M15
Scirpus cespitosus-Erica tetralix wet heath

Synonymy

Scirpetum cespitosi Tansley 1939 *p.p.*; *Molinietum caeruleae* Tansley 1939 *p.p.*; *Trichophoreto-Eriophoretum caricetosum* McVean & Ratcliffe 1962; *Molinia-Myrica* mire McVean & Ratcliffe 1962, Birks 1973, Ratcliffe & Hattey 1982; *Molinieto-Callunetum* McVean & Ratcliffe 1962, Birks 1973, Prentice & Prentice 1975, Evans *et al.* 1977; *Trichophoreto-Callunetum* McVean & Ratcliffe 1962, Birks 1973, Prentice & Prentice 1975, Evans *et al.* 1977, Hill & Evans 1978; *Narthecio-Ericetum tetralicis* Moore (1964) 1968, *sensu* Birse 1980; *Erica tetralix-Molinia caerulea* sociation Edgell 1969; *Trichophorum cespitosum* nodum Edgell 1969; *Trichophorum cespitosum-Carex panicea* Association Birks 1973, Adam *et al.* 1977; *Narthecium-Campylopus atrovirens* nodum Prentice & Prentice 1975; Blanket bog communities Adam *et al.* 1977; *Calluno-Molinietum* Hill & Evans 1978; Mire noda 3 & 4 Daniels 1978 *p.p.*; *Trichophorum germanicum-Calluna vulgaris* Association McVean & Ratcliffe 1962 *emend.* Birse 1980; *Molinia caerulea-Potentilla erecta* community Bignal & Curtis 1981; *Trichophorum cespitosum-Eriophorum angustifolium* mire Ratcliffe & Hattey 1982; *Ericetum tetralicis* Dierssen 1982; Disturbed peatland 3.ii Hulme & Blyth 1984.

Constant species

Calluna vulgaris, *Erica tetralix*, *Molinia caerulea*, *Potentilla erecta*, *Scirpus cespitosus*.

Rare species

Campylopus atrovirens var. *falcatus*, *C. setifolius*.

Physiognomy

The *Scirpus cespitosus-Erica tetralix* wet heath is a compendious vegetation type with few constants and wide variation in the pattern of dominance and in the associated flora. *Molinia caerulea*, *Scirpus cespitosus*, *Erica tetralix* and *Calluna vulgaris* are all of high frequency throughout and, by and large, it is mixtures of these species that give the vegetation its general stamp. But sometimes one of them, or occasionally even two, can be missing and their proportions are very diverse, varying not only with natural differences in climate and soils, but also very markedly with treatment. Of the four species, *Molinia* is the most consistent overall and it is often abundant, so some accounts have included the community within a *Molinietum* (e.g. Tansley 1939; see also McVean & Ratcliffe 1962, Edgell 1969, Bignall & Curtis 1981) or a *Molinieto-Callunetum*, where dominance is shared with *Calluna* (McVean & Ratcliffe 1962, Birks 1973, Prentice & Prentice 1975, Evans *et al.* 1977, Hill & Evans 1978). In other stands, *Scirpus* is very prominent, such that vegetation of this kind has been characterised as part of a *Scirpetum* (e.g. Tansley 1939, Edgell 1969) or, where *Calluna* is again also abundant, as communities like the *Trichophoreto-Callunetum* of McVean & Ratcliffe (1962) or its equivalents (Birks 1973, Prentice & Prentice 1975, Evans *et al.* 1977, Hill & Evans 1978, Birse 1980). Such units as these subsume a considerable amount of the variation in dominance within the community, but other combinations of species are quite common: *Molinia* sometimes dominates with *Scirpus*, or with both *Scirpus* and *Calluna*; and *E. tetralix*, which is generally subordinate in cover, can be abundant too, often with *Molinia*, as in many of the Welsh stands described by Ratcliffe & Hattey (1982).

Then, in the various sub-communities, some other plants make a contribution to the shrubby cover. *Erica cinerea* and *Vaccinium myrtillus* are of generally low frequency throughout but they are preferential to particular kinds of *Scirpus-Erica* wet heath and can attain local abundance, though usually with less than 25% cover. More striking is *Myrica gale* which, in other subcommunities, can be found as a low-cover occasional but which thickens up locally to dominate in a canopy 50 cm or so tall. Such vegetation has generally been characterised as a distinct *Molinia-Myrica* nodum (e.g. McVean & Ratcliffe 1962, Birks 1973), but, as where *Myrica* shows the same behaviour in other mire types, this variation can be readily subsumed within the community.

Typically, the dominants make up an extensive cover, though only 2–3 dm tall except where *Myrica* figures, and other vascular plants are often represented only as scattered individuals or in small clumps or tufts. Few of the associates are common throughout and one species notable for its scarcity here is *Eriophorum vaginatum*. In general appearance, this community often looks like a blanket mire, frequently occurs with such vegetation or replaces it, and grades floristically to it, but the low frequency of *E. vaginatum* overall, and its characteristically low cover when it does occur, provide one good separation between the *Scirpus-Erica* wet heath and the ombrogenous Sphagnetalia communities. Continuity, on the other hand, is stressed by the common occurrence here of *Potentilla erecta* and, particularly in the moister stands, of *Polygala serpyllifolia*, *Narthecium ossifragum* and *Eriophorum angustifolium*, all of which also characterise the *Scirpus-Eriophorum* blanket mire, the ombrogenous bog whose range coincides very closely with that of the *Scirpus-Erica* wet heath.

