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Institutionen för skogens ekologi och skötsel

# How is the distribution of the epiphytic lichen *Usnea longissima* affected by forest structure and logging history within stands?

*Hur påverkar skogsstrukturen och huggningshistoriken förekomsten av den epifytiska laven Usnea longissima på beståndsnivå?*

**Ylva Linnman Wänglund**

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Handledare: Lars Östlund & Torbjörn Josefsson
Examinator: Johnny Schimmel

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This report presents an MSc thesis at the Department of Forest Ecology and Management, Faculty of Forest Sciences, SLU. The work has been supervised and reviewed by the supervisor, and been approved by the examinator. However, the author is the sole responsible for the content.

SLU
Institutionen för skogens ekologi och skötsel
901 83  UMEÅ

# Contents

# Abstract

The boreal forests of Sweden have gone through radical changes during the last c. 100 years due to human activities. Many species, dependent on undisturbed forests with long canopy continuity and old-growth characteristics, are threatened today due to the loss of these habitats. Consequently, there is an urgent need to increase the understanding of these species ecology and habitat demands, so that the right type of habitats can be protected and in quantities enough to support sustainable populations. Studies of the forest history can give enhanced insights into a species habitat demands that might not be possible to learn by simply observing the present forest structure where the species occur. The overall aim of this study was to analyse how the distribution of the old-growth dependent epiphytic lichen *Usnea longissima* Ash. is related to past and present forest structures and logging history in two separate forest stands, both with high occurrence of this lichen. Field studies of the present occurrence of *U. longissima*, the forest structure and traces of past forestry were complemented with aerial photograph interpretations of changes in the forest structure during a 50 year period. Analysis of correlations between the occurrence of *U. longissima* and different stand variables were made at sample plot level and in addition, differences between sub areas, with different abundance of the lichen, were analysed at each study site. The studied forest stands differed in many aspects and both had gone through large changes during the last 50 years due to earlier logging events. At one of the study sites, *U. longissima* mainly occurred in patches that did not have too high canopy closure and timber volume and with minor effects of logging. At the other site, located on a mountain, the occurrence of *U. longissima* was highest in patches that were not too open and where the changes in canopy cover and tree species composition had been small. *U. longissima* was found in patches with rather different forest structure and therefore it is likely that the variations in microclimate, rather than the forest structure per se, is of decisive importance for the distribution of the lichen within a forest stand. This study shows that *U. longissima* can occur in high numbers in forest stands that has gone through relatively large changes, but also that the highest abundance of the lichen often is found in less disturbed patches. Therefore, the results suggest that forests where *U. longissima* occur can be managed by careful selective logging as long as the old-growth structures with an open, but not too open canopy are preserved – allowing for enough light, but preserving the air humidity and the shelter from wind.


**Keywords:** *Usnea longissima*, epiphytic lichen, forest history, stand structure, canopy openness.

# Sammanfattning

Sveriges boreala skogar har genomgått stora förändringar på grund av mänskliga aktiviteter under det senaste ca 100 åren. Många arter, vilka är beroende av skogar med lång trädkontinuitet och gammelskogskaraktärer, är idag hotade på grund av förlusten av dessa habitat. Därför finns det ett stort behov av att öka förståelsen för dessa arters ekologi och habitatkrav, så att rätt typ av habitat kan skyddas i tillräckligt stor utsträckning för att upprätthålla livskraftiga populationer. Skogshistoriska studier kan ge ökad insikt i en arts habitatkrav som kanske inte är möjlig att uppnå endast genom att studera den nuvarande skogsstrukturen där arten förekommer. Det övergripande målet med den här studien var att analysera hur utbredningen av den epifytiska gammelskogslaven långskägg (*Usnea longissima* Ash.) är relaterad till tidigare och nuvarande skogsstruktur och huggningshistorik i två separata skogsbestånd, båda med rikliga förekomster av laven. Fältstudier av den nuvarande utbredningen av långskägg, skogsstrukturen och spår av skogsbruk komplimenterades med flygbildstolkningar av hur skogsstrukturen förändrats under en 50-årsperiod. Analyser av sambanden mellan långskäggsförekomsten och olika beståndsvariabler gjordes på provytenivå och dessutom analyserades skillnader mellan delområden med olika frekvens av träd med långskägg på vartdera studieområde. De studerade skogsbestånden skilde sig åt i flera avseenden och båda hade genomgått stora förändringar under de senaste 50 åren på grund av tidigare huggningar. I ett av studieområdena förekom långskägg främst på platser som inte hade för hög slutenhet och volym och som endast i mindre omfattning var påverkade av skogsbruk. I det andra studieområdet, vilket utgjordes av en bergssluttning, fanns de rikligaste långskäggsförekomsterna på platser som inte hade för öppen skogstruktur och där förändringar av slutenheten och trädslagssammansättningen endast hade varit små. Långskägg påträffades på platser med relativt olika skogsstruktur och det är därför möjligt att det är variationerna i mikroklimatet, snarare än skogsstrukturen i sig, som är av avgörande betydelse för utbredningen av långskägg inom ett skogsbestånd. Denna studie visar att långskägg kan förekomma i stora mängder i skogsbestånd som har genomgått relativt stora förändringar, men också att de rikligaste förekomsterna finns på platser där störningarna har varit mindre. Resultaten tyder på att skogar med långskägg kan skötas genom skonsam plockhuggning så länge den öppna, men inte för öppna gammelskogsstrukturen bevaras, så att ljusinsläppet blir tillräckligt samtidigt som luftfuktigheten och skyddet från vind bibehålls.

**Nyckelord:** *Usnea longissima*, epifytiska lavar, skogshistorik, beståndsstruktur, slutenhet.

# Introduction

The area of natural forests (i.e. forests with relatively minor human impact) has decreased dramatically in northern Sweden during the last 100 years due to the increasing demand for timber products. Natural disturbances, like gap dynamics and wildfire, have been replaced by forest management methods that radically have altered the forest structures and disturbance regimes (Linder & Östlund 1998, Kuuluvainen 2002). Natural disturbances create environmental heterogeneity in space and time and this is one of the most important factors determining biodiversity (Kuuluvainen 2002). Many threatened species are dependent on relatively undisturbed forests with long canopy continuity and old-growth characteristics. Consequently, the loss of natural, old-growth forests is a threat to the survival of such species (Linder & Östlund 1998).

There is an urgent need to increase the understanding of the ecology and habitat demands of today's threatened species so that the right type of habitats can be protected and in quantities enough to support sustainable populations. A complicating factor is that sometimes the place, where a species occur today, is not necessarily the optimal habitat for it. Species that are dependent on long forests canopy continuity, like many epiphytic lichens, often have low dispersal abilities. Therefore it has to be taken in to account that the structure of forest where a species is found today might have been altered a lot since the species first colonised it. For example the current population might be only a small remnant of a previously much bigger population. Consequently studies of the forest history can give enhanced insight into a species habitat demands and give clues to the future prospect of the species survival.

Forests with rich occurrence of certain lichens also often host many endangered invertebrates and fungi. Therefore these lichens can be utilised as indicator species for ecosystems with rich occurrences of many threatened species (Olsen & Gauslaa 1991, Nitare 2000). However, the understanding of lichens responses to site factors and disturbances must increase so that efficient methods for restoring lichen populations in managed forests can be developed (Will-Wolf et al 2006a).

*Usnea longissima* Ach. is an epiphytic lichen dependent on old-growth spruce forests (Esseen et al 1981, Esseen & Ericson 1982, Olsen & Gauslaa 1991). The distribution of this lichen has strongly decreased in many parts of Europe due to increasing logging and air pollutions during the last c. 100 years (Esseen & Ericson 1982). Epiphytic lichens often have poor dispersal ability and therefore dispersal into young forests after intensive logging or clear cutting is limited (Dettki et al 2000, Muir et al 2006). *U. longissima* is considered to be strongly affected by modern forestry and does not survive clear cutting, but under optimal conditions it can spread into young forests and in Norway it has been observed in a 35 years old forest (Turander & Oldhammer 2003). In forests where *U. longissima* does occur, its distribution on stand level is patchy and unpredictable (Olsen & Gauslaa 1991, Gauslaa et al 1998, Josefsson et al 2005). This fact is one of the main sources of inspiration to this study. Most studies of epiphytic lichens have investigated differences between forest stands and few have focused on the distribution of lichens within stands. Therefore, this study was carried out within two different forest stands with different stand characteristics but still hosting a large number of trees with *U. longissima*. The study design allowed for a spatially precise approach, but also for a comparison of the two study sites.

The overall aim of this study was to analyse how the distribution of *U. longissima* is related to past and present forest structures and logging history in two separate forest stands, both with high occurrence of this lichen. The specific questions I wanted to answer were: (1) in what aspects does the forest structure differ between the two study sites (forest stands), (2) does the present distribution of *U. longissima,* within stands, have any correlation to stand variables like canopy closure, basal area, tree age and timber volume in sample plots, (3) do sub areas with different density of trees with *U. longissima* differ when it comes to stand structure, (4) what is the logging history in areas with occurrence of *U. longissima*, (5) is there any correlation between previous timber harvestings and the distribution of *U. longissima* and (6) how has the canopy cover and tree species composition changed since the middle of the 20$^{th}$ century (interpreted from aerial photographs)?

# Materials and methods

## *The study area*

The study area is situated in the county of Västernorrland in the middle boreal forest zone of Sweden, about 14 km west-southwest of the town of Kramfors. In this area inventories were carried out at two different locations, Sör-Lappmyran and Hugstmyrhöjden (Figure 1). The distance between the two study sites is approximately 4 km.

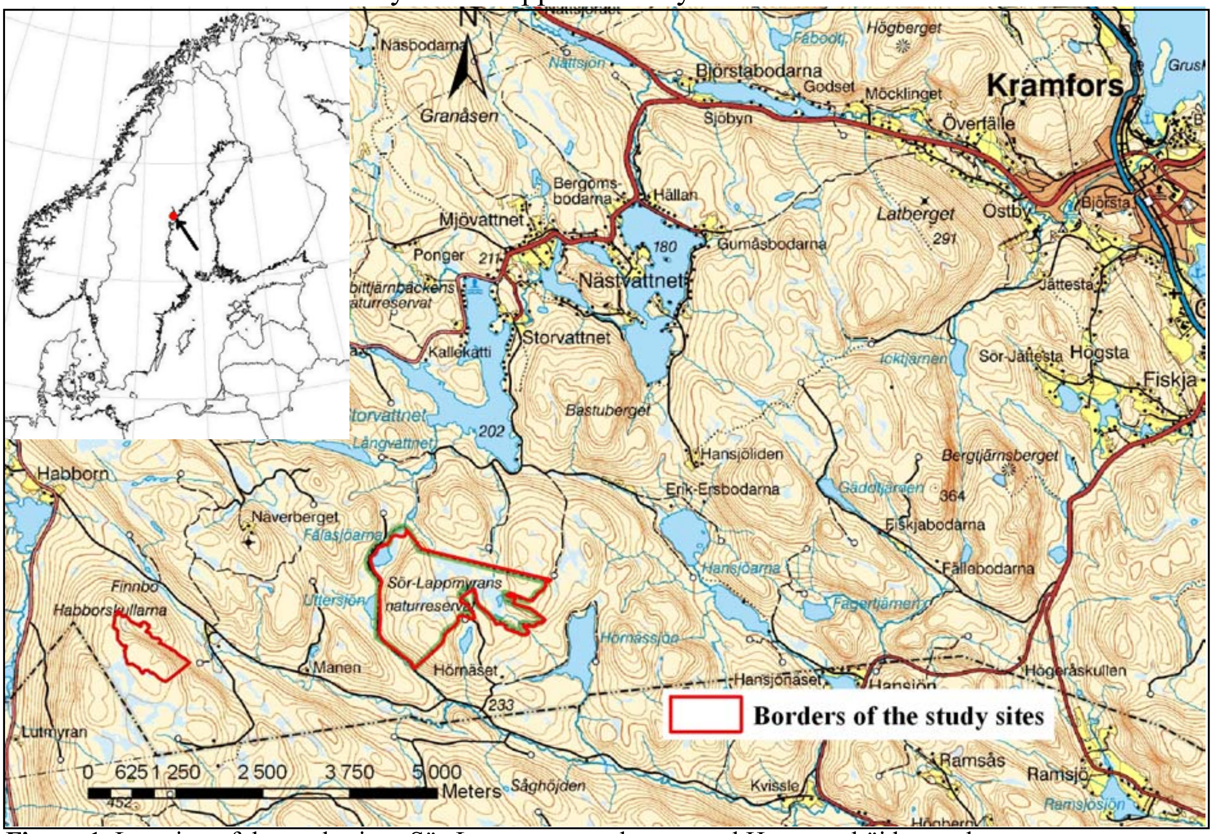



**Figure 1.** Location of the study sites, Sör-Lappmyran to the east and Hugstmyrhöjden to the west.


Sör-Lappmyran was designated a nature reserve in 1998 and one of the main purposes was to preserve the rich occurrence of the epiphytic lichen *U. longissima*. The site Hugstmyrhöjden is a mountain, on which *U. longissima* thrive on the slow growing spruces. This site is not formally protected as a nature reserve, but is listed as a site which should not be logged by the forest owner. Both Sör-Lappmyran and Hugstmyrhöjden is owned by the forest company

Svenska Cellulosa Aktiebolag (SCA). The mean precipitation in the area is approximately 725 mm per year and the mean annual temperature about 3ºC (Alexandersson 2001). The bedrock is primarily sedimentary gneiss of greywacke origin with dikes or small massifs of granite, pegmatite and aplite (Lundqvist 1990) and the soil is mainly sandy till (and peat) with medium boulder frequency (Lundqvist 1987).

