

From: Bryophytes & Lichens  
in a Changing  
Environment, pp. 2

Kimmerer  
EFB 446/646

# The role of bryophytes and lichens in terrestrial ecosystems

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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  $\alpha$  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 mm<sup>3</sup> rock per individual per day, resulting in weathering at 0.7–1.1 metric tons ha<sup>-1</sup> yr<sup>-1</sup> (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 *Lecidea* 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 *Lecidea* 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

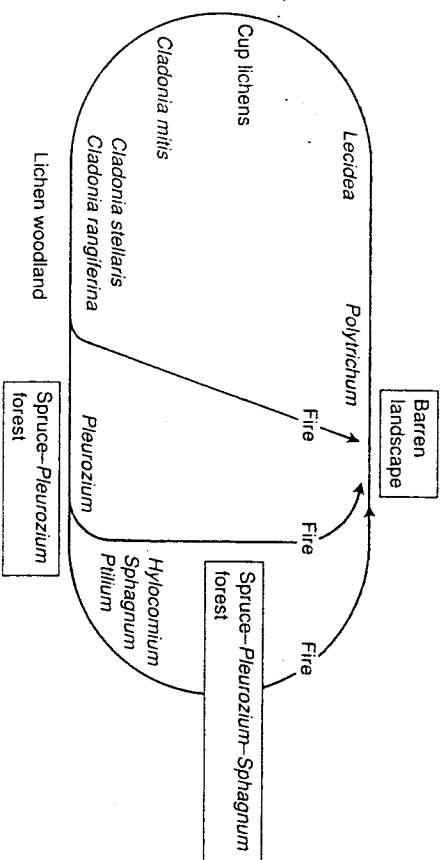


Fig. 2.1 Schematic representation of fire-induced succession in Canadian boreal forests (after Foster 1985).

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 *Lecidea* 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

