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Effect of Logging on the Threatened Epiphytic Lichen *Usnea longissima*: a Comparative and Retrospective Approach

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Usnea longissima is a conspicuous circumboreal "beard lichen" draping tree canopies in moist coastal and mountainous forests. It is extirpated in many European and North-American localities, presumably due to industrial forestry and air pollution, but still has a stronghold in parts of Scandinavia and U.S. and Canadian Pacific Northwest. Using a retrospective approach, we reconstructed the stand histories in 24 plots (0.1 ha) of mature Norway spruce (*Picea abies*) forest stands in Lillehammer, Norway, of which 21 was selected due to the presence of *U. longissima*. Number of trees with *U. longissima* present within plots varied from 4 to 37 and number of visible thalli from 12 to 469. The detailed stand reconstructions were done by means of tree-ring analysis of 517 living trees and the size and decay stage of 1423 stumps from logging and 467 dead trees. Total harvested volume during the last 100 years ranged 100–370 m^3ha^{-1} (representing 40–350% of the present-day standing volume), and present amount of dead wood ranged 2–87 m^3ha^{-1} (1.0–37% of the standing volume). All stands had been selectively logged 2–4 times during the last 100 years, of which 5 stands almost to a clearcut appearance. We used a variety of present-day and historic forest structural variables, both at the scale of study plots and individual trees, to predict the occurrence and abundance of *U. longissima*. Although most forest stand variables failed in this respect, there were indications of a certain negative influence of the historic logging activity. Number of thalli present on trees showed a unimodal relationship to present-day tree density, indicating that medium dense forest stands are most favorable for *U. longissima*. We tentatively suggest that selective logging, securing lichen-rich trees, may be a viable management option to keep tree density at a moderate level in the long run, thereby enhancing growth and establishment of *U. longissima*.

Keywords dendroecology, epiphytic lichens, forest history, historic logging, *Picea abies*, selective logging, stand reconstruction, *Usnea longissima*
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1 Introduction

Modern commercial and large scale industrial forestry profoundly alters natural stand structure and landscape mosaics, thereby influencing a variety of organisms inhabiting forest ecosystems. Forest clearcutting practices followed by dense monocultures pose a threat to a wide range of species depending on late seral stages (e.g. Esseen et al. 1997, Siitonen 2001). During the last decade or so a greater attention from end consumers of forestry-related products has pushed forward stronger regulations as to how forests are harvested and managed. This, in turn, has led forest managers to request scientific advices to guide forest operational procedures (e.g. Kohm and Franklin 1997, Rametsteiner and Simula 2003).

Epiphytic lichens are particularly vulnerable to changes in tree density and canopy closure (Dettki and Esseen 1998, Sillett and Goslin 1999). Among this group, *Usnea longissima* Ach. (Methuselah's beard lichen) has received special attention, partly because of its conspicuous tinsel-like appearance, but also because it seems to loose ground in many regions of former high abundance (Esseen et al. 1981, Olsen and Gauslaa 1991, Rolstad and Rolstad 1996, 2008a, Josefsson et al. 2005). It is currently redlisted as a threatened species in many European countries (Kålås et al. 2006, Nordic Lichen Society 2008), and considered a sensitive species in several North-American regions (Doell 2004; USDA Forest Service 2008). It is still fairly common in the North-American Pacific Northwest, and has a few strongholds in boreal Scandinavia (Esseen et al. 1981, Keon and Muir 2002, Rolstad and Rolstad 2008a, b). Despite of *U. longissima* being one of the most studied red-listed lichen species in Fennoscandia, relatively little is known about its tolerance to logging operations (Esseen et al. 1981, Rolstad and Rolstad 1999, Keon and Muir 2002, Josefsson et al. 2005, Gauslaa et al. 2007).

On request from forest managers in Lillehammer, Norway, we were invited to survey and monitor populations of *U. longissima* as part of a long-term experimental study. Prior to the logging experiments we conducted historic and present-day comparisons of forest structure and lichen abundance. Here we report the results of the retrospective and comparative part of the study 1) by unraveling the logging history in forest stands inhabited with *U. longissima*, and 2) by evaluating how present stand structure, historic logging activity, and single tree growth patterns may have influenced *U. longissima* abundances.

2 Material and Methods

2.1 Study Area

The study area is located in the valley Saksumdalen in the municipality of Lillehammer, in south-central Norway (61°05'N, 10°17'E). Elevation ranges from 350 to 700 m a.s.l. and the area has a mean annual precipitation of 800 mm and mean annual temperature of 2°C. July is the warmest month of the year and reaches a mean temperature of 14°C, whereas January is the coldest with an average of –10°C (Moen 1999). The bedrock is primarily sandstone with schist and feldspar, and the soils are thick unsorted glacial deposits in the hillsides but sparse in top areas. The region is in the middle boreal vegetation zone (Moen 1999), and Norway spruce (*Picea abies* (L.) Karst.) is the almost totally dominating tree species. Other tree species, like birch (*Betula pubescens* Ehrh.), rowan (*Sorbus aucuparia* L.), and willow (*Salix caprea* L.) occur very sparsely in the area, and they probably do not influence the *U. longissima* population. *Vaccinium myrtillus* L. forest is the predominating vegetation type in the study area, however, also areas of small-fern forest are common.

The Saksumdalen valley has farms that settled more than 1000 years ago. However, after the Black Death epidemic (1349–50) no farms in the valley were inhabited and it was not until late 1500s when several were re-occupied (Rugsveen and Stang 1996). As early as 1610 three water-driven sawmills were located in the neighboring parishes, and these were probably important in this settler time after the Black Death (Mathisen 2002). During the 16- and 1700s the small rivers and creeks in the area were used for timber transport, and in the 1790s local farmers sold fuel wood to the glassworks at Vingrom (10–15 km down the Rinna creek). Small dams were therefore constructed in most of the creeks. In 1821 the farms even sold timber to traders in Oslo, 170 km to the south. The timber floating down the Rinna creek peaked in 1914 and 1921, with 123 000 and 100 000 logs, respectively. However, due to large variations in timber prices the logging activity fluctuated widely, as only 1400 logs were floated in 1922 (Mathisen 2002).

During the mid-1900s a shift in logging practice occurred when clearcutting and planting were introduced after centuries with single-tree and selective cuttings. Between 1925 and 1935 25 000–45 000 plants were annually sold from local forest nurseries to this district, and this number increased dramatically to 300 000 plants annually in the late 1950s (Fåberg Skogråd 1961). Thus, the previously selectively cut forests were gradually replaced by clearcuts and young forests, effectively managed for timber and pulp resulting in increased standing volumes and forest yields. Today, the mature forest stands are remnants from the previous period of selective logging, whereas younger stands originated after clearcutting and replanting.

Environmental surveys were conducted in 2002–2003 in Lillehammer municipality to upgrade forest planning databases (Mjøsen Skogeierforening 2005, Gjerde et al. 2007). A special search was launched to identify locations of *U. longissima*, based on previous knowledge of this species in the area (Gaarder 1997). A total of 82 sites with presence of *U. longissima* were found, of which 76 were protected as woodland key habitats (Mjøsen Skogeierforening 2005). The present study was conducted within a landscape section of ca. 30 km^2, on both sides of the Saksumdalen valley (Fig. 1). Old forest covered 40% of the forested part of the landscape, with individual stands varying in size from <1 ha to ca 25 ha.

