Reconstructing 100–150 years of logging history in coastal spruce forest (*Picea abies*) with special conservation values in central Norway

KEN OLAF STORAUNET[1], JØRUND ROLSTAD[1] and RUNE GROVEN[2]

[1]*Norwegian Forest Research Institute, Høgskoleveien 12, N-1432 Ås, Norway and* [2]*Department of Forest Sciences, Agricultural University of Norway, P.O. Box 5044, N-1432 Ås, Norway*

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Coastal spruce forests of central Norway harbour a unique assemblage of epiphytic lichens and are given high priority with respect to conservation of biodiversity. To assess the historical impact of logging during the last 100–150 yrs, 31 remnant stands were studied by means of tree-ring analysis of 2199 trees and the decay stage of 1605 stumps. No stands had been clear-cut, but all had been selectively logged at least twice during the last 150 yrs. Total harvested timber volume ranged from 65 to 409 $m^3 ha^{-1}$ (31–124% of present-day standing volume) and the selective logging kept standing volume low (40–200 $m^3 ha^{-1}$) during 1890–1930. Present-day stand characteristics were strongly correlated with site productivity and topographic position within the ravine valleys. Low amounts of dead wood at sites with high historical logging activity was the only consistent relationship found after covariance of site productivity, topographic position and deciduous trees were taken into account. The results indicate that old-growth stand characteristics, such as reversed J-shaped age distributions and dead wood in advanced decay classes, can be obtained 100–150 yrs after intensive selective logging. *Key words: central Norway, coastal spruce forest, forest history, growth release, logging activity, Picea abies, stand reconstruction, stump decay.*

INTRODUCTION

In recent years attention has focused on the consequences of modern forestry methods on biological diversity (Hunter 1990, Hansen et al. 1991, Anon. 1992, Boyce & Haney 1997), particularly with regard to threatened and vulnerable species (Virkala et al. 1993, Berg et al. 1994, Franklin et al. 1996). Recognizing that approaches for conserving biodiversity can be based on different nature conservation measures as well as on specific forest management practices (Kotar 1997), considerable effort has been devoted to the task of defining a common basis for sustainable forestry (Liljelund et al. 1992, Anon. 1993, Christensen et al. 1996). One central issue, among others, has been the inherent problem of defining what constitutes an old-growth forest (Hunter 1989, Hunter & White 1997).

The coastal spruce forests in central Norway receive enough precipitation to be classified as "boreal rain forest" (Holien & Tønsberg 1996). The region is given special emphasis by the Norwegian Ministry of the Environment when they discuss and evaluate the present conservation status of coniferous forests in Norway (Anon. 1995). The coastal spruce forests contain species of lichens that are endemic or have their primary European distribution here, referred to as the "Trøndelag phytogeographical element" (Holien & Tønsberg 1996). Several of these species are included in the Norwegian Red List of threatened species (Anon. 1999). This has given rise to a debate between forest owners and timber industry on the one hand, and environmental organizations on the other, as to how these remnant forest stands should be managed to preserve their biological diversity in the future (Sved & Søraa 1993, Hals 1994, Falkeid 1995, Christensen 1997).

It is well known that the forests in this region have been utilized for several hundred years (Mørkved 1949). It is also believed that the lichen species in the Trøndelag phytogeographical element can tolerate moderate selective logging and thinning (Holien & Tønsberg 1996). However, no quantitative studies have been undertaken to document explicitly the frequency and magnitude of the logging activity during the last 100 yrs. Knowledge about the historical development of these sites can guide the prospective management, regarding both those areas that are (and will be) protected by means of nature reserves, and those that are allocated to forest utilization. Therefore, using dendroecological methods, the aim of this study was (1) to date and quantify logging events in selected stands of coastal spruce forests, (2) to reconstruct stand histories in detail, and (3) to explore how the logging history has influenced present-day forest structure. The possible impact on the lichen flora is treated by Rolstad et al. (2000).

MATERIALS AND METHODS

Study area

The study area is located in the Namdalen valley in central Norway, in the municipalities of Namsos, Overhalla, Grong and Høylandet. In total, 31 sites of coastal spruce forest were surveyed, scattered throughout the valley from 15 km south-west of Namsos to 15 km north-east of Grong, a distance of approx. 70 km (Fig. 1). The region is situated within the middle and southern boreal zone (Moen 1987). The climate is highly oceanic with yearly precipitation averaging more than 1200 mm, evenly distributed throughout the year with more than 220 days of measurable precipitation (Førland 1993*a*, *b*). The average annual temperature is 5°C. January is the coldest month with an average temperature of − 6°C, while July is warmest with an average temperature of 14°C (Aune 1993*a*, *b*). All study sites are situated below the marine limit, which is 140–150 m above present sea level (Sveian 1991), i.e. the soil is

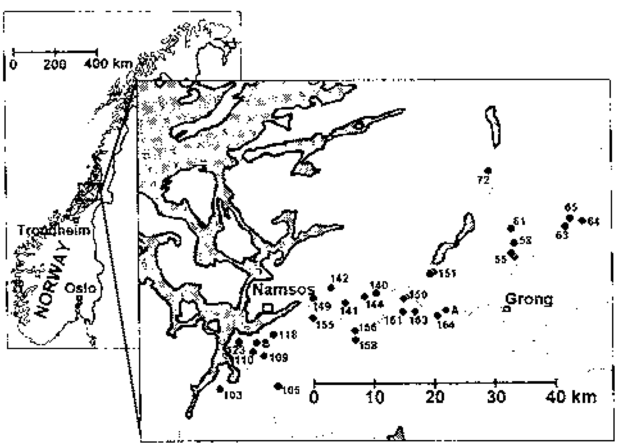

Fig. 1. Study area in Namdalen, central Norway, and the location of the 31 study sites. Numbers are referred to in Table 1.

ocean and fjord depositions of clay and silt. V-shaped ravine valleys created by water erosion are common features in the landscape. These valleys typically have a distance from the bottom to the top of 50 m and a difference in elevation < 20 m. Today these sites offer a moist microclimate, assumed to be an important prerequisite for the occurrence of many lichen species.

Holien & Tønsberg (1996) distinguish two main types of coastal spruce forests: the Namdalen type, characterized by an almost total dominance of Norway spruce [*Picea abies* (L.) Karst.], and the Fosen-Brønnøy type, representing a mixed spruce–deciduous forest, with birch (*Betula pubescens* Ehrh.), alder [*Alnus incana* (L.) Moench], willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) often comprising a large proportion of the tree stands. In the Namdalen region, alder and birch occur sparsely at riverbanks and riparian zones, on sites subject to small-scale erosion disturbances. This study was conducted within the Namdalen region.

An important vegetation characteristic is the wealth of epiphytic lichens. Within the ravine systems below the marine limit, the Lobarion pulmonariae community is dominated by species such as *Lobaria pulmonaria* (L.) Hoffm., *L. scrobiculata* (Scop.) DC., *Nephroma* spp., *Peltigera collina* (Ach.) Schrader and *Pseudocyphellaria crocata* (L.) Vainio. *Erioderma pedicellatum* (Hue) P. M. Jørg., *Lobaria hallii* (Tuck.) Zahlbr. and *Fuscopannaria ahlneri* (P. M. Jørg.) P. M. Jørg. occur almost exclusively in the coastal spruce forest (Holien & Tønsberg 1996).

