

Field Measurements of the Growth Rates of Forage Lichens, and the Implications of Grazing by Svalbard Reindeer

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Abstract

Mean relative growth rates of lichens on Brøggerhalvøya, Svalbard, (78°60' N, 12°0' E, Norwegian High Arctic) ranged from 2.4 (*Alectoria nigricans*) to 10.6 (*Cladonia rangiferina*) mg.g⁻¹ per week. This related to a seasonal increase of between 2.5% and 11.2% of original dry mass. The number of species and percentage cover of lichens were greater inside than outside three long-term reindeer exclosures, suggesting that through their indiscriminate trampling and selective grazing Svalbard reindeer have the ability to completely alter lichen community structure, in both the short and long term. The lichen communities are only likely to be able to re-establish if there is a significant reduction in the reindeer population for at least 20 years, such as could occur by a complete emigration of deer from the area. Reduced lichen forage availability has potentially serious implications for the reindeer population.

Keywords: Lichens, relative growth rates, grazing, Svalbard, reindeer

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1. Introduction

Cetraria nivalis, *C. islandica* and *C. delisei* were key components of the vegetation community of Brøggerhalvøya, a peninsula of north west Spitsbergen, and major winter forage species for non-migratory Svalbard reindeer (Staaland et al., 1993). However, the relative composition and extent of the formerly widespread lichen heath communities has changed since the introduction and subsequent exponential population expansion of reindeer. Reindeer are highly selective grazers (Mathiesen, 1999), and chose to eat lichens when available despite the low nutritional quality of this forage (see Longton, 1992, for a review). Preferential herbivory has removed *Cetraria nivalis*, *Cladonia uncialis*, and *Cladonia rangiferina*, followed by less discriminate grazing and trampling of the other species (Holand et al., 1981; Wegner et al., 1992; Ditlefsen, 2000).

Brøggerhalvøya has probably been reindeer-free since the beginning of the last century (Wollebæk, 1926; Lønø, 1959). In 1978 twelve Svalbard reindeer (*Rangifer tarandus platyrhynchus*) were successfully transferred from an established population near Longyearbyen. The numbers of deer on Brøggerhalvøya increased exponentially with an average annual growth rate of 25% over 15 years and then declined sharply from 360 to 80 animals in 1993/94, a winter with severe icing conditions (Aanes et al., 2000). The population has since increased to around 150 individuals in 2000 (R. Aanes, pers. com.), giving a present population density of around 1.6 animals/km².

Published data are unavailable both from this region of Svalbard and for much of the High Arctic on the annual net primary production of forage lichens, and their potential to recolonize following heavy grazing pressure and physical damage by trampling. Indeed, Crittenden (2000) underlined the pressing need for data on lichen growth rates for use in determining the carrying capacity of reindeer ranges.

It is hypothesized that the cover and composition of the lichen community has been affected by the changes observed in the reindeer population. This study aimed to: i) characterise the field growth rates of intact lichen thalli of a range of forage species measured throughout a summer growing season; ii) outline the changes in lichen composition and cover brought about by the introduction of reindeer; and iii) indicate the implications of the productivity of the lichen herbage for a High Arctic reindeer population.

2. Materials and Methods

Study area

Brøggerhalvøya is a peninsula on the north west of Spitsbergen (78°60'N,



Figure 1. Map of the study area showing position of enclosures.

12°0'E) with a total area of 221 km². It is isolated from the surrounding land areas by outlet glaciers terminating in the fjords to the north and south. The centre of the peninsula is comprised of mountains and glaciers, surrounded by a relatively flat coastal area (Fig. 1). Around 93 km² of the peninsula has a vegetation coverage of over 5%, although only about 28 km² has over 50% coverage (Øritsland et al., 1980; Brattbakk, 1986). The area has a mean June-August temperature of 2.5°C, and a mean summer daily precipitation of 1 mm (Norwegian Meteorological Institute).

Reindeer exclosures

Long-term reindeer exclosures (10 × 10 m, 2 m high) were established in 1978 prior to the release of reindeer onto Brøggerhalvøya (Øritsland, 1987). One exclosure was erected on each of three vegetation types; moderate snowbed, exposed ridge, and a ridge underneath a bird cliff (see Fig. 1 for positions of exclosures). The exclosures were placed to represent the vegetation types locally (L.B. Jacobsen, pers. com.). Extensive surveys in Brøggerhalvøya (E.J. Cooper, unpublished data) in 1999 and 2000 suggest that the vegetation types around the exclosures are also representative for the majority of vegetated areas on Brøggerhalvøya.