2.2 Field Work

All field work was performed in 2005. Based on the information from the environmental inventory we established 21 circular study plots of 0.1 ha in size in mature spruce stands with presence of *U. longissima*. Within different stands hosting groups of lichen-bearing trees, the plots were centered on the tree with maximum number of visible thalli. We aimed at distributing the plots among stands to maximize the variation in the abundance of the lichen, thereby increasing the statistical power to detect possible relationships between lichen abundance and forest stand and logging characteristics. For this reason we also included three plots without visible signs of *U. longissima*, randomly selected within stands of similar stand structures as those with *U. longissima*, resulting in a total of 24 study plots (Fig. 1, Table 1). Seven of the 21 study plots were situated in forest stands where we performed a study of experimental selective logging. These loggings were carried out in 2006 and 2007 in cooperation with local forest entrepreneurs and the forest owners association (Mjøsen Skog BA), and the results will be reported elsewhere. Because these experimental logging operations were an important part of the project, it should be noted that the stand selection sample was skewed towards forest stands having relatively high timber volumes, since it is not relevant to do selective logging in forest stands having low timber volume.

For all living trees ≥4 cm (n = 1922) within the study plots we recorded diameter at breast height (DBH, 1.3 m above ground level) (only trees ≥10 cm DBH in five of the plots), and 20–25 of the biggest and the oldest trees in each plot (n = 517) were cored 30–50 cm above the ground level to achieve as many tree-rings as possible. Stumps (≥10 cm at stump height) (n = 1423) from previous logging events and dead trees (snags and logs, ≥10 cm DBH) (n = 467) were recorded and categorized according to the degree of decay and diameter. We assigned the stumps and logs according to an eight-grade decay classification scheme, where category 1 was recently cut or fallen and 8 was almost completely decomposed (see Groven et al. 2002 for description of the decay classes). Snags were categorized according to the number of branch orders present, where category 1 snags had only first order branches (main branch from the stem), category 2 snags had also second-order branches (growing on first order branches), and so on (Storaunet 2004). This categorization has shown to be a good indicator of the number of years since the death of the tree.

To survey *U. longissima*, all trees in the plots were carefully checked from the ground using binoculars. As an index of lichen abundance, we

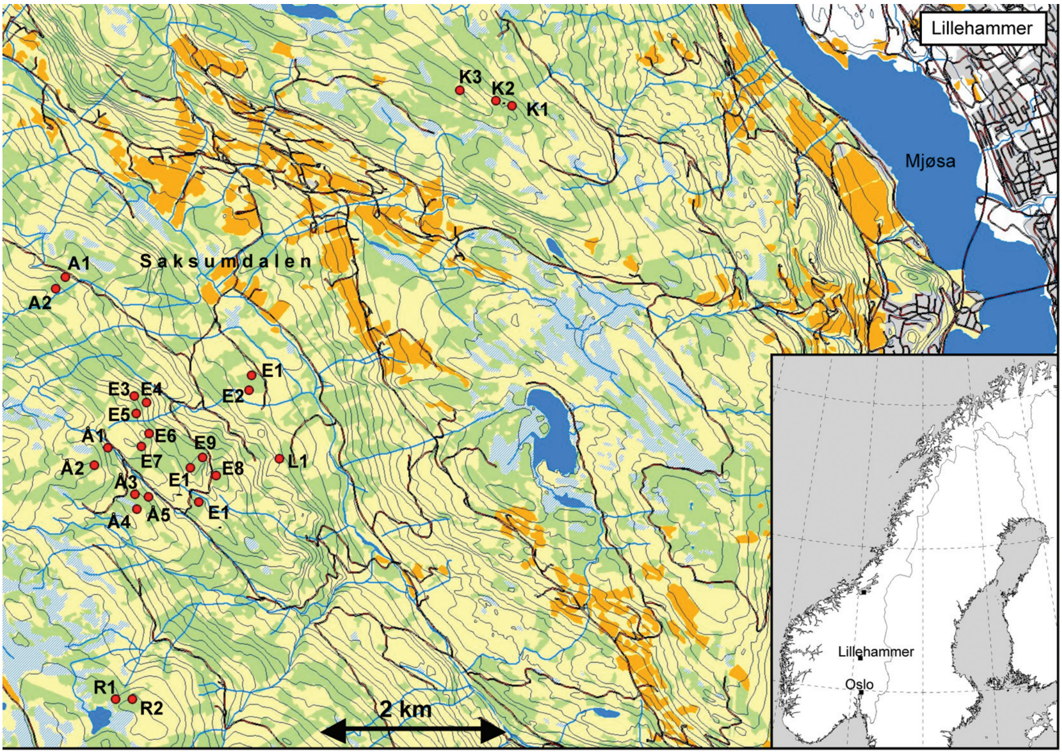

Fig. 1. Map of the study area with location of the study plots marked as numbered red dots. Green: old forest; yellow: young planted forest; orange: cultivated land; blue: ponds and lakes; light blue: mires.

counted all visible pendant branches of lichen thalli, irrespective of the length of the branches. Single-stranded thallus branches were fairly easy to recognize due to the relatively sparse occurrences of thalli. However, because many small thallus fragments were most likely overlooked, we underestimated the total population sizes (Gauslaa et al. 1998). In the forest stands where experimental selective loggings were planned, the number of lichen thalli was counted on all trees throughout the whole experimental areas. From these records we calculated three different variables describing the lichen population; 1) number of trees per plot with the lichen present (occurrence), 2) total number of thalli per plot (abundance), and 3) mean number of lichen thalli per tree bearing the lichen within plots (density). Since the latter variable was highly skewed, with many trees with few thalli and few trees with many thalli, we log-transformed the values before averaging number of thalli per tree within plots. Around all trees with *U. longissima* present, we measured the basal area (m^2ha^{-1}) using a relascope. All trees with the lichen present were mapped in a GIS system and marked in the field.

2.3 Laboratory Procedures and Calculations

Increment cores were shaved with a scalpel to obtain a good surface, and zinc paste was used to make the tree-ring boundaries more visible. Tree rings were measured with the digital WinDendro system (Guay et al. 1992) with an accuracy of 0.01 mm. To determine the age of trees when increment cores failed to hit the pit, we estimated the length of the missing radius by matching the curvature of the inner rings to concentric circles drawn on a clear plastic sheet (Applequist 1958, Motta and Nola 2001). The mean ring width of the 10 innermost rings was used to estimate the number of rings in the missing radius.

Table 1. Plot characteristics, forest structure characteristics, historical logging data, and records of *Usnea longissima* as recorded in 24 study plots of 0.1 ha in Saksumdalen, Lillehammer. Note that study plots marked with an asterisk have no *U. longissima* present.

No.	Altitude (m a.s.l)	Site index**	Standing volume (m^3ha^{-1})	No. of trees ≥10 cm DBH (ha^{-1})	Median stand age (years)	Volume of snags (m^3ha^{-1})	Volume of logs (m^3ha^{-1})	Total harvested volume (m^3ha^{-1})	No. of stumps (ha^{-1})	No. of logging events	No. of trees with *U. long.* present	Tot. no. of *U. long.* thalli	Max. no. of thalli	Median no. of thalli
A1	490	G14	99	720	141	2	17	374	1000	3	20	100	18	3
A2	490	G14	204	620	112	18	18	194	620	4	4	17	7	4.5
Å1	600	G17	257	510	160	4	32	131	340	3	11	110	35	5
Å2	655	G14	234	480	162	30	30	199	650	3	4	21	11	4.5
Å3	585	G14	203	590	157	0.4	23	204	610	2	13	76	20	3
Å4	595	G11	168	540	163	8	34	122	440	2	7	76	50	3
Å5	565	G17	221	630	137	14	44	183	510	3	33	270	45	6
E1	330	G14	138	610	162	18	5	156	470	2	7	66	30	4
E2*	335	G14	150	560	173	32	16	127	450	3	0	0	0	0
E3	540	G14	251	710	106	14	6	238	600	2	9	28	11	2
E4	530	G14	197	440	174	2	22	161	530	3	10	45	13	2.5
E5	550	G14	171	640	108	1	5	139	580	3	7	34	11	3
E6	565	G17	228	470	147	6	77	150	330	3	8	38	12	3.5
E7	580	G14	175	570	145	29	36	191	610	3	37	271	38	5
E8	530	G14	235	760	157	3	17	204	540	3	36	469	50	8
E9	520	G17	272	710	144	17	47	103	300	2	23	193	28	5
E10*	530	G14	235	660	153	15	72	175	600	3	0	0	0	0
E11	525	G11	117	780	143	6	8	96	440	2	15	123	40	6
L1	360	G11	184	920	158	11	5	335	1120	3	6	12	6	1
K1	685	G14	165	540	98	22	3	172	470	2	23	125	27	3
K2	700	G11	167	640	124	1	1	246	700	2	12	125	30	5
K3	730	G11	145	750	100	2	2	230	760	2	7	45	28	3
R1*	730	G11	181	600	137	2	9	187	440	2	0	0	0	0
R2	740	G14	187	490	155	22	19	178	450	3	20	126	15	6