The Norwegian Directorate for Nature Management recently undertook a survey of the lichen flora in the coastal spruce forest in the Namdalen valley (Anon. 1997). Here locations were classified into three categories of conservation value, mainly based on the occurrence of rare lichen species. In the present study, study sites were established in 26 locations from this report. In addition, one site in an already established nature reserve and one site in another ravine location (Brennmoen) were studied. The objective was to sample from all three conservation categories and to distribute the locations throughout the entire valley. In three of the largest locations study sites were established in two different places, because these locations had an extensive area and a large topographical variation. This gave a total of 31 study sites (Table 1).

Fieldwork

Within the locations, study sites were established where the two characteristic species *Pseudocyphellaria crocata* and *Fuscopannaria ahlneri* occurred most abundantly (Rolstad et al. 2000). Five circular plots, each of 0.02 ha, were sampled, and the central sample plot was located where *P. crocata* and *F. ahlneri* were most common. The distances to the four other sample plots were 50 m to the north, east, south and west, respectively. When tree density was low the sample plots were enlarged (≤ 0.08 ha). The sample plots were categorized as bottom, slope or plateau, according to their topographic position in relation to the ravines. A fourth category contained miscellaneous plots that did not fit into the ravine gradient. For each study site a ravine bottom index was calculated as the proportion of the sample plots situated at the bottom of the ravines. Site index, defined as top height at a reference age of 40 yrs, was determined from site index curves for Norway spruce (Tveite 1977).

Diameter of all living trees ≥ 10 cm at breast height (DBH = 1.3 m above ground level) was recorded, and all living trees with DBH ≥ 10 cm were cored, a total of 2199 trees. The trees were cored at breast height partly because growth responses were easier to discern than at ground level, and partly for the greater convenience of the fieldwork. Trees with DBH between 3 and 9 cm were counted. Stumps and fallen dead wood (logs) ≥ 10 cm at stump height and breast height, respectively, were recorded and categorized according to degree of decay and diameter. A sampling scheme of eight decay classes (where 1 is recently cut/fallen, and 8 is almost completely decayed) was applied (Arnborg 1942, Hofgaard 1993, Groven et al. submitted.

Laboratory procedures and calculations

Increment cores were prepared in the laboratory with a scalpel, and tree-ring widths were measured with a micrometer (accuracy of 0.01 mm) at 20 or 40× (Stokes & Smiley 1968). To determine the age of trees when increment cores failed to reach the pith, the length of the missing radius was estimated by matching the curvature of the inner rings to concentric circles drawn on a clear plastic sheet. The mean ring width of the 10 innermost rings and the estimated missing radius were used to estimate number of rings in the missing radius. Age at breast height was transformed to total age according to the following relationship:

$$\log(y) = 1.25 - 0.568 \times \log(x), \ (p = 0.0004, r^2 = 0.29, n = 45)$$

where y is number of years from ground level to breast height, and x is average ring width of the 10 oldest rings at breast height. This relationship was estimated from coring 45 randomly selected trees at ground level and breast height, respectively.

To identify growth responses to logging events changes in the rate of radial increment growth for each tree were examined using the following procedure: for each core the average tree-ring width was compared between two consecutive 10-yr periods. This comparison was done for all years, starting 10 yrs from the pith or the oldest ring. A growth release was defined as a 100% or more increase in average radial increment (Fajvan & Seymour 1993). If the average ring width of the 10 yrs preceding a growth increase was larger than 1 mm, the criterion for defining a growth release was reduced to 50% increase (moderate release, cf. Lorimer & Frelich 1989). This was done because a fast-growing tree is less likely to respond to logging than a slow-growing tree. If there were several subsequent years that exceeded the thresholds, the event was dated according to the year when the percentage increase was largest (Fajvan & Seymour 1993). Following a logging event an unknown proportion of the remaining trees will react. A logging event was defined if a year was followed by a 10-yr period with more than 15% of the trees showing growth releases. The number of logging events in the nineteenth century contains elements of uncertainty because there were few available trees to disclose growth releases from this period.

The age of stumps in different decay classes was determined by selecting 120 living trees adjacent to stumps that had only one 100% growth release. This growth-release criterion indicates release from suppression of small understory trees in response to the death or harvest of nearby canopy trees (Lorimer & Frelich 1989). To estimate the harvested timber volume for each logging event, the recorded stumps were allocated to the dated logging events according to their decay class and the stump datings (see Groven et al. submitted, for further details). To estimate the tree diameter at breast height, the relationship

$$\text{DBH} = 0.81 \times \text{D}_{\text{stump height}} - 0.1 \ (p < 0.0001, r^2 = 0.97, n = 108).$$

was used. This relationship was estimated from measuring the diameter of 108 randomly selected trees at

Table 1. *Study site characteristics, historical logging data and forest stand characteristics, as recorded in 31 study sites of coastal spruce forest in Namdalen, central Norway. Site no. refer to Anon. (1997).*

Study site data					Logging data			Forest stand characteristics						
Site no.	Study site	Altitude (m a.s.l.)	Area of location (ha)	Area of study site (ha)	Total harvested volume (m^3ha^{-1})	No. of stumps (ha^{-1})	No. of logging events 1900–1996	Standing volume (m^3ha^{-1})	No. of trees ≥ 10 cm DBH (ha^{-1})	Median stand age (yrs)	% Deciduous trees	Volume of logs (m^3ha^{-1})	No. of logs (ha^{-1})	No. of trees 3–9 cm DBH (ha^{-1})
55.1	Gartlandselva nedre, west	85	86.0	0.123	178	490	4	245	490	146	0	10	30	200
55.2	Gartlandselva nedre, south	90	86.0	0.134	104	250	4	281	430	167	0	7	20	320
58	Gartlandselva midtre	90	12.5	0.111	161	250	3	261	450	160	0	20	50	350
61	Helmersetran	90	4.0	0.100	92	350	2	278	760	102	9	34	90	470
63	Kvernbekken	100	29.5	0.100	92	350	3	142	430	135	0	8	50	610
64	Solbakken	115	19.0	0.100	185	530	4	180	540	118	2	9	20	540
65	Skogvoll	105	14.0	0.100	122	650	2	204	630	166	2	5	40	660
72	Nedre Flakkan	90	4.0	0.100	176	310	2	276	500	138	0	12	60	240
103	Storolsengmyra	20	5.5	0.100	209	890	4	338	800	128	20	16	70	570
105	Langmyra	45	2.5	0.100	144	550	3	209	640	97	8	19	70	360
109	Bognmyra	55	2.5	0.100	134	310	1	299	770	153	0	26	40	580
110	Dølaelva	55	4.0	0.100	147	440	3	354	810	161	0	19	60	500
118	Sæva	35	10.5	0.160	129	290	3	200	600	118	0	3	10	510
123	Selneselva	20	4.5	0.100	409	1300	3	329	910	98	1	2	10	870
140	Rygg	50	2.0	0.100	104	380	3	229	490	130	0	1	10	250
141	Vestmyr	15	9.0	0.100	147	520	3	270	770	122	4	10	40	370
142	North of Stormyra	35	1.0	0.100	113	400	2	186	530	104	4	12	30	220
144	Lauvset	45	2.5	0.100	115	420	3	276	620	116	0	20	80	290
149	Lindset, south-east	30	3.0	0.100	189	730	4	178	420	147	0	34	120	410
150.1	Foss/Grande, plateau	50	20.5	0.100	323	870	3	274	610	174	0	2	10	290
150.2	Foss/Grande, ravine	70	20.5	0.120	180	600	3	266	620	137	1	2	20	480
151.1	Flenga, east	25	25.0	0.160	207	520	2	310	640	122	5	7	20	400
151.2	Flenga, south	20	25.0	0.105	65	320	3	176	700	117	5	9	70	390
155	Øvre Sandmoelva	15	3.5	0.100	97	340	3	258	1040	113	24	18	240	490
156	Homstad	50	2.5	0.123	122	390	2	394	680	125	1	31	110	150
158	Brannen	60	4.5	0.100	243	750	3	307	740	99	1	3	20	290
161	Skogly	75	8.0	0.100	223	670	2	285	800	124	3	4	40	450
163	Engan/Kattmoen	65	25.0	0.100	191	450	4	312	570	90	9	26	40	310
164	Skistad	60	3.0	0.100	148	270	3	418	530	104	2	12	40	270
A	Brennmoen, ravine	40	5.0	0.060	99	330	3	209	630	77	45	80	270	820
B	Nature reserve Dølaelva	45	9.5	0.111	117	310	2	191	540	153	0	8	30	320
	Median				147	420	3	270	620	124	1	10	40	390
	Mean				160	490	2.9	262	630	127	5	15	60	420
	SD				71	230	0.8	66	150	25	9	15	60	170
	Min.				65	250	1	142	420	77	0	1	10	150
	Max.				409	1300	4	418	1040	174	45	80	270	870