At the site Sör-Lappmyran, inventories were carried out on the hills west and south of the mires Lappmyran and Sör-Lappmyran. These are the parts which have richest occurrence of *U. longissima*. Other epiphytic lichens like *U. filipendula* Stirt., *Alectoria sarmentosa* (Ash.) Ash., *Bryoria* spp. and *Lobaria pulmonaria* (L.) Hoffm. are abundant here. The red-listed lichen *Bryoria nadvornikiana* (Gyeln.) Brodo & D. Hawksw. also occurs here. The ground vegetation is dominated by *Vaccinium myrtillus* (L.) and mosses like *Hylocomium splendens* (Hedw.) Schimp., *Pleurozium schreberi* (Brid.) Mitt. and *Dicranum* spp., but also the less common *Plagiothecium undulatum* (Hedw.) can be found. Norway spruce [*Picea abies* (L.) Karst.] dominates the forest, but there are also birch (*Betula* spp.) and Scots pine (*Pinus sylvestris* L.) scattered over the forest stand and in some places the occurrence of large Aspen (*Populus tremula* L.) is rich. The elevation in the nature reserve ranges from 270 to 360 m above sea level (a.s.l.), and the studied parts are situated between c. 310 and 360 m a.s.l.

The inventoried area on Hugstmyrhöjden is at a higher elevation than Sör-Lappmyran, i.e. between c. 400 and 455 m a.s.l. The forest here is dominated by Norway spruce, although less dense than the forest in the nature reserve, and there are fewer Scots pine trees. The ground vegetation composition is similar to Sör-Lappmyran, but the productivity is lower because of the harsher climate, due to the higher elevation and exposure to the north. The upper part of Hugstmyrhöjden is also more exposed to wind and snow, therefore top breaks on older spruces are more common here and the trees are generally shorter.

## *Forest history of the study area*

The study area is located in a region called Ådalen, the river valley of Ångermanälven. Ådalen was one of the most important areas for the development of the forest industry in northern Sweden (Björklund 1992). Already at the end of the 16$^{th}$ century settlements were established at Mjövattnet and Nästvattnet close to the two study sites (Figure 1) by Finnish immigrants (Gothe 1948). The combined effect of colonisation and population growth induced an agrarian development. The impact on the forest increased as a result of slash and burn cultivation, grazing by cattle and felling of trees for firewood and building material (Östlund 1993). However, it was only the immediate surroundings of the settlements and summer farms that were affected by this agrarian forest utilisation (Östlund 1993). It was not until later, in the early 18$^{th}$ century, that the forest utilisation started to have a more profound impact at larger scales. During this time the demand for charcoal for the ironworks significantly increased.

During the first decade of the sawmill epoch (in the middle of the 19$^{th}$ century) the forests in the river valley of Ångermanälven was heavily exploited and forest fires, due to human activities, was common (Johansson 2003). The development of the Swedish timber products industry was closely related to the industrial revolution in western Europe and the increasing demand for sawmill products. In the middle of the 19$^{th}$ century, when the demand for sawn products increased rapidly on the European market, the forest exploitation in the area was intensified (Lundberg 1984). Regeneration of forests after fires had almost ceased during the end of the 19$^{th}$ century (Fahlgren 1995). At the same time large-scale logging (high-grading) was introduced, which resulted in removal of the large diameter trees (mainly Scots pine) and a drastic reduction of the standing volume, creating more open forests with smaller conifer trees and more deciduous trees (Östlund 1993).

The pulp industry was established in northern Sweden in the late 19$^{th}$ century and therefore it was possible to use smaller trees and also Norway spruce (Björklund 1992). From the 1850's to the 1930's the felling intensity continuously increased and since the logging companies accepted thinner and thinner dimensions, forests that had already been subject to high-grading could be exploited again (Linder & Östlund 1992). Although thinner dimensions now had a market, there was a strong resistance against the clear cutting method. Selection felling was still the prevailing method since it was believed that remaining trees would increase their growth and that tree seedlings would naturally regenerate in the gaps of felled trees. Later experiences, however, showed that there was not sufficient growth increment or regeneration (Johansson 2003). During the time of World War I and II the export of timber decreased, but the need for fuel wood increased, which again changed the utilisation of the boreal forests (Östlund 1993). Eventually modern forestry utilisation with clear cuttings started in the middle of the 20$^{th}$ century (Arpi 1959). Today both Hugstmyrhöjden and Sör-Lappmyran are mainly surrounded by much younger forests and north of Sör-Lappmyran there are plantations of the exotic species lodge pole pine (*Pinus contorta* Dougl. ex Loud.). Both study sites are bordered by clear cuts with young trees on the south-east sides.

## *Morphology and ecology of Usnea longissima*

The epiphytic lichen *U. longissima* has a pendulous growth form and can become several meters long (Figure 2). The 1-2 mm thick thallus is pale green-grey and sparsely branched or unbranched, but has plenty of 1-2 cm long fibrils (Nitare 2000). The main stem lacks continuous cortex tissue, and therefore the grey-white and somewhat elastic core can be seen between the fibrils (Esseen & Ericson 1982). In contrast to the majority of fruticose epiphytic lichens *U. longissima* usually lacks holdfast and is instead loosely winded around branches (Gauslaa 1997). By occupying the space between the branches and having little contact with the substratum the competition with other lichens is reduced (Gauslaa 1997).

**Figure 2.** Long thallus of *Usnea longissima*. Photo by the author.

*U. longissima* has a widespread and incomplete circumpolar distribution (Ahlner 1948). In Europe the largest populations occur in Scandinavia, mainly in south-eastern Norway (Gauslaa et al 1998). In Sweden it is rare and grows almost exclusively on spruce in older forests that have not been subject to forestry to any lager extent (Ahlner 1948, Nitare 2000). Today the distribution of *U. longissima* reaches from the provinces of Värmland to Medelpad and the coast of Västerbotten with the highest abundance in the eastern part of the proveniences of Ångermanland and Medelpad (the county of Västernorrland) (Figure 3) (Ahlner 1948, Nitare 2000). There are also some isolated occurrences in the county of Norrbotten (Nitare 2000).

**Figure 3.** Occurrence of *U. longissima* in Sweden. Source: Nitare 2000.

The habitat consists of moist, slow growing and old spruce forests. In these forests *U. longissima* can be found on north and east facing slops, but also in the vicinity to mires, i.e. places where the local climate has a constantly high and even humidity (Esseen et al 1981, Nitare 2000). The distribution within tree canopies is usually limited to the lower parts, not often higher than 7 meters above ground (Olsen & Gauslaa 1991). There is also a large variation of the lichen distribution between neighbouring trees (Gauslaa et al 1998). The lichen is often found on the highest mountains in the landscape but close to the coast it can occur on lower elevations (Nitare 2000). Light is also an important factor determining the distribution and growth of *U. longissima* (Gauslaa 1997, Nybakken et al 2007) and it is believed to be very susceptible to draught and wind (Esseen et al 1981, Nitare 2000). *U. longissima* is often found in places that are shaded in the middle of the day, but that still receives much light (Olsen & Gauslaa 1991). In localities with *U. longissima* many trees are old and some of them have reduced vitality. Top breaks and dead trees also occur (Esseen & Ericson 1982, Olsen & Gauslaa 1991).

*U. longissima* has traditionally been used as a symbol of virgin forests since it is believed to be extremely sensitive to environmental disturbances, i.e. due to its very specific habitat demands and low dispersal ability (Esseen et al 1981). Under favourable conditions with large populations of *U. longissima* the lichen seems to have better dispersal ability (Keon 2002, Turander & Oldhammer 2003). In Sweden the dispersal is solely vegetative, for example through spread of small thallus fragments down the canopy or by wind (Gauslaa 1997). This dispersal strategy is of great importance for *U. longissima* together with many other filamentous lichens (Esseen 1985). Vegetative dispersal can, less commonly, also occur by formation of soredia and isidia, which enables the lichen to spread longer distances (Olsen & Gauslaa 1991, Gauslaa 1997). Apothecia formation is unusual and has never been observed in Sweden (Ahlner 1948, Nitare 2000).

## *Study design and field inventories*

Maps, showing areas with high occurrences of *U. longissima* in the study sites, were provided by the County Administrative Board (CAB) of Västernorrland. On these maps a 75×75 m cell-sized grid was placed in order to obtain coordinates for the sample plots (circles, 0.1 ha in size). In field, however, it was discovered that the lichen had a very patchy distribution and consequently in many sample plots there was no *U. longissima*, but right outside the border there were trees with the lichen. In order to receive enough sample plots with occurrence of *U. longissima* the grid was condensed (half the cell size) in these places.

The field inventory was carried out in the late summer of 2007. At each sample plot, basal areas for each tree species and for dead trees were recorded using a relascope. Randomly chosen trees were cored using increment borers (Ø 4.5 mm). Also, two trees of representative species for the sample plot and with the largest diameter in breast height were cored and their heights (dominant height) were measured with a hypsometer. All trees were cored as close to the germination point as possible. Trees affected by rot were cored at breast height. The timber volume per hectare was determined for each sample plot using a table (Karlsson & Westman 1987) where the inputs were basal area and dominant tree height. Stumps that could indicate logging were counted and categorised into different classes: 1) stumps of Norway spruce and 2) stumps of Scots pine 3) birches with a bouquet like growth form, which can indicate earlier logging of fire wood. The number of trees with *U. longissima* and their coordinates were recorded. Coordinates for the trees with *U. longissima* and the centre of the sample plots were determined using a GPS (Swedish topographic system RT90). The altitude for each sample plot was also given by the GPS. Notes about the vegetation, terrain, location etc at each sample plot were also recorded.

Analyses of sub areas of the study sites were performed in order to distinguish possible spatially-dependent differences that could explain the distribution of *U. longissima* within the stands. The sample plots on each of the two study sites were subjectively divided into three smaller sub areas where the forest structure was more similar (Figure 7). The division was also based on the number of trees with *U. longissima* in the sample plots and some sample plots were not included in any sub area since they were located in areas of the study sites with extremely patchy distribution of the lichen. At each study site sub areas with low, medium and high abundance of *U. longissima* were distinguished.

