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The role of bryophytes and lichens in terrestrial ecosystems

ROYCE E. LONGTON
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2.1 Introduction

The importance of bryophytes and lichens in primary succession has long been recognized. Otherwise these plants have generally been regarded as troublesome to identify when compiling relevés but of little significance in the functioning of mature communities. This attitude has recently changed with the use of mosses and lichens as pollution monitors, and it has also been realized that they play a significant role in the functioning of undisturbed communities (Longton 1984; Seaward 1988; Slack 1988). Nowhere is the importance of mosses and lichens greater than in polar tundra and in northern forests and mires, which have so far been less modified by human activity than other, more complex ecosystems. Such communities are ideally suited to the study of fundamental ecosystem processes, and their cryptogamic component was intensively investigated during the International Biological Programme (Longton 1988*d*). Global warming is likely to be most intense at high latitudes, and the role of bryophytes and lichens in boreal and polar communities is therefore emphasized in this account.

2.2 Succession

2.2.1 Primary succession on rock

Vegetation has developed through colonization of bare areas by pioneer organisms, followed by the gradual displacement of the pioneers in a series of successional communities. The component biota are believed to modify edaphic and microclimatic conditions in ways that favour members of the next community, with which they therefore become unable to compete. Succession thus reflects interaction between abiotic factors and the influ-

ence of the successional species. It may culminate in the establishment of relatively stable, climax vegetation. Bryophytes and lichens are commonly prominent during succession and undoubtedly influence rates of change, although climax vegetation appears to be determined principally by climate interacting with drainage patterns and the chemistry of surface rocks.

Adaptations enabling lichens to colonize rock surfaces include longevity, tolerance of desiccation and extreme temperatures, and low growth rates commensurate with the slow release of mineral nutrients from the substratum (Topham 1977). Many mosses show similar characteristics. Crustose lichens are often the first visible colonizers, giving way to foliose lichens or small cushion-forming mosses and later to fruticose lichens associated with mats and turfs of larger bryophytes. However, species composition, growth-form representation (Hale 1983; Richards 1984), and the relative abundance of bryophytes and lichens vary in relation to moisture, rock type, and other factors within a climatic region.

Once established, mosses and lichens promote soil formation by accelerating physical and chemical weathering, by trapping wind-blown organic and inorganic material, and by contributing directly to undecomposed organic matter. They appear also to concentrate several essential elements, including K, P, and S (Syers and Iskandar 1973; A. J. E. Smith 1982; Ugolini and Edmunds 1983), and may increase the availability of N, which is typically low in young soils.

Physical weathering is promoted by expansion and contraction of α appressed, partially endolithic crustaceous lichens as their water content varies, and by penetration of rhizines of foliose species which leads to the influx of water and thus to frost action. Lichens induce chemical weathering by liberating oxalic acid, carbonic acid and lichen compounds, which may crystallize on the outer surface of hyphae bringing them into direct contact with the rock. Although of high molecular weight, lichen compounds are slightly water-soluble and act as metal chelating agents (Rundel 1978).

SEM studies have confirmed the incidence of weathering beneath lichen thalli (Ascaso 1985; Jones and Wilson 1984; Viles 1987), where etching of the rock creates irregular surfaces susceptible to physical weathering. Garty and Delarea (1987) described how germinating ascospores of *Caloplaca aurantia* establish contact with free-living cells of a green alga, presumably *Trebouxia*, in pits in weathered roof tiles, with dust particles becoming trapped in the young thallus. Penetration of lichens into rock, also with incorporation of rock particles into the thalli, has been demonstrated on Antarctic quartz mica-schist (Walton 1985*d*). Direct evidence of substantial weathering comes from antarctic sandstones, where the surface periodically peels off due to cementing material between the rock crystals being dissolved by substances released from endolithic lichens (Friedmann 1982).

Snails feeding on endolithic lichens in desert limestone ingest up to 9 mm³ rock per individual per day, resulting in weathering at 0.7–1.1 metric tons ha⁻¹ yr⁻¹ (Schachak *et al.* 1987).

Whether lichen-associated weathering on such a scale is widespread remains unclear. Free-living fungi show greater ability than either fungi or algae isolated from lichens to chelate ferric iron in culture (Williams and Rudolph 1974). Brodo (1973) considered that weathering, humus formation, and entrapment of wind-blown particles by lichens are very slow. Thalli of *Rhizocarpon geographicum* on Arctic rocks may be several thousand years old (Andrews and Barnett 1979) confirming that lichen colonization does not always initiate rapid succession. Indeed, lichens or bryophytes may retard weathering by protecting surfaces from erosion, by insulating against freeze–thaw cycles, or by absorbing precipitation and further reducing frost shattering (Lindsay 1978). Danin *et al.* (1983) considered that lichen cover accelerates weathering in dry environments but protects the rock surface under wet conditions. The importance of lichens in weathering and pedogenesis is critically assessed by Jones (1988).

While crustose lichens are normally the first visible colonizers of newly exposed rocks, their presence is not always necessary to permit subsequent establishment of mosses, often in cracks or depressions. Moss rhizoids and associated fungi penetrate at least 5 mm into some rocks (Hughes 1982). Moreover, mosses grow faster than lichens, giving a greater capacity to trap wind-blown material and to contribute organic matter to developing soil (A. J. E. Smith 1982). Oosting and Anderson (1939) considered these processes of greater significance than the influence of cryptogams on weathering in their classic study of granite outcrops in North Carolina. The first colonizers, crustose and foliose lichens such as *Verrucaria nigrescens* and *Parmelia conspersa*, were regarded as unimportant in aiding establishment by other species. The effective pioneer was the moss *Grimmia laevigata* which formed spreading cushions. As the margins advanced, *G. laevigata* was displaced in the centre by communities dominated successively by the fruticose lichen *Cladonia leporina*, by *Selaginella rupestris* and by *Polytrichum ohioense*. As these communities spread laterally concentric zonation became established. Eventually, soil thickness in the centre of the mats increased, paving the way for angiosperm dominated vegetation. Many variations on this theme have been described (Topham 1977).

2.2.2 Primary succession on inorganic particulates

Several plant forms can act as pioneers on sand, gravel, and glacial till. Mosses and grasses are often the first macrophytes, with little association between the two (Corner and Smith 1973; Fridriksson 1975; Worsley and

Ward 1974). Indeed, on South Georgia some moraines subject to cryoturbatic disturbance are colonized first by grasses, with mosses later becoming established in older grass tufts. In contrast, crustose lichens appear first on more stable soils, subsequently giving way to colonies of mosses in which flowering plants become established (Heilbron and Walton 1984; Smith 1984).

Cryptogams undoubtedly influence pedogenesis on immature mineral soils by contributing organic matter and through their impact on nutrient cycling and their stabilizing effect on soil temperature and moisture regimes (Rouse and Kershaw 1971; Edward and Miller 1977). Usnic acid and other sparingly soluble lichen compounds are mobile, and Dawson *et al.* (1984) suggested that they contribute significantly to podsolization and profile development in coniferous woodland and alpine tundra soils. Mucher *et al.* (1988) showed that the occurrence of cryptogams, including species of *Diploschistes*, *Xanthoparmelia* (lichens), *Bryum*, *Desmatodon* (mosses), and *Taraxionia* (liverwort) was positively associated with the formation of a surface crust which prevents erosion of red earths in Australian rangelands. Soils beneath the mosses and lichens also had water and nutrients concentrated near the surface, and the cryptogams were considered desirable in terms of seed lodgement and germination.

2.2.3 Primary succession in water

Mosses are also important in successional processes that convert water bodies to dry land. In boreal regions, *Sphagnum* spp., associated with sedge rhizomes, form floating mats that extend outwards from the shore, increase in thickness, and eventually support plants characteristic of mires and later of mesic communities. Thus forest may develop on a floating raft of peat (Virt and Slack 1975; Tallis 1983). Benthic mosses such as *Drepanocladus* and *Scorpidium* spp. are influential in the early stages of other Arctic hydroseres by accelerating accumulation of organic matter and inorganic sediments on lake bottoms (Pohlinn 1935).

2.2.4 Auto-succession

While climax vegetation often develops through successive replacement of one community by another there is growing evidence that some vegetation develops by auto-succession. Muller (1952) defined this as 'a succession consisting of a single stage, in which pioneer and climax species are the same'. It occurs particularly where climatic severity so restricts the number of species that competition is minimized and displacement fails to occur. Originally described in alpine vegetation in Scandinavia (Muller 1952), auto-succession also predominates among luxuriant cryptogamic commu-

nites in the cold Antarctic, where there is little evidence of competition, or replacement of one community by another (Smith 1972; Longton and Holdgate 1979). Nor is this pattern restricted to areas of extreme climatic severity. Oosting and Anderson (1939) noted in North Carolina that successional change was very slow and that 'some places may actually be in a condition of pioneer equilibrium'.

2.2.5 Secondary succession

Bryophytes and lichens are prominent in succession following the destruction of established vegetation. An abundance of *Fumaria hygrometrica* on burnt-over ground, and of other small acrocarpous mosses on disturbed roadside verges, is a familiar sight throughout temperate regions. The nutrient relationships of *F. hygrometrica* on soils enriched by fire are discussed by Southorn (1977) and Dieterl (1979), but the impact of these pioneer mosses on soil development has not been investigated.

Mosses and lichens are both prominent in secondary succession in the boreal forest, where lightning-induced fire is a recurrent factor. The following (Ahti 1977) is one of several characteristic lichen sequences: 1. Bare soil; 1-3 years after fire; 2. Crustose lichen stage, 3-10 years, characterized by *Leclidea* spp.; 3. Cup lichen stage, 10-30(-50) years, characterized by species of *Cladonia* subgenus *Cladonia*, e.g. *C. crispata*; 4. First reindeer lichen stage, 30(-50)-80(-120) years, characterized by species of *Cladonia* subgenus *Cladina*, e.g. *C. rangiferina*; 5. Second reindeer lichen stage, beginning after 80(-120) years, characterized by *Cladonia* (*Cladina*) *stellaris*. The moss *Ceratodon purpureus* and the thallose hepatic *Marchantia polymorpha* are also among the earliest colonizers of bare soil, while *Polytrichum juniperinum* and *P. piliferum* are associated with *Leclidea* spp. during the crustose lichen stage.