Other occasionals in the community include *Nardus stricta*, *Juncus squarrosus*, *Agrostis canina* ssp. *canina*, *Festuca ovina/vivipara* and, occurring more sparsely, *Blechnum spicant*, *Huperzia selago*, *Pedicularis sylvatica*, *Festuca rubra*, *Carex binervis*, *Juncus acutiflorus*, *J. effusus*, *J. conglomeratus* and *J. articulatus*. Enrichment among the vascular flora is of two kinds and helps define some of the sub-communities, involving an increase in Nardo-Callunetea species in the *Vaccinium myrtillus* sub-community or plants of the Caricion nigrae (or even the Caricion davallianae) in the *Carex panicea* sub-community. In general terms, however, this vegetation is of an impoverished character.

Bryophytes common throughout are likewise few in number. There are usually some Sphagna but they do not form the consistently luxuriant ground cover typical of the Sphagnetalia mires. The most frequent species overall are *Sphagnum capillifolium* and *S. subnitens* with *S. palustre*, *S. recurvum* and *S. auriculatum* becoming common in wetter stands, and each of these can attain some measure of abundance. *S. papillosum*, such an important component of the plane of Sphagnetalia bogs, is much more restricted here. *S. compactum* and *S. tenellum*, which are characteristic of the eastern, lowland counterpart of this community, the *Ericetum tetralicis*, are scarce but the *Scirpus-Erica* wet heath likewise provides an occasional locus for *S. molle*.

Other bryophytes found at moderate frequency include *Hypnum cupressiforme/jutlandicum*, *Hylocomium splendens*, *Aulacomnium palustre*, *Dicranum scoparium* and *Diplophyllum albicans* with, following the same general pattern as seen among the vascular plants, some enrichment in dry, heathy stands or those with some soligenous influence.

Lichens do not occur consistently throughout the *Scirpus-Erica* wet heath but they can be locally prominent, particularly in the *Cladonia* sub-community where *C. impexa*, *C. uncialis*, *C. arbuscula* and *C. pyxidata* are preferentially frequent.

Sub-communities

***Carex panicea* sub-community:** *Trichophoreto-Eriophoretum caricetosum* McVean & Ratcliffe 1962; *Molinia-Myrica* mire McVean & Ratcliffe 1962, Birks 1973, Ratcliffe & Hattey 1982; *Molinieto-Callunetum* McVean & Ratcliffe 1962 *p.p.*, Birks 1973 *p.p.*; *Narthecio-Ericetum tetralicis* Moore (1964) 1968, *sensu* Birse 1980 *p.p.*; *Erica tetralix-Molinia caerulea* sociation Edgell 1969; *Trichophorum cespitosum-Carex panicea* Association Birks 1973, Adam *et al.* 1977; *Narthecium-Campylopus atrovirens* nodum Prentice & Prentice 1975. This sub-community, which is typically found as small stands, often in obvious soakways or water-tracks, is the richest and floristically most distinct kind of *Scirpus-Erica* wet heath. *Molinia* and *E. tetralix* retain high frequency throughout and the former especially is often abundant. *Scirpus*, on the other hand, is rather patchy and especially sparse on the more sloppy ground and *Calluna*, too, is typically of low cover and poor vigour. *Myrica* occurs frequently and quite often forms an extensive, low canopy but *E. cinerea* and *V. myrtillus* are hardly ever found.

Potentilla erecta and *Polygala serpyllifolia* are very commonly accompanied here by *Narthecium ossifragum* and *Eriophorum angustifolium*, but more obviously preferential are *Drosera rotundifolia* (and occasionally *D. anglica* and *D. intermedia*) and a variety of Caricion nigrae and Caricion davallianae species such as *Carex panicea*, *C. echinata*, *C. nigra*, *C. pulicaris*, *C. demissa*, *C. dioica*, *Selaginella selaginoides*, *Pinguicula vulgaris*, *Succisa pratensis*, *Viola palustris*, *Juncus bulbosus/kochii* and *Dactylorhiza maculata* ssp. *maculata*. *Schoenus nigricans* also occurs occasionally, sometimes with local abundance.

The bryophyte element, too, has distinctive features. Among the Sphagna, *S. capillifolium* is rather patchy, but *S. subnitens* occurs commonly though it is often exceeded in abundance by *S. palustre* and *S. recurvum*; *S. auriculatum* can also sometimes be found. More striking is the occasional occurrence of *Breutelia chrysocoma*, *Drepanocladus revolvens*, *Campylium stellatum*, *Scorpidium scorpioides*, *Aneura pinguis*, *Campylopus atrovirens* (including the rare var. *falcatus*), *C. setifolius* and *C. shawii*, the last three typically on shallow but very wet peat.

The local abundance of *Myrica* in this sub-community does not disrupt the overall floristic character of the vegetation, though under denser canopies the associates tend to thin out, such that in extreme cases there is little more beneath than patchy *Molinia* with scattered *E. tetralix*, *Potentilla erecta*, *Succisa pratensis*, a little

Carex panicea, *C. echinata*, *Juncus acutiflorus* or *J. effusus* and a carpet of *Sphagnum palustre*. Such vegetation could be distinguished as a variant.

