M18

Erica tetralix-Sphagnum papillosum raised and blanket mire

Synonymy

Eriophoretum vaginati Rankin 1911*a*; *Sphagnetum* Regeneration Complex Tansley 1939, Godwin & Conway 1939 *p.p.*; Marginal *Sphagnetum* Godwin & Conway 1939; *Sphagnum* community, Type A 'moss' Pearsall 1941; Dissected moss Pearsall 1941; *Pleurozia purpurea-Erica tetralix* Assoziation, Sub-assoziation von *Andromeda polifolia* Braun-Blanquet & Tüxen 1952; Flat & hummock communities Ratcliffe & Walker 1958; *Erico-Sphagnetum magellanici*, Sub-Atlantic race Moore 1968 *p.p.*; *Trichophoreto-Eriophoretum*, Typical facies Eddy *et al.* 1969; *Sphagnum papillosum-Erica tetralix* & *Calluna vulgaris-Eriophorum vaginatum* noda, Normal Series Tallis 1973; *Erico-Sphagnetum papillosi* Moore (1964) 1968 *emend.* Birse 1980 *p.p.*; *Calluna-Eriophorum Sphagnetum* community Bignal & Curtis 1981; *Trichophorum cespitosum-Eriophorum vaginatum* community Bignal & Curtis 1981; *Erica-Sphagnum magellanicum* nodum Ratcliffe & Hattey 1982 *p.p.*; *Erico-Sphagnetum magellanici* Dierssen 1982.

Constant species

Calluna vulgaris, Erica tetralix, Eriophorum angustifolium, E. vaginatum, Sphagnum capillifolium, S. papillosum, S. tenellum, Odontoschisma sphagni.

Rare species

Andromeda polifolia, Sphagnum imbricatum.

Physiognomy

The *Erica tetralix-Sphagnum papillosum* mire is a raised and blanket bog community generally dominated by Sphagna, with ericoid sub-shrubs and monocotyledons often playing a subordinate role, though becoming more important on drier ground and, some of them at least, increasing in prominence with particular kinds of treatment. The vegetation can be found as extensive, undulating carpets comprising irregular mosaics of the different structural elements or, on mires with strongly-differentiated surface microrelief, it can comprise the lawn and hummock components, with the plants more clearly zoned in relation to the height of the water-table and with Rhynchosporion assemblages occupying the wettest hollows.

The bulkier vascular plants typically form a low and patchy canopy, 2 dm or so tall, with *Calluna vulgaris, Erica tetralix* and *Eriophorum vaginatum* being the commonest species, *Scirpus cespitosus* a little less frequent. Often, none of these is truly dominant, small bushes or tussocks occurring scattered through the *Sphagnum* carpet, but, over lawns and hummocks, they can show a stronger pattern of local prominence, *E. tetralix* tending to predominate on wetter ground, where shoots of *Eriophorum angustifolium* can also be abundant, *Calluna, Scirpus* and *E. vaginatum* being concentrated on the drier areas. In such situations, the last two can grow more tussocky, though *Calluna* usually has the higher covers and *E. vaginatum* never really attains the important role it has in the *Calluna-Eriophorum* mire. *Molinia caerulea*, more so than *Scirpus*, is relatively scarce here compared with its prominence in the *Scirpus-Eriophorum* mire, but it can be occasionally abundant, extending down on to wetter flats and becoming more tussocky on hummocks, and it can increase greatly in frequency and cover where better-aerated peats occur within or around stands of the community, as on the drying centres of raised mires, on well-drained rands and where there is some soligenous influence in surface soakways or marginal lagg streams. This is well seen in maps and transects in the studies by Godwin & Conway (1939) of Cors Goch glan Teifi in Dyfed and by Ratcliffe & Walker (1958) and Boatman *et al.* (1981) of the Silver Flowe mires in Galloway. Some stands transitional to such *Molinia*-dominated vegetation can therefore often be included within the community and drying raised mires, which are common, often show a shift in this direction (see below).

Apart from *Calluna* and *E. tetralix*, no other sub-shrub occurs throughout the community. *Myrica gale* is

occasionally found in the wetter *Sphagnum-Andromeda* sub-community and, with *Molinia*, it can increase in prominence in soligenous zones, but it is less characteristic here than in the *Scirpus-Eriophorum* mire and rather patchy in its distribution: it becomes commoner in south-west Scotland and parts of Wales, for example, but it is decidedly scarce in Strathclyde (Bignal & Curtis 1981). Drier areas within stands of the community, most notably on the tops of taller and decaying hummocks such as figure frequently in the *Empetrum-Cladonia* sub-community, often have some *Empetrum nigrum* ssp. *nigrum*, but the Arctic-Alpine *E. nigrum* ssp. *hermaphroditum*, *Vaccinium vitis-idaea* and *V. uliginosum* which, together with the Arctic-Subarctic *Rubus chamaemorus*, become so important in the *Calluna-Eriophorum* mire, are all very scarce here: like the *Scirpus-Eriophorum* mire, the *Erica-Sphagnum* mire is largely a low-altitude community. *Vaccinium myrtillus* is similarly very infrequent, even on drying mires.

Of the remaining vascular associates, few are common, and all of these are preferential to the *Sphagnum-Andromeda* sub-community, characteristic of wetter areas on undisturbed mires. In such situations, *Drosera rotundifolia* and *Narthecium ossifragum* occur frequently but both plants are found in other types of ombrogenous bog, being especially common in the *Scirpus-Eriophorum* mire and lower-altitude stands of the *Calluna-Eriophorum* mire, and more distinctive of the *Erica-Sphagnum* mire are two Continental Northern species, *Vaccinium oxycoccos* and *Andromeda polifolia*, whose British distributions are largely centred in the regions where the community is found. *Andromeda*, though somewhat patchy even in the *Sphagnum-Andromeda* sub-community, is particularly diagnostic, occurring in similar vegetation in Ireland (Braun-Blanquet & Tüxen 1952) and in northern Germany (e.g. Moore 1968) though, in mainland Europe, also being found in montane and boreal Sphagnion fusci mires.