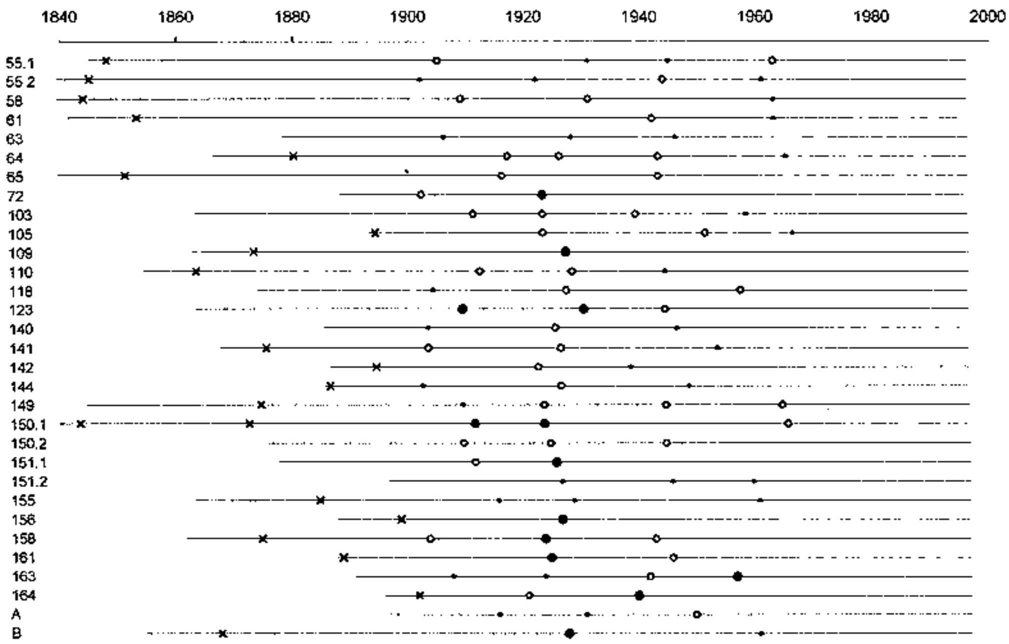

Fig. 2. Dating of logging events and harvested volumes for 31 study sites of coastal spruce forest in Namdalen, central Norway. The time lines begin at a sample depth of 20 trees. ●: >80 m^3ha^{-1}; ○: 40–80 m^3ha^{-1}; •: <40 m^3ha^{-1}; ×: unknown harvested volume. Numbers on the left refer to study site number in Table 1.

breast height and stump height, respectively. The DBH together with the diameter/height relationship were then used to calculate harvested stem volumes (formulae after Vestjordet 1967). This is a single-entry volume calculation, also called a tariff table (e.g. Avery & Burkhart 1994), using the diameter to estimate the volume of single trees. The diameter/height relationship was derived from five sample trees in each stand separately (Fitje & Vestjordet 1977) and was assumed to be constant between 1900–1996.

Diameter distributions and standing volumes at each site during the period 1900–1996 were reconstructed. Diameters of cored trees were reconstructed by using the measured tree-ring widths. The diameters of rotten trees were reconstructed by using the average ring width for the particular study site. This was also done for trees that were "raised" on stumps prior to the respective logging events. After adding bark thickness, the standing volumes in the study sites were calculated (Vestjordet 1967, Groven et al. submitted).

Partial correlation coefficients from multiple regression models were used to examine relationships between variables independent of covariates. Multiple regressions are sensitive to deviations from normality and outliers. Therefore, before analysis, the data distributions were carefully checked and non-normal variables corrected applying logarithmic, arcsine and square root transformations (Zar 1984). Statistical tests were two-tailed and based on a 0.05 significance level, except for the partial correlations where a significance level of 0.10 was applied to increase the power of the tests.

RESULTS

Logging activity and stand history

The logging activity deduced from tree-ring analysis dated back 100–150 yrs, depending on the number of old trees in the stands. All study sites had been logged at least twice and a maximum of five times during this period (Fig. 2). On average three logging events were dated during the last 100 yrs, with an average rotation time of 20 yrs. None of the stands had been clear-cut. Total harvested timber volume averaged 160 m^3ha^{-1} and varied from 65 to 409 m^3ha^{-1} (Table 1). This constituted 31–124% of present-day standing volume. The number of stumps ha^{-1} averaged 490 (range 250–1300), which was slightly lower than the present-day average tree density, 640 trees ha^{-1} (range 420–1040). Nine study sites had at least as many stumps as living trees. Stumps averaged 26 cm (range 21–34) in diameter at stump height, corresponding to 21 cm in breast height, approximately the same as the present-day average stem diameter (DBH = 22 cm). Stump diameter was not correlated with decay class ($r = 0.03$, $p > 0.20$, $n = 1605$), indicating that the size of the harvested trees had not changed during the period 1900–1960 when most of the logging took place. There was no relationship between total harvested volume and number of logging events after 1900 ($r = 0.16$, $n = 31$, $p > 0.20$) (Table 2a), which means that trees were harvested either in a few large or several small loggings. Stumps decomposed completely in 100–120 yrs and the relationship between age and decay class appeared to be linear (Fig. 3). The decomposition time constrained how far back in time the stands could be reconstructed.

Logging activity was low in late 1800s, peaked in 1920s and ceased after 1960s (Fig. 4). The halt in logging activity after 1965 was due to a shift in the harvest regime, from selective logging to clear-cutting. This temporal variation was also reflected in the distribution of stumps and logs in different decay classes (Fig. 5). As many as 82% of the stumps were classified to decay class 4–6, dating back to 1910–1950 (Fig. 3). Only 2% of the stumps were classified to decay class 1–2, corresponding to the halt in selective logging after 1965. Logs in decay class 5–8 constituted only 15% of all logs. There was a peak in the distribution of logs in decay class 3 (Fig. 5), reflecting that logs had started to accumulate after the selective logging ceased in the 1960s.