Typical sub-community: *Trichophoreto-Callunetum*, *Sphagnum* facies McVean & Ratcliffe 1962, Birks 1973; *Molinieto-Callunetum* McVean & Ratcliffe 1962, Prentice & Prentice 1975, Evans *et al.* 1977, all *p.p.*; *Narthecio-Ericetum tetralicis* Moore (1964) 1968; *Trichophorum cespitosum* nodum Edgell 1969; *Trichophoreto-Callunetum*, Typical & *Eriophorum* facies Prentice & Prentice 1975; *Trichophoreto-Callunetum* Evans *et al.* 1978; *Calluno-Molinietum* Hill & Evans 1978; Mire nodum 3 Daniels 1978; *Trichophorum-Calluna* Association Birse 1980; *Molinia-Potentilla erecta* nodum Bignal & Curtis 1981 *p.p.*; *Trichophorum cespitosum-Eriophorum angustifolium* mire Ratcliffe & Hattey 1982. This sub-community shows virtually the complete range of possible permutations of the dominants from the kind of *Trichophoreto-Callunetum* described by McVean & Ratcliffe (1962) in which *Scirpus* and *Calluna* share dominance, with but little *Molinia* or *E. tetralix*, through stands in which *Molinia* and *Calluna* predominate (as in classic *Molinieto-Callunetum*) or *Molinia* and *E. tetralix*, to what is almost a pure *Molinietum*. *Myrica gale* is also quite common, though generally not abundant, and there is sometimes a little *E. cinerea*.

This kind of *Scirpus-Erica* wet heath shares with the previous sub-community frequent records for *Narthecium ossifragum* and *Eriophorum angustifolium* but the small sedges distinctive there are generally sparse, with only *C. panicea* and *C. echinata* occurring occasionally and the other poor- and rich-fen associates are very uncommon. In the other direction, some stands grade to the *Cladonia* or *Vaccinium* sub-communities, with *Nardus* and *Juncus squarrosus* showing local prominence. Positive features among the vascular element are rather weak, though it is here that *Eriophorum vaginatum* tends to occur, as a low-cover occasional.

A little better defined is the rise to fairly high frequency and local abundance of *Sphagnum papillosum* and, when this occurs with moderate amounts of *S. capillifolium* and *S. subnitens*, and a little *Odontoschisma sphagni*, the community makes its closest approach to the *Scirpus-Eriophorum* mire. Typically, however, the cover of these species, and of *S. palustre*, *S. recurvum* and *S. auriculatum*, is very variable and patchy. And, in some stands, Sphagna are very sparse and mosses such as *Racomitrium lanuginosum*, *Dicranum scoparium*, *Hypnum cupressiforme* and *Campylopus paradoxus* provide most of the cover.

***Cladonia* spp. sub-community:** *Trichophoreto-Callunetum*, lichen facies McVean & Ratcliffe 1962; *Trichophoreto-Callunetum*, *Rhacomitrium* facies Birks 1973; *Trichophoreto-Callunetum*, *Cladina* facies Prentice & Prentice 1975; Mire nodum 3 Daniels 1978; *Trichophorum-Calluna* Association Birse 1980 *p.p.*; *Narthecio-Ericetum* Moore (1964) 1968 *sensu* Birse 1980 *p.p.*; Disturbed peatland 3.ii Hulme & Blyth 1984. All four of the possible dominants retain high frequency here but *Calluna* shows a fairly strong tendency to predominate and there is commonly a little *E. cinerea*. Among the associates, *Potentilla erecta* remains constant but *Polygala serpyllifolia* and, more so, *Narthecium* are reduced in frequency, and *Eriophorum angustifolium* and *Myrica* are very scarce.

Most of the distinctive features of the vegetation, however, are among the ground cover. Sphagna are but poorly represented, with only *S. capillifolium* attaining occasional records. *Racomitrium lanuginosum* and *Hypnum cupressiforme/jutlandicum* become frequent but more obvious is the variety and abundance of *Cladonia* spp., particularly *C. impexa* and *C. uncialis*, with *C. arbuscula*, *C. pyxidata*, *C. coccifera* and *C. gracilis* more weakly preferential.

***Vaccinium myrtillus* sub-community:** *Juncus squarrosus* bog McVean & Ratcliffe 1962; *Trichophoreto-Callunetum*, *Juncus squarrosus* facies Prentice & Prentice 1975; *Trichophoreto-Callunetum* Hill & Evans 1978; *Molinia caerulea-Potentilla erecta* community Bignall & Curtis 1981 *p.p. Scirpus* and *E. tetralix* both become rather uneven in their occurrence here and rarely have high cover, mixtures of *Molinia* and *Calluna* generally dominating, quite often with some *Vaccinium myrtillus*. And, very commonly, there are small tussocks of *Nardus*, *Juncus squarrosus*, *Deschampsia flexuosa* and, more occasionally, some *Anthoxanthum odoratum*, *Festuca ovina/vivipara*, *F. rubra*, *Luzula multiflora* and *Carex pilulifera*, and *Galium saxatile* sometimes joins *Potentilla erecta*, so the overall impression is of vegetation intermediate between a blanket mire and a rough Nardetalia sward.

The bryophyte component, too, reflects this trend with most of the Sphagna infrequent and even *S. capillifolium* of low cover, their place being taken by *Hypnum cupressiforme/jutlandicum*, *Dicranum scoparium*, *Pleurozium schreberi*, *Plagiothecium undulatum*, *Polytrichum commune* and *Rhytidiadelphus loreus*. In this element, as well as among the vascular plants, this sub-community comes closest to the northern form of the *Ericetum tetralicis*, though the reduced role of *Molinia* there and the high frequency of *Sphagnum compactum* and *S. tenellum* will usually serve as distinguishing features. More problematic is the similarity of this *Vaccinium* sub-community to run-down forms of blanket mire vegetation, such as the *Juncus squarrosus-Rhytidiadelphus loreus* sub-community of the *Scirpus-*

Eriophorum bog, but this is a very real reflection of the convergence of these vegetation types on drying peat which has been subject to particular treatments.

Habitat

The *Scirpus-Erica* wet heath is characteristic of moist and generally acid and oligotrophic peats and peaty mineral soils in the wetter western and northern parts of Britain, being especially associated with thinner or better-drained areas of ombrogenous peat, though also extending into places with soligenous influence. Grazing and burning have important effects on the floristics and structure of the vegetation, and draining and peat-cutting have extended its coverage on to once deeper and wetter peats.