Lichen growth rate

Intact lichen thalli were needed for the experiment; however, none were found on an original search of Brøggerhalvøya. Therefore thalli were collected from within the exclosure at the base of the bird cliff, Steinflåstupet (number 1 in Fig. 1) from an area of 1 × 1 m designated by the Norwegian Polar Institute for all future destructive sampling. The thalli were cleaned of moss and small stones, dried to constant mass in a desiccator at room temperature for approximately 36 hours, and weighed to an accuracy of ±0.1 mg, before being rehydrated and set in clear perforated plastic pots (40 mm diameter) with moss. A thin net, of mesh size 10 mm was fastened over the pots to prevent the samples from blowing away, but allowing light and rain water to enter. The lichens were protected from reindeer grazing throughout the growing period, but otherwise experienced the natural climatic conditions of the area.

The growth rates of seven replicates of each of six different lichen species were calculated from the difference in dry mass of the thalli in the 10 weeks growing season between snow melt in late June and snow fall in early September 1999. Thalli with a reduction in mass during the summer were not used in subsequent calculations. The species studied were: *Cetraria nivalis* (L.) Ach., *Cetraria islandica* (L.) Ach., *Cetraria delisei* (Bory) Th. Fr., *Cladonia uncialis* (L.) Wigg., *Cladonia rangiferina* (L.) Wigg., *Alectoria nigricans* (Ach.) Nyl. (nomenclature follows Thomson (1984)).

Relative growth rate (RGR) was calculated as $(\ln W_2 - \ln W_1) / (t_2 - t_1)$ where W_1 and W_2 are initial mass and final mass respectively; t_1 is initial time (i.e. zero) and t_2 is the time of the final harvest. In this case, $(t_2 - t_1) = 10$ weeks.

Impact of reindeer grazing and trampling

In summer 1999, 12 quadrats, of size 50 × 50 cm were placed at random, within

each enclosure (leaving a 1 m boundary along the inside edge where no measurements were taken), and also in an adjacent area that had always been available for grazing. The composition and percentage cover of lichens were measured and compared inside and outside the enclosures. The area designated for destructive sampling in enclosure 1 was not used for the subsequent measurements of percentage cover of lichens.

Statistical analysis

The proportion of quadrats and the percentage cover were not normally distributed so the following specific methods were used for their analyses (see Herzberg et al., 2000, for an example). The analysis of percent cover of each taxon was performed in two steps: 1) an analysis of the proportion of quadrats with the species present, and 2) the analysis of the percentage cover given that the species is present. The analysis of proportions was done using logistic regression (Agresti, 1990), with the number of quadrats where the species was present as the response variable, and enclosure, species and location (in vs. out) as predictor variables. We investigated interactions between each factor. We also aimed at assessing differences and similarities between species by defining groups of species, and models based on different species grouping were compared. The goodness of fit of a model was assessed using the Pearson Chi-square (sum of squared Pearson residuals of the model). A model with a Pearson Chi-square or residual deviance less than 2 times the number of degrees of freedom was taken as satisfactory (Lindsey, 1999). Model selection was done using the Akaike's Information Criterion (AIC), defined as $-2 * \log\text{-likelihood} + 2 * \text{number of parameters of the model}$ (Akaike, 1973; Burnham and Anderson, 1998). The AIC aims at finding the best model in the sense of a compromise between bias and variance of the parameter estimates (too simple models result in biased estimates, and too complicated models result in large sampling variances). The model(s) with the lowest AIC was used for further inference. We used parameter estimates to investigate relative effects on the different groups. The analysis of percentage cover (number of quadrats with different covers: 0–5%, 6–20%, 21–40%, 41–60%, 61–80% and 81–100%) was based on log-linear models (Agresti, 1990). As for the analysis of proportions, the goodness-of-fit of the models was assessed using the residual deviance and the Pearson Chi-square, and model selection was based on AIC.