Cladonia spp. or *Stereocaulon paschale* carpet the ground beneath white spruce (*Picea glauca*) in open lichen woodland in the north of the Canadian boreal forest. Lichen woodland may be a climax community on sandy soils under dry, continental climates (Ahti 1977; Johnson 1981), although Klein (1982) considers it dependent on the regular occurrence of fire. In moist habitats (Matkawa and Kershaw 1976), and more generally in oceanic areas, closure of the tree canopy occurs and fruticose lichens become replaced by the large, welf-forming pleurocarpous mosses *Hylacomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*, often associated with tall turf-forming mosses (*Dicranum* spp.) and colonized by foliose lichens such as *Peltigera* spp. (Fig. 2.1). These plants may later be overgrown by *Sphagnum* spp. which blanket the forest floor causing waterlogging and reductions in pH, decomposition rates, nutrient availability, and forest productivity (Foster 1985). Paludification, resulting in

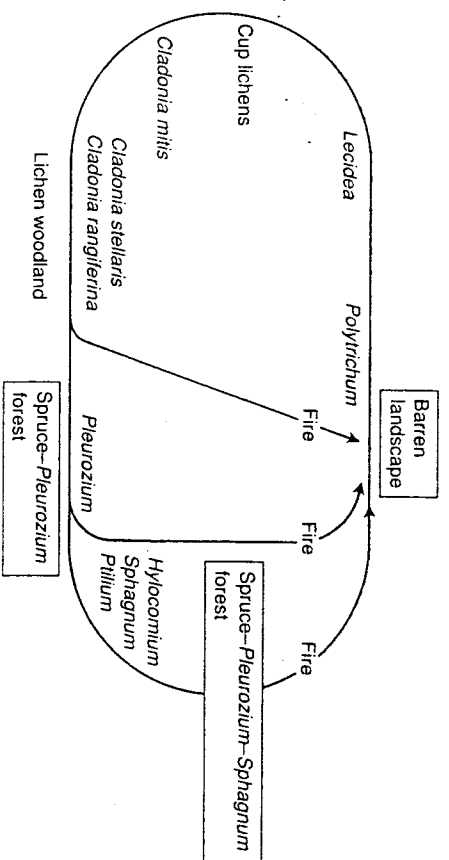


Fig. 2.1 Schematic representation of fire-induced succession in Canadian boreal forests (after Foster 1985).

degeneration of forests following invasion of *Sphagnum* spp., occurs widely in northern regions (Tallis 1983; see also Chapter 7).

Cryptogams modify environmental conditions throughout the post-fire sequence. Before colonization, there is wide diurnal temperature fluctuation at the ground surface, with high maxima inimical to many plants during sunny weather. Colonization by *Polytrichum* and *Leclidea* spp. increases surface albedo, thus reducing net radiation, and accumulating organic matter retains moisture so that absorbed energy is increasingly dissipated as latent heat. Maximum surface temperatures therefore decline, favouring the establishment of fruticose lichens which have a similar, but enhanced, effect. Their elimination following closure of the canopy apparently results from light limitation of photosynthesis (Kershaw 1985). Besides stabilizing soil temperature and moisture regimes, cryptogams are major contributors of organic matter to the soil, leading to acidification of the surface layers, even though accumulation of organic matter may be accompanied by increases in exchangeable cations (Filion and Payette 1989).

2.2.6 Cyclic succession

Bryophytes and lichens are commonly involved in cyclic succession. This occurs in subclimax communities where directional succession is reversed, as where thalli of pioneer epilithic lichens, such as *Parmelia saxatilis* and *Placopsis contortuplicata* in the cold Antarctic (Lindsay 1978), slowly expand to form roughly circular colonies which die and become eroded from the centre outwards. This restores a bare surface that may be recolonized by

the same, or ecologically related species. A more dynamic situation was revealed by John's (1989) analysis of lichens on a rock slide in the Rocky Mountains. A diversity of crustose lichens and more competitive foliose species gave total cover as high as 84 per cent, but most species were represented by a large proportion of small (presumably young) thalli, suggesting that active recruitment continued. There was little evidence of succession towards climax forest, and John suggested that cyclic succession, initiated by death or erosion of older thalli, was maintaining the diverse community: species distribution was also thought to be influenced by allelopathic substances released by some of the crustose species. Cryptogams are also involved in cyclic processes that result in temporal change in species composition at a given point within a climax community, for example in association with the pattern of growth and regeneration of *Calluna vulgaris* bushes in heathland (Fig. 2.2).

2.2.7 Succession and strategies.

Both primary and secondary succession are normally marked by a progressive increase in species diversity, although diversity may decline slightly in the climax community. This applies to the ecosystem as a whole (Odum 1971), and to the cryptogamic component (Magomedova 1980; Filion and Payette 1989). It implies that competition becomes more intense as succession proceeds. In a parallel trend, there is a tendency for r-selection to predominate in pioneer communities, giving way to K-selection in the climax, a pattern also evident among bryophytes (During 1979) and lichens (Topham 1977; Rogers 1988). Ahti (1982) considered some species of *Cladonia*, such as *C. crispata*, to be r-selected since they are effective colonizers with a capacity for rapid population growth, early maturation, and abundant production of small ascospores. Later species, such as *C. stellaris*, show K-selection as they operate as large, long-lived perennials in stable communities and show a lower, primarily asexual reproductive effort. Similarly *Funaria hygrometrica*, a pioneer moss following fire on Spanish dunes had a higher reproductive effort, in terms of both spore output and investment in sporophyte tissue, than the perennial *Tortella flavovirens* in nearby woodland (Longton 1988b). In many groups a trend from r-selection to K-selection is marked by an increase in diaspore size. This pattern is less clear among bryophytes and lichens, where one species may produce show and asexual diaspores in a range of sizes, and many ruderal mosses show shuttle strategies marked by large spores (During 1979).

Rogers (1990) has recently related an assemblage of over 30 lichen species to Grime's (1979) triangular ordination of strategies. He confirmed that species of relatively stable vegetation, such as *Cladonia alpestris*, lie near

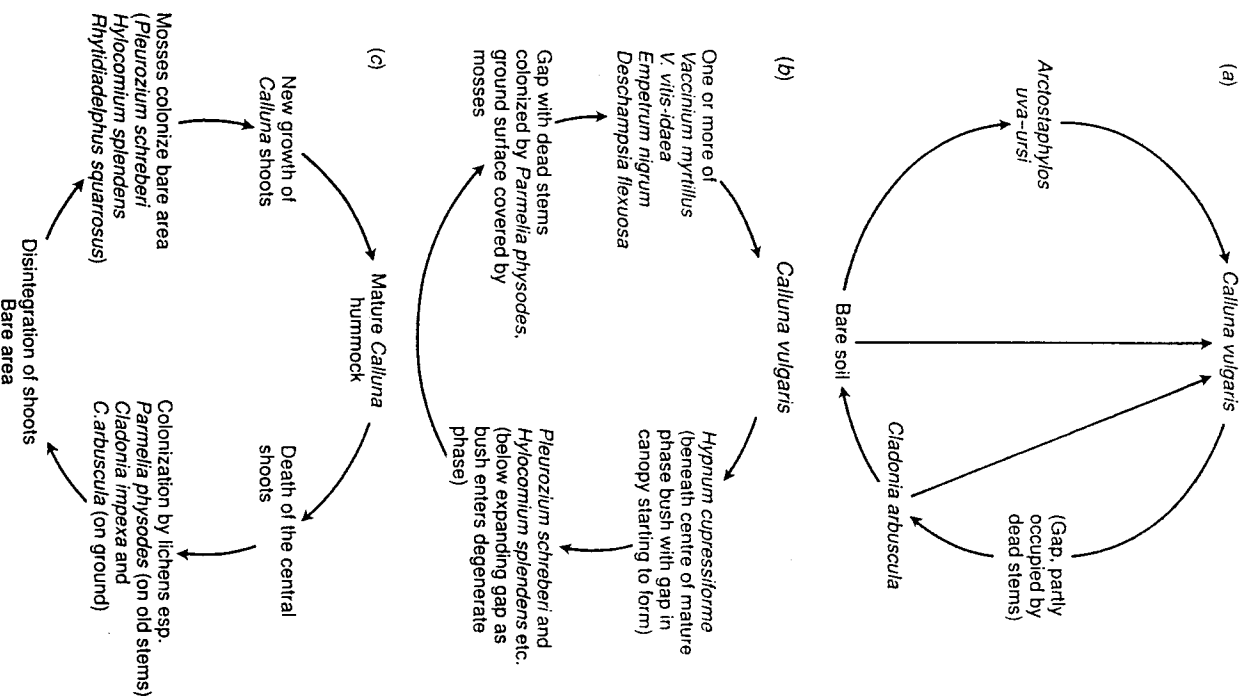


Fig. 2.2 Examples of cyclic succession in *Calluna*-dominated communities in Scotland, indicating the importance of mosses and lichens in (a) a *Calluna-Arcostaphylos* community; (b) a *Calluna-Vaccinium* community; (c) a dune heath. (*Parmelia physodes* = *Hypogymnia physodes*; *Cladonia impexa* = *C. portentosae*, *Hypnum cupressiforme* is probably *H. julandicum*). Reproduced from Gimingham (1972) by permission of Chapman and Hall.

the competitor pole of the ordination on the basis of large size and high relative growth rate. His findings also suggest that strategies among pioneer species may vary with substrate, as lithophytes such as *Rhizocarpon obscurata* and epiphylls such as *Porina epiphylla* showed the characteristics of stress tolerators and ruderals respectively. A detailed consideration of bryophyte and lichen strategies in different communities is presented in Chapter 1.

2.3 Production and phytomass

Bryophytes and lichens are dominant in many tundra and mire communities. They also contribute substantially to phytomass in a number of other vegetation types, of which only selected examples can be considered here. Grassland (Van Tooren *et al.* 1988) and coastal desert (Nash *et al.* 1977) are among further types of vegetation with significant cryptogamic components. Methods of assessing cryptogamic production and phytomass, and their reliability, are discussed by Longton (1988a), Russell (1988), and Russell and Botha (1988).