Quite often of greater prominence than all these plants, however, are the Sphagna. Their abundance here frequently led early authors to describe the community as a *Sphagnetum* (e.g. Tansley 1939, Godwin & Conway 1939, Pearsall 1941) and the prevailing red-brown tinge of the most important species contributes greatly to the characteristically sombre hue of this vegetation. As in the *Scirpus-Eriophorum* mire, both *Sphagnum papillosum* and *S. capillifolium* are very common throughout, but here *S. tenellum* also attains constancy (though usually in less abundance than these two) and the total cover and luxuriance of the carpet are typically greater. A more obvious preferential feature is the frequent occurrence, particularly in the wetter vegetation of the *Sphagnum-Andromeda* sub-community, of *S. magellanicum*, a species rather unevenly represented in other ombrogenous mires, but here a major peat-builder. *S.*

subnitens, *S. palustre*, *S. cuspidatum*, *S. auriculatum* and, particularly where there is some eutrophication, *S. recurvum*, can also be found occasionally. Among Sphagna of more restricted occurrence in Britain, this community provides an occasional locus for *S. pulchrum* and, sometimes forming pronounced domes, *S. fuscum* and *S. imbricatum*. *S. fuscum* is rather more characteristic in Britain of certain kinds of high-altitude *Calluna-Eriophorum* mire (where it provides a link with the Sphagnion fusci bogs) but *S. imbricatum* seems especially distinctive of this community: it is rather local in its occurrence now (a little less so in equivalent Irish vegetation), but its readily-identifiable sub-fossil remains often figure very prominently in the peats of raised bogs on which the *Erica-Sphagnum* mire is still found (e.g. Godwin & Conway 1939, Pigott & Pigott 1963, Green 1968, Moore 1968).

Over more gently undulating surfaces, the Sphagna are distributed in a rather irregular patchwork but, with increasing differentiation of hummocks and hollows, they show a vertical stratification. *S. papillosum* is primarily a species of the surrounds to wetter depressions and of flats and it often predominates there, with *S. magellanicum* and a little *S. tenellum*. *S. magellanicum* extends a little higher above the water-table than *S. papillosum* but, on hummock sides and tops, both typically give way to an abundance of *S. capillifolium*, and the balance between these species helps define the two sub-communities. In the wettest hollows, semi-aquatic Sphagna become more important in the transition to Rhynchosporion pool vegetation.

Other bryophytes characteristically play a subordinate part in the ground cover but some are frequent and can be locally abundant. As in the *Scirpus-Eriophorum* mire, these can include some leafy hepatics: *Odontoschisma sphagni* and *Mylia anomala* are both very common here and can occur as conspicuous patches among the Sphagna. *Pleurozia purpurea*, on the other hand, strongly preferential among our ombrogenous mires to the most oceanic situations, is generally absent from this vegetation, except in transitional stands (like some of those on the Silver Flowe mires: Ratcliffe & Walker 1958). *Aulacomnium palustre* and *Hypnum cupressiforme/jutlandicum* also occur frequently and there are occasional records for *Pohlia nutans*, *Polytrichum alpestre*, *Campylopus paradoxus* and *Plagiothecium undulatum*. Hypnaceous mosses, notably *Pleurozium schreberi* and *Rhytidiadelphus loreus*, together with *Racomitrium lanuginosum*, are fairly uncommon in wetter situations but they become much more frequent in the *Empetrum-Cladonia* sub-community. It is there, too, that lichens make their strongest contribution to this kind of mire vegetation, larger species like *C. impexa*, *C. uncialis* and *C. arbuscula* being especially good preferentials and together often of moderately high cover.

Sub-communities

***Sphagnum magellanicum-Andromeda polifolia* sub-community:** *Eriophorum vaginati* Rankin 1911*a*; *Sphagnetum* Regeneration Complex, Stages 3 & 4 Tansley 1939; *Sphagnetum* Regeneration Complex, middle stages Godwin & Conway 1939; *Sphagnum* community, Type A 'moss' Pearsall 1941; Flat communities Ratcliffe & Walker 1958; *Erico-Sphagnetum magellanici*, Sub-Atlantic race Moore 1968 *p.p.*; *Sphagnum papillosum-Erica tetralix & Calluna vulgaris-Eriophorum vaginatum* noda, Normal Series Tallis 1973; *Erico-Sphagnetum papillosi*, Typical subassociation Moore (1964) 1968 *emend.* Birse 1980 *p.p.*; *Erica-Sphagnum magellanicum* nodum, *Andromeda polifolia-Rhynchospora alba* complex Ratcliffe & Hattey 1982 *p.p.* All the vascular constants of the community are of high frequency here but very often none of them is dominant and, in the wetter conditions that are characteristic in this kind of *Erica-Sphagnum* mire, *Calluna* is often of rather poor growth and *Eriophorum vaginatum* and *Scirpus* do not show a markedly tussocky habit, though all three of these can increase a little in stature and cover where the vegetation runs up the lower surrounds of well-differentiated hummocks.

Typically, however, it is the Sphagna that make the most obvious immediate impression, forming an extensive and luxuriant carpet in which *S. papillosum*, often here with abundant *S. magellanicum*, predominates around the hollows and over extensive undulant lawns. *S. tenellum* and *S. capillifolium* are also both constant and usually of low cover in wetter situations but the latter can become firmly established on more substantial carpets raised just above the water level and begin to form the hummocks that mark the transition to the drier vegetation of the *Empetrum-Cladonia* sub-community. Much more locally, *S. fuscum* or *S. imbricatum* can be found as prominent hummocks. Then, there is occasionally a little *S. subnitens* or *S. palustre* in the lawn and, in wetter hollows, *S. cuspidatum* or *S. auriculatum*, species which thicken up considerably, replacing *S. papillosum*, in the transition to Rhynchosporion pools. The horizontal and vertical patterning typically found among the Sphagna in this kind of vegetation is very well shown in the quadrats and sections illustrated in Godwin & Conway (1939) and Ratcliffe & Walker (1958). It is probably also best to include in this sub-community the hummock vegetation developed within the extensive *Sphagnum recurvum* lawns of some Cheshire basin mires (e.g. Sinker 1962, Green & Pearson 1968, Tallis 1973*a*).

Scattered through this ground, in addition to the vascular constants, are frequent individuals of *Drosera rotundifolia*, *Narthecium ossifragum* and, a little less commonly but still strongly preferential, *Vaccinium oxycoccos* and *Andromeda polifolia*. Then, around the Rhynchosporion pools, *Rhynchospora alba* and *Drosera anglica* can occasionally be found: these, particularly the former, figure very frequently in the stands of Ratcliffe & Hattey (1982) because of the strictly-maintained use of standard sized quadrats which obviously transgressed vegetation boundaries. In the other direction, towards well-differentiated hummocks, *Empetrum nigrum* ssp. *nigrum* is sometimes seen among the thickening *Calluna* and, in the ground layer, the shift towards *S. capillifolium* can be accompanied by the more frequent occurrence of *Cladonia* spp. and *Pleurozium schreberi*. Typically, however, all these species are of low frequency in this sub-community.