Like its counterpart in the south and east of Britain, the *Ericetum tetralicis*, the *Scirpus-Erica* wet heath is typical of more acid soils (surface pH being generally between 4 and 5) that are too dry or freely drained for the development of Sphagnetalia mires and too wet for Calluno-Ulicetalia heaths. The community shares many of its major species with the bogs of the north and west of Britain, and grades to such vegetation on deeper peats with a high and stagnant water-table, but important peat-builders like *Eriophorum vaginatum*, *Sphagnum papillosum* and *S. magellanicum*, and their distinctive blanket mire associates such as *Pleurozia purpurea*, *Odontoschisma sphagni*, *Mylia anomala* and *M. taylori*, are of restricted occurrence here and help separate the communities. Conversely, the *Scirpus-Erica* wet heath extends on to drier ombrogenous peats and thin humic tops to podzolised soils, where the *Sphagnum* cover becomes attenuated and hypnoid mosses, lichens and Nardo-Callunetea herbs like *Nardus* and *Juncus squarrosus* increase their frequency, but *Erica cinerea* and *Vaccinium myrtillus* remain fairly confined and are generally of low cover. As in the *Ericetum*, this vegetation thus takes much of its basic character from species tolerant of the intermediate soil moisture regime and able to thrive with the reduced competition from plants better adapted to the extremes (Rutter 1955, Bannister 1966, Gimingham 1972): *Erica tetralix*, *Calluna*, *Molinia* and, more important here than in the wet heaths of the south and east, *Scirpus cespitosus*.

Environmental conditions favouring the development of the *Scirpus-Erica* wet heath are of widespread occurrence in the north and west, where high rainfall permits (or has, in the past, permitted) the accumulation of acid peat, not only in topogenous hollows, but over flatter plateaus and quite steep slopes, even on pervious and calcareous substrates and at low altitudes. This community is almost wholly confined to areas with a present annual precipitation in excess of 1200 mm, and generally with more than 1600 mm (*Climatological Atlas* 1952), at least 180 wet days yr^{-1} (Ratcliffe 1968) and next to no potential water deficit. And within this zone, it is largely a community of the lowlands and submontane fringes, occurring almost at sea-level in the far north-west of Scotland and with a mean altitude of less than 250 m. In drier areas, it tends to be found at progressively higher altitudes, a feature well seen in traversing central Scotland where it eventually reaches over 500 m in the Cairngorms though, with this climatic shift, the *Scirpus-Erica* wet heath is largely replaced by the *Ericetum tetralicis* with its characteristic ground carpet of *Sphagnum compactum* and *S. tenellum*.

On the blanket of ombrogenous peat which clothes much of the ground in north-west Britain, the community typically occurs on well-humified deposits which are fairly dry or which at least show no stagnation. In areas with the highest rainfall, this generally means that it is found on sloping ground with a moderately thin cover of peat, giving way on flatter areas to blanket mire proper or, in regions where gentler slopes are rare, as in the west-central Highlands, comprising the bulk of the cover of ombrogenous mire vegetation. With decreasing precipitation, it occurs on progressively shallower slopes, with sometimes quite thick peat, which constitute the wettest ground locally. Again, this is best observed in moving across central Scotland: the contrast between Glen Torridon, in the west with more than 2000 mm of rain, and Glen Clova, in the east with about 1200 mm, is well illustrated in McVean & Ratcliffe (1962: Figure 20). This simple relationship is complicated by aspect since, on north-facing slopes, the community can run up on to steeper ground (of 30° or more at Glen Shiel, for example) and, on south-facing hills, is more restricted to gentler slopes. Overall, the *Scirpus-Erica* wet heath has geographical and altitudinal ranges roughly comparable to those of the *Scirpus-Eriophorum* mire, but occurs over a greater range of slopes (0–42°, mean 8°, for the former; 0–25°, mean 4°, for the latter) and, on more undisturbed ombrogenous peats, is found on shallow deposits (usually less than 2 m).

The community also extends, particularly in areas of higher rainfall or where there is local drainage impedence, on to peaty podzols with but a few centimetres of humic top, where blanket mire proper cannot develop but from which heaths are excluded by periodic waterlogging (McVean & Ratcliffe 1962, Edgell 1969, Birse 1980). And it occurs widely on once deeper and wetter blanket peats and, in some areas, on raised mires which have become dry and eroded, or which have been drained, frequently burned, cut-over and disturbed (McVean & Ratcliffe 1962, Birks 1973, Birse 1980, Bignall & Curtis 1981, Hulme & Blyth 1984).

Much of the floristic and structural variation within and between the sub-communities can be accounted for in terms of differences in water relations in the generally intermediate kind of habitat characteristic of the

Scirpus-Erica wet heath. The Typical sub-community is generally found on deeper peats kept fairly moist by a moderately high water-table and it is here that the community makes its closest approach to the blanket mire vegetation typical of the region, with a substantial suite of Oxycocco-Sphagnetea species and quite vigorous *Sphagnum* growth, *Eriophorum vaginatum* figuring occasionally at low covers and *S. papillosum* showing local abundance. In such stands, *Calluna* is often poorly-grown or, quite often, totally absent, suffering from waterlogging and without the advantage of any differentiation of drier hummocks which maintain its frequency and abundance on blanket mires (Bannister 1964*b*, *c*, *d*; Gimingham 1972). *E. tetralix* is thus the commonest ericoid in such situations in mixtures with *Molinia* and *Scirpus*. Still within the Typical sub-community, but on somewhat drier and usually shallower peats, often on steeper slopes, the balance among the dominants shifts, with *Calluna* often gaining ascendance with *Scirpus*, and *Sphagnum* cover declines, *S. papillosum* in particular disappearing.

