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Using a spatially precise approach to analyse the occurrence of Usnea longissima in relation to present and past stand structure –
a case study in boreal Scandinavia

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Examensarbete i biologi, 20 p
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Januari 2004

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ABSTRACT

To maintain biodiversity in managed forests, long-term trends in forest structure and ecological processes must be understood since these have a decisive influence on the distribution of many forest species, especially epiphytic lichens. To enhance the understanding of the complex occurrence of *Usnea longissima* Ash. at the stand level, a spatially precise investigation of present and past stand structure was made in an area in boreal Sweden. Field studies of present occurrence of *U. longissima* and present forest structure were complemented with dendrochronological analysis and interpretation of different historical sources. Stand structure at present was more or less similar all over the study area. No occurrence of forest fires during the last centuries and absence of forestry operations since the 1930s were most important for the occurrence of *U. longissima*. However, the distribution of the lichen within the study area could not be explained by present stand structure. Instead, several essential factors affecting the distribution of *U. longissima* could be related to past stand structure, especially the extent and intensity of previous logging operations and the subsequent stand development. Possibly, pre-industrial forest use and modest selective cuttings may occasionally have contributed to a maintained open forest structure. Evidently, *U. longissima* appears to be favoured by long-term stability in forest structure, including a somewhat open forest dominated by *Picea abies*, moderate re-growth of trees and absence of large-scale disturbances. The results indicate that stand history has an important influence on the distribution of epiphytic lichens such as *U. longissima* and should be considered to achieve a comprehensive management of boreal forests. Furthermore, the use of a spatially precise approach may elucidate many different factors and is practicable for interpreting forest history and long-term changes in habitat conditions.

SAMMANFATTNING

En förutsättning för att bedriva ett effektivt skogsbruk samtidigt som en hög biodiversitet bibehålls är fördjupad kunskap om långsiktiga förändringar av skogsstrukturen och ekologiska processer. Utbredningen av många skogslevande arter, i synnerhet epifytiska lavar, styrs till stor del av dessa faktorer. Syftet med denna studie var att öka kunskapen kring långskäggslavens (*Usnea longissima* Ash.) komplicerade utbredning på beståndsnivå i norra Sverige. Förutom en fältstudie av långskäggsförekomst och nuvarande beståndsstruktur användes två olika skogshistoriska metoder, närmare bestämt dendrokronologi och tolkning av olika historiska dokument. Studieområdet hade inte påverkats av skogsbruk sedan 1930-talet och några tecken på skogsbrand under de senaste seklen återfanns ej. Dessa faktorer är avgörande för förekomsten av *U. longissima* i studieområdet. När det gäller utbredningen av *U. longissima* i området kunde denna relateras till beståndshistoriken, framför allt omfattningen av tidigare huggningar samt efterföljande beståndsutveckling. Möjligen kan förindustriellt agrart bruk av skogen samt småskalig plockhuggning i vissa fall ha bidragit till en bibehållen öppen skogsstruktur. Långskäggslaven tycks således gynnas av en beständig och något öppen skogsstruktur med dominans av gran (*Picea abies* L. Karst), långsam tillväxt samt frånvaro av storskaliga störningar. Resultat visar att beståndshistorik har stor inverkan på förekomsten av epifytiska lavar såsom långskäggslav och bör därför beaktas vid skötseln av våra boreala skogar. Djupgående studier på små områden hjälper till att belysa många olika faktorer samt är användbara för tolkning av skogshistoria och långsiktiga förändringar av olika habitat.

INTRODUCTION

A key question in multiple-use management of boreal forest ecosystems is to understand how long-term trends in habitat characteristics affect the distribution of threatened species. Since intensive forest management has replaced natural disturbance factors such as wildfire and natural tree-mortality almost completely (Linder 1998, Niklasson & Granström 2000, Axelsson 2001), ecological processes and forest structures have been thoroughly altered. These changes in forest use have had a significant impact on the ecosystems at different spatial levels. As a result, many forest-dwelling species have been reduced in numbers or even gone extinct (Gärdenfors 2002).

Many epiphytic lichens are dependent on forests with old-growth characteristics and are therefore especially sensitive to forestry, for example *Evernia divaricata* (L.) Ach. and *Ramalina thrausta* (Ach.) Nyl. (Rose 1976, Gauslaa 1997, Esseen et al 1996). The main reasons for this appears to be their inability to withstand changes in the abiotic environment and substrate quality and availability (Esseen et al 1996) but also the configuration of landscape elements (Dettki & Esseen 1998). Since most epiphytic lichens depend on stable habitat conditions over time, changes in tree species composition and age structure of the forest stand might alter the biodiversity and even decrease the abundance of many epiphytic lichens (Uliczka & Angelstam 1999, Dettki 2000). In Scandinavia and North America the epiphytic lichen *Usnea longissima* Ach. is regarded as particularly disadvantaged by modern forestry and has therefore been the subject of much scientific research (Esseen et al 1981, Esseen & Ericson 1982, Dynesius 1984, Gauslaa 1997, Rolstad & Rolstad 1999, Keon 2001, Peterson & McCune 2002). The distribution of *U. longissima* is limited by many factors, of which intensive industrial logging is considered as the most important (Esseen & Ericson 1982).

In 1994 the new Swedish Forestry Act came into force, in which timber production and protection of biodiversity were given equal importance. Pressure from nature conservation organisations in addition to new scientific research had set focus on how forestry affected ecological processes and forest structure and new policies were introduced (Bernes 1994, Anon 2001). Accordingly, the loss of epiphytic lichens and other organisms in managed forests has lead to an emerging interest in the fundamental requirements for ecological sustainability of the boreal forest ecosystems (Berg et al 1994, Thor 1998, Esseen et al 1999, Uliczka & Angelstam 1999, Dettki 2000). As an example, critical habitat components such as old conifer trees and deciduous trees but also the amount of dead wood are now regarded as crucial for biodiversity and should therefore be restored (Angelstam 1998, Axelsson et al 2002, Kuuluvainen et al 2002, Nordlind & Östlund 2003, Andersson & Östlund 2004). However, to achieve an efficient management, knowledge about the forest history should also be considered (Östlund 1993, Östlund & Zackrisson 2000, Groven et al 2002, Hellberg et al 2003). The use of historical records related to forest exploitation can reveal past changes in stand structure and species composition (Ericsson et al 2000, Axelsson et al 2002), age distribution (Axelsson & Östlund 2001) and effects on biodiversity (Groven et al 2002). For the purpose of this study, stand history is best illustrated through dendrochronological analysis and interpretation of historical documents, for example stand descriptions and forest inventory maps from Regional Forestry Boards and forest companies.

The aim of this study was to analyse the occurrence of *U. longissima* in relation to a spatially precise stand history. Objectives were to: 1) combine written historical documents and information based on dendrochronological analysis to describe the stand history since the 1860s in an area where *U. longissima* is found 2) analyse occurrence of *U. longissima* in relation to present and past forest structure 3) discuss processes in maintaining populations of particularly vulnerable epiphytic lichens such as *U. longissima* in boreal forest ecosystems 4) assess the use of a stand level approach for interpreting stand history and long-term changes in habitat conditions.

MATERIALS AND METHODS

Description of the study area

The study was carried out in a small area called Fällebodhöjden, located in the county of Västernorrland in the middle boreal forest zone of Sweden (Sjörs 1963). The area, situated 10 km west of Kramfors, is owned by the forest company SCA and comprises 23 ha (Fig. 1). The site was chosen using the following criteria: 1) occurrence of *U. longissima* 2) no forestry reported during the last 50 years and 3) availability of historic forest inventory data.

Fällebodhöjden is situated on a small plateau surrounded by mires and clear cuts (Fig. 2). Elevation ranges from 320 m to 380 m above sea level. Bedrock in this region is mainly metamorphic grey wacke with granite intrusions and soils are mainly sandy moraines (Fredén 2002). Norway spruce (*Picea abies* L. Karst) on mesic dwarf shrub type stands with *Vaccinium myrtillus* L. and *Deschampsia flexuosa* (L.) Trin. dominate the forest. The forest structure is multi-layered and characterised by frequent small glades. Scattered deciduous trees, mainly birches (*Betula spp.*) and goat willow (*Salix caprea* L.) also occur, while aspen (*Populus tremula* L.) and mountain ash (*Sorbus aucuparia* L.) are less abundant. A mixture of Norway spruce and Scots pine (*Pinus sylvestris* L.) dominates forest sites at higher elevations, while Norway spruce covers the southernmost part of the study area. Here also some large aspen trees occur. In the central parts of the study area the forest is less dense and contains large trees of birch and Scots pine. These parts of Fällebodhöjden also display the highest

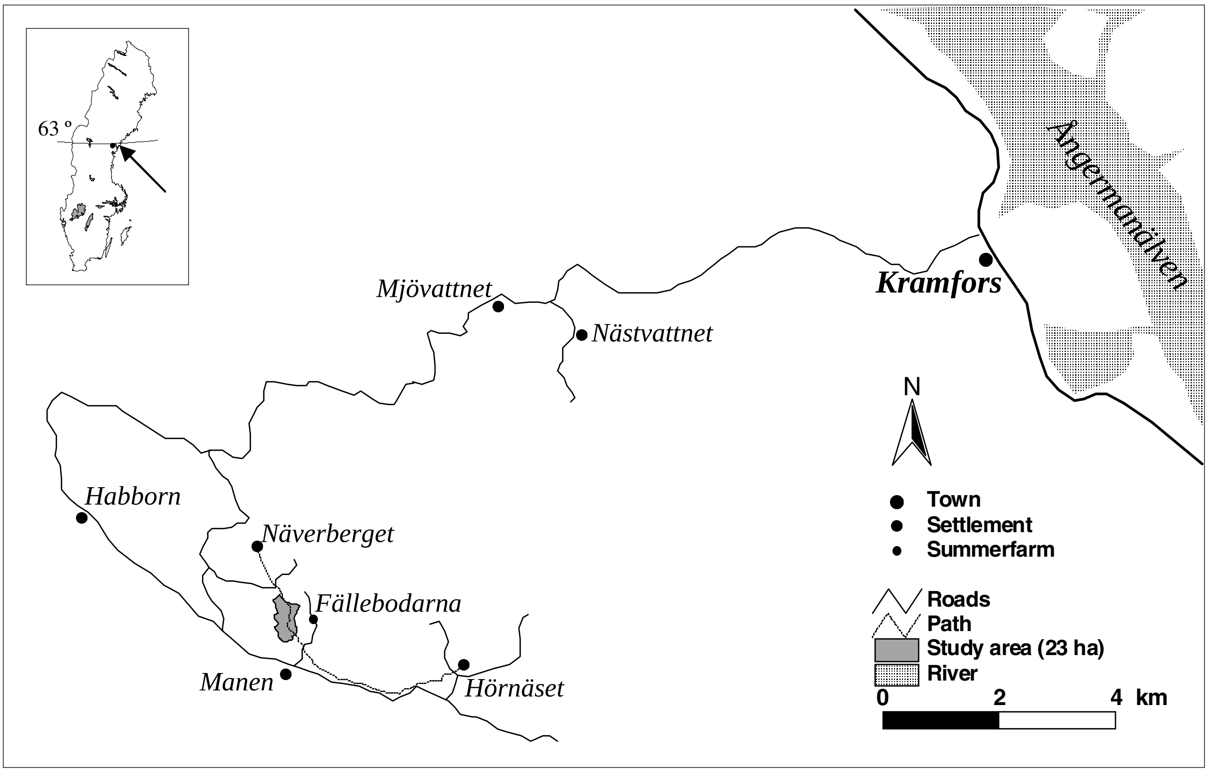

Fig. 1. Location of the study site Fällebodhöjden.

abundance of epiphytic lichens. Additionally, the central-eastern parts contain scattered specimens of juniper (*Juniperus communis* L.). Some areas are considerably moister and the ground-layer is dominated by different *Sphagnum*-species. The eastern part of the forest is denser and contains the largest trees and the highest amount of dead wood. In this part of the area the occurrence of *Dryopteris carthusiana* (Vill.) H.P. Fuchs is evident. Within the study area several epiphytic lichens occur, for example *U. longissima, U. filipendula* Stirt., *Lobaria pulmonaria* (L.) Hoffm., *Alectoria sarmentosa* (Ach.) Ach., *Bryoria capillaries* (Ach.) Brodo & D. Hawksw., *B. nadvornikiana* (Gyeln.) Brodo & D. Hawksw. and *B. fuscescens* (Gyeln.) Brodo & D. Hawksw.