***Empetrum nigrum* ssp. *nigrum-Cladonia* spp. sub-community:** *Sphagnetum* Regeneration Complex, Stage 5 Tansley 1939; *Sphagnetum* Regeneration Complex, later stages Godwin & Conway 1939; Marginal *Sphagnetum* Godwin & Conway 1939; Dissected moss Pearsall 1941; Medium & tall hummocks Ratcliffe & Walker 1958; *Erico-Sphagnetum magellanici*, Sub-Atlantic race Moore 1968 *p.p.*; *Trichophoreto-Eriophoretum*, Typical facies Eddy *et al.* 1969 *p.p.*; *Erico-Sphagnetum papillosi*, Typical & *Rhytidiadelphus* subassociations Moore (1964) 1968 *emend.* Birse 1980 *p.p.*; *Erica-Sphagnum magellanicum* nodum, *Sphagnum papillosum-Erica tetralix* type Ratcliffe & Hattey 1982 *p.p.* Where this sub-community forms the medium and taller hummock element of mire vegetation within stretches of the last sub-community, the drawing of a boundary between the two can be quite difficult but, in their extreme forms, they are quite distinct. First, in comparison with the *Sphagnum-Andromeda* sub-community, *Calluna*, *Scirpus* and *E. vaginatum* tend to have higher covers here, the first in particular becoming more vigorous and abundant but the last two also growing markedly more tussocky. Then, there is frequently some *Empetrum* among them, this becoming especially prominent on the tops of decaying hummocks. By contrast, the preferential herbs of the *Sphagnum-Andromeda* sub-community all decline in frequency here, particularly *Drosera rotundifolia* and *Andromeda*, a little less strikingly *Narthecium* and *Vaccinium oxycoccos*.

Second, there are obvious differences in the composition and structure of the ground layer. Among the Sphagna, the balance shifts towards a strong dominance of *S. capillifolium*, with *S. papillosum* still very frequent but much less abundant, *S. tenellum* rather patchy, though locally prominent and *S. magellanicum* only occasional and of low cover. And other mosses now become frequent among the thickening vascular plants, with *Pleurozium schreberi* and *Rhytidiadelphus loreus* especially good preferentials, *Hypnum cupressiforme/jutlandicum* also increasing somewhat and *Racomitrium*

lanuginosum, *Dicranum scoparium* and *Polytrichum commune* becoming occasional. *Odontoschisma sphagni* and *Mylia anomala* both remain common but other hepatics, notably *Cephalozia connivens*, *C. bicuspidata*, *Calypogeia muellerana*, *Cladopodiella fluitans* and *Kurzia pauciflora*, now appear with some frequency. The other noticeable difference is the increase in larger *Cladonia* spp., notably *C. impexa*, *C. uncialis* and *C. arbuscula*, each of which can be locally abundant. On especially dry surfaces, as on the tops of the tallest hummocks, even *Sphagnum capillifolium* is reduced, with its shoots decaying and, where *Calluna*, *Scirpus* or *E. vaginatum* do not have a vigorous hold, there is often just a crown of *Empetrum* and *Racomitrium* or encrusting lichens, like *Cladonia gracilis*, *C. coccifera* and *C. pyxidata*, on exposed peat.

Habitat

The *Erica tetralix-Sphagnum papillosum* mire is characteristic of waterlogged ombrogenous peats, typically at low altitudes in the moderately oceanic parts of Britain. It is pre-eminently a community of raised bogs, comprising the bulk of the cover on their active plane, but it can also be found within stretches of blanket mire, and it occurs, too, on acidic topogenous peats in some basin mires. The typical habitat has been very widely affected by various treatments, notably peat-cutting, burning and draining, and these have often modified the vegetation or reduced it to fragmentary stands.

Raised bogs have developed where local accumulation of topogenous deposits has elevated the mire surface above the immediate controlling influence of the ground water-table, leading to the establishment of ombrogenous conditions on the plane. They are found primarily in the lowlands and are particularly associated with the flood-plains of mature river valleys, where flat tracts of alluvium have provided a suitable base for deep and often extensive peat accumulation. Most occur adjacent to large estuaries, as on the Somerset Levels, at Cors Fochno in Dyfed, around Morecambe Bay and at Bowness, Wedholme, Glasson and Kirkconnell on the Solway, where the *Erica-Sphagnum* mire can be found (or once did occur) close to sea-level; but broad valleys far inland, and sometimes at altitudes over 200 m, have also provided locations, as at Cors Goch glan Teifi in Dyfed, Rhos Goch in Powys and alongside the Forth in the Flanders Moss complex (Ratcliffe 1977). Such sites are concentrated in a broad belt running south-west to north-east between the Severn–Humber and Clyde–Moray lines and, though the initiation of raised mire development seems often to have coincided with climatic deterioration at the Boreal/Atlantic transition about 7000 years ago, these bogs subsist today under relatively low rainfall. For the most part, they receive between 800 and 1200 mm annual precipitation (*Clima-*

tological Atlas 1952) with 140–180 wet days yr^{-1} (Ratcliffe 1968), considerably less than either of our two other ombrogenous bogs, the *Scirpus-Eriophorum* and *Calluna-Eriophorum* mires. Characteristically, raised bogs have a domed profile, but the slope of the ground under the *Erica-Sphagnum* mire is usually very near to zero, so run-off is very slight and the active growth of the bog is not so strongly dependent on a high precipitation/evaporation ratio. Indeed, remnants of raised mires survive in what are now very dry areas, as on Thorne Waste in West Yorkshire/Lincolnshire and at Woodwalton in Cambridgeshire, where annual rainfall is less than 600 mm, and on the former site healthy fragments of the *Erica-Sphagnum* mire can be found.