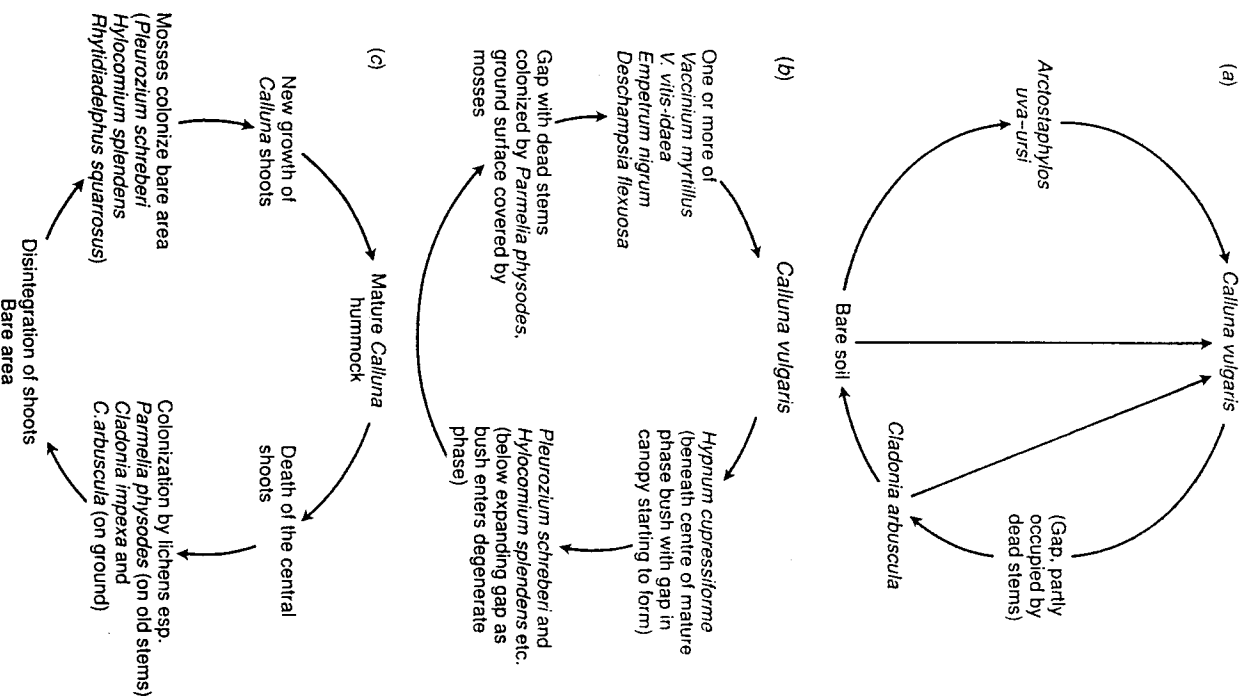


Fig. 2.2 Examples of cyclic succession in *Calluna*-dominated communities in Scotland, indicating the importance of mosses and lichens in (a) a *Calluna-Arcostaphylos* community; (b) a *Calluna-Vaccinium* community; (c) a dune heath. (*Parmelia physodes* = *Hypogymnia physodes*; *Cladonia impexa* = *C. 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<sup>-2</sup> (Longton 1974; Ino 1983). Total phytomass is only 5–200 g m<sup>-2</sup> in the typical open communities (Longton 1974; Kappen 1985), but reaches 1000 g m<sup>-2</sup> in occasional closed stands of mosses and of epilithic fruticose lichens. Green phytomass alone was 1097 g m<sup>-2</sup> 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<sup>-2</sup> yr<sup>-1</sup> but turnover is slow (Vestal 1988), with organic matter in the surface layers of rock reaching 46–177 g m<sup>-2</sup> (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 *Callitregon* 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<sup>-2</sup> 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<sup>-2</sup> for green shoots, 20 000–30 000 g m<sup>-2</sup> for phytomass above permafrost,

and up to 46 000 g m<sup>-2</sup> for total phytomass including permanently frozen material to the base of a bank 1 m deep. Estimates of 250 g m<sup>-2</sup> for annual production and 800–1750 g m<sup>-2</sup> 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<sup>-2</sup>. 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<sup>-2</sup>; bryophyte production has been recorded as only 150–250 g m<sup>-2</sup>, 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 m<sup>2</sup>, 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<sup>-2</sup> for *Dirichium strictum* in dry fellfield to 1028 g m<sup>-2</sup> 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<sup>-2</sup> in cool Antarctic tussock grassland compared with 100–150 g m<sup>-2</sup> in mild Arctic spruce woodland (Longton 1979b). Similarly, productivity of *Cladonia rangiferina* on South Georgia may reach 100–1130 g m<sup>-2</sup> yr<sup>-1</sup> (Lindsay 1975; Smith 1984), whereas maximum values reported by Andreev (1954) for Arctic cladonias were only 17–27 g m<sup>-2</sup> yr<sup>-1</sup>.

#### *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 ( $\text{g m}^{-2}$ ) 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
<b>ARCTIC</b>											
<b>Wet meadow</b>											
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
<b>Grass heath</b>											
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
<b>Dwarf shrub heath</b>											
<i>Cassiope tetragona</i> heath	Devon I	18	90	20	4	132	159(+228)	1041	423	48	1899
<b>Fellfield</b>											
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
<b>Barren</b>											
<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
<b>ANTARCTIC</b>											
<b>Grass heath</b>											
<i>Festuca contracta</i> heath	South Georgia	340	350	150	2	842	425(+1598)	1642	500	12	4177
<b>Herbfield</b>											
<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).