An increase in the vigour of *Calluna*, the appearance of *E. cinerea*, *Racomitrium lanuginosum* and lichens, marks the shift to the *Cladonia* sub-community on steeper, often convex as opposed to concave, slopes with a generally shallower and more sharply-draining cover of peat, or gentle slopes with peaty podzols or a much-eroded peat mantle. *E. cinerea* can perform moderately well on the drier surfaces here (Bannister 1964*a*, *d*, 1965), perhaps better than in comparable situations around valley mires, where higher levels of ferrous ions seem to restrict its transgression from the surrounding dry heaths (Jones 1971*a*, *b*).

The Typical sub-community also grades in another direction to the Carex sub-community with an increase in soligenous influence. Water movement through the peat is probably considerable within some stands of the Typical sub-community itself, particularly where these occur in slight hollows or flats that receive and shed surface and sub-surface water draining off surrounding slopes (McVean & Ratcliffe 1962, Birks 1973). Here, there is probably enhanced aeration and some modest nutrient-enrichment of the peat, with *Molinia* in particular being able to capitalise on this amelioration of the environment (Loach 1966, 1968*a*, *b*, Sheikh & Rutter 1969, Sheikh 1969*a*, *b*, 1970). Such conditions are much more pronounced in the *Carex* sub-community which typically occupies areas where downwash is concentrated or narrow soakways, often of gentle slope but with a continuous through-put. The soils in such situations are usually shallow peats over gleyed mineral profiles or undifferentiated stony hill-wash, with a surface pH noticeably higher than usual, generally between 5 and 6, and probably some increase in calcium and major nutrients (McVean & Ratcliffe 1962, Edgell 1969, Birks 1973, Prentice & Prentice 1975). Here the *Scirpus-Erica* wet heath shows quite strong floristic affinities with Scheuchzerio-Caricetea poor fens, with an increase in semi-aquatic Sphagna and species such as *Carex panicea*, *C. echinata*, *C. nigra*, *Viola palustris* and *Juncus bulbosus/kochii*, and even provides a locus in the community for rich-fen plants like *Selaginella selaginoides* and *Pinguicula vulgaris*.

It is also in this kind of *Scirpus-Erica* wet heath that *Myrica gale* makes its most obvious contribution to the vegetation. It occurs occasionally in the Typical sub-community, usually with low cover (and also in the *Scirpus-Eriophorum* blanket mire) but reaches its greatest abundance on the better-aerated and more mineral-rich irrigated peats here, quite often with much strongly-tussocky *Molinia*, but with a consequent reduction in the variety of associates among the dense and shaded cover. Where streams flow from stretches of ombrogenous peat, this kind of vegetation often runs down on to the periodically-flooded flats where there may be modest deposition of fine mineral matter (McVean & Ratcliffe 1962, Birks 1973). In more nutrient-poor situations, *Myrica* may be of considerable importance in producing nitrogen-enrichment of the system by N-fixation in its root nodules (Bond 1951, 1967, Sprent *et al.* 1978).

Superimposed on these lines of variation related to natural edaphic differences are the diverse effects of treatments which influence the proportional contributions of the dominants and the composition of the associated flora. The natural surface drying of ombrogenous peats which has taken place with climatic changes in the recent post-Glacial has probably been greatly speeded by human activities such as deforestation and burning, which have been virtually universal in some parts of the range of the *Scirpus-Erica* wet heath, and more recently by direct drainage. Such activities have probably extended the cover of the community on to the wasting margins of once-wetter peats and, within the *Scirpus-Erica* wet heath itself, they tend to shift the composition of the vegetation away from the more *Sphagnum*-rich kind of the Typical sub-community through the more *Calluna*-rich to the distinctly heathy *Cladonia* sub-community. This latter vegetation is especially well represented on the deforested morainic country of the western Highlands, and, at higher altitudes, on ground that has probably been much burned. In extreme cases, *Calluna* and the other ericoids have been virtually eliminated and *Scirpus* reduced to scattered tussocks, with much of the cover made up of hummocks of *Racomitrium*, patches of *Cladonia* spp. and a surface crust of lichens over a thin and patchy mantle of humus with exposed gravel and stones between (McVean & Ratcliffe 1962). Where wastage has not been so extreme but where ericoids have been virtually lost, cessation of burning may favour a vigor-

ous recovery of *Molinia* as against *Scirpus*: *Molinia*-dominated stands of the Typical sub-community are especially extensive in the western Highlands and in Galloway (McVean & Ratcliffe 1962). Other *Scirpus-Erica* wet heaths with an abundance of *Molinia* may have been derived from the *Carex* sub-community by elimination of *Myrica*. Where there has been frequent but more carefully-controlled burning, *Calluna* may be encouraged as a dominant, particularly where the community extends into less oceanic regions: in the east-central Highlands, for example, stands of the Typical and *Cladonia* sub-communities form part of poorer-quality grouse-moors (Birse 1980).

Grazing by sheep and deer, sometimes combined with burning, has also had some influence on the vegetation, particularly where it extends on to drier ground. Such a mixture of treatments may be partly responsible for the composition of the *Vaccinium* sub-community. The grazing-sensitive bilberry is present only at small covers but is often accompanied by mixtures of Nardetalia herbs and hypnoid mosses characteristic of sub-montane swards on base-poor and ill-drained ground where grazing is heavy.