Table 2.1 Vegetation zones in polar regions (Longton 1988a)

Zone	Highest mean monthly air temperature (°C)	Characteristics of the vegetation
Mild polar	6–10 (to 12)	Extensive grass heath, dwarf shrub heath, mire, and other closed phanerogamic vegetation. <i>Sphagnum</i> abundant in many mires, though local in the mild Antarctic. Fellfields on the drier uplands.
Cool polar	3–7	Open fellfields and barrens predominant but mire, dry meadow, and other closed angiosperm-dominated communities locally extensive in favourable habitats. Dwarf shrub heaths of restricted occurrence or absent. <i>Sphagnum</i> seldom a major component of mires.
Cold polar	0–2	Closed stands of bryophytes, lichens, or algae extensive where wet or mesic conditions occur, with open cryptogamic vegetation on drier ground. Herbaceous phanerogams subordinate to cryptogams or absent. Liverworts frequent.
Frigid polar	<0	Vegetation largely restricted to scattered colonies of mosses, lichens, or algae, and to endolithic micro-organisms. Phanerogams absent. Liverworts very rare.

2.3.1 Polar tundra

Polar regions are highly variable in climate and vegetation. Four intergrading vegetation zones may be recognized based on growth-form representation. The zonation is correlated with mean summer temperature (Table 2.1).

The frigid Antarctic

The frigid Antarctic has no counterpart in the Arctic. Mean air temperature normally remains below 0°C throughout the year, and aridity is a major limiting factor. The entirely cryptogamic vegetation is largely restricted to sparse, open communities of algae and small turf- and cushion-forming mosses such as *Bryum* and *Grimmia* spp. on the predominantly mineral soil and of lichens, including crustose, foliose, and fruticose species, on rocks (Longton 1979a). The few estimates of annual production in open moss communities are all <5 g m⁻² (Longton 1974; Ino 1983). Total phytomass is only 5–200 g m⁻² in the typical open communities (Longton 1974; Kappen 1985), but reaches 1000 g m⁻² in occasional closed stands of mosses and of epilithic fruticose lichens. Green phytomass alone was 1097 g m⁻² in an exceptional stand of mosses (Seppelt and Ashton 1978). Endolithic lichens are a major component of the biota. Their productivity is estimated at <5 mg m⁻² yr⁻¹ but turnover is slow (Vestal 1988), with organic matter in the surface layers of rock reaching 46–177 g m⁻² (Friedmann 1982).

Cold polar regions

Mean air temperatures in the more oceanic cold Antarctic reach only 0–2°C in summer, but mean winter temperatures may remain as high as –8 to –10°C. Precipitation is light but frequent. The terrain is rugged with much bare ground in the uplands; there are only two native angiosperms, but luxuriant cryptogamic communities are developed extensively close to sea level. These include deep banks of tall turf-forming mosses, notably *Polytrichum alpestre* and *Chorisodontium aciphyllum*, on mesic slopes with carpets and large hummocks of *Calliigon* spp., *Drepanocladus* spp., and other pleurocarps in seepage areas and permanently wet situations. Associations of *Andrya* with *Usnea*, *Himantornia* spp. and other fruticose lichens occur on inland rocks, while species of *Caloplaca*, *Xanthoria*, and crustose lichens clothe exposed coastal rocks. Annual production ranges from 200–900 g m⁻² in closed moss turf and moss carpet communities (Longton 1970; Davis 1981), levels comparable with those in temperate grassland. Phytomass is also large in the moss turfs, reaching 300–1000 g m⁻² for green shoots, 20 000–30 000 g m⁻² for phytomass above permafrost,

and up to 46 000 g m⁻² for total phytomass including permanently frozen material to the base of a bank 1 m deep. Estimates of 250 g m⁻² for annual production and 800–1750 g m⁻² for phytomass have been reported for fruticose lichens (Smith 1984).

Cool and mild polar regions

Flowering plants are conspicuous in cool and mild polar tundra (Table 2.1), in areas where mean temperatures in summer are typically 3–10°C. Bryophytes and lichens are abundant associates, and are dominant in communities such as *Racomitrium* heath and lichen heath. Production generally increases along a xeric → hydric gradient. It is higher in Antarctic than in Arctic regions (Longton 1988a; Russell 1990), probably because of greater precipitation and soil enrichment by marine sources of N and P.

Turf- and cushion-forming mosses including *Andreaea* and *Dirichium* spp., with mat-forming pleurocarps such as *Hylacomium*, *Hypnum*, and *Racomitrium* spp., grow between cushions of *Dryas* spp. and other flowering plants in xeric fellfields. Associated species include crustose (e.g. *Lecidea*, *Ochrolechia* spp.), fruticose (*Sphaerophorus* spp.) and foliose (*Parmelia*, *Solorina*) lichens. Grass heath is one of the most extensive mesic vegetation types in the Arctic. It is formed by caespitose grasses and sedges, including species of *Kobresia* and *Carex*, associated with abundant cryptogams. Mosses include tall turfs of *Dicranum*, *Dirichium*, and *Polytrichum*, and mats of *Hypnum* or *Racomitrium* spp., while species of *Cetraria*, *Cladonia*, *Stereocaulon*, and other fruticose lichens are often prominent.

Total annual production in these communities is generally <60 g m⁻². The contribution of mosses to both production and phytomass varies between stands but is often substantial, and while lichen production is low, lichens commonly form a significant proportion of above-ground phytomass (Table 2.2). This contribution reaches 44 per cent in mesic graminoid communities in Alaska (Webber 1978). Strikingly high ratios of phytomass:production of up to 70:1 have been recorded for mosses in arctic grass heaths. Annual production in grass heaths, herbfields and other mesic communities on cool Antarctic islands reaches 850–1650 g m⁻²; bryophyte production has been recorded as only 150–250 g m⁻², but mosses again contribute significantly to above ground production and phytomass. These points are illustrated in Table 2.2, which also emphasizes the sparse total production, with insignificant moss and lichen components, in the extensive barrens that characterize the more arid parts of the North American cool Arctic.

Arctic wetlands are dominated by grasses and sedges with rhizomes embedded in an understorey of mosses. These include large, turf-forming acrocarps, e.g. species of *Mesita* and *Cindidium*, and carpet-forming

pleurocarps like *Calliergon* and *Drepanocladus* spp. Hepatics also occur and *Sphagnum* spp. are abundant, particularly in the mild Arctic. Total annual production is normally 100–300 g m², with bryophytes representing 10–45 per cent of the total and exceeding the above-ground vascular plant component at wetter sites. Below ground parts of flowering plants often form the major component of both production and phytomass. High phytomass:production ratios again characterize the bryophytes. Lichen production is generally low and phytomass variable (Table 2.2).

Production in individual colonies of cool Antarctic mosses reaches the remarkably high levels recorded for continuous stands in the cold Antarctic, estimates ranging from 27 g m⁻² for *Dirichium strictum* in dry fellfield to 1028 g m⁻² for *Pohlia mahlenbergii* and *Tortula robusta* in streams (Clarke *et al.* 1971; R. I. L. Smith 1982; Russell 1985). Production in individual colonies is again higher in the cool Antarctic than in comparable arctic situations, with annual production in *Polytrichum alpestre* estimated as 450–500 g m⁻² in cool Antarctic tussock grassland compared with 100–150 g m⁻² in mild Arctic spruce woodland (Longton 1979b). Similarly, productivity of *Cladonia rangiferina* on South Georgia may reach 100–1130 g m⁻² yr⁻¹ (Lindsay 1975; Smith 1984), whereas maximum values reported by Andreev (1954) for Arctic cladonias were only 17–27 g m⁻² yr⁻¹.

Adaptations of polar bryophytes and lichens

Polar environments are characterized by a cool, usually short growing season and low solar irradiance. Continental regions experience severe winter cold and low precipitation, while the immature soils are typically deficient in P and available N. These conditions impose severe limitations on the growth of vascular plants, and yet mosses and lichens are abundant and the mosses may be highly productive. Factors underlying the success of bryophytes and lichens in polar regions are discussed in depth by Kershaw (1985) and Longton (1988a).

Mosses and lichens are remarkably similar in terms of attributes favourable in polar regimes. Many show a broad response of net assimilation rate (NAR) to temperature, often with maxima at 10–15°C but with substantial rates of both net assimilation and dark respiration maintained at temperatures close to or below 0°C (Fig. 2.3). Light compensation and saturation levels are typically lower than in vascular plants, and both decrease at low temperature. This permits positive net photosynthesis under cool, low-light conditions. Some species become photosynthetically active beneath snow cover in spring, and maintain positive net assimilation for 24 hours per day in mid-summer (Oechel and Sveinbjörnsson 1978), while physiological responses show acclimatization to changing conditions

Table 2.2 Representative data for annual net production and phytomass (g m^{-2}) in mild and cool polar vegetation

Vegetation Type	Locality	Annual net production					Phytomass				
		Vascular plants					Vascular plants				
		Above-ground	Below-ground	Bryophytes	Lichens	Total	Above-ground*	Below-ground	Bryophytes	Lichens	Total
ARCTIC											
Wet meadow											
Cotton grass-dwarf shrub tundra	Demster, Alaska	87	—	69	<5	—	66(+102)	2372	4753	69	7362
Wet sedge-moss meadow	Devon I, Canada	46	130	103	0	279	78(+120)	1295	1097	0	2592
Hummocky sedge-moss meadow	Devon I	45	104	33	0	182	86(+187)	2023	908	0	3208
Frost-boil sedge-moss meadow	Devon I	58	119	15	0	193	112(+202)	1332	1100	0	2748
Grass heath											
Graminoid steppe	Elef Ringness I, Canada	13	13	32	<1	58	13(+74)	88	2128	20	2323
Moss-graminoid meadow	King Christian I, Canada	5	5	32	<1	42	41	23	2136	10	2210
Dwarf shrub heath											
<i>Cassiope tetragona</i> heath	Devon I	18	90	20	4	132	159(+228)	1041	423	48	1899
Fellfield											
Cushion plant-lichen fellfield	Devon I	15	3	2	3	23	89(+298)	57	15	49	508
Cushion plant-moss fellfield	Devon I	27	5	20	2	54	126(+192)	50	600	23	991

Table 2.2 (cont.)

Vegetation Type	Locality	Annual net production					Phytomass				
		Vascular plants					Vascular plants				
		Above-ground	Below-ground	Bryophytes	Lichens	Total	Above-ground	Below-ground	Bryophytes	Lichens	Total
Barren											
<i>Papaver radicata</i> barren	Devon I	0.5	1.0	0.1	0	1.5	310(+8.2)	0.9	2.4	0	15
ANTARCTIC											
Grass heath											
<i>Festuca contracta</i> heath	South Georgia	340	350	150	2	842	425(+1598)	1642	500	12	4177
Herbfield											
<i>Acaena magellanica</i> herbfield	South Georgia	885	500	250	0	1635	1300(+517)	7536	221	0	9574
<i>Pleurophyllum hookeri</i> herbfield	Macquarie I	314	550	146	4	1014	139(+266)	1920	393	9	2727

*Living (+standing dead)
Data from various sources as indicated in Longton (1988a)

during the growing season (Fig. 2.3). On the negative side, moderate illumination at low temperature causes photoinhibition in some mosses (Adamson *et al.* 1988) and lichens (Kappen *et al.* in press).

