

Effects of reindeer grazing on understorey vegetation in dry *Pinus sylvestris* forests

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Abstract. Data on floristic composition and environmental variables were collected in floristically homogeneous oligotrophic pine (*Pinus sylvestris*) forests with heath-like understorey vegetation in eastern Fennoscandia, and ordinated by non-linear multidimensional scaling (NMDS) in order to study the effect of lichen grazing by reindeer on the understorey vegetation. The study sites included areas with varying grazing pressure, as well as 50-yr old grazing exclosures.

Sites rich in respectively bryophytes and lichens were placed at opposite ends of the ordination axes, and heavily grazed sites were placed in between them. Reindeer grazing increased the abundance of bryophytes, especially *Dicranum* spp. and *Pleurozium schreberi*. Grazing changed the vegetation to the extent that it resembled more mesotrophic sites, but this did not show any relationship with tree volume or other site productivity indicators. This was observed both in the ordination and, in a more compelling way, when exclosures with adjacent grazed areas were compared. No such signs were evident at ungrazed sites, where especially *Cladina* spp. spatially replace *Cladonia* spp. and tiny bryophytes like *Barbilophozia* spp., *Polytrichum* spp. and *Pohlia nutans* during succession. *Cladina stellaris* had almost disappeared from the most intensively grazed sites.

The soil at ungrazed sites was characterized by high Al and Fe concentrations and bryophyte-rich sites by high Mn concentrations. Shannon's diversity index, depth of humus layer and proportion of bare ground also increased in sites getting richer in bryophytes.

Keywords: Boreal ecosystem; *Cladina*; *Cladonia*; *Dicranum*; Non-linear multidimensional scaling; *Rangifer tarandus*; Succession.

Nomenclature: Hämet-Ahti et al. (1986) for vascular plants, Ahti (1981) for lichens, Koponen et al. (1977) for bryophytes, except for *Dicranum* in which Nyholm (1986) is followed.

Introduction

Lichen-rich forests, usually with *Pinus sylvestris* as a dominant tree, occur on dry sandy soils in Finland. They are heavily grazed by semidomestic reindeer. In

the beginning of the 1900s the number of reindeer was above 100 000 (Kautto et al. 1986), and by 1959 - 1960 it had reached 140 000 (Alaruukka 1964). In 1983 - 1984 the number exceeded 200 000 (Kautto et al. 1986) and in the winter of 1991 - 1992 it was 265 000 (Anon. 1993). As a consequence reindeer have to be fed with hay or imported lichens during winter (Mattila 1981; Helle & Aspi 1982; Kojola et al. 1993). Today, trampling and grazing of lichens by reindeer is a major factor controlling the vegetation cover and has led to significant variation in the forest floor plant cover in northern Finland.

Several authors (Du Rietz 1925; Söyrinki 1939; Nordhagen 1943; Skuncke 1969; Brown & Mikola 1973; L. Oksanen 1978; Helle & Aspi 1982; Leader-Williams et al. 1987; Staaland & Olesen 1992; Staaland et al. 1993) have described the effects of reindeer grazing on vegetation. Many studies are speculative in nature, however, since exclosures were only rarely used (L. Oksanen 1978; Leader-Williams et al. 1987).

The response of vegetation to grazing depends on the geographical location. In oceanic areas a change in vascular plant abundance has been reported, e.g. native *Poa flabellata* was replaced by introduced weedy *Poa annua* in South Georgia (Leader-Williams et al. 1987), in St. Matthew Island in the Bering Sea, and in Scandinavian mountains, lichens were replaced by graminoids like *Carex bigelowii* and *Festuca ovina* (L. Oksanen 1978; Klein 1987). In continental and intermediate parts between continental and oceanic sectors of the Fennoscandian mountains the thick *Cladina stellaris* carpet is replaced by vascular plants, bryophytes and other lichens (Du Rietz 1925; Nordhagen 1943; Söyrinki 1939). However, in the absence of ungrazed control areas, it is impossible to say which of the characteristics of vegetation are due to reindeer grazing and which are natural (Oksanen & Ahti 1982; Oksanen 1983). Succession in vegetation is very slow, according to Jalas (1953) it takes at least 50 to 80 years after fire to reach the mature *Cladina stellaris* stage in central Finland. In northern Finland this may be even longer.