The different quadrats measured are unlikely to represent independent observations as they are spatially close. Such positive spatial autocorrelation should result in a poor goodness of fit, i.e., a residual deviance or Pearson Chi-square larger than expected under the hypothesis of independence, a phenomenon called over-dispersion (Burnham and Anderson, 1998). The absence

Table 1. Relative growth rate (RGR) of field-grown lichens in the Ny Ålesund area, Brøggerhalvøya, Svalbard.

Species	Mean RGR (SE) mg.g ⁻¹ per week	Mass increase in 10 weeks as a percentage of original mass (SE)
<i>Cetraria nivalis</i>	5.97 (0.78)	6.2 (0.8)
<i>Cetraria islandica</i>	6.03 (1.33)	6.3 (1.4)
<i>Cetraria delisei</i>	6.01 (0.90)	6.2 (1.0)
<i>Cladonia rangiferina</i>	10.58 (0.80)	11.2 (0.9)
<i>Cladonia uncialis</i>	4.74 (0.43)	4.9 (0.4)
<i>Alectoria nigricans</i>	2.43 (0.90)	2.5 (0.9)

Table 2. The number of quadrats (maximum twelve) recording each lichen species within and outside of each of three exclosures on Brøggerhalvøya, Svalbard. Exclosure 1 was on a ridge underneath a bird cliff; exclosure 2 was on an exposed ridge and exclosure 3 was in a moderate snowbed (see Fig. 1 for locations).

Species	Exclosure 1		Exclosure 2		Exclosure 3		Total
	in	out	in	out	in	out	
<i>Alectoria nigricans</i>	5	-	-	-	-	-	5
<i>Cetraria cuculata</i>	6	-	-	-	-	-	6
<i>Cladonia uncialis</i>	11	-	-	-	-	-	11
<i>Cladonia rangiferina</i>	12	8	-	-	-	-	20
<i>Cetraria nivalis</i>	12	2	1	-	-	-	15
<i>Cetraria islandica</i>	12	2	10	4	3	7	38
<i>Cetraria delisei</i>	4	1	12	10	12	12	51
<i>Stereocaulon</i> sp.	-	5	12	10	5	10	42
Number of species	7	5	4	3	3	3	

of large over-dispersion in most models used in the paper indicates that there is no strong spatial autocorrelation between quadrats, and therefore there is not a severe problem for the statistical analyses.

3. Results

Lichen growth rate

Mean relative growth rate ranged from 2.4 (*A. nigricans*) to 10.6

(*C. rangiferina*) mg.g^{-1} per week (Table 1). This relates to a growing season increase of between 2.5% and 11.2% of original dry mass.

Impact of reindeer grazing and trampling

Table 2 shows the presence of each lichen species, given by number of quadrats (out of a total of 12) inside and outside each enclosure. There was a greater number of species inside enclosure 1 and 2 than outside, but no difference for enclosure 3. Enclosure 1 had the greatest number of species present, and the greatest difference in cover between inside and outside. The differences in community composition between the enclosures can be explained by the placement of the enclosures in different vegetation types. The percentage cover of any particular species in the quadrats was grouped into categories with different covers: 0–5%, 6–20%, 21–40%, 41–60%, 61–80% and 81–100%. There were no quadrats with any species occupying greater than 81% cover. The number of quadrats in the various categories for the most common lichen species encountered are shown in Fig. 2. There was a lower percentage cover outside the enclosures compared to inside for all species except *Stereocaulon* sp.

Analysis of proportions

We first investigated which interactions were needed between the factors 'species', 'enclosure' and 'location'. The best model was a model including the three-order interaction: enclosure, species and location (see Table 3). Such a model is difficult to use as it means that differences between the two locations (inside and outside) differed both between species and enclosures. The model without the third-order interaction was about as adequate judging from the AIC values. This model means that species did not occur in the same proportion in the different enclosures, and that species differed in the proportions with respect to location, and that the differences between the two locations varied between enclosures. Pooling the species in two groups (instead of having only species specific parameters) for the difference inside-outside resulted in a model with a similar fit to the data. The groups contained the following species: group 1. *Cetraria nivalis*, *C. cuculata*, *C. islandica*, *C. delisei*, *Cladonia uncialis*, *C. rangiferina*, *Alectoria nigricans*, group 2. *Stereocaulon* sp.