General history of the study area

The utilisation of the boreal forests in northern Sweden reach far back in time, from Neolithic hunter/gatherer societies, agrarian colonisation and establishment of ironworks to the introduction of modern forestry and human recreation activities in the 20th century. Due to low human population density, the historical influence on the environment in these parts of Scandinavia has been low. However, when large-scale logging was introduced in the late 19th century there was a sharp increase in impact on the forest (c.f. Östlund 1993). The studied area (drained by the river Ångermanälven) is one of the most important regions in the development of the Swedish forest industry, which in addition to hydropower and mining constitute the very foundations of the Swedish industrialisation and development of welfare (Lundberg 1984, Björklund 1992). In the 1920s the productive forest area of the Ångermanälven region was estimated to 18 858 km^2 with a standing volume of 29.3 million m^3: the largest productive forest region in northern Sweden (Wik 1950).

Fig. 2. The southernmost part of Fällebodhöjden, surrounded by clear-cuttings, viewed from the south. (Photo by the author.)

The earliest known farm settlements near the study area were established by Finnish immigrants during the 16th century, who for different reasons (mainly war and years of famine) colonised remote forests in the central parts of Sweden (Fig. 3). These immigrants descended mainly from the Savolax area in eastern Finland, where years of warfare between Sweden and Russia resulted in serious oppression of the civilian population (Wedin 2001). The first settlements, Mjövattnet and Nästvattnet, near the study area can be dated to late 16th century, while several other settlements were established by Finnish immigrants during the 17th and 18th century (Gothe 1948). In old population registers at the Regional archive in Härnösand, Näverberget (which is the farm closest to the study area) is mentioned a new settlement in the 1850s (Table 1). Through agrarian development and an enhanced population growth, impact on the forest increased and changed. Slash and burn cultivation, grazing and cutting for building material and firewood were the primary causes.

Fig. 3. Demonstration of a plough used for slash and burn cultivation by Finnish immigrants 1912. (Photo courtesy of Forest Library, Swedish University of Agricultural Sciences.)

However, this agrarian forest utilisation was primarily concentrated to the immediate surroundings of the settlements (c.f. Östlund 1993). Also the use of "summer farms" was common in these parts of Sweden. Summer farms were used for grazing, from approximately June to August, to ease the pressure on the forests near the home farm and make use of the outlying land in a practical way (Kardell & Olofsson 2000). Most of the summer farms are now abandoned and completely overgrown or used for recreation purposes. However, several summer farms were in use near Fällebodhöjden until the 1940s (Frödin 1948, Sjölander pers. comm.), for example Fällebodarna, which was situated adjacent to the study site (Fig. 1). Small-scale production of tar (produced from pine snags and stumps) also occurred in the area (Sjölander pers. comm.), for example near the settlement Manen a tar pile was in use during the second part of the 19th century (Fig. 1).

An intensified utilisation of the forests in the Kramfors area began in the early 18th century, when demands for charcoal for the ironworks increased dramatically, this demonstrating the economic value of the enormous forested areas of northern Sweden (Almquist 1909, Hamilton 1983). The importance of the ironworks down the river valleys in northern Sweden has been significant, although they were to give way to the rapidly expanding sawmill industry. In the mid 19th century a new phase in forest use began. A dramatically increased exploitation of the Swedish boreal forests was triggered by the rapidly increasing demand for sawn wood products on the European market (Almquist 1909, Östlund 1993). A gradual decrease in custom duties in several countries (England, for example) in addition to technical advances created new potential for the Swedish export industry, which in turn resulted in the economic upswing in Sweden during the 1870s (Almquist 1909, Granström 1987). River mouths became the central points for shipping of forest products and large sailing-ships were leaving the Härnösand harbour carrying massive loads of timber.

The exploitation of the vast forest areas along the river Ångermanälven was completely dependent on the supply of labour and access to log-floating systems. The workers were recruited from the agrarian population but were primarily employed seasonally, mainly during the winter. Accordingly, permanent employment was not common until the 1950s (Embertsén 1976). Trees were felled by hand (Fig. 4) while horses were used for skidding and hauling, techniques that would be improved by better sleighs and winter roads (Embertsén 1976). The logging operations in the late 19th century (denoted as high grading) removed most of the larger trees, mainly Scots pine, which reduced the standing volume significantly (Östlund 1993). The structural effects on the forest after high grading operations were dramatic, leaving mainly small-dimensioned trees of Norway spruce and deciduous trees (Fig. 5). The timber was transported using the spring flood down several rivers to different sawmill companies (Fig. 6). Until 1851-52, when the first steam-powered sawmill was constructed in Kramfors, hydro-powered sawmills were being used (Höglund 1957, Embertsén 1976).

Table 1. Unpublished sources used for data collection.

A. Landsarkivet, Härnösand [Regional archive]
- Inskrivningsmyndigheten i Härnösands domsaga arkiv [Registration Authority of Härnösand judicial district archive]
  - Vol. DI:III Näverberget 1^2 i Gudmundrå socken (1876-1931)
- Inskrivningsdomaren i Ångermanland Södra arkiv [Registration Authority of Ångermanland southern judicial district archive]
  - Vol. CII: a:1 and CI: a:2 (1933-1968)
- Landskontoret i Västernorrlands läns arkiv [The County of Västernorrland archive]
  - Vol. EIII:89 Mantals och Skattskrifnings Längd för år 1850, Ångermanlands södra fögderi

B. Lantmäteriet, Gävle [Swedish National Land Survey Office]
- Flygfoto 1:30000 18H 5g 1958 [Aerial photographs]

C. NIN – Näringslivsarkiv i Norrland, Härnösand [Archive of trade and industry in Northern Sweden]
- Graningeverken AB
  - Skogsindelningar – kartor [Forest inventory maps and descriptions]
    - Tub 18 Mjövattnet 1892 + beståndsbeskrivningar
    - Tub 83 Mjövattnet 1771-75, 1845
    - Tub 84 Näverberget 1866, 1866, 1939, 1939-40

D. SCA Centralarkiv Merlo, Timrå [SCA central archive]
- Sunds AB
  - F: 3 Taxeringsinstrument 1895-1912 [Forest surveys]
    - Diverse brev, taxeringar mm. [Various letters, forest surveys]
      - 14. Skogsräkning å hemmanen Westeråsen, Habbarn, Näverberg, Elgberget m.fl.
      - 31. Transumt (20/5 1896) av E. Hessels taxeringsinstrument över Eriksdals Ångsågs Aktiebolags skogar år 1890
    - Fabian Gyllenhammar taxering av fastigheter och arrendeskogar 1897-1902 [Forest surveys]
      - 15. 7/7 1896 Eriksdals Ångsågs AB’s hemman och arrendeskogar i Gudmundrå, Ytterlännes och Wiksjö socknar
- Svanö AB
  - 2. Skogsbruk (Skogsvårdsstyrelsen, beståndsbeskrivningar, skogsindelningar, handlingar 1931-1952) [Forestry (Forestry Boards, stand descriptions, management plans)]
    - Arealuppgift: skogstillgång, avverkningsstatistik och kulturarbeten för Svanö, Dynäs & Wäija A/B:s egna skogar 1923-51. Ej insorterad. Sektion 26.11
    - 261.53 Äldre skogsindelningshandlingar, sammandrag mm. 1931-46. Volym 15. Sektion 27:1
    - 261.7 Arealuppgifter, skogstillgångar mm. 1923-1937. Volym 16. Sektion 27:2
    - 266.301 Sammandrag över Svanö AB’s skogsfastigheters arealer och kubikmassor 1933, 1942-46 och 1947-51, Volym 22. Sektion 27.2

E. SCA SKOG AB lokalkontor, Ullånger [SCA local administration office]
- Graningeverken AB
  - Arkiv: skogsindelningar – kartor mm. [Archive: management plans and maps]
    - Karta över Block II omfattande Sandvikens A.B. tillhöriga Byn Hörnäset uti Gudmundrå socken 1926
    - Karta över Block III omfattande reg.nr. 1^2 inom Näverbergets by uti Gudmundrå socken 1938, S.C. AB
    - Flygfoto 1:30000 18h 5g 1976 + beståndsbeskrivningar

F. Skogsvårdsstyrelsens distriktskontor, Sollefteå [Forestry District office of the National Board of Forestry]
- Arkiv: Skogsbruksplaner fastighetsvisa Fjällsjö – Gudmundrå 1951-1963 [Archive: management plans]
  - FXIIe: Volym 5. Skogsvårdsplan för fastigheten Hörnäs 2:1 i Gudmundrå socken 1961 + karta

These sawmills were dependent on small tributary streams with waterfalls to operate the water wheel. During the period 1850-1886 the Swedish sawmill-industry expanded dramatically (Sällström-Nygren 1967, Embertsén 1976). The utilisation of steam-powered sawmills meant that these could be placed near the coast in close connection to the harbours. Also, the use of thin saw blades contributed to an increased production and accordingly enhanced export prospects (Sällström-Nygren 1967). Near the study area, close to the settlement Näverberget, a steam-powered sawmill was constructed in the 1860s (Wik 1950). During the first half of the 20th century, several other sawmills were in use near Fällebodhöjden, for example close to the settlement Manen (Sjölander pers. comm.) However, hydro powered sawmills were not abandoned immediately. Even in the late 19th century a considerable part of the sawmills in the Västernorrland county were still powered with huge water wheels (Höglund 1957). During this period and in the early 20th century further technical improvements and extensions of the existing road network made it possible to carry out forestry even in more remote parts (Embertsén 1976). The introduction of pulpwood manufacturing also meant that thinner trees and trees of lower quality could be logged (Jäghagen 1996). The belief in the inexhaustible boreal forests of northern Sweden eventually led to degenerated ecosystems and in accessible areas, shortage forests suitable for timber (Östlund 1993, Östlund et al 1997, Ericsson et al 2000).