** Site index of productivity is defined as height of trees at the age of 40 years (Tveite and Braastad 1981).

To identify growth responses to logging events in single trees we examined the radial growth pattern for abrupt and sustained growth increases (Lorimer 1980, 1985, Groven et al. 2002, Fraver and White 2005). Norway spruce is a shade-tolerant species, and small trees and saplings are able to respond to gap openings. We compared the average tree-ring width between two consecutive 10-yr periods and calculated both the relative change (Groven et al. 2002) and the absolute change in radial growth (Fraver and White 2005). This was done for all years, starting from the oldest ring. Threshold values for defining a growth release were set to 100% increase for relative changes and 0.55 mm for absolute changes. The 0.55 mm-threshold value was estimated as the 90%-percentile out of all possible growth changes in all trees, as suggested by Fraver and White (2005). Finally, we compared these defined calculated releases with the tree-ring growth pattern of the trees to ascertain the timing of the release. Following a logging event an unknown proportion of the remaining trees will respond with increased radial growth. A logging event was defined if a year was followed by a 10-yr period with ≥20% of the trees showing growth releases.

The recorded stumps were allocated to logging events according to their decay class and stump decay rates (see Groven et al. 2002 for further details). To estimate the tree diameter at breast height, the following relationship was used:

$$\mathrm{DBH} = 0.89 \times \mathrm{DSH}\ (r^2 = 0.94) \qquad (1)$$

This relationship was estimated from 445 living trees that were measured both at stump (DSH) and at breast height (DBH). To estimate the height of trees ≥10 cm DBH we used the following relationship:

$$\mathrm{H} = 12.5 \times \ln(\mathrm{DBH}) - 21.5\ (r^2 = 0.64) \qquad (2)$$

This relationship was based on height measurements of 70 trees in the same forest stands. The diameter (DBH, in cm) together with the tree height (H, in meters) was then used to calculate historic stem volumes (formulae from Vestjordet 1967).

Diameter distributions and standing volumes at each site during the period 1900–2005 were reconstructed. Diameters of cored trees were reconstructed by using the measured tree-ring widths, whereas trees not cored and the trees that were "raised" on stumps prior to logging events were reconstructed by using the average tree-ring width for the particular site. After adding estimates for bark thickness, the historic standing volumes in the study sites were calculated (Vestjordet 1967, Groven et al. 2002). The stand reconstructions was performed following the same procedures as described in Groven et al. (2002) and Storaunet et al. (2000).

To analyze if single-tree growth during the last decades influenced the occurrence and abundance of *U. longissima* on trees today, we constructed several tree-ring derived variables. We calculated average tree-ring widths over the last 5, 10, and 20 years, and several *growth-indices* (*GI*) with different time windows. E.g. the GI noted *10 yr / 20 yr* was calculated as:

$$GI\ 10\,yr\ /\ 20\,yr = \frac{mean\ tree\,ring\ width\ 1996-2005}{mean\ tree\,ring\ width\ 1976-1995} \qquad (3)$$

After calculating the GI *10 yr / 10 yr* for all years between 1950 and 2005, we finally selected the maximal and the minimal GI during this period to check if certain extreme growth events had influenced the presence and abundance of *U. longissima*.

We calculated the amount of old forest within circles of 100 m, 200 m, and 500 m radius around the study plots to check for possible relationships between the *U. longissima* populations and the amount of old forest in the vicinity. This was done in the GIS system based on the forest planning data from the forest owners association (Mjøsen Skog BA).

2.4 Statistics

In general, we used non-parametric Spearman rank correlation coefficients to examine relationships between different past and present forest stand characteristics at the study plot level. We explored parametric regression models with different link functions and log-transformations to assure that our inference from the rank correlations were correct. In general, the parametric tests did not increase power of the tests, so unless otherwise stated, only results from the rank correlations are shown. Statistical significance levels for Spearman rank correlation tests refer to Zar (1999). The same procedure was used to evaluate relationships between the different variables describing the plot-level *U. longissima* population and the present and historic forest characteristics.

At single-tree level we tested whether size, age, and growth of trees influenced *U. longissima* populations using two lines of evidence: 1) Present-absent data, i.e. the *occurrence* of lichens were checked with Mann-Whitney U-tests and logistic regression models using trees with and without visible thalli as a binary variable. 2) For trees bearing the lichen, we checked correlations between *U. longissima abundance* and the tree-level explanatory variables by Spearman rank analyses and general linear models. Similar to the analyses done at plot level, the parametric models did not improve the statistical power of the tests, hence, only results from the rank analyses are reported.

To evaluate the relationship between number of *U. longissima* thalli on trees and stand density (basal area, m^2ha^{-1}) around these trees, we compared the observed relationship with 10 000 randomized samples of the same data. In this permutation test the significance level was calculated as the relative number of randomizations that attained an F-value larger than the observed one.

Statistical rank analyses were performed using the StatView 5.0 software package (SAS Institute Incorporated, Cary, North Carolina), whereas the logistic regression and general linear models were performed using S-Plus® 6.2 software (Insightful Corporation, Seattle, Washington). The randomizations were accomplished in a small self-written program in Visual Basic for Applications (VBA in Microsoft® Excel).

3 Results

3.1 Stand Structure, Logging Activity, and Stand History

The study sites appear today as mature and over-mature spruce forests. Canopy trees have diameters of 25 to 45 cm DBH and total ages of 100–170 years (Fig. 2, Fig. 3). The oldest recorded tree was 313 years (at site Å4). Several plots contained high numbers of small trees, resulting in reversed J-shaped DBH distributions (e.g. site A1, E2, E4, E5, E6, Å4), whereas others had almost even DBH distributions (site A2, E7, E10, K3, R2, Å5) (Fig. 2). Standing volume in plots ranged 100–270 m^3ha^{-1}, and number of living trees ≥10 cm DBH ranged 440–990 ha^{-1}, whereas the amount of dead wood varied from 2 to 87 m^3ha^{-1} (corresponding to 1–37% of the volume of living trees) (Table 1). Fallen dead wood was two times more abundant than snags. Dead wood showed a high proportion of well decayed logs, with 72% classified to decay class 5–7 (Fig. 4).

The logging activity deduced from tree-ring analyses in the study plots dated back 90–150 years, depending on the ages of the cored trees. The sites had been logged between two and four times during this period, with an average rotation period of 24 years (Fig. 5, Fig. 6). This was evident both in the amount of decayed stumps in different decay classes (Fig. 4), and also in the many growth releases in the tree-ring series. Total harvested volume averaged 187 m^3ha^{-1} and varied almost 4-fold from 96 to 370 m^3ha^{-1}, corresponding to the number of stumps that averaged 565 ha^{-1} (range 300–1100). This was approximately the same as the number of living trees today (average 620 ha^{-1}) (Table 1). Stumps averaged 27 cm in diameter at stump height, corresponding to 24 cm in breast height; about the same as present-day average stem diameter of 23 cm (trees >10 cm DBH).