These two models were barely satisfactory with respect to their goodness of fit (without pooling: residual deviance 29.08 on 14 d.f.; with pooling 41.55 on 20 d.f.). Parameter estimates for the difference 'in vs. out' showed that proportions were much lower in the outer part for the fruticose lichens in group 1 (-5.29 ; S.E. = 0.91548; $t = -5.78$, $P < 0.0001$), but that this difference was lower for *Stereocaulon* sp. (-3.30 , S.E. = 0.97).

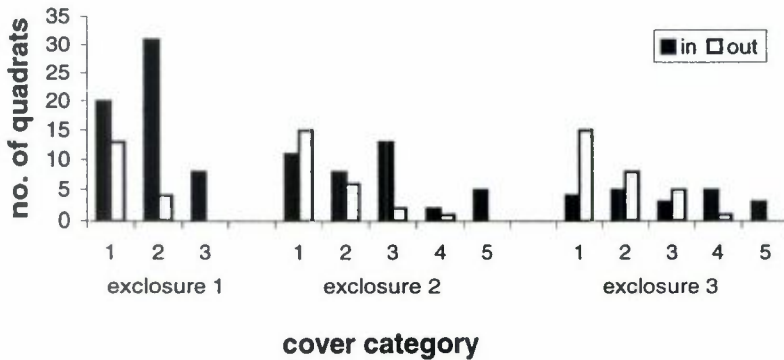


Figure 2. The number of quadrats in different categories of cover of *Cetraria nivalis*, *Cetraria cuculata*, *Cetraria islandica*, *Cetraria delisei*, *Cladonia uncialis*, *Cladonia rangiferina*, *Alectoria nigricans*, and *Stereocaulon* sp. species inside and outside of each of the long-term reindeer exclosures. The categories 1–5 represent a cover of 0–5%, 6–20%, 21–40%, 41–60% and 61–80%, respectively.

Analysis of percentage cover

The best model in terms of AIC was a model including the main effects of 'species' and 'exclosure', and the interaction between 'location' and 'group' (Table 4). This model means that species did not occur with the same cover, and that groups differed in cover with respect to location. Pooling the species in two groups (instead of having only species specific parameters) for the difference inside-outside resulted in a model with a better fit to the data. Parameter estimates showed as for the proportions a much larger effect on cover for the fruticose lichens of group 1 than for *Stereocaulon* sp.

4. Discussion

Lichen growth rate

The growth rates presented here for High Arctic lichens are in the same range – for similar rainfall – as the rates found by Kärenlampi (1971) in the classic study on lichen growth rates in Subarctic Finland. However, the annual growth was lower on Svalbard as the rainfall was lower and the growing season shorter than in the Finnish system.

The growth rate of *Cladonia rangiferina* was much higher than that of the other species studied. Kärenlampi (1971) also found that this species grew faster than *Cetraria nivalis*, and attributed the difference to either differences

Table 3. Akaike's Information Criterion for the different statistical models used to analyse the variability in proportions. The best models are indicated in bold.

Model	AIC
Species + exclosure	369.62
Species + exclosure + location	341.35
Species * exclosure + location	120.04
Species * exclosure + group * location	109.34
Species * exclosure + species * location	101.37
Species * exclosure + exclosure * location + group * location	97.55
Species * exclosure + exclosure * location + species * location	97.08
Species * exclosure * location	96.00

Table 4. Akaike's Information Criterion for the different statistical models used to analyse the variability in cover. The best model is indicated in bold. Only the interactions with cover are described (see text for explanations).

Model	AIC
No effect	281.76
Species + exclosure + location	191.18
Species * exclosure + location	213.31
Species + exclosure + group * location	189.60
Species + exclosure + species * location	208.85
Species + exclosure + exclosure * location	192.70
Species + exclosure + exclosure * location + group * location	192.76
Species + exclosure + exclosure * location + species * location	215.14

in morphology or physiology. *Alectoria nigricans* had the lowest growth rate in this study. It is one of several species that are damaged by grazing (Elvebakk and Hertel, 1996; Wegner et al., 1992), and its slower growth hampers subsequent re-establishment. The lichens studied here gained 2.5–11.2% of their original mass in a 10 weeks growing season; it is therefore estimated that it would take between 9 and 40 years (depending on the species) to re-grow.