Zonation and succession

Zonations within stands of the *Scirpus-Erica* wet heath and between the community and other vegetation types generally reflect variations in the soil moisture regime, sometimes with attendant differences in base- and nutrient-status. Such patterns are often overlain by the effects of treatments and, in some cases, the community may represent a seral intermediate between blanket mire and either dry heath or grassland. Without burning or grazing, less-damaged stands might be able to revert to blanket mire or progress to woodland. Much vegetation of this kind has been replaced by coniferous forest after draining of the ground.

The intermediate character of the *Scirpus-Erica* wet heath frequently finds spatial expression in its occurrence as a zone between Sphagnetalia bogs and Calluno-Ulicetalia heaths, the particular nature of the vegetation types and their proportions in the zonations varying with geographical locality, altitude and the character of the terrain. Most often, at lower altitudes in western Britain, where the community is best developed, it occurs in close association with the *Scirpus-Eriophorum* blanket mire, grading to it in hollows and over gently-undulating ground where there is accumulation of deeper peat with a high and stagnant water-table. More *Sphagnum*-rich stands of the Typical sub-community may form a more or less gradual transition to the blanket mire, being replaced, on more free-draining slopes, first by less *Sphagnum*-rich stands of this sub-community, then by the *Cladonia* sub-community over thinner, drier peats. This, in turn, can give way to dry heath on sharply-draining podzols, generally some form of *Calluna-Erica cinerea* or *Calluna-Vaccinium* heath, though often dominated overwhelmingly by *Calluna*, a physiognomic feature which can extend a considerable way into the wet heath, where there has been more controlled burning, and which can therefore blur the upper part of the vegetation sequence.

In areas with lower rainfall, the whole zonation tends to move downslope, the *Sphagnum*-rich Typical sub-community, rather than the *Scirpus-Eriophorum* blanket mire, occupying the wettest ground in hollows and the *Cladonia* sub-community extending less far up the surrounding slopes before being replaced by drier heath. A similar effect on the upper part of the zonation can be seen where the communities occur over south-facing slopes where the drier heath component can be especially extensive; on northerly aspects, on the other hand, the *Scirpus-Erica* wet heath transgresses far on to steeper ground (McVean & Ratcliffe 1962).

Increased water movement through the peats is often marked by a rise in the proportion of *Molinia* through stands of the Typical sub-community and, where soligenous influence is most pronounced, with enhanced aeration and sometimes an increase in base-status and perhaps nutrient content, stretches of the *Carex* sub-community may clothe gentler slopes or occur within definite soakways, running through both the *Scirpus-Erica* wet heath and the *Scirpus-Eriophorum* mire and quite often along streams that drain from the peat through surrounding heaths and grasslands. Very frequently, such zones of water movement are marked most obviously by the presence of *Myrica*, a feature readily discerned from a distance on the ground or from aerial photographs.

Where the *Scirpus-Erica* wet heath extends to higher altitudes, as it does in Scotland and more locally in northern England and Wales, it can also be found in association with the *Calluna-Eriophorum* blanket mire, typically forming a zone below it where the peat thins out on steeper or convex slopes. In the north-west Highlands, the community often forms an altitudinal band separating the two kinds of blanket mire and grading in each direction to them. Further east in Scotland, where the *Scirpus-Eriophorum* bog becomes increasingly rare, the *Scirpus-Erica* wet heath can occur below the *Calluna-Eriophorum* mire in transitions to drier heath or grassland (McVean & Ratcliffe 1962, Birks 1973, Birse 1980). Generally, however, in this part of Britain, the community is replaced in such sequences by the *Ericetum tetralicis*.

Fragments of these kinds of zonations are of widespread occurrence where the climate or the terrain is unsuitable for the development of the full sequence and each of the sub-communities can be found alone in vegetation patterns. The Typical and *Cladonia* sub-

communities, for example, often mark out the most ill-drained patches of ground in gently-undulating landscapes clothed with grasslands and heaths over podzols with varying degrees of drainage impedence and shallow peat accumulation. And the *Carex* sub-community is of widespread occurrence along fairly base-poor soakways in tracts of heaths and grasslands, well away from stands of other kinds of *Scirpus-Erica* wet heath or blanket mire (Edgell 1969). In such situations, it may pass, along the water-tracks, to different types of soligenous mire according to the degree of base- and nutrient-enrichment of the incoming waters.

Even where extensive zonations occur, however, they have been very widely affected by treatments. Less severe burning and/or grazing can impose a uniformity of dominance over much of the sequence, masking the transition from one vegetation type to another. More drastic or long-continued treatments, particularly where these accentuate the effects of natural degeneration of peatlands, have a more profound influence on the floristics. It is likely that some stands of the *Scirpus-Erica* wet heath have been derived from blanket mire as a result of a combination of climatic change, burning and grazing. Sphagnetalia communities affected by these factors tend to lose their luxuriant carpet of Sphagna and to show an increase in either *Racomitrium lanuginosum* and lichens or Nardetalia herbs and hypnoid mosses (McVean & Ratcliffe 1962), trends which can be seen, for example, in the *Cladonia* and *Juncus-Rhytidiadelphus* sub-communities of the *Scirpus-Eriophorum* blanket mire. Elimination of *Eriophorum vaginatum* from these vegetation types can produce assemblages which are indistinguishable from the *Cladonia* and *Vaccinium* sub-communities of the *Scirpus-Erica* wet heath and extensive mosaics of these vegetation types can be seen on many areas of degenerating ombrogenous peat. Deep sheet-erosion may lead to a replacement of the *Carex* sub-community in such patterns by the *Carex echinata-Sphagnum* mire in widespread systems of runnels (Birks 1973), and where the wasting peat is washed down over the slopes below, there can be transitions to Nardetalia grasslands with much *Nardus* and *Juncus squarrosus*.