Fig. 4. Tree felling with axe during winter 1937. (Photo courtesy of Forest Library, Swedish University of Agricultural Sciences.)

Fig. 5. Forest structure after intensive high grading operations during the late 19th century, Jokkmokk 1919. (Photo courtesy of Forest Library, Swedish Agricultural Sciences.)

Ownership of forest properties has changed considerably over time in this region (Almquist 1909, Fahlén 1917, Höglund 1957). Within the study area and its surroundings several forest companies have been active. The estate, which is named Näverberget 1^2 and includes the study area, was according to old forest surveys at SCAs central archive owned by private smallholders but managed by Eriksdals Ångsåg AB in the late 19th century (Table 1). During the 1890s the company, founded in 1890 (Höglund 1957), acquired several forest properties nearby the study area, while Näverberget 1^2 remained private until the 1930s. As described in documents provided by the Regional archive in Härnösand, Näverberget 1^2 was owned by 7 different private smallholders between 1866 and 1933 (Table 1). However, according to old forest inventory maps provided by the Archive of trade and industry in Northern Sweden, Graningeverken AB became the new owner of the estate in 1968 (Table 1). Until then Sandvikens Cellulosa AB and Svanö AB had been managing the forests surrounding Fällebodhöjden and Näverberget. Following a merger of SCA and Graningeverken, SCA is the present owner of the forest estate.

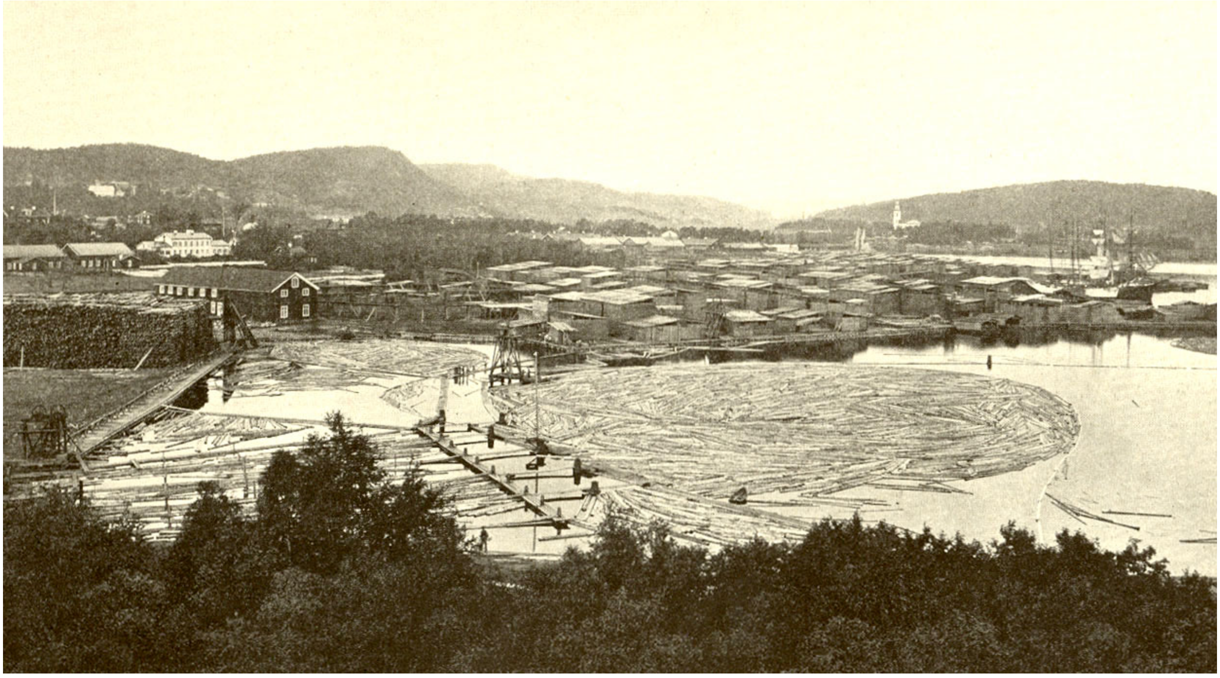

Fig. 6. View of the old timber yard at Bollsta Bruk, near Kramfors, in the late 19th century. (Photo extracted from Almquist 1909.)

Description of the fruticose epiphytic lichen Usnea longissima

U. longissima is an epiphytic lichen with an almost circumboreal distribution and associated to a variety of tree species and forest ecosystems (Ahlner 1948, Ahti 1977). However, during the 20th century its abundance has decreased markedly throughout its range, for example in the boreal forest of Scandinavia (Esseen et al 1981, Esseen & Ericson 1982, Nitare 2000). The pendulous lichen is characterised by its length and sparsely- or unbranched strand with frequent 1-2 cm long fibrils (Fig. 7). The light blue-green main stem lacks continuous cortex-tissue, while the white core is somewhat elastic (Moberg & Holmåsen 1990). In Sweden *U. longissima* is nationally protected and considered threatened according to the IUCN Red list of Swedish species (Gärdenfors 2000). The distribution of *U. longissima* in Sweden is concentrated to the southern and middle part of the boreal belt with a stronghold in the eastern part of the Västernorrland County (Fig. 7). It occurs in relatively open stands, predominantly on upper parts of north- and east facing slopes but also next to mires and moist areas (Esseen & Ericson 1982, Thor & Arvidsson 1999). *U. longissima* has an unpredictable pattern of occurrence at the stand level and often displays a patchy distribution in apparently homogenous stands, mainly in the lower part of Norway spruce canopies (Esseen & Ericson 1982, Gauslaa et al 1998). It may be found on both living and dead trees and often in areas with high occurrence of top breaks, caused by large accumulation of snow in the canopies (Esseen et al 1981, Esseen & Ericson 1982).

Areas containing *U. longissima* are characterised by high and stable atmospheric humidity and fairly narrow temperature amplitudes (Esseen & Ericson 1982, Thor & Arvidsson 1999). The main substrate in Sweden is Norway spruce, although other species of tree may hold lichen fragments. However, these thalli often originates from a nearby Norway spruce (Esseen & Ericson 1982). Thalli of *U. longissima* often grow unattached to the substrate and more or less wound round twigs or down the tree trunk (Fig 8). It seldom occurs higher than 9 metres from ground level (Gauslaa 1997). In Sweden the dispersal is solely vegetative. At a stand level small thallus fragments are spread horizontally by the wind or vertically down the tree canopy (Esseen & Ericson 1982, Gauslaa 1997). Dispersal of soredia and isidia are less common and are thought to be of greater importance at the landscape level (Gauslaa 1997). Several variables, such as air quality (Esseen & Ericson 1982), tree age (Rolstad & Rolstad 1999), mineral composition of the substrate (Gauslaa et al 1998), light (Gauslaa 1997), dispersal and stand age (Keon 2001) have been suggested as factors affecting its distribution. Furthermore, it is believed that *U. longissima* and several other rare

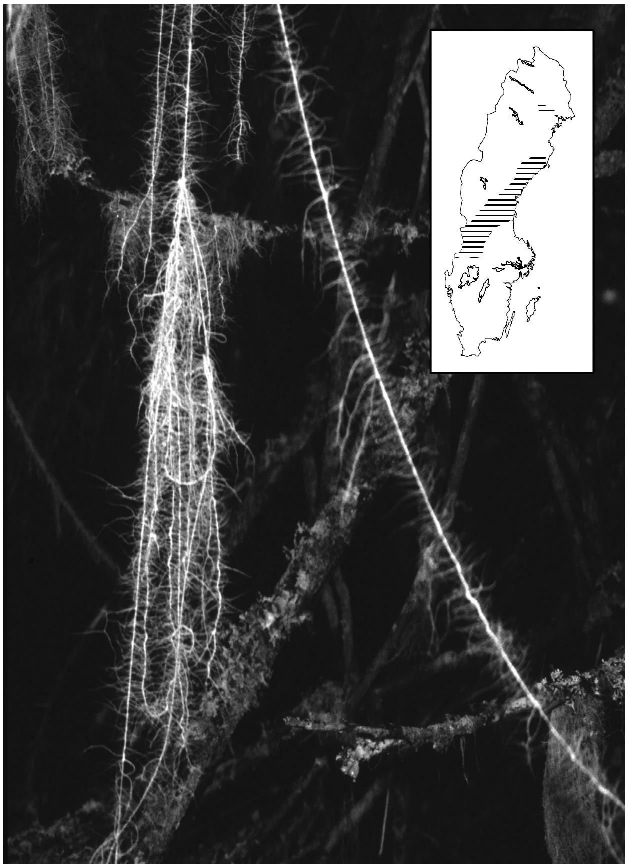

Fig. 7. Close-up photo on *U. longissima.* Inset map shows its distribution in Sweden. Data extracted from Andersson & Williamsson (1993), Thor & Arvidsson (1999), Gärdenfors (2000), Nitare (2000). (Photo by the author.)

Fig. 8. Extremely long thalli formation of *U. longissima* down a Norway spruce trunk. (Photo by the author.)

epiphytic lichens are dependent on spruce forests with long forest continuity (Esseen & Ericson 1982, Nitare 2000). As has been described by Dettki et al (2002) old growth stands may function as an important source of lichen propagules.

Study design and sampling of the inventory

Fig. 9. Forestry marking on Norway spruce, made in the 1930s. (Photo by the author.)

The environmental data used in this study were collected from transect analyses and sample plots in the study site Fällebodhöjden during September 2003. By using a 50x50 meters cell-size grid, transects and sample plots could be obtained. 28 transects, running in an east-west direction, were placed with starting points along a main line running from south to north. Trees with occurrence of *U. longissima* > 5m height, stumps related to forest exploitation, fire scars and culturally modified trees (CMTs) were recorded within 12.5 meters along each side of the transects. CMTs were recorded since they may give significant information of past utilisation of the forest (Andersson & Östlund 2002, Östlund et al 2002). Marking of trees intended for felling was a common procedure in late 19th and early 20th century and some of these are still visible on old trees (Fig. 9). Also, five potential fire scars were sampled using a chainsaw. The position and direction of all objects were determined using GPS (Swedish topographic system RT90) and compass. Stumps were classified into three categories: class 1) stumps of Scots pine felled by axe >120 years ago, class 2) stumps of Scots pine felled by handsaw or chainsaw <120 years ago and class 3) stumps of Norway spruce felled by handsaw or chainsaw <120 years ago. Stumps descending from the high grading period during the second half of the 19th century can be distinguished from stumps created during later logging operations. High grading included only old-growth Scots pine trees cut by axe, predominately during the winter, which resulted in slanted and fairly tall stumps with large diameter (Tirén 1937, Östlund & Lindersson 1995). Additionally, all objects were numbered and described.

In 24 sample plots, basal area and tree height were recorded by using relascope and hypsometer. These variables were later used to estimate canopy openness and basal area. Classification of forest-floor vegetation according to Ebeling (1978), altitude and occurrence of downed dead wood were also noted. A total of 121 trees within the sample plots were cored using increment borers (ø 4 and 5 mm). The trees were randomly chosen when estimating the basal area of the sample plot. Samples were taken as near the germination point as possible. Tree age was later determined in laboratory by using scalpel, zinc paste and stereo magnifier. In cases when the increment cores failed to reach the pith, a transparent plastic sheet with concentric circles drawn was used to estimate the length of the missing radius (Groven et al 2002). Additionally, the ages of 33 trees with occurrence of *U. longissima* and 6 trees with markings were determined in the same way. Trees with markings were cored with an increment borer (ø 10 mm). To analyse differences in tree age between trees with and trees without occurrence of *U. longissima,* a non-parametric statistical test (Wilcoxon Two-sample Test) was conducted.