The aim of this study was to investigate the effect of grazing by reindeer on the vegetation structure and soil characteristics of dry oligotrophic *Pinus sylvestris* heaths by comparing ungrazed and grazed sites using exclosures established 30 to 50 yr ago. These were compared with 'natural' pine heath forests all around Lapland and the Kola Peninsula. The forests of the Western Kola Peninsula are ungrazed. This information might become very important in the near future with respect to the massive pollution in the western Kola Peninsula, and because there are plans by Finnish reindeer keepers to rent lichen heaths in nearby areas in Russia. These areas have not yet been grazed and the lichen carpet may protect the soil from pollution. Grazing of these areas may lead to most undesirable consequences.

Material and Methods

Study area and sampling

The study sites are situated in northern Finland and in the Kola Peninsula (Fig. 1), according to Tuhkanen (1984) in intermediate parts between oceanic and continental sectors of the northern boreal zone, except the two southernmost sites, which belong to the middle boreal zone (Ahti et al. 1968). The study sites were located on glaciofluvial sand deposits including some gravel material. The dominant tree species in all sites was *Pinus sylvestris* – hence this species was excluded from the vegetation analyses. Some stands included *Betula pubescens* and *Picea abies*. The age of the pines varied between 80 and 200 yr. The growth parameters for *Pinus sylvestris* and climatological data are given in Table 1. The climatological data were calculated according to Ojansuu & Henttonen (1983), but their model does not extend to the Kola Peninsula or Norway.

Two types of vegetation data were used:

1. At 20 sites average cover values from 15 quadrats of 1 m² located regularly on the circumference of three circular plots (five per each) of 13.8 m diameter at 40 m distance from each other were analysed at each site (Tikkanen & Mikkola 1991). The sites in Finland have been grazed to a varying extent by reindeer; those in the Kola Peninsula (Russia) were ungrazed.

2. At four sites average cover values from 10 quadrats of 1 m² located on two parallel 10-m lines (five per each), 40–100 m from each other. At each site, two plots were located at each side of the fence. The reindeer fence was originally built in the end of the 1940s to prevent reindeer from crossing the border to Russia, and it was generally maintained in a good condition. In western Lapland the fence was built in the 1960s as lichen reserve for reindeer. Thus, we had exclosures

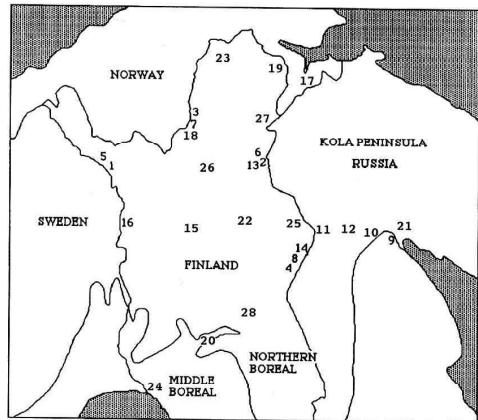


Fig. 1. Location of the study sites. 1 - 4 ungrazed and 5 - 8 grazed sites. 1, 5 = Muonio; 2, 6 = Raja-Jooseppi; 3, 7 = Angel; 4, 8 = Naruska; 9 = Pirenga; 10 = Upoloksa; 11 = Kovdor; 12 = Yena; 13 = Raja-Jooseppi; 14 = Sätsi; 15 = Aska; 16 = Muonio; 17 = Svanvik; 18 = Angel; 19 = Sevettijärvi; 20 = Tennilä; 21 = Imandra; 22 = Lokka; 23 = Kevo; 24 = Kemi; 25 = Ainiärvi; 26 = Rajala; 27 = Kessi; 28 = Kemijärvi. The border separating the middle and northern boreal zones is according to Hämet-Ahti et al. (1968).

available of 50 yr and 30 yr old, respectively. Field work was carried out in 1992 and 1993.

