is the one performed by Gilbert (1991, 2002) in Great Britain. In this small-scale study, 71% of 14 *Lobaria amplissima* (Scop.) Forssell fragments remained after one year, a result that was stable also after 10 years. After 20 years survival among the transplanted thalli was 40%. Although the transplantation experiments performed in this thesis were monitored for only one year, some of the obtained results can be seen as promising for long-term survival among the fragments (I, V).

E. divaricata fragments were able to grow at all transplantation sites, with new growth found in 12.5% of the fragments at the old-growth site and in 27.5% at both the near-optimal forest site and the clear-cut border site, in line with Keon and Muir (2002). Shoots were typically 2-5 mm after one year, which is as much as can be expected for fruticose species, even compared to thalli that have not suffered from the stress associated with fragmentation and transplantation (Hale

1974). It is likely that frequencies of new growth would have been even higher if only marginal parts of the *E. divaricata* lichen material had been used (Ott 1987, Honegger 1996). Since stress responses after transplantation may be due to initial costs of adaptations to the new abiotic environment, short-term chlorosis or reductions in growth rates can be misleading with reference to the long-term vitality of the lichens (Gauslaa and Solhaug 1996, Nash 1996, Hilmo 2002, Hedenås and Ericson 2003). This is supported by the present thesis, which indicates that both *E. divaricata* and *R. dilacerata* are able to recover from temporary declines in vitality (I).

Although 'wind' was diagnosed as a cause of mortality fairly evenly among the different transplantation sites in this thesis, a characteristic U-shape of the *E. divaricata* fragments at the clear-cut border site suggests that wind might be of particular importance at this site (I). Results obtained by Esseen (1985), Esseen and Renhorn (1998), and Hilmo and Holien (2002) indicate that the low cover of epiphytic lichens at forest edges may be due to high rates of mechanical damage caused by e.g. high wind speeds and snow abrasion. This shows that estimations of both growth rates and biomass losses are needed to assess the possibilities for long-term biomass accumulation in restored populations.

Transplantation of epiphytic lichens as a tool for conservation

For many endangered species, the habitats of remnant populations are often both very small and isolated from other habitats that potentially could harbour the species. In cases when creation of habitat corridors is considered inefficient or impossible, artificial dispersal is a conservation management technique that could provide a window of opportunity to lower the risk of random losses of endangered populations. When the availability of suitable substrates is limiting, habitat restoration approaches should have a large potential to be useful. However, in the case of many epiphytic lichen species, such solutions have a severe drawback in the fact that suitable substrates and habitats have a quite long deliverance time. Also in this case, artificial dispersal could constitute a valuable conservation tool for restoration, either within present sites of occurrence or in new habitats.

Still, this does not lend support to the conclusion that artificial dispersal can be seen as a cost-efficient alternative to the preservation of habitats. The classic set-aside approach to conservation (with or without management interventions to maintain desired successional phases) does not only preserve the few red-listed species that are easily detected in surveys, but also the multitude of species that are not so easily observed. Therefore, restoration should be seen as a last resort when set-aside conservation options no longer suffice to preserve biodiversity. However, for many of the species threatened today, detrimental temporal gaps in the supply of suitable habitats and substrates are to be expected in the future. This thesis shows that artificial dispersal of lichen fragments could be one of the tools utilised in the effort to meet this challenge. Transplantations can also be seen as a way to increase resource efficiency in terms of optimising species richness in protected habitats. By increasing patch occupancy, risks of random losses of local populations can be lowered, and the costs of set-aside protection can benefit more species at each protected site.

Species-specific patterns of PSII activation time lags and water-holding capacity

