

Growth, population density and population structure of *Cetraria nivalis* during 240 years of primary colonization

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Abstract: The growth of the alpine lichen *Cetraria nivalis* was followed in a chronosequence of 240 years of primary colonization in a glacier foreland in the Jotunheimen mountain range and National Park in Norway. The largest thallus of *C. nivalis* was 96 mm in diameter. It was found in the area that had been exposed for a maximum of 240 years. If this individual thallus became established at about the time the habitat was exposed, its average annual diameter increase has been 0.4 mm per year. The growth curve of *C. nivalis* does however exhibit a pattern of fast growth in the first years followed by a decrease in growth rate. In contrast the population density of *C. nivalis* increases through time in a linear manner, from 0.4 thalli/m² in the areas recently exposed to 10.5 thalli/m² in the sites exposed for maximum of 240 years. This suggests a fairly stable flow of propagules over the landscape through the years. The size distribution (population structure) of thalli within the foreland is skewed, with many small individuals and few big ones.

Key words: *Flavocetraria nivalis*, lichen growth, population density, reindeer lichens

Introduction

The yellow-white lichen heaths of dry alpine habitats in the Northern Hemisphere form a distinct feature in the colour mosaic of the landscape. The prominence of these patches in the landscape has led to their delimitation as a distinct plant community or association, the *Cetrarietum nivalis* (Samuelsson 1917; DuRietz 1925; Dahl 1956). In Norway the dominant lichen species of these habitats is the bright yellow *Cetraria nivalis*. Contributing to the light colour are also the lichens *Cetraria cucullata*, *Alectoria ochroleuca* and species of *Stereocaulon* and *Cladonia*. Growing predominantly on barren, wind-exposed ridges with little snow-cover they form an important part of the food available for reindeer during winter (Scott & Rouse 1995; Svihus & Holand 2000; Ferguson *et al.* 2001; den Herder *et al.* 2003). Their exposed location in the landscape and easy absorption of water also make them emi-

nently suitable for environmental monitoring of air pollution (Crete *et al.* 1992; Strandberg 1997; Mols *et al.* 2000; Riget *et al.* 2000; Kelly & Gobas 2001), as well as for studies of the effects of radiation and climate (Schipperges *et al.* 1995; Bjerke *et al.* 2005a, b). The yellow lichens are also used as an indicator of snow-patterns in the planning of roads, railway lines and cottage building sites in alpine landscapes.

A general impression is that lichens in alpine habitats grow slowly (Beschel 1957, 1963). But exactly how slowly? With current scenarios of climate change predicting substantial modification in alpine vegetation and the extent of glaciers, knowledge of the relevant time scale or rate of ecological processes in these areas acquires added significance (Beniston 1994; Chapin *et al.* 1994; Reynolds & Tenhunen 1996). Most data on lichen growth in alpine habitats have been provided by quaternary geologists and physical geographers using lichenometry to date recently glaciated substrata or rock falls by estimating growth rates of certain crustose lichen species (e.g. Beschel 1957; Haines-Young 1983; Innes 1985a;

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Bickerton & Matthews 1993; McCarthy & Smith 1995; McCarroll *et al.* 1998). Questions of lichen biology have not been their primary concern. Yet we know that basic life-history parameters such as growth rate are major determinants of the potential for a species to colonize, re-colonize and persist in a habitat (Grime & Hunt 1975; Walker *et al.* 1986; Huston & Smith 1987; Stearns 1992). The temporal scale of the dynamics in alpine habitats may, however, easily exceed the average research grant, research career or even human life-span, and this poses a challenge to any study of lichen life-histories. One way to circumvent these limitations has been to study lichens in a series of habitats where the approximate times of exposure are known, relating thallus size and development to substratum age (Beschel 1950, 1957, 1961, 1963). Glacier forelands provide a natural laboratory for such studies (Pickett 1989; Matthews 1992).

The aim of the present study was to provide knowledge of the thallus growth, population growth and population structure of *Cetraria nivalis*. The growth of this lichen has previously been studied for short periods in terms of biomass and herbivory (fungivory) (den Herder *et al.* 2003). We here present the results of a long-term study of population growth and structure.