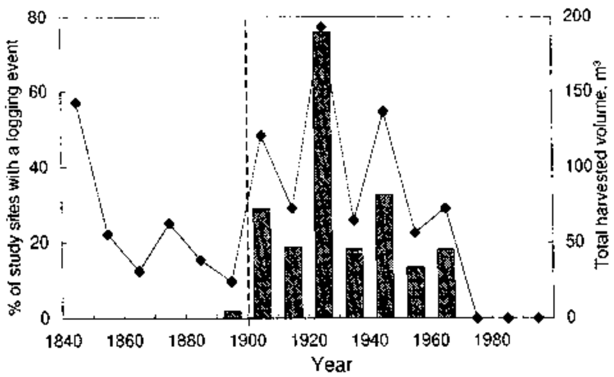

Fig. 4. Temporal distribution of the total harvested timber volume (bars) and the percentage of study sites with a logging event (line with indications, ◆) in each decade during 1840–1990, in Namdalen, central Norway. The vertical broken line indicates that harvested volume could not be estimated prior to 1900 owing to stump decay.

Although none of the study sites was clear-cut, they were selectively logged down to 40–100 m^3ha^{-1}, often several times between 1900 and 1960. Twelve study sites had their lowest standing volume between 1900 and 1910, 11 were at the lowest between 1920 and 1930 and six had the lowest volume after 1940 (Fig. 6). Present standing volumes were three to six times higher than the minimum estimated volumes between 1900–1940 and two to three times higher than standing volume in 1960. Although the study sites had low standing volumes during the early part

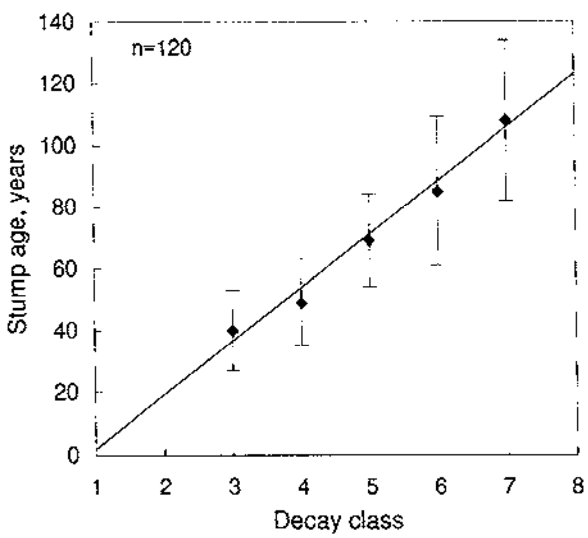

Fig. 3. Relationship between decay class (1: recently cut; 8: almost completely decayed) and stump age of 120 dated stumps in Namdalen, central Norway. Lines denote individual standard deviation and linear regression. No stumps were dated in decay classes 1, 2 or 8.

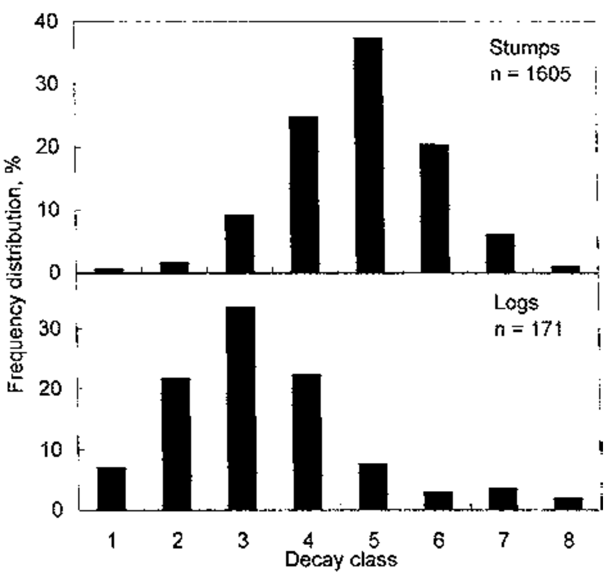

Fig. 5. Frequency distribution of stumps and logs in relation to decay class (1: recently cut/fallen; 8: almost completely decayed). Data are from all 31 study sites of coastal spruce forest in Namdalen, central Norway.

Table 2. *Correlation matrices for forest stand characteristics and logging variables in 31 study sites of coastal spruce forest in Namdalen, central Norway: (a) non-corrected coefficients; (b) partial coefficients corrected for ravine index and site index; (c) partial coefficients corrected for ravine index, site index and percentage deciduous trees*

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(a)										
(1) Harvested volume (m^3ha^{-1})	1.00									
(2) No. of logging events 1900–1996	0.16	1.00								
(3) Standing volume (m^3ha^{-1})	0.38	−0.22	1.00							
(4) No. of trees (≥10 cm) ha^{-1}	0.14	−0.23	0.39	1.00						
(5) No. of trees (<10 cm) ha^{-1}	0.06	0.04	−0.22	0.37	1.00					
(6) Median stand age	0.06	−0.07	−0.06	−0.31	−0.11	1.00				
(7) No. of logs ha^{-1}	−0.44	−0.05	−0.02	0.23	0.09	−0.27	1.00			
(8) Percentage deciduous trees	−0.21	0.14	0.00	0.45	0.34	−0.60	0.58	1.00		
(9) Ravine bottom index	−0.32	0.16	−0.32	−0.34	0.05	−0.06	0.26	0.08	1.00	
(10) Site index	0.28	−0.09	0.57	0.17	−0.45	−0.43	−0.21	0.02	−0.05	1.00
(b)										
(1) Harvested volume (m^3ha^{-1})	1.00									
(2) No. of logging events 1900–1996	0.27	1.00								
(3) Standing volume (m^3ha^{-1})	0.19	−0.15	1.00							
(4) No. of trees (≥10 cm) ha^{-1}	0.02	−0.18	0.27	1.00						
(5) No. of trees (<10 cm) ha^{-1}	0.24	−0.01	0.07	0.56	1.00					
(6) Median stand age	0.19	−0.11	0.22	−0.32	−0.38	1.00				
(7) No. of logs ha^{-1}	−0.36	−0.12	0.24	0.40	−0.01	−0.40	1.00			
(8) Percentage deciduous trees	−0.21	0.14	0.01	0.51	0.40	−0.65	0.60	1.00		
(c)										
(1) Harvested volume (m^3ha^{-1})	1.00									
(2) No. of logging events 1900–1996	0.27	1.00								
(3) Standing volume (m^3ha^{-1})	0.20	−0.16	1.00							
(4) No. of trees (≥10 cm) ha^{-1}	0.11	−0.29	0.36	1.00						
(5) No. of trees (< 10 cm) ha^{-1}	0.33	−0.06	0.07	0.41	1.00					
(6) Median stand age	0.07	−0.03	0.31	0.02	−0.17	1.00				
(7) No. of logs ha^{-1}	−0.31	−0.20	0.24	0.13	−0.27	−0.01	1.00			

Correlation coefficients corresponding to significance levels (η) of 0.10, 0.05 and 0.01 are 0.30, 0.36 and 0.45, respectively. The smallest detectable correlation coefficient with $\eta = 0.10$ and power = 0.80 is 0.45.