Plant cover was estimated using a percentage scale of <0.5% (transformed to 0.25 for computations), 0.5%, 1, 2, 3, 4, 5, 10, 15, 20, etc., with 5% intervals up to 100%. The four *Dicranum* species recorded, *D. brevifolium*, *D. drummondii*, *D. majus* and *D. scoparium*, were lumped. Unidentified *Cladonia* species also include *C. macrophylla*, *C. pleurota* and *C. pyxidata*. Different subspecies of *Cladonia gracilis* (Ahti 1980) were not distinguished. *Cladonia gracilis* coll., particularly on the northernmost sites, include some *C. maxima*, and *Cladina arbuscula* includes *C. mitis* – which is perhaps not a distinct species (Ruoss 1987). The vegetation data are presented in Table 2 in a 1 - 9 transformed scale (L. Oksanen 1976). This because Oksanen uses a 1-5 scale, i.s.o. of a 1-9 scale. Only those species occurring in more than four sites were included.

For the soil nutrient analyses 10 humus samples were collected from each plot in August-September 1991. The thickness of the humus layer was measured. Roots were separated by hand and the samples from each plot pooled. The humus layer was so thin at two of the sites (1 and 8) that no analysis was possible. Soil nutrients at one site (26) were not determined.

The pH of the soil samples was determined in 0.01 M CaCl₂ (1:2 by volume) with a glass electrode after shaking for 1 h and resting for 30 min. The contents of plant available nutrients were determined by extracting

Table 1. Mean climatological, *Pinus sylvestris* growth, and mean cover data for bryophytes, lichens and vascular plants at the study sites (Fig. 1). Climatological data were not estimated separately for the exclosures. S.E. = Standard error.

	\bar{x}	S.E.	range
Precipitation (mm/yr)	475	9	395 - 540
Mean annual temperature ($^{\circ}$ C)	-1.4	0.1	-2.1 - 0.8
Temperature sum ($^{\circ}$ C)	690	26	475 - 985
Number of stems (ha^{-1})	785	94	135 - 2200
Basal area ($m^2 ha^{-1}$)	13	1	4 - 22
Diameter at breast height (cm)	16	1	7 - 25
Height (m)	10	0.6	6 - 17
Volume ($m^3 ha^{-1}$)	85	8.6	21 - 191
Cover bryophytes (%)	50	6.3	1 - 100
Cover lichens (%)	23	5.1	1 - 80
Cover vascular plants (%)	23	2.5	3 - 60

5 g of fresh soil with 50 ml of 0.5 N ammonium acetate ($pH = 4.65$) for 1 hr. The extracts were filtered and the concentrations of P, K, Ca, Mg, S, Al, Fe, Mn, Zn, Mo, Cu and Ni determined in the soil laboratory of the Finnish Forest Research Institute using standard methods (Halonen et al. 1983). Cu and Ni concentrations were below the detection limit in most cases and were not included in the nutrient data. Total N was determined by the micro-Kjeldahl method with tube digestion (Kubin 1978). Organic matter content (OM) was determined as loss in weight on ignition at 485 $^{\circ}$ C for two hours. Total N concentration is expressed as mg/OM and exchangeable nutrients as μ g/g OM.

Data analysis

Data were ordinated with Non-Metric Multidimensional Scaling (NMDS; DECODA software of Minchin 1988). The method was selected because it has been found to be the best ordination method for detecting vegetation gradients (Minchin 1987).

The idea of NMDS is to find a representation of data in few dimensions so that distances in the ordination reflect the similarities between sample plots as closely as possible. The ordination finds the gradient structure in vegetation, if the similarity index between sample plots has a close relation to the separation of sample plots along gradients. Simulation studies by Faith et al. (1987) showed that the Bray-Curtis index with double standardization (first to unit maximum for each species, then to unit sample total) has the desired good rank order similarity with the gradient location. This index and standardization were therefore used.