In Paper IV, *U. longissima* and *B. bicolor* exhibited very slow PSII activation rates, with full activation of photosynthesis only reached 24 h after liquid hydration of both species. In addition, *P. norvegica* and *L. amplissima* exhibited rather significant activation time lags, with approximately 90% of full activation of photosynthesis being reached by both species after 4 h (IV). However, since the activation curve for *P. norvegica* is more linear (cf. IV) the impact of activation time lags on realised activity will be much greater for this species. Compared to previous findings relating to PSII activation time lags, with suboptimal photosynthetic activity recorded up to 1 h after liquid hydration (Lange *et al*. 1986, Palmqvist 2000), the four rare hydrophilic species in the present study appear to be significantly hampered; the most pronounced effects were recorded for *U. longissima* and *B. bicolor*. Since only fully vital lichen material was used, we consider that these differences are likely to be a consequence of species-specific differences in their photosynthetic responses to drought. At least two possible, and not necessarily exclusive, explanations for these observed time lags can be suggested: 1) either the thylakoid or Calvin cycle enzymes are not sufficiently protected during desiccation, resulting in slow repair; 2) the metabolic systems have been protected sufficiently during desiccation, but the “unfolding” of these protective mechanisms is a very slow process.

To complement this picture, results show that *U. longissima* and *B. bicolor* have a much lower capacity for holding water within the thalli and for maintaining photosynthetic activity at low water potentials, compared to *L. amplissima*, *P. norvegica*, and *P. glauca* (cf. Lange and Ziegler 1986). Since the metabolic cost of activation is basically the same for each activation event, a poor water-holding capacity may reduce the likelihood of positive net growth especially during shorter potentially active periods. This is clearly reflected in the markedly shorter mean wet times and the lower realised activity levels recorded for *U. longissima* and *B. bicolor* in the simulations performed in Paper IV.

Possibly, the pronounced activation time lags found especially for *U. longissima* and *B. bicolor* may protect against unnecessary and costly unfolding of the protective systems required to cope with desiccation. With the constraints added by photosynthetic activation time lags, such a strategy would only be viable in habitats where long wet periods with sufficient light are sufficiently frequent to allow positive net growth. When analysing the distribution patterns of the two species, it is clear that they are much more abundant in areas with high precipitation rates and an overall oceanic climate, and in areas where microclimatic conditions create long periods of hydration associated with sufficient irradiation (Thor and Arvidsson 1999). In contrast, *P. glauca* and *L. amplissima* have a low moisture compensation-point and exhibit rapid activation of photosynthesis, which may allow for peaks of positive net photosynthetic gas exchange to occur during brief hydration events e.g. from dew (cf. Green *et al*. 2002, Lange 2003, and Lange *et al*. 2006).

Effects of species-specific activation time lags on potential *vs.* realised photosynthetic activity

In Paper III and IV, we could see that incorporation of species-specific activation time lags into the simulations revealed large differences among the studied species. Irrespective of microhabitat, the total accumulated realised activity for *P. glauca* and *L. amplissima* during rainy periods was only reduced by 1% (*La* five sites, *Pg* six sites) to 2% (*La* at one site) compared to the potential activity. In addition, during the humid periods, the realised activity levels were consistently very high, being reduced by 1-5% compared to the potential activity, with a single exception of a 9% reduction for *Pg* at Kulbäcken Calm 20 m. For *P. norvegica*, the total realised activity during rainy periods was only 89% (Kulbäcken Turbulent 1m and Calm 1m) to 82% (Lögdeälven Calm 1m) of the potential activity, and 76% (Kulbäcken Turbulent 1m) to 62% (Stenträskbäcken Calm 1m) during humid periods, depending on microhabitat. For *U. longissima* and *B. bicolor*, PSII activation time lags reduced the realised activity significantly compared to the potential activity. For these two species, the quotas (q values) between potential and realised activity values during the rainy periods were 61% (*Ul*) and 77% (*Bb*) at Stenträskbäcken Turbulent 1m, to 49% (*Ul*) and 69% (*Bb*) at Lögdeälven Turbulent 20 m. During the humid periods the values were 41% (*Ul*) and 59% (*Bb*) at Kulbäcken Turbulent 1m, down to the very low levels of 19% (*Ul*) and 38% (*Bb*) at Stenträskbäcken Calm 1m.

Factors of importance for viability in natural and restored populations

Macroclimate

Results obtained in this thesis show distinct differences among naturally established *P. norvegica* populations in the two study regions (II). Many of these are likely to be due to macroclimatic differences such as precipitation patterns, air humidity levels, and frequencies of foggy days, which affect establishment, growth, and abundance of lichen thalli (Boucher and Nash 1990, Halonen et al. 1991, Muir et al. 1997, Ward and Robinson 2000, Davie 2003). One prominent difference was a distinctly higher abundance of thalli in the oceanic region, with 6.78 (sd ±5.09) thalli per tree, compared to 2.97 (±8.94) in the continental region (II). While higher bark pH levels in the oceanic region failed to explain the observed differences, there was a good correspondance at site level between abundance and annual wet precipitation. For example, the three sites with the highest annual wet precipitation levels have on average 7.0-8.8 (±5.2-3.8) thalli per tree, while the three most continental sites have 1.7-1.9 (±3.3-4.3) thalli, respectively (II).