The length of time needed for lichen to recover after damage depends on the severity of grazing or trampling. Very light grazing tends to thin out individuals (Gaare, 1986), and may stimulate regrowth, but heavier grazing, such that the top part of the lichen thallus is removed, decreases growth

substantially, greatly increasing the length of time required for recovery (Ahti, 1959). The extent of the damage to the lichen cover on Brøggerhalvøya is so great that many years without grazing or trampling by reindeer would be needed to allow a restoration of lichen cover to the former level.

Impact of reindeer grazing and trampling

In 1978 one enclosure was set up in each of the vegetation types; this experimental design may be criticised due to pseudoreplication. However, within the historically imposed limitations, the data shown here are very clear: there are significantly fewer species and percentage ground cover of lichen outside than inside the enclosures. Outside, there was limited coverage of the less preferred *C. delisei*, and hardly any other lichen species were represented. Only a few small, broken and unattached pieces of *C. islandica* and *C. nivalis* were found. Very few rotten basal parts of thalli were seen, suggesting that most of the lichens had been removed some time ago.

Data presented here for 'outside the enclosures' are representative of Brøggerhalvøya in general as revealed by searching a total of 1080 50 × 50 cm quadrats for the presence of lichen (E.J. Cooper, unpublished data). This contrasts markedly with a nearby peninsula, Sarsøyra, on which no reindeer have been recorded before 1994. A study carried out in 1999 revealed that lichen species diversity, and thallus and patch size were much greater on this peninsula than on the overgrazed Brøggerhalvøya (E.J. Cooper, unpublished data).

The area inside the enclosures is representative of vegetation present on Brøggerhalvøya before the reindeer introduction, or of that which can grow in the absence of deer. The differences between enclosed and open plots in the number of species and percentage cover of lichen are therefore assumed to be due to the presence of reindeer. Reindeer graze selectively, but may cause much damage to lichen mats by trampling (Ahti, 1959; Crittenden, 2000). Even though lichens have the ability to regrow from a broken thallus, their growth is slower than that of intact thalli (Cooper et al., 2001) and they are vulnerable to being wind disturbed.

Implications for reindeer population

Introduced ungulate populations have been shown to follow a pattern of irruption with subsequent decline (Caughley, 1970; Leader-Williams, 1988). Reindeer population declines have often been associated with depletion of lichens that were important winter herbage (Klein, 1968). Whether the

population dies out completely, or eventually builds up again depends on the resilience of the vegetation to grazing (Leader-Williams, 1988). However, lichens grow extremely slowly, and are thus vulnerable to being completely overgrazed if they are an important part of the reindeer's diet. Lindsay (1973) noted that reindeer had already overgrazed the macrolichens from dry meadows and fellfield communities of South Georgia within 12 years of their introduction. He suggested that the ultimate result of such an introduction would be the loss of *Cladonia rangiferina* and *Cetraria islandica* from vegetation communities accessible for grazing, with survival only in isolated inaccessible locations. Reindeer densities at the time (0.7 to 1.1 animals km⁻²) were comparable to those on Brøggerhalvøya.

Studies on the food intake of Svalbard reindeer gave values for their average daily intake of 0.98, 2.30 and 1.94 kg dry mass/day during winter (January–March), summer (August) and autumn (September), respectively (Nilssen, 1986). The deer were young (1.5 years old, 49–56 kg) fenced-in, and provided with an excess of food. From this an estimate of 537.7 kg of food is required annually. A study by Staaland (1986) of rumen contents of Svalbard reindeer in the summer gives an estimate of a daily summer intake for an 80 kg animal of 3.5 kg and yearly intake of 650 kg.

Microhistological analysis of reindeer faeces from Brøggerhalvøya gives a value for lichen of 20% of the total plant fragments in summer and 40% in winter (Holand et al., 1981). These faecal samples were collected in 1979 and 1980 when there were still plenty of lichens in the area and so can be assumed to be from reindeer with free choice of forage species. This possibly under-represents the total amount of lichen in the diet, because lichens are easily digested (Mathiesen, 1999). If, however, we use these values, we obtain a conservative estimate of 170 kg of lichens consumed annually by each deer.

Measurements taken in 1979 (Brattbakk, 1986) give a rough estimate of standing crop of lichens on Brøggerhalvøya of 13991 kg. This is enough lichen for 82 deer-years. If there were no change in forage selected, it would be expected that the total standing crop of lichens would have been eaten by 1984, based on a record of reindeer numbers. Only a change in forage species, especially during winter, would allow the continued population growth recorded on Brøggerhalvøya. A shift in grazing preference to different vegetation types, and in composition of plant fragments in faeces had already been noted in 1988 (Scheie and Grøndal, 1990).