NMDS is an iterative procedure, and convergence to a unique solution is not guaranteed. Therefore, the analysis was made with 10 random starting configurations. With two dimensions, the ordinations with lowest stress were practically identical, as assessed by Procrustean

Table 2. Floristic composition of the sites; sites 1-8 are in exclosures. Species cover scale: 1 = < 0.5%; 2 = 0.5 - 1.0%; 3 = 1 - 2%; 4 = 2 - 4%; 5 = 4 - 8%; 6 = 8 - 16%; 7 = 16 - 32%; 8 = 32 - 64%; 9 = > 64%.

	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2
	1524738639804621509623547178																		
<i>Cladonia amaurocraea</i>	11	--	11	---	-----														
<i>Polytrichum piliferum</i>	31	--	11	--	1	--	--	11	11	11	1	1	1	1	1	1	1	1	1
<i>Cetraria nivalis</i>	11	-	61	11	11	2	-	1	--	1	1	1	1	1	1	1	1	1	1
<i>ICmadophila ericetorum</i>	11	--	1	--	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Stereocaulon</i> sp.	16	-	22	12	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Diphastiastrum complanatum</i>	---	114	--	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cladina stellaris</i>	9297184669191187117111	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cladonia cervicornis</i> ¹	--	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cladina rangiferina</i>	6877877874463667665446454552																		
<i>Vaccinium uliginosum</i>	--	1633	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cladonia arborea</i>	171686787163754665556545231																		
<i>Cladonia</i> spp.	--	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cetraria ericetorum</i>	11	-	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cladonia coccifera</i>	11	-	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cladonia phyllophora</i>	---	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Calluna vulgaris</i>	--	14	12	17	3	14	5	1	42	1	65	--	1	1	1	1	1	1	1
<i>Cladonia fimbriata</i>	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
<i>Cladonia uncialis</i>	11	12	11	11	42	17	17	23	44	51	34	22	62	11	11	11	11	11	11
<i>Pinus sylvestris</i>	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
<i>Dicranum fuscescens</i>	-	11	11	12	32	41	7	16	71	11	63	17	84	6	-	11	12	13	14
<i>Cladonia deformis</i>	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
<i>Cladonia chlorophaea</i>	--	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Pohlia nutans</i>	--	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
<i>Cladonia crispata</i>	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
<i>Vaccinium vitis-idaea</i>	4463657657465566666567667765																		
<i>Empetrum nigrum</i>	2162546534365562156556537663																		
<i>Cladonia cornuta</i>	211111111111111111111111111113214111																		
<i>Polytrichum juniperinum</i>	-2111-11111111-11131-45111-1																		
<i>Cetraria islandica</i>	1--1---11-111111-1--1112-1																		
<i>Peltigera aphthosa</i>	---	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cladonia gracilis</i>	1111111111111111111111111111151111																		
<i>Nephroma arcticum</i>	---	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Dicranum</i> spp.	----	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Pleurozium schreberi</i>	-1231151556257578677784389																		
<i>Dicranum polysetum</i>	-1--1----1-1-1-11111-1-3-4-1																		
<i>Polytrichum commune</i>	-----1-----1---1-1-1-11111																		
<i>Cladonia botrytes</i>	-----1-----1-1-1-1-1-1-1-1																		
<i>Ptilidium ciliare</i>	--1-111111-1-21-1-13111611																		
<i>Betula pubescens</i>	-----1-----1-1-11111111																		
<i>Deschampsia flexuosa</i>	--11-----112-1-1141																		
<i>Ledum palustre</i>	-----1-----3---1441																		
<i>Vaccinium myrtillus</i>	-----11-14-1-445---5657																		
<i>Barbilophozia hatcheri</i>	-----1-----1-1--141-																		
<i>Hylocomium splendens</i>	-----3---1---56																		
'ssp. <i>verticillata</i>																			

analysis (Schönemann & Carroll 1970), and one of them was selected for further analysis. With three or four dimensions, the ordinations with the lowest stress fell into two or more different groups. Only two-dimensional solutions are discussed here.