The marginal *P. norvegica* populations display both morphological and distributional responses to the more continental climate. Although not quantified, thalli at the continental sites generally were much flatter, which possibly might be a response to the drier climate (Larson and Kershaw 1976, Kershaw 1985). In addition, thalli occurred further out on the branches in the continental region (II), which could indicate lower degrees of interspecific competition (Hilmo 1994) or that establishment is facilitated at microsites more exposed towards rain. The fact that thalli in the continental region on average are smaller, but in spite of this fact more abundantly covered with diaspores, could indicate that overall growth rates are slower in the fringe habitats (II). Reduced growth-rates in marginal habitats are in accordance with results obtained by Palmqvist and Sundberg (2000) and Hyvärinen (1992).

However, close to the watercourses in the continental region, it was found that both abundances of thalli and average sizes surpassed those found in the oceanic region (discussed further below). This indicates that local sources of humidity can outweigh the effect of lower precipitation levels. In accordance with Glenn et al. (1997), results obtained in this thesis show that infections by nodule-producing parasites were much less frequent in *P. norvegica* thalli in the continental region, compared to the oceanic region (II). Also, results indicate that infections may be less lethal in the continental fringe habitats (II).

As will be discussed further below, results indicate that both close proximity to water and less acidic bark pH values are essential for the occurrence *P. norvegica* in the continental fringe habitats, while being insignificant in the oceanic core habitats (II). Possibly, suboptimal humidity and bark pH levels hamper germination and/or survival of small thalli, resulting in a comparatively low proportion of successful establishments. This hypothesis is supported further by the fact that the frequency of trees hosting *P. norvegica* in the fringe habitats declined dramatically with increasing distance to the watercourse, while no such pattern was found at the oceanic sites (II). Other studies have indicated that lichens during the process of germination are particularly sensitive to unfavourable microclimatic conditions (Ott 1987, Scheidegger et al. 1995, Hilmo and Holien 2002).

Sources of microclimatic humidity

The microclimatic monitoring performed in Paper III and IV revealed that the availability of humidity may differ to a large extent among seemingly similar stream sites within a homogenous climatic region. In the three streams, effects of the physical habitat are confounded with seasonal variations in precipitation and temperature, and should therefore primarily be seen as examples of different microclimatic scenarios. As such, we can see that for wet time caused by rain ranged from 8107 min at Stenträskbäcken to 3183 min at Lögdeälven. However, for wet time caused by humid air the pattern was reversed, ranging from 4749 min at Lögdeälven to 2227 min at Stenträskbäcken (IV). At Kulbäcken, total wet time for the microhabitats adjacent to calm water was, on average, 91.9% of the time recorded for the microhabitats adjacent to turbulent water. The equivalent values for Stenträskbäcken and Lögdeälven were 68.1% and 156%, respectively. At Kulbäcken, total wet time 20 m from the stream was 74.6% of the wet time registered 1m from the stream. At Stenträskbäcken and Lögdeälven, the differences were even more pronounced, with the average wet time 20 m from the stream being 66.5% and 61.5%, respectively, of the 1 m values.