## *Canopy closure*

In field, two photographs of the canopy were taken in the centre of each sample plot by placing a digital camera horizontally on a stool and taking one picture with the camera in a north-south direction and one in the east-west direction. The photographs were later analysed in Adobe Photoshop CS2, version 9.0. Each picture was converted to black and white by giving it a threshold value so that all pixels with a lower colour value became black and the pixels with a higher colour value became white. In the histogram, the channel luminescence was selected and a histogram without cache stored data was chosen. This way the percentage of pixels darker than the threshold value was received. The method gave a precise measurement of the canopy closure in the middle of the sample plots. The canopy closure was defined as the percentage of dark pixels and can also be looked upon as the proportion of the sky obscured by the canopy. For further information about this method see Korhonen et al 2006.

## *Age and growth response analyses*

In laboratory the ages of the cored trees were determined using a stereo magnifier, scalpel and zinc paste. A transparent plastic sheet with concentric circles was used to calculate the amount of missing tree rings on the samples where the increment cores had missed the pith. In total the age of 232 trees were determined, 123 from Sör-Lappmyran and 109 from Hugstmyrhöjden, out of which 10 trees from each study site were carrying *U. longissima*. In addition, two bouquet birches were cored in order to obtain information about when felling of birch for fire-wood had been carried out on Hugstmyrhöjden. Also, one big birch (not in bouquet form) was cored in attempt to find out when the generation of birches, which has been subject to firewood felling on Hugstmyrhöjden, had originated.

During the age estimations the cores were also checked for growth responses which can indicate disturbance events. A growth response was defined as an increment in mean tree ring width with at least 100 % between two successive 10-year periods. Growth responses can indicate logging events but also other disturbances that results in better growth conditions for some trees, e.g. storm felling and self thinning. To identify possible logging events the amount of trees with growth responses within a 10-years period from every year since 1775 was estimated. Similar methods for analysing logging events have been used by Groven et al (2002) and Josefsson et al (2005).

### Aerial photographs

Aerial photographs from the study sites taken in 1958 were analysed and compared to aerial photographs from 1999 (the newest aerial photographs available). These photographs were provided by the National Land Survey of Sweden in Gävle. The photos from 1985 were in black and white, while the ones from 1999 were in infra-red. From these photographs the tree species composition, canopy cover (volume density) and number of tree layers could be interpreted and the tree height could be measured. The tree species composition was interpreted as the proportions of Scots pine, Norway spruce and deciduous trees. Canopy cover interpretations were in terms of volume density, i.e. the volume of a stand in relation to the volume of a completely closed stand in accordance to some reference table (Karlsson & Westman 1987). In this way changes in the forest structure were studied. All the sample plots from the field inventories were analysed by a professional aerial photograph analyst.

### Statistical analyses

To relate the number of trees with *U. longissima* to independent forest stand variables (canopy closure, tree age, timber volume, basal area, tree height, number of stumps and canopy cover in 1958 and 1999) linear regression analysis was used. Furthermore, stepwise multiple regressions were performed to analyse which combinations of independent variables most effectively explained the occurrence of *U. longissima* within stands. Analysis of variance (ANOVA) was used to analyse differences in forest stand variables between the sub areas displaying different abundance of *U. longissima*. The outcomes of the results were reported significantly different on the basis of a significance level of $\alpha$=0.05. All statistical analysis were preformed using MINITAB® 14.1 software.

## Results

### General stand structure at the study sites

The forest at both sites was characterised by a partially open stand structure with a relatively uneven age-composition (Table 1). The forest structure on Sör-Lappmyran was relatively uniform. Hugstmyrhöjden, on the other hand had a more variable forest structure with rather open forest on the summit of the mountain and denser on the hillsides. Therefore variables like basal area and canopy closure varied more between the sample plots here. On average, Hugstmyrhöjden also had a less dense forest structure with lower values of basal area, timber volume and canopy closure compared to Sör-Lappmyran.

Norway spruce dominated the forest stands at both study sites, but Scots pine and deciduous trees, *Betula* spp. and *P. tremula*, also occurred (Figure 4). Large individuals of these deciduous species were found on Sör-Lappmyran. The trees on Hugstmyrhöjden were generally older and shorter compared to the trees on Sör-Lappmyran.

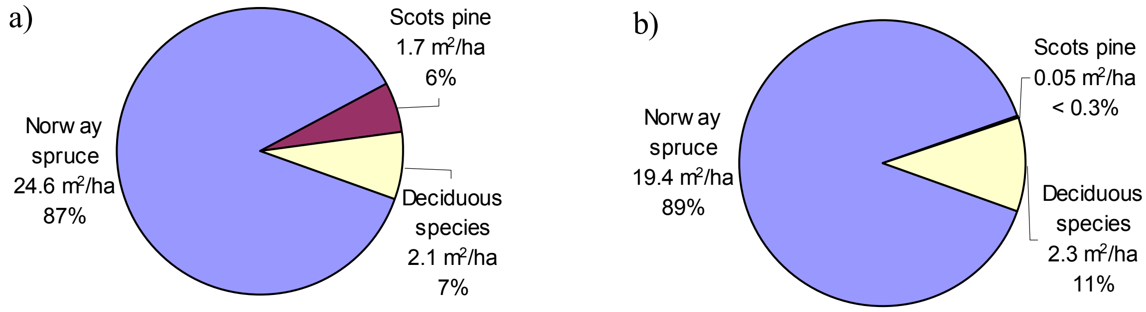



**Figure 4.** Mean basal area and tree species composition for Sör-Lappmyran to the left (a) and Hugstmyrhöjden to the right (b). The percentage values are percent of mean basal area for all species together.

*U. longissima* was relatively common at both study sites (Table 1), but with an aggregated distribution within the stands and therefore no lichen were found on many sample plots (Figure 5). In total 223 trees with *U. longissima* were found on the sample plots at the study sites; 116 on Sör-Lappmyran and 107 on Hugstmyrhöjden. The lichen was growing on both living and dead trees, mainly on Norway spruce, but two birches with several thalli were found on Sör-Lappmyran. Trees with *U. longissima* were generally older than trees without the lichen, especially on Hugstmyrhöjden. Noteworthy, the average age of the trees with *U. longissima* on Hugstmyrhöjden was higher than the age of the oldest cored tree with the lichen on Sör-Lappmyran. Only one of the trees with *U. longissima* was younger then 100 years and the oldest one were 172 and 245 years on Sör-Lappmyran and Hugstmyrhöjden respectively (Table 1). However, two trees without *U. longissima* older than 300 years were found on Hugstmyrhöjden. The oldest one, a Norway spruce, was 362 years old.

**Table 1.** Stand characteristics derived from field sampling in 45 sample plots at Sör-Lappmyran and Hugstmyrhöjden. [a] Average value for the two thickest trees on every sample plot.

| | **Sör-Lappmyran** | | **Hugstmyrhöjden** | |
|---|---|---|---|---|
| **Variables** | Mean | Range | Mean | Range |
| No. of sample plots | 23 | | 22 | |
| Basal area ($m^2$/ha) | 28 | 15-49 | 22 | 12-39 |
| Dominant height (m) [a] | 22 | 16.0-27.1 | 19 | 12.4-25.8 |
| Timber volume ($m^3$/ha) | 241 | 100-355 | 160 | 75-380 |
| Canopy closure (digital photos) (%) | 50 | 14-75 | 34 | 10-67 |
| Tree age (years) | 130 | 62-260 | 137 | 54-362 |
| Age of trees with *U. longissima* (years) | 138 | 112-172 | 174 | 89-245 |
| Trees with *U. longissima* (no./ha) | 50 | 0-290 | 49 | 0-290 |
| Norway spruce stumps (no./ha) | 80 | 0-250 | 55 | 0-130 |
| Scots pine stumps (no./ha) | 39 | 0-80 | 20 | 0-110 |
| Bouquet birch (no./ha) | 4 | 0-40 | 30 | 0-120 |
| Stumps total (no./ha) | 123 | 40-270 | 105 | 10-190 |

The forest at both study sites have been affected by selective logging of Scots pine, Norway spruce and birch. Sör-Lappmyran had more stumps of Norway spruce and Scots pine, while the quantity of bouquet birch was much higher on Hugstmyrhöjden. However, the number of stumps in total was highest on Sör-Lappmyran (Table 1). Another trace of human impact was ditches on the mires in vicinity to the study site on Sör-Lappmyran.

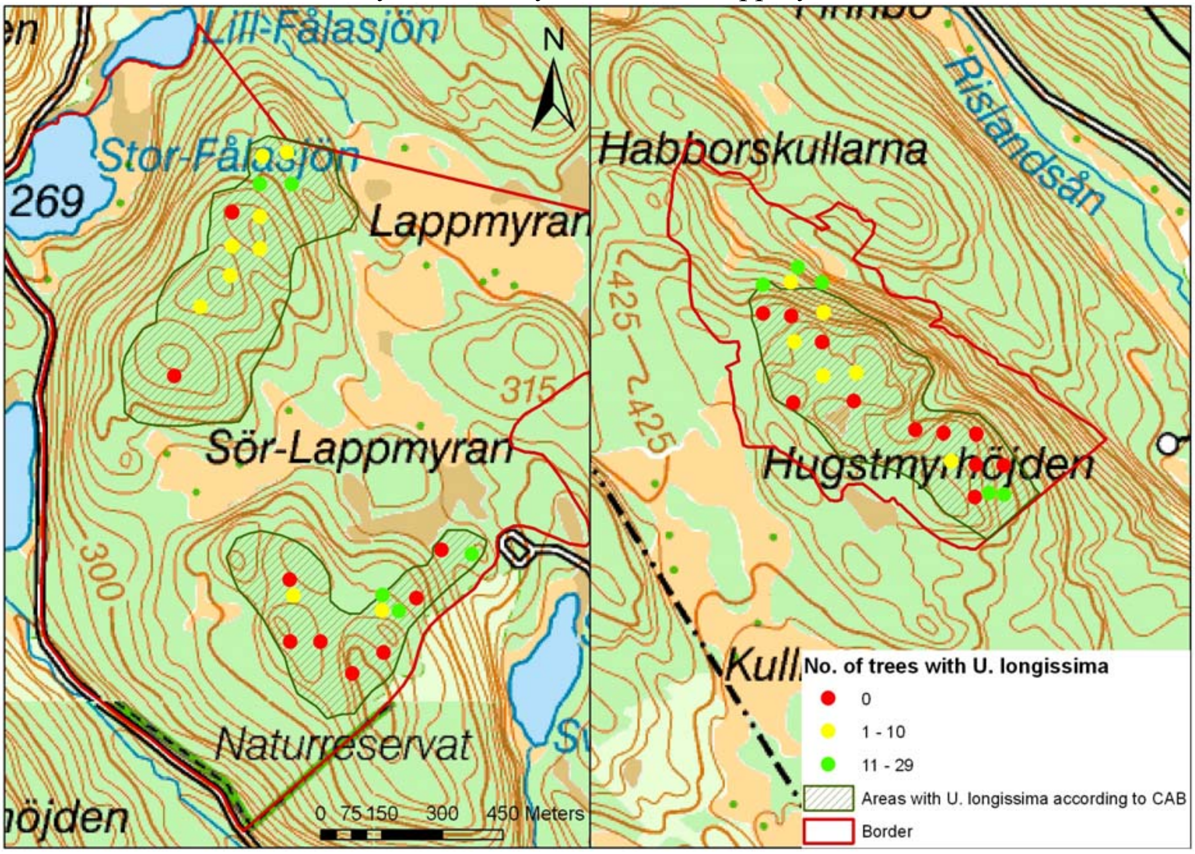



**Figure 5.** The distribution of the sample plots on Sör-Lappmyran (left) and Hugstmyrhöjden (right). The sample plots are divided into tree classes based on the number of trees with *U. longissima*. Green striped areas are areas with high occurrences of *U. longissima* according to the County Administrative Board (CAB).