Material and Methods

The study was conducted in the foreland of the Hellstugubreen glacier in the Jotunheimen National Park, southern Norway, 61°35'N, 8°26'E. Jotunheimen is a remnant of the mountain range created by large tectonic overthrusts of Precambrian crusts and sediments during the Caledonian orogeny (Milnes & Koestler 1985). The bedrock in the study area consists of highly metamorphic rocks such as pyroxen-granulite, pyroxen-gneisses and ultramafic rocks. The quaternary geology of Jotunheimen is summarized by Holmsen (1982). The Hellstugubreen glacier is situated in a distinctly U-shaped valley and connects to a larger complex of glaciers associated with the alpine peak systems of Hellstugutindane and Memurutindane. The glacier front is presently at 1465 m altitude, and the lowermost parts of the foreland at 1418 m. The foreland forms an elongate area along the valley in front of the glacier. The maximum extension of the foreland is c. 1100 m.

During the so-called 'Little Ice Age' Norwegian glaciers advanced considerably, reaching a maximum in

c. 1740–1750 AD (Hoel & Werenskiold 1962). Since then the glaciers have 'retreated', occasionally interrupted by minor advances. The geologist P. A. Øyen in 1901 marked the front of Hellstugubreen, and the dynamics and retreat of the glacier have subsequently been studied in detail by Liestøl (1962), the Norwegian Polar Research Institute and the Norwegian Water and Electricity Council (Norsk Polarinstitutt 1962, 1969; Norges Vassdrags- og elektrisitetsvesen 1965; Norges Vassdrags- og elektrisitetsvesen og Norsk Polarinstitutt 1980). The outermost moraine in the foreland is assumed to have been deposited c. 1740–1750. For the 150 years up to 1901 there are no detailed recordings of the retreat of the glacier, but a comparison of the area exposed up to 1901 with that exposed during the 20th Century indicates that glacier retreat up to 1901 was rather slow. In the 20th Century a slightly exponential (close to linear) increase in the areas exposed per year has occurred. The grazing pressure in the Hellstugubreen area is negligible. There is no wild stock of reindeer in Jotunheimen, only a small domestic herd kept in the eastern parts of the National Park, outside our research area.

Cetraria nivalis (L.) Ach. is one of the most common fruticose lichens in alpine areas of the Northern Hemisphere. The lichen grows on silt, sand, clay and pebbly ground characteristic of dry ridges. The rather loose attachment of the lichen to its substratum causes it to form small, circular and dome-shaped mats to prevent it being blown off. In late and fairly undisturbed stages of vegetation development, the individual mats join into a more or less continuous cover of the habitat (this latter stage was not reached in the 240 year chronosequence studied here). Only rarely does the species produce apothecia with sexually generated ascospores (none observed in the present study). Instead, the lichen disperses by fragmentation. When dry it is brittle, and if stepped on will be crushed into many small fragments. Fragments of *C. nivalis* are among the most common lichens found in snow drifts in the Scandinavian mountains (DuRietz 1931). For the purpose of this study, the term 'thallus' is used to describe all 'individuals' (or clones) of *C. nivalis* ranging from single lobes to discrete mats comprised of many lobes which probably have arisen from a single propagule.

The field work was carried out in the summer from July to September 1994. Only the eastern half of the foreland was studied due to steepness and danger of rock falls in the western part. Eleven linear transects were laid out radially from a large boulder marked "NP88" in red paint, lying mid-front of the glacier (Fig. 1). The boulder was marked by the Norwegian Polar Research Institute in 1988 indicating the ice front, which has since retreated a few more metres. At every fifth metre along the transects a sample plot of 0.5 × 0.5 m (0.25 m²) was examined. Altogether 1396 quadrats were recorded.

All individual thalli of *C. nivalis* present in the plots were counted, and their maximum diameter measured non-destructively with a clear plastic ruler to the nearest mm. Altogether 1302 individual thalli were examined.