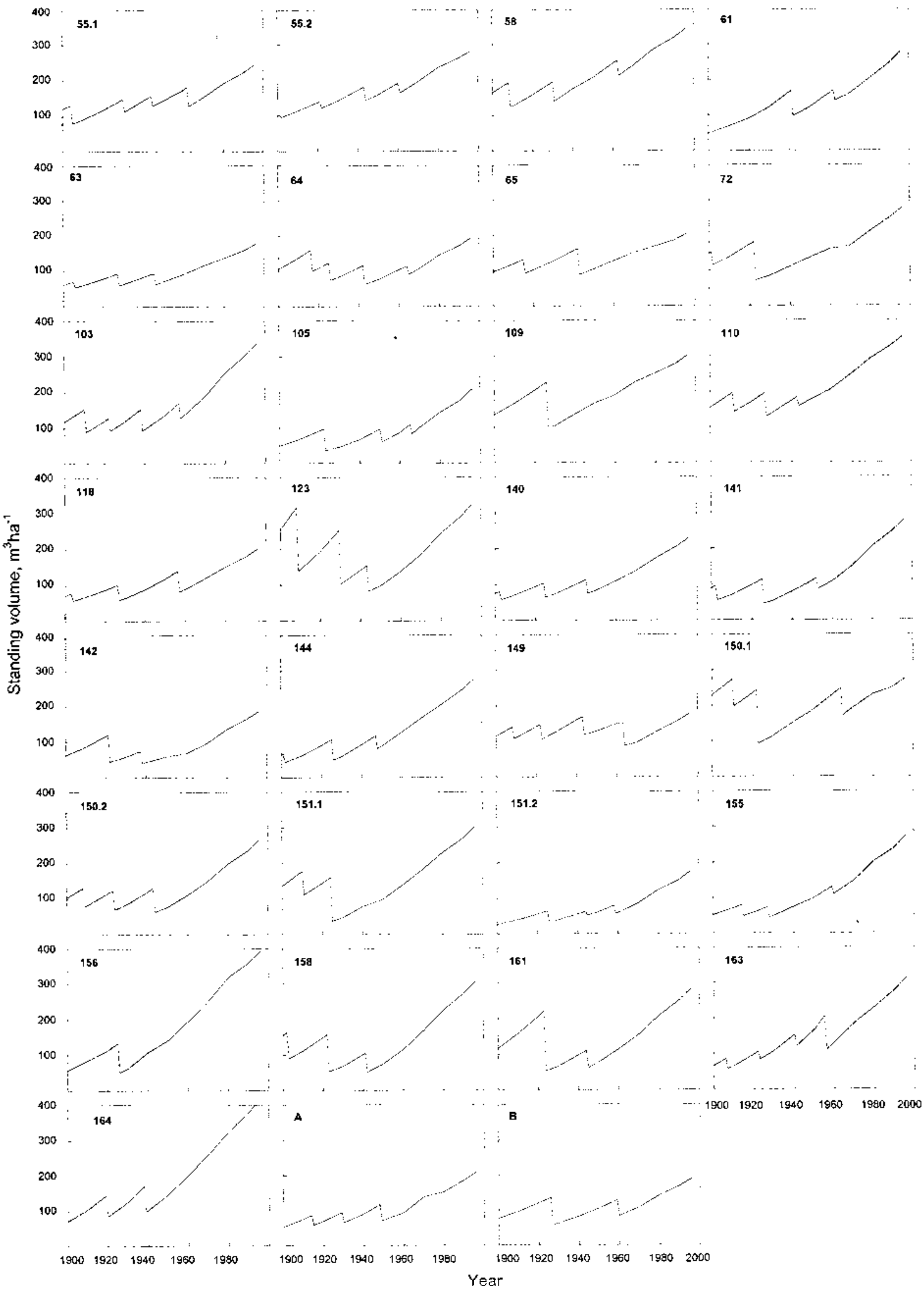

Fig. 6. Reconstructed standing volume (m^3ha^{-1}) in 31 study sites of coastal spruce forest during 1900–1996 in Namdalen, central Norway. Upper left numbers denote study site number according to Table 1.

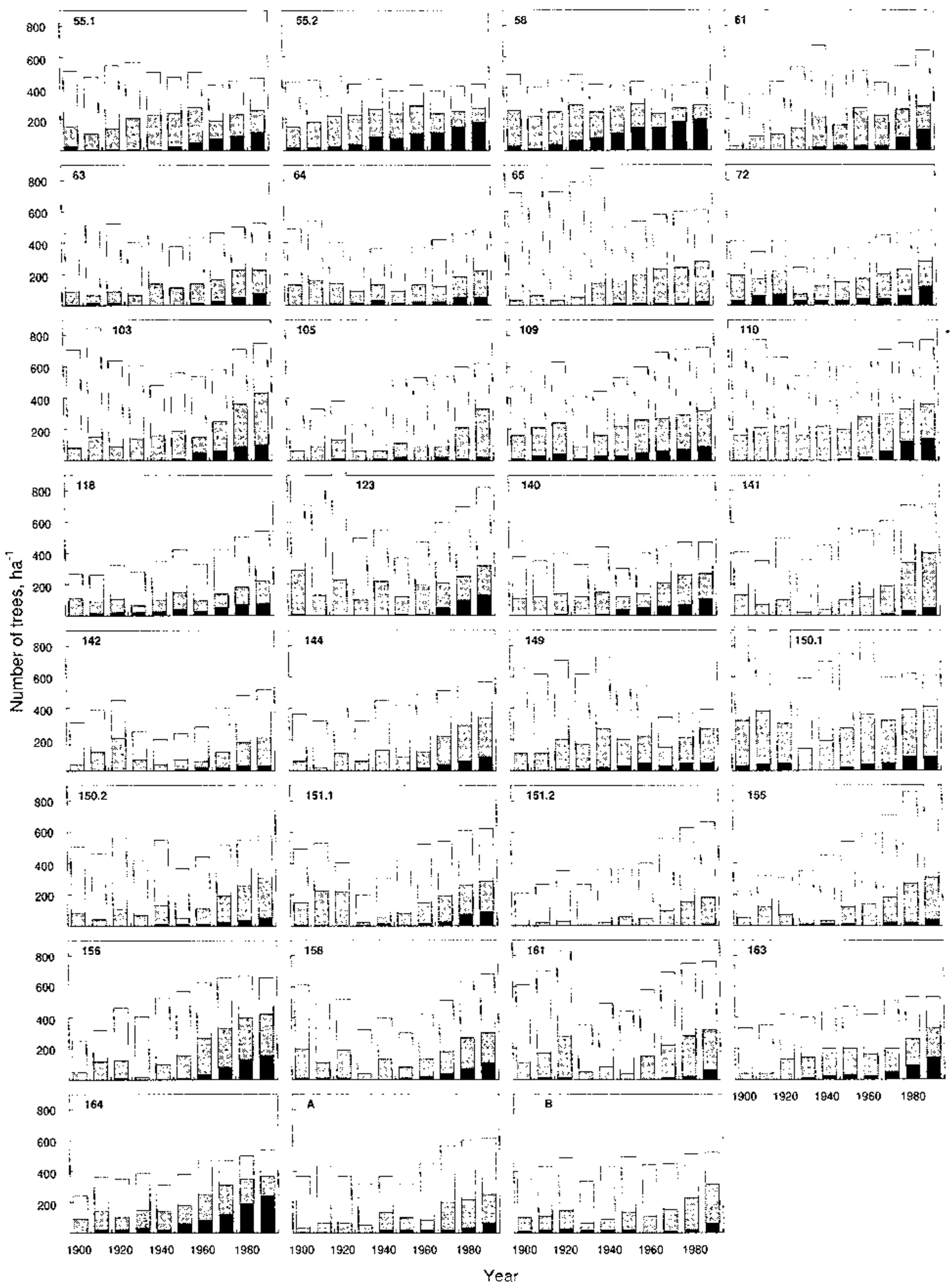

Fig. 7. Reconstructed number of trees per ha ($\geq$ 10 cm DBH) at the turn of each decade during 1900–1990 in 31 study sites of coastal spruce forest in Namdalen, central Norway. All tree species are included and the trees are distributed among three diameter classes (white: 10–19 cm DBH; grey: 20–29 cm DBH; black: $\geq$ 30 cm DBH). Upper left numbers denote study site number according to Table 1.

of the twentieth century, the total number of trees ha^{-1} was fairly constant (Fig. 7). In fact, 17 sites had their maximum number of trees ha^{-1} before 1950. The proportion of large trees (≥ 20 cm DBH) increased during the few last decades and this was the main reason for the increase in standing volume. Until the 1940s the study sites were almost devoid of trees ≥ 30 cm DBH.

