The Tenth Arctic Ungulate Conference,
9–13 August, 1999, Tromsø, Norway.

Aspects of the ecology of mat-forming lichens

P. D. Crittenden

School of Biological Sciences, University of Nottingham, Nottingham NG7 2RD, UK
(Peter.Crittenden@nottingham.ac.uk).

Abstract: Lichen species in the genera *Cladonia* (subgenus *Cladina*), *Cetraria, Stereocaulon* and *Alectoria* are important vegetation components on well-drained terrain and on elevated micro-sites in peatlands in boreal-Arctic regions. These lichens often form closed mats, the component thalli in which grow vertically upwards at rhe apices and die off in the older basal regions; they are therefore only loosely attached to the underlying soil. This growth habit is relatively unusual in lichens being found in <0.5% of known species. It might facilitate internal nutrienr recycling and higher growth rates and, together with the production of allelochemicals, it might underlie the considerable ecological success of mar-forming lichens; experiments to critically assess the importance of these processes are required. Mat-forming lichens can constitute in excess of 60% of the winter food intake of caribou and reindeer. Accordingly there is a pressing need for data on lichen growth rates, measured as mass incremenr, in order to help determine the carrying capacity of winter ranges for rhese herbivores and to better predict recovery rates following grazing. Trampling during the snow-free season fragments lichen thalli; mat-forming lichens regenerate very successfully from thallus fragments provided trampling does nor re-occur. Frequent recurrence of trampling creates disturbed habitats from which lichens will rapidly become eliminated consistent with J.P. Grime's CSR strategy theory. Such damage to lichen ground cover has occurred where reindeer or caribou are unable to migrate away from their winter range such as on small islands or where political boundaries have been fenced; it can also occur on summer range that contains a significant lichen component and on winter range where numbers of migrarory animals become excessive. Species of *Stereocaulon,* and other genera that contain cyanobacteria (most notably *Peltigera* and *Nephroma*), are among the principal agents of nitrogen fixation in boreal-arcric regions. *Stereocaulon*-dominated subarctic woodlands provide excellent model systems in which to investigate the role of lichens in nitrogen cycling. Mat-forming lichens are sensitive indicators of atmospheric deposition partly because they occur in open situations in which they intercept precipitation and particulates directly with minimal modification by vascular plant overstoreys. Data from both the UK and northern Russia are presented to illustrate geographical relationships between lichen chemistry and atmospheric deposition of nitrogen and acidity. The ecology of mat-fotming lichens remains under-researched and good opportunities exist for making significant contributions to this field including areas that relate directly to the management of arctic ungulates.

Key words: acid rain, allelopathy, grazing, growth, lichens, nitrogen fixation, recycling, trampling.

Rangifer, 20 (2–3): 127–139

Introduction

That lichens are eaten by reindeer and caribou is one of the better known facts about lichens amongst lay people of mid latitudes. It is also quite widely understood that lichens are symbiotic organisms and not plants in the strict sense. Although they are primary producers, and frequently have dimensions of small vascular plants, they are in fact composed of fungi deriving nutrition (carbon and sometimes nitrogen) from unicellular or filamentous algae and/or cyanobacteria in mutualistic symbiotic associations. Accordingly, it is strictly inappropriate to refer to lichens as organisms but for the sake of brevity it is often convenient to do so. Lichen-forming fungi constitute about one fifth of the fungal kingdom (Hawksworth *et al.,* 1995) and there is evidence that lichens represent an ancient association that was present amongst terrestrial crust communities during the early to mid Paleozoic Era (Shear, 1991; Taylor *et al.,* 1995). Yet because of

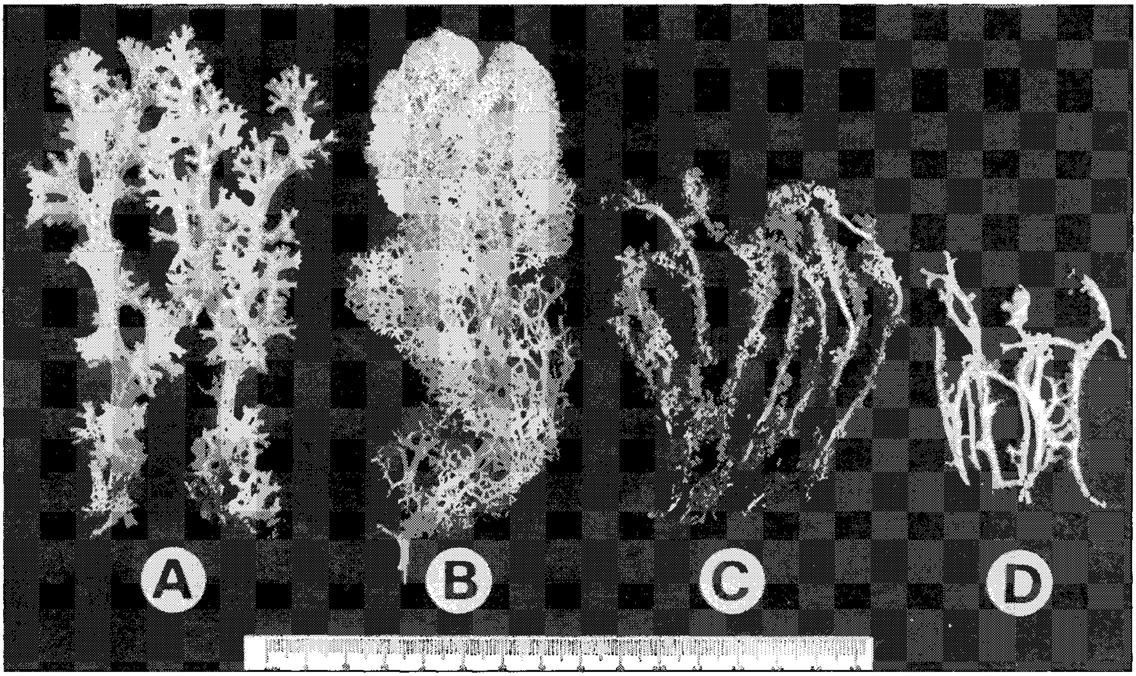

Fig. 1. Examples of mat-forming lichens. a) *Cladia retipora* (Australasia), b) *Cladonia stellaris,* c) *Stereocaulon paschale* and d) *Cetraria cucullata* (boreal-arctic zone). *Cladia retipora* occurs in coastal and alpine heathlands in Australasia. *Cladonia stellaris* is the supreme example of a mat-forming lichen and possibly one of the world's most abundant fungi; species that are morphologically similar to *C. stellaris* occur in the Southern Hemisphete e.g. *C. pycnoclada, C. leptoclada* and *C. confusa,* which locally form extensive ground cover.

their minor economic importance the biology of lichens remains poorly understood in comparison to the other principal types of terrestrial mutualistic "plant" symbioses (i.e. mycorrhizas and legumes/ actinorrhizas).

Lichens grow on substrata that are deficient in nitrogen and phosphorus, and that are subject to frequent episodes of acute drought. Such substrata are relatively abundant in boreal-arctic regions. In particular, the poorly developed to skeletal soils typical of high latitudes frequently support lichen-rich ground cover. According to Larson (1987) lichen-dominated vegetation covers approximately 8% of the world's terrestrial surface and much of this is in the Subarctic and Arctic. However, factors that control the development of lichen-dominated terrain remain incompletely understood. Such vegetation appears to be largely restricted to well-drained surfaces, including elevated microsites in peat bogs (Kershaw, 1977; Foster & Glaser, 1986; Ahti & Oksanen, 1990); these are sites in which vascular plant vigour is reduced due to low soil fertility and/or that are at an early successional stage following fire. Precipitation does not appear to determine the frequency of lichen-dominated terrain; for example, lichen woodland is abundant in both north-central Canada (*c.* 300 mm annual precipitation) and Labrador (*c.* 800 mm) although the relative importance of particular lichen species may differ (Kershaw, 1977). The most ecologically successful terricolous lichens are mat-forming species of the genera *Cladonia* (subgenus *Cladina*), *Cetraria, Stereocaulon,* and *Alectoria* (Fig. 1). Certain key species in these genera can form extensive ground cover in subarctic lichen woodland, forest tundra and tundra heathlands. They form the principal component of lichen intake by reindeer and caribou on their winter ranges (e.g. Miller, 1976; Holleman & Luick, 1977; Boertje, 1990), although epiphytic species are also important in the diet of some populations (e.g. Rominger *et al.,* 1994). This review focuses on aspects of the ecology of mat-forming lichens.