The logging events were distributed in time from the 1880s to the 1970s, with peak logging activity in the 1920s and in the 1950s, and a sharp decline thereafter (Fig. 5, Fig. 6). This halt in logging was due to a general shift in harvesting regime, from selective logging to clear-cutting

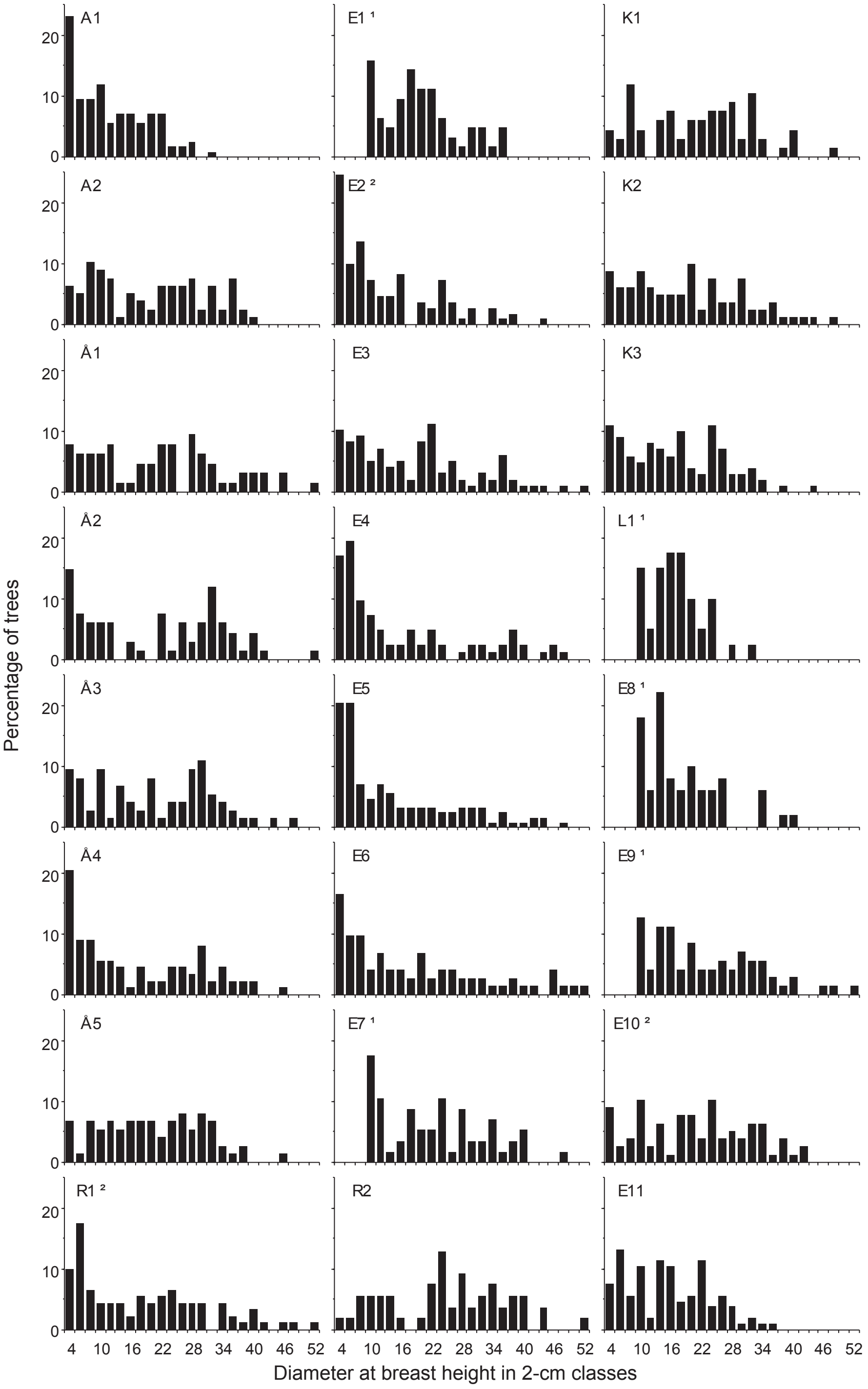

Fig. 2. Diameter distribution of trees ≥4 cm measured at breast height for 24 study plots in Saksumdalen, Lillehammer. In study plots marked ¹, only trees ≥10 cm DBH were measured, and plots marked ² had no trees with *U. longissima* present.

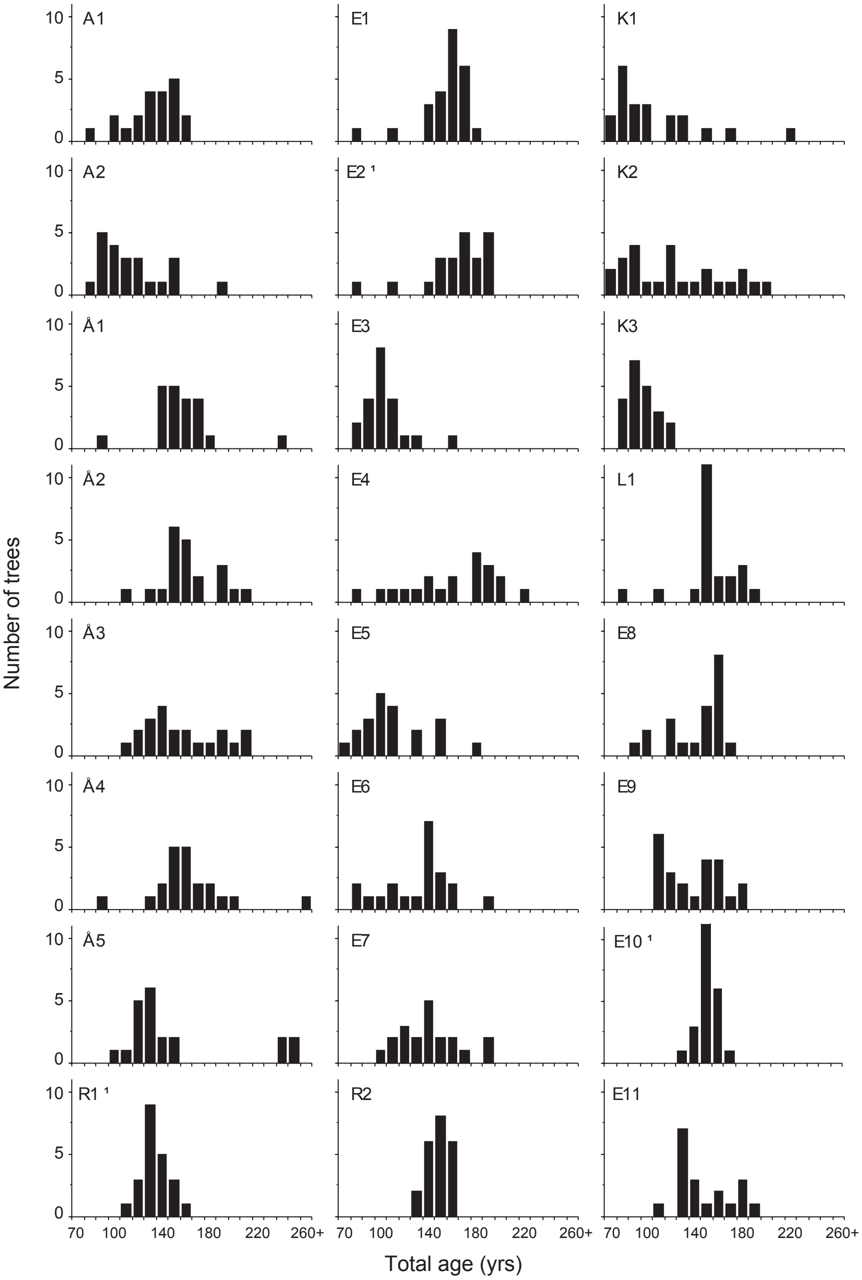

Fig. 3. Age distribution of the 20–25 cored Norway spruce trees in 24 study plots in Saksumdalen, Lillehammer. Plots marked ¹ had no trees with *U. longissima* present.