Species scores corresponding to the NMDS ordination of sample plots were calculated by weighted averaging. Hence, the species ordination could be presented graphically with the sample plot ordination, in the same way as in Correspondence Analysis (ter Braak 1986).

In common vegetation science parlance, NMDS is an unconstrained method, i.e. it is based on site similarities only, and does not maximize correlations with environmental variables. The advantage of unconstrained

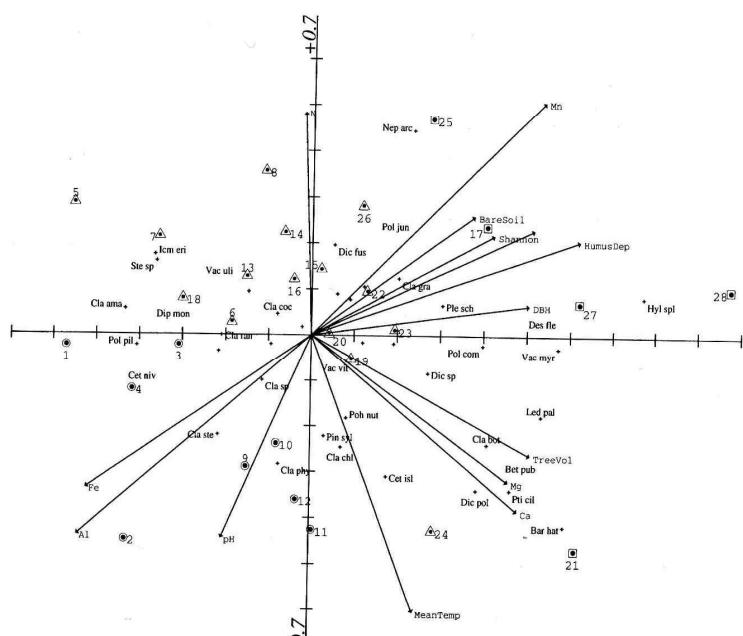


Fig. 2. Scores of the 28 study sites and species along NMDS ordination axes 1 and 2. Arabic numerals refer to the study sites given in Fig. 1. Species name abbreviations include the first three letters of the genus and species names given in Table 2. DBH = diameter of trees at breast height, SpecNum = number of species. Circles include ungrazed sites in the Kola Peninsula and exlosures, triangles include grazed sites and squares naturally bryophyte-rich sites.

analysis is that the ordination will not be dependent on the environmental variables that incidentally are used, and it is possible to detect vegetation gradients for which no environmental variables are available (Kantvilas & Minchin 1989). However, it is possible to assess the correlations between unconstrained ordination and environmental variables. It is not meaningful to compute correlations between ordination axes and environmental variables, since it is only the configuration which is reflected in NMDS, and the direction of an axis is arbitrary. Instead, the gradient direction must be found, by means of correlation analysis. The environmental variables are presented as arrows (Fig. 2). The direction of the arrow indicates the direction of the gradient, and the length the correlation. In this way, the interpretation is similar as in correspondence analysis (ter Braak 1986).

The significance of canonical correlations was assessed with the Monte Carlo technique (500 permutations). Only environmental variables with a significant correlation ($p < 0.05$) with the ordination configuration are shown in Fig. 2. Nearly significant variables Bare soil ($p = 0.056$), pH ($p = 0.051$), and N ($p = 0.054$) are also displayed.

Species diversity at each site was analyzed by the change in species diversity using the exponent of the Shannon index $\exp [H'] = -\sum p_i \ln p_i$.