Increasingly, to the north-west of Britain, individual raised mires lose their integrity within the smothering mantle of blanket peat that has developed in the wetter climate but certain stretches of mire seem to retain something of the character of raised bog, particularly over local depressions or on cols. Such transitional situations provide a suitable location for the *Erica-Sphagnum* mire at unusually high altitudes, up to 500 m or more. They occur occasionally in Wales, at Cors Goch in Powys, for example which provides the most southerly station for *Andromeda*, and on the Pennines, on Stainmore (Pearsall 1941) and at Moor House (Eddy *et al.* 1969), but are especially plentiful in the Borders and south-west Scotland, at sites like the Irthinghead mires, on the Silver Flowe (Ratcliffe & Walker 1958) and in Strathclyde (Bignal & Curtis 1981; see also Ratcliffe 1977). At the other extreme, the *Erica-Sphagnum* mire also extends on to some basin bogs, where more strictly topogenous peats have acquired a character verging on the ombrogenous towards their centre. Such sites are quite plentiful over the drift-smeared terrain within the limit of the Final Glaciation and the community is represented on some of them in the north-west Midlands, at Chartley and Wybunbury Mosses, for example, which have a *schwingmoor* character (Sinker 1962, Green & Pearson 1968, Tallis 1973*a*), and around the Eden valley in Cumbria, at Tarn, Moorthwaite, Cumwhitton and Cliburn Mosses (Ratcliffe 1977).

In this range of site types, the *Erica-Sphagnum* mire is characteristic of virgin surfaces where there is consistent waterlogging, at least on the flats and around the hummock bases, by a high and stagnant water-table. The peats are often deep, typically deeper than under the *Scirpus-Eriophorum* and *Calluna-Eriophorum* blanket mires and sometimes up to 10 m or more. However, although at the base of raised and basin mires they are derived from herbaceous fen vegetation with interposed brushwood, they are uniformly acidic at the surface, with a pH of around 4, and oligotrophic. Under such conditions, the Sphagna show very luxuriant growth on the active mire plane and make the major contribution

to the accumulating peats, with *Eriophorum vaginatum* constant and confirming the Sphagnetalia character of the vegetation, but generally making the minor contribution to accumulation. The balance of the major structural elements in the vegetation, the Sphagna and the bulky vascular plants, is thus more like that in the *Scirpus-Eriophorum* mire than in the *Calluna-Eriophorum* mire but, if anything, the Sphagna are of greater importance than in the *Scirpus-Eriophorum* mire. For reasons which are unclear, *Sphagnum magellanicum* shows a quite marked preference for this community, frequently joining *S. papillosum* as an abundant component of the undulant flats developed at or just above the level of the water-table.

These flats tend to be more extensive here than in the *Scirpus-Eriophorum* mire and surface relief is often not so strongly differentiated. On many raised mires, Cors Fochno and Glasson Moss being good, more intact examples, the patterning is on rather a large scale and of low amplitude, though the size of the bog seems to have some effect on the relief, smaller raised mires in similar climatic conditions often showing more pronounced undulations, as at Rhos Goch and at Wem Moss in Shropshire, a feature which becomes more exaggerated where rainfall is lower and sporadic, as on Penmanshiel Moor in Berkwickshire (Ratcliffe 1977). And, where the *Erica-Sphagnum* mire extends into more oceanic areas, the pool element can become as extensive and ordered as on some blanket mires, a situation well seen in the Silver Flowe complex (Ratcliffe & Walker 1958, Lindsay *et al.* 1984). Where hummocks and hollows are well differentiated, they show the characteristic zonation of Sphagna and vascular plants in relation to the height of the water-table (see below), but whether bog growth always involves a cyclical alternation of hummock and hollow at particular points is debatable. Although it was from classic raised bogs with the *Erica-Sphagnum* mire that the theory of the 'regeneration complex' was first described in Britain (Osvald 1923, 1939, Tansley 1939, Godwin & Conway 1939), stratigraphical investigation does not always reveal the tell-tale lenses of the different Sphagna and, as in the *Scirpus-Eriophorum* mire, some surface-patterning may be a quasi-permanent feature.

Other distinctive floristic features of the *Erica-Sphagnum* mire reflect the moderately oceanic character of the climate over the region where the community is centred. Compared with the *Scirpus-Eriophorum* mire, for example, *Molinia* is less important here within the bog vegetation itself, though it is often very abundant on drier or better-drained areas in close proximity to the community, and *Sphagnum auriculatum* does not figure so prominently in the transitions to the Rhynchosporion pools. *Potentilla erecta*, *Polygala serpyllifolia* and *Pedicularis sylvatica* are also much reduced on ombrogenous peats with the move to less oceanic conditions, and

Pleurozia purpurea and *Campylopus atrovirens*, though recorded in transitional stands, as on the Silver Flowe (Ratcliffe & Walker 1958) and in similar vegetation in Ireland (Moore 1968), are generally absent. In the other direction, the *Erica-Sphagnum* mire only very occasionally penetrates into the cooler, wet climate characteristic of the *Calluna-Eriophorum* mire, which accounts for the scarcity here of plants like *Rubus chamaemorus*, *Vaccinium vitis-idaea*, *V. uliginosum* or *Empetrum nigrum* spp. *hermaphroditum*, the contrast between the communities being well seen on Stainmore (Pearsall 1941) and at Moor House (Eddy *et al.* 1969). Positive floristic responses to climate are few, but the Continental Northern *Vaccinium oxycoccos* and particularly *Andromeda* are very good preferentials.

Floristic and structural differences between the subcommunities are strongly related to variations in ground moisture and thus partly a reflection of the differentiation of surface relief. The *Sphagnum-Andromeda* subcommunity is the more distinct of the two and is consistently associated with wetter conditions, comprising the bulk of the cover where flats and low hummocks predominate. Under such conditions, there is an especially luxuriant carpet of Sphagna, frequent occurrences of lawn plants like *Drosera rotundifolia*, *Narthecium*, *Vaccinium oxycoccos* and, particularly over slightly raised areas, *Andromeda*, poorly-developed tussockiness in *Eriophorum vaginatum* and *Scirpus*, and often puny *Calluna*. Such vegetation parallels that in the *Drosera-Sphagnum* sub-community of the *Scirpus-Eriophorum* mire, containing occasional records for Rhynchosporion plants where there are transitions to bog pools, though generally lacking any indicators of soligenous influence, which is rare on the surface of raised mires. The *Sphagnum-Andromeda* sub-community can also come very close in its floristics to the *Narthecio-Sphagnetum*, the typical Sphagnetalia mire of lowland valley bogs: this is especially true on some of the Cheshire mosses where *Scirpus* and *Eriophorum vaginatum*, two good distinguishing species between the communities, become scarcer.