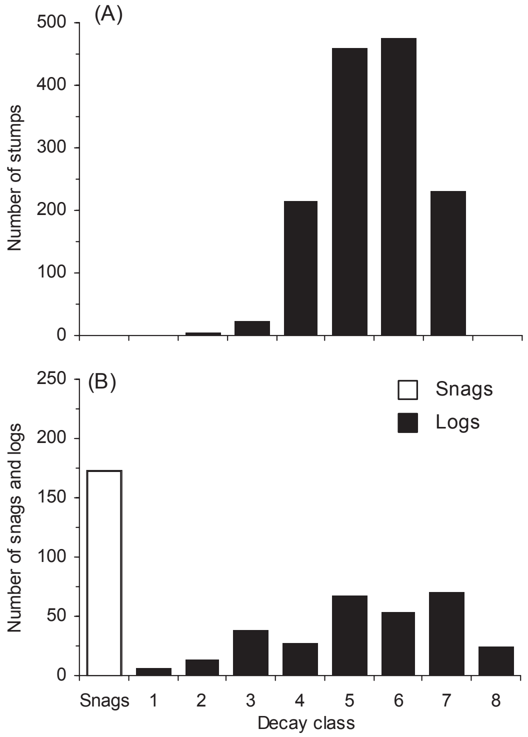

Fig. 4. Frequency distribution of stumps from logging (A) and of snags and logs (B) in relation to decay class (1: recently dead/fallen/cut, 8: almost completely decayed). Data are pooled totals for all 24 study plots.

practices. This temporal change was also reflected in the distribution of stumps in different decay classes, with 83% classified to decay class 5–7 (originating during 1910–1940) and only 2% to decay class 2 and 3 (Fig. 4).

Most stands had gained considerable volume during the last 50 years, and with a few exceptions (most notably A1) present-day standing volumes were the highest recorded during the historic studied period of ca 100 years. Although no stands had been completely clearcut, five stands approached clearcut appearance (site E3, E5, E11, K3, R1), with lowest volumes <20 m^3ha^{-1} after the logging events.

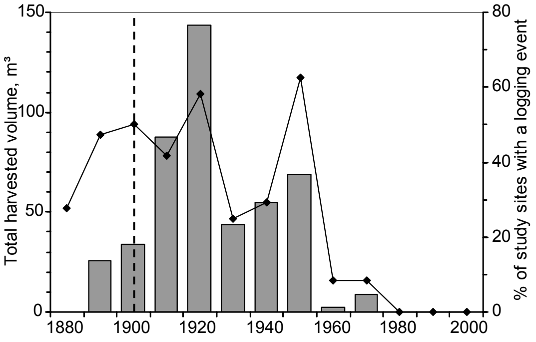

Fig. 5. Temporal distribution of total harvested volume (bars) and the percentage of study sites with a logging event (line with indications) in each decade during 1880–2000. The vertical broken line indicates that harvested volume could not be completely estimated before the 1900s due to decomposition of stumps. Data are pooled for all 24 study plots.

3.2 Relationships Between Historic Logging and Present-day Stand Structure

Because most of the logging occurred 50–100 years ago, many relationships with present stand structures were weak (Table 2). Notably, the lowest recorded historic volume correlated negatively to number of trees ≥10 cm DBH, and positively to stand age and number of fallen dead trees. This implies that if stands had been very open, they displayed more trees, younger trees, and fewer fallen dead trees today. Along this line, the harvested volume after 1940 tended to correlate negatively with present standing volume and positively with present number of living trees (Table 2). Thus, sites with historic high logging activity had low present volumes but high numbers of smaller trees.

Somewhat surprisingly, there was no relationship between the historic lowest recorded volume and the total amount of logging. This was because some sites had been subjected to a few heavy loggings, whereas other sites had been harvested in several smaller operations, with the total amount of harvested timber being about the same. There was also no relationship between the lowest recorded volume and the year that this low volume took place, implying that minimum

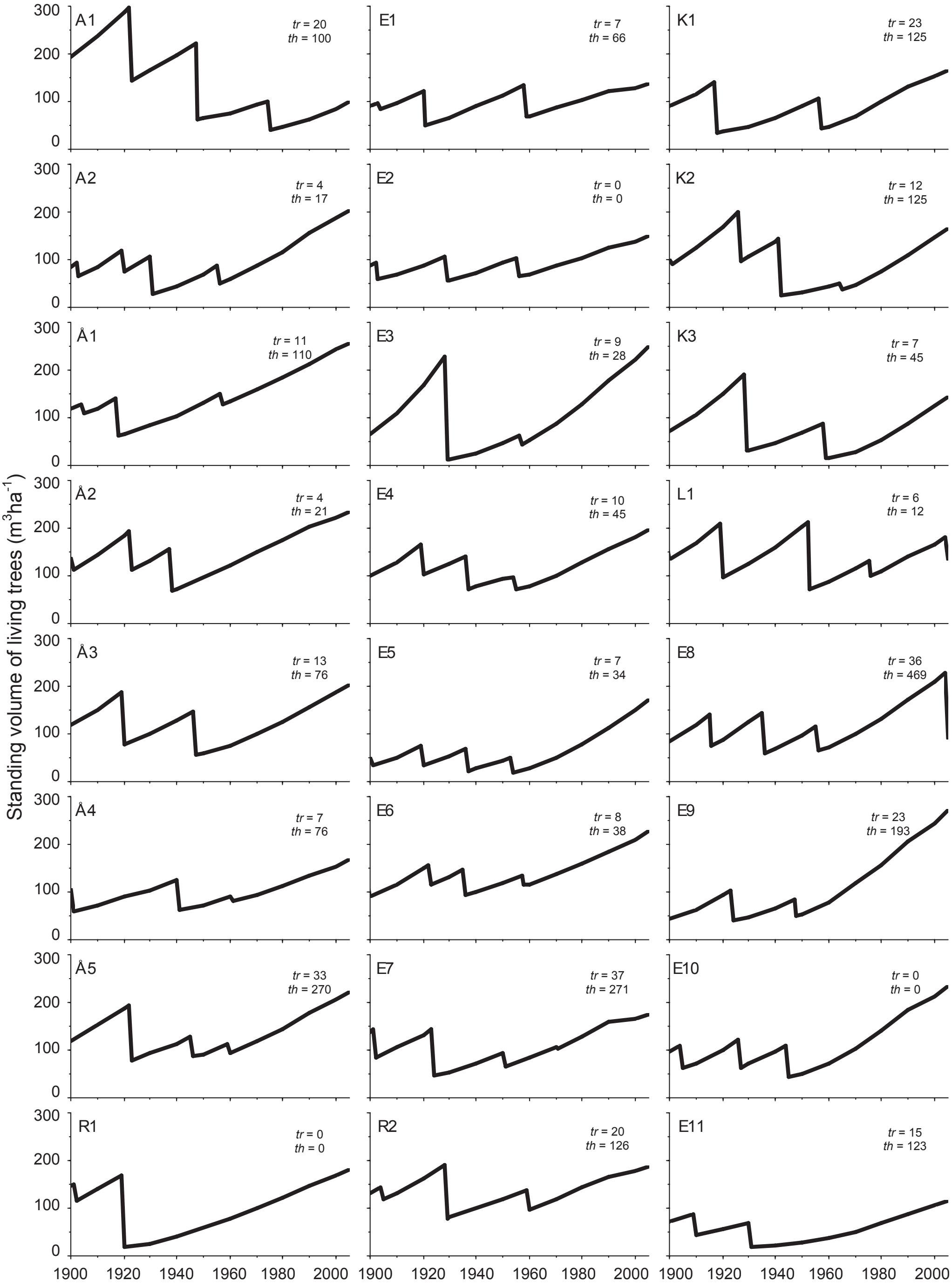

Fig. 6. Reconstructed standing volume (m^{3}ha^{-1}) in the 24 study plots in Saksumdalen, Lillehammer. Upper left numbers denote plot number according to Table 1, whereas numbers to the right show number of trees (*tr*) with presence of *Usnea longissima* and total number of *U. longissima* thalli (*th*) on these trees.

stand volume occurred at different time periods at different locations. However, there was a clear positive relationship between the total amount of logging (number of stumps) and the year of lowest historic volume, meaning that the sites that had been most heavily logged were at their lowest volume in more recent times than those sites that had been logged more lightly (Table 2, Fig. 6).