In combination with species-specific activation time lags, these data also have far-reaching consequences for the different lichens' ability to utilise hydration in the monitored habitats. For example, the favourable humidity patterns recorded in the habitat Stenträskbäcken Turbulent 1m produced realised activity values of 42.4 and 41.4, respectively, for the rapidly activated and efficiently water-holding species *L. amplissima* and *P. glauca*. For *P. norvegica*, which has a water-holding capacity equal to that of *L. amplissima* and *P. glauca*, but has quite pronounced PSII activation time lags, the total realised activity for Stenträskbäcken Turbulent 1m was 33.9. Finally, for the two species that are limited both by rapid desiccation and long activation time lags, *B. bicolor* and *U. longissima*, the total realised activities were 27.5 and 20.3, respectively in the same microhabitat. For the least hospitable microclimatic scenarios included in the simulations, the total realised activity at Lögdeälven Turbulent 20 m was 10.0 and 9.5 for *L. amplissima* and *P. glauca*, respectively, 7.0 for the intermediate *P. norvegica*, and very low for *B. bicolor* and *U. longissima*, being 4.9 and 3.2 respectively. For all species, but especially for *U. longissima* and *B. bicolor*, realised activity was reduced even more during hydration events caused by humid air. Palmqvist and Sundberg (2000) point out that there is an additional limitation caused by the restriction of metabolic activity to wet occasions, since rain also results in lower light fluxes, particularly in shaded habitats such as under dense forest canopies. This line of argument further highlights the possible importance of stream habitats, which often provide, simultaneously, relatively high levels of both irradiance and air humidity (Brosofske *et al.* 1997, Danehy and Kirpes 2000).

In the *P. norvegica* survey, the ANOVAs showed that thalli abundance in the peripheral populations is strongly affected by close proximity to open water (II). Results from the microclimatic monitoring campaigns (III, IV) indicate that these observed aggregations very well may be due to increased levels of air humidity (cf also Brosofske et al. 1997, Danehy and Kirpes 2000). In the oceanic region, no such effect was found in Paper II, but is detected in a recent transplantation study by Hilmo, O., Rocha, L., Holien, H., Gauslaa, Y. (ms in prep.) where diaspores of *Lobaria pulmonaria* (L.) Hoffm. and *L. scrobiculata* are used. Although thalli sizes were smaller, areas of necrotic tissue were larger, and abundances lower in the continental region, it was found that within 10 metres from the streams, areas of necrotic tissue were lower, and both numbers of lichen thalli per tree (8.22 ± 14.5) and mean values for thalli area surpassed the average levels found in the oceanic region (II). An increase in diaspore cover increased close to the streams in both regions further underscores the positive effect of watercourses on viability in the continental *P. norvegica* populations (II).

In Paper IV, the simulations performed for *P. norvegica*, *L. amplissima*, *B. bicolor*, *U. longissima*, and *P. glauca* revealed that both close proximity to the streams and turbulent water were beneficial for both potential and realised activity values among the studied species (IV). On average, the microhabitats 20 m from the streams had a potential activity during rainy periods that was 69% of the values found 0.5 m from the streams, and a realised activity that was 68% of the 0.5 m values. During rainy periods, the microhabitats adjacent to calm water had a potential activity that was 83%, and a realised activity that was 82% of the turbulent water values. Correspondingly, for humid air periods, values at 20 m from the stream were 35% (potential) and 34% (realised) of the 0.5 m values. Moreover, microhabitats adjacent to turbulent water had both absolute levels of realised activity, and q values that were higher than values obtained adjacent to calm water. On average, the *turbulent* water values were 34% (potential) and 35%

(realised) of the calm water values. Possibly, the presence of aerosols dispersed from rushing water might contribute to lichen hydration in these habitats (cf also Lange et al. 1986, 1988, Tønsberg et al. 1996, McCune et al. (2002). All differences (over all stream sites, for potential and realised activity) for turbulent *vs*. calm water, and 0.5 *vs*. 20 m, were found to be significant according to Tukey tests, comparing the means.

Further, simulation results suggest that both topographical differences and tree basal area may influence the photosynthetic performance of the studied species (IV, cf. Danehy and Kirpes 2000). Generally, the positive effect of close proximity to the stream was stronger in the relatively steep ravine of Stenträskbäcken, where significant interactions were usually at the 0.001** probability level. In contrast, at Lögdeälven, where the turbulent water is wide and relatively slow-moving, sun-exposed, and the topography is relatively flat, differences between the four microhabitats were smaller, with respect to both potential and realised activity. For all species, a relatively dense canopy cover had a positive effect on realised activity caused by rain, but a negative effect on realised activity caused by humid air (IV). These patterns seem completely reasonable, since a low degree of canopy openness generally will slow down evaporation, while a high degree of canopy openness will facilitate the formation of dew and fog during the night and reduce morning temperature.