Since 1994, reindeer have been observed on Sarsøyra, a peninsula to the south of Brøggerhalvøya. It is assumed that they migrated over the sea ice or glaciers in search of food, as there is significantly more lichens on Sarsøyra (E.J. Cooper, unpublished data), and the area now supports about 100 reindeer (R. Aanes, pers. com).

Possible causes of error

There are several possible causes of error in the lichen growth measurements. First, the physical environment in the plastic pots was unnatural and may have affected growth. Enclosure in these pots may have affected temperature or humidity when compared to lichen growing on the ground surface. Second, contact with the soil was removed so there was no possibility of mineral nutrition from the base (Barashkova, 1963), although the nutrients from rainwater were accessible. Kärenlampi (1971), however, found no difference in photosynthetic capacity in *Cladonia alpestris* after one year's growth in plastic boxes. The errors thus incurred are likely to be minimal. Third, drying the lichens inside at room temperature may have resulted in a small loss of mass due to increased respiration. However, this was an inevitable consequence of the method and applied to all lichen species equally.

5. Conclusion

Mean relative growth rates of lichens on Brøggerhalvøya ranged from 2.4 (*Alectoria nigricans*) to 10.6 (*Cladonia rangiferina*) mg.g^{-1} per week, relating to a seasonal increase of between 2.5% and 11.2% of original dry mass. The number of lichen species and percentage cover of lichens were greater inside than outside three long-term reindeer exclosures on Brøggerhalvøya. This suggests that through their indiscriminate trampling and selective grazing, Svalbard reindeer have the ability to alter lichen community structure, in both the short and long term. The lichen communities are only likely to be able to re-establish if there is a significant reduction in the reindeer population for at least 20 years, such as could occur by a complete emigration of deer from Brøggerhalvøya.

The lichen productivity and distribution throughout Brøggerhalvøya is not great enough to support the present population of deer during winter. Reduced lichen forage availability could potentially induce a population crash due to starvation, or force the deer to either: change their dependency on lichens as an important contributor of winter forage, or; to migrate to areas of greater lichen availability. Indications exist that some of these processes may have already occurred in this area.

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REFERENCES

- Aanes, R., Sæther, B-E., and Øritsland, N.A. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography* **23**: 437–443.
- Agresti, A. 1990. *Categorical Data Analysis*. Wiley and Sons, New York.
- Ahti, T. 1959. Studies on the caribou lichen stands of Newfoundland. *Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo'* **30**: 1–44.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: *Second International Symposium on Information Theory*. B.N. Petrov and F. Csaki, eds. Akademiai Kiado, Budapest, pp. 267–281.
- Barashkova, E.A. 1963. Nutrition of *Cladonia rangiferina* (L.) Web. through the dead part of the podetium. *Botaniceskij Zurnal* **48**: 588–591.
- Brattbakk, I. 1986. Flora og vegetasjon. In: *Svalbardreinen og dens livsgrunnlag*. N.A. Øritsland, ed. Universitetsforlaget, Oslo. pp. 15–34.
- Burnham, K.P. and Anderson, D.R. 1998. *Model Selection and Inference. A Practical Information Theoretic Approach*. Springer-Verlag, New York.
- Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* **51**: 53–72.
- Cooper, E.J., Smith, F.M., and Wookey, P.A. 2001. Increased rainfall ameliorates the negative effect of trampling on the growth of High Arctic forage lichens. *Symbiosis* **31**: 153–171.
- Crittenden, P.D. 2000. Aspects of the ecology of mat-forming lichens. *Rangifer* **20**: 127–139.
- Ditlefsen, A.M. 2000. *Reinbeite på Brøggerhalvøya, Svalbard- en oppfølgende beiteøkologisk undersøkelse III*. Hovedoppgave ved Institutt for biologi og naturforvaltning, Norges Landbruks Høgskole, Ås. 57 pp.
- Elvebakk, A. and Hertel, H. 1996. A catalogue of Svalbard plants, fungi, algae and cyanobacteria. Part 6. Lichens. In: *A Catalogue of Svalbard Plants, Fungi, Algae and Cyanobacteria*. A. Elvebakk and P. Prestrud, eds. Norsk Polarinstitut, Oslo. pp. 271–359.
- Gaare, E. 1986. Does grazing influence growth of the reindeer lichen *Cladina mitis*? *Rangifer*, special issue, **1**: 357–358.
- Hertzberg, K., Yoccoz, N.G., Ims, R.A., and Leinaas, H.P. 2000. The effects of spatial habitat configuration on recruitment, growth and population structure in Arctic Collembola. *Oecologia* **124**: 381–390.
- Holand, Ø., Leifseth, A.B., and Persen, E. 1981. *Nyetablering av rein på Brøggerhalvøya-Svalbard. En beiteøkologisk undersøkelse*. Hovedoppgave ved Institutt for biologi og naturforvaltning, Norges Landbruks Høgskole, Ås 196 pp.