3.3 *Usnea longissima* and the Surrounding Forest

Although the study was not explicitly designed to evaluate possible patterns at the landscape scale, we checked if the amount of old forest around the study plots explained the occurrence and abundance of *U. longissima*. The amount of old forest within a 100 m, 200 m, and 500 m circle around the plots averaged 77% (range 49–100%), 58% (33–95%), and 43% (27–74%), respectively. None of the variables came close to significantly explaining the variation in lichen population ($p > 0.20$ for all comparisons). Neither did they explain any residual variation in multiple regression models including other plot-level variables.

3.4 *Usnea longissima* at the Forest Plot Level

At the outset we included three plots devoid of *U. longissima* but otherwise apparently similar to the other 21 plots with lichens. Expectedly, they did not differ in present-day stand structure, but neither did they differ with respect to any historic logging variables (Table 1, Fig. 2, Fig. 3, Fig. 6). Although these plots might have differed in other unknown aspects, they had no explanatory power in predicting lichen abundance and were therefore excluded from these analyses.

Within the 21 plots with *U. longissima*, the number of thalli per tree varied from single individuals to >50 thalli, with a clear negative exponential distribution (Fig. 7). Despite large variation in tree density (440–920 ha^{-1}), standing volume (100–270 m^{3}ha^{-1}), and median stand age (98–174 years), none of the present-day stand structural variables explained the occurrence, abundance, or density of *U. longissima* (Table 3,

Table 2. Spearman rank correlation (r_S) matrix between different present-day forest structural and historic logging characteristics, in 24 study plots in Saksumdalen, Lillehammer. r_S values corresponding to significance levels of 0.01, 0.05, and 0.10 are 0.52, 0.41, and 0.34, respectively. (Numbers in first row refer to variable numbers in first column.)

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
(1) Productivity	1.00													
(2) Standing volume, m^{3}ha^{-1}	0.59	1.00												
(3) No. of trees ≥10 cm DBH, ha^{-1}	−0.35	−0.24	1.00											
(4) Median stand age, yrs	0.09	0.11	−0.42	1.00										
(5) Avg. age of 5 oldest trees, yrs	0.13	0.08	−0.38	0.68	1.00									
(6) Volume of snags, m^{3}ha^{-1}	0.29	0.12	−0.27	0.19	0.09	1.00								
(7) Volume of logs, m^{3}ha^{-1}	0.61	0.60	−0.40	0.41	0.41	0.28	1.00							
(8) Total no. of stumps, ha^{-1}	−0.36	−0.19	0.38	−0.22	−0.17	−0.16	−0.38	1.00						
(9) Total harvested volume, m^{3}ha^{-1}	−0.28	−0.01	0.36	−0.30	−0.31	−0.23	−0.33	0.84	1.00					
(10) No. of stumps cut after 1940, ha^{-1}	−0.26	−0.36	0.34	−0.05	0.09	−0.17	−0.22	0.56	0.43	1.00				
(11) Harvested volume after 1940, m^{3}ha^{-1}	−0.25	−0.35	0.34	0.01	0.09	−0.18	−0.23	0.49	0.42	0.96	1.00			
(12) Lowest volume during 1900–2005, m^{3}ha^{-1}	0.42	0.30	−0.53	0.69	0.60	0.26	0.56	−0.19	−0.12	0.01	0.08	1.00		
(13) Time (year) of lowest volume	−0.20	−0.12	0.33	−0.07	−0.17	−0.47	−0.21	0.67	0.49	0.25	0.25	−0.07	1.00	
(14) No. of logging events during 1900–2005	0.41	0.29	−0.20	0.24	0.06	0.28	0.37	0.21	0.09	−0.04	−0.11	0.51	0.27	1.00

Table 3. Spearman rank correlation coefficient (r_S) between three measures of *Usnea longissima* and different forest structure and historical characteristics. 21 study plots with presence of *U. longissima* were included. r_S values corresponding to significance levels of 0.05 and 0.10 are 0.44 and 0.37, respectively. Significance level (ά) of 0.05 and effect size (r) of 0.30 gives power = 0.28, whereas ά = 0.10 and r = 0.40 gives power = 0.61.

Variable	No. of trees with *U. long.*	No. of *U. long.* thalli	No. of *U. long.* thalli per tree
Productivity	0.32	0.22	0.16
Standing volume, m^{3}ha^{-1}	0.05	–0.01	0.08
No. of trees ≥10 cm DBH, ha^{-1}	0.10	0.05	0.07
Median stand age, yrs	–0.18	–0.06	0.10
Avg. age of 5 oldest trees, yrs	0.05	0.08	0.16
Volume of snags, m^{3}ha^{-1}	–0.04	0.07	–0.05
Volume of logs, m^{3}ha^{-1}	0.24	0.24	0.14
Total no. of stumps, ha^{-1}	–0.28	–0.36	–0.43
Total harvested volume, m^{3}ha^{-1}	–0.05	–0.18	–0.36
No. of stumps cut after 1940, ha^{-1}	–0.03	0.02	–0.02
Harvested volume after 1940, m^{3}ha^{-1}	0.07	0.13	0.04
Lowest volume during 1900–2005, m^{3}ha^{-1}	0.04	0.07	–0.01
Time (year) of lowest volume	–0.25	–0.40	–0.46
No. of logging events during 1900–2005	–0.09	–0.16	–0.24

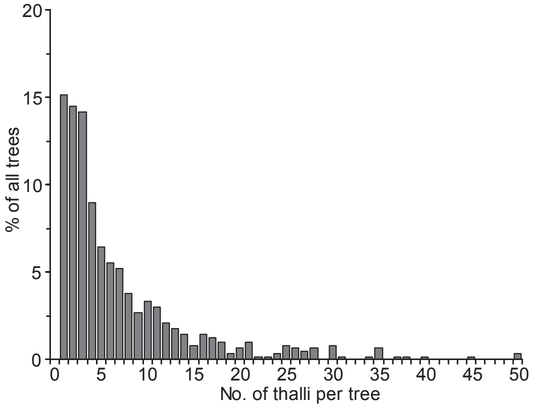

Fig. 7. Distribution of 635 trees related to number of *Usnea longissima* thalli on the trees. Included are all trees bearing *U. longissima* recorded in the study area, both in study plots and in the experimental logging areas.

Fig. 8A–D). In a second-order polynomial regression model present-day tree density explained a significant (p = 0.02) part of the variation (34%) in number of thalli per tree (Fig. 8B). However, this was due to a distinct outlier with high tree density (site L1), and removing this plot reduced the explanatory power to 5% (p = 0.66).