Results

Ungrazed reindeer-lichen-dominated sites and bryophyte-rich sites are found at opposite ends in the NMDS ordination space, and extensively grazed sites in-between (Fig. 2). These ungrazed lichen-rich sites were characterized by certain *Cladina* and *Cladonia* species, by *Cetraria nivalis*, and by one bryophyte, *Polytrichum piliferum*. High Al and Fe-concentrations and pH characterize the same corner in the ordination space. Bryophyte-rich sites had abundant *Barbilophozia hatcheri*, *Hylocomium splendens* and *Pleurozium schreberi*, and also the dwarf shrubs *Ledum palustre* and *Vaccinium myrtillus*. High Mn concentration, species number, cover of bare ground and thick humus layer were correlated with low Al, Fe and pH. Most species were fairly indifferent as regards to habitat choice in these dry oligotrophic Scots pine forests, but the Shannon index ranged from 2.30 to 11.77, with an increase towards the moss-rich sites.

At grazed sites (5-8, 13-16, 18-20, 22-24, 26) the cover of lichens and bryophytes was ca. the same, with a total average of 64 %. The cover of dwarf shrubs was generally ca. 20%, but ca. 55 % at sites 17 and 21, where dwarf shrubs were dominant instead of bryophytes.

Floristically, the grazed sites were characterized by a low cover of *Cladina stellaris* (4 %) and a high cover of *C. arbuscula*, *Cladonia uncialis* (in total 36 %) and a relatively high cover of *Dicranum* spp. (7 %) compared to ungrazed sites (0.25 %). *Calluna vulgaris* was a characteristic dwarf shrub.

Exclosures

At the fenced ungrazed sites the dominant species was *C. stellaris* (63 % cover) and the total cover of lichens was 92 %. At the adjacent grazed sites the total cover of lichens was 75 %, and the cover of *C. stellaris* was only 4 %. The total cover of mosses was 1 % and 12 % in ungrazed and grazed sites, respectively. Comparisons of the cover values for the species at these sites are presented in Fig. 3. Amongst the mosses especially *Dicranum* spp. benefitted from grazing.

A comparison of the nutrient levels of the exclosures showed that grazed sites were characterized by elevated N-contents, but 30–60 % lower values for exchangeable nutrients (Table 3). However, only P showed a statistically significant difference ($p = 0.013$).

Discussion

Reindeer grazing increased the abundances of bryophytes, especially *Dicranum* spp. and *Pleurozium schreberi*. This was observed both in the ordination, and in a more compelling way when exclosures were compared with adjacent grazed areas. No signs of increased bryophyte abundance were evident at ungrazed sites, where especially reindeer lichens (*Cladina* spp.) spatially replace lichens of the 'first reindeer lichen stage' (Ahti 1959, 1977, mainly *Cladonia* spp.) and tiny bryophytes (such as *Barbilophozia* spp., *Pohlia nutans* and *Polytrichum* spp.). When reindeer lichens are devoured by reindeer, other species like *Dicranum* spp. are able to spread.

The effects of reindeer grazing have not directly been investigated in forest vegetation, but several authors have speculated on the effects of grazing in extant vegetation (Helle & Aspi 1982; Oksanen & Ahti 1982; Oksanen 1986; Ahti & Oksanen 1990). Most studies delimited the vegetation type by the dominance of lichens in the forest floor. Bryophyte-rich sites are easily excluded from the survey, or regarded as belonging to a different vegetation type than slightly grazed *Cladina*-rich vegetation. Consequently, when scientists assumed that they compared sites with different grazing pressure, they may have compared more xeric (assumed heavily grazed) with less xeric sites (assumed slightly grazed). Oksanen & Ahti (1982) and Oksanen (1984) assumed

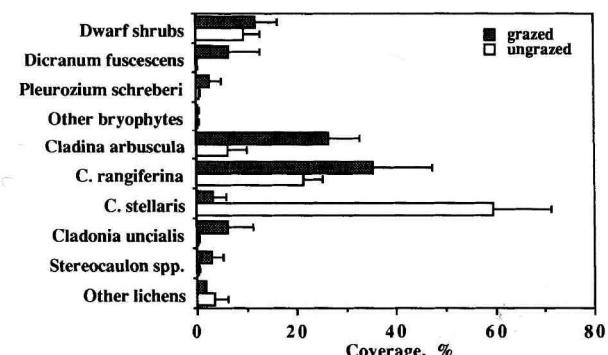


Fig. 3. The cover of species at exclosures showing differences between ungrazed (1-4) and grazed (5-8) sites.

that the estimated decrease in area of Finnish *Cladina* site type in Lapland in forestry surveys from 1922 to 1956, is due to the narrowing concept of the *Cladina* site type. However, our recent study indicates that the abundance of bryophytes may have increased due to increasing reindeer numbers (Alaruikka 1964; Kautto et al. 1986; Anon. 1993).