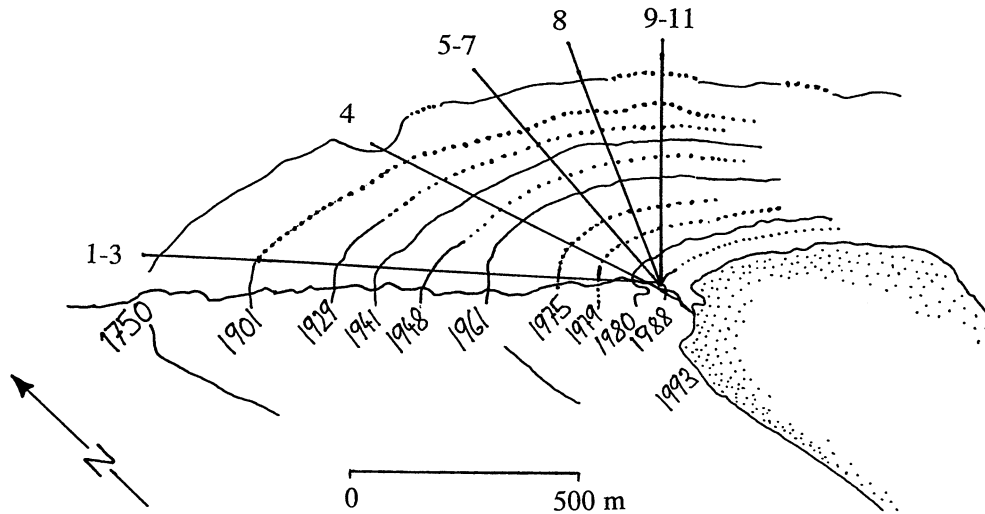


FIG. 1. The eastern part of the Hellstugubreen glacier foreland with dated moraines and sampling transects 1–11. Dotted lines indicate less prominent ridges.

A new site exposed by the melting ice of the glacier is thereafter continuously exposed to new colonization. For this reason the chronosequence approach based on the biggest individual thallus in each dated area can only be reliably used to estimate the *maximum* growth of the lichens. In the present study we present plots of the mean of the five biggest thalli. This measure is commonly used in lichenometrical studies because the size of a single thallus may sometimes reflect an exceptionally favourable habitat, for example a bird-manured boulder (cf. Innes 1985a).

Results

Growth

The largest thallus of *C. nivalis* was 96 mm in diameter. It was found in the area that had been exposed for a maximum of 240 years. If this thallus became established at about the time the habitat was exposed, its average annual increase in diameter was 0.4 mm per year. The growth curve of *C. nivalis* does however exhibit an apparently distinct pattern of fast growth in the first years followed by a decrease in growth rate (Fig. 2).

Population density

Small thalli of *C. nivalis* are already present in the most recently exposed parts of

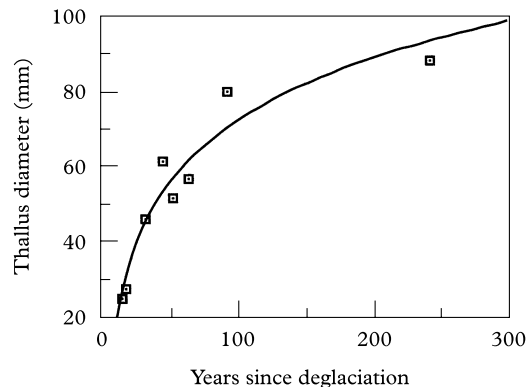


FIG. 2. Growth curve for *Cetraria nivalis*, generated by fitting a logarithmic growth model to observations of the average of the five largest thalli in a given time interval ($r^2=0.929$, $P<0.001$ for the fitted line).

the glacier foreland, indicating very effective dispersal and colonization ability. There was a steady, linear increase in density through the 240 years of population development (Fig. 3).

Population structure

The size structure of *C. nivalis* within the foreland was skewed, with many small thalli and only few larger ones (Fig. 4).