On somewhat drier peats, the *Sphagnum-Andromeda* sub-community is replaced by the *Empetrum-Cladonia* type, which can therefore be seen on virgin mires on the tops of taller hummocks, as in the later stages of the 'regeneration complex' (Tansley 1939, Godwin & Conway 1939) and the 'medium and tall hummocks' of Ratcliffe & Walker (1958); over more extensive surfaces which are maintained in a drier state, as in the 'marginal *Sphagnetum*' on Cors Goch glan Teifi (Godwin & Conway 1939); and on peats at higher altitudes which have become dissected by erosion channels (Pearsall 1941). In this less strongly-waterlogged environment, dominance among the Sphagna shifts to *S. capillifolium*, *Cladonia* spp. and hypnaceous mosses become prominent among

the increasingly tussocky *Eriophorum vaginatum* and *Scirpus* and vigorous *Calluna*, and *Empetrum nigrum* ssp. *nigrum* spreads on the eroding surfaces. In the process, the *Erica-Sphagnum* mire loses some of its distinctive character, *Vaccinium oxycoccos* and particularly *Andromeda* becoming scarce, and the vegetation closely approaches that of drier forms of the *Scirpus-Eriophorum* mire. Indeed, drier areas of peat on mires towards the more oceanic limit of the community, where *Erica cinerea* becomes conspicuous as a coloniser, develop vegetation indistinguishable from the *Cladonia* subcommunity of the *Scirpus-Eriophorum* mire, a situation well seen in Strathclyde (e.g. Bignal & Curtis 1981).

The surface-drying of whole raised mires may be, in part, a natural phenomenon, recurrence surfaces, often here with abundant remains of *Sphagnum imbricatum*, testifying to past episodes of wetter conditions (Godwin & Conway 1939, Tallis 1961, Walker & Walker 1961, Green 1968). But there is no doubt that, in very many cases, the process has been hastened by treatment, more especially by combinations of peat-cutting, burning and draining, sometimes with grazing. Very few of our raised bogs or basin mires, lying as they do in relatively accessible lowland landscapes, have escaped these kinds of interference. Much early activity was largely confined to their margins and often perfunctory in character but, in some sites, and, in recent years, more universally, the effects have been more drastic, with extensive drainage and abandonment, reclamation for agriculture or forestry, or the wholesale stripping of peat, originally for local burning, now for horticultural use. In extreme cases, the entire original surface of the mire, or very nearly all of it, has been removed by peat-cutting, such that the raised bog vegetation of the *Erica-Sphagnum* type has been totally lost, as on Holme Fen and at Woodwalton in Cambridgeshire (Poore 1956*b*), or severely reduced to fragments, as on Shapwick Heath in Somerset and at Thorne Waste, or restricted to sections of the bog, as at Bowness and Wedholme. Elsewhere cutting has been more confined but attempts at drainage have lowered the water-table, a situation seen at Kirkconnell Flow and on Flanders Moss, and where this has been combined with burning and grazing, the effects have been pronounced. Accidental fires, like those at Glasson Moss, have sometimes damaged more intact sites. In some basin mires carrying the *Erica-Sphagnum* vegetation, there has been a marked eutrophication of incoming waters by fertiliser run-off which has curtailed any tendency to the development of ombrogenous nuclei, a phenomenon clearly visible at sites in Cheshire and Shropshire (Poore & Walker 1959, Sinker 1962, Green & Pearson 1968, Tallis 1973).

In such situations as these, the *Sphagnum-Andromeda* sub-community tends to suffer first and most, its extensive *Sphagnum* carpet being very susceptible to surface drying or burning, recovering only slowly from episodes of damage or not at all where the effects of interference are sustained. Often, then, its cover is reduced to wetter or unburned remnants of the mire surface, though it does seem to be able to regenerate on new wet areas, such as abandoned shallow peat-cuttings. At Moorthwaite and Cumwhitton Mosses, for example, two basin mires in Cumbria, there is vigorous growth over old cut surfaces and sporadic regeneration can even be seen in the very dry climate at Thorne Waste (Ratcliffe 1977). And *Andromeda* is one of the distinctive plants of this kind of *Erica-Sphagnum* mire which can positively thrive after burning, even though the richness of the accompanying flora has been lost, at least temporarily (e.g. Sinker 1962). The often quite marked variation in the representation of different associates in this subcommunity at particular sites may be attributable to their differential rates of recovery from frequently complex patterns of interference.

The *Empetrum-Cladonia* sub-community, characteristic as it is of drier peat, may actually be favoured by certain kinds of treatment, particularly by surface or marginal drainage which lowers the water-table over part or all of the mire, allowing its extension from drier hummocks over what were originally wet lawns and hollows. In other cases, it can become prominent on remaining baulks of peat on cut surfaces with the intervening areas occupied by the regenerating *Sphagnum-Andromeda* sub-community or modified vegetation. Such prominence may, however, be a temporary interlude prior to extensive invasion by woody plants no longer held in check by waterlogging (see below). Even on relatively intact mires, with only slight shifts in the water regime or infrequent episodes of burning or grazing, there can be changes in the abundance of particular species within tracts of reasonably well-preserved *Erica-Sphagnum* mire. The local prominence of *Scirpus* and *Molinia*, for example, on Cors Goch glan Teifi may be partly related to past treatment (Godwin & Conway 1939, Ratcliffe 1977).

Zonation and succession

Zonations between the sub-communities of the *Erica-Sphagnum* mire are related to the height of the water-table and transitions to other vegetation types to the degree of stagnation and to the extent of soligenous influence. Treatments can modify these patterns greatly and permit the replacement of the community by other herbaceous vegetation or by woodland.

Internal patterning within virgin stands of the *Erica-Sphagnum* mire characteristically reflects the differentiation of surface microrelief. As noted above, this is generally less pronounced than in the more oceanic *Scirpus-Eriophorum* mire, though it shows some variation with climate and also with the size of the bog. Often

the *Sphagnum-Andromeda* sub-community predominates over extensive wet lawns, with the *Empetrum-Cladonia* sub-community marking out raised areas, frequently slight and of irregular disposition, in other cases more prominent and ordered, with a clearer zonation among the plants in relation to the height of the water-table. Where pools occur in the hollows, there are transitions from the *Sphagnum-Andromeda* sub-community to Rhynchosporion vegetation, with a shift in the *Sphagnum* carpet to semi-aquatic species and a reduction in many of the vascular plants characteristic of the mire plane, notably *Calluna*, *Scirpus* and *E. vaginatum*. As on the *Scirpus-Eriophorum* mire, a fringe of *Rhynchospora alba* often marks this switch, but here the Rhynchosporion vegetation is typically represented by the *Sphagnum cuspidatum/recurvum* community, the *Sphagnum auriculatum* type of bog pool generally being confined to sites in areas with a somewhat more oceanic climate, where the mire vegetation itself is of a transitional character (as on the Silver Flowe: Ratcliffe & Walker 1958). Usually, *S. cuspidatum* is the predominant pool species but, where mire surfaces have become eutrophicated, *S. recurvum* often becomes abundant (see below).