It might be hypothesised that with a more continental climate, resulting in overall levels of humidity that are insufficient for efficient lichen metabolism, differences due to elevated evaporation would become increasingly important. In addition to the sources of hydration studied in the present thesis, evaporation from seepage areas can be significant (Bosveld 1999, Ward and Robinson 2000, Davie 2003), and may be an important factor for the occurrence of hydrophilic epiphytic lichens in swamp forests (Kuusinen 1996). In essence, this means that e.g. a wet, *Sphagnum*-dominated ground floor might have a similar effect on evaporation as the open water surface of a stream. To some extent, this might be valid for the sites in the continental region. At two of the three sites with broad seepage areas bordering the streams (Kjolån and Storbekken), the outer limit of the *P. norvegica* population roughly coincided with the transition of ground vegetation from *Sphagnum* to dwarf-shrub vegetation. In conclusion, results from the *P. norvegica* survey and simulations incorporating species-specific activation time lags indicate that restoration measures on suboceanic lichens preferably can be concentrated to the immediate vicinity of watercourses (II, IV), and (optional) to sites with less acidic bark pH values (II, see below). However, other sites with presumed high levels of air humidity, such as swamp forests or steep northern slopes, could also have a potential as suitable restoration sites.

Substrate quality

In accordance with the patterns detected for proximity to open water, the effect of bark pH on thalli abundance was in the present study strongly dependent of region (II). In the continental region, the ANOVAs revealed a very strong positive effect of less acidic bark pH values on the abundance of *P. norvegica*, a pattern which was absent in the oceanic region (II). Since bark pH values were significantly higher in the oceanic region compared to the continental region (II), one interpretation might be that most trees in the oceanic region had a bark pH above a threshold value facilitating establishment and/or growth of *P. norvegica*. The ANOVAs also revealed a strong combinatory effect in the continental region of bark pH and proximity to water on thalli abundance (II), in line with recent findings by Hilmo, O., Rocha, L., Holien, H., Gauslaa, Y. (ms in prep.). Since there also was a positive correlation in this region between bark pH and proximity to the watercourse (II), these factors are likely to interact in producing the observed aggregation of lichen thalli. Positive synergy effects between humidity and bark pH have been suggested also by Rolstad et al. (2001) to explain the affinity of many lichen species for valley bottoms. Although the importance of bark pH for cyanolichens has been demonstrated in a number of studies (e.g. Bates 1992, Gustafsson and Eriksson 1995, Gauslaa and Holien 1998, Goward and Arsenault 2000, Wolseley and James 2000, van Herk 2001), no papers have previously shown a positive effect of high bark pH values on the occurrence of chlorolichens in boreal forests (cf. also Gauslaa and Holien 1998, Gauslaa et al. 1998).

Results from the *P. norvegica* survey also showed that in the continental region, thalli growing on dead wood substrate were larger than those growing on living wood (II). Very often, the largest thalli were found on relatively thick, broken-off dead branches. One possible interpretation of this might be that the development of large thalli is so slow that growth becomes limited by the process of self-pruning (Leemans 1991, Makinen et al. 2003). Therefore, as indicated also by results from the transplant experiment, one important consideration when performing transplantations of endangered species would be to choose as stable substrates as possible (I, II).

Can habitat restrictions among hydrophilic lichens be explained by activation time lags?

For total daylight simulations, the q values show a rather constant relative efficiency among the species irrespective of microhabitat. However, the absolute values for both potential and realised activity differ greatly among the twelve different microhabitats. This highlights the influence of habitat characteristics and/or seasonal variations in hydration patterns on photosynthetic output. If we consider the very large differences in accumulated realised activity reported here for different species/habitat combinations (42.4 for *L. amplissima* at Stenträskbäcken Turbulent 1m and 3.2 for *U. longissima* at Lögdeälven Turbulent 20m), we can see that the potential for positive net growth may differ by a factor of 13. At Stenträskbäcken Calm 1m, the q value of 0.19 obtained during humid air activation for *U. longissima*, suggests that, for this very slowly activating species, PSII activation time lags can reduce the realised photosynthetic activity by a factor of five under certain microclimatic conditions.