Although in the far west, blanket mire seems to be able to regenerate in less-disturbed areas of wet ground (McVean & Ratcliffe 1962), it seems unlikely that progression to the *Scirpus-Erica* wet heath or beyond can be readily reversed. Cessation of burning, especially on peat that is naturally well-aerated or where there has been draining, may precipitate a vigorous expansion of *Molinia* and, in some areas, blanket mires and wet heath seem to have converged into vast tracts of *Molinia*-dominated grasslands in which Sphagnetalia or Sphagno-Ericetalia species play a relatively minor role, mosaics among them being shaded out or at least masked by the dominant. Invasion of the *Scirpus-Erica* wet heath by woody species is probably theoretically possible over most, if not all, its altitudinal range but widespread deforestation has often removed potential seed-parents, and continued grazing by stock and deer and sporadic burning may be enough to set back succession continually. *Betula pubescens* and *Pinus sylvestris* are the most likely invaders of the characteristic soils here, especially on the drier ground of the *Cladonia* and *Vaccinium* sub-communities, but seedlings are rarely found. Coniferous plantations, on the other hand, have been established over extensive stretches of drained ombrogenous peat, some of which probably carried the *Scirpus-Erica* wet heath.

Distribution

The community occurs widely at lower altitudes in western and northern Britain, being particularly well represented in the western Highlands of Scotland, in south-west Scotland and Wales and, less extensively, in the Lake District and on Dartmoor and Exmoor. The distribution of the sub-communities is imperfectly known and, though the Typical and *Carex* types are especially common in western Scotland and the *Cladonia* and *Vaccinium* types in somewhat drier regions, all probably occur throughout the range of the community. In the eastern and southern lowlands of Britain, the *Scirpus-Erica* wet heath is replaced by the *Ericetum tetralicis* which, with increasing dryness of the climate, becomes progressively restricted to topogenous mires.

Affinities

The *Scirpus-Erica* wet heath brings together a variety of vegetation types on better-aerated ombrogenous peats in north-west Britain, uniting communities that have previously been distinguished to a great extent on the dominance of either *Scirpus*, *Calluna* or *Molinia*, very susceptible to variations in treatment (Tansley 1939, McVean & Ratcliffe 1962, Birks 1973, Prentice & Prentice 1975, Evans *et al.* 1977, Hill & Evans 1978), or on the degree of soligenous influence (McVean & Ratcliffe 1962, Edgell 1969, Birks 1973, Prentice & Prentice 1975). Although it embraces a fairly wide range of variation, particularly in including vegetation transitional to Caricion nigrae poor fens, the community holds together well as one of our two wet heaths, floristically intermediate between Sphagnetalia mires and Calluno-Ulicetalia heaths. With its south-eastern counterpart, the *Ericetum tetralicis*, floristic variation in which roughly parallels that found here, it can be placed unequivocally in the Sphagno-Ericetalia (= Ericetalia Moore (1964) 1968), with its single alliance, the Ericion tetralicis, comprising western European mires and wet heaths on shallower peats. The definition in this scheme retains some of the major divisions made among these vege-

tation types by McVean & Ratcliffe (1962) and fills out the description provided by Moore (1968) of what he termed the *Narthecio-Ericetum tetralicis*, the Ericion community characteristic of more Atlantic regions, like western Britain, Eire and Normandy (as in Duvigneaud 1949). Vegetation of this same general kind has also been recorded from Scandinavia by Nordhagen (1922), Böcher (1943), Tveitnes (1945), Knaben (1950), Faegri (1960), Skogen (1965) and Dierssen (1982).

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Floristic table M15

	a	b
Molinia caerulea	V (4–8)	V (1–9)
Potentilla erecta	V (1–4)	V (1–6)
Erica tetralix	V (1–4)	V (1–6)
Calluna vulgaris	IV (1–4)	IV (1–8)
Scirpus cespitosus	III (1–8)	IV (1–8)
Narthecium ossifragum	V (1–4)	V (1–6)
Eriophorum angustifolium	IV (1–4)	III (1–6)
Myrica gale	IV (4–8)	III (1–8)
Sphagnum palustre	IV (1–6)	III (1–8)
Carex panicea	V (1–4)	II (1–4)
Carex echinata	V (1–4)	II (1–4)
Drosera rotundifolia	IV (1–4)	II (1–4)
Pinguicula vulgaris	IV (1–4)	I (1)
Sphagnum recurvum	III (1–8)	II (1–4)
Breutelia chrysocoma	III (1–4)	I (1–4)
Succisa pratensis	III (1–3)	I (1–3)
Carex pulicaris	III (1–4)	I (1)
Selaginella selaginoides	III (1–3)	
Juncus bulbosus/kochii	II (1–4)	I (1–3)
Carex nigra	II (1–6)	I (1–3)
Viola palustris	II (1–3)	I (1–3)
Campylopus atrovirens	II (1–4)	I (1–3)
Euphrasia officinalis agg.	II (1–3)	I (1)
Schoenus nigricans	II (1–6)	I (2)
Sphagnum auriculatum inundatum	II (1–4)	I (1)
Carex demissa	II (1–4)	I (1)
Drosera anglica	II (1–2)	I (2–4)
Drepanocladus revolvens	II (1–3)	I (1–4)
Aneura pinguis	II (1–3)	I (1)
Campylium stellatum	II (1–4)	
Scorpidium scorpioides	II (1–3)	