Natural zonations from the *Erica-Sphagnum* mire to other vegetation types are often related to the degree of stagnation in the peats and, on raised bogs, this characteristically lessens towards the margins where there is a more steeply-sloping surround or rand of sometimes considerable width. Over this, the freely-drained con-

ditions exclude the *Erica-Sphagnum* mire and it is typically replaced by vegetation in which *Molinia* is the leading species, a pattern well seen in the maps and transects of Cors Goch glan Teifi (Godwin & Conway 1939) and some of the Silver Flowe mires (Ratcliffe & Walker 1958, Boatman *et al.* 1981). The overwhelming dominance of *Molinia*, and the consequent exclusion of associates from this zone, sometimes make it difficult to determine the exact character of this vegetation but it can usually be referred to the Junco-Molinion. Gradations between this and the *Erica-Sphagnum* mire of the bog dome are rarely abrupt and transitional vegetation can sometimes be clearly identified as *Scirpus-Erica* wet heath, often the *Sphagnum* sub-community which has some representation of Sphagnetalia species (as in the 'intermediate bog' of Ratcliffe & Walker 1958). Elsewhere, such gradual transitions can be incorporated within the *Erica-Sphagnum* mire itself, the change being essentially confined to gentle shifts of dominance as the rand is approached (Figure 16).

Rands are sometimes dissected by erosion channels in which there is some clear soligenous influence but, in normal circumstances, these do not eat back on to the bog dome itself and direct transitions from the *Erica-Sphagnum* mire to soligenous mires are rare on raised bogs. Nonetheless, the distinctive vegetation of the lagg zone beyond the rand is an integral part of the large-scale pattern in this kind of habitat and it is typically some kind of Caricion nigrae poor fen, often the *Carex echinata-Sphagnum* mire, with some invasion by woody

Figure 16. Changes in raised mire zonations from more natural sequence of communities (foreground) to that on drying bog surfaces (background).
M1 *Sphagnum auriculatum* bog pool community
M6 *Carex echinata-Sphagnum* mire
M15b *Scirpus-Erica* wet heath, Typical sub-community

M18a *Erica-Sphagnum* bog, *Sphagnum-Andromeda* sub-community
M18b *Erica-Sphagnum* bog, *Empetrum-Cladonia* sub-community
M25a *Molinia-Potentilla* mire, *Erica* sub-community
W4 *Betula-Molinia* woodland
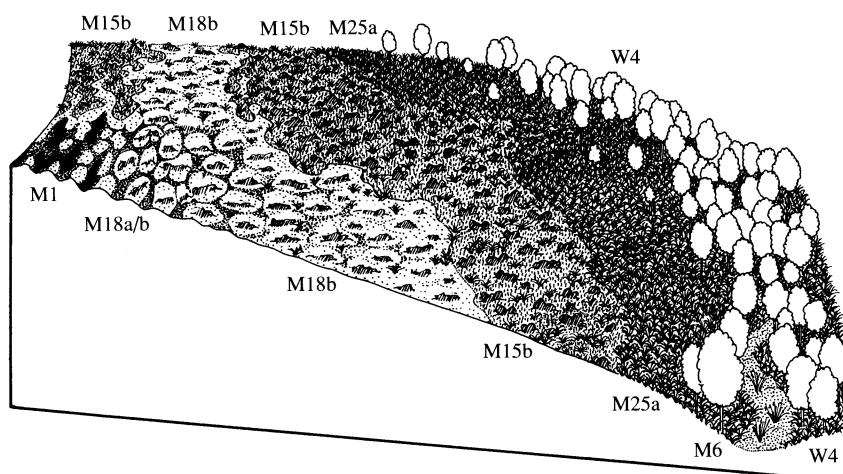
plants producing *Salix-Galium* or *Betula-Molinia* woodland or, where there is some greater degree of base enrichment, the *Alnus-Carex* woodland. This type of pattern can be seen at Cors Fochno, Rhos Goch and Glasson Moss.

Where the *Erica-Sphagnum* mire is represented on basin mires, the community can be found in closer juxtaposition with both soligenous and topogenous vegetation which, with some base- and/or nutrient-enrichment from the incoming waters, often shows a slight shift towards a more calcicolous or eutrophic character. At Llyn in Powys, for example, Cors Graianog in Gwynedd and Cumwhitton, the *Erica-Sphagnum* mire occurs with the *Potentillo-Caricetum* and there are sometimes close associations with the *Carex-Sphagnum warnstorfii* or *Carex-Sphagnum squarrosum* mires or even with vegetation approaching the *Carex-Calliergon* mire, again with varying colonisation by *Salix* spp. and *Betula pubescens*.

Where the *Erica-Sphagnum* mire occurs in conditions approaching those of blanket bog, the vegetation pattern may preserve some features of the raised mire system, with a rand on most of the circumference, or just on one side (as on Snibe and Brishie bogs, respectively, in the Silver Flowe complex: Ratcliffe & Walker 1958), passing gradually over its other edges to blanket mire proper or, where there is a transition to steeper valley-side slopes, to *Scirpus-Erica* wet heath on thinner, drier peats. In other cases, ill-defined patches of the *Erica-Sphagnum* mire occur embedded within tracts of blanket bog where the peat mantle deepens over cols or sub-surface hollows. Usually, at the lower altitudes of which the community is characteristic, it is the *Scirpus-Eriophorum* mire which provides the context, as in southern Scottish sites like Mochrum Lochs and Kilquhockadale Flow (Ratcliffe 1977, Bignal & Curtis 1981), though towards the Pennines and particularly at higher altitudes, this is replaced by the *Calluna-Eriophorum* mire, as around Irthinghead on the Cumbria/Northumberland border, on Stainmore (Pearsall 1941) and at Moor House (Eddy *et al.* 1969). At lower levels soligenous soaks can sometimes be found in close association with the *Erica-Sphagnum* mire, with a cover of the *Carex* sub-community of the *Scirpus-Erica* wet heath or some type of *Carex echinata-Sphagnum* mire. At higher altitudes, surface erosion features are sometimes found with systems of gullies fretting the surface and the *Eriophorum angustifolium* community in pools.