## *Relationships between present stand structures and the distribution of Usnea longissima at sample plot level*

The number of trees with *U. longissima* compared to basal area, number of stumps, canopy closure, timber volume and tree height showed no significant correlations (data not shown) in any of the study sites. However, there was a significant correlation between amount of trees with *U. longissima* and mean age on Sör-Lappmyran (F= 4.65, $p$<0.05) (Figure 6a). The number of trees with *U. longissima* increased with higher mean age also at Hugstmyrhöjden, although not significantly (F= 4.08, $p$=0.057) (Figure 6b).

a)

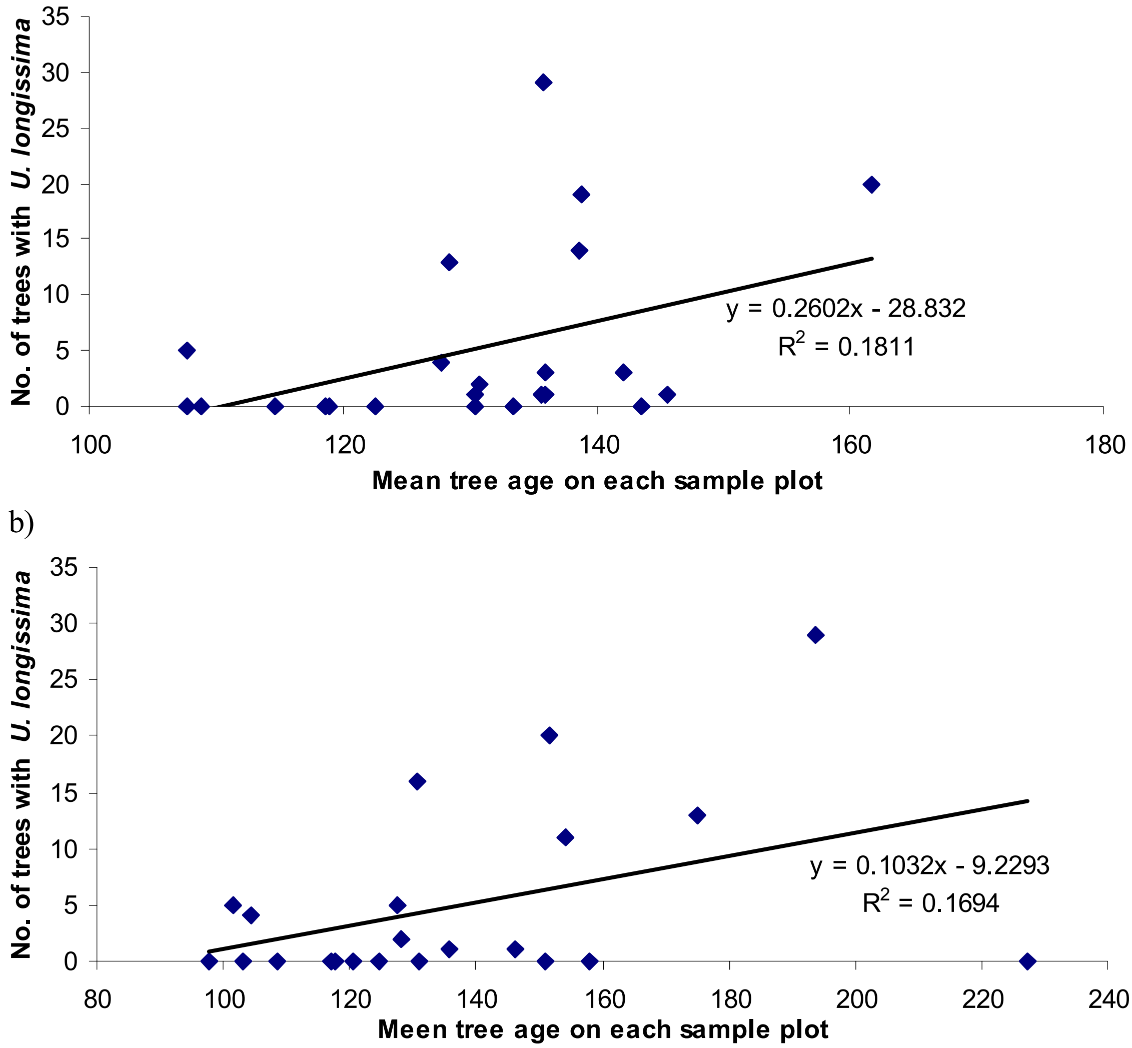



**Figure 6.** The relationship between the number of trees with *U. longissima* and average age of the cored trees on each sample plot on Sör-Lappmyran (a) and Hugstmyrhöjden (b).

When comparing the canopy closure with the number of stumps, a significant correlation was found on Hugstmyrhöjden; the canopy closure decreased with increasing number of stumps (F= 6.34, $p$<0.05). No such relationship was detected on Sör-Lappmyran. Other significant correlations were the relationship between basal area and canopy closure on both study sites (F=6.52, $p$<0.05 for Sör-Lappmyran and F=28.43, $p$<0.000 for Hugstmyrhöjden), the relationship between canopy cover 1999 (aerial photographs) and basal area (F=6.33, $p$<0.05 for Sör-Lappmyran and F=23.32, $p$<0.000 for Hugstmyrhöjden) and the relationships between canopy closure (digital photos) and canopy cover 1999 (aerial photos) (F=5.45, $p$<0.05 for Sör-Lappmyran and F=15.87, $p$<0.05 for Hugstmyrhöjden).

In the multiple regression analyses, relating the number of trees with *U. longissima* to all the studied stand variables, tree age and basal area in combination was the best predictor of the number of trees with *U. longissima* on Sör-Lappmyran (F=6.33, $p$<0.05) (Table 2). The number of trees with *U. longissima* was positively correlated to tree age and negatively correlated to basal area. Also tree age and timber volume in combination emerged as a predictor of the number of trees with *U. longissima*, (F=5.39, $p$<0.05) (Table 2). The number of trees with the lichen was negatively correlated to timber volume and positively correlated to tree age (Table 2). On Hugstmyrhöjden, tree age in combination with the number of Scots pine stumps was the best predictor of the number of trees with *U. longissima* (F=4.27, $p<0.05$) as it was positively correlated to tree age and negatively correlated to the amount of Scots pine stumps.

**Table 2.** Results of the stepwise multiple regression analyses between the number of trees with *U. longissima* and tree age (TA), basal area (BA), timber volume (TV) and stumps of Scots pine (SSP) for 23 sample plots on Sör-Lappmyran and 22 sample plots on Hugstmyrhöjden. Independent variables were included in the model when $p<0.05$, except for number of Scots pine stumps ($p=0.064$).

| Response | Predictor | $R^2$ | $p$ |
|---|---|---|---|
| No. of trees with *U. longissima* - Sör-Lappmyran | TA (+), BA (-) | 0.387 | 0.007 |
| No. of trees with *U. longissima* - Sör-Lappmyran | TA (+), TV (-) | 0.350 | 0.013 |
| No. of trees with *U. longissima* - Hugstmyrhöjden | TA (+), SSP (-) | 0.310 | 0.029 |

## *Relationships between present stand structures and the distribution of Usnea longissima in sub areas of the study sites*

The sub areas with high and medium abundance of *U. longissima* were situated close to each other while the sub area with low lichen abundance was separated from the other sub areas in both study sites (Figure 7). The mean values of trees with *U. longissima* per sample plot on each sub area on Sör-Lappmyran were: high: 14.50, medium: 1.67, low: 0.17. For Hugstmyrhöjden the corresponding values were: high: 11.20, medium: 1.40, low: 0.67.

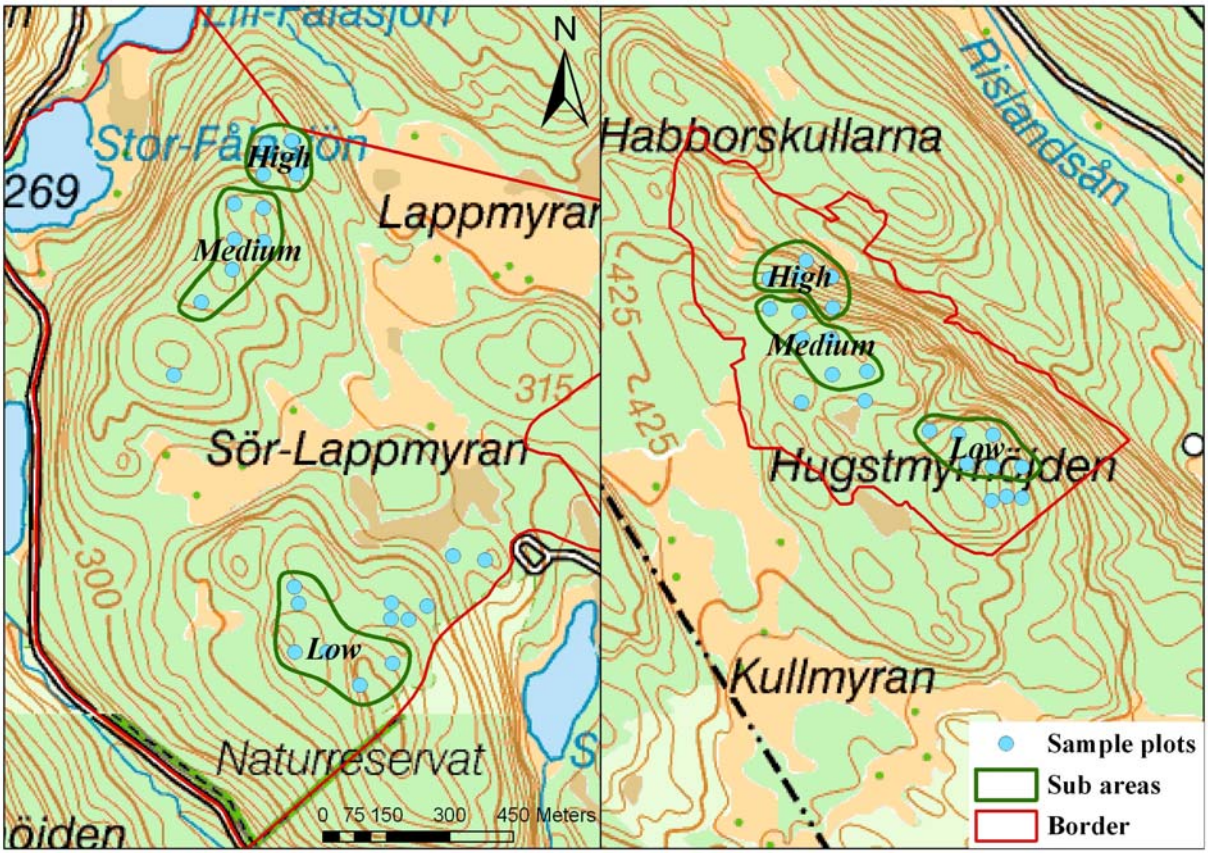


**Figure 7.** The sample plots on each study site divided into sub areas; High – high abundance, Medium – medium abundance and Low – low abundance of *U. longissima*. Sör-Lappmyran to the left and Hugstmyrhöjden to the right. © Lantmäteriverket Gävle 2007. Medgivande I 2007/2346.

When comparing sub areas with different abundance of *U. longissima*, significant differences in mean tree age of the two oldest trees was found on Sör-Lappmyran (Table 3). The mean age for the two oldest trees on each sample plot increased with the abundance of trees with *U. longissima*.

On Hugstmyrhöjden significant differences in basal area, number of stumps of Norway spruce, number of Bouquet birch and canopy cover in 1999 were detected (Table 3). The basal area was highest in the sub area with high abundance of *U. longissima* and lowest in the sub area with low lichen abundance. The mean number of Norway spruce stumps was lower in the sub area with low abundance of *U. longissima* compared with the other two sub areas, while the amount of bouquet birches decreased with increasing abundance of lichen. Also the canopy cover was significantly lower on the sub area with low abundance of *U. longissima* than on the other two sub areas.