All samples were further analysed to detect possible growth responses that may indicate disturbance events. Consequently, mean tree-ring width was compared between two consecutive 10-year periods. A growth response was defined as an increase in mean tree width between two successive periods of more than 100%. Several factors (including logging events) may give rise to growth responses. Logging events were interpreted from a diagram showing the proportion of trees with growth release following years with dated growth releases. In addition, this was related to other data, i.e. historical sources and occurrence of stumps and forestry markings. The method used for analysing logging events resemble previous studies on tree age and logging history carried out in Norway by Groven et al (2002).

Also distribution of tree species, diameter breast height (DBH) > 5 cm and vitality of trees were recorded in a total of eight sample plots (0.1 ha), four plots within an area with occurrence of *U. longissima* and four plots randomly chosen within the study area. Vitality of the trees was classified into two categories: living and dead trees.

Historical maps and forest management plans

The primary sources used in this study were stand descriptions and forest inventory maps from forest companies that have managed the forest within the study area during different time periods since the 1870s (Table 1). The historical documents and maps were principally provided by SCAs archive in Merlo, NIN in Härnösand and SCAs local administration office in Ullånger. The historical sources were applied with careful source criticism. Data on DBH, tree species composition and number of trees were used to estimate the standing volume in the area in the late 19th century. Changes in stand characteristics, including stand age and canopy openness, tree species composition and standing volume were interpreted using forest inventory maps, stand descriptions, management plans and aerial photographs. By using GIS (ArcView 3.2 program), digital maps showing the distribution of snags of different classes, trees with occurrence of *U. longissima* and CMTs were produced. The forest inventory maps were scanned and geo-referenced to fit digital topographic maps provided by SCAs local administration office in Bollsta and the Swedish Land Survey. Different forest stands were processed into polygons and stand development and then analysed using the GIS overlay procedure. Literature on the local history, including Finnish immigration, forestry and industrial development, was consulted. As a complement to the written sources, information from private smallholders near the study area and personal from the County Board of Västernorrland was used.

RESULTS

Stand structure and occurrence of Usnea longissima according to transect and sample plot inventory

The forest of Fällebodhöjden displayed fairly similar stand characteristics over the whole area, although smaller areas deviated in some respects. Mean tree height within sample plots was 19 m (ranging from 12 m to 26 m) while canopy openness varied between 0.35 and 0.75 (mean: 0.6). The number of living trees within the study area was mainly represented by Norway spruce (83 %) with deciduous spp. (15.5 %) subdominant and Scots pine trees (1.5 %) scattered over the area (Fig. 10). A comparison between areas with *U. longissima* and areas without showed no distinct differences in present stand characteristics such as amount of downed dead wood (data not presented here), tree species composition, tree size and tree vitality including top breaks on trees (Table 2). Average tree age in the study area was 133 years (n=154). While the age of the living Norway spruces with *U. longissima* varied between 102 and 265 years (n=33), most were 110 to 160 years old (Fig. 11). Trees without *U. longissima* displayed a similar age structure, however a bit younger and with some Norway spruces less than 100 years old and some unusually old (>350 years). A significant difference in mean tree age was found between trees with *U. longissima* (149 years) and trees without (129 years) ($Z = 3.81$, $P < 0.05$).

Table 2. Stand characteristics taken from eight sample plots (0.1 ha) with and without occurrence of *U. longissima*. All trees > 5 cm DBH were counted. Data derived from field sampling.

	***U. longissima* present**	***U. longissima* absent**
Tree species (%)		
Betula sp.	16.7	13.8
Picea abies	81.1	83.6
Pinus sylvestris	2.0	1.6
Populus tremula	0.2	
Sorbus aucuparia		1.0
Tree size (mean DBH)		
Betula sp.	14.5	13.3
Picea abies	16.8	16.5
Pinus sylvestris	37.6	34.4
Populus tremula	44.0	
Sorbus aucuparia		9.0
Tree vitality (%)		
Living trees	83.8	83.3
Dead trees	16.2	16.7
Top breaks on trees		
Average height (m)	3.49	3.52
Proportion of trees (%)	9.7	8.2

Within the study area, *U. longissima* was detected on a total of 56 trees, of which only 9 % had a stem diameter less than 10 cm DBH. The number of trees with *U. longissima* was estimated to be 3.4/ha. *U. longissima* was recorded on both dead and living trees but was found only on Norway spruce and predominantly in the south-central part of Fällebodhöjden. At this location some trees were extremely lichen rich and contained long free-hanging specimens. The forest was characterised by an open and multi-layered stand structure with slow growing trees, while the topography featured a more hilly terrain with drier site conditions and occurrence of *Vaccinium vitis-idaea* L., *Cladonia rangiferina* (L.) F.H. Wigg. and *C. arbuscula*

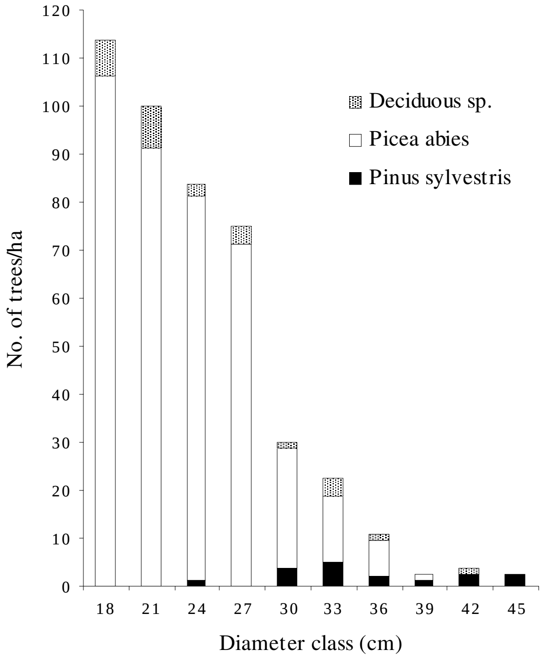

Fig. 10. Diameter distribution of tree species in 2003. Data derived from field sampling.

(Wallr.) Flot. (Fig. 12). Thalli of the lichen found in the northern and eastern part of the study area were confined to small gaps, while specimens found in the central part showed no such pattern. Here the forest structure was still multi-layered and open but somewhat denser than the south-central part of the study area.

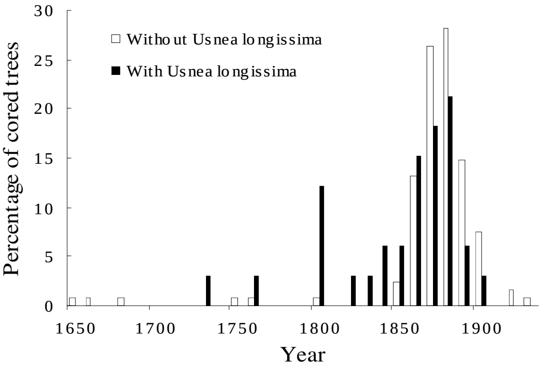

Fig. 11. Age structure of Norway spruce in 10-year intervals for trees > 5 cm DBH, showing trees with (filled bars) and without (open bars) occurrence of *U. longissima*. Data derived from field sampling.

Reconstruction of stand characteristics 1860-2003

Stand structure within the study area has changed considerably during the last 150 years. Prior to the 1860s, large trees of Scots Pine and slow growing trees of Norway spruce dominated the forest, while deciduous trees are thought to have occurred less frequently (no precise data on tree species composition was found from this period). In a forest survey over the Näverberget estate from 1896 (including Fällebodhöjden), the forest was described as dying and with limited re-growth. According to the logging data, most of the large Scots pine trees were felled before 1890 (Fig. 13 B), leaving a thinned even-aged stand of restricted Norway spruce and deciduous trees. In 1890 the proportion of Scots pine had diminished to about 3 %, but some of the trees still exceeded 45 cm in DBH (Fig. 14). Through further selective logging operations in the first decades of the 20th century, additional Scots pine and large diameter Norway spruce trees were felled (Fig. 13 C-D). As a result, the remaining forest was characterised by stands of pure Norway spruce or Norway spruce and Scots pine (Fig. 15). In the 1930s the occurrence of deciduous trees were noticeably low, but has thereafter increased substantially (Fig. 15). In 1933 the standing volume of timber within the study area and its surroundings was 99 m^3/ha. However, during the last century the standing volume has increased, except for a temporary decline in the late 1930s (Fig. 16). In 1938 old forest (>120 years) covered less than 23 % of the study area and was confined to stands number 2 and 5 (Fig. 17). In stand number 4 the forest was even younger than 80 years. Today the study area is covered completely by a multi-aged forest with an average stand age exceeding 120 years (Fig. 17) and the standing volume of timber is around 200 m^3/ha. Furthermore, at present time

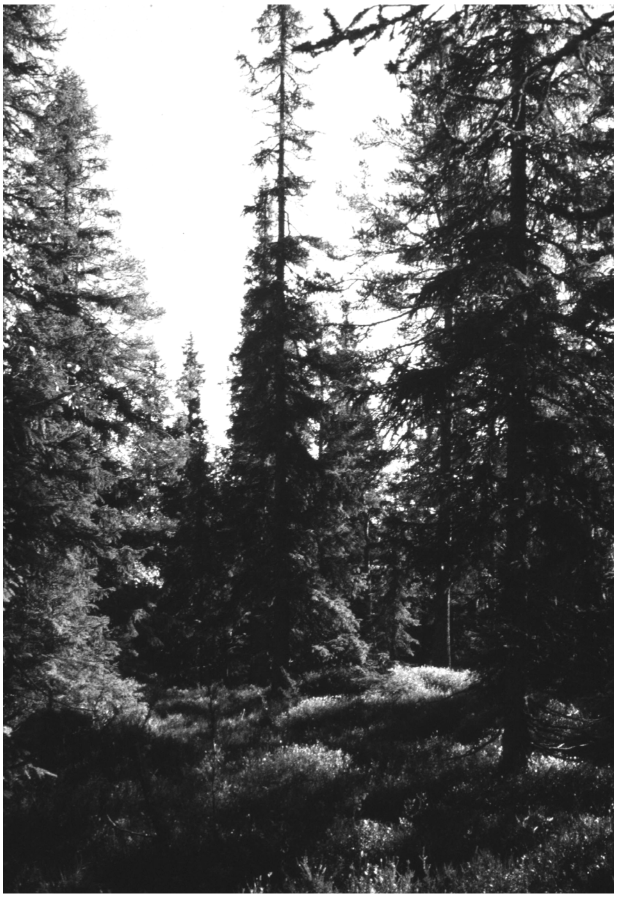

Fig. 12. Stand structure at the main location for occurrence of *U. longissima*. (Photo by the author.)