Such zonations as these have been very widely affected by treatments, particularly at lower altitudes where there has been a long history of local, but sometimes intensive, exploitation of peatlands and where many raised and basin mires now remain, much modified and safeguarded only by statutory protection, within intensive agricultural landscapes. The influences of treat-ments have been very diverse, partly because histories of interference have been complex, and partly because different communities in the vegetation patterns are affected in different ways by peat-cutting, burning and draining. But some general effects can be discerned. First, lowering of the water-table, and surface-damage by burning on raised and basin mires, tend to shift the balance within the *Erica-Sphagnum* mire towards the *Empetrum-Cladonia* sub-community and sometimes towards more overwhelming dominance by *Calluna*, *E. vaginatum*, *Scirpus* or, increasing beyond its usual low cover here, *Molinia*. Such changes can occur over entire mire surfaces but they often show first around the margins, where the rand vegetation extends its cover inwards, and at the centre, such that the *Erica-Sphagnum* mire is reduced to a narrowing ring. Increasing climatic dryness makes raised mires particularly susceptible to such modifications (Godwin & Conway 1939).

Continuations of such a trend would be expected to convert the *Erica-Sphagnum* mire to the *Scirpus-Erica* wet heath with the loss of *Eriophorum vaginatum* and the luxuriant *Sphagnum* lawns, but particular sites often show a complex patchwork of vegetation intermediate between the two, with local dominance of ericoids, *Scirpus* and *Molinia*, the balance between which is also affected by burning and grazing. Establishment of dry Calluno-Ulicetalia heath may follow but, very commonly, once the surface has ceased to be waterlogged, invasion by woody plants supervenes. *Betula pubescens* (with *B. pendula* on drier peats) and *Pinus sylvestris* are the major colonisers. The former can come to dominate in *Betula-Molinia* woodland or, where drying out has proceeded further, in birch-dominated stands of the *Quercus-Betula-Dicranum* woodland. The pine, though usually seeding in from plantation stock, can form a canopy to vegetation very similar to the natural *Pinus-Hylocomium* woodland in which *E. tetralix* or *Empetrum* can persist under more open covers and where such characteristic species as *Pyrola minor* or *Listera cordata* sometimes appear. Pine woodland of this kind can be seen colonising the community at Moorthwaite Moss and Kirkconnell Flow.

Second, peat-cutting often contributes to the surface drying of raised and basin mires but it also results in patterns of its own which fret the bog surface with systems of hollows and baulks. Where the hydrological regime has not been too grossly disrupted, such uneven ground may preserve something of the natural pattern of virgin mires, with the two sub-communities disposed according to the wetness of the ground, but with an artificial regularity over the surface. Often, however, the impact has been more drastic, so that complex mosaics of secondarily-developed communities remain, with poor fens, wet and dry heath, bracken stands and *Salix*

and birch woodland all jumbled together: this is well shown over parts of the Somerset Levels and on Thorne Waste.

Eutrophication of the mire surface or of the ground waters around is often an attendant feature of such gross disturbance and even sites which have remained reasonably intact can show marked effects of enrichment from, for example, fertiliser run-off or drift. This is especially prevalent in some of the Cheshire and Shropshire mires, where it has resulted in a spread of *Sphagnum recurvum*, from its usual confines in pools over extensive wet lawns in which the *Sphagnum-Andromeda* sub-community of the *Erica-Sphagnum* mire is reduced to scattered (though sometimes apparently actively-growing) patches on slightly raised areas (Sinker 1962, Green & Pearson 1968, Tallis 1973*a*).

Stratigraphical studies clearly show that, in raised and basin mires, vegetation of the *Erica-Sphagnum* type has developed as the climax of a hydroseral succession, the commonest sequence of which has been open water, swamp, fen, woodland and bog, the stages to fen often taking less than 1000 years, the later phases sometimes much longer (e.g. Walker 1970). Although there is evidence in the peats of periods of drier climate since the initiation of ombrogenous accumulation, the community seems to persist on active surfaces at the present time, provided treatments are not too disruptive of the hydrological regime.

Distribution

The *Erica-Sphagnum* mire is of widespread but local occurrence through the lowlands of Wales and north-west Britain up to the Clyde–Moray line, with a few outlying sites in lowland southern England. In many areas, its extent has been much reduced and its vegetation modified by exploitation of peatlands, but good stands remain in parts of Wales, around the Solway, in the Borders and in south-west Scotland. Both sub-communities occur throughout the range.

Affinities

Although vegetation of this kind was early recognised as distinctive among our range of bog types (e.g. Rankin 1911*a*, Tansley 1939, Godwin & Conway 1939, Pearsall 1941, Osvald 1949), it is generally subsumed within a *Sphagnetum* which included parts of other communities, and the major interest of which was often taken to be its supposed pattern of regeneration. And, being essentially a vegetation type of lowland areas outside north-west

Scotland, it did not figure in McVean & Ratcliffe (1962), whose two major ombrogenous communities, the *Scirpus-Eriophorum* and *Calluna-Eriophorum* mires, have tended to provide the basis for subsequent descriptive accounts.