In contrast, *L. amplissima* has a highly efficient metabolism, aided both by relatively rapid activation and a very high water-holding capacity. The high capacity for growth is also consistent with the fact that thalli of this species are thick and very large, up to Ø 1m. This leads us to conclude that the observed habitat restrictions of *L. amplissima* to humid micro- and macroclimates are the result of some other factor than the capacity for positive growth in the adult thalli.

Possibly, the hydrophilic distributional pattern of *L. amplissima* instead is related to a dependence of high humidity levels during e.g. reproduction, establishment and/or the juvenile phase. Similar discrepancies between potential and realised niches have been found both for *L. pulmonaria* (Gauslaa *et al.* 2006) and *L. pulmonaria* and *L. oregana* (Antoine and McCune 2004).

It is well documented that hydrophilic species often are aggregated close to streams (particularly with turbulent water), and in dense habitats sheltered from the wind (e.g. Thor and Arvidsson 1999). These distribution patterns coincide well with the habitat features that generate high values of realised activity among the slowly activated species studied here. As has been shown in the present study, the consequences of activation time lags for the photosynthetic performance of the studied hydrophilic species are far-reaching, and may well be of sufficient magnitude to explain, to a large extent, the observed habitat restrictions exhibited by rare hydrophilic lichens.

Using dynamic modeling as a tool to predict lichen water-related activity

In Paper III, we used activation of photosynthetic electron transport as an indirect marker of photosynthetic activation, since it allows rapid responses to be tracked and large numbers of samples to be screened with relative ease. Incorporation of species-specific activation time-lags into a dynamic model revealed marked differences between the photosynthetic capacity of species in the studied microhabitats (III; IV). Although this represents a major step forward towards understanding lichen growth potential in different microclimatic scenarios, a complete prediction of the overall growth potential of lichens from the model developed here would require inclusion of a variable for respiration (cf. Sundberg et al. 1999). The hydration status of a lichen thallus and the environmental conditions in the habitat may affect lichen respiration in several ways, complicating attempts to determine general correlations between their growth rates and environmental variables (Lange and Green 2006).

To develop a more complete lichen growth model it will be necessary to include functions for different aspects affecting lichen respiration, such as light conditions *per se* during the daytime (Jonsson Čabrajić A, Moen J and Palmqvist K, unpublished data); the ratio between light and dark active periods (Lange and Green 2006); respiration in relation to fluctuating temperature (Lambers 1985; Sundberg et al. 1999); resaturation respiration effects (Sundberg et al. 1999); and respiration in relation to different water sources (Lange and Green 1996; Green et al. 2002; Pintado and Sancho 2002). Nevertheless, we believe that in habitats with frequent, brief hydration events, i.e. habitats where the negative effects of photosynthetic activation time lags will have the largest impact, these respiration effects would probably increase rather than reduce the differences indicated by the model developed and applied Papers III and IV. In addition, it is also possible that slow activation may be caused by a slow uncoupling of the complete photosynthesis for lichens with high carbon fixation capacity, and particularly those with high levels of Rubisco. High carbon fixation rates once fully activated could then theoretically compensate for suboptimal assimilation rates during the activation phase. However, as for respiration, in habitats with frequent, brief hydration events the negative effects of slow activation will have a larger impact.

Biogeographical considerations for efficient conservation management

The survey performed on natural *P. norvegica* populations in this thesis has shown that both population dynamics and the importance of habitat characteristics can differ significantly among different regions (II). A higher overall abundance of *P. norvegica* in the oceanic region suggests that a possibly shorter life-span (II) is well compensated for by better conditions for germination and establishment of new thalli. As has been shown by the simulations performed in Paper III and IV, sufficient hydration from humid air and rain becomes increasingly more important the more hampered the studied species are by activation time lags. Since slow activation reduces photosynthetic output proportionally more when wet time is divided into many, brief events (III), it is intuitive that oceanic macroclimates such as e.g. in the Trøndelag region in central Norway should be beneficial for slowly activating species.