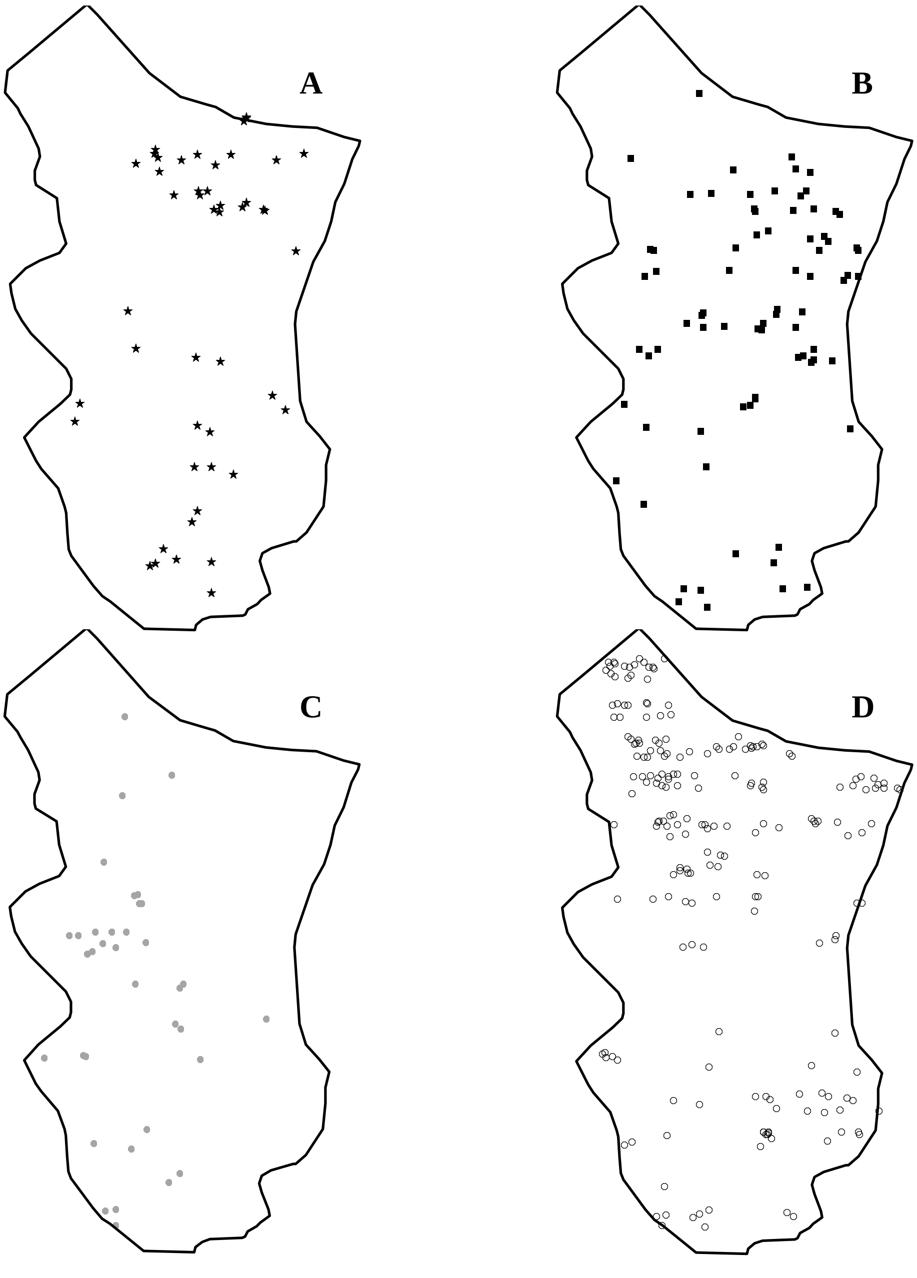

Fig. 13. Distribution of a) trees marked for felling ★, b) class 1 stumps ■, c) class 2 stumps ● and d) class 3 stumps ○ within the study site in 2003. Data derived from field sampling.

the area features twice as many trees in each class up to 45 cm DBH compared to in 1890. However, very large trees (DBH >45 cm) existed in 1890, but are now completely absent (Fig. 14). A comparison of canopy openness in 1938 and 2003 displayed changes in all areas except the central parts (stand number 2) of the study area, which today contains the highest concentration of trees with *U. longissima* (Table 3). Furthermore, no traces of clear-cutting operations were found within the study area.

Dating of logging events

Stumps of all three categories were found within Fällebodhöjden (Fig. 13 B-D). Stumps of class 1 (Scots pine felled >120 years ago) were evenly distributed over the study area (7/ha) and are thought to derive from the earliest logging within the study area. Mean height and diameter of class 1 stumps were 60 cm and 40 cm respectively. Stumps of class 2 (Scots pine felled <120 years ago) were less common (3/ha) and confined to the west-central parts. The mean height of these stumps was 35 cm and mean diameter 30 cm. Many of the class 2 stumps had a straight cut surface and in some cases small pieces of bark left on the sides. Stumps of class 3 (Norway spruce felled <120 years ago) were found all over the area (18/ha) but concentrated to the northwest part. These stumps were often completely overgrown with bryophytes and ericaceous vegetation. Accordingly, the northern part of the study area displayed the highest concentration of stumps related to forestry, while the south-central part, which is the main location of *U. longissima*, contained few stumps of all three classes. However, logging operations were evident all over the study area, including areas with occurrence of *U. longissima*. Positive growth release, indicating historical loggings was detected in 23 % (n=37) of the cored trees. During

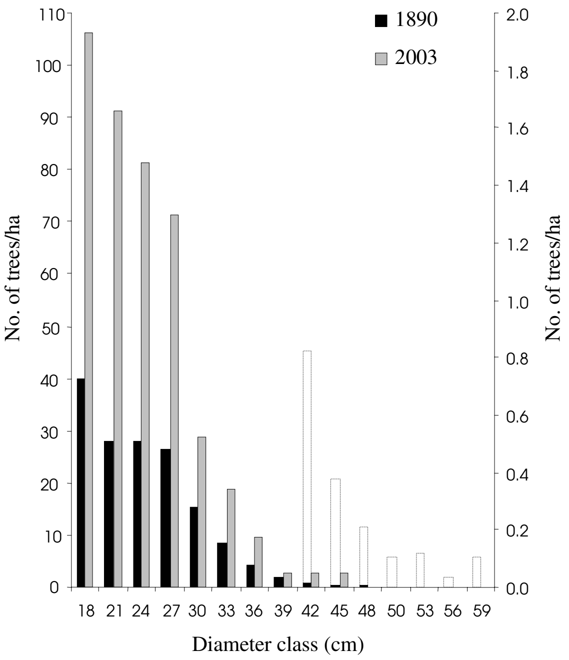

Fig. 14. Diameter distribution of conifer trees in 1890 (black bars) and 2003 (grey bars). Filled bars are plotted against the left Y-axis; open bars (plotted on the right Y-axis) represents expansions, for clarity, of frequencies less than 1 tree/ha. Data from 1890 (including the study site and estates in the surroundings) extracted from document Sunds AB, 2.Skogsbruk, F:3: 14 in Table 1. Data from 2003 derived from field sampling.

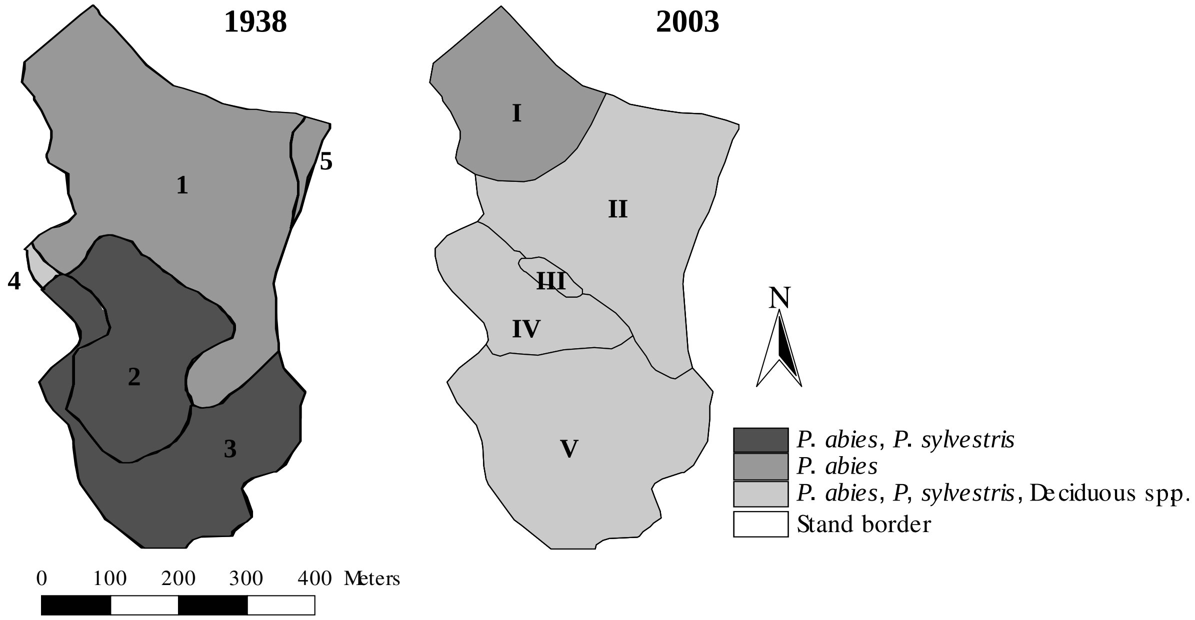

Fig. 15. Stand borders and tree composition in 1938 and 2003. All areas are dominated by *P. abies* but with occurrence of *P. sylvestris* or deciduous spp. and *P. sylvestris*. Stands are numbered 1-5 and I-V for 1938 and 2003 respectively. Data extracted from field sampling and document Graningeverken, arkiv: Karta över Block III 1938 in Table 1.

the last 150 years three distinct periods of positive growth release were detected within the study area: 1857-1868, 1913-1922 and 1937-1946 (Fig. 18).

Occurrence of CMTs and traces of fire events

The mean number of culturally modified trees (CMTs) per hectare was 4.8, more or less evenly distributed over the study area. A total of 111 trees with CMTs were identified, of which 22 were trail markings from the old path between the settlements Näverberget and Hörnäset (Fig. 1) and 47 were markings related to forestry, indicating previous logging operations. Forestry markings were found on Norway spruce and birches within the study area apart from the very northwest section and less frequently within the south-central area (Fig. 13 A). 6 of the markings were dated to 1929, 1936 (3), 1940 and 1941. Another common type of CMT detected, was birches scarred to produce axe-handles. However, 18 % of the CMTs could not be classified.

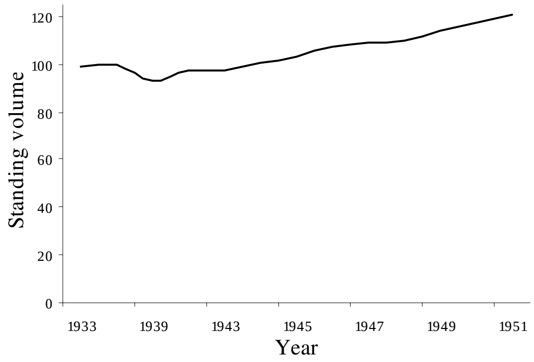

Fig. 16. Standing volume in m^3/ha for the study site and estates in the surroundings included. Data 1933-1951extracted from documents Svanö AB, 2.Skogsbruk: arealuppgift 1923-51, 261.53, 261.7 and 266.301 in Table 1.