c	d	15
V (4–7)	V (1–9)	V (1–9)
V (1–4)	V (1–4)	V (1–6)
V (1–4)	IV (1–5)	V (1–6)
V (4–8)	V (1–9)	IV (1–9)
IV (1–6)	III (1–6)	IV (1–8)
III (1–4)	II (1–4)	III (1–6)
I (1–4)	II (1–4)	III (1–6)
I (4)	I (2–4)	III (1–8)
	I (1–6)	II (1–8)
I (1–4)	I (1–4)	II (1–4)
	I (1)	II (1–4)
	I (1)	II (1–4)
I (1)	I (1)	I (1–4)
	I (1–4)	I (1–8)
I (1–3)	I (1–4)	I (1–4)
I (1–3)	I (1–4)	I (1–4)
	I (1)	I (1–4)
	I (1)	I (1–3)
I (1)	I (1–3)	I (1–4)
I (1)	I (1–4)	I (1–6)
	I (1–3)	I (1–3)
I (1–3)		I (1–4)
	I (1)	I (1–3)
		I (1–6)
		I (1–4)
		I (1–4)
		I (1–4)
		I (1–4)
		I (1–3)
		I (1–4)
		I (1–3)

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Pleurozia purpurea	II (1–3)				I (1–3)
Dactylorhiza maculata maculata	II (1–3)				I (1–3)
Carex dioica	I (1–3)				I (1–3)
Menyanthes trifoliata	I (1–4)				I (1–4)
Sphagnum papillosum	I (4)	III (1–9)	I (1–6)	I (1–4)	II (1–9)
Juncus acutiflorus	I (1)	II (1–4)	I (4)	I (1)	I (1–4)
Odontoschisma sphagni	I (1)	II (1–3)	I (1–3)	I (1)	I (1–3)
Sphagnum auriculatum auriculatum	I (1)	II (1–4)	I (1)		I (1–4)
Eriophorum vaginatum		II (1–4)	I (1–3)	I (1–4)	I (1–4)
Campylopus paradoxus		II (1–3)	I (1–3)	I (1–2)	I (1–3)
Erica cinerea	I (1)	II (1–4)	V (1–6)	I (1–4)	II (1–6)
Hypnum cupressiforme	I (1–4)	II (1–3)	III (1–5)	II (1–8)	II (1–8)
Racomitrium lanuginosum	I (1–3)	II (1–4)	III (1–6)	I (1)	I (1–6)
Cladonia impexa	I (1)	I (1–3)	II (1–3)	I (1–4)	I (1–4)
Cladonia uncialis	I (1)	I (1)	II (1–3)	I (2)	I (1–3)
Vaccinium myrtillus		I (1–3)	I (1)	IV (1–6)	II (1–6)
Nardus stricta	II (1–4)	II (1–4)	II (1–6)	III (1–6)	II (1–6)
Juncus squarrosus	I (1)	II (1–4)	I (1–2)	III (1–4)	II (1–4)
Dicranum scoparium	I (1)	II (1–3)	I (1)	III (1–4)	II (1–4)
Hypnum jutlandicum	I (1)	I (1–4)	II (1–4)	III (1–9)	II (1–9)
Deschampsia flexuosa	I (1–3)	I (1)	I (1–4)	III (1–4)	I (1–4)
Pleurozium schreberi	I (1–4)	I (1–3)	I (1–3)	III (1–6)	I (1–6)
Plagiothecium undulatum	I (1)	I (1–3)	I (1–4)	II (1–4)	I (1–4)
Galium saxatile	I (1)	I (1)	I (1)	II (1–4)	I (1–4)
Anthoxanthum odoratum	I (1)	I (1–3)	I (1)	II (1–5)	I (1–4)
Polytrichum commune	I (1)	I (1–3)	I (1)	II (1–4)	I (1–4)
Festuca ovina	I (1–6)	I (1–4)	I (1)	II (1–6)	I (1–6)
Luzula multiflora	I (1)	I (1)		II (1–3)	I (1–3)
Carex pilulifera		I (1)	I (1)	II (1–4)	I (1–4)
Rhytidiadelphus loreus		I (1–3)	I (1–3)	II (1–4)	I (1–4)
Cladonia chlorophaea			I (1)	II (1–4)	I (1–4)
Polygala serpyllifolia	III (1–4)	III (1–4)	II (1–2)	II (1–4)	III (1–4)
Sphagnum capillifolium	III (1–4)	III (1–6)	II (1–5)	II (1–4)	III (1–6)
Sphagnum subnitens	III (1–4)	II (1–6)	I (1–3)	II (1–6)	II (1–6)

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Floristic table M15 *(cont.)*

	a	b
Agrostis canina canina	I (1)	II (1–5)
Hylocomium splendens	I (1–4)	I (1–3)
Aulacomnium palustre	I (1–2)	I (1–3)
Festuca vivipara	I (1–4)	I (1–2)
Diplophyllum albicans	I (1)	I (1–4)
Pedicularis sylvatica	I (1–3)	I (1–4)
Empetrum nigrum nigrum	I (1)	I (1–3)
Blechnum spicant	I (1)	I (1–2)
Carex binervis	I (1)	I (1)
Huperzia selago	I (1)	I (1–3)
Juncus conglomeratus	I (4)	I (1–3)
Rhytidiadelphus squarrosus	I (1–3)	I (1)
Festuca rubra	I (1–4)	I (1–3)
Sphagnum compactum	I (1–3)	I (1–6)
Juncus articulatus	I (1–4)	I (1)
Danthonia decumbens	I (1–4)	I (1–2)
Juncus effusus	I (1–4)	I (1–4)
Calypogeia muellerana	I (1)	I (1–3)
Leucobryum glaucum		I (1–4)
Pteridium aquilinum		I (1–4)
Agrostis stolonifera		I (1–3)
Agrostis capillaris		I (1–3)
Calypogeia fissa		I (1–3)
Sphagnum tenellum		I (1–4)
Cladonia arbuscula		I (1–2)
Pedicularis palustris	I (