In general, most variables expressing the historic logging activity also performed poorly in explaining abundances of *U. longissima* (Table 3, Fig. 8E–J). Two relationships should be mentioned though. First, number of thalli per tree appeared to decrease with increasing number of stumps from logging (p = 0.05), and total number of thalli tended to decrease in a similar way (p = 0.10) (Table 3, Fig. 8). However, site L1 also stood out as an outlier in both of these cases. Although the trends were upheld, they lost their statistical significance when this site was removed from the analysis (p = 0.13 and 0.25, respectively). Accordingly, one would expect that more recent loggings should have had a more profound impact on the present amount of *U. longissima*. However, this was not the case, since both the number of stumps and the harvested volume after 1940 were less influential in explaining lichen abundance (Table 3).

Second, number of thalli per tree was negatively correlated with the year of lowest recorded volume (r_s = –0.46, p = 0.04, Fig. 8J), but it was not correlated with the lowest volume *per se*. This means that those sites that were at their lowest volumes recently harbored less lichens than those with lowest volumes in the past, but

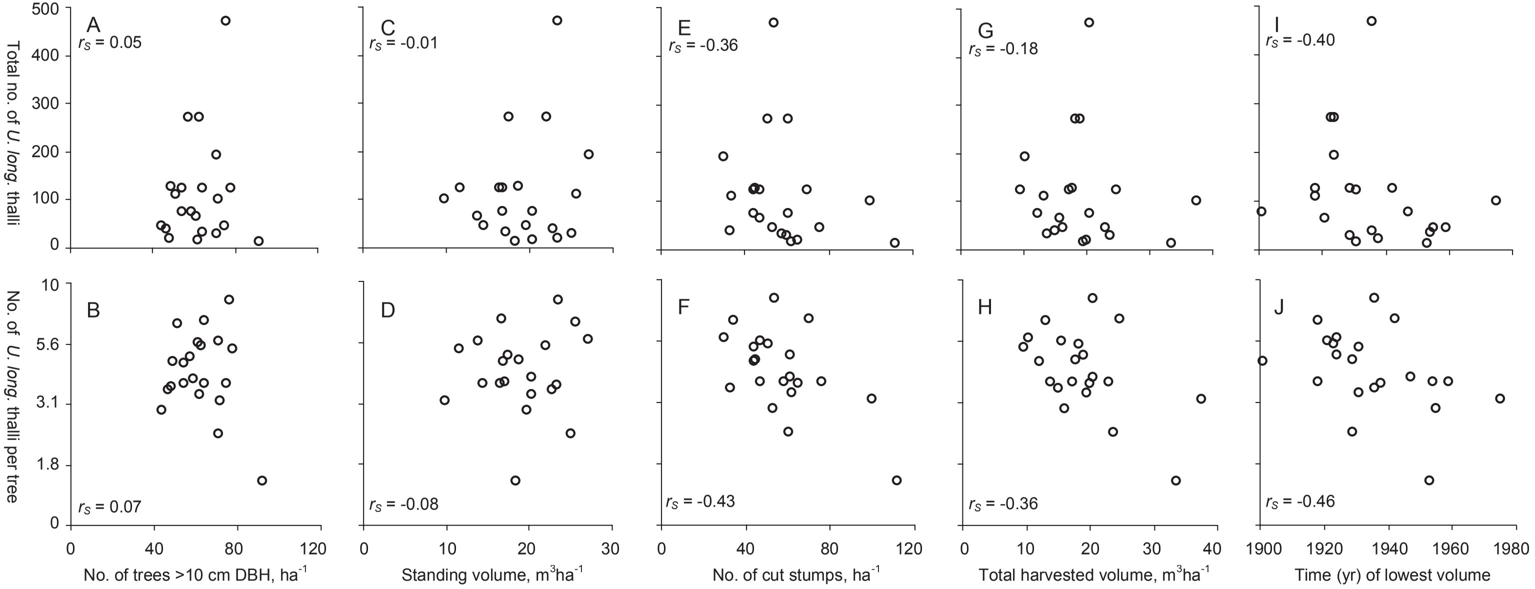

Fig. 8. Relationships between the amount of *Usnea longissima* and different variables representing present stand characteristics and historic logging activity, in Saksumdalen, Lillehammer. Only the 21 study plots with presence of *U. longissima* were included. Spearman's rho (r_S) is shown for the relationships. r_S values corresponding to significance levels of 0.05 and 0.10 are 0.44 and 0.37, respectively. Note that the y-axes on the lower panels (B, D, F, H, and J) are logarithmically scaled.

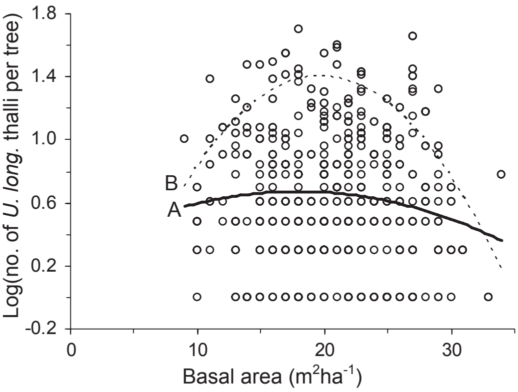

Fig. 9. The relationship between the number of *Usnea longissima* thalli per tree and the basal area (m^{2}ha^{-1}) around the same tree. Line A (thick, solid line) shows the fitted 2nd-order polynomial regression line using all trees (n = 429), whereas line B (thin, dotted line) shows the fitted line using only the three highest ranked values of number of thalli for each value of basal area (n = 68). Permutation tests showed significance levels of these observed patterns of p = 0.029 (line A) and p = 0.045 (line B), respectively. Note that the y-axis is logarithmically scaled. (See text for further details.)

how low the volume was, appeared insignificant. However, because those sites that were at their lowest volumes recently also were the most heavily logged (see above), the lower number of thalli at these sites might as well be due to the total historic amount of logging, rather than the year of lowest volume. When removing the effect of logging in a multiple regression model, the year of lowest volume totally lost its statistical significance ($r_p < 0.01$).

3.5 *Usnea longissima* at the Single-Tree level

At the single-tree level we used basal area as a proxy for stand density. When relating number of thalli per tree to basal area, a second-order polynomial function fitted the data best. We also fitted a second-order function to the three highest ranked values for number of thalli (Fig. 9). The permutation test showed that a statistically significant higher number of thalli occurred around medium basal area values (15–25 m^{2}ha^{-1}), both when using the whole data set (n = 429; exact permutation test: p = 0.029) and the subsample of maximum values (n = 68; p = 0.045). These results corroborated the finding at the forest stand level, indicating that moderately dense forest stands harbored most *U. longissima*.

The dataset from cored trees used in the tree-ring analysis was suitable for evaluating possible relationships of lichen occurrence and abundance. *U. longissima* was present on 138 and absent on 337 of the cored trees. Trees with and without the lichen did not differ in size or age (Table 4). However, there were statistically significant, albeit rather small, differences between the two groups for several tree growth variables, indicating that trees with low absolute growth (mean tree-ring width last 10 yrs) and more strongly declining growth (*GI 10 yr / 20 yr*) had higher occurrences of *U. longissima*. Although the differences were not large in absolute terms, the results were corroborated by the fact that the minimum value of the *GI 10 yr / 10 yr* in the period after 1950, and after 1975, also differed between the groups, whereas the corresponding maximum values did not (Table 4). This latter result implies that trees with the lichen present today had experienced more pronounced events of declining growth during the last several decades than those without the lichen.

To see if these observed patterns of occurrence translated to the abundance of *U. longissima*, we explored the correlations between the different tree-ring growth variables and the number of *U. longissima* thalli recorded on the 138 cored trees where it was present. This exercise did not support our findings regarding lichen occurrence, as most rank tests showed p-values >0.30 (Table 4). Thus, whereas there were small but statistically significant differences regarding tree growth parameters explaining lichen occurrence, no such pattern explained lichen abundance.