Table 3. Canopy openness in 1938 and 2003 (within borders 1-5 corresponding to 1938 years stand borders). Data derived from field sampling and extracted from document Graningeverken, arkiv: Karta över block III 1938 in Table 1.

Stand number	Openness 1938	Openness 2003
1	0.7	0.55
2	0.6	0.6
3	0.5	0.6
4	0.7	0.55
5	0.9	0.65

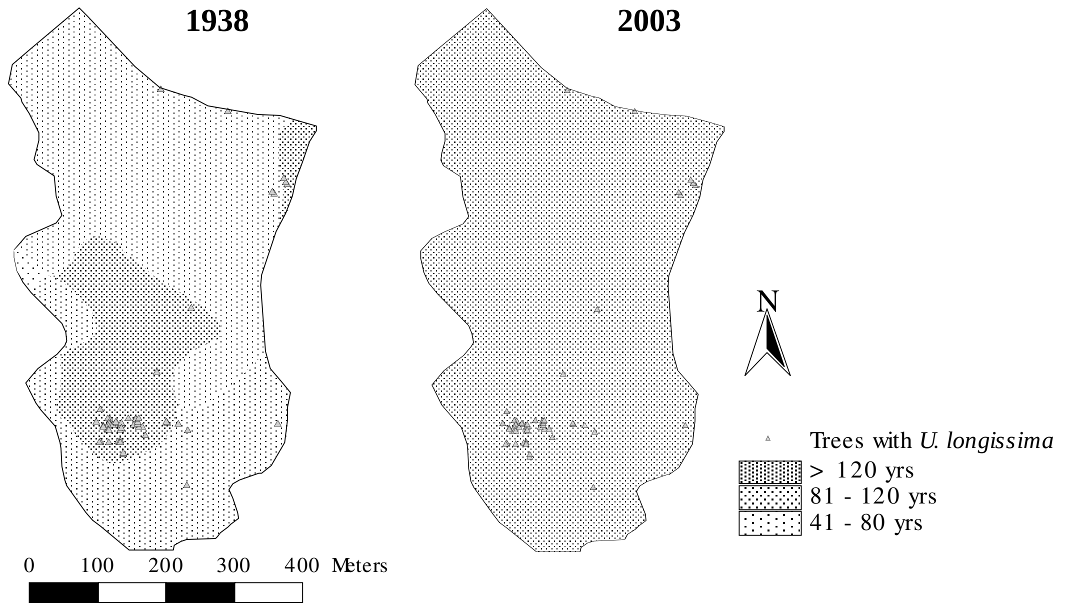

Fig. 17. Age structure in 1938 and 2003. Present distribution of *U. longissima* is plotted on both maps. Data extracted from field sampling and document Graningeverken, arkiv: Karta över Block II 1926 and Karta över block III 1938 in Table 1.

Since no reliable scars or traces of larger fires were detected in Fällebodhöjden, no forest fire seems to have occurred during at least two centuries. One tree hit by lightning was found, but this event seems not to have affected the surrounding forest. However, according to old management plans provided by the Forestry District Office archive in Sollefteå, a forest fire occurred south of the study area in the late 19th century, leaving large amounts of burnt stumps and snags of Scots pine (Table 1).

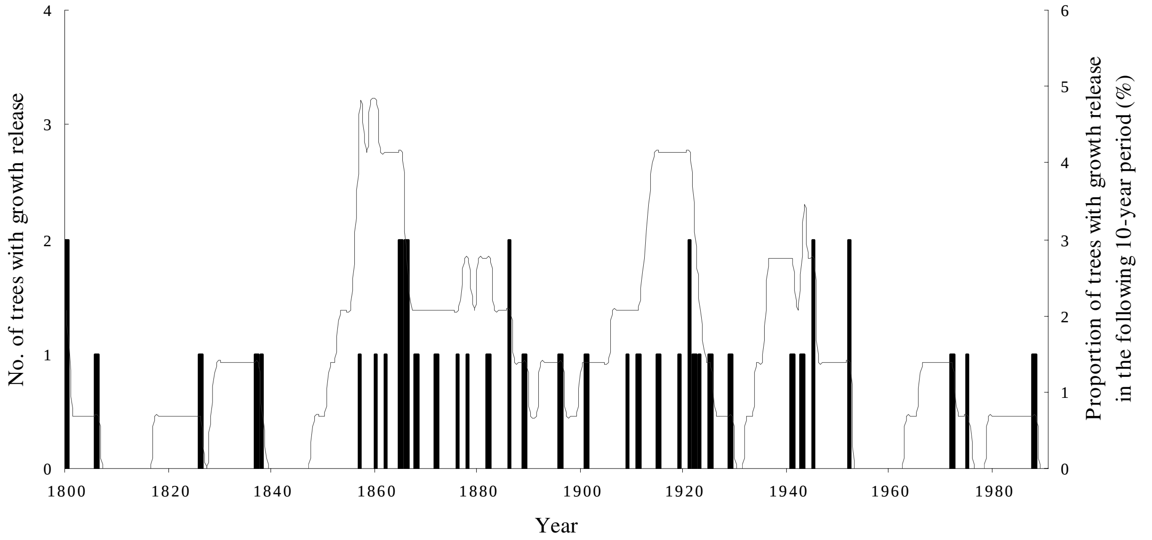

Fig. 18. Number of cored trees with growth release per year (filled bars) and the percentage of cored trees with growth release in the following 10-year period (line). Data derived from field sampling.

DISCUSSION

Research on the occurrence of *U. longissima* have focused on ecological factors such as present habitat characteristics (Esseen et al 1981), morphological characters (Gauslaa 1997), nutritional status of the substrate, (Gauslaa et al 1998), age of the substrate (Rolstad & Rolstad 1999) and habitat conditions and dispersal (Keon 2001). Many factors seem to affect the distribution of *U. longissima*, especially substrate quality and availability, microclimate and also stand age. However, neither of these factors alone nor a specific combination of factors has given a sufficient explanation to the intricate occurrence of *U. longissima*. Furthermore, a basic but unverified assumption that forest continuity is of great importance permeates much literature on this species (c.f. Ahlner 1948, Olsen & Gauslaa 1991, Nitare 2000). In this study I have explored the possibility to analyse spatial distribution of *U. longissima* in relation to a detailed stand history and thus deepen the discussion on continuity.

Present stand structure and distribution of Usnea longissima

The survey of the present stand structure did not reveal any differences in tree species composition, tree size, tree vitality and top breaks on trees between areas with *U. longissima* and areas without. Furthermore, similar stand structure was found throughout the studied area (Table 2). However, tree size and presence of *U. longissima* displayed a reliable pattern, since more than 90 % of the trees holding *U. longissima* had a stem diameter larger than 10 cm

DBH. A likely explanation for this is that large trees can host more thalli than small trees, i.e. the branch surface area is bigger. Furthermore, every tree smaller than 10 cm DBH holding *U. longissima* were positioned right next to a much larger tree, also with occurrence of *U. longissima*. This indicates that the occurrence of *U. longissima* on small trees is dependent on dispersal of small thallus fragments from larger trees nearby, which has also been proposed by Esseen et al (1981), Esseen (1985) and Gauslaa (1997).

Trees containing *U. longissima* displayed a slightly different age structure than trees without it (Fig. 11). As an example, a certain part of the cored trees containing *U. longissima* germinated during the first half of the 19th century, yet very few of the cored trees without the lichen did. In addition, a few exceptionally old specimens of Norway spruce without *U. longissima* were found but also some quite young, while trees containing *U. longissima* displayed no such pattern (Fig. 11). However, regardless of occurrence of *U. longissima* most trees germinated between 1850 and 1900, which points to a strong influence of disturbances during this period. Consequently tree age is less important for the occurrence of *U. longissima*. This statement is supported by previous studies carried out in Norway by Esseen & Ericson (1982) and Rolstad & Rolstad (1999). Furthermore, the small differences in age structure may in the present study be a result of different sample sizes.

Fig. 19. Photo on *U. longissima*. Unlike many other epiphytic lichens, *U. longissima* seldom attaches to the substrate through holdfasts. Instead it decreases the competition from other lichens by minimising contact with branches and additionally, occupying the space between them. (Photo by the author.)

U. longissima was found solely on Norway spruce but showed no obvious preference for living or dead trees. The results are consistent with earlier studies (Esseen & Ericson 1982, Gauslaa 1997, Rolstad & Rolstad 1999) and gives support to the assumption that tree species but not tree vitality affect the distribution of *U. longissima* and that the thallus fragments seen from the ground probably are derived from populations higher up in the canopy. The somewhat open, multi-layered stand structure and differing topography of the south-central part of Fällebodhöjden clearly provides suitable conditions for *U. longissima* (Fig. 20). These habitat characteristics resemble conditions described in Ahlner (1948), Esseen & Ericson (1982) and Thor & Arvidsson (1999) and may be an important explanation to the uneven distribution of *U. longissima* within the study area. However, in areas with habitat conditions resembling those in the south-central part no specimens were found. On the contrary, several thalli were found in areas without these typical habitat conditions but in those cases confined to small canopy openings. Absence of

U. longissima and other epiphytic lichens in apparently suitable habitats may also be due to poor dispersal ability, as proposed by Esseen & Ericson (1982) and Dettki et al (2000).

Reconstructions of stand characteristics including past human utilisation and logging events

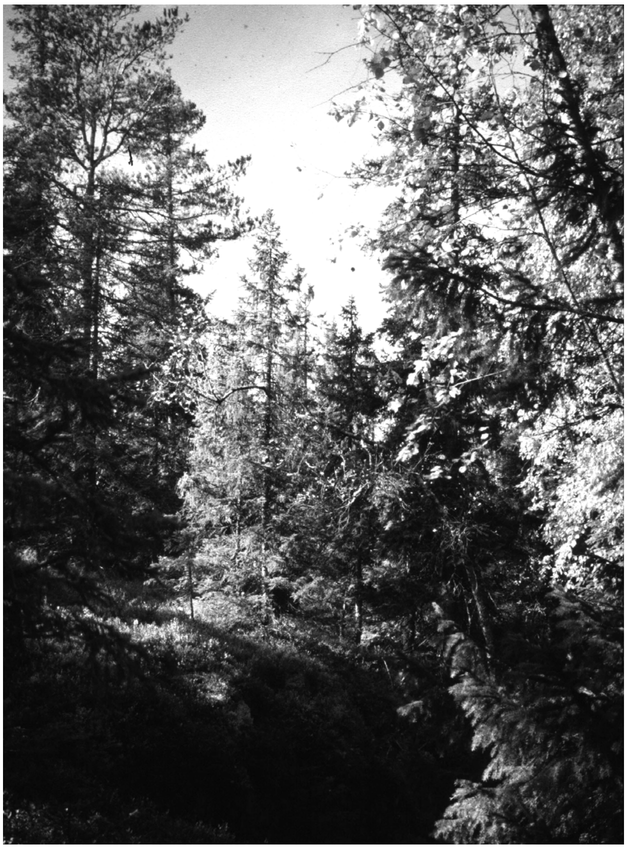

Fig. 20. Stand structure at the main location of *U. longissima*, just 10 meters from the position were the photo displayed in figure 12 was taken. (Photo by the author.)