Other notable differences between the sub areas on Hugstmyrhöjden, which did not turn out to be significant, were increasing dominant height with increasing abundance of *U. longissima* and higher timber volume on the sub area with high abundance of *U. longissima* (Appendix 2). Also, the sub areas with high and medium abundance of *U. longissima* did not differ much in canopy closure, but the sub area with low abundance of the lichen had noticeable lower canopy closure. This is the opposite to what was found on Sör-Lappmyran, where canopy closure, basal area and timber volume were lower in the sub area with high abundance of *U. longissima* (Appendix 1). In fact, the canopy closure and timber volume was almost as low here as in the sub area with low abundance of *U. longissima* on Hugstmyrhöjden. On Hugstmyrhöjden the number of Scots pine stumps did not differ much between the sub areas with high and medium abundance of *U. longissima*, but it was much higher in the area with low abundance of the lichen. Total number of stumps was slightly lower (not significantly) in the area with high lichen abundance, which was also the case on Sör-Lappmyran.

**Table 3.** One way ANOVA test for differences in forest stand variables between sub areas with different abundance of *U. longissima*. Only the variables showing a significant difference ($p< 0.05$) between the sub areas are displayed (both study sites included).

| Predictor | Sub area | Mean | StDev | F | *p* |
|---|---|---|---|---|---|
| Average age, 2 oldest trees | High | 170.38 | 28.74 | 4.72 | 0.029 |
| Sör-Lappmyran | Medium | 147.58 | 5.56 | | |
| | Low | 135.92 | 16.23 | | |
| Basal area | High | 27.20 | 6.83 | 6.56 | 0.011 |
| Hugstmyrhöjden | Medium | 23.80 | 6.38 | | |
| | Low | 15.33 | 3.56 | | |
| Norway spruce stumps | High | 8.00 | 2.35 | 8.29 | 0.005 |
| Hugstmyrhöjden | Medium | 7.60 | 2.07 | | |
| | Low | 2.00 | 3.46 | | |
| Bouquet birch | High | 0.40 | 0.89 | 3.96 | 0.045 |
| Hugstmyrhöjden | Medium | 3.00 | 2.00 | | |
| | Low | 5.67 | 4.59 | | |
| Canopy cover 1999 (%) | High | 76.40 | 13.69 | 7.71 | 0.006 |
| Hugstmyrhöjden | Medium | 75.60 | 4.16 | | |
| | Low | 51.50 | 14.69 | | |

## *Changes in forest structure and the distribution of Usnea longissima within stands*

Stumps indicating logging events were found all over the two study sites, including areas with occurrence of *U. longissima*. Also 111 growth responses, indicating responses to disturbance events, was detected on 86 of the examined trees. On Sör-Lappmyran, three periods with increased number of trees with growth responses were detected: 1898-1909, 1926-1934, and 1968-1977. The growth response data from Hugstmyrhöjden was more difficult to interpret since no distinct peaks were detected. However, there seemed to be three periods with increased amount of growth responses here as well, although not as clear: in the late $19^{th}$ century, in the beginning of the $20^{th}$ century and the last period in the mid $20^{th}$ century. The two birches that were cored to obtain information about when firewood logging had been carried out on Hugstmyrhöjden were dated to 1942 and 1910. The birch representing the generation of birches subjected to firewood felling on Hugstmyrhöjden had originated in 1887.

The aerial photography interpretations revealed large changes in canopy cover during the last 50 years. On the aerial photography of Hugstmyrhöjden from 1958 a large clear cut area was detected on the south and west sides of the study site. Apart from this, both study sites were surrounded by continuous old forests in 1958. The aerial photographs also showed that the canopy cover was much more variable on Hugstmyrhöjden than on Sör-Lappmyran, both in 1958 and 1999 (Table 4). The canopy cover has increased considerably since 1958 at both study sites.

**Table 4.** Canopy cover in percent 1958 and 1999. Data form aerial photographs.
Mean values for all sample plots.

| | **Sör-Lappmyran** | | **Hugstmyrhöjden** | |
|---|---|---|---|---|
| **Variables** | Mean | Range | Mean | Range |
| Canopy cover 1958 (%) | 71 | 50-95 | 54 | 10-85 |
| Canopy cover 1999 (%) | 80 | 55-110 | 65 | 25-100 |

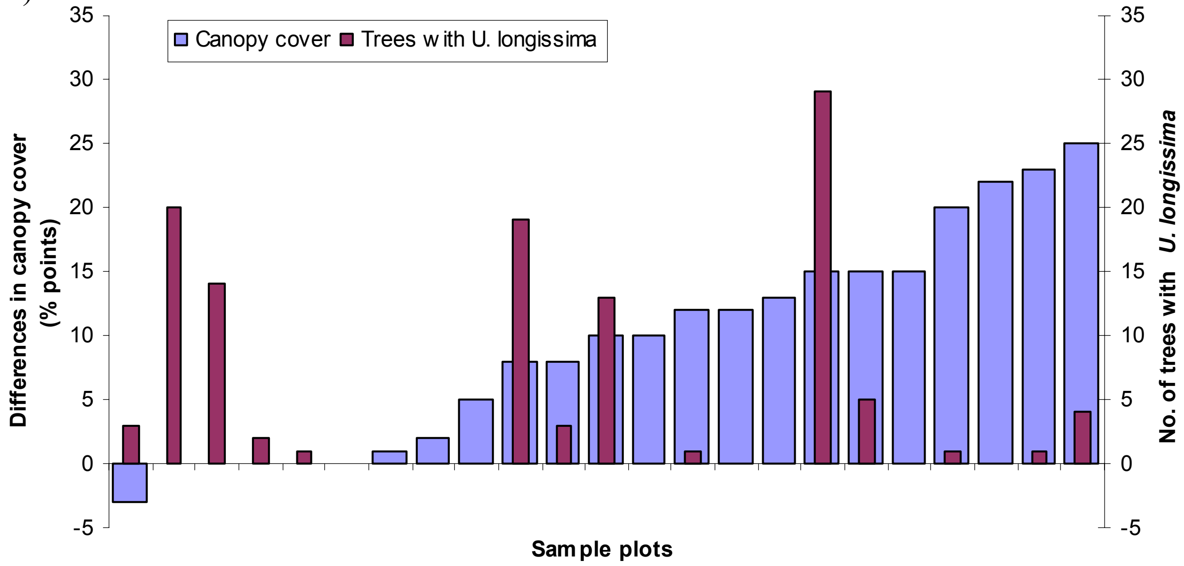
On Sör-Lappmyran canopy cover in the sub areas did not differ significantly (Appendix 1). On Hugstmyrhöjden, however, the canopy cover in 1958 and 1999 was significantly lower on the sub area with low abundance of *U. longissima* than on the other two sub areas (Table 3 and 5).

**Table 5.** One way ANOVA tests for differences in the canopy cover in 1958 between sub areas on Hugstmyrhöjden. Data from aerial photographs.

| **Predictor** | **Sub area** | **Mean** | **StDev** | **F** | ***p*** |
|---|---|---|---|---|---|
| Canopy cover 1958 (%) | High | 70.80 | 9.93 | 14.23 | 0.001 |
| Hugstmyrhöjden | Medium | 65.80 | 7.16 | | |
| | Low | 40.83 | 12.01 | | |

Most of the sample plots with high occurrence of *U. longissima* on Sör-Lappmyran had gone through small changes in canopy cover (<15 percentage points), but some had not gone through any changes at all (Figure 8a). On Hugstmyrhöjden, the canopy cover on most of the sample plots with high occurrence of *U. longissima* (>10 trees) has remained stable during the last 50 years (Figure 8b).

a)




b)

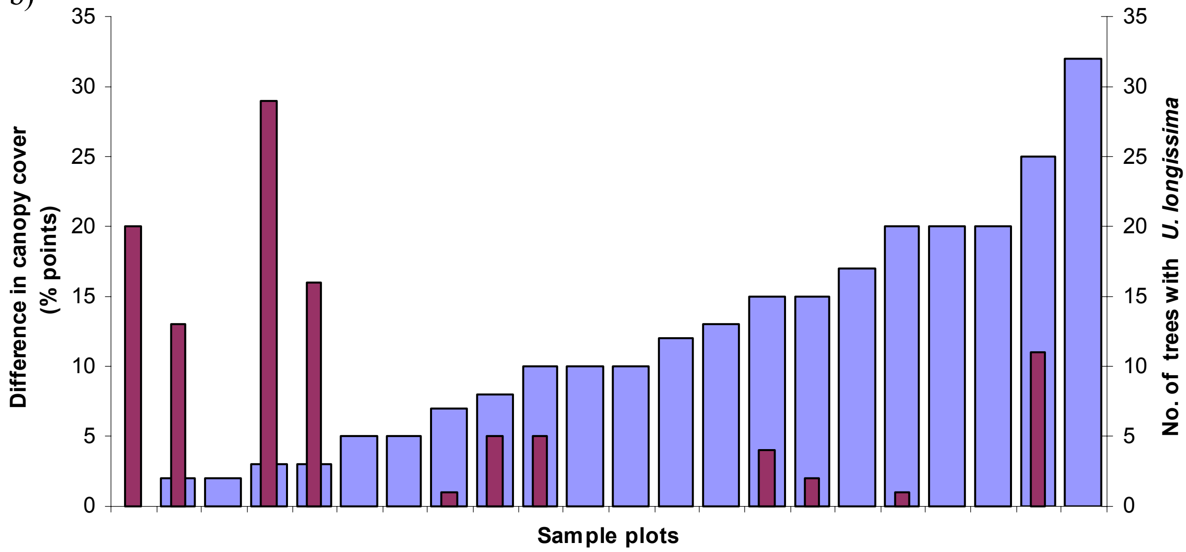



**Figure 8.** Differences (in percentage points) in canopy cover between 1958 and 1999 (left y-axis) in relation to the number of trees with *U. longissima* in 2007 (right y-axis) on Sör-Lappmyran (a) and Hugstmyrhöjden (b).

When comparing the tree species composition in 1958 and 1999, some clear changes have taken place. On Sör-Lappmyran the proportion of Norway spruce has generally increased with 10-20 percentage points (Figure 9a) and the proportions of Scots pine and deciduous trees have decreased. The same pattern is evident on sample plots with *U. longissima* (Figure 9a). On Hugstmyrhöjden, the change in tree species composition was less pronounced, with exception for one of the sample plots where deciduous trees increased with more than 60 percentage points, while the proportion of Norway spruce and Scots pine decreased substantially (Figure 9b). Almost 50 % of the sample plots with occurrence of *U. longissima* displayed no difference in tree species composition between 1958 and 1999 (Figure 9b).