However, of course this does not make it less necessary to make the most of the options for conservation and restoration available in the fringes of distribution for suboceanic species. Our simulations revealed that both close proximity to streams and the presence of turbulent water had a strong positive impact on realised activity among the slowly activated species, a pattern that coincides with observed distribution patterns of hydrophilic species (IV). These results also coincide well with the observations made for natural *P. norvegica* populations in the continental fringe habitats (II). Here, patterns of thalli abundance, thalli area and necrosis suggest that, within the zone of elevated humidity around the streams, conditions for germination and establishment are fully comparable to those in the oceanic region (II). In view of the scarcity of protected habitats in central Norway, the present thesis suggests that both set-aside protection and restoration of fringe populations can be of great importance to the conservation of endangered suboceanic lichens in Scandinavia. As discussed above, microclimatic humidity (II, III, IV) and less acidic bark pH levels (II) are important environmental constraints for *P. norvegica* in the continental fringe populations, while being insignificant in the oceanic core populations (II). Therefore, these factors could constitute important criteria for identification of suitable restoration sites for suboceanic species in continental fringe environments.

Conclusions

The following conclusions can be drawn from this thesis:

1) Artificial dispersal of lichen fragments can result in very high levels of survival, vitality, and new growth, indicating that artificial dispersal can constitute a valuable tool for restoration of endangered lichen populations (I). The mode of transplantation is of vital importance to fragment vitality, and may need modification to suit the characteristics of the habitat and species involved (I).

2) Resource efficiency in transplantations can be optimised by minimising the size of transplanted fragments (I), and by preparing transplant surfaces with an adhesive solution of the hydrogel Ac-Di-Sol® when performing transplantations of isidia (V).

3) In the natural population survey in Paper II, we found distinct differences in thalli abundance among the *P. norvegica* populations in the core and fringe habitats, and that the marginal *P. norvegica* populations display both morphological and distributional responses to the more continental climate (II). Both less acidic bark pH values and close proximity to open water are important for the occurrence of *P. norvegica* in the continental region, while insignificant in the oceanic core environments (II).

4) Results from the *P. norvegica* survey challenge the common assumption that conditions as a rule are more beneficial, and populations more vital, within the distributional core of a certain species. As indicated by e.g. thalli abundances and sizes within 10 m bordering the streams, conditions for germination and establishment within this zone are fully comparable to those in the oceanic region. In view of the scarcity of protected habitats in central Norway, this thesis suggests that both set-aside protection and restoration of fringe populations can be of great importance to the conservation of endangered suboceanic lichens in Scandinavia (II).

5) As has been shown in this thesis, habitat, microsite, and substrate quality strongly affects vitality in naturally established populations (II), and both short-term survival and prospects for long-term viability in transplanted populations (I). Restorative transplantations should therefore be concentrated to habitats and substrates that can be viewed as optimal for the species in question, in order to enhance the possibilities for long-term viability and persistence of the population. The model developed in Paper III and used in Paper IV may provide a tool for identifying such suitable habitats.

6) Laboratory studies have revealed the previously unknown occurrence of significant PSII activation time lags among the studied hydrophilic species (IV). For *U. longissima* and *B. bicolor*, full activation of photosynthesis was not reached until 24 h after liquid hydration of both species. Also for *P. norvegica* and *L. amplissima* rather significant activation time lags were found, with approximately 90% of full activation being reached after 4 h.

7) Simulations have shown that for three of the four studied hydrophilic species, species-specific PSII activation time lags can, in combination with microclimatic

differences, control photosynthetic performance in a most dramatic manner. For *U. longissima*, activation time lags can under certain microclimatic conditions, reduce potential photosynthetic activity by a factor of five, and that *B. bicolor* is almost as severely affected.

8) In the simulations, both close proximity to streams and the presence of turbulent water had a consistent strong positive impact on realised activity among the studied species (IV). Thus, the observed aggregations of *P. norvegica* close to the streams in the continental fringe habitats may well be due to a dependence of elevated levels of microclimatic humidity provided by the stream (II).

9) The distribution patterns of hydrophilic lichens coincide very well with habitat features that generate high realised activity among the slowly activated species studied here. The occurrence of pronounced activation time lags, which is reported for the first time in the present study, may therefore be one of the physiological causes explaining habitat restrictions in rare hydrophilic lichens.

10) Results obtained in the present thesis - from the transplantation studies, the natural population survey, and the performed PSII activity simulations – recurrently underscore the importance of separating the processes of dispersal, immobilisation and establishment, when studying lichen distributional patterns.

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