Present-day stand characteristics

All study sites were situated in connection with ravine valleys or brooklets and their general appearance was that of mature forest. Median stand age was 127 yrs (range 77–174 yrs; Table 1) and none of the stands were even-aged. Maximum tree age ranged from 149 to 291 yrs and 6.3% of the trees regenerated prior to 1800. Standing volume of living trees ranged from 142 to 418 m^3ha^{-1} (average 262 m^3ha^{-1}) and the site index varied between 8 and 17 (average 14).

The most conspicuous characteristics of the forest stands were the low amounts of logs and the low proportions of deciduous trees (Table 1). The average percentage of deciduous trees (≥ 10 cm DBH) was only 4.8% (median 1%). At 13 study sites no deciduous trees were recorded at all, and at only three sites did the proportion of deciduous trees exceed 10%. Two-thirds of the deciduous trees were alder, one-third was birch, and only a few specimens of willow and rowan were recorded. The number of logs constituted 9.2% (median 6.3%) of the number of living trees (≥ 10 cm). Based on stem volume, the average proportion of logs was 6.1% (median 4.7%) of the standing volume. As many as 16 study sites had less than 10 m^3 logs ha^{-1} and only four sites had more than 30 m^3 logs ha^{-1}. Snags were almost absent, comprising <1% of the number of living trees.

Most stand characteristics were correlated with the ravine bottom index and the site index (Table 2a). Ravine bottoms had lower standing volume, fewer trees (≥ 10 cm DBH) and a tendency for more logs compared with ravine slopes and plateaux. Standing volume increased and the number of trees ≤ 10 cm DBH and stand age decreased with increasing site index. To explore the relationships between forest stand characteristics, independent of topographic position and site productivity, correction was made for the ravine bottom index and the site index in a multiple regression model (Table 2b). After ravine bottom and site indices were adjusted for, the percentage of deciduous trees was positively related to number of trees ≥ 10 cm ($r = 0.51$), number of trees ≤ 10 cm ($r = 0.40$) and number of logs ($r = 0.60$), and it was strongly negatively correlated to stand age ($r = -0.65$). There were negative relationships between stand age and number of trees ≥ 10 cm ($r = -0.32$), number of trees ≤ 10 cm ($r = -0.38$) and number of logs ($r = -0.40$). However, after correcting for the covariance of percentage of deciduous trees, the partial correlations between stand age and the other stand characteristics were no longer significant (Table 2c). The only significant correlations that were upheld, after removing the covariance of deciduous trees, were positive relations between standing volume and number of trees ≥ 10 cm DBH, and between number of trees ≥ 10 cm and trees ≤ 10 cm.

Influence of previous logging

The harvested timber volume was negatively correlated with the ravine bottom index ($r = -0.32$) and positively correlated with the site index ($r = 0.28$) (Table 2a), suggesting that the logging activity had been lower in the ravine bottoms and higher on more productive sites. This explains the spurious positive correlation between harvested volume and standing volume ($r = 0.38$), which was no longer significant when ravine bottom and site indices were accounted for ($r = 0.19$, $p > 0.20$, Table 2b). Since the 1960s, when the selective logging ceased, stands gained considerable volume, especially on the more productive sites. The number of logs was negatively correlated with harvested volume ($r = -0.44$), and this relationship was upheld after ravine bottom and site indices were corrected for ($r = -0.36$). In addition, after adjusting for the covariation of deciduous trees, number of logs and harvested volume were negatively correlated, albeit more weakly ($r = -0.31$, Table 2c). None of the other stand characteristics was found to correlate significantly with harvested volume; most notably, there was no relationship between harvested volume and stand age. The proportion of deciduous trees was low in most study sites. However, at some sites, where groups of deciduous trees occurred, stumps were almost lacking. This was indicated by a negative, albeit non-significant ($r = -0.21$), correlation between the percentage of deciduous trees and harvested volume (Table 2b).

DISCUSSION

All study sites had been extensively harvested by means of selective logging during the last 100–150 yrs. The logging activity in the latter half of the nineteenth century appeared to be low compared with the first half of the twentieth century. The logging almost ceased in the 1890s, which is the 10-yr period with lowest activity. A rapid increase in logging activity in the early 1900s peaked in the 1920s, a decade when almost 80% of the surveyed sites were logged. No logging events were recorded after the 1960s. These results generally agree with the trend in logging activity described in historical records (Mørkved 1949, Tveite 1964). Mørkved (1949) describes a short period of low timber utilization in the late 1800s due to both low timber prices and a general concern about overexploitation of the forest resources. In the beginning of twentieth century timber prices increased and the minimum dimension requirements for sale were reduced, partially as a result of the introduction of pulping industries in the region. The amount of timber floated down the river valley of Namdalen more than doubled between 1900 and 1910 (Mørkved 1949). The present results therefore support statements that the forests in this region were strongly depleted and sparsely stocked around 1900 and throughout the first decades of the twentieth century (e.g. Barth 1916, Mørkved 1949, Tomter 1994).

The number of logging events decreased from the 1920s to the 1960s, when it ceased. This decline was caused by the shift from selective logging to clear-cutting practices. The selective logging was accompanied by natural regeneration of the stands. After clear-cutting was introduced, the harvested areas were reforested with seedlings grown in local forest nurseries in the Namdalen region. In this respect, the transition period from selective logging to clear-cutting is mirrored in the sales statistics from the forest nurseries, which increased rapidly in the period from 1940 to 1960 (Mørkved 1949, Grande 1988).

Historically, the international demand for wood products led to a timber frontier through Fennoscandia during the last centuries, from south-west to north-east (Östlund 1993, Angelstam 1996). This exploitation gradually transformed the forested landscape from old-growth forest to today's heavily managed stands. Studies from northern Sweden show that old-growth conditions still prevailed during the latter part of the nineteenth century, because the timber frontier had not reached the region (Östlund 1993, Östlund & Linderson 1995, Östlund et al. 1997). In north-western Russia old-growth forests still remain (Angelstam 1996). The present results show that coastal spruce forests of central Norway already were strongly depleted 100–150 yrs ago. On a large scale, shorter distances to the international markets can explain this difference (Östlund 1993). In addition, the locations studied here are situated near farms and close to transport rivers, and they are among the most productive sites in the region, thereby increasing their suitability for timber harvest.

Some of the growth releases in the 1840s, defined here as logging events, may have been responses to a severe hurricane ("Gærn-natta") that occurred in this area October 1837. This hurricane resulted in large areas with wind-thrown trees throughout the Namdalen valley and the event is described in several historical sources (Bilton 1840, Eide 1926, Mørkved 1949). In most of the study sites the sample depth of tree-rings was low in the latter part of the nineteenth century, and there was no supporting evidence from stumps.