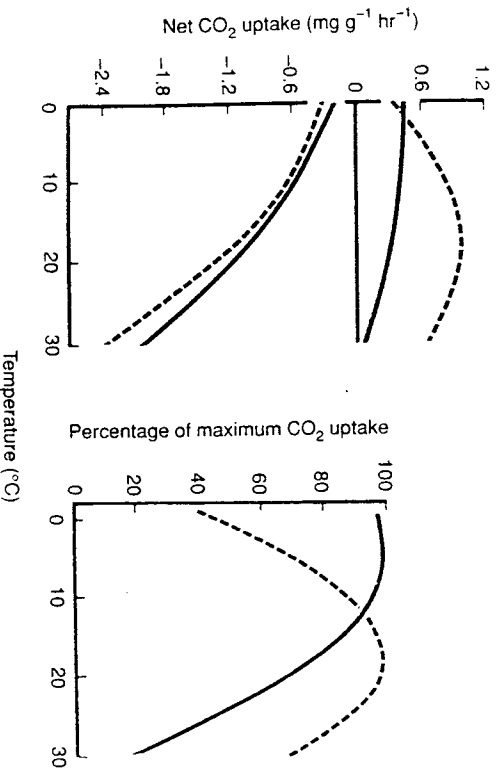


Fig. 2.3 Temperature responses of net photosynthesis and dark respiration in the moss *Polytrichum alpinum* from wet meadow in Alaska in early summer (solid line) and late summer (broken line). Data from Oechel and Sveinbjörnsson (1978).

Many mosses and lichens are poikilohydric (Proctor 1990). They have little access to soil moisture, but lack an effective cuticle, thus enabling them to absorb water through much of their surface. However, this results in rapid water loss under drying conditions, and in compensation the cytoplasm is desiccation-tolerant. The plants become inactive when dry, but resume normal metabolism rapidly on re moistening. This feature may also be adaptive in polar environments as the plants are able to utilize short periods of favourable conditions whenever they occur. Rates of drying, and the length of active periods, are influenced by the spatial organization of individuals within the colony, leading to correlation between growth-form and habitat. Poikilohydry may also enhance frost resistance, by conferring tolerance of cytoplasmic dehydration resulting from extra-cellular ice formation.

These features are also shown by mosses and lichens at lower latitudes, and many ecologically important tundra cryptogams occur in boreal and temperate communities. Lechowicz (1982) found no correlation with latitude of origin in respect of maximum NAR, saturating irradiance, or optimum water content for photosynthesis in lichens, although there was a

significant trend of decreasing optimum temperature for net photosynthesis with increasing latitude. Some Antarctic lichens have temperature optima below 0°C, but this results from enhanced respiration at high temperatures (Lange and Kappen 1972) rather than from high NAR under cold conditions.

Some mosses show inherent intraspecific variation between polar and temperate populations. Clinal variation in leaf length and annual shoot elongation in *Polytrichum alpestre* results in short, compact turfs in cold, dry polar environments (Longton 1979b). Maximum NAR declines with increasing latitude of origin in *P. commune* and other mosses (Sveinbjörnsson and Oechel 1983; Kallio and Saarnio 1986). Comparable variation occurs within lichen species, for example between populations of *Alectoria ochroleuca* from contrasting arctic environments (Larson and Kershaw 1975), but cultivation difficulties have prevented confirmation of a genetic basis. There is also evidence of adaptive physiological variation between species characteristic of different polar habitats (Kershaw 1985).

2.3.2 Boreal forests

A continuous understorey of bryophytes and lichens is characteristic of boreal forests, where prolonged severe winters alternate with mild summers at mean July temperatures up to 20°C. As a broad generalization, the predominant cryptogams are *Cladonia* spp. and other fruticose lichens on dry soils, particularly in open woodland in the north, and large, wet-forming pleurocarpous mosses, notably *Hylacomium splendens* and *Pleurozium schreberi*, under mesic conditions. *Sphagnum* spp. become abundant at wetter sites.

Phyтомass of *Cladonia stellaris* may exceed 300 g m⁻² in mature lichen woodland, with the lichen carpet over 10 cm deep (Ahti 1977). Maximum production occurs in younger, shallower lichen stands (Andreev 1954), because NAR is depressed in older colonies due to respiration below the level of effective light penetration (Sveinbjörnsson 1987). Ahti (1977) considered that the most productive lichen stands for reindeer grazing were at the first reindeer lichen stage, with a depth of 4–6 cm, phyтомass of 50–150 g m⁻², and annual production of 6–16 g m⁻². Boreal forests may also support abundant epiphytic lichens including foliose species such as *Hypogymnia physodes* and *Platismatia glauca*, and finely branched fruticose species, e.g. *Pseudocercaria*, *Usnea* and *Alectoria*, spp. hanging in festoons from trunks, branches, and twigs. Phyтомass of arboreal lichens may reach 500 kg ha⁻¹ of forest (Scott 1962).

Abundance of mosses varies between different communities. In Alaska, green phyтомass of *Hylacomium splendens* and *Pleurozium schreberi* was 170–290 g m⁻² under spruce at densities up to 7000 shoots m⁻². Mean

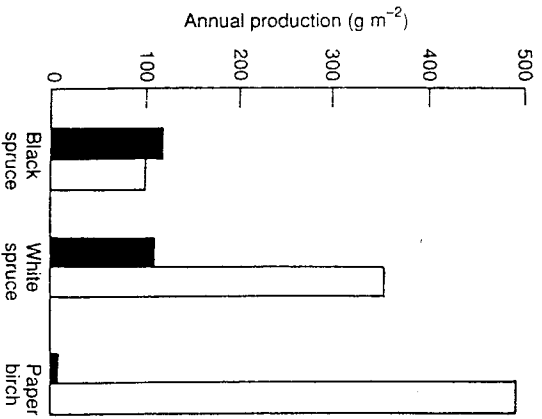


Fig. 2.4 Annual production of mosses (black) and the above-ground component of trees (white) in selected forest types in interior Alaska. Data from Oechel and Van Cleve (1986).

mass density was often less than 10 shoots m^{-2} in successional stands of *Betula* and *Populus* spp., with phytomass only 4–6 $g m^{-2}$. Annual moss production was negligible in the deciduous forests, but ranged from 70–150 $g m^{-2}$ under spruce, where it commonly exceeded above-ground tree production (Fig. 2.4). Comparable production by the large pleurocarpous mosses has been reported in other coniferous forests (Tamm 1953; Weetman 1968; Pakarinen 1978). As ectohydric mosses, *H. splendens* and *P. schreberi* derive water largely from precipitation, and thus seasonal timing and annual extent of growth vary with rainfall patterns (Busby *et al.* 1978; Longton and Greene 1979; Vitt 1990).

2.3.3 Temperate forests

Many temperate deciduous forests have a sparse growth of cryptogams on the ground, as at sites in New Hampshire where bryophyte phytomass was only 2–3 $g m^{-2}$ (Forman 1969). However, Rieley *et al.* (1979) reported bryophyte phytomass of 1600–2900 $g m^{-2}$ in Welsh oakwoods (*Quercus petraea*), as compared with only 250–300 $g m^{-2}$ for the herb layer. The dominant mosses included ectohydric pleurocarps such as *Planozium schreberi* and *Rhytidiadelphus loreus*, and partially endohydric acrocarps including *Dicranum majus* and *Polytrichum formosum*. Production was estimated as 170–210 $g m^{-2}$ for the mosses and 120 $g m^{-2}$ for the herbs.

Shading by shrub and herb layers and dense tree litter, falling in autumn at what is often the beginning of the moss growing season (Pitkin 1975), may be important in limiting cryptogams on deciduous wood floors.

The greatest abundance of bryophytes and lichens in temperate forests is on rotting wood and as epiphytes. European epiphytic communities were described in detail by Barkman (1958). Abundance of epiphytes is greatest in oceanic regions, and Nadkarni (1984) estimated the mean phytomass of bryophytes on *Acer macrophyllum* in temperate rainforest in Washington State as c. 800 $g m^{-2}$ of tree surface, 27 $kg tree^{-1}$ or 5000 $kg ha^{-2}$ of forest. Epiphytic lichen phytomass has been estimated at 100–1800 $kg ha^{-1}$ in a range of North American temperate forests, with annual production from 50–500 $kg ha^{-1}$ (Pike 1978). Evergreen *Nothofagus* forests in southern Chile may also have a rich, luxuriant flora of lichens and bryophytes including an abundance of leafy hepatics (Greene *et al.* 1985; Guzman *et al.* 1990).

2.3.4 Mires

Mosses form a continuous understorey in mires from sub-Arctic to temperate and locally tropical regions, and are commonly the predominant peat-formers. Species of *Cladonia*, *Peltigera*, and other lichens are sometimes prominent, but probably contribute little to net production. *Sphagnum* spp. are the principal bryophytes in ombrotrophic bogs and nutrient-poor fens, while pleurocarpous mosses in the Amblystegiaceae and Brachytheciaceae are characteristic under minerotrophic conditions in richer fens (see Chapter 7). Associated species include graminoids and hepatics, with ericoids particularly in bogs. The gradient from bogs to rich fens is marked by increases in pH, Ca, Mg, and Na, but there is little variation in P and available N (Vitt 1990). Mires generally show a hummock–hollow topography with different mosses arranged along the resulting hydrological gradient.

Clymo and Hayward (1982) note that annual production of *Sphagnum* spp. has been recorded as 100–150 $g m^{-2}$ for hummocks, 500 $g m^{-2}$ in lawns, and 600–800 $g m^{-2}$ in pools over a wide latitudinal range. However, from literature data Moore (1989) detected a weak tendency for production to decrease in line with mean annual temperature towards the north. Although *Sphagnum* production within a mire is, in general, positively correlated with water availability, production on hummocks exceeds that in lawns under some circumstances (Moore 1989; Vitt 1990).