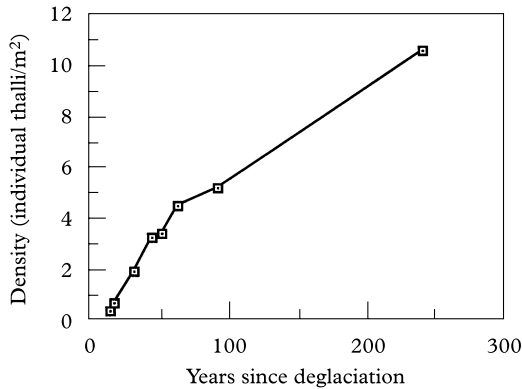


FIG. 3. The increase in density of *Cetraria nivalis* during 240 years of primary colonization.

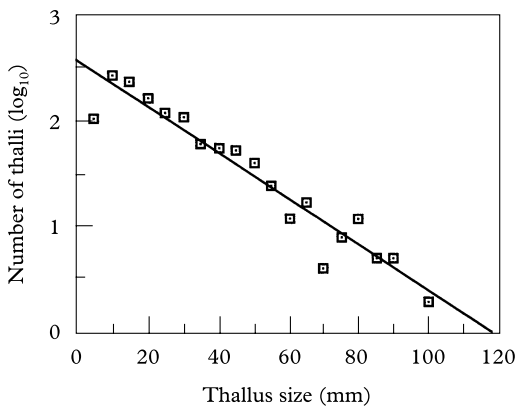


FIG. 4. The population structure (size distribution of thalli) of *Cetraria nivalis* in the Hellstugubreen glacier foreland ($r^2=0.91$, $P<0.001$, for the fitted line).

Discussion

The growth curve of *C. nivalis* is similar to that of several other lichens, with growth progressively slowing down as size increases. Beschel (1958) suggested a general four-phase partition of lichen growth into (a) a juvenile phase with slow growth, (b) a “great period” during which the thallus grows exponentially at a maximum rate, (c) a mature phase where growth becomes linear and approaching a maximum size, and (d) a period of senescence where the thallus stops growing and disintegrates (see also Armstrong 1974, 1976; Hill 2002; Clayden *et al.* 2004). One cause of the slowing growth

in *C. nivalis* may be the change in morphology with size. Larger thalli (>50 mm diameter) of *C. nivalis* are often beautifully dome-shaped, a growth form which in alpine plants is variously interpreted as an adaptation to wind resistance and water retention (Spomer 1964).

The growth curves are based on the five largest thalli in each time interval and should thus be considered maximum rates for the species under the given environmental circumstances. It is important to note also that particular curves of growth observed cannot be interpreted as *the* definite growth pattern of a species. The expression of life history traits may to a substantial degree be environmentally determined, and the same species may thus perform differently under other environmental conditions (Beschel 1957, Innes 1985b). The fruticose growth form of *C. nivalis* implies that the thallus also grows in the vertical dimension, and that the horizontal diameter measure is a good estimate of habitat cover but a less precise indication of biomass. The relationship between horizontal diameter and biomass remains to be studied, and can unfortunately only be studied destructively, by removing thalli and measuring their dry weight. It should be noted, however, that in no case did the height of *C. nivalis* in the foreland exceed *c.* 60 mm.

The almost linear change in population density through the chronosequence indicates that the propagule supply and deposition are fairly constant through time, and also that each thallus does indeed derive from a single fragment. A few of the big thalli may be aggregated but in general their dome-shaped growth form suggests an origin from a single fragment. The effect of possible local recruitment from established thalli within the foreland appears to be negligible in the temporal scale studied here. It is notable that within the 240 year chronosequence the cover of *C. nivalis* did not reach the stage of large mats of continuous cover, sometimes several square meters wide, commonly observed on ‘mature’ dry lichen heaths.

Compared with other lichen species in the same habitat, the population growth of

C. nivalis is moderate, reaching a total of 1302 thalli in the 1396 quadrants examined. The population of *Umbilicaria cylindrica* in the same set of sample squares was in contrast 64700 thalli (Hestmark et al. 2004b), while those of *Allantoparmelia alpicola* and *Melanelia stygia* were 65 thalli and 481 thalli respectively (Hestmark et al. 2004a).