The stand structure within Fällebodhöjden has varied considerably during the last 150 years. Past forest utilisation, early logging operations but limited impact by recent forestry in addition to the long-term absence of forest fires have all contributed to present stand characteristics. In the 1860s the first logging operations within Fällebodhöjden took place. Since then at least two additional selective cutting have occurred. The most conspicuous signs of this are the many stumps of different age and size, but also forestry markings such as blazes on trees planned to be felled or blazes indicating borders for logging operations (Fig. 13 A-D). The logging blazes detected on birches from the 1930-40s indicate that deciduous trees were felled during World War II for fuel and gas production (Ericsson et al 2000). In this study the inventory of stumps and forestry markings are supported by the tree-ring width analysis, in which at least three separate periods of growth release could be detected. However, the percentage of the trees displaying a growth release since 1800 was quite low (Fig. 18). Nevertheless, when using all variables together three different logging events were identified.

The first logging event was interpreted as high grading of Scots pine and seems to have affected the forest structure all over the study area (Fig. 13 B). These logging operations represented a loss of the largest trees but more importantly changed habitat conditions for Norway spruce under-growth (Tirén 1937). In some stands high grading resulted in slow re-growth and death of trees. In an early forest survey from 1896 the forest in the surroundings of Fällebodhöjden was described as damaged by previous cuttings:

> “Wid afverkningen har den kraftigaste skogen afverkats med förbigående endast af mer eller mindre felaktiga träd samt undermåliga sådana, hvadan den nu befintliga skogen, synnerligast i södra delen af halfva denna trakt, utgöres snart sagt, uteslutande af tynande och döende gles granskog med ringa eller ingen återväxt…” [At the time of the logging operations only the largest and healthiest trees have been cut, leaving a thin and dying spruce forest with insignificant re-growth, especially in the southernmost part of the area…] (Text translated and extracted from document Sunds AB, F:3: 14 in Table 1).

In areas with an especially dense forest structure, the increase of canopy openness may have favoured populations of epiphytic lichens such as *U. longissima* temporarily. However, in other stands these logging operations resulted in noticeable growth responses and recruitment of new trees. As a consequence, the majority of the trees in Fällebodhöjden germinated during the late 19th century (Fig. 11). This sudden change in habitat conditions may indeed have influenced the occurrence of *U. longissima*. In areas with strong growth response of the trees, this should have affected *U. longissima* and several epiphytic lichens negatively, since it is sensitive to abrupt changes in substrate quality and availability and also change in micro-climate (Esseen & Ericson 1982, Gauslaa et al 1998, Esseen et al 1999).

However, more pronounced effects on stand structure probably took place during the selective logging operations in the first half of the 20th century, particularly in the northern part of the study area (Fig. 13 C-D). These loggings of Norway spruce, Scots pine and deciduous species are indicated by the many stumps of class 2 and 3. The change in habitat structure (including reduction of substrate and most likely removal of trees containing important sources of epiphytic lichens) also affected the distribution of old-growth forest (Fig. 17). Hence, this seems to be a decisive factor for explaining the present distribution of *U. longissima* within the study area. Furthermore, the standing volume within Fällebodhöjden in the early 20th century is assumed to have been very low. A reconstruction of stand characteristics in the area during the 1930-50s, displayed a general increase of standing volume between 1935 and 1951 (Fig. 16). Since then the standing volume has continued to increase steadily. Especially important was also that no signs of forestry or other disturbance events could be detected from the period after the last logging operation in the 1930s.

As has been stated in previous studies, stand age is of greater importance for the distribution of *U. longissima* than the age of single trees (Esseen & Ericson 1982, Rolstad & Rolstad 1999). Occurrence of *U. longissima* seemed strongly connected to stands with a continuous old age structure and modest effects of logging operations during the last ca 100 years, while areas outside the main location for *U. longissima* were all heavily affected by previous forestry, especially selective logging operations in the 1930s (Fig. 13 B-D & 17). This is especially interesting since present forest structure (tree age and size and species composition) does not differ whatsoever in the studied area. Noticeably, more than 86 % of the trees containing *U. longissima* were found within areas correspondent to stands number 2 and 5, which even in 1938 were covered by a forest more than 120 years old (Fig. 17). Additionally, the area within the borders of stand 2 also displayed no significant changes in canopy openness between 1938 and 2003 (Table 3). This supports the hypothesis that *U. longissima* is favoured by long-term stability in forest structure, including a somewhat open forest and absence of large-scale disturbances.

Interpretation of local stand history and persistence of Usnea longissima

As shown above, a key factor explaining the occurrence of *U. longissima* lies within the local forest history. Clearly, stand characteristics, including an open, multi-layered stand structure, stable environmental conditions and a somewhat hilly terrain constitute the basic conditions for its occurrence. However, stand history has a decisive influence on the complex distribution of *U. longissima* within a forest.

My interpretation is thus that *U. longissima* was more abundant before the commencement of the high grading operations in the 1860s, not just at the stand level but also at the landscape level. This is based on the following reasons: 1) the study area and its surroundings are characterised by slow growing Norway spruce trees and contain a number of suitable areas with the basic conditions for *U. longissima* 2) an open stand structure and a multi-aged forest with long persistence are thought to have dominated the region prior to the logging operations and 3) the present occurrence of *U. longissima* in the Kramfors region is still fairly high at the landscape level (Rydkvist pers. comm.). However, this interpretation does not require the presence of an untouched natural forest landscape before the 1860s. On the contrary, agrarian utilisation of the forest within Fällebodhöjden and its surroundings are thought to have occurred for several hundred years. During the field study, signs of such past human utilisation of the forest were observed all over the area. Culturally modified trees of different kinds and the earlier occurrence of summer farms nearby clearly demonstrate the agrarian influence on the forest. The extent to which these have affected the habitat conditions for *U. longissima* is not known. However, the use of forests for grazing often results in a lowered primary production and therefore also contributes to a more open stand structure (Tirén 1948, Kardell & Olofsson 2000) which in turn may have favoured several epiphytic lichens, including *U. longissima* (Norstedt 1991, Thor & Arvidsson 1999).

The extent of the high grading operations in the 1860s as well as the subsequent stand development seems to be essential factors influencing the long-term trends in habitat characteristics on a stand level. Previous studies have shown that at least two different scenarios may be distinguished: 1) intensive high grading followed by forest fire and 2) moderate high grading followed by forest fire. In this study an additional scenario is proposed: 3) moderate high grading with no subsequent forest fire. The first two scenarios have been described by Axelsson et al (2002) and are assumed to have generated deciduous-dominated forests and mixed deciduous forests respectively. Under these circumstances, the forest structure was completely altered and similar scenarios would have been devastating for the existence of *U. longissima* within the study area. In the third scenario specimens of *U. longissima* may have been able to survive the logging event in stands with favourable habitat conditions, although only if the cuttings were modest and depending on the amount and distribution of Norway spruce trees left behind after logging, which has also been emphasised by Esseen & Ericson (1982).

The selective logging operations in the early 20th century are also thought to be important components of the complex distribution of *U. longissima* within stands. Where these cuttings have been intense, they may be an important reason to the absence of *U. longissima* in seemingly suitable habitats. The negative effects of the intensive cuttings may also have been aggravated by *U. longissimas* limited dispersal ability (cf. Esseen & Ericson 1982, Dettki et al 2000). Furthermore, a decisive factor to occurrence of *U. longissima* in Fällebodhöjden is absence of recent industrial forestry operations, including extensive thinning and clear cuts. Consequently, a continuous old age structure and moderate re-growth of trees after modest selective cuttings seem to be prerequisites for the present occurrence of *U. longissima* in areas affected by forestry. However, the importance of a continuous old age structure should not be confused with various theories of continuity, since the latter concept is rather unclear and therefore often misused (cf. Ohlson et al 1997, Nordén & Appelqvist 2001, Rolstad et al 2002).

Management implications

In general, modern forestry has been considered to have a negative effect on the occurrence of *U. longissima* (Ahlner 1948, Esseen et al 1981, Esseen & Ericson 1982, Moberg & Holmåsen 1990, Norstedt 1991, Nitare 2000). Nonetheless, this study shows that stands with *U. longissima* can be sustained even if they have been affected by previous logging operations.

This in turn indicates that an adaptive forest management may include careful selective logging. However, this refers to management on a stand level and assumes that populations of *U. longissima* within the area of interest are highly viable. Most importantly, further studies encompassing several areas are needed before any recommendations on management can be made. At a landscape level, the relationship between distributions of *U. longissima* and old-growth forest seems stronger and therefore demands even more careful management, due to the poor dispersal ability of *U. longissima*, among other things (Esseen & Ericson 1982). Based on my results other important questions arise: How abundant was *U. longissima* before the high grading operations in the 1860s? Which other factors are the most important in determining the distribution of *U. longissima* on a stand level? To what extent can selective logging operations be accomplished in an area were a viable population of *U. longissima* is to be sustained? These questions need to be answered if a comprehensive management strategy is to be formulated. However, a specially directed forest management aimed at the persistence of moderately open stands and abolishing of clear cuts in low productive areas may favour the maintenance of viable populations of *U. longissima* and other rare epiphytic lichens in boreal Scandinavia.

Studies that interpret forest history and long-term changes in habitat conditions at a stand level do not only provide information with high spatial resolution, they also identify the most important variables and suggest how other studies may be designed when including several areas. Furthermore, by using a spatially precise approach many different factors are made visible. In short, knowledge about previous stand structure and forest history on a stand level can play a significant role in future forest management, where management of high biodiversity and restoration is an important aim. This in turn can generate a deeper ecological understanding of essential natural processes and guide managers in their efforts to maintain the existence of threatened species such as *U. longissima* and other epiphytic lichens.

ACKNOWLEDGMENTS

First of all I would like to thank my supervisors Lars Östlund and Erik Hellberg for inspiration and encouragement and for giving me constructive comments on the manuscript. I also thank all personal at the Dept. of Forest Vegetation Ecology, Swedish University of Agricultural Sciences, especially Anders Jäderlund, Anna Shevtsova and Henrik von Stedingk. Thanks also to Per-Anders Esseen at the Dept. of Ecology and Environmental Science, Umeå University for advice on the field study and comments on the manuscript; Kjell-Åke Hermansson and personal at SCA Merlo arkiv, Landsarkivet in Härnösand, Näringslivsarkiv i Norrland and the Regional Forestry Boards of Sollefteå and Härnösand for access to archives and assistance with historical documents and maps; Jan-Erik Larsson for field assistance; Sven Rasmussen for valuable comments on the manuscript and language improvements; Tomas Rydkvist at the County Board of Västernorrland for introducing me to the study area; Åke Sjölander for information on the local history of the study area; Anna Mamhidir for comments on the manuscript; SCA represented by Per Österberg, Claes-Göran Erson and Erik Viklund for providing of accommodation, geographical and forest data and availability to the study area. This study was financed by Svenska Cellulosa Aktiebolag, SCA.