The high logging activity recorded in the 1920s is not mirrored in the general trend in forestry activity in the area. This result may have been confounded by climatic fluctuations. The radial growth in the northern boreal zone is mostly controlled by the temperature of the growing season (Kalela-Brundin 1999). If a logging event takes place in a period with increasing temperatures, growth releases in tree-ring widths may be more pronounced, thereby increasing the chance of detecting a logging event. Conversely, if a logging event takes place during a period with decreasing temperatures, the tree-ring signal caused by logging may be masked. However, the method of reconstructing stand history used in this study is shown to be robust to errors in the dating of logging events (Groven et al. submitted). In addition, this would not affect the total harvested volume because it was calculated on the basis of cut stumps.

Despite a six-fold difference in harvested timber volume among the study sites, stand history explained only minor parts of the variation in present stand structure. Several factors may account for this lack of relationship. First, much of the variation in stand structure was due to site productivity and the topographic position within the ravine valleys. Secondly, the selective logging ceased in the 1960s, allowing the stands to gain volume during more than 40 yrs. Most of the stands more than doubled their standing volume during this period. Finally, the selective logging practice presumably gave little room for abundant regeneration, especially with respect to deciduous trees.

The only consistent relationship between logging history and present forest structure was that of fallen dead wood. Although about one-third of the dead wood comprised deciduous logs, the negative relationship between logging and number of logs was still present after correcting for deciduous trees. There were very few logs in older decay stages (decay class 5–8; 9 logs ha^{-1}). Downed logs in younger decay stages (decay class 1–4) were five times more abundant (43 logs ha^{-1}), showing that the amount of dead wood had started to accumulate during the last 40 yrs. Lack of dead wood in advanced decay classes was the stand characteristic that differed most from old-growth forest condition (e.g. Linder et al. 1997, Kuuluvainen et al. 1998).

It is not known whether the low proportion of deciduous trees is a natural feature of old-growth condition in this region, primarily because no virgin old-growth stands presently can serve as unmanaged control sites. At sites where groups of deciduous trees occurred, there were often signs of mudslides, showing as patches of bare soil or depressions in the ground. In some ravine bottoms, alder was growing at riparian zones that had been exposed to early spring floods. On this basis, the local occurrence of deciduous trees, especially alder, may have been related to small-scale, natural disturbances. In these cases, stumps from previous logging had probably been eroded by the mudslides or covered by sediments from floods. This may explain the negative association between the percentage of deciduous trees and harvested volume.

None of the studied locations could presently be considered old-growth stands, mostly because they lacked dead wood in late decay stages. From a conservation perspective one may ask how long it takes to achieve old-growth conditions. Hörnberg et al. (1995) showed that the age structure of stands of spruce swamp forests in boreal Sweden indicated forest stand continuity of at least 300 yrs. Ohlson et al. (1997) suggest that 300 yrs is sufficient to develop old-growth qualities and high biodiversity in these forests after major disturbances. The present results indicate that this period would presumably be considerably shorter in stands that have been subject to selective logging. Some 50–70 yrs ago many of the study sites were devoid of larger trees (>30 cm DBH) and they had very low standing volumes. Today, these sites were in a mature condition and coarse woody debris had started to accumulate. In another 50–70 yrs without logging, these locations may be characterized by small-scale gap dynamics. Many of the sites will have large amounts of dead wood, both as snags and logs, as well as large trees. Thus, most of the old-growth stand characteristics will be present 100–150 yrs after the stands were strongly depleted.

The most important conservation motive for preserving these coastal spruce forests has been to safeguard the assemblage of rare epiphytic lichens, the "Trøndelag phytogeographical element". The present results suggest that the lichen flora presumably can be preserved by means of moderate selective logging (Rolstad et al. 2000), confirming the views of Holien et al. (1995) and Holien & Tønsberg (1996). This management practice, as applied to maintain and restore natural stand structures on uneven-aged Norway spruce sites, is reviewed by Fries et al. (1997). However, little is known about other focal taxa affiliated with old-growth characteristics in the coastal spruce forests, even though several liverworts are found to occur in the forest type (Holien & Tønsberg 1996). Holien & Tønsberg (1996) also report that the region may have a depauperate fungal flora owing to the scarcity of dead wood. Cavity-nesting birds, e.g. the tree-toed woodpecker (*Picoides tridactylus*), preferentially excavate and breed in snags. These birds are very rare today. Selective logging usually precludes old-growth elements such as snags and fallen dead wood. To ensure the whole suite of old-growth flora and fauna a certain proportion of the remnant stands should be preserved as nature reserves.

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REFERENCES

Angelstam, P. 1996. The ghost of the forest past – natural disturbance regimes as a basis for reconstruction of biologically diverse forests in Europe. *In* DeGraaf, R. M. & Miller, R. I. (eds). Conservation of Faunal Diversity in Forested Landscapes, pp. 287–337. Chapman & Hall, London. ISBN 0-412-61890-7.

Anon. 1992. Agenda 21: Rio Declaration: Forest Principles: Drafts. United Nations Conference on Environment and Developement, Rio de Janeiro, 496 pp. ISBN 92-1-100482-9.

Anon. 1993. Forest Ecosystem Management Team. Forest ecosystem management: an ecological, economic, and social assessment., US Government Printing Office, Washington, DC, No. 1993-793-071. (Irregular pagination.)

Anon. 1995. Opptrapping av barskogvernet fram mot år 2000. (Barskogvernmeldingen). Stortingsmelding nr. 40, Miljøverndepartementet, Oslo, 25 pp. (In Norwegian.)

Anon. 1997. Boreal regnskog i Midt-Norge. Direktoratet for naturforvaltning, Rapport 2, 326 pp. ISBN 82-7072-276-6. (In Norwegian with English abstract.)

Anon. 1999. Nasjonal rødliste for truete arter i Norge 1998. Norwegian Red List 1998. Direktoratet for naturforvaltning, Rapport 3, 161 pp. ISBN 82-7072-344-2. (In Norwegian with English summary.)

Arnborg, T. 1942. Lågaföryngringen i en sydlappländsk granurskog. Svenska SkogsvFörb. Tidskr. 40: 47–78. (In Swedish.)

Aune, B. 1993*a*. Det norske meteorologiske institutt. Månedstemperatur. 1: 7 mill. Nasjonalatlas for Norge, kartblad 3.1.6. Statens kartverk, Hønefoss.

Aune, B. 1993*b*. Det norske meteorologiske institutt. Årstemperatur. 1: 2 mill. Nasjonalatlas for Norge, kartblad 3.1.5. Statens kartverk, Hønefoss.

Avery, T. E. & Burkhart, H. E. 1994. Forest Measurements, 406 pp. McGraw-Hill, New York. ISBN 0-07-002556-8.

Barth, A. 1916. Norges skoger med stormskridt mot undergangen. Tidsskri. Skogbr. 24: 123–154. (In Norwegian.)

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, J. & Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8: 718–731.

Bilton, W. 1840. Two Summers in Norway. By the Author of 'The Angler in Ireland', Vol. 1, 332 pp. Saunders and Otley, London.

Boyce, M. S. & Haney, A. (eds).1997. Ecosystem Management. Applications for Sustainable Forest and Wildlife Resources, 361 pp. Yale University Press, New Haven. ISBN 0-300-06902-2.

Christensen, N. L., Bartuska, A. M., Brown, J. H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J. F., MacMahon, J. A., Noss, R. F., et al. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecol. Applic. 6: 665–691.