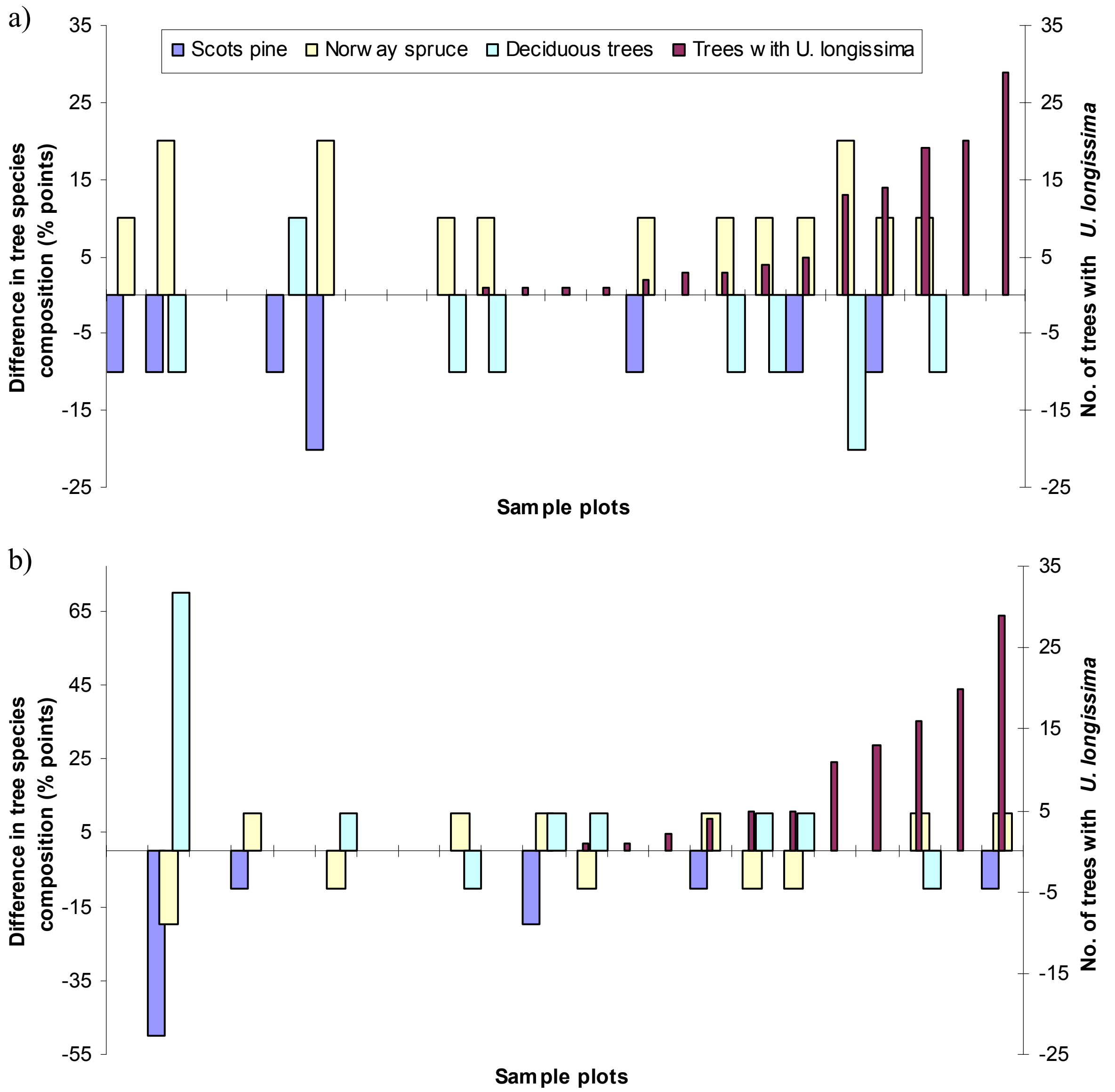



**Figure 9.** Differences in tree species composition between 1958 and 1999 (left y-axis) compared with the number of trees with *U. longissima* in 2007 (right y-axis) on Sör-Lappmyran (a) and Hugstmyrhöjden (b).

# Discussion

### *General stand structure at the study sites*

The studied forest stands on Sör-Lappmyran and Hugstmyrhöjden differ in many aspects (tree density and size, forestry history etc), but they are both today apparently good habitats for *U. longissima*. The productivity is usually lower on summits (Hugstmyrhöjden) than in valleys and on smaller hills (Sör-Lappmyran). Therefore the difference in mean basal area, tree height and timber volume can be explained by lower productivity, higher frequency of broken treetops and harsher climate conditions on the summit of Hugstmyrhöjden.

Judging from the stump data, Sör-Lappmyran seems to have been more affected by past logging of conifer trees, while felling of birch for firewood have been carried out to a larger extent on Hugstmyrhöjden. This could further have affected the forest structure in different ways at the two study sites. High-grading of Scots pine (Figure 10) has affected both study sites in the late $19^{th}$ century. The growth response data could indicate that high-grading was probably carried out around 1880 on Hugstmyrhöjden and around 1900 on Sör-Lappmyran. Traces of high-grading and past forestry practices are not unusual in forests where *U. longissima* and many other sensitive macrolichens occur (Esseen & Ericson 1982, Rolstad et al 2001). Another type of human impact (not accounted for in this study) that might have affected *U. longissima* is ditching of mires which could have made the local climate less humid.

**Figure 10**. Scots pine stump from the high-grading period. Photo by the author.

On Sör-Lappmyran early high-grading and subsequently minor thinning of conifers for pulpwood could explain the occurrence of large aspens and birches which most likely were favoured by logging, giving them space to regenerate and co-dominate the canopy in some patches. Under more natural conditions deciduous trees usually become out competed by the more shade tolerant Norway spruce and regeneration mostly occurs in gaps in old growth forests or after fire (Kuuluvainen & Juntunen 1998). No traces of forest fire were found on the study sites, but limited effort was put in to searching for such traces. However, Sör-Lappmyran contains several mires and is in general a mesic site which makes it a potential fire refuge. Forests not subjected to large-scale disturbance by fire in the past are typically sites where *U. longissima* can be found (Esseen et al 1981, Esseen & Ericson 1982, Rolstad & Rolstad 1999).

Logging on the summit of Hugstmyrhöjden could explain the relationship between present canopy closure and number of stumps here. Compared to the denser forest on the hillside the forest on the summit contained somewhat more stumps, probably because it is difficult to fell trees on steep slopes. Moreover, it seems likely that birches (subject to firewood logging) were more abundant on the summit of the mountain than on the more productive hillsides were Norway spruce could out compete them. The forest on the summit was probably already less dense compared to the hillsides, but by removing trees an even more open forest structure was created. On both study sites logging in the early 20$^{th}$ century created a more open forest structure which, during the last decades, has become denser again.

***Relationships between present stand structures and the distribution of Usnea longissima at sample plot level***

The number of trees with *U. longissima* increased with increasing tree age, which is not surprising since larger populations of *U. longissima* usually are found on older trees (Esseen et al 1981) and in older forest stands (Rolstad &Rolstad 1999, Keon 2001). Also, species richness and abundance of epiphytic lichens has been found to be positively correlated to stand age (Dettki & Esseen 1998, Price & Hochachka 2001). The relationship between tree age and the distribution of *U. longissima* may therefore indicate that places were the lichen grows today have been less disturbed in the past.

The multiple regressions revealed that the number of trees with *U. longissima* also had a negative correlation to basal area and timber volume on Sör-Lappmyran. The reason why no such correlation was detected on Hugstmyrhöjden is probably because the sample plot with the highest number of trees with *U. longissima* was situated in the open forest on the upper part of the mountain, while most of the other sample plots with many trees with *U. longissima* were situated in the denser forest on the hillside. In other words sample plots with large numbers of *U. longissima* were found in both comparatively dense as well as in open forest structure on Hugstmyrhöjden.

It was surprising that, on sample plot level, only the number of Scots pine stumps (and no other kinds of stumps) on Hugstmyrhöjden were correlated to the number of trees with *U. longissima*. In an area close to the study sites Josefsson et al (2005) found that the distribution of *U. longissima* was correlated to earlier logging, i.e. more lichen was found in stands that were less affected by forestry. Therefore, stronger correlations between the number of trees with *U. longissima* and the number of stumps were expected to be found. Overall, the stand structures on sample plot level were expected to be a better predictor of the distribution of *U. longissima* considering that the lichen is believed to be associated with relatively open forest structures (Josefsson et al 2005) and natural forests (Esseen et al 1981). However, the present study was carried out on a spatially precise scale in old-growth forests. Therefore, although the canopy closure, basal area, timber volume etc varied a lot, the local environmental conditions might be rather similar throughout the studied part of the forest – a potential contribution to the explanation of why *U. longissima* occurs in seemingly different stand structures.

***Relationships between present stand structures and the distribution of Usnea longissima in sub areas of the study sites***

The analyses of sub areas showed that the only significant difference between the sub areas on Sör-Lappmyran (Figure 7) was increasing age of the oldest trees the higher the abundance of *U. longissima*. However, the basal area, canopy closure and timber volume was lower on the sub area with high abundance of *U. longissima*, which is in agreement with previous studies showing that the lichen prefers relatively open forest structure (Josefsson et al 2005). Also, tree density usually decreases with increasing age of the forest (Rolstad & Rolstad 1999). It was also interesting that the number of stumps was slightly lower in the sub area with high abundance of *U. longissima*, which suggests that the lower canopy closure here is not caused by logging, but is rather a result of natural dynamics that take place in old forests.

The abundance of the lichen was expected to decrease with increasing basal area of trees (Asplund 2004), but on Hugstmyrhöjden it was the other way around. The explanation could be that *U. longissima* is less successful in the open forest (lower basal area) on the wind exposed summit of Hugstmyrhöjden. More difficult to explain is the higher number of Norway spruce stumps in the areas with high abundance of the lichen. This might be due to that more spruces and fewer birches probably were growing here when the logging were carried out, while the area with low abundance of *U. longissima* had a higher proportion of birch. Therefore, the logging was concentrated to birch on the south-east summit of the mountain and, in larger extent, to Norway spruce in the north part of the study site. This could also explain the decreasing number of bouquet birches with increasing lichen abundance.

The analyses of sub areas highlighted the large differences in forest structure between Sör-Lappmyran and Hugstmyrhöjden. The correlations (although not statistically significant) between the number of trees with *U. longissima* and important variables (timber volume and canopy closure) turned out to be inversed when comparing the two study sites. This clearly shows that *U. longissima* can live in rather different forest structures. The explanation can be different logging history and different environmental conditions. The pattern of more *U. longissima* in less dense forest on Sör-Lappmyran and the opposite on Hugstmyrhöjden (more *U. longissima* in denser forest) might be explained by the fact that Hugstmyrhöjden is more exposed to wind and drought on the highest elevations were the forest is rather open (due to natural conditions and logging). *U. longissima* is usually not found in wind exposed places (Olsen & Gauslaa 1991), therefore the microclimate conditions are better for *U. longissima* in the denser forest on the eastern and northern hillsides of Hugstmyrhöjden. The lichen has been found to typically grow in north and east facing slopes that are shaded during the middle of the day, resulting in conditions with high air humidity, because of reduced temperature and evaporation (Esseen et al 1981), but still much light reception in lower parts of the canopy due to the inclination (Esseen et al 1981, Olsen & Gauslaa 1991). These conditions explain why *U. longissima* occurs in high abundance where the timber volume and canopy closure is much higher at Hugstmyrhöjden compared to the sub area with high abundance of the lichen at Sör-Lappmyran.

***Changes in forest structure and possible explanations of the patchy distribution of Usnea longissima***

Both study sites have gone through large changes during the last 50 years; the canopy cover has increased and Norway spruce generally makes up a bigger proportion of the three species composition today than in 1958. This is not astonishing since the forests at the study sites earlier have been subject to logging and after that successively have become denser again. For example, the increased proportion of deciduous trees on some sample plots at Hugstmyrhöjden could be due to logging of birch for firewood that were carried out before the aerial photograph was taken in 1958; since than new birches have established here. The canopy cover varies much on Hugstmyrhöjden, both in 1958 and 1999, which likely is a reflection of the natural nutrient and climate gradients on the mountain, but could also partly be due to logging. Interestingly, the canopy cover seemed to have gone through comparable small changes on most of the sample plots with many trees hosting *U. longissima* at Hugstmyrhöjden, which suggests that the lichen thrive better in stable environments. This pattern was not as evident on Sör-Lappmyran, but then again the stand variables where not as varying here.

Several small outtakes of trees at Hugstmyrhöjden (not affecting the whole study site at the same occasion) have been carried out during the last two centuries. This is suggested by the indistinct peaks in the growth response data and by the age structure, with some very old Norway spruces on Hugstmyrhöjden, which also indicates that logging have been more concentrated to birches. The dating of the three additionally cored birches matches the growth response data and the generation of birches subjected to firewood logging had probably germinated after the high-grading. Compared to Sör-Lappmyran, the cored trees on Hugstmyrhöjden had a more widespread age distribution. However, both study sites are characterised by wide age distribution, which is typical for natural old-growth spruce forests where *U. longissima* occur (Esseen & Ericson 1982); Olsen and Gauslaa (1991) found that trees adjacent to trees with *U. longissima,* in two localities in Norway, were 78-260 years old and there was no specific age class dominating.