A high cover of bryophytes is regarded as an indicator of more productive forest sites (Cajander 1949; Carleton 1990; Nieppola & Carleton 1991), but despite possible increases in bryophyte abundances, there is hardly any corresponding change in forest productivity. This was obvious in the present study, as the pine tree volume did not depend on the species composition of the understorey vegetation. Classifying bryophyte-rich sites to more productive types reflects the belief that the vegetation is controlled by the abiotic environment only, disregarding any role of herbivory.

It has been assumed that in most parts of Finnish Lapland *Cladina stellaris* would be the dominant species in the absence of grazing (Ahti 1961, 1977; Oksanen & Ahti 1982; Oksanen 1986; Ahti & Oksanen 1990). Grazing changes the vegetation towards the so-called 'first reindeer lichen stage' naturally occurring 30–40 yr after fire (Ahti 1959, 1977) where *Cladina mitis* (included in *C. arbuscula* in this paper) would be the dominant species. When the grazing pressure increases, it is natural to assume that this would lead to an increase of crustose lichens (e.g. *Trapeliopsis granulosa*, *Placynthiella uliginosa*, *P. oligotropha*), minute cup lichens (*Cladonia* spp.) and ephemeral bryophytes (e.g. *Pohlia nutans*, *Polytrichum piliferum*, *Buxbaumia aphyllo*), resulting in a vegetation similar to early successional stages after fire (Sarvas 1937; Scotter 1964; Maikawa & Kershaw 1976; Nimis 1981; Foster 1985). This was assumed from field data by Oksanen & Ahti (1982). Our study indicates that this shift may only occur in most xeric sites, whereas in most sites grazing brings about an increased abundance of forest bryophytes (*Dicranum*

Table 3. Total nitrogen content mg g⁻¹ organic matter, plant available nutrients µg g⁻¹ organic matter, pH(CaCl₂) and thickness (cm) of the organic layer at the sites. - = not determined.

Sites	N	P	K	Ca	Mg	S	Elements						pH	humus
							Al	Fe	Mn	Zn	Mo	Na		
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	22	47	170	440	64	42	320	200	28	7	0	36	2.9	1.5
3	31	32	74	220	53	26	300	200	14	3	0.5	21	3.3	1.8
4	18	65	220	520	60	53	440	100	38	10	1.1	54	2.9	1.8
5	33	23	44	240	26	15	39	8	27	3	0.2	10	2.9	1.0
6	19	26	61	260	37	21	160	81	21	4	0.6	15	3.0	1.9
7	31	25	78	190	56	25	290	120	10	3	0.4	18	3.1	1.7
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	15	48	127	500	75	47	227	32	35	9	0.7	29	3.0	2.2
10	16	33	126	471	61	31	109	10	26	6	0.4	57	2.9	1.2
11	17	56	205	1170	126	36	254	96	25	8	0	131	3.6	1.1
12	14	63	215	710	102	49	168	32	47	9	0	37	3.2	2.2
13	28	41	310	540	120	60	330	110	62	9	0.5	28	2.8	2.2
14	22	38	150	510	75	37	92	5	29	9	0.5	34	2.7	2.7
15	13	39	170	360	71	35	88	39	52	6	0.3	40	2.8	2.2
16	24	31	140	390	45	27	74	10	24	5	0.3	54	2.8	2.0
17	23	44	171	599	140	37	19	6	66	7	0.2	42	2.7	2.7
18	20	42	140	520	90	32	39	41	58	5	0.3	35	2.7	2.2
19	23	41	170	690	150	41	100	18	44	9	0.4	42	2.7	3.8
20	26	62	200	740	86	49	120	24	95	10	0.6	56	2.9	2.5
21	21	27	104	485	74	22	36	6	28	5	0.2	16	2.8	2.5
22	27	37	170	740	95	34	21	3	76	7	0.3	35	2.8	2.8
23	24	55	180	780	130	40	24	3	50	7	0.3	61	2.7	3.0
24	20	68	210	970	210	58	140	35	32	17	0.8	84	3.0	2.0
25	23	51	150	650	65	30	12	2	120	8	0.2	32	2.9	2.6
26	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27	21	61	230	830	130	41	15	4	130	11	0.2	35	2.8	2.9
28	30	74	260	750	110	43	18	2	110	9	0.3	32	2.8	3.0