The mat-forming habit

Mat-forming lichens grow acropetally (i.e. at their apices) and vertically upwards while in mature mats the thallus bases die off. Thus the upper living parts of the mats are often supported physically by a deep layer of dead, structurally intact, thallus or necromass. This growth habit is relatively unusual in lichens being found in <0.5% of the 13 500 known species; the vast majority of lichens are firmly attached to their substrata. Precipitation and dry deposition of dust particles and gases are believed to be the primary sources of N and P for lichen growth. Thus in deep mats, zones of depletion develop in the lower strata due to interception of light and nutrients by the surface layers. Several authors have discussed the horizontal stratification of microclimate and thallus morphology that occurs within lichen mats (Carstairs & Oechel, 1978; Lechowicz, 1983; Pakarinen, 1985; Sveinbjörnsson, 1987; Coxson & Lancaster, 1989; Crittenden, 1991). Thallus below the light compensation depth (i.e. the depth at which photosynthetic CO_2 assimilation equals respiratory loss of CO_2) represents a respiratory burden and is therefore expendable. In the northern hemisphere, *Cladonia stellaris* is the supreme example of a mat-forming lichen.

Lichens, being essentially fungal mycelia, are poikilohydric, i.e. their water status is coupled to that of the atmosphere. Under the influence of evaporative forces lichens lose water becoming dry and largely metabolically inactive. A widely held view is that lichens are C-limited because photosynthetic activity is restricted to intermittent periods of adequate water availability. However, there is evidence that the more productive mat-forming lichens are N and/or P limited (Crittenden *et al.*, 1994). Several of the above authors have suggested that N and P in senescing basal parts of lichen thalli might be remobilized and translocated to the growing apices. Such internal recycling would be ecologically advantageous because it would permit a higher growth rate at the apices than could be sustained by new atmospheric supplies alone. This, in turn, would result in a higher rate of necromass production and deeper mats with the capacity to cast deep shade. In vascular plant ecology the development of a tall closed canopy is a mechanism by which some plant species exclude potential competitors and exert dominance (Grime, 1979). The capacity to recycle nutrients, which would be dependent on the loss of attachment between living thallus and the substratum, might underlie the ecological success of mat-forming lichens.

There is conflicting information on the occurrence of viable seed banks beneath lichen ground cover. Johnson (1975) failed to find germinable seeds in spruce-lichen woodland soils in the Northwest Territories in Canada whereas I have found abundant viable seeds beneath mats of *Cladonia stellaris* and *Stereocaulon paschale* in Finnmarksvidda in Norway. It is probable that seeds that descend to the bottom of mats will suffer light-deprivation sufficient to inhibit either germination or seedling growth (Kershaw, 1977) while Allen (1929) described seedlings in lichen mats being uprooted or damaged by the expansion of dry mats upon rehydration. Thus vascular plant species reproducing by small seeds may be excluded from well-developed lichen mats. However, studies in Sweden (Steijlen *et al.,* 1995; Zackrisson *et al.*, 1995) have shown that *Cladonia*-dominated ground cover in coniferous forests is a more favourable environment for the establishment and survival of spruce and pine seedlings than vegetation dominated by either *Empetrum hermaphroditum* or *Pleurozium schreberi.* Germination of pine and spruce seeds is not completely suppressed by light deprivation (Sarvas, 1950) and it is possible that a larger seed size might sustain the growth of pine and spruce seedlings through the lichen canopy into the 'photic' zone. However, Cowles (1982) found the centres of deep lichen cushions to be formidable barriers to the establishment of spruce in lichen woodland in northern Quebec whereas, in contrast, polygonal cracks that form in desiccated mats were favourable sites for establishment.

Allelopathic activity

Lichens produce a diverse range of secondary chemical products, many of them phenolic derivatives, and most being unique to lichens (Fahselt, 1994). Such products probably have several functions in the lichen thallus. Since many have antimicrobial properties, and/or are effective in deterring potential herbivores, it seems reasonable to suggest that one of their functions is chemical defence of the thallus (Lawrey, 1986, 1989). The yellow compound usnic acid is one of the more potent lichen products in terms of antimicrobial activity and is produced commercially as a pharmaceutical (Vartia, 1973); it occurs in a large number of lichen genera and is a typical compound for the subgenus *Cladina*; for example, it contributes about 2% of the dry mass of *C. stellaris* (Huovinen & Ahti, 1986). Although most lichen secondary products are only sparingly soluble in water, it has been suggested that trace quantities released into the soil from healthy thalli during rainfall, and from decomposing thalli, might inhibit the growth of neighboring vascular plants. Species of *Cladonia* (subgenus *Cladina*) have been reported to retard growth and mycorrhizal development in boreal forest trees (Brown & Mikola, 1974; Fisher, 1979). This is an attractive idea because such allelopathic effects provide yet another mechanism by which a plant can reduce the growth rate of its neighbours and exert dominance. However, despite a sizeable literature on this topic (reviewed by Lawrey, 1984; 1986) the importance of allelopathy in the ecological success of mat-forming lichens still remains to be critically assessed.

There are several potential pitfalls in experiments designed to test for allelopathic interactions between plants (Harper, 1975; Qasem & Hill, 1989). One of these is that quantities of metabolites to which test plants are exposed can greatly exceed those occurring in nature so that reported toxic effects can be exaggerated, if not entirely a product of the experimental conditions. Thus lichen extracts prepared using organic solvents (e.g. Goldner *et al.*, 1986) or by homogenizing thalli in water (e.g. Brown & Mikola, 1974; Kaitera *et al.*, 1996) may contain ecologically improbable concentrations of metabolites. Cowles (1982) conducted a field experiment in northern Quebec, that has been frequently cited in the literature, to investigate the effects of lichens on the growth of spruce. He removed lichen ground cover from plots in lichen woodland and found that this had a negative effect on the growth of black spruce as indicated by a reduction in the rate of branch elongation. This negative effect might have resulted from enhanced evapotranspiration since it could be counteracted by covering lichen-free plots with polyethylene sheet. Cowles also investigated the potential role of lichen allelopathy by soaking lichen mats in barrels of water for 24 h and then applying the filtrate to lichen-free plots covered with polyethylene sheet to compensate for the lost insulating effect of the lichens. This procedure was repeated daily during the snow-free seasons for 4 y and resulted in a negative growth response of broadly similar magnitude to the positive effect of lichen cover. However, the author does not indicate the frequency with which lichen in the barrels was renewed during the experiment; water that has passed through a dense mass of dead, and possibly fermenting, lichen is likely to differ markedly in chemical composition from rainfall that has percolated through a living lichen stand. It should also be remembered that lichens are not the only producers of allelochemicals in these ecosystems: evidence suggests that ericaceous shrubs (Pellissier, 1993; Nilsson *et al.*, 1993; Inderjit & Mallik, 1997; Yamasaki *et al.*, 1998) and feather mosses (Steijlen *et al.*, 1995) also produce phytotoxins that inhibit the establishment and/or growth of trees (see discussion of seed banks above).