Mean *Sphagnum* production in mires varies from year to year, but is generally 70–400 $g m^{-2}$, with most values for pleurocarpous mosses in fens in the lower half of this range (Vitt 1990). The ratio of moss:vascular plant production also varies. Annual production of *Sphagnum* spp. at Stordalen,

northern Sweden, was 70 g m^{-2} , compared with 59 g m^{-2} for the above-ground plus 24 g m^{-2} for the below-ground angiosperm component (Rosswall *et al.* 1975). In contrast, annual production of *Sphagnum* and of vascular plants at Moor House, northern England, was estimated as 213 g m^{-2} and 659 g m^{-2} respectively (Forest and Smith 1975; Heal *et al.* 1975). The relative contribution of bryophytes to above-ground standing crop may exceed their contribution to production due to slow decomposition. At Stordalen, mean annual moss production exceeded above-ground vascular plant production by 1.2:1, whereas the green phytomass of the sphagna (300 g m^{-2}) exceeded that of vascular plants by 1.6:1 (Rosswall *et al.* 1975).

2.3.5 Tropical rain forests

General descriptions of tropical forest lichens (Sipman and Harris 1989) and bryophytes (Pócs 1982; Richards 1984; Gradstein and Pócs 1989) indicate that the ecological role of these plants, particularly lichens, remains unclear. The bryophytes and lichens are primarily epiphytic, and they increase in diversity and abundance with altitude. Perhaps in response to the prevailing high humidity, the corticolous bryophytes commonly exhibit growth-forms where the photosynthetic shoots are solitary rather than aggregated into colonies, although they are usually attached to a primary shoot system adherent to the substratum. Solitary growth-forms include the dendroid type (e.g. *Rhodobryum*), the bracket form where the green shoots spread horizontally (e.g. *Leiomela*, *Spiridens*), the hanging type where the long spreading branches grow vertically downwards (e.g. *Meteoriaceae*), and feather forms where the spreading shoots are more or less pinnately branched (e.g. *Hypopterygium*). The latter should not be confused with wet-forming pleurocarps of the boreal forest, which are sometimes referred to as 'feather mosses'. The bryophyte and lichen communities of tropical forests are described in detail in Chapter 9.

In studies along altitudinal gradients Frahm (1990) recorded bryophyte phytomass as generally below $10\text{--}12 \text{ g m}^{-2}$ of tree trunk at altitudes up to 1000 m, rising in montane regions to 140 g m^{-2} in Peru and 400 g m^{-2} (exceptionally to 800 g m^{-2}) in Borneo. The differences between localities were thought to reflect local rather than regional factors. For Borneo, these values represent phytomass of under 1 kg ha^{-1} of forest below 1000 m, rising to $200\text{--}500 \text{ kg ha}^{-1}$ (exceptionally to 1300 kg ha^{-1}) in the upper montane region. Even higher values of $10\text{--}300 \text{ kg ha}^{-1}$ were recorded for high-altitude epiphytic bryophytes in Tanzania (Pócs 1982). Although representing a small proportion of community phytomass, Pócs estimated that bryophytes absorb up to $30\text{--}000 \text{ l ha}^{-1}$ of water during a single rain event, a figure exceeding that elsewhere in the canopy. They were therefore

considered of great importance in maintaining soil nutrient status, limiting erosion, and in stabilizing the flow in rivers to the benefit of lowland agriculture.

Richards (1984) suggested that the low bryophyte biomass in humid lowland forests is due to a combination of continuous heat and humidity inducing respiration at rates not balanced by day-time photosynthesis in deep shade, and Frahm (1990) has provided supportive experimental evidence. Conversely the cooler, brighter, but equally humid conditions in the elfin woodland canopy are clearly favourable for many species.

2.4 Herbivory

A striking feature emerging from these data is the high phytomass:production ratios typical of bryophytes and lichens, particularly in tundra and mires. This is consistent with low rates of decomposition and herbivory (Frankland 1974; Lawrey 1986). Nevertheless, these plants form an important food resource for a wide range, if undoubtedly a minority, of animals, including both generalist and specialist feeders.

2.4.1 Lichens

Lichens are important winter food for many ungulates due to their availability when other food is in short supply (Richardson and Young 1977; Robbins 1987). They represent 60–70 per cent of the winter diet of caribou and reindeer (*Rangifer tarandus*), who reach the lichens by digging craters in soft woodland snow. *Cladonia* and *Cetraria* spp. are preferred to nitrogen-fixing lichens (Kallio 1975). Rundel (1978) cites earlier reports that *Cladonia stellaris* is preferred to *C. arbuscula* and *C. rangiferina*, which contain the bitter-tasting and possibly inhibitory depside fumaroprocetraric acid, but other authors consider *C. stellaris* less acceptable than related lichens (Gaare and Skogland 1975). Arboreal species of *Alectoria*, *Evernia*, and *Usnea* are also eaten. Reindeer herders in Fennoscandia fell lichen-covered trees to provide food during adverse conditions (Hustich 1951).

Lichens in some respects represent low quality food, the preferred species being deficient in protein, lipids, and several essential elements. Captive animals lose weight on a lichen diet unless given a nitrogen supplement (Staaland *et al.* 1984). However, the preferred lichens contain abundant carbohydrate (Scotter 1972), are readily digestible by *R. tarandus* which possesses the enzyme lichenase (White and Trudell 1980; Slack 1988), and provide an effective energy source in winter. This and other aspects of its nutritional relationship with lichens (Longton 1988a) led Klein (1982) to postulate that *Rangifer* evolved in response to a lichen-based Arctic food niche unoccupied by other animals.

One reindeer needs at least 2 kg dry weight of lichen daily in winter and browses about 2000 m² in six months. Overgrazing can increase the lichen regrowth period from 2–5 years to 10–15 or even 100 years (Slack 1988). Careful management of lichen pastures is therefore vital, as domesticated reindeer in Eurasia and free-ranging caribou in North America remain an important dietary component of indigenous Arctic people. This task is hindered by human interference in the form of pipelines and highways which alter migration routes. At the same time, increasing sulphur and nitrogen pollution in the Arctic pose a direct threat to the lichens. Accumulation and retention by lichens of radionuclides, from atmospheric weapon tests and the Chernobyl accident, has led to disturbing concentrations in meat and its human consumers (Hanson 1982; MacKenzie 1986), while accumulation of heavy metals by both lichens and mosses has implications for other food webs.

Bryophytes and lichens provide habitats in which a wide array of invertebrates, from protozoans to insects, find concealment and a stable environment, particularly as regards humidity. Some animals, e.g. lepidopteran caterpillars, mimic lichens as defence against predation (Seaward 1988), while both mosses and lichens are found attached to the backs of tropical forest weevils, apparently helping to camouflage the animals (Gressitt *et al.* 1965). The relationships range from accidental to cases where particular animals are seldom found except in association with mosses or lichens. Not all the animals concerned eat cryptogams. Animals regularly feeding on lichens include molluscs and mites, as well as springtails (Collembola), barklice (Psocoptera) and moths. Some feed almost exclusively on lichens (e.g. the orbaitid mites *Pimodius detritidis* and *Domotioria plantizaga*), while others eat lichens only when alternative food is unavailable. Springtails, in particular, may occur on lichens in vast numbers and their grazing can cause major damage. Invertebrates eat lichens by scraping the surface (molluscs), chewing (many insects) or piercing cells and sucking out their contents (prostitomatid mites). Details are given by Gerson and Seaward (1977) and Seaward (1988).

Rundel (1978), while noting that overall levels of herbivory on lichens are low, regarded consumption as irregular, with a variety of vertebrates and invertebrates consuming some species in considerable quantity. Low nutrient content, difficulties in metabolizing the polysaccharide lichenin, the patchiness of lichens as a resource, and morphological features, such as the gelatinous sheaths covering members of the Collembataceae, were considered inhibitory to feeding. Rundel pointed out that lichens with a high nitrogen content, while potentially the most nutritious, were normally among the least grazed, as supported by Lawrey's (1983) field observations and feeding trials. Rundel (1978) reviewed circumstantial evidence that

nitrogen-fixing lichens may be protected by terpenes while pulvinic acid derivatives, anthraquinones, depsidones, and depsides such as fumarprotocetraric acid were regarded as potentially defensive in some other types of lichen. However, acetone extracts from several lichens, containing depsides, depsidones, and usnic acid, had no significant effect on larvae of the gypsy moth (*Lymantria dispar*), whereas aqueous extracts reduced feeding and growth. The larvae are generalist feeders not normally attacking lichens. Glycosides and polypeptides were suggested as the active compounds in aqueous extracts (Blewitt and Cooper-Driver 1990). Lawrey (1986) concluded that unpalatability of lichens to invertebrates is based in part on chemical defence, that chemical defence is related to the nutritional value of the lichens, but that further research is required to assess the generality of the anti-herbivore role of lichen substances.

2.4.2 Bryophytes

Unlike lichens, mosses are seldom eaten in quantity by *Rangifer tarandus*, and their digestibility by caribou is low (Person *et al.* 1980; White and Trudell 1980; Thomas and Kroeger 1981). However, mosses are eaten in winter by herds on Arctic islands which have no access to abundant lichens, and on Svalbard the caribou appear to have evolved adaptations to a bryophytic diet, notably an enlarged caecum-colon complex (Staland *et al.* 1979). Mosses are freely consumed by other Arctic and alpine vertebrates, including geese, voles, and particularly lemmings (*Lemmus* spp.).

North American populations of *L. sibiricus* fluctuate through 4–6 year cycles, peak numbers reaching 100–200 individuals ha⁻¹ (Batzli *et al.* 1980). Plant consumption may then reach 25 per cent of above-ground production, with mosses such as *Callitregon*, *Dicranum*, and *Polytrichum* spp. forming 5–20 per cent of the diet in summer and 30–40 per cent in winter (Bunnell *et al.* 1975). However, captive lemmings lost weight on a moss diet, due to low ingestion and poor digestibility (Batzli and Cole 1979). Lemmings may eat mosses because of winter availability and relatively high concentrations of calcium, magnesium, and iron. Low digestibility could increase the value of mosses as a mineral source by increasing the intake required to satisfy energy requirements (Batzli and Cole 1979). Prins (1982) has further speculated that Arctic animals benefit from ingesting arachidonic acid, a highly unsaturated fatty acid with a low melting point (–49.5°C). Largely restricted to mosses among plants, this compound is present in unusually high concentrations in the blood of Arctic animals and could protect animal cell membranes, and increase limb mobility, at low temperatures.