REFERENCES

Personal Communication

Rydkvist, Tomas, Länsstryrelsen Västernorrlands län.

Sjölander, Åke, owner of the settlement Näverberget.

Literature

Ahlner, S. 1948. Utbredningstyper bland Nordiska barrträdslavar. Acta Phytageographica Suecica **22**: 1-257.

Ahti, T. 1977. Lichens of the boreal coniferous zone. In Seaward, M.R.D. (ed.) *Lichen ecology*. (pp. 145-181) Academic Press, London.

Almquist, J.A. 1909. Graningenverken - historisk skildring. Stockholm.

Andersson, I. & Williamson, M. 1993. Usnea longissima new for the province of Norrbotten, N. Sweden. Svensk Botanisk Tidskrift **87**: 354.

Andersson, R. & Östlund, L. 2002. Träd med kulturspår i skogen. Svensk Botanisk Tidskrift **96**: 53-62.

Andersson, R. & Östlund, L. 2004. Spatial patterns, density changes and implications in biodiversity for old trees in the boreal landscape of northern Sweden. Biological Conservation (In press).

Angelstam, P.K 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science **9**: 593-602.

Anon 2001. Skogsvårdslagen: Handbok. Skogsstyrelsen, Jönköping.

Axelsson, A-L. 2001. Forest landscape change in boreal Sweden 1850-2000 – a multi-scale approach. PhD Dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

Axelsson, A-L. & Östlund, L. 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. Forest Ecology and Management **147(2-3)**: 109-122.

Axelsson, A-L., Östlund, L. & Hellberg, E. 2002. Changes in mixed deciduous forests of boreal Sweden 1866-1999 based on interpretation of historical records. Landscape Ecology **17**: 403-418.

Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. 1994. Threatened plant, animal and fungus species in Swedish forests – distribution and habitat associations. Conservation Biology **8**: 718-731.

Bernes, C. (ed.) 1994. Biological diversity in Sweden : a country study. Monitor 14. Swedish Environmental Protection Agency, Solna.

Björklund, J. 1992. Skogsindustrins utveckling före andra världskriget några perspektiv på Västerbottens län. *In:* Björklund, J. (ed.) & Östlund. L. (ed.) KSLA Rapport 64. Norrländsk skogshistoria (pp. 61-67). Umeå.

Dettki, H. & Esseen, P-A. 1998. Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. Ecography **21**: 613-624.

Dettki, H. 2000. Epiphytic lichens in Boreal forest landscapes: influence of forestry and spatial structure. PhD Dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

Dettki, H., Klintberg, P. & Esseen, P-A. 2000. Are lichens in young forests limited by local dispersal? Ecoscience **7(3)**: 317-325.

Dysenius, M. 1984. Klövberget gränsberg med gammelskog och långskägg. Länstyrelsen, Västernorrlands län, 1984:2.

Ebeling, F. 1978. Nordsvenska skogstyper. Sveriges skogsbruksförbund, Stockholm.

Embertsén, S. 1976 Logging and transport in the Kramfors forests of SCA 1911-1965. STUDIA FORESTALIA SUECICA 134, Stockholm.

Ericsson, S., Östlund, L. & Axelsson, A-L. 2000. A forest of grazing and logging: Deforestation and reforestation history of a boreal landscape in central Sweden. New Forests **19**: 227-240.

Esseen, P-A., Ericson, L., Lindström, H. & Zackrisson, O. 1981. Occurrence and ecology of *Usnea longissima* in central Sweden. Lichenologist **13(2)**: 177-190.

Esseen, P-A & Ericson, L. 1982. Spruce forests with the lichen *Usnea longissima* in Sweden. Rapport PM 1513, Swedish Environmental Protection Agency, Solna.

Esseen, P-A. 1985. Litter fall of epiphytic macrolichens in two old *Picea abies* forests in Sweden. Canadian Journal of Botany **63**: 980-987.

Esseen, P-A., Renhorn, K-E. & Pettersson, R. B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications **6**: 288-238.

Esseen, P-A., Hedenås, H. & Ericson, L. 1999. Epifytiska lavar som mångfaldsindikatorer. Skog & Forskning **2**: 40-45.

Fahlén, H. 1917. Svanö Aktiebolag 1867-1917. Stockholm.

Fredén, C. (ed.) 1994. Geology. National Atlas of Sweden, KartCentrum, Vällingby.

Frödin, J. 1948. Ångermanlands fäbodar. Meddelanden från Uppsala Universitets geografiska institution 56, Uppsala University, Uppsala.

Gauslaa, Y. 1997. Population structure of the epiphytic lichen *Usnea longissima* in a boreal *Picea abies* canopy. Lichenologist **29(5)**: 455-469.

Gauslaa, Y., Ohlson, M. & Rolstad, J. 1998. Fine-scale distribution of the epiphytic lichen *Usnea longissima* on two even-aged neighbouring *Picea abies* trees. Journal of Vegetation Science **9**: 95-102.

Gothe, R. 1948. Finnkolonisationen inom Ångermanland, södra lappmarken och Jämland. Stockholm.

Granström, L. 1987. Mellan bark och ved. Arvidsjaur.

Groven, R., Rolstad, J., Storaunet, K.O. & Rolstad, E. 2002. Using forest stand reconstructions to assess the role of structural continuity for late-successional species. Forest Ecology and Management **164**: 39-55.

Gärdenfors, U. (ed.) 2000. Rödlistade arter i Sverige 2000 - The 2000 Red List of Swedish Species ArtDatabanken, SLU, Uppsala.

Hamilton, H. 1983. Hundra år i skogen. Sveriges Skogsvårdsförbund/Skogen Förlag. Djursholm.

Hellberg, E., Hörnberg, G., Östlund, L. & Zackrisson, O. 2003. Vegetation dynamics and disturbance history in three deciduous forests in boreal Sweden. Journal of Vegetation Science **14**: 267-276.

Höglund, H. 1957. Såg vid såg jag såg… Sundsvall.

Jäghagen, K. 1996. Alla tiders skog: skogsskötsel för mångfald. Skogsägarnas riksförbund, Stockholm.

Kardell, L. & Olofsson, M. 2000. Klövsjös fäbodar. Rapport 87, Institution of Environmental Assessment, Swedish University of Agricultural Sciences, Uppsala.

Keon, D.B. 2001. Factors limiting the distribution of the sensitive lichen *Usnea longissima* in the Oregon Coast Range: habitat or dispersal? M.S. Thesis. Oregon State University, Corvallis, USA.

Kuuluvainen, T., Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J. & Tukia, H. 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silvia Fennica **36(1)**: 409-422.

Linder, P. 1998. Stand structure and successional trends in forest reserves in boreal Sweden. PhD Dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

Lundberg, O. 1984. Sawmill Companies and society. Economic, social and political transformation in the district of Örnsköldsvik 1860-1900. PhD Dissertation. Department of Economic History, Umeå University, Umeå.

Moberg, R. & Holmåsen, I. 1990. Lavar – en fälthandbok. Interpublishing AB, Stockholm.

Niklasson, M. & Granström, A. 2000. Number and sizes of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. Ecology **81**: 1484-1499.

Nitare, J. (ed,) 2000. Signalarter. Skogsstyrelsen, Jönköping.

Nordén, B. & Appelqvist, T. 2001. Conceptual problems of Ecological Continuity and its bioindicators. Biodiversity and Conservation **10**: 779-791.

Nordlind, E. & Östlund, L. Retrospective comparative analysis as a tool for ecological restoration: a case study in a Swedish boreal forest. FORESTRY **76(2)**: 243-251.

Norstedt, G. 1991. Långskäggslav i Nätra fjällskog. Länstryrelsen, Västernorrlands län 1991:1.

Olsen, S.R. & Gauslaa, Y. 1991. *Usnea longissima*, a lichen of ancient forest, threatened on Nordmarka, SE Norway. Svensk Botanisk Tidskrift **85**: 342-346.

Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation **81**: 221-231.

Östlund, L. 1993. Exploitation and structural changes in the north Swedish boreal forest 1800-1992. PhD Dissertation. Swedish University of Agricultural Sciences, Umeå, Sweden.

Östlund, L & Lindersson, H. 1995. A dendrochronological study of the exploitation and transformation of a boreal forest stand. Scandinavian Journal of Forest Research **10(1)**: 56-64.

Östlund, L., Zackrisson, O. & Axelsson, A-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Candian Journal of Forest Research **27**: 1198-1206.

Östlund, L. & Zackrisson, O. 2000. The forest history of boreal Sweden: a Multidisciplinary approach. *In:* Agnoletti, M. (ed.) & Anderson, S. (ed.) IUFRO 3. Methods and approaches in forest history. (pp. 119-128). Cambridge.

Östlund, L., Zackrisson, O. & Hörnberg, G. 2002. Trees on the border between nature and culture – Culturally modified trees in boreal Sweden. Environmental History **7(1)**: 48-68.

Peterson, E. B. & McCune, B. 2002. The importance of hotspots for lichen diversity in forests of Western Oregon. The Bryologist **106(2)**: 246-256.

Rolstad, J. & Rolstad, E. 1999. Does tree age predict the occurrence and abundance of *Usnea longissima* in multi-aged submontane *Picea abies* stands? Lichenologist **31(6)**: 613-625.

Rolstad, J., Gjerde, I., Gundersen, V.S. & Saetersdal, M. 2002. Use of indicator species to assess forest continuity: a critique. Conservation Biology **16(1)**: 253-257.

Rose, F. 1976. Lichenological indicators of age and environmental quality in woodlands. *In:* Brown, D.H., Hawksworth, D.H. & Bailey, R.H. (ed.). Lichenology: Progress and problems. (pp. 279-307). London, Academic Press.

Sjörs, H. 1963. Amphi-Atlantic zonation. Nemoral to Artic. North biota and their history, Oxford, London.

Sällström-Nygren, C. 1967. Vattensågar och ångsågar i Norrland under 1800-talet. Meddelanden från Ekonomisk-Historiska institutionen vid Göteborgs Universitet 10, Göteborg.

Thor, G. 1998. Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. Biodiversity and Conservation **7**: 59-72.

Thor, G. & Arvidsson, L. (red.) 1999. Rödlistade lavar i Sverige – Artfakta. [Swedish Red Data Book of Lichens]. ArtDatabanken, SLU, Uppsala.

Tirén, L. 1937. Skogshistoriska studier i trakten av Degerfors i Västerbotten. Meddelande Statens skogsförsöks-anstalt **30(1-2)**: 67-322.

Tirén, O. 1948. Skogsbete – Kulturbete: några vunna erfarenheter från Västerbottens län. Skogsvårdsstyrelsens arbetsfält 1948:1, Stockholm

Uliczka, H. & Angelstam, P. 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. Ecography **22**: 396-405.

Wedin. M. (ed.) 2001. Det skogsfinska kulturarvet. FINNSAM, Falun.

Wik, H. 1950. Norra Sveriges sågverksindustri från 1800-talets mitt fram till 1937. Geographica, Papers from the geographical institute, Upsala University Nr 21, Kartografiska Institutet AB, Stockholm.