P. D. Crittenden and R. P. Beckett (unpubl.) investigated the effects of lichen-modified rainwater on mycorrhizal development and growth in the cultivated cranberry (*Vaccinium macrocarpon*) grown in sand-solution culture. Mats of *Cladonia stellaris* and *Stereocaulon paschale* were reconstructed on stainless steel grilles superimposed over rain gauges in lichen-rich birch woodland at Kevo, northern Finland, following the method of Crittenden (1983). Water that percolated through the mats during natural rainfall events was collected quantitatively, filtered to pass 0.22 µm and applied in 5 ml aliquots to the surface of the sand surrounding each *Vaccinium* plant; these additions were repeated at intervals of several hours until all water that had been collected during a rainfall event was exhausted. Control plants received either unmodified rainfall or deionized water, and the *Vaccinium* was grown either in the mycorrhizal (inoculated with the fungus *Hymenoscyphus ericaea* [Smith & Read, 1997]) or non-mycorrhizal states and under either low or high nitrogen regimes (2.7 or 27 parts N/10^6, respectively, in applied nutrient solutions). The only statistically significant effect of lichen-modified rainwater during a three month growth period was an *increase* in the extent of mycorrhizal infection in the low nitrogen treatment (Fig. 2). In this experiment the quantities of lichen products added to the experimental plants were probably ecologically relevant. The two lichen species supported over the replicate rain guages appeared to remain in a healthy state: they increased in dry mass during the experiment and did not release K^+ into the percolating rain water, indicating cell membrane integrity (see Buck & Brown, 1979; Tarhanen *et al.*, 1996). The promorion of ericoid mycorrhizal development may have been due to utilization by the mycorrhizal fungus of exogenous organic carbon present in the lichen-modified rainfall thus promoting more effective colonization of the rhizosphere prior to establishing infection points. It is debatable whether this effect would be evident in podzolic soils containing abundant soluble organic compounds. Nonetheless,

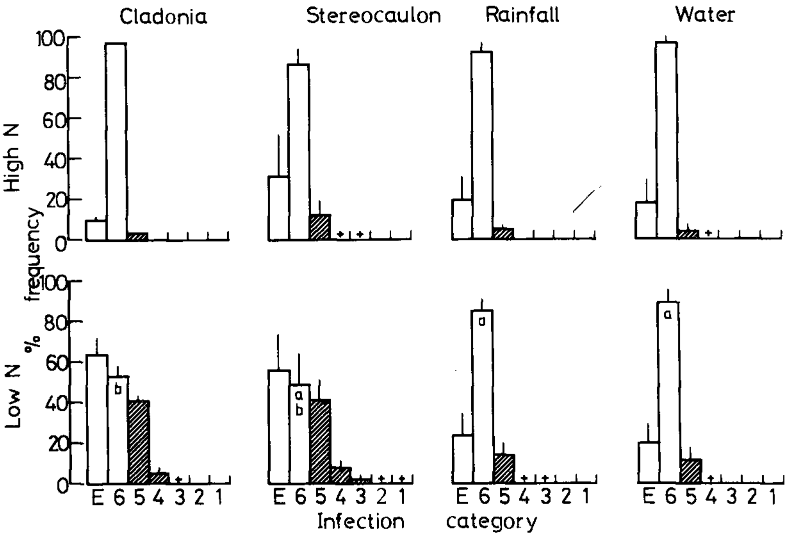

Fig. 2. The effect of lichens on mycorrhizal infection in the cultivated cranberry (*Vaccinium macrocarpon*). Plants wete watered with lichen-modified rainwater (*Cladonia*, or *Stereocaulon*), unmodified rainwater or deionized water, and harvested at 107 days from planting. Plants in the low N treatment received 2.7 parts/ 10^6 NH_4^+-N in nutrient solution, high N plants received 27 parts/ 10^6 NH_4^+-N. Root subsamples were stained in cotton and lactophenol and scanned with a light microscope at a magnification of x 200, each field of view being assessed for mycorrhizal infection according to the scale of Read and Stribley (1975): category 1, 98-100% of cortical cells infected; category 2, 75-98% infected; category 3, 50-75% infected; category 4, 25-50% infected; category 5, 0-25% infected; category 6, no infection. The frequency of fields of view in which extramatricullar hyphae were visible (E) was also noted. (Number of fields of view per sample ranged between 228-985; mean values [n = 3] are plotted with 1 standard error; + = ≤ 2%). Frequencies of category 6 infection level with the same letter are not significantly different (P>0.05, ANOVAR and Duncan's multiple tange test). The combined frequency of category 6 infection level for low N plants receiving lichen leachates was significantly lower (P<0.05) than fot low N plants receiving rainfall or water.

the results do not support the popular belief that lichens inhibit mycorrhizal development. My own observations in lichen woodland are that shrubs and trees rooting beneath lichen mats have well-developed mycorrhizal associations.

Co-existence with vascular plants

Terricolous lichens grow on oligotrophic sandy or podzolic soils on at least moderately well-drained terrain. Vascular plants adapted to these conditions have low growth rates (Grime, 1979) and have the capacity to absorb simple and complex organic forms of nitrogen either directly (Kielland, 1994; Schimel & Chapin, 1996) or via mycorrhizal associations (Smith & Read, 1997; Näsholm *et al.*, 1998), thus largely by-passing the need for microbiologically-driven mineralization processes. Vascular plants show plasticity in their root/shoot ratio and typically develop larger root systems in nutrient deficient soils (e.g. Chapin, 1980; Tilman & Wedin,1991) increasing the carbon cost of mineral nutrient recovery. Clearly, with increasing nutrient scarcity there is a limit to how "rooty" a plant can become given the increased respiratory cost of expanding below-ground biomass. As this limit is approached and plant vigour declines, a point will be reached at which productive terricolous mat-forming lichens can co-exist with vascular plants (cf. Manseau *et al.*, 1996).

Lichens do not have root systems and are probably almost entirely dependent on atmospheric deposition for supplies of N and P (Crittenden *et al.*, 1994). The seasonal intake of these elements by lichens may be substantially less than their vascular plant neighbours but the carbon cost of this acquisition is probably small in comparison. Thus the growth rates of above-ground phytomass in lichens and vascular plants could be similar or, in extremely nutrient poor soils, greater in lichens. Being rootless, lichens are largely uncoupled from soil water and thus must tolerate periods of desiccation during which metabolic activity is minimal. Lichen ecophysiologists tend to view desiccation negatively since it is believed that this limits lichen growth rates. In addition, there is evidence that rewetting of lichen thalli (e.g. during the onset of rainfall) is itself associated with a carbon cost (e.g. Lechowicz, 1981; Dudley & Lechowicz, 1987). However, because precipitation is one of the major processes that delivers nutrients to lichens, periods of desiccation between infrequent precipitation events might decrease the carbon cost of nutrient capture. However, fertilization of these oligotrophic communities can increase plant growth rates and result in the competitive exclusion of lichens (e.g. Persson, 1981; Jonasson, 1992). It is quite common in the Subarctic for well-drained terrain to experience acute summer droughts that could be lethal to fine roots of trees and dwarf shrubs which develop close to the soil surface. Thus, in addition to paucity of soil mineral nutrients, periodic drought may also be a significant factor suppressing vascular plant vigour and promoting the development of lichen ground cover.

Lichen growth and the impact of trampling and grazing

Terricolous lichens typically constitute in excess of 60% of the winter food intake by reindeer and caribou (Miller, 1976; Boertje, 1990). Lichen consumption declines markedly during the summer months when graminoids and dwarf shrubs comprise the major food items. Crête *et al.* (1990) estimated that the average lichen biomass on the winter range of the Rivière George caribou herd (*c.* 680 000 individuals in 1988) in northern Quebec averaged 1223 kg ha^{-1} and that in 1987 0.5-0.9% of this was consumed annually. The significance of this consumption is dependent on lichen productivity; unfortunately, as the authors point out, appropriate data on lichen growth are largely lacking. Sveinbjörnsson (1990) has discussed some of the approaches available for measuring lichen growth rate: these range from morphological analyses (that to my knowledge have never been critically evaluated) to simulation modelling based on net CO_2-exchange measurements. Probably the best method, and possibly the only method that should be considered for long-term productivity determination, is the measurement of mass increment (Jónsdóttir *et al.,* 1998). Few investigators have measured mass-increment in lichens and only Kärenlampi (1971), Hooker (1980), Crittenden (1983, 1989; summarized in Crittenden *et al.,* 1994) and Hyvärinen & Crittenden (1998a) have done so for mat-forming lichens. The method suffers from the criticism that lichen thalli must be detached from the ground (or underlying necromass) in order to make the initial (time zero) weighing. The effect of such detachment has not been fully investigated.

In northern Finland, thalli of *Cladonia stellaris* and *Stereocaulon paschale* that were pre-weighed and inserted into reconstructed lichen mats increased in dry mass by at least 26% per year (Crittenden *et al.*, 1994). This equates with a mean relative growth rate (RGR) of *c.* 0.004 mg mg^{-1} d^{-1}, a value that compares favourably with those recorded by Kärenlampi (1971) for the same species using a similar method. However, Kärenlampi showed that in wet years RGR for *C. stellaris* could rise to 0.005-0.01 d^{-1}. It is instructive to compare these lichen RGR values with those for vascular plants. Grime & Hunt (1975) measured the RGR of plant species in the local flora of the Sheffield region in the UK under optimum conditions of temperature and supplies of light, water and nutrients. Of the 132 species screened *Urtica dioica* was found to have the highest mean RGR of 0.3 d^{-1} and *Vaccinium vitis-idaea*, a species that frequently co-occurs with mat-forming lichens in the boreal-Arctic, had the lowest value of 0.03 d^{-1}. When *V. vitis-idaea* was grown in organic top-soil collected from beneath *C. stellaris* mats in Finnmarksvidda, Norway, but otherwise under favourable conditions of light, temperature and water supply, mean RGR values of 0.016 d^{-1} were observed (Crittenden, 1989). Thus, under harsher field conditions (e.g. exposure to periodic summer drought, lower temperatures) it is not improbable that RGR of *V. vitis-idaea* would approach that of *C. stellaris* consistent with the co-existence of the two species. The measured growth rates for *C. stellaris* and *S. paschale* are in broad general agreement with the observation that recovery of *C. stellaris* ground cover that is harvested by man for ornamental purposes in northern Finland takes 5-6 years (Søchting, 1984). Virtala (1992) estimated that lichen biomass in overgrazed lichen woodland in Fennoscandia could recover from 300 kg ha^{-1} to 1000 kg ha^{-1} in about 9 years, and to 2000 kg ha^{-1} in 16 years.

Mat-forming lichens are relatively loosely attached to the ground. I have argued above that this loss of firm attachment to the substratum may have permitted an increased productivity in those species adopting this growth habit. Lichen species that form deep mats (e.g. *C. stellaris, C. mitis, S. paschale*) are generally resticted to sheltered sites experiencing comparatively low wind speeds: these are woodlands and low arctic tundra sites with at least moderate winter snow cover (Larson & Kershaw, 1975; Larsen, 1980). The extent to which the distribution of these species is linked to snow depth, and whether this link is causal, is not known. In contrast, other species such as *Cetraria nivalis* and *Alectoria ochroleuca* frequently occur on exposed sites experiencing minimal winter snow cover (Larson & Kershaw, 1975; Petzold & Mulhern, 1987; Ahti & Oksanen, 1990). Lichens beneath deep snow are afforded protection against trampling by reindeer and caribou herds on their winter ranges (Miller, 1976). In order to graze terricolous lichens the animals excavate craters in the snow. This causes mechanical damage to mats over and above the loss due to consumption; estimates of this wastage range between to 2 - 10 times the lichen mass ingested (Virtala, 1992). Kauppi (1990) has shown that in middle Finland *C. stellaris*-dominated lichen mats that become covered with debris, such as conifer needles and bark fragments, can fully recover in 3-8 years; comparable distutbance effects might occur due to deposition of faeces and mat-fragments in areas where caribou and reindeer have cratered intensively (Miller, 1976).

In summer, dry lichen mats are destroyed rapidly by trampling (cf. Bayfield, Urquhart & Cooper, 1981). In the case of migratory herds such damage may be largely confined to migration routes (Boertje, 1990) or to summer ranges where these have a significant lichen component. For example, Manseau *et al.* (1996) have reported marked depletion of lichens in tundra used by migratory caribou as summer range in northern Quebec. My own observations in shrub tundra between Vorkuta and the Polar Ural Mountains in Russia suggest that reindeer herding has largely eliminated mat-forming lichens from the ground cover in this region. Here, *Cladonia arbuscular* can be found in most 1 m^2 quadrats randomly located on well-drained terrain but usually only in trace quantities, possibly indicating that efficient foraging is as least as important as ttampling; Moser, Nash & Thompson (1979) made a similar observation in Alaskan tundra. According to Ahti & Oksanen (1990) and Vilchek (1997), depletion of lichen cover in tundra due to reindeer herding is widespread in Russia.

Severe degradation of winter range owing to summer trampling can also occur where migratory movements are prevented by artificial barriers at political boundaries or by the stocking of small islands (Anon, 1974; Oksanen, 1978; Swanson & Barker, 1992; Väre *et al.,* 1996). Deterioration of winter range in northern Finland, a result primarily of summer-time trampling, is particularly marked and on a scale that is evident in satellite images (Käyhkö & Pellikka, 1994; Väre *et al.,* 1996). Where numbers of migratory animals exceed the range carrying capacity then excessive winter-time foraging can also lead to depletion of the lichen resource. Such a situation has been described for caribou in northern Quebec (Arseneault *et al.,* 1997) and Alaska (Moser, Nash & Thompson; 1979), and for reindeeer in Finnmarksvidda (E. Gaare, pers. comm.; Kashulina *et al.,* 1997) and Russia (Vilchek, 1997).

Mat-forming lichens appear to regenerate well following fragmentation. This is exemplified by lichen monocultures established at the Kevo Subarctic Research Station in northern Finland by P. Kallio in 1971. Kallio cleared vegetation from 1 m x 1 m plots on the floor of an open stand of Scots pine and then spread 200 g crushed thalli of a single lichen species into each. Monocultures of *Cl. stellaris, Cl. rangiferina, Ce. nivalis* and *S. paschale* had developed by 1978 and in 1998 most species were present as luxurious mats. Many lichen-forming fungi in the genera *Cladonia* and *Stereocaulon* can be readily isolated into pure culture by plating small (60-200 µm long) alga-free fragments of macerated thallus onto agar (Crittenden *et al.,* 1995) and this may also be indicative of the importance of fragmentation as a means of dispersal and regeneration in these important lichen genera.

Kallio's lichen plots demonstrate that mat-forming lichens can regenerate following a massive disturbance if subsequently left undisturbed but where disturbance recurs frequently lichens will not recover. The reason for this is succinctly explained by Grime's (1979) CSR sttategy theory which states that no plant strategy has evolved that can facilitate survival in habitats that are subject to high levels of both stress and disturbance. Since mat-forming lichens are supremely good toleratots of environmental stress then, in accordance with Grime, they must also be intolerant of frequent disturbance. Thus lichens are rapidly eliminated from summer range by repeated trampling and will only recover if ungulate numbers are reduced (cf. Virtala, 1992).

Nitrogen fixation

Lichens that contain a cyanobacterium fix nitrogen. An important finding of the International Biological Programme's Tundra Biome investigations was that cyanobacterial lichens (principally of the genera *Peltigera, Stereocaulon* and *Nephroma*) are among the major agents of nitrogen fixation in the

Subarctic and Arctic (Stewart, 1976). There has been a sufficiently large number of studies of nitrogenase activity in lichens to provide a relatively good understanding of which genera and species are the most active fixers (e.g. *Peltigera* spp.) and how rates of nitrogenase activity are controlled by environmental factors such as thallus water content, temperature and incident light (Kershaw, 1985).

But what is the ecological significance of nitrogen fixation by lichens? There have been several attempts to produce annual rates of N input by lichens in both northern boreal forests (Billington & Alexander, 1983) and tundra habitats (Gunther, 1989; Getsen *et al.,* 1997). However, almost invariably these estimates have been derived from the results of the acetylene reduction assay, an analogue enzymatic teaction which, at best, only gives an approximate measure of absolute nitrogen fixation rates. Where feasible, annual rates of nitrogen fixation can probably be more appropriately obtained from the product of growth (as mass increment - see above) and thallus nitrogen concentration but as yet such calculations have not been made [with the exception of Crittenden (1989)]. Further, estimates of N input by lichens have not been placed in context with other N fluxes in the ecosystems under study. Larsen (1980) constructed a schematic N cycle for the boreal forest which incorporated an estimate of nitrogen fixation for *S. paschale* derived from acetylene reduction data of Crittenden & Kershaw (1979). This suggested that nitrogen fixation by this species $\leq$20 kg ha^{-1} y^{-1}) could potentially provide much of the annual N requirement of vascular plants (10-40 kg ha^{-1} y^{-1}) in upland spruce forest. *Stereocaulon paschale* is an active nitrogen fixer that has the potential to form extensive, almost monospecific, groundcover in lichen-woodlands. Such ecosystems are abundant in north-central Canada (Kershaw, 1977) and parts of Russia (Lavrenko & Sochava, 1956; Karev, 1961) and will make excellent model systems in which to investigate some key questions that to date remain unexplored. For example, by which pathways and in what quantities does N_2 fixed by lichens reach vascular plants? Does the presence of N_2-fixing lichens influence rooting patterns, and promote the growth, of shrubs and trees? These questions have a direct beating on the primary productivity of lichen-rich ecosystems. Moreover, N_2-fixing lichens are particularly sensitive to air pollution (e.g. Hallingbäck & Kellner, 1992) giving added significance to these questions. Species of *Peltigera* and *Nephroma* ate likely to be among the first lichens to be eliminated from subarctic areas affected by acid rain and there is a pressing need to better understand their ecological role.

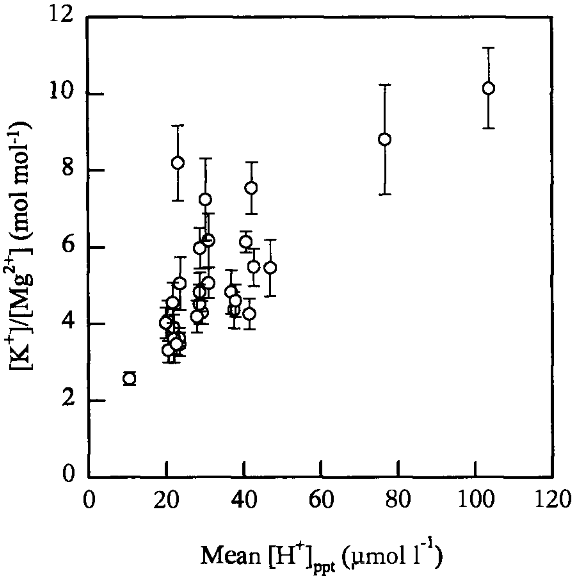

Fig. 3. The relationship between mean values (with ±1 standard error) of the ratio [K$^+$]:[Mg^{2+}] (n=5-10) in the apices of *Cladonia portentosa* and hydrogen ion concentration in precipitation ([H$^+$]$_{ppt}$) at 31 sites in the British Isles.

Response to pollution

Lichens are renowned for their ability to accumulate pollutants and for their usefulness as indicators of pollution loads. Perhaps of most significance for reindeer and caribou production is the capacity for lichens to intercept and accumulate radionuclides in atmospheric deposits (Nevstrueva *et al.,* 1967; Taylor *et al.*, 1988; Feige *et al.*, 1990; Baskaran *et al.*, 1991; Strandberg, 1997). The food chain concentrating effect has been implicated as the cause of an increased incidence of cancer among some native peoples in the Arctic (Crittenden, 1995).

There is now growing interest in the impact of acid rain in northern latitudes. Acid rain contains elevated concentrations of both acidity and N, principally as nitrate. The concentration of NO_3^- in precipitation has steadily increased in northern latitudes during the past century (Brimblecombe & Stedman, 1982; Rodhe & Rood, 1986; Fischer *et al.*, 1998). Recent studies have shown mat-forming lichens to be sensitive indicators of N and acid deposition. Using *Cladonia portentosa* in British

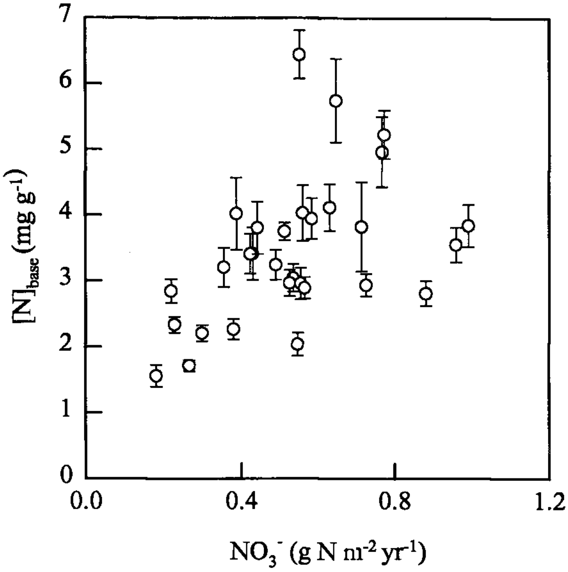

Fig. 4. The relationship between mean values (with ±1 standard error) of total nitrogen concentration (n=5-10) in a horizontal stratum of *Cladonia portentosa* between 40-50 mm from the thallus apices ($[N]_{base}$) and wet deposition of NO_3^- as a function of total N deposition.

heathlands as a model system, Hyvärinen & Crittenden (1996; 1998b) showed that the ratio $K^+ : Mg^{2+}$ in the thallus apices was highly correlated with H^+ concentration in precipitation (Fig. 3), and that thallus N concentration was related to total N deposition (Fig. 4). While a preliminary study could not find any evidence that the growth of *C. portentosa* was impaired by acid rain (Hyvärinen & Crittenden, 1998a) it was often absent from eutrophicated heathlands. This is probably owing to competitive exclusion by mosses and vascular plants, the growth of which is believed to be stimulated by elevated N deposition driving a change from slower to faster growing species. Mat-forming lichens may provide particularly sensitive indicators of atmospheric chemistry because (i) they occur in open situations where they intercept atmospheric deposits directly and largely unmodified by plant canopies, (ii) they are partially isolated from the chemical status of underlying soil by a layer of necromass, and (iii) they are very efficient scavengers of inorganic N (and probably P) in precipitation (Crittenden, 1983; 1989; Hyvärinen & Crittenden, 1998c). For example, nitrogen concentration in the apical 5 mm of *C. stellaris* was measured at sites distributed along a 240 km long transect across the taiga-tundta ecotone in northern Russia and found to gradually decrease from south to north (Fig. 5). This change probably reflects a south to north decrease in N deposition due to either a decline in total precipitation (ranging from *c.* 1200 mm at the southern end of the transect to *c.* 620 mm at the northern end) or a pollution gradient, or both. However, a comparable gradient in nitrate concentration in winter snow pack was not observed (Walker, Crittenden & Young, unpubl.).

Ecosystems at high latitudes are classically N-limited and potentially responsive to N pollution. This is likely to increase in the future due to such activities as exploitation of oil and gas reserves located deep within the Subarctic. Nitrogen pollution has been implicated as a factor contributing to increased growth rates of northern boreal forest trees (D'Arrigo *et al.*, 1987; Myneni *et al.*, 1997; Nadelhoffer *et al.*, 1999). The effect on lichens will depend on the N load. Species containing cyanobacteria, such as *Stereocaulon, Peltigera* and *Nephroma* may be particularly susceptible to increased N and acid deposition although the latter species are not favoured by reindeer or caribou. However, increased vascular plant vigour could result in the competitive exclusion of terricolous lichens in the most

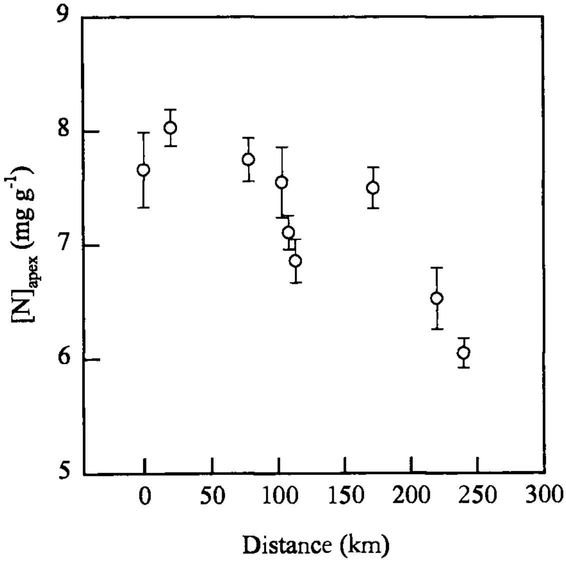

Fig. 5. Variation in mean values (with ±1 standard error) of total nitrogen concentration (n=18) in the apical 5 mm of *Cladonia stellaris* along a 240 km transect in the Usa River catchment, notthem Russia. The transect extends from Vangyr (lat 64°14'N, long 59°12'E) in the boreal forest northwatds to the Khosedayu River in the tundra (lat 67°15'N, long 59°37'E).

affected areas. Søchting (1990; 1995) considers this to be a contributory factor in the decline of *Cladonia* (subgenus *Cladina*) spp. in Danish heathlands. In some of the most eutrophicated heathlands in the Netherlands and the UK there has been an incursion of graminoids resulting in competitive exclusion of not only lichens but also ericaceous shrubs: in these areas heathlands are changing into grasslands (Aerts & Heil, 1993; Marrs, 1993).

Concluding remarks

The majority of lichen research is curiosity-driven and takes place in countries without reindeer industries. It attracts minimal financial support and lichenologists are not generally accustomed to having end-users who consider lichens of practical importance. Perhaps it is not surprising, therefore, that lichenology is poorly equipped to address some of the range management issues facing reindeer herding. One way forward is for those working in reindeer range management to identify key questions that they think lichenologists should address. These can be publicised in international fora and will hopefully provide incentive for research on topics that are currently neglected and perhaps viewed as unfashionable. The rate of mass increase in mat-forming lichens is clearly one such topic.

Acknowledgements

Fig. 3 was reproduced with kind permission of the *New Phytologist* and Fig. 5 is previously unpubl. output from TUNDRA, a collaborative research project supported by the EC Environment and Climate Research Programme (contracr nr. ENV4-CT97-0522, climate and natural hazards). I thank T. K. Sorensen for translating a Danish text.

References

Aerts, R & Heil G. W. (eds.). 1993. *Heathlands: patterns and processes in a changing environment.* Kluwer Academic Publishers, Dordrecht, pp. 238.

Ahti, T. & Oksanen, J. 1990. Epigeic lichen communities of taiga and rundra regions. – *Vegetatio* 86: 39–70.

Allen, A. E. 1929. Influence of *Cladonia* ground cover on the establishment of Seedlings. – *Ecology* 10: 354–355.

Anon. 1974. Reindeer overgraze in South Georgia. – *Nature* 248: 639.

Arseneault, D., Villeneuve, N., Boismenu, C., Leblanc, Y. & Deshaye, J. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Québec: an application of fire history and Landsat data. – *Journal of Applied Ecology* 34: 65–78.

Baskaran, M., Kelley, J. J., Naidu, A. S. & Holleman, D. F. 1991. Environmental radiocesium in subarctic and arctic Alaska following Chernobyl. – *Arctic* 44: 346–350.

Bayfield, N. G., Urquhart, U. H. & Cooper, S. M. 1981. Susceptibility of four species of *Cladonia* to disturbance by trampling in the Cairngorm Mountains, Scotland. – *Journal of Applied Ecology* 18: 303–310.

Billington, M. M. & Alexander, V. 1983. Site-to-site variations in nitrogenase activity in a subarctic black spruce forest. – *Canadian Journal of Forest Research* 13: 782–788.

Boertje, R. D. 1990. Diet quality and intake requirements of adult female caribou of the Denali herd, Alaska. – *Journal of Applied Ecology* 27: 420–434.

Brimblecombe, P. & Stedman, D. H. 1982. Historical evidence for a dramatic increase in rhe nitrate component of acid rain. – *Nature* 298: 460–462.

Brown, R. T. & Mikola, P. 1974. The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. – *Acta Forestalia Fennica* 141: 1–22.

Buck, G. W. & Brown, D. H. 1979. The effect of desiccation on cation location in lichens. – *Annals of Botany* 44: 265–277.

Carstairs, A. G. & Oechel, W. C. 1978. Effects of several microclimatic factors and nutrients on net carbon dioxide exchange in *Cladonia alpestris* (L.) Rabh. in the Subarctic. – *Arctic and Alpine Research* 10: 81–94.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. – *Annual Review of Ecology and Systematics* 11: 233–260.

Cowles, S. 1982. Preliminary results investigating the effect of lichen ground cover on the growth of black spruce. – *Naturaliste canadien* 109: 573–581.

Coxson, D. S. & Lancaster, J. 1989. The morphological basis of variation in ner photosynthetic and respiratory responses of the mar-forming lichen species *Stereocaulon virgatum* and *S. tomentosum.* – *Canadian Journal of Botany* 67: 167–176.

Crête, M., Morneau, C. & Nault, R. 1990. Biomasse et espèces de lichens terrestres disponibles pour le caribou dans le nord du Québec. – *Canadian Journal of Botany* 68: 2047–2053.

Crittenden, P. D. 1983. The role of lichens in the nitrogen economy of subarctic woodlands: nitrogen loss from the nitrogen-fixing lichen *Stereocaulon paschale* during rainfall. – *In:* J. A. Lee, S. McNeill & I. H. Rorison (eds.). *Nitrogen as an ecological factor.* Blackwell Scientific Publications, Oxford, pp.43–68.

Crittenden, P. D. 1989. Nitrogen relations of mar-forming lichens. – *In:* L. Boddy, R. Marchant & D. J. Read (eds.). *Nitrogen, phosphorus and sulphur utilization* *by fungi.* Cambridge University Press, Cambridge, pp. 243–268.

Crittenden, P. D. 1991. Ecological significance of necromass production in mat-forming lichens. – *Lichenologist* 23: 323–331.

Crittenden, P. D. 1995. Lichens and radioactive fallout over north west Russia – *British Lichen Society Bulletin* 77: 34–35.

Crittenden, P. D. & Kershaw, K. A. 1979. Studies on lichen dominated systems. XXII. The environmental control of nitrogenase activity in *Stereocaulon paschale* in spruce-lichen woodland. – *Canadian Journal of Botany* 57: 236–254.

Crittenden, P. D., Kałucka I. & Oliver E. 1994. Does nitrogen supply limit the growth of lichens? – *Cryptogamic Botany* 4: 143–155.

Crittenden, P. D., David, J. C., Hawksworth, D. L. & Campbell, F. S. 1995. Attempted isolation and success in the culturing of a broad specrrum of lichen-forming and lichenicolous fungi. – *New Phytologist* 130: 267–297.

D'Arrigo, R., Jacoby, G. C. & Fung, I. Y. 1987. Boreal forests and atmosphere-biosphere exchange of carbon dioxide. – *Nature* 329: 321–323.

Dudley, S. A. & Lechowicz, M. J. 1987. Losses of polyol through leaching in subarctic lichens. – *Plant Physiology* 83: 813–815.

Fahselt, D. 1994. Secondary biochemistry of lichens. – *Symbiosis* 16: 117–165.

Feige, G. B., Niemann, L. & Jahnke, S. 1990. Lichens and mosses - silent chronisrs of the Chernobyl accident. – *Bibliotheca Lichenologica* 38: 63–77.

Fischer, H., Wagenbach, D., & Kipfstuhl, J. 1998. Sulfate and nitrate firn concentrations on the Greenland ice sheet – 2. Tempotal anthropogenic deposition changes. – *Journal of Geophysical Research – Atmospheres* 103: 21935–21942.

Fisher, R. F. 1979. Possible allelopathic effects of reindeer-moss (*Cladonia*) on Jack pine and white spruce. – *Forest Science* 25: 256–260.

Foster, D, R. & Glaser, P. H. 1986. The raised bogs of south-eastern Labrador, Canada: classification, distribution, vegetation and recent dynamics. – *Journal of Ecology* 74: 47–71.

Getsen, M. V., Kostyaev, V. Ja. & Patova, E. N. 1997. Role of nitrogen-fixing cryptogamic plants in the tundra. – *In:* R.M.M. Crawford (ed.). *Disturbance and recovery in Arctic lands.* Kluwer Academic Publishers, Dordrecht, pp. 135–150.

Goldner, W. R., Hoffman, F. M. & Medve, R. J. 1986. Allelopathic effects of *Cladonia cristatella* on ectomycorrhizal fungi common to bituminous strip-mine spoils. – *Canadian Journal of Botany* 64: 1586–1590.

Grime, J. P. 1979. *Plant strategies and vegetation processes.* J. Wiley and Sons, Chichester, pp. 222.

Grime, J. P. and Hunt, R. 1975. Relative growth-rate: its range and adaptive significance in a local flora. – *Journal of Ecology* 63: 393–422.

Gunther, A. J. 1989. Nitrogen fixation by lichens in a Subarctic Alaskan watershed. – *Bryologist* 92: 202–208.

Hallingbäck, T. & Kellner, O. 1992. Effects of simulated nitrogen rich and acid rain on the nittogen-fixing lichen *Peltigera aphthosa* (L.) Willd. – *New Phytologist* 120: 99–103.

Harper, J. L. 1975. Review of "Allelopathy" by E.L. Rice. – *Quarterly Review of Biology* 50: 493–495.

Hawksworth, D. L., Kirk, P. M., Sutton, B. C. & Pegler, D. N. 1995. *Ainsworth and Bisby's dictionary of the fungi,* 8th Ed. CAB International, Wallingford, 616 pp.

Holleman, D. F. & Luick, J. R. 1977. Lichen species preference by reindeer. – *Canadian Journal of Zoology* 55: 1368–1369.

Hooker, T. N. 1980. Growth and production of *Cladonia rangiferina* and *Sphaerophorus globosus* on Signy Island, South Orkney Islands. – *British Antarctic Survey Bulletin* 50: 27–34.

Huovinen, K. & Ahti, T. 1986. The composition and contents of aromatic lichen substances in the genus *Cladina.* – *Annales Botanici Fennici* 23: 93–106.

Hyvärinen, M. & Crittenden, P. D. 1996. Cation ratios in *Cladonia portentosa* as indices of precipitation acidity in the British Isles. – *New Phytologist* 132: 521–532.

Hyvärinen, M. & Crittenden, P. D. 1998a. Growth of the cushion-forming lichen, *Cladonia portentosa,* at nitrogen-polluted and unpolluted heathland sites. – *Environmental and Experimental Botany* 40: 67–76.

Hyvärinen, M. & Crittenden, P. D. 1998b. Relationships between atmospheric nitrogen inputs and the vertical nitrogen and phosphorus concentration gradients in the lichen *Cladonia portentosa.* – *New Phytologist* 140: 519–530.

Hyvärinen, M. & Crittenden, P. D. 1998c. Phosphate uptake in *Cladonia portentosa.* – *Lichenologist* 30: 297–301.

Inderjit & Mallik, A. U. 1997. Effects of *Ledum groenlandicum* amendments on soil characteristics and black spruce seedling growth. – *Plant Ecology* 133: 29–36.

Johnson, E. A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. – *Canadian Journal of Botany* 53: 2933–2941.

Jonasson, S. 1992. Plant responses to fertilization and species removal in tundra related ro community sttucture and clonality. – *Oikos* 63: 420–429.

Jónsdóttir I. S., Crittenden P. D. & Jägerbrand A. 1998. *Measuring growth rate in bryophytes and lichens.* Supplement to ITEX Manual, 2nd ed. (U. Molau & P. Mölgaard (eds.). Danish Polar Centre, Copenhagen.

Kaitera, J. A., Helle, T. & Jalkanen, R. E. 1996. The effect of *Alectoria sarmentosa, Bryoria fuscescens* and *Bryoria fremontii* extracts and usnic acid on growth of *Gremmeniella abietina* in vitro. – *Canadian Journal of Botany* 74: 352–359.

Kärenlampi, L. 1971. Studies on the relative growth rate of some fruticose lichens – *Reports from the Kevo Subarctic Research Station* 7: 33–39.

Karev, G. I. 1961. Kormovaya baza severnogo olenevodstva. - *In:* P.S. Zhigunov (ed.). *Severnoe olenevodstvo,* 2nd ed. Izdatel'stvo Sel'skokhozystvennoy Literatury, Zhurnalov i Plakatov, Moskva. pp. 188-254. (Translated into English by Israel Program for Scientific Translations, 1968).

Kashulina, G., Reimann, C., Finne, T. E., Halleraker, J. H., Äyräs, M. & Chekushin, V. A. 1997. The state of the ecosystems in the central Barents region: scale, factors and mechanisms of disturbance. – *Science of the Total Environment* 206: 203–225.

Kauppi, M. 1990. The effect of litter and waste wood on a *Cladina stellaris* carpet. – *Aquilo Series Botanica* 29: 33–38.

Käyhkö, J. & Pellikka, P. 1994. Remote sensing of the impact of reindeer grazing on vegetation in northern Fennoscandia using SPOT XS data. – *Polar Research* 13: 115–124.

Kershaw, K. A. 1977. Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. – *Canadian Journal of Botany* 55: 393–410.

Kershaw, K. A. 1985. *Physiological ecology of lichens.* Cambridge University Press, Cambridge, pp. 293.

Kielland, K. 1994. Amino acid absorprion by Arctic plants: implications for plant nutrition and nitrogen cycling. – *Ecology* 75: 2373–2383.

Larsen, J. A. 1980. The boreal ecosystem. Academic press, New York, 500 pp.

Larson, D. W. 1987. The absorption and telease of water by lichens. – *Bibliotheca Lichenologica* 25: 351–360.

Larson, D. W. & Kershaw, K. A. 1975. Studies on lichen-dominated systems. XI. Lichen-heath and winter snow cover. – *Canadian Journal of Botany* 53: 621–626.

Lavrenko, E. M. & Sochava, V. B. eds. 1956. *Rastitel' nyy pokrove SSSR* (*Descriptio Vegetationis URSS*). Akademia nauk SSSR, Moskva-Leningrad.

Lawrey, J. D. 1984. *Biology of lichenized fungi.* Praeger, New York, pp.407.

Lawrey, J. D. 1986. Biological role of lichen substances. – *Bryologist* 89: 111–122.

Lawrey, J. D. 1989. Lichen secondary compounds: evidence for a correspondence between antiherbivore and antimicrobial function. – *Bryologist* 92: 326–328.

Lechowicz, M. J. 1981. The effects of climatic pattern on lichen productivity: *Cetraria cucullata* (Bell.) Ach. in the arctic tundra of northern Alaska. - *Oecologia* 50: 210–216.

Lechowicz, M. J. 1983. Age dependence of photosynthesis in the caribou lichen *Cladina stellaris.* – *Plant Physiology* 71: 893–895.

Manseau, M., Huot, J. & Crête, M. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. – *Journal of Ecology* 84: 503–513.

Marrs, R. H. 1993. An assessment of change in *Calluna* heathlands in Breckland, Eastern England, between 1983 and 1991. – *Biological Conservation* 65: 133–139.

Miller, D. R. 1976. *Biology of the Kaminuriak population of barren-ground caribou.* Part 3: *Taiga winter range relationships and diet.* Canadian Wildlife Service Report Series No. 36. Environment Canada Wildlife Service, Ottawa, pp. 42.

Moser, T. J., Nash, T. H., III, & Thomson, J. W. 1979. Lichens of Anaktuvuk Pass, Alaska, with emphasis on the impact of caribou grazing. – *Bryologist* 82: 393–408.

Myneni, R. B., Keeling, C. D., Tucker C. J., Asrar, G., & Nemani, R. R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. – *Nature* 386: 698–702.

Nadelhoffer, K. J., Emmett, B. A., Gundersen, P., Kjønaas, O. J., Koopmans, C. J., Schlepp, P., Tietema, A. & Wright, R. F. 1999. Nitrogen deposirion makes a minor conrribution to carbon sequestration in temperate fotests. – *Nature* 398: 145–148.

Näsholm, T., Ekblad, A, Nordin, A., Giesler, R., Högberg, M. & Högberg, P. 1998. Boreal forest plants take up organic nitrogen. – *Nature* 392: 914–916.

Nevstrueva, M. A., Ramzaev, P. V., Moiseer, A. A., Ibatullin, M. S. & Teplykh, L. A. 1967. The natute of ^{137}Cs and ^{90}Sr transport over the lichen-reindeer-man food chain. – *In:* B. Åberg & F. P. Hungate (eds.). *Radioecological concentration processes.* Pergamon Press, Oxford, pp. 209–215.

Nilsson, M.-C., Högberg, P., Zackrisson, O. & Fengyou, W. 1993. Allelopathic effects by *Empetrum hermaphroditum* on development and nitrogen uptake by roots and mycorrhizae of *Pinus silvestris.* – *Canadian Journal of Botany* 71: 620–628.

Oksanen, L. 1978. Lichen grounds of Finnmarksvidda, northern Norway, in relarion to summer and winter grazing by reindeer. – *Reports from the Kevo Subarctic Research Station* 14: 64–71.

Pakarinen, P. 1985. Mineral element accumulation in bog lichens. – *In:* D. H. Brown (ed.). *Lichen physiology and cell biology.* Plenum Press, New York, pp. 185–192.

Pellissier, F. 1993. Allelopathic inhibition of spruce germination. – *Acta Œcologica* 14: 211–218.

Petzold, D. E. & Mulhern, T. 1987. Vegetation distributions along lichen-dominated slopes of opposing aspect in the eastern Canadian Subarctic. – *Arctic* 40: 221–224.

Persson, H. 1981. The effect of fertilization and irrigation on the vegetation dynamics of a pine-heath ecosystem. – *Vegetatio* 46: 181–192.

Qasem, J. R. & Hill, T. A. 1989. On difficulties with allelopathy methodology. – *Weed Research* 29: 345–347.

Read, D. J. & Stribley, D. P. 1975. Some mycological aspects of the biology of mycorrhiza in the Ericaceae. – *In:* F.E. Sanders, B. Mosse & P. B. Tinker (eds.). *Endomycorrhizas.* Academic Press, London, pp. 105–117.

Rodhe, H. & Rood, M. J. 1986. Temporal evolution of nitrogen compounds in Swedish precipitation since 1955. – *Nature* 321: 762–764.

Rominger, E. M., Allen-Johnson, L. & Oldemeyer, J. L. 1994. Arboreal lichen in uncut and partially cut subalpine fir stands in woodland catibou habitat, northern Idaho and southeastern British Columbia. – *Forest Ecology and Management* 70: 195–202.

Sarvas, R. 1950. Effect of light on the germination of forest tree seeds. – *Oikos* 2: 109–119.

Schimel, J. P. & Chapin, F. S., III. 1996. Tundra plant uptake of amino acid and NH_4^+ nitrogen in situ: plants compete well for amino acid N. – *Ecology* 77: 2142–2147.

Shear, W. A. 1991. The early developmenr of tettestrial ecosystems. – *Nature* 351: 283–289.

Smith, S. E. & Read, D. J. 1997. *Mycorrhizal symbiosis* 2nd. ed. Academic Press, San Diego, 605 pp.

Søchting, U. 1984. Stjerne-Rensdyrlav. – *Naturens Verden* 1984 (11): 377–382.

Søchting, U. 1990. Reindeet lichens injuted in Denmark – *British Lichen Society Bulletin* 67: 1–4.

Søchting, U. 1995. Lichens as monitors of nitrogen deposition. – *Cryptogamic Botany* 5: 264–269.

Steijlen, I., Nilsson, M.-C. & Zackrisson, O. 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichen and feather moss. – *Canadian Journal of Forest Research* 25: 713–723.

Stewart, W. D. P. 1976. Nitrogen fixation. – *Philosophical Transactions of the Royal Socioty of London* 274: 341–358.

Strandberg, M. 1997. Distribution of ^{137}Cs in a low arctic ecosystem in West Greenland. – *Arctic* 50: 216–223.

Sveinbjörnsson, B. 1987. Reindeer lichen producrivity as a function of mat thickness. – *Arctic and Alpine Research* 19: 437–441.

Sveinbjörnsson, B. 1990. Reindeer lichen productivity: problems and possibilities. – *Rangifer,* Special Issue No. 3: 91–98.

Swanson, J. D. & Barker, M. H. W. 1992. Assessment of Alaska reindeer populations and range conditions. – *Rangifer* 12: 33–43.

Tarhanen, S., Holopainen, T., Poikolainen, J. & Oksanen, J. 1996. Effect of industrial emissions on membrane permeability of epiphytic lichens in northern Finland and the Kola Peninsula industrial areas. – *Water, Air, and Soil Pollution* 88: 189–201.

Taylor, H. W., Svoboda, J., Henry, G. H. R. & Wein, R. W. 1988. Posr-Chernobyl ^{134}Cs and ^{137}Cs levels at some localities in Northern Canada. – *Arctic* 41: 293–296.

Taylor, T. N., Hass, H., Remy, W. & Kerp, H. 1995. The oldest fossil lichen. – *Nature* 378: 244.

Tilman, D. & Wedin, D. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. – *Ecology* 72: 685–700.

Väre, H., Ohtonen, R. & Mikkola, K. 1996. The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in nottheastern Fennoscandia. – *Ecography* 19: 245–253.

Vartia, K. O. 1973. Antibiotics in lichens. – *In:* V. Ahmadjian & M. E. Hale (eds.). *The lichens.* Academic Press, New York, pp. 547–561.

Vilchek, G. E. 1997. Arctic ecosystem stability and disturbance: a western Siberian case history. – *In:* R. M. M. Crawford (ed.). *Disturbance and recovery in Arctic lands.* Kluwer Academic Publishers, Dordrecht, pp. 179–189.

Virtala, M. 1992. Optimal harvesting of a plant-herbivore system: lichen and reindeer in northern Finland. – *Ecological Modelling* 60: 233–255.

Yamasaki, S. H., Fyles, J. W., Egger, K. N. & Titus, B. D. 1998. The effect of *Kalmia angustifolia* on the growth, nutrition, and ectomycorrhizal symbiotic community of black spruce. – *Forest Ecology and Management* 105: 197–207.

Zackrisson, O., Nilsson, M.-C., Steijlen, I. & Hörnberg, G. 1995. Regeneration pulses and climate – vegetation interactions in nonpyrogenic boreal Scots pine stands. – *Journal of Ecology* 83: 469–483.