Collared lemmings (*Dicrostonyx groenlandicus*) have been observed eating *Polytrichum* gametophytes in summer (Longton 1980), but captive animals

are only capsules when offered fruiting *Funaria arctica* (Pakarinen and Vitt 1974). In temperate regions, grouse chicks and timlice eat moss capsules (Richardson 1981), and capsules are freely eaten in some north American forests (Slack 1988). There are few reports of moss gametophytes being eaten by temperate or tropical vertebrates, and Rieley *et al.* (1979) suggested that preferential grazing of grasses by sheep leads to the abundance of bryophytes in Welsh oakwoods.

Some invertebrates also prefer capsules. Harvester ants (*Messor* sp.) collect capsules of *Crossidium cassiniere* in the Negev Desert, presumably opportunistically as the moss does not fruit every year (Loria and Herrstadt 1980). In Britain several species of slug (*Atrion* spp.) preferred capsules to gametophyte shoots of *Brachythecium rutabulum*, *Mnium hornum*, and *Funaria hygrometrica*, in the field and in laboratory trials. Young green capsules were heavily predated at some sites and were eaten in preference to brown capsules containing spores (Davidson and Longton 1987; Davidson *et al.* 1990). Protonema was eaten freely in the laboratory, but shoot consumption was negligible except for *Funaria hygrometrica*, a finding in agreement with the view that annuals invest less in defense than perennials (Gime 1979).

Studies reviewed by Gerson (1982, 1987) and Slack (1988) have confirmed that moss gametophytes are eaten by a range of invertebrates including species of tardigrades, gastropods, crustaceans, mites, and many groups of insects. Animals whose diet appears to comprise principally bryophytes include a scorpion fly (*Boreus brunalis*; Gerson 1982) and the tardigrade *Echiniscus testudo* (Morgan 1977). Gerson (1982) considered few moss feeders to be host specific, a view challenged by Whitehouse (1985). A common pattern of consumption involves stripping leaf lamina cells while leaving the midrib and any specialized border cells intact (Wyatt and Stoneburner 1989; Davidson *et al.* 1990). Other common moss feeders include aphids and mites that pierce the cells and suck out the contents.

A few quantitative assessments indicate that consumption may be locally high. Rock grasshoppers (*Trimerotropis saxatilis*) were estimated to eat *Grimmia laevigata* at 391 mg m⁻² yr⁻¹ in south-east USA (Duke and Crossley 1975), while weevils (*Ectomorphnus similis*) each consumed 1.67 mg of *Brachythecium rutabulum* per day (37 per cent of body weight) on a cool Antarctic island (Smith 1977). In general, however, consumption of moss gametophytes, including *Sphagnum* spp., appears to be remarkably low (Clymo and Hayward 1982; Longton 1988a; Davidson *et al.* 1990). Thus food intake by the microfauna in two cold Antarctic moss communities ranged from 200–300 g m⁻² yr⁻¹, but was principally bacteria, fungi, algae, and dead organic matter: living mosses and lichens contributed <0.2 g m⁻² yr⁻¹ (Davis 1981).

Bryophyte gametophytes generally have a lower calorific value than leaves of associated angiosperms (Forman 1968; Pakarinen and Vitt 1974), as reflected in lower protein and carbohydrate contents (Skre *et al.* 1975). However, the differences are generally small, and in the slug-grazing study ash-free calorific values of immature capsules, which were consumed, were no higher than those of the rejected leafy shoots (Davidson *et al.* 1990). Other factors that could contribute to the low acceptability of bryophytes include the presence of inhibitory compounds and low nitrogen content, particularly in *Sphagnum* (Clymo and Hayward 1982).

In mosses, low digestibility, as demonstrated for caribou and lemmings, is likely to be a major factor restricting consumption. With *Atrion* spp., examination of faeces suggested that moss cells passed through the animals intact when starved individuals ate shoots of *Brachythecium rutabulum* and *Mnium hornum* (Davidson *et al.* 1990). The concentration of phenolic compounds was greater in shoots than in immature capsules of these species, and certain phenolics were released from the shoot only after severe hydrolysis, suggesting an intimate association with the cell wall. One such compound, ferulic acid, was present in the shoots but not in young capsules of *M. hornum* (Davidson *et al.* 1989). It is also recorded from hydrolysed *Sphagnum* shoots (Bland *et al.* 1968). Phenolic polymers occur in the walls of other mosses (Erikson and Miksche 1974; Logan and Thomas 1985), and could make the walls indigestible and impenetrable to fungal hyphae. In angiosperms, wall-bound hydroxycinnamic acids, especially ferulic acid, are considered to represent a primitive defence against pathogens and herbivores (Swain 1977; Fry 1983). Such a mechanism in mosses would help to account for the low incidence of herbivory, low rates of decomposition (see below), and the strong representation of arthropods with sucking mouthparts among the invertebrate consumers.

Aqueous and methanol extracts of moss shoots had no inhibitory effect on feeding by *Atrion* spp. (Davidson *et al.* 1990), but antifedants have been reported from the cytoplasm of numerous hepatics and it is possible that mosses and liverworts show essentially different mechanisms of antitherbivore defence. Asakawa (1990) states that biologically active compounds in hepatics are principally terpenoids and lipophilic aromatic compounds located in oil bodies, e.g. the sesquiterpene lactone plagiocliline A which showed potent antifedant activity against the African army worm *Spodoptera exempta*. Other examples were summarized by Ando and Matsuo (1984) and Gerson (1982).

2.5 Defence against micro-organisms

Many hepatics harbour endophytic fungi (Pocock and Duckett 1985), and

a wide range of fungi has been reported as parasites on mosses and liverworts (Felix 1988; During and Van Tooren 1990). However, both bryophytes and lichens appear to be relatively immune from damaging attack by bacteria and fungi, and more than 50 per cent of species tested from both groups are known to produce inhibitors to the growth of such organisms. Lichen compounds appear to be particularly inhibitory to fungi and gram-positive bacteria, with the most effective substances including usnic acid, pulvinic acid derivatives, and some types of depside and depsidone (Vartia 1973). There is evidence that some compounds are effective against both herbivores and microorganisms (Lawrey 1989). Banerjee and Sen (1979) suggested that bryophytes more commonly contain inhibitors against bacteria than fungi, but antifungal activity has recently been reported in many mosses and liverworts (Ando and Matsuo 1984; Asakawa 1990).

A variety of compounds is again involved, including polyphenolics, fatty acids, and lunnaric acid. Little is known about their mode of operation in nature. Lawrey (1986) referred to work by Malicki indicating that usnic acid leached from terricolous lichens inhibits bacterial decomposers in the soil, suggesting a role in regulating decomposition and in nutrient cycling. He also suggested that antibiotic activity of lichen substances may be largely responsible for the remarkable longevity of some lichens, with the defence constitutive rather than induced since the compounds are produced regardless of the presence of micro-organisms or grazers.

2.6 Decomposition

The limited grazing of bryophytes and lichens implies that much of their phytomass passes into the detritus pathway. However, these plants often decompose more slowly than angiosperms. Rates of lichen decomposition in Arctic communities appear generally to be low. Mean loss of lichen phytomass after two years at Fennoscandian tundra sites was only 13 per cent, compared with values up to 37 per cent for angiosperms (Rosswall *et al.* 1975). Slow decomposition has also been reported of tundra lichens in Alaska (Williams *et al.* 1978) and of *Cladonia stellaris* in lichen woodland (Moore 1984). In contrast, rapid decomposition has been reported for *Cladonia mitis* in boreal forest (Fyles and McGill 1987) and for boreal (Weetman 1982) and temperate epiphytic lichens (Pike 1978; Guzman *et al.* 1990). The latter authors reported decomposition from 40–90 per cent within one year in *Sticta hypochra* and *Pseudoglyphellaria* spp. in Chilean *Nothofagus* forests. Current evidence suggests that decomposition rates among lichens may be highest in nitrogen-fixing types with low C:N ratios, as suggested by Crittenden and Kershaw (1978).

Decomposition rates are variable, but often low among bryophytes. Rates in Antarctic species increase along a gradient of increasing soil moisture and tissue mineral content, and of decreasing tissue C:N ratios (Russell 1990). Annual rates in the cold Antarctic range from 0–3 per cent in tall turves of *Polytrichum* and *Chorisodontium* spp. to 14–25 per cent in wet carpets of *Calliergon* and *Drepanoladus* spp. and 40 per cent in *Brachythecium austrosalebrosum* in a minerotrophic flush (Collins 1973). Decomposition accounts for <10 per cent of annual bryophyte production in tundra sites generally (Heal *et al.* 1981). New growth of mosses takes 5–12 years to decompose in Canadian spruce forest, resulting in a thick layer of partially decomposed *Pleurozium schreberi* on the ground (Weetman 1968; Fyles and McGill 1987). Kibertus (1968) gave a corresponding figure of five years for *Pseudoscleropodium purum* in French pine forests, and considered that this species plays a major role in humus formation despite relatively low annual production (39 g m⁻²). Pócs (1982) indicated that epiphytic bryophytes contribute significantly to humus formation in Tanzanian elfin forest. A higher proportion of *Sphagnum* production than of the associated angiosperms is preserved as peat (Clymo and Hayward 1982).

The acidic, waterlogged, anaerobic conditions created by *Sphagnum* spp. contribute to slow decomposition in mires. Low nitrogen content could also reduce decomposition rates of *Sphagnum*, and of mosses growing under aerobic non-waterlogged conditions such as the cold Antarctic moss turfs. Walton (1985b) considered high levels of holocellulose and crude fibre inhibitory to decomposition of similar vegetation in the cool Antarctic, while Kibertus *et al.* (1970) found cell walls of *Pseudoscleropodium purum* resistant to attack by micro-organisms, possibly for reasons associated with the low incidence of herbivory in other mosses. Moss tissue may remain alive for many years after it becomes brown (Longton 1972), possibly retaining biologically active compounds.

2.7 Nutrient cycling

Bryophytes and lichens require a similar range of elements to other plants, and through growth and decomposition they inevitably participate in nutrient cycling. They clearly dominate the process in many tundra and mire communities, and their role elsewhere could be distinctive, and possibly disproportional in relation to production. Mineral uptake and release by bryophytes and lichens have been critically discussed by Nieboer *et al.* (1978), Brown (1984), Brown and Beckett (1985), Kershaw (1985), and Brown and Bates (1990).