In summary, the analyses in the present study show that patches with high abundance of *U. longissima* have older trees and slightly lower timber volume, basal area and canopy closure than patches where the lichen is absent or low in abundance on Sör-Lappmyran. Also, these patches have gone through comparable small changes in canopy cover, but the proportion of spruce has generally increased at the expense of pine and birch. The lichen exists in patches with minor effects of logging and where the canopy closure and timber volume is not too high. On Hugstmyrhöjden the patterns of *U. longissima* in relation to basal area, timber volume and canopy closure is the opposite of Sör-Lappmyran; the abundance of *U. longissima* is higher where the basal area, timber volume and canopy closure is higher. Also, the lichen occurs in significantly higher abundance in areas where the number of Norway spruce stumps and canopy cover are higher and the number of Scots pine stumps and bouquet birches are lower. *U. longissima* exists in patches that are not too open, i.e. more protected form the harsh climate on the exposed summit of the mountain, and where the changes in canopy cover and tree species composition has been small.

The clear cut that was seen south-west of Hugstmyrhöjden in the aerial photography form 1958 seemed to be rather young and was probably created during the 1950's. Presumable the forest on summit of Hugstmyrhöjden were thinned at the same time since the sample plots adjacent to the former clear cut have become much denser today. The growth response data also indicates that some disturbance event, logging by suggestion, might have taken place on Hugstmyrhöjden in the middle of the 20$^{th}$ century. The clear cut could also have affected the distribution of *U. longissima* since the edge effect can reach far into the persisting forest and cause dehydration and injures on *U. longissima* (Esseen & Ericson 1982). However, today recently created clear cuts (Figure 11) exist only a few hundred meters, some times within tens of meters, from patches with high occurrences of *U. longissima,* suggesting that the edge effects have not reached that far into the stands or that the lichen can tolerate the changes. It must though be kept in mind that no changes of the occurrence of *U. longissima* have been studied here, therefore it is not possible to make conclusions about the effects of the clear cuts.

**Figure 11.** View from the clear cut on the south-east part of Hugstmyrhöjden. The sample plot with the highest number of trees with *Usnea longissima* is located only c. 100 meters inside the forest to the left. The view shows the surrounding forest landscape with younger forests and clear cuts. Photo by the author.

It is also not possible to tell whether the populations of the lichen have decreased or increased, but considering the general decline of *U. longissima* in Sweden (Esseen & Ericson 1982, Turander & Oldhammer 2003), it seems likely that a decrease has taken place at the studied sites as well. The decline of old-growth forest lichens, which has been observed during the last century, can have an explanation in the increasing shade in old forests. Increasing shade can be caused by $CO_2$ and N fertilisations and climatic changes, but also by reduced domestic grazing, fires and selective logging (Gauslaa et al 2007). Moreover, sudden changes in substrate quality and availability as well as changed microclimate are believed to affect *U. longissima* and other epiphytic lichens negatively (Esseen et al 1981, Gauslaa et al

1998, Johansson & Ehrlén 2003). The abundance and species richness of epiphytic lichens are therefore considered to be negatively correlated with logging intensity (Dettki & Esseen 1998). However, many lichens associated with natural forests have survived in forest stands where only careful selective logging has been carried out (Olsen & Gauslaa 1991). For example Rolstad et al (2001) found no significant correlations between logging history and the present abundance of the eight macrolichens they studied. Also, Molinari et al (2005) found that the forest with *U. longissima* they studied was not a fire-free, long-continuity forest, which traditionally is believed to be the lichens habitat (Esseen et al 1981).

There are several possible explanations for the distribution of *U. longissima* in the studied stands. At least tree explanations about how the logging have affected the lichen can be put forth: (1) Many trees previously hosting *U. longissima* have been cut during the logging events, which resulted in disappearance of parts of the population and due to the relatively slow accumulation of lichen biomass over time (Dettki & Esseen 1998, Dettki et al 2000), recovery has not yet taken place. Today's patchy distribution of the lichen in the stands then is a relict of a previously denser population. (2) The logging events have altered the stand structure in ways that have disfavoured *U. longissima*, i.e. the forest grew faster and became denser after the logging, decreasing the light penetration. The changed forest structure might also have altered the humidity and wind conditions. Again this has disfavoured the lichen and resulted in a small fragmented population today. (3) The logging has favoured the lichen. If the outtake of trees was limited the growth and density increment (thinning effect) of the forest might have been only small or did not take place at all. Under these conditions the changed, slightly more open forest structure probably favoured *U. longissima* since light is a growth limiting factor even in open old forests (Nybakken et al 2007). In this case perhaps the occurrence of the lichen previously was greater in stands surrounding the sites and now only outliers of the population remain in the studied stand.

One potential scenario is a combination of all three explanations described above. In some places the logging has disfavoured *U. longissima*, in others it has been favouring, depending on logging intensity and the local environmental conditions before and after the logging. For example, logging events on the summit of Hugstmyrhöjden have most likely increased the wind exposure, disfavouring the lichen. It is also possible that the logging first favoured the lichen by increasing the openness and light and later resulted in worse conditions when the canopy closure increased. Asplund (2004) found that *U. longissima* is favoured by openness in the canopy north of the host tree, but towards south it is advantageously with a less open canopy. On one sample plot on Hugstmyrhöjden a distinct different between the east and west side of the sample plot were found; eleven trees with *U. longissima* were found and 17 stumps, but all the trees with *U. longissima* grew on the east half and the stumps were found on the west half of the sample plot. These findings indicate that the distribution of trees and stumps can be of importance for the distribution of the lichen at sample plot scale. However, essential to *U. longissima* is that it receives enough light and at the same time enough moisture to allow photosynthesis, moreover, it needs protection from wind and the right nutrients. These conditions can be fulfilled in different ways, the important thing for the lichen is that they are fulfilled, not how (Asplund 2004).

Of course not only logging have affected the distribution of *U. longissima*; geographic location, air pollutions and climate also correlate with the distribution of epiphytic lichens (Will-Wolf et al 2006b), but these processes operate at a larger scale than the studied one.

***Evaluation of the study method***

The results on Hugstmyrhöjden would presumably have been different if the inventories had been carried out further downhill where the number of trees with *U. longissima* was more abundant, but the choice of location made interesting comparisons of different environments possible. Another inventory (unpublished study) was carried out by the County Administrative Board of Västernorrland (Bader pers. comm.) on Hugstmyrhöjden earlier during the same summer the present study was preformed. This inventory searched for trees with *U. longissima* all over the forest stand and, in accordance with the present study, much more trees with *U. longissima* were found on the hillsides (north and east of the mountain) than on the summit. When comparing the lichen data from the present study with the total distribution of trees hosting *U. longissima*, most often sample plots (present study) with many trees hosting *U. longissima* were located in areas with high abundance of the lichen (the study by CAB) and sample plots with little or no *U. longissima* were located in areas with low abundance of the lichen. However, due to the patchy distribution of *U. longissima*, some sample plots where no lichen was found were located in patches surrounded by a lot of trees with *U. longissima*. Therefore, the relatively low number of sample plots in relation to this patchy distribution is a source of error.

The canopy closure measured form the digital photographs were lower than the canopy cover measured from the aerial photographs because they represent different measurements of the canopy openness. However, there was a significant correlation between canopy closure and canopy cover and also between basal area and canopy closure on both study sites, which indicate that the method of measuring canopy closure in field gives reliable results. It most also be mentioned that the precision of the coordinates, determined by GPS in field, could have resulted in a discrepancy between the locations of the sample plots on the aerial photographs and their actual location. However, the GPS was left in the centre of the sample plots for at least half an hour before the coordinates were written down.

In future studies with similar approaches I suggest that the total number of trees on each sample plot is counted, so that it is possible to calculate the relationship between the number of trees with *U. longissima* and the total number of trees, which statistically is a better measure of the occurrence of *U. longissima*. It is possible that the impact of logging on *U. longissima* can be better understood if the positions of stumps are determined. With knowledge of stump positions and the stand structure variations on sample plot level, correlations between the distribution of *U. longissima* and these variables on sample plot level can be found. Gauslaa et al (1998) studied the chemical differences in the year shoots of trees with and without *U. longissima* and found that the concentrations of individual elements differed slightly. Perhaps a combination of studies of the environmental conditions (light, humidity, nutrients etc.) carried out on tree level, and studies of stand structure and forest history on stand level, is the best approach if the mysterious distribution of *U. longissima* within tens of meters should be fully understood.

***Management implications and recommendations***

Dispersal ability is considered a limiting factor for many epiphytic lichens. However, Muir et al (2006) suggests that dispersal limitations are of greatest importance when forestry affect relatively large areas and remove a considerable proportion of the substrate hosting the lichens and when such events reoccur before the lichen populations have re-established. In the same study it is also suggested that if forestry practices are altered, so that epiphytic lichens with dispersal limitations are given chances to establish in young forests, they will do so if the microclimate and substrate conditions are not limiting here. *U. longissima* grows faster in open and sunny places and, like the folios lichens *Lobaria pulmonaria* (Figure 11) and *Pseudocyphellaria crocata*, synthesises more sun protecting substances as an acclimatisation to the light exposure (Nybakken et al 2007). *U. longissima* seem to be more limited by light than these two lichens, since they grow better in less sun exposed places while, in transplantation experiments, *U. longissima* grew better the more sun it received. However in direct sunshine it desiccates and become photosynthetically inactive (Gauslaa et al 2007). Therefore, and also due to the low rate of canopy branches that can catch detached thalli, *U. longissima* is not likely to establish in windy clear cuts or stands with low tree density, suggesting that not only limited dispersal ability determine where the lichen grows (Gauslaa et al 2007). Gauslaa et al (2007) also found that a high lichen biomass can be formed at younger stand ages in oceanic forests compared to continental forests, since the rainfall is higher there. However in dense young forests light becomes a severely limiting factor (Gauslaa et al 2007, Nybakken et al 2007). The solely vegetative dispersal can also be a part of the explanation to why *U. longissima* is found in relatively open forests, since openness is essential to supply branches far down the trunk with light. To little light kills the bottom branches of the canopy and then there is nothing to catch the downward dispersing thallus fragments (Gauslaa 1997).

**Figure 12.** *Lobaria plumonaria* at Sör-Lappmyran. Photo by Hanna Millberg.

The analyses of changes in stand structure suggest that *U. longissima* can occur in high amounts in forest stands that has gone through relatively large changes, but also that the highest abundance of the lichen often is found in less disturbed patches. The results from the present study therefore suggest that forests where *U. longissima* occur can be managed by careful selective logging as long as the old-growth structures with an open, but not too open canopy are preserved – allowing for enough light, but preserving the air humidity and the shelter from wind. This is in accordance with other studies of *U. longissima* (e.g. Rolstad & Rolstad 1999, Josefsson et al 2005) and other epiphytic lichens (e.g. Rolstad et al 2001, Muir et al 2006). A combination of natural and anthropogenic processes with long history at the sites where *U. longissima* and other endangered species occur might be the best way of maintaining biological values (Molinari et al 2005). Modified logging procedures can be a way of maintaining and restoring lichen communities in managed forests. However, when managing forests with rare and patchy distributed species by selective logging, it should be taken into consideration that, just by chance, the species can be locally eliminated if attention is not paid to which trees are cut (Rolstad et al 2001). I suggest that the forest stands in the present study and other similar stands with *U. longissima* should be left for free development, but can be managed by careful selective logging in areas with *U. longissima* where the forest is too dense. However, if loggings are carried out they must be preceded by careful markings of trees with *U. longissima* to avoid felling such trees and perhaps also adjacent trees. Also, the canopy closure should not be reduced to below 30 % or in wind exposed places, not below 45 %.