Lichen populations exhibit size-structures ranging from strongly skewed to the almost perfectly 'normal' (Gaussian) distribution (Hestmark 1992; Ramstad & Hestmark 2001; Hestmark et al. 2004b). Skewed size-structures of the kind observed for the total population of *C. nivalis* have received different interpretations. Available models predict that the size-structure of populations will change over time, reflecting notably intraspecific competition (review by Hara 1988). The standard prediction is that the skew will increase, towards a population with many small and a few big dominant individuals. However, the scattered occurrence of *C. nivalis* individuals suggests that intraspecific competition is not a significant factor in creating the skewed pattern. Skew may instead indicate the presence of different cohorts of recruitment, with the smallest thalli being the last to colonize. If the 'propagule rain' is indeed fairly constant as suggested by the linear growth in density, new small thalli must become established constantly. As the glacier melts, the available area for such new recruitments steadily increases, and this may explain why the distribution of thallus sizes is not linear but exponential. Size differences may also reflect local differences in the availability of nutrients for growth (cf. Hestmark 2000). There was no indication that large thalli exhibited signs of senescence or decay. Similar problems have been encountered in the interpretation of size-structures in lichenometry (Innes 1985a, 1986) but also in vascular plants invading glacier forelands (Whittaker 1993).

REFERENCES

- Armstrong, R. A. (1974) Growth phases in the life of a lichen thallus. *New Phytologist* **73**: 913–918.
- Armstrong, R. A. (1976) Studies on the growth rates of lichens. In *Lichenology: Progress and Problems* (D. H. Brown, D. L. Hawksworth and R. H. Bailey, eds): 309–322. New York: Academic Press.
- Beniston, M. (ed.) (1994) *Mountain Environments in Changing Climates*. London: Routledge.
- Beschel, R. (1950) Flechten als Altersmasstab Rezenter Moränen. *Zeitschrift für Gletscherkunde und Glacialgeologie* (Neue Folge), **1**: 152–161.
- Beschel, R. (1957) Lichenometrie im Gletschervorfeld. In *Jahrbuch 1957 des Vereins zum Schutze der Alpenpflanzen und -Tiere*. 1–22. München.
- Beschel, R. (1958) Flechtenvereine der Städte, Stadtflechten und ihr Wachstum. *Berichte der Naturwiss.-Medizin. Vereins Innsbruck* **52**: 1–157.
- Beschel, R. (1961) Dating rock surfaces by lichen growth and its application to glaciology and physiography (lichenometry). In *Geology of the Arctic*. Vol. 2. (G. O. Raasch, ed.): 1044–1062. Toronto: University of Toronto Press.
- Beschel, R. (1963) Observations on the time factor in interactions of permafrost and vegetation. In *Proceedings of the 1st Canadian Conference on Permafrost* (J. E. Brown, ed.). 43–56. Ottawa: NRCC.
- Bickerton, R. W. & Matthews, J. A. (1993) "Little Ice Age" variation of outlet glaciers from Jostedal-breen ice-cap, southern Norway: a regional lichenometric-dating study of ice-material moraine sequences and their climatic significance. *Journal of Quaternary Science* **8**: 45–66.
- Bjerke, J. W., Elvebakk, A. & Dominguez, B. (2005a) Seasonal trends in usnic acid concentration of Arctic, alpine and Patagonian populations of the lichen *Flavocetraria nivalis*. *Phytochemistry* **66**: 337–344.
- Bjerke, J. W., Gwynn-Jones, D. & Callaghan, T. V. (2005b) Effects of enhanced UV-radiation in the field on the concentration of phenolics and chlorophyll fluorescence in two boreal and arctic-alpine lichens. *Environmental and Experimental Botany* **53**: 139–149.
- Chapin, F. S., Walker, L. R., Fastie, C. L. & Sharman, L. C. (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* **64**: 149–175.
- Clayden, S. R., Pentecost, A. & Dawson, R. J. M. (2004) Growth of the lichen *Rhizocarpon lecanorinum*, with comments on Aplin-Hill and lichenometric curves. *Symbiosis* **37**: 379–393.
- Crete, M., Lefebvre, M. A. & Zikovsky, L. (1992) Cadmium, lead, mercury and Cesium-137 in fruticose lichens in Northern Quebec. *Science of the Total Environment* **121**: 217–230.
- Dahl, E. (1956) Rondane Mountain Vegetation in South Norway and its Relation to the Environment. *Det Norske Videnskaps-Akademi, Skrifter. I. Matematisk-Naturvidenskapelig Klasse 1956*. **3**: 1–374.
- DuRietz, G. E. (1925) Zur Kenntnis der flechtenreichen Zwergstrauchheiden im kontinentalen Südnorwegen. *Svenska växtsociologiska Sällskapets Handlingar* **8**: 1–60.
- DuRietz, G. E. (1931) Studier över vinddriften på snöfält i de skandinaviska fjällen. Ett bidrag till de