Table 4. Comparisons of size, age, and different tree-ring derived growth variables between mature trees with and without presence of *Usnea longissima*. The Mann-Whitney unpaired two-group test checks for differences between trees with and without presence of *U. longissima*, whereas the Spearman rank test checks for correlations between *U. longissima* abundance (no. of thalli on trees) and the different size, age, and growth variables. Data showing trees from all study plots pooled.

Variable	Trees with *U. long.*, mean	Trees without *U. long.*, mean	Mann-Whitney Z-value	Mann-Whitney p-value	Spearman rank Z-value	Spearman rank p-value
Sample size	138	337			138	
DBH, cm	31.6	32.6	–1.27	0.21	1.01	0.29
Total age, yrs	146	145	0.29	0.77	–0.20	0.84
Mean tree-ring width last 5 yrs, mm	0.98	1.09	–1.81	0.07	0.41	0.69
Mean tree-ring width last 10 yrs, mm	0.89	1.00	–2.01	0.04	0.39	0.70
Mean tree-ring width last 20 yrs, mm	0.99	1.10	–1.62	0.11	0.17	0.87
GI 5 yr / 5 yr	1.22	1.21	0.45	0.65	1.01	0.31
GI 10 yr / 10 yr	0.81	0.86	–1.88	0.06	0.57	0.57
GI 10 yr / 20 yr	0.74	0.81	–2.44	0.01	–0.20	0.85
GI 10 yr / 10 yr, max-value after 1950	1.62	1.71	–0.36	0.72	–0.82	0.41
GI 10 yr / 10 yr, min-value after 1950	0.52	0.56	–2.91	0.004	0.34	0.74
GI 10 yr / 10 yr, max-value after 1975	1.16	1.21	–0.87	0.38	–2.07	0.04
GI 10 yr / 10 yr, min-value after 1975	0.57	0.61	–2.66	0.008	–0.11	0.92

4 Discussion

4.1 Logging Activity and Present Stand Structures

All study sites had been extensively logged from the 1880s up to the 1950s, with peak logging activity in the 1910s and the 1920s, corresponding to the years of maximum timber floating in 1914 and in 1921. Although stand-replacement logging was widely accepted after World War II, a majority of the sites continued to be selectively logged throughout the 1950s. With three exceptions (A1, K2 and L1) selective logging ceased after 1960, where two of these were minor loggings and the third was logged during the making of an operation road.

Harvested volumes during logging events varied tremendously, from barely noticeable to almost clearcut (e.g. 95% cut at site E3 in 1920s, Fig. 6). However, despite a four-fold difference in total harvested volume among study sites, the stand history explained only minor parts of the variation in present stand structure. The main reason for this is that almost all stands were left unmanaged after 1960, thereby allowing stands to gain volume for several decades and conceal possible historic tracks today. Many stands more than doubled their standing volumes after the 1950s (cf. Fig. 6).

4.2 Possible Effects on *Usnea longissima*

No characteristics of present-day forest stands convincingly explained the occurrence and abundance of *U. longissima*. We found a statistically significant unimodal relationship between tree density and average number of thalli per tree, a pattern that was sensitive to one outlying plot value. The pattern, however, recurred at the single-tree level, with peak thalli densities around basal areas of 15–25 m^2ha^{-1}, corresponding to stand volumes of 130–220 m^3ha^{-1}. *U. longissima* is known to have highest growth rates in open habitats, enabling the photosynthesizing green-alga to be active for longer periods, provided that the microclimate is sufficiently humid (Gauslaa and Solhaug 1996, Keon and Muir 2002, Gauslaa et al. 2007). On the other hand, loss rates, in terms of wind break-off and mortality due to light-damage to the photobiont, also seem to be highest in open, exposed habitats (Keon and Muir 2002). A medium open canopy that provides ample diffuse light and prevents thalli from dehydration and wind damage may well be optimal for sustained growth of *U. longissima* populations (Josefsson et al. 2005).

We found higher *U. longissima* occurrences on trees having lower absolute growth and more strongly declining growth during the recent decades. However, no trend was found when we tried to predict lichen abundance from the same growth related variables among trees with the lichen present. Being careful not to put too much emphasis on this finding, it is known that many epiphytic lichens grow more vigorously on slow-growing, or otherwise stressed, trees. This may be due to such trees offering more stable growing conditions, or to provide more favorable chemical micro-environment for establishment and growth (Gauslaa and Holien 1998, Gauslaa et al. 1998).

Although variation was large, and statistical relationships susceptible to outliers, there was a tendency for *U. longissima* to be more abundant at sites less influenced by logging activity and if the historically lowest standing volume appeared long time ago. Notably, the data also showed that the stands that were less logged, and were at their lowest volume a long time ago, also had lower tree densities, higher volumes, and older stand ages today. Thus, less logged stands appeared today with fewer, bigger, and older trees than their more heavily logged counterparts. Two processes may have contributed to this observed pattern in *U. longissima*. First and foremost, during logging events lichen populations most probably declined as much as or more than the actual proportion of timber that was harvested. This is because most thalli are found on the biggest trees, and trees were cut regardless of lichens being present or not. Second, although the selective loggings temporarily opened up the canopy, letting through more light, and thereby created better growing conditions for the remaining lichens, this effect may have been of rather short duration. Subsequent re-growth of the stands, during the last 50 years or more, increased the canopy cover, and thereby presumably slowed down lichen growth. Without experimental evidence, it is not possible to disentangle these factors. Finally, we should not exclude the possibility that other region-wide negative factors (e.g., air pollution in the 1970s and -80s (van Herk et al. 2003)) or that the lichen have immigrated into the forest stands later, may have obscured the effects of logging that otherwise would have been present.

4.3 Management Implications

Although our results are not conclusive, it is clearly shown that *U. longissima* is still present in many stands with a long history of heavy logging. This shows that it can tolerate, and maybe even benefit from, selective logging, provided that lichen-rich trees are spared. However, because those stands that were most heavily logged in the past, have the highest forest stand density today, it is not possible to separate the direct effect of logging and the more indirect effects of canopy closure. Because *U. longissima* grows better in open habitat, it is tempting to suggest that most stands of today are too dense and therefore sub-optimal.

The peak number of lichen thalli appeared at basal-area of 15–25 m^2ha^{-1}, corresponding to a standing volume of living trees of about 130–220 m^3ha^{-1}. If we assume medium-sized trees (0.25–0.30 m^3) as a basis, this represents 400–600 trees ha^{-1}. With certain reservations due to the fact that our sample plots were skewed toward forest stands having relatively high timber volumes, we tentatively suggest that selective logging may be a viable management options in such stands with *U. longissima* present. A conservative approach may be to leave 100–150 m^3ha^{-1} (~400 medium-sized trees ha^{-1}). This roughly corresponds to half the present-day standing volume and tree density in many of the surveyed stands. Prior to logging, we urge that the lichen flora is thoroughly surveyed, and that trees with *U. longissima* are marked in the field so they are not incautiously cut. Finally, it is important to evaluate how suitable the forest stands are for selective logging (e.g., following Lexerød and Eid 2006), since certain forest conditions may result in increased vulnerability to wind throws.

U. longissima is presently categorized as Endangered in the Norwegian Red List (Kålås et al. 2006). Environmental certification standards in Norway do not allow forest stands with red-listed species to be clearcut. Given the relatively high number of *U. longissima* locations in certain areas, which is the case in our study area, selective logging may be a better alternative than a hands-off policy. However, care should be taken in planning and implementation of such operations, until we better understand the habitat requirements and responses of *U. longissima*. Some answers to these questions will hopefully be brought about by the experimental loggings accomplished in relation to this study.

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