Since many epiphytic lichens have limited dispersal ability a recommendation is to decrease the size of logging units in order to facilitate the dispersal of epiphytic lichens between old-growth forests and to moderate the microclimate in harvested areas (Muir et al 2006). To increase and improve the dispersal opportunities for epiphytic lichen in managed boreal forests, retention and restoration of old-growth forests should be included in forest management all over the landscape (Dettki et al 2000, Keon 2001). Knowledge about sensitive and threatened species is important when selecting areas for nature conservation since far from all red-listed species occur in high biodiversity spots (Gjerde et al 2004). Patch isolation can have negative effects on the occurrence of epiphytic lichens (Johansson & Ehrlén 2003). Thus, although *U. longissima* can spread long distances by soredia and isidia and perhaps also by birds (Keon 2002, Östlund 2006), the chance of it ending up in a place where it succeeds to germinate and grow is small considering how distantly separated old-growth forests are today (Lidén et al 2004). Artificial dispersal has also been proposed as a way of establishing new populations or enlarging present populations of endangered lichens (Lidén et al 2004). However, artificial dispersal ought to be seen as a last way of saving endangered species, since actions to increase the species habitat areas and connectivity is the best way of securing their long-term survival and at the same time increasing biodiversity. The old-growth forest stands that remain in the landscape today are important lifeboats for dispersal limited species and species that require the exclusive environmental conditions and substrates, e.g. dead wood (Atlegrim & Sjöberg 2004), that is characteristic of old-growth forests (Muir et al 2006). Maintenance and protection of these forests and future potential habitats is required if *U. longissima* and many other old-growth species should be able to live on in the boreal forests of Scandinavia.

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# Appendix 1

| Predictor | Sub area | Mean | StDev | SS | MS | F | *p* | S | $R^2$ | $R^2$(adj) |
|---|---|---|---|---|---|---|---|---|---|---|
| Basal area | High | 24.00 | 6.22 | 136.3 | 68.2 | 1.71 | 0.219 | 6.310 | 20.85% | 8.67% |
| | Medium | 31.17 | 4.45 | | | | | | | |
| | Low | 30.17 | 7.78 | | | | | | | |
| Dominant height | High | 21.28 | 2.37 | 12.41 | 6.21 | 1.32 | 0.300 | 2.166 | 16.91% | 4.13% |
| | Medium | 22.93 | 1.66 | | | | | | | |
| | Low | 21.03 | 2.47 | | | | | | | |
| Timber volume | High | 175.00 | 58.74 | 22875 | 11438 | 2.85 | 0.094 | 63.370 | 30.47% | 19.77% |
| | Medium | 270.00 | 39.62 | | | | | | | |
| | Low | 250.00 | 82.46 | | | | | | | |
| Canopy closure (digital photos) (%) | High | 31.33 | 20.16 | 1718 | 859 | 3.13 | 0.077 | 16.550 | 32.54% | 22.16% |
| | Medium | 54.08 | 12.03 | | | | | | | |
| | Low | 56.24 | 18.00 | | | | | | | |
| Average age | High | 133.26 | 22.35 | 958 | 479 | 2.76 | 0.100 | 13.170 | 29.82% | 19.02% |
| | Medium | 136.84 | 6.10 | | | | | | | |
| | Low | 119.69 | 10.69 | | | | | | | |
| Average age, 2 oldest trees | High | 170.38 | 28.74 | 2867 | 1433 | 4.72 | 0.029* | 17.430 | 42.05% | 33.14% |
| | Medium | 147.58 | 5.56 | | | | | | | |
| | Low | 135.92 | 16.23 | | | | | | | |
| Norway spruce stumps | High | 4.25 | 5.06 | 11.4 | 5.7 | 0.39 | 0.686 | 3.824 | 5.64% | 0.00% |
| | Medium | 6.33 | 4.03 | | | | | | | |
| | Low | 6.00 | 2.53 | | | | | | | |
| Scots pine stumps | High | 4.25 | 2.63 | 0.83 | 0.42 | 0.07 | 0.936 | 2.495 | 1.02% | 0.00% |
| | Medium | 3.67 | 2.73 | | | | | | | |
| | Low | 3.83 | 2.14 | | | | | | | |
| Bouquet birch | High | 0.00 | 0.00 | 5.1 | 2.55 | 1.97 | 0.179 | 1.138 | 23.27% | 11.46% |
| | Medium | 0.00 | 0.00 | | | | | | | |
| | Low | 1.17 | 1.84 | | | | | | | |
| Total no. of stumps | High | 8.50 | 3.42 | 15 | 7.5 | 0.38 | 0.692 | 4.446 | 5.51% | 0.00% |
| | Medium | 10.00 | 4.94 | | | | | | | |
| | Low | 11.00 | 4.47 | | | | | | | |
| Canopy cover 1958 (aerial photos) (%) | High | 63.75 | 12.50 | 178 | 89 | 1.00 | 0.395 | 9.436 | 13.33% | 0.00% |
| | Medium | 72.33 | 3.33 | | | | | | | |
| | Low | 68.33 | 11.26 | | | | | | | |
| Canopy cover 1999 (aerial photos) (%) | High | 77.50 | 2.89 | 7.1 | 3.5 | 0.04 | 0.964 | 9.785 | 0.58% | 0.00% |
| | Medium | 79.17 | 9.77 | | | | | | | |
| | Low | 78.17 | 12.19 | | | | | | | |

Results from one way ANOVA on each variable that could explain the distribution of *U. longissima* in the three sub areas on Sör-Lappmyran. Mean values of trees with *U. longissima* /sample plot on each sub area: high: 14.50, medium: 1.67, low: 0.17. *p*-values marked with * shows a significant difference between the sub areas.

# Appendix 2

| Predictor | Sub area | Mean | StDev | SS | MS | F | *p* | S | $R^2$ | $R^2$(adj) |
|---|---|---|---|---|---|---|---|---|---|---|
| Basal area | High | 27.20 | 6.83 | 416.5 | 208.3 | 6.56 | 0.011* | 5.636 | 50.22% | 42.56% |
| | Medium | 23.80 | 6.38 | | | | | | | |
| | Low | 15.33 | 3.56 | | | | | | | |
| Dominant height | High | 22.29 | 3.34 | 44.15 | 22.07 | 2.45 | 0.125 | 3.000 | 27.39% | 16.22% |
| | Medium | 20.10 | 3.16 | | | | | | | |
| | Low | 18.27 | 2.55 | | | | | | | |
| Timber volume | High | 228.00 | 92.91 | 30948 | 15474 | 3.30 | 0.070 | 68.530 | 33.64% | 23.43% |
| | Medium | 131.00 | 42.19 | | | | | | | |
| | Low | 135.00 | 62.29 | | | | | | | |
| Canopy closure (digital photos) (%) | High | 43.59 | 16.29 | 922 | 461 | 1.74 | 0.214 | 16.290 | 21.09% | 8.95% |
| | Medium | 41.56 | 13.15 | | | | | | | |
| | Low | 26.98 | 18.42 | | | | | | | |
| Average age | High | 137.47 | 27.63 | 335 | 167 | 0.15 | 0.860 | 33.130 | 2.29% | 0.00% |
| | Medium | 129.44 | 11.79 | | | | | | | |
| | Low | 140.27 | 46.17 | | | | | | | |
| Average age, 2 oldest trees | High | 181.50 | 61.33 | 1026 | 513 | 0.20 | 0.823 | 50.890 | 2.96% | 0.00% |
| | Medium | 166.30 | 36.72 | | | | | | | |
| | Low | 184.83 | 51.44 | | | | | | | |
| Norway spruce stumps | High | 8.00 | 2.35 | 126.55 | 63.28 | 8.29 | 0.005* | 2.762 | 56.06% | 49.30% |
| | Medium | 7.60 | 2.07 | | | | | | | |
| | Low | 2.00 | 3.46 | | | | | | | |
| Scots pine stumps | High | 0.40 | 0.89 | 60.1 | 30.05 | 3.62 | 0.056 | 2.881 | 35.77% | 25.89% |
| | Medium | 0.60 | 0.55 | | | | | | | |
| | Low | 4.50 | 4.55 | | | | | | | |
| Bouquet birch | High | 0.40 | 0.89 | 75.9 | 37.95 | 3.96 | 0.045* | 3.095 | 37.87% | 28.31% |
| | Medium | 3.00 | 2.00 | | | | | | | |
| | Low | 5.67 | 4.59 | | | | | | | |
| Total no. of stumps | High | 8.80 | 2.59 | 32 | 16 | 1.44 | 0.272 | 3.333 | 18.14% | 5.55% |
| | Medium | 11.20 | 3.11 | | | | | | | |
| | Low | 12.17 | 3.97 | | | | | | | |
| Canopy cover 1958 (aerial photos) (%) | High | 70.80 | 9.93 | 2892 | 1446 | 14.23 | 0.001* | 10.080 | 68.65% | 63.83% |
| | Medium | 65.80 | 7.16 | | | | | | | |
| | Low | 40.83 | 12.01 | | | | | | | |
| Canopy cover 1999 (aerial photos) (%) | High | 76.40 | 13.69 | 2253 | 1126 | 7.71 | 0.006* | 12.080 | 54.27% | 47.24% |
| | Medium | 75.60 | 4.16 | | | | | | | |
| | Low | 51.50 | 14.69 | | | | | | | |

Results from one way ANOVA on each variable that could explain the distribution of *U. longissima* in the three sub areas on Hugstmyrhöjden. Mean values of trees with *U. longissima* /sample plot on each sub area: high: 11.20, medium: 1.40, low: 0.67. *p*-values marked with * shows a significant difference between the sub areas.

## SENASTE UTGIVNA NUMMER

2007:15 Författare: Lisa Werndin
Effekter av gödsling i äldre tallbestånd på renbetesväxter i fält- och bottenskikt

2008:1 Författare: Anna Bylund
En analys av SCA Skog AB's metod för egenuppföljning av gallringar

2008:2 Författare: Lars Johansson
Plantering av gran (*Picea abies* L. Karst) på kalhyggen och självföryngring under högskärmar av björk (*Betula pendula* och *Betula pubescens*) – Föryngringsresultat 7-10 år efter avverkning

2008:3 Författare: Nathalie Enström
Heavy metal accumulation in voles, shrews and snails after fertilisation with pelletized and granulated municipal sewage sludge

2008:4 Författare: Jenny Sallkvist
Relationer mellan Norske Skog och de privata skogsägarna i Jämtland

2008:5 Författare: Emma Sandström
Skötsel av tätortsnära skogliga rekreationsområden. Besökares upplevelser i norra och södra Sverige

2008:6 Författare: Tobias Norrbom
Askgödsling och dess lämplighet i torvmarksskogar tillhörande Sveaskog Förvaltnings AB – en litteraturstudie

2008:7 Författare: Camilla Göthesson
Privata skogsägares inställning till frivilliga naturvårdsavsättningar samt kvalitets- och tillväxthöjande skogsskötselåtgärder

2008:8 Författare: Sakura Netterling
Tropical rain forest recovery after cyclone and human activity on Savai'i, Samoa – A field study of tree species composition and distribution

2008:9 Författare: Håkan Nilsson
Resultat från tre klonförsök med Fågelbär, *Prunus avium* L, i södra Sverige

2008:10 Författare: Anna Nylander
Trädslagsinverkan på markvegetationens utveckling i odlingsförsök med tall och contorta

2008:11 Författare: Cecilia Persson
Tillväxt och potentiell sågtimmerkvalitet i gallringsmogna jämförelseplanteringar med *Pinus contorta* och *P. sylvestris*

2008:12 Författare: Anna Sjöström
Fuktkvotens inverkan på oljeupptag och pigmentinträngning i gran (*Picea abies* L. Karst) och tall (*Pinus sylvestris* L.) vid impregnering med Linotechmetoden.

2008:13 Författare: Alexander Ross
Ifrågavarande kronopark skall benämnas Skatan – En skogshistorisk analys av Ekoparken Skatan

2008:14 Författare: Hampus Roffey
Fågelbär (*Prunus avium* L.) – Överlevnad, höjdutveckling och skador i unga planteringar på småländska höglandet

2008:15 Författare: Jenny Andersson
Ekologisk landskapsplan för fastigheten Götebo 1:5

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