- nordiska fjäll-lavarnas spridningsbiologi. *Botaniska Notiser* (1931): 31–44.
- Den Herder, M., Kytoviita, M. E. D. & Niemala, P. (2003) Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. *Ecography* **26**: 3–12.
- Ferguson, M. A. D., Gauthier, L., & Messier, F. (2001) Range shift and winter foraging ecology of a population of Arctic tundra caribou. *Canadian Journal of Zoology* **79**: 746–758.
- Grime, J. P. & Hunt, R. (1975) Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology* **63**: 393–422.
- Haines-Young, R. H. (1983) Size variation of *Rhizocarpon* on moraine slopes in southern Norway. *Arctic and Alpine Research* **15**: 295–305.
- Hara, T. (1988) Dynamics of size structure in plant populations. *Trends in Ecology and Evolution* **3**: 129–133.
- Hestmark, G. (1992) Sex, size, competition and escape—strategies of reproduction and dispersal in *Lasallia pustulata*. *Oecologia* **92**: 305–312.
- Hestmark, G. (2000) The ecophysiology of lichen population ecology. *Bibliotheca Lichenologica* **75**: 397–403.
- Hestmark, G., Skogedal, O. & Skullerud, Ø. (2004a) Growth in the alpine saxicolous lichens *Allan-toparmelia alpicola* and *Melanelia stygia*. *Nova Hedwigia* **78**: 301–309.
- Hestmark, G., Skogedal, O., & Skullerud, Ø. (2004b) Growth, reproduction and population structure in four alpine lichens during 240 years of primary colonization. *Canadian Journal of Botany* **82**: 1365–1362.
- Hill, D. J. (2002) Measurement of lichen growth. In *Protocols in Lichenology: Culturing, Biochemistry, Ecophysiology and Use in Biomonitoring* (I. Kranner, R. P. Beckett & A. K. Varma, eds): 255–278. Berlin: Springer.
- Hoel, A. & Werenskiold, W. (1962) Glaciers and snowfields of Norway. *Norsk Polarinstittutt Skrifter* **114**. Oslo, Norway.
- Holmsen, P. (1982) Jotunheimen. Beskrivelse til kvar-tærgeologisk oversiktskart m 1: 250.000 (med fargetrykt kart). *Norges Geologiske Undersøkelse, Skrifter* **374**: 1–47.
- Huston, M., & Smith, T. (1987) Plant succession: life history and competition. *American Naturalist* **130**: 168–198.
- Innes, J. L. (1985a) Lichenometry. *Progress in Physical Geography* **9**: 187–254.
- Innes, J. L. (1985b) Moisture availability and lichen growth: The effects of the snow cover and streams on lichenometric measurements. *Arctic and Alpine Research* **17**: 417–424.
- Innes, J. L. (1986) The size-frequency distributions of the lichens *Sporastatia testudinea* and *Rhizocarpon alpicola* through time at Storbreen, south-west Norway. *Journal of Biogeography* **13**: 283–291.
- Kelly, B. C. & Gobas, F. A. P. C. (2001) Bioaccumulation of persistent organic pollutants in lichen-caribou-wolf food chains of Canada's Central and Western Arctic. *Environmental Science and Technology* **35**: 325–334.
- Liestøl, O. (1962) Special investigations on Hellstugubreen and Tverrabreen. *Norsk Polarinstittutt, Skrifter* **114**: 175–207.
- Matthews, J. A. (1974) Families of lichenometric dating curves from Storbreen gletschervorfeld, Jotunheimen, Norway. *Norsk geografisk Tidsskrift* **28**: 215–235.
- Matthews, J. A. (1992) *The Ecology of Recently-deglaciated Terrain*. Cambridge: Cambridge University Press.