Although the *Erica-Sphagnum* mire shows a virtually continuous gradation into the *Scirpus-Eriophorum* type, a feature recognised by Braun-Blanquet & Tüxen (1952) and Ratcliffe & Walker (1958), and extends into habitats transitional to the blanket bog context typical of the latter, it shows sufficient peculiar characteristics to be worth recognising as a separate kind of ombrogenous vegetation best developed in the raised mire habitat. Moore (1968) was the first to accord British vegetation of this kind this status, placing it in an *Erico-Sphagnetum magellanici*, a broadly-defined Erico-Sphagnion association centred on the *eigentliches Hochmoor* of Osvald (1923), corresponding roughly with the range of *Sphagneta* diagnosed by Kastner & Flössner (1933) and Schwickerath (1940) and characteristic of the lowlands of north-west Europe. Moore (1968) recognised three geographical races within the community, extending from the extreme Atlantic conditions of central Ireland (where the vegetation had first been described by Braun-Blanquet & Tüxen (1952)), through a sub-Atlantic zone across Britain, Belgium and Germany (e.g. Jonas 1933, Schwickerath 1940, Vanden Berghen 1948), into the sub-continental parts of Europe (e.g. Vanden Berghen 1948, Tüxen & Soyrinki 1958, Jahns 1962). As defined here, using our own data and samples from Birse (1980) and Bignal & Curtis (1981), the *Erica-Sphagnum* mire falls firmly in the central type, distinguished from the first by the low frequencies of *Molinia*, *Pleurozia purpurea* and *Campylopus atrovirens*, and from the third by the high frequencies of *Scirpus* and *Sphagnum papillosum*. We have followed Birse (1980) in using *S. papillosum*, rather than *S. magellanicum*, which is preferential but not constant, to name the community, though his *Erico-Sphagnetum papillosi* also contains vegetation which would here be placed in the *Scirpus-Eriophorum* and *Calluna-Eriophorum* mires. In addition to *S. magellanicum*, the community is separated from these two other ombrogenous Erico-Sphagnion mires by the preferential occurrence of *Andromeda*, *Vaccinium oxycoccos* and the now very local *S. imbricatum*. It can be distinguished from the *Narthecio-Sphagnetum*, the Erico-Sphagnion community which replaces it in valley mires in lowland, southern Britain, by *Andromeda*, *Scirpus* and *Eriophorum vaginatum*.

Floristic table M18

	a	b	18
Calluna vulgaris	V (1–8)	V (1–9)	V (1–9)
Erica tetralix	V (1–7)	V (1–4)	V (1–7)
Eriophorum angustifolium	V (1–6)	V (1–8)	V (1–8)
Sphagnum papillosum	IV (1–8)	V (1–9)	V (1–9)
Eriophorum vaginatum	IV (1–7)	V (1–8)	IV (1–8)
Sphagnum capillifolium	IV (1–6)	V (1–8)	IV (1–8)
Sphagnum tenellum	IV (1–3)	IV (1–5)	IV (1–5)
Odontoschisma sphagni	IV (1–4)	IV (1–3)	IV (1–4)
Sphagnum magellanicum	IV (1–8)	II (1–4)	III (1–8)
Narthecium ossifragum	IV (1–7)	II (1–3)	III (1–7)
Drosera rotundifolia	IV (1–3)	I (1–3)	II (1–3)
Vaccinium oxycoccos	III (1–4)	II (1–3)	II (1–4)
Andromeda polifolia	III (1–3)		I (1–3)
Rhynchospora alba	I (1–4)		I (1–4)
Myrica gale	I (1–4)		I (1–4)
Drosera anglica	I (1–2)		I (1–2)
Empetrum nigrum nigrum	II (1–6)	IV (1–6)	III (1–6)
Pleurozium schreberi	II (1–4)	IV (1–5)	III (1–5)
Cladonia impexa	II (1–3)	IV (1–4)	III (1–4)
Rhytidiadelphus loreus	I (2)	IV (1–4)	II (1–4)
Cladonia uncialis	I (1–4)	III (1–6)	II (1–6)
Cladonia arbuscula	I (1–4)	III (1–3)	II (1–4)
Cephalozia connivens		III (1–3)	II (1–3)
Calypogeia muellerana	I (1)	II (1–3)	I (1–3)
Hypogymnia physodes	I (1)	II (1–3)	I (1–3)
Polytrichum commune	I (1–2)	II (1–3)	I (1–3)
Dicranum scoparium	I (1–3)	II (1–3)	I (1–3)
Cephalozia bicuspidata	I (1–3)	II (1–3)	I (1–3)
Kurzia pauciflora	I (1–4)	II (1–4)	I (1–4)
Cladopodiella fluitans		II (1–3)	I (1–3)
Racomitrium lanuginosum	I (2)	II (1–4)	I (1–4)
Mylia anomala	III (1–6)	III (1–4)	III (1–6)
Aulacomnium palustre	III (1–5)	III (1–3)	III (1–5)
Scirpus cespitosus	III (1–6)	III (1–6)	III (1–6)
Sphagnum cuspidatum	II (1–6)	II (1–2)	II (1–6)
Hypnum jutlandicum	II (1–5)	II (1–3)	II (1–5)
Molinia caerulea	II (1–4)	II (1–4)	II (1–4)
Sphagnum recurvum	I (1–5)	I (1–3)	I (1–5)
Hypnum cupressiforme	I (1–3)	I (1–3)	I (1–3)
Sphagnum palustre	I (2–3)	I (1–2)	I (1–3)
Polytrichum alpestre	I (1–2)	I (1–3)	I (1–3)
Pohlia nutans	I (1–4)	I (1–3)	I (1–4)
Sphagnum subnitens	I (3–4)	I (1–3)	I (1–4)
Rubus chamaemorus	I (1–4)	I (1–2)	I (1–4)

Plagiothecium undulatum	I (1)	I (1–3)	I (1–3)
Vaccinium myrtillus	I (1–3)	I (1–3)	I (1–3)
Vaccinium vitis-idaea	I (1)	I (1–3)	I (1–3)
Sphagnum pulchrum	I (1–4)	I (1–2)	I (1–4)
Deschampsia flexuosa	I (1–3)	I (1)	I (1–3)
Juncus squarrosus	I (1–2)	I (1–3)	I (1–3)
Campylopus paradoxus	I (1–3)	I (1)	I (1–3)
Lophozia ventricosa	I (1–3)	I (1–2)	I (1–3)
Cladonia gracilis	I (1–3)	I (1–3)	I (1–3)
Sphagnum fuscum	I (1–3)	I (1)	I (1–3)
Number of samples	118	77	195
Number of species/sample	15 (8–21)	24 (16–30)	17 (8–30)
Herb height (cm)	25 (15–40)	18 (13–30)	22 (13–40)
Herb cover (%)	71 (10–100)	57 (35–75)	67 (10–100)
Bryophyte height (mm)	56 (20–150)		
Bryophyte cover (%)	63 (2–100)	91 (75–95)	71 (2–100)
Altitude (m)	206 (10–530)	250 (15–550)	209 (10–550)
Slope (°)	0 (0–2)	0 (0–2)	0 (0–2)
Soil pH	4.0 (3.3–4.7)		

a *Sphagnum magellanicum-Andromeda polifolia* sub-community

b *Empetrum nigrum nigrum-Cladonia* sub-community

18 *Erica tetralix-Sphagnum papillosum* raised mire (total)

M18   *Erica tetralix-*
       Sphagnum papillosum
       raised mire

b   *Empetrum nigrum* ssp.
       nigrum-Cladonia spp.
       sub-community