Christensen, T. B. 1997. Hogger skogbruket mangfoldet i filler? Bellona magasin 1997(2): 37–39. (In Norwegian.)

Eide, E. 1926. Granskogens foryngelsesforhold i Namdalstraktene. Meddr norske SkogforsVes. 2(7): 49–86. (In Norwegian with German summary.)

Fajvan, M. A. & Seymour, R. S. 1993. Canopy stratification, age structure, and developement of multicohort stands of eastern white pine, eastern hemlock, and red spruce. Can. J. For. Res. 23: 1799–1809.

Falkeid, S. 1995. Biologisk mangfold – Bråk om kystbarskog. Skogeieren 81(4): 3–4. (In Norwegian.)

Fitje, A. & Vestjordet, E. 1977. Stand height curves and new tariff tables for Norway spruce. Medd. Nor. inst. skogforsk. 34(2): 23–68. (In Norwegian with English summary.)

Førland, E. 1993a. Det norske meteorologiske institutt. Nedbørhyppighet. 1: 7 mill. Nasjonalatlas for Norge, kartblad 3.1.2. Statens kartverk, Hønefoss.

Førland, E. 1993b. Det norske meteorologiske institutt. Årsnedbør. 1: 2 mill. Nasjonalatlas for Norge, kartblad 3.1.3. Statens kartverk, Hønefoss.

Franklin, A. B., Gutiérres, R. J., Noon, B. R. & Ward, J. P. Jr. 1996. Demographic characteristics and trends of Northern Spotted Owl populations in northwestern California. Stud. Avian Biol. 17: 83–91.

Fries, C., Johansson, O., Petterson, B. & Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. For. Ecol. Manage. 94: 89–103.

Grande, P. O. 1988. Kvatningen planteskole. *In* Namdal Skogselskap 1913–1988, pp. 27–41. Hojem Trykkeri, Namsos. (In Norwegian.)

Groven, R., Rolstad, J., Storaumet, K. O. & Rolstad, E. Using forest stand reconstructions to assess the role of structural continuity for late-successional species. For. Ecol. Manage. (submitted).

Hals, A. 1994. Den trønderske kystgranskogen – Nå står den for tur. Skogeieren 80(11): 16–18. (In Norwegian.)

Hansen, A. J., Spies, T. A., Swanson, F. J. & Ohmann, J. L. 1991. Conserving biodiversity in managed forests. BioScience 41: 382–392.

Hofgaard, A. 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. J. Veg. Sci. 4: 593–601.

Holien, H. & Tønsberg, T. 1996. Boreal rain forest in Norway – the habitat for lichen species belonging to the Trøndelag phytogeographical element. Blyttia 54: 157–177. (In Norwegian with English summary.)

Holien, H., Gaarder, G. & Håpnes, A. 1995. *Erioderma pedicellatum* still present, but highly endangered in Europe. Graphis Scripta 7: 79–84.

Hörnberg, G., Ohlson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration pattern and long-term continuity in boreal old-growth *Picea-abies* swamp forests. J. Veg. Sci. 6: 291–298.

Hunter, M. L. Jr. 1989. What constitutes an old growth stand? J. For. 87: 33–35.

Hunter, M. L., Jr 1990. Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity, 370 pp. Prentice-Hall, Englewood Cliffs, NJ. ISBN 0-13-959479-5.

Hunter, M. L., Jr & White, A. S. 1997. Ecological thresholds and the definition of old-growth forest stands. Nat. Areas J. 17: 292–296.

Kalela-Brundin, M. 1999. Climatic information from tree rings of *Pinus sylvestris* L. and a reconstruction of summer temperatures back to AD 1500 in Femundsmarka, eastern Norway using PLS analysis. Holocene 9: 59–77.

Kotar, J. 1997. Silviculture and ecosystem management. *In* Boyce, M. S. & Haney, A. (eds). Ecosystem Management. Applications for Sustainable Forest and Wildlife Resources, pp. 265–275. Yale University Press, New Haven. ISBN 0-300-06902-2.

Kuuluvainen, T., Syrjanen, K. & Kalliola, R. 1998. Structure of a pristine *Picea abies* forest in northeastern Europe. J. Veg. Sci. 9: 563–574.

Liljelund, L. E., Pettersson, B. & Zackrisson, O. 1992. Skogsbruk och biologisk mångfald. Svensk Bot. Tidskr. 86: 227–232. (In Swedish.)

Linder, P., Elfving, B. & Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. For. Ecol. Manage. 98: 17–33.

Lorimer, C. G. & Frelich, L. E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. 19: 651–663.

Moen, A. 1987. The regional vegetation of Norway; that of Central Norway in particular. Norw. J. Geogr. 41: 179–226. (In Norwegian with English summary.)

Mørkved, K. L. 1949. Skogbruk og treforedling i Namdal. Historisk streiftog, 316 pp. F. Bruns Bokhandels Forlag, Trondheim. (In Norwegian.)

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. Biol. Conserv. 81: 221–231.

Östlund, L. 1993. Exploitation and structural changes in the north Swedish boreal forest 1800–1992. Swedish Univ. of Agric. Sci., Dept of Forest Vegetation Ecology, Umeå. Dissertations in Forest Vegetation Ecology 4, 30 pp. ISBN 91-576-4754-2.

Östlund, L. & Linderson, H. 1995. A dendrochronological study of the exploitation and transformation of a boreal forest stand. Scand. J. For. Res. 10: 56–64.

Östlund, L., Zackrisson, O. & Axelsson, A. L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Can. J. For. Res. 27: 1198–1206.

Rolstad, J., Gjerde, I., Storaunet, K. O. & Rolstad, E. 2000. Epiphytic lichens in coastal spruce forest of Central Norway in relation to present-day forest structure and historic logging. Ecol. Applic. (in press).

Stokes, M. A. & Smiley, T. L. 1968. An Introduction to Tree-ring Dating, 73 pp. University of Chicago Press, Chicago.

Sved, R. & Søraa, J. 1993. Trøndelags ukjente regnskoger. Natur Miljø 1993(6): 4–8. (In Norwegian.)

Sveian, H. 1991. Namsos. Kvartærgeologisk kart, 1723 IV, med beskrivelse. 1:50 000. Norges geologiske undersøkelse, Oslo.

Tomter, S. M. (ed.). 1994. Statistics of Forest Conditions and Resources in Norway. NIJOS, Ås, 103 pp. ISBN 82-7464-076-4.

Tveite, B. 1977. Site index curves for Norway spruce (*Picea abies* (L.) Karst). Medd. Nor. inst. skogforsk 33(1), 84 pp. (In Norwegian with English summary.)

Tveite, S. 1964. Skogbrukshistorie. *In* Seip, H. K. (ed.). Skogbruksboka. Bind 3: Skogøkonomi, pp. 17–75. Skogforlaget, Oslo. (In Norwegian.)

Vestjordet, E. 1967. Functions and tables for volume of standing trees. Norway spruce. Meddr norske SkogforsVes. 22: 539–574. (In Norwegian with English summary.)

Virkala, R., Alanko, T., Laine, T. & Tiainen, J. 1993. Population contraction of the white-backed woodpecker *Dendrocopus leucotos* in Finland as a consequence of habitat alteration. Biol. Conserv. 66: 47–53.

Zar, J. H. 1984. Biostatistical Analysis, 718 pp. Prentice Hall, Englewood Cliffs, NJ. ISBN 0-13-077595-9.