2.7.1 Nitrogen fixation

Nitrogen fixation is carried out by lichens with cyanobacterial photobionts, and by cyanobacteria and heterotrophic bacteria growing in the moist, often warm, low-oxygen environment within bryophyte colonies. Terricolous lichens such as *Stereocaulon paschale*, and micro-organisms epiphytic on mosses, provide significant inputs of N in dry and wet habitats respectively in tundra and boreal forest. Fixation may reach 50–400 mg N m⁻² yr⁻¹ (Kallio 1975; Alexander *et al.* 1978). It was considered of major importance in nitrogen-deficient northern ecosystems by Dowding *et al.* (1981), although these rates are lower than for biological fixation in temperate regions. In contrast, Gunther (1989) indicated fixation by lichens to be of minor overall significance in Alaskan forests. Bacteria epiphytic on mosses provide a major nitrogen input in mires (Basilier *et al.* 1978; Rosswall and Granhall 1980), and contribute significantly in other communities including grassland (Vlassak *et al.* 1973), epiliths (Snyder and Wullstein 1973; Jones and Wilson 1978), and tropical forests where epiphyllous liverworts are important hosts (Bentley 1987). Epiphytic lichens contribute substantial fixed nitrogen in some temperate and tropical forests and other communities (Forman 1975; Pike 1978).

2.7.2 Other sources of nutrients

Apart from biological nitrogen fixation, mineral nutrients enter terrestrial ecosystems through weathering and aerial deposition of particulates and of ions in solution in precipitation. The influence of cryptogams on weathering has already been considered, and it is suspected that lichens are particularly effective at releasing nutrients from trapped particulates (Nieboer *et al.* 1978). Elements in solution enter plants via the same route as water. They are likely to pass directly into actively growing aerial parts of mosses and lichens, with internal transport in a transpiration stream from below important only in partially endohydric bryophytes.

Lichens, and particularly mosses, can take up nutrients from dilute solutions (Babb and Whitfield 1977; Williams *et al.* 1978), in part because of their high cation exchange capacities. They are therefore likely to enhance retention of nutrients dissolved in precipitation, often enriched as runoff from taller vegetation, by incorporating part of the input directly into shoot tissue. Retention of precipitation in capillary spaces within the colonies, whence it may evaporate or drain slowly into the underlying substratum, could also reduce nutrient losses, both from the new input in precipitation and by leaching from the pool already present in the soil. Humus, to which mosses may contribute substantially, also helps maintain

soil fertility by reducing drainage and through chemical association with mineral ions (Longton 1984; Nadkarni 1984).

The relative importance to cryptogams of nutrients dissolved in precipitation or throughfall, as opposed to soil moisture, has been debated ever since Tamm (1953) demonstrated that annual input in precipitation would account for annual accumulation by *Hylacomium splendens* of all major nutrients except N (Nieboer *et al.* 1978; Longton 1980, 1988a; Brown 1984; Brown and Bates 1990; Van Tooren *et al.* 1990). The ability of bryophytes to remove elements from rainfall or artificial solutions percolating through the colonies has been confirmed for mosses from the cold Antarctic (Allen *et al.* 1967), from British woodlands (Rieley *et al.* 1979; Bates 1990), and for mats of bryophytes, lichens, and other cryptogamic epiphytes in Amazonian forests (Herrera *et al.* 1978). Both lichens and mosses in boreal woodland have been shown to retain nitrogen compounds applied in solution (Crittenden 1983; Weber and Van Cleve 1984), while epiphytic lichens from temperate forests took up N and the divalent cations Ca⁺⁺ and Mg⁺⁺ during laboratory misting experiments (Pike 1978).

The reverse process may also occur, however, and these results do not imply that bryophytes and lichens obtain no minerals from their substratum. The moisture gradient that commonly develops in lichen colonies will result in upward movement of soil moisture and dissolved nutrients (Nieboer *et al.* 1978). Bates and Farmer (1990) showed that *Plurizium schroberi* can take up Ca from both a layer of CaCO₃ placed on the ground beneath the colony and from dilute solutions sprayed on the leaves. Thus both soil and precipitation are likely to supply nutrients to mosses and lichens, their relative importance depending on age, growth form, and other characteristics of individual species, and on climatic and other external factors (Longton 1980). However, the influence of these plants in retaining part of the atmospheric input is likely to be significant, particularly in tropical forests, boreal and polar communities, ombrogenous mires, and other systems deficient in available N and other essential nutrients.

2.7.3 Nutrient release

Nutrients taken up by bryophytes and lichens may be released and made available to other organisms by leaching, upon death and decomposition, following fire, or to a limited extent by herbivory. However, a proportion is retained indefinitely as undecomposed organic matter, and in some communities bryophytes and lichen compete effectively with vascular plants for nutrients available in limiting quantities.

Some authors consider that lichens conserve much of their N until death and decomposition (Lindsay 1978). However, there is ample evidence that N fixed by lichens, and by bacteria epiphytic on bryophytes, is released and

utilized by other organisms. Crittenden (1983) reported leaching of organic nitrogen compounds from *Stereocaulon paschale* by rainfall, and cited evidence for transfer of N to nearby mosses. N is also freely leached from nitrogen-fixing epiphytic lichens (Pike 1978). Alexander *et al.* (1978) considered that N fixed by bacteria on tundra mosses is important in short-term turnover, studies with ^{15}N indicating release of $\text{NH}_4\text{-N}$ and its transfer to mosses and vascular plants. Biological fixation is likely to be particularly important during primary succession. An association between *Funaria hygrometrica* and cyanobacteria occurred widely during colonization of Surtsey, and growth of the moss was enhanced by nitrogen compounds released by the latter (Rodgers and Henriksson 1976). Jones and Wilson (1978) reported that ^{15}N fixed by *Nostoc* growing on mosses on limestone rock was digested by invertebrates and taken up by mosses and vascular plants in laboratory experiments.

Some elements are also likely to be freely released from mosses and lichens by leaching, losses following thawing or rehydration perhaps being particularly important (Hooker 1977; Brown 1984). Bates (1990) reported that spraying KH_2PO_4 solution on *Pseudoscleropodium purum* resulted in only temporary enhancement of P and K content in the moss. A small proportion of the addition was collected in throughfall beneath the colony, and Bates concluded that most was released from the moss and either utilized by micro-organisms or remained uneluted in the litter.

In other cases nutrients absorbed by cryptogams are made available by decomposition. Weeman (1968) found that tree roots were concentrated at the base of the moss layer in black spruce forest. He considered that decomposing mosses provided a collecting point for elements, particularly N, absorbed by the moss from throughfall. A similar conclusion was reached by Weber and Van Cleve (1984) following studies of ^{15}N uptake by *Hylocomium splendens* and *Pleurozium schreberi*. Involvement of mycorrhizal fungi in transferring P from *H. splendens* to spruce trees was suspected by Chapin *et al.* (1987). Brown and Bates (1990) point out that the P might equally have been taken up by the fungi and passed to the trees in the absence of mosses. The importance of mosses in this process may be determined by the rate at which leaching would occur without the moss layer.

The examples of nutrient release so far considered imply that mosses and lichens enhance nutrient availability to other organisms. This seems certain to apply in some situations, for Sendstad (1981) found that removal of lichen cover, principally *Cetraria delisei*, from lichen heath on Svalbard resulted in reduced concentrations of soil organic matter and of macronutrients. During (1990) considered that nutrient release from bryophytes in chalk grassland, while unimportant over whole sites, might contribute to

the vigour and survival of seedlings in dense moss patches. In other cases, however, mosses may decrease nutrient availability. This applies particularly to N, which may be retained in association with phenolic compounds in the cell wall (Berg 1984), and to divalent cations such as Ca^{++} and Mg^{++} that remain strongly bound to anionic exchange sites in the cell wall. These factors apply in dead as well as living tissue. Release of H^+ ions in exchange for divalent cations is one cause of acidity in *Sphagnum*-dominated mires (Clymo and Hayward 1982). Lichens appear to be less effective at retaining Ca^{++} and Mg^{++} than mosses (Nieboer *et al.* 1978).

As examples, Dowling *et al.* (1981) estimated that 50 per cent of the Ca in mesic tundra meadows on Devon Island was in the bryophytes, with a turnover time of 22 years. Absorption of N and other nutrients by *Sphagnum* is considered to reduce their availability to vascular plants in mires (Pakarinen 1978; Woodin *et al.* 1985). Oechel and Van Cleve (1986) suggest that nutrient immobilization by an increasing phytomass of mosses reduces vascular plant productivity as succession proceeds from deciduous to coniferous woodland in Alaska, despite the beneficial effect of bryophytes on nutrient cycling noted above.

There are many intriguing possibilities concerning the influence of bryophytes and lichens on nutrient cycling. That these plants have a significant effect in some communities where they are abundant can hardly be doubted, but further research is required to quantify the effects and to assess their generality.

2.8 Conclusion

This chapter has been mainly concerned with the role of bryophytes and lichens in succession, energy flow, nutrient cycling, and other fundamental ecosystem processes. Although largely unquantified, their influence is likely to be both significant and distinctive, by virtue of moderate levels of production, limited palatability to herbivores and often low rates of decomposition combined with the high water-holding and cation exchange capacities that characterize the resulting biomass. At the same time, bryophytes and lichens also interact directly with other organisms in a variety of ways, for example by providing habitats and camouflage for invertebrates, nesting material for animals, and conditions that may in some cases favour and in others discourage seed germination and establishment (During and Van Tooren 1990). Phenolic compounds from lichens epiphytic on oaks are absorbed by the host leading to reductions in NAR and to defoliation (Gimenez and Vicente 1989), and a range of allelopathic compounds are released by both lichens (Lawrey 1986) and bryophytes (Asakawa 1990). *Sphagnum* spp. control the environment of bogs by creating

acid, waterlogged, anaerobic conditions and by retaining N and divalent cations. These and other interactions are considered in the reviews of Gerson and Seaward (1977), Richardson and Young (1977), Seaward (1988), and Slack (1988).

These various relationships could alter dramatically in the coming decades even if, as seems likely, SO_2 emissions to which mosses and lichens are particularly sensitive can be controlled. Thus agricultural problems associated with any intensification of the drying trend in sub-Saharan Africa could be exacerbated if reduced humidity or forest clearance in montane regions leads to a reduction in the phytomass, and therefore water-holding capacity, of epiphytic bryophytes. However, the most dramatic effects can be anticipated at high latitudes, particularly if a rise in mean annual temperature of anything approaching the levels of $8\text{--}10^\circ\text{C}$ sometimes forecast for northern regions (Garrels 1982) is accompanied by shifts in rainfall patterns and a continuing rise in nitrogen deposition.