spp., *Pleurozium schreberi*). In Finland, these species traditionally regarded as indicators of more productive forest site types (Cajander 1949). Many authors assume that these bryophytes follow reindeer lichens in post-fire succession after ca. 150 yr (Hustich 1951; Loaman 1964a, b; Nimis 1981; Foster 1985), to the extent that these forests have been called '*Pleurozium* woodland' (Foster 1985). However, the latter type of woodland may be dependent rather on site factors (Mattila 1981; Carroll & Bliss 1982; Seponnen 1985; Tonteri et al. 1990; Nieppola & Carleton 1991) or geographical area and climate (Ahti & Oksanen 1990).

A new and somewhat surprising observation is that forest bryophytes could be favoured by reindeer grazing. This underlines the fact that one should be careful using the term retrogression in the context of succession.

Stereocaulon is known to characterize the initial stage of lichen stands or disturbances in the lichen carpet (Jalas 1950, 1953; Aartolahti 1973). In our study, *Stereocaulon* was abundant only at Muonio (site 5, grazed), NW Finland. This part of Finland is known for the occurrence of *Stereocaulon* in grazed sites (Oksanen & Ahti 1982; Seponnen 1985), but it seems to be fairly rare also here, as it is in Sweden (Skuncke 1969). In continental Canada *Stereocaulon* may replace *Cladina stellaris* in the succession of *Picea mariana* forests (Maikawa & Kershaw 1976; Kershaw 1977).

In some studies, lichens and bryophytes have been found to be useful indicator species of edaphic conditions (Cajander 1949; Carleton 1990). Most of the species occurring at the study sites were wide-ranging generalists that are well adapted to minor environmental changes in their habitats. These species may be particularly useful in the case of infertile lichen-rich sites with only a few, usually indifferent vascular plants. Lichens and bryophytes also enable comparisons between continents by means of lichen synusiae (Nimis 1981), since the similarity of lichen floras in widely separated areas is greater than that of the vascular floras (Kornaś 1972). Comparisons between sites may become biased, however, if successional stages are not recognized. Heavy grazing resulted in heterogeneous patchy occurrences of species. In our study there was a difference both in species abundance and in species composition. Various *Cladonia* species easily invade at sites in which the soil has been disrupted, in the present case by reindeer.

Grazing seemed to increase the pH and to decrease Al and Fe in the soil. This may be due to decrease in lichen substances like usnic acid after lichens have been grazed by reindeer. Organic acids are known to render both Al and Fe more soluble (Haug 1984). Mn reacted opposite to these elements and its concentration was highest at mossy sites. Low pH stimulates leaching of Mn (Kazda & Zvacek 1989). Grazed sites of the exclosures were characterized by elevated N content

and by decrease of other element concentrations when compared to ungrazed sites.

In conclusion, grazing of lichens by reindeer in oligotrophic *Pinus sylvestris* forests resulted in vegetation types bearing a resemblance to more mesotrophic sites characterized by a moss-rich habitat. These were heterogeneous types of a successional nature. Different types of disturbance, e.g. grazing, forest fire and logging, are likely to produce different successional stage gradients. By including exclosures (e.g. grazed and ungrazed) of otherwise similar adjacent study sites in the analyses, it is possible to evaluate the stages of vegetation succession and the relationships between them.

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