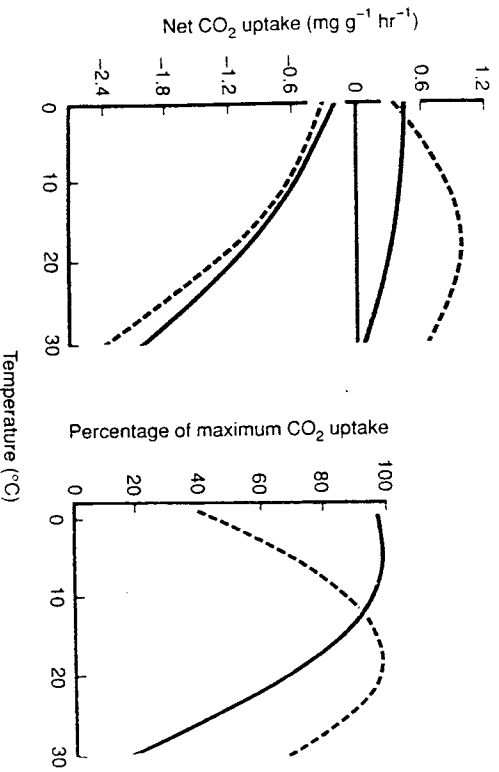


Fig. 2.3 Temperature responses of net photosynthesis and dark respiration in the moss *Polytrichum alpinum* from wet meadow in Alaska in early summer (solid line) and late summer (broken line). Data from Oechel and Sveinbjörnsson (1978).

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<sup>-2</sup> 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<sup>-2</sup>, and annual production of 6–16 g m<sup>-2</sup>. 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<sup>-1</sup> 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<sup>-2</sup> under spruce at densities up to 7000 shoots m<sup>-2</sup>. Mean



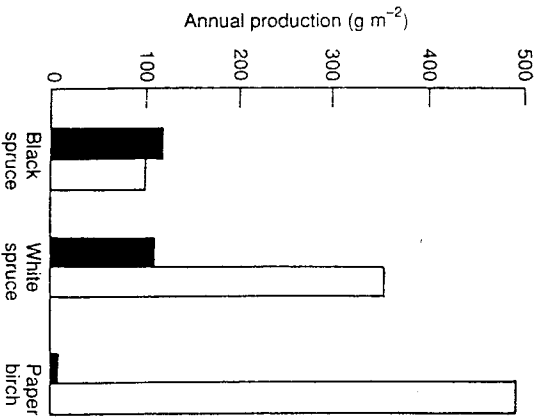


Fig. 2.4 Annual production of mosses (black) and the above-ground component of trees (white) in selected forest types in interior Alaska. Data from Oechel and Van Cleve (1986).

mass density was often less than 10 shoots m<sup>-2</sup> in successional stands of *Betula* and *Populus* spp., with phytomass only 4–6 g m<sup>-2</sup>. Annual moss production was negligible in the deciduous forests, but ranged from 70–150 g m<sup>-2</sup> 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<sup>-2</sup> (Forman 1969). However, Rieley *et al.* (1979) reported bryophyte phytomass of 1600–2900 g m<sup>-2</sup> in Welsh oakwoods (*Quercus petraea*), as compared with only 250–300 g m<sup>-2</sup> 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<sup>-2</sup> for the mosses and 120 g m<sup>-2</sup> 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<sup>-2</sup> of tree surface, 27 kg tree<sup>-1</sup> or 5000 kg ha<sup>-2</sup> of forest. Epiphytic lichen phytomass has been estimated at 100–1800 kg ha<sup>-1</sup> in a range of North American temperate forests, with annual production from 50–500 kg ha<sup>-1</sup> (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<sup>-2</sup> for hummocks, 500 g m<sup>-2</sup> in lawns, and 600–800 g m<sup>-2</sup> 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<sup>-2</sup>, 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  $70 \text{ g m}^{-2}$ , compared with  $59 \text{ g m}^{-2}$  for the above-ground plus  $24 \text{ g m}^{-2}$  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  $213 \text{ g m}^{-2}$  and  $659 \text{ g m}^{-2}$  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 ( $300 \text{ g m}^{-2}$ ) 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  $1000 \text{ m}$ , rising in montane regions to  $140 \text{ g m}^{-2}$  in Peru and  $400 \text{ g m}^{-2}$  (exceptionally to  $800 \text{ g m}^{-2}$ ) in Borneo. The differences between localities were thought to reflect local rather than regional factors. For Borneo, these values represent phytomass of under  $1 \text{ kg ha}^{-1}$  of forest below  $1000 \text{ m}$ , rising to  $200\text{--}500 \text{ kg ha}^{-1}$  (exceptionally to  $1300 \text{ kg ha}^{-1}$ ) 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  $30\ 000 \text{ l ha}^{-1}$  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.