- Kärenlampi, L. 1971. Studies on the relative growth rate of some fruticose lichens. *Reports from the Kevo Subarctic Research Station* 7: 33–39.
- Leader-Williams, N. 1988. *Reindeer on South Georgia: The Ecology of an Introduced Population*. Cambridge University Press, Cambridge.
- Lindsay, D.C. 1973. Effects of reindeer on plant communities in the Royal Bay area of South Georgia. *British Antarctic Survey Bulletin* 35: 101–109.
- Lindsey, J.K. 1999. On the use of corrections for overdispersion. *Applied Statistics* 48: 553–561.
- Longton, R.E. 1992. Role of bryophytes and lichens in terrestrial ecosystems. In: *Bryophytes and Lichens in a Changing Environment*. J.W. Bates and A.M. Farmer, eds. Clarendon Press, Oxford. pp. 32–76.
- Lønø, O. 1959. Reinen på Svalbard. *Flora* 12: 40–70.
- Klein, D.R. 1968. The introduction, increase and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management* 44: 640–657.
- Mathiesen, S.D. 1999. Comparative aspects of digestion in reindeer. Ph.D. Thesis, Department of Arctic Biology and Institute of Medical Biology, University of Tromsø, Norway.
- Nilssen, K. 1986. Svalbardsreinenens energetikk. In: *Svalbardreinen og dens livsgrunnlag*. N.A. Øritsland, ed. Universitetsforlaget Oslo, pp. 92–102.
- Scheie, J.O. and Grøndal, F.A. 1990. *Reinen på Brøggerhalvøya. En oppfølgende beiteøkologiske undersøkelse*. Hovedoppgave ved Institutt for Biologi og Naturforvaltning, Norges Landbruks Høgskole, Ås. 54 pp.
- Staaland, H. 1986. Svalbardreinenens ernæring. In: *Svalbardreinen og den livsgrunnlag*. N.A. Øritsland, ed. Universitetsforlaget AS, Oslo, pp. 72–91.
- Staaland, H., Scheie, J.O., Grøndahl, F.A., Persen, E., Leifseth, A.B., and Holand, Ø. 1993. The introduction of reindeer to Brøggerhalvøya, Svalbard: grazing preference and effect on vegetation. *Rangifer* 13: 15–19.
- Thomson, J.W. 1984. *American Arctic Lichens. 1. The Macrolichens*. Columbia University Press, New York.
- Wegner, C., Hansen, M., and Jacobsen, L.B. 1992. Effekter av reinbeite ved Kongsfjoden, Svalbard. *Norsk Polarinstitutt Meddeler* 121: 31–41.
- Wollebæk, A. 1926. The Spitsbergen reindeer (*Rangifer tarandus Spetsbergensis*). In: *Resultater av de norske understøttede Spitsbergensekspeditioner I*: 1–71. Det Norske Vitenskapsakademi, Oslo.
- Øritsland, N.A., Ødegaard, H., Frøyland, E., and Brattbakk, I. 1980. Use of satellite data and the IBM-ERMAN system in mapping of reindeer grazing range on Svalbard. In: *Proceedings of the 2nd International Reindeer/Caribou Symposium Røros, Norway, 1979*. E. Reimers, E. Gaare, and S. Skjenneberg, eds. Direktoratet for vilt og ferskvannsfisk. pp. 174–177.
- Øritsland, N.A. 1987. *Norsk Polarinstitutt Årbok, 1986*. Oslo, pp. 38–40.