- McCarroll, D., Shakesby, R. A. & Matthews, J. A. (1998) Spatial and temporal patterns of Late Holocene rockfall activity on a Norwegian talus slope: a lichenometric and simulation-modelling approach. *Arctic and Alpine Research* **30**: 51–60.
- McCarthy, D. P. & Smith, D. J. (1995) Growth curves for calcium-tolerant lichens in the Canadian Rocky Mountains. *Arctic and Alpine Research* **27**: 290–297.
- Milnes, A. G. & Koestler, A. G. (1985) Geological structure of Jotunheimen, southern Norway (Sognefjell-Valdres cross-section). In *The Caledonide orogen – Scandinavia and Related Areas* (D. G. Gee and B. A. Sturt, eds.): 457–474. Chichester: John Wiley.
- Mols, T., Paal, J. & Fremstad, E. (2000) Response of Norwegian alpine communities to nitrogen. *Nordic Journal of Botany* **20**: 705–712.
- Nesje, A. & Dahl, S. O. (2000) *Glaciers and Environmental Change*. London: Arnold.
- Norges Vassdrags- og Elektrisitetsvesen (1965) Hellstugubreen. 1: 10000, ekvidist. 10 m.
- Norges Vassdrags- og Elektrisitetsvesen og Norsk Polarinstittutt (1980) Hellstugubreen. 1: 10000, ekvidist. 10 m.
- Norsk Polarinstittutt (1962) Hellstugubreen. 1: 10 000, ekvidist. 10 m.
- Norsk Polarinstittutt (1969) Hellstugubreen. 1: 10 000, ekvidist. 10 m.
- Pickett, S. A. (1989) Space-for-time substitution as an alternative to long-term studies. In *Long-term Studies in Ecology. Approaches and Alternatives* (G. E. Likens, ed.): 110–135. New York: Springer.
- Ramstad, S. & Hestmark, G. (2001) Population structure and size-dependent reproductive effort in *Umbilicaria spodochroa*. *Mycologia* **89**: 453–458.
- Reynolds, J. F. & Tenhunen, J. D. (eds) (1996) *Landscape Function and Disturbance in Arctic Tundra*. (Ecological Studies **120**) Berlin: Springer.
- Riget, F., Asmund, G. & Aastrup, P. (2000) The use of lichen (*Cetraria nivalis*) and moss (*Rhacomitrium lanuginosum*) as monitors for atmospheric deposition in Greenland. *Science of the Total Environment* **245**: 137–148.
- Samuelsson, G. (1917) Studien über die Vegetation der Hochgebirgsgegenden von Dalarne. *Nova acta regiae Soc. Scientiarum Upsaliensis*. Ser IV. 4 (8): 1–252.

- Schipperges, B., Kappen, L. & Sonesson, M. (1995) Intraspecific variations of morphology and physiology of temperate to arctic populations of *Cetraria nivalis*. *Lichenologist* **27**: 517–529.
- Scott, P. A. & Rouse, W. R. (1995) Impacts of increased winter snow cover on upland tundra vegetation—a case example. *Climate Research* **5**: 25–30.
- Spomer, G. G. (1964) Physiological ecology studies of alpine cushion plants. *Physiologia Plantarum* **17**: 717–724.
- Stearns, S. C. (1992) *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Strandberg, M. (1997) Distribution of Cs-137 in a low arctic ecosystem in West Greenland. *Arctic* **50**: 216–223.
- Svihus, B. & Holand, O. (2000) Lichen polysaccharides and their relation to reindeer/caribou nutrition. *Journal of Range Management* **53**: 642–648.
- Walker, L. R., Zasada, J. C. & Chapin, F. S. (1986) The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* **67**: 1243–1253.
- Whittaker, R. J. (1993) Plant population patterns in a glacier foreland succession: pioneer herbs and later-colonizing shrubs. *Ecography* **16**: 117–136.

Accepted for publication 28 May 2005