The effects of environmental change on the distribution and abundance of mosses and lichens will be determined in part by direct responses, but will also be strongly influenced by associated effects on angiosperms. Thus the abundance of cryptogams in arctic tundra is dependent in large measure on the failure of flowering plants to assume dominance under the cool summer conditions currently prevailing in polar regions. It is unclear how far this results from the effects of low temperature directly on growth or indirectly on rates of nutrient cycling and the resulting deficiencies of available N and P (Chapin 1983). A significant rise in CO_2 concentration, temperature, and nitrogen availability could combine to increase the abundance of angiosperms and thus eliminate the highly distinctive tundra communities composed principally of mosses and lichens. This effect could be enhanced if increasing concentrations of atmospheric CO_2 lead to generally increased rates of biological nitrogen fixation, as demonstrated in the temperate lichen *Lobaria pulmonaria* (Norby and Sigal 1989). Conversely, loss of an insulating layer of cryptogams would accelerate any melting of permafrost initiated by rising temperature, perhaps resulting in extensive disruption of the land surface and its vegetation cover, and providing opportunities for cryptogams in successional communities. Existing cryptogamic vegetation will probably survive longer in the Antarctic where summer temperatures are lower than at comparable Arctic latitudes and barriers to migration more effective.

permitted by individual genotypes, combined with poikilohydry and the consequent ability to switch rapidly between states of metabolic activity and rest as dictated by external conditions at any time of the year (Longton 1988a). Moreover, bryophytes can survive as small populations in microhabitats where conditions are far different from those prevailing in an area generally. Thus some Arctic endemics have their closest relations among tropical floras and are viewed as having survived in the Arctic since a period of temperate or subtropical conditions in the early Tertiary (Steele 1978). Other species, however, particularly those that are already rare and have limited dispersal ability through failure to produce spores, could face extinction given a significant shift in climate.

The impact on the global ecosystem of significant changes in the distribution of bryophytes and lichens is difficult to predict. However, it is abundantly clear that release of C from undecomposed mosses in peat could substantially accentuate the process of global warming. Figures in Clymo and Hayward (1982) indicate that peatlands cover about 150×10^6 ha (>1 per cent of the Earth's land surface) and contain some $300\,000 \times 10^6$ metric tons of peat, of which perhaps half is *Sphagnum* with a further component of other mosses. Assuming a 40 per cent carbon content the peat contains $120\,000 \times 10^6$ metric tons of C. This is equivalent to 24 years' emission from fossil fuel at the current rate of 5000×10^6 tons yr^{-1} , and to more than 50 per cent of total emission from this source since 1860, according to estimates in Liss and Crane (1983), Moore *et al.* (1989), and Roty and Marland (1986). Any disruption of northern mires that results in rapid decomposition of the peat could thus have most serious implications. The message is clear for those who plan to convert peatlands to forest! Again, it is the combination of climatic change, leading to warmer and possibly drier conditions, with increased nitrogen deposition that could be particularly significant. Lee *et al.* (1990) show that nitrogen levels in severely polluted areas are already supraoptimal for *Sphagnum* and could favour growth of angiosperms, while enhanced nitrogen levels will also accelerate decomposition.

Finally, the potential significance of currently accumulating bryophyte phytomass as a carbon sink should not be overlooked. Assuming annual *Sphagnum* production at 200 g m^{-2} over $100\,000$ ha of mire (Clymo 1983) gives 200×10^6 metric tons dry weight or 80×10^6 metric tons C. Similarly, a conservative estimate of annual moss production in the boreal forest at 100 g m^{-2} over half the area indicated by Longton (1988b) gives

the rise in atmospheric CO₂ concentrations must surely be achieved by implementing a wide range of measures, many with individually small effects. Encouraging production of slowly decomposing bryophyte phytomass, and its subsequent storage in a useful form, e.g. as insulation material, is one such approach.

References

- Adamson, H., Wilson, M., Selkirk, P., and Seppelt, R. D. (1988). Photoinhibition in antarctic mosses. *Polarforschung*, **58**, 103–11.
- Ahti, T. (1977). Lichens of the boreal coniferous zone. In *Lichen ecology*, (ed. M. R. D. Seaward), pp. 145–81. Academic Press, London.
- Ahti, T. (1982). Evolutionary trends in cladoniform lichens. *Journal of the Hattori Botanical Laboratory*, **52**, 331–41.
- Alexander, V., Billington, M., and Schell, D. M. (1978). Nitrogen fixation in arctic and alpine tundra. In *Vegetation and production ecology of an Alaskan arctic tundra*, (ed. L. L. Tieszen), pp. 539–58. Springer, New York.
- Allen, S. E., Grimsshaw, H. M., and Holdgate, M. W. (1967). Factors affecting the availability of plant nutrients on an Antarctic island. *Journal of Ecology*, **55**, 381–96.
- Ando, H. and Matsuo, A. (1984). Applied bryology. *Advances in Bryology*, **2**, 133–224.
- Andreev, V. N. (1954). Prirost kormovyykh lishainikov i priemy ego regulirovaniya. *Geobotanika* **9**, 11–74.
- Andrews, J. T. and Barnett, D. M. (1979). Holocene (Neoglacial) moraine and periglacial lake chronology, Barnes Ice Cap, N.W.T. Canada. *Boreas*, **8**, 341–58.
- Asakawa, Y. (1990). Terpenoids and aromatic compounds with pharmacological activity from bryophytes. In *Bryophytes their chemistry and chemical taxonomy*, (eds H. D. Zinsmeister and R. Mues), pp. 369–410. Oxford Science Publications, Oxford.
- Ascaso, C. (1985). Structural aspects of lichens invading their substrata. In *Surface physiology of lichens*, (eds C. Vicenti, D. H. Brown, and M. Estrella Legaz), pp. 87–113. Universidad Complutense de Madrid, Madrid.
- Babb, T. A. and Whitfield, D. W. S. (1977). Mineral nutrient cycling and limitation of plant growth in the Truelove Lowland ecosystem. In *Truelove Lowland, Devon Island, Canada: a high arctic ecosystem*, (ed. L. C. Bliss), pp. 589–606. University of Alberta Press, Edmonton.
- Banerjee, R. D. and Sen, S. P. (1979). Antibiotic activity of bryophytes. *The Bryologist*, **82**, 141–53.
- Barkman, J. J. (1958). *Phytosociology and ecology of cryptogamic epiphytes*. Van Gorcum, Assen.
- Basilier, K. Granhall, U., and Senström, T. -A. (1978). Nitrogen fixation in wet minerotrophic moss communities of a subarctic mire. *Oikos*, **31**, 236–46.
- Bates, J. W. (1990). Interception of nutrients in wet deposition by *Pseudocleropodium parvum*: an experimental study of uptake and release of potassium and phosphorus. *Lindbergia*, **15**, 93–8.
- Bates, J. W. and Farmer, A. M. (1990). An experimental study of calcium acquisition and its effects on the calcifuge moss *Pleurozium schreberi*. *Annals of Botany*, **65**, 87–96.
- Batzli, G. O. and Cole, F. R. (1979). Nutritional ecology of microtine rodents: digestibility of forage. *Journal of Mammalogy*, **60**, 740–50.
- Batzli, G. O., White, R. G., MacLean, S. E., Preika, F. A., and Collier, B. D. (1980). The herbivore-based trophic system. In *An arctic ecosystem: the coastal tundra at Barron, Alaska*, (eds J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell), pp. 335–410. Hutchinson and Ross, Dowden.
- Bentley, B. L. (1987). Nitrogen fixation by epiphylls in a tropical rainforest. *Annals of the Missouri Botanical Garden*, **74**, 234–41.
- Berg, B. (1984). Decomposition of moss litter in a mature Scots pine forest. *Pedobiologia* **26**, 301–8.
- Bland, D. E., Logan, A., and Menshun, M. (1968). The lignin of *Sphagnum*. *Phytochemistry*, **7**, 1373–7.
- Blewitt, M. R. and Cooper-Driver, G. A. (1990). The effects of lichen extracts on feeding by exypt moths (*Lymantria dispar*). *Bryologist*, **93**, 220–1.
- Brodo, I. M. (1973). Substrate ecology. In *The lichens*, (eds V. Ahmadjian and M. E. Hale), pp. 401–41. Academic Press, New York.
- Brown, D. H. (1984). Uptake of mineral elements and their use in pollution monitoring. In *The experimental biology of bryophytes*, (eds A. F. Dyer and J. G. Duckett), pp. 229–55. Academic Press, London.
- Brown, D. H. and Bates, J. W. (1990). Bryophytes and nutrient cycling. *Botanical Journal of the Linnean Society*, **104**, 129–47.
- Brown, D. W. and Beckett, R. P. (1985). Minerals and lichens: acquisition, localization and effect. In *Surface physiology of lichens*, (eds C. Vicenti, D. H. Brown, and M. Estrella Legaz), pp. 127–49. Universidad Complutense de Madrid, Madrid.
- Bunnell, F. L., MacLean, S. F., and Brown, J. (1975). Barrow, Alaska, USA. In *Structure and function of tundra ecosystems*, (eds T. Rosswall and O. W. Heal), pp. 73–124. *Ecological Bulletins (Stockholm)*, **20**.
- Busby, J. R., Bliss, L. C., and Hamilton, C. D. (1978). Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomentypnum nitens* and *Hylacomium splendens*. *Ecological Monographs*, **48**, 95–110.
- Chapin, F. S. (1983). Direct and indirect effects of temperature on arctic plants. *Polar Biology*, **2**, 47–52.
- Chapin, F. S., Oechel, W. C., Van Cleve, K., and Lawrence, W. (1987). The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. *Oecologia (Berlin)*, **74**, 310–15.
- Clarke, G. C. S., Greene, S. W., and Greene, D. M. (1971). Productivity of bryophytes in polar regions. *Annals of Botany*, **35**, 99–108.
- Clymo, R. S. (1983). Peat. In *Mires: swamp, bog, fen and moor. General studies*, (ed. A. J. P. Gore), pp. 159–224. Elsevier, Amsterdam.
- Clymo, R. S. and Hayward, P. M. (1982). The ecology of *Sphagnum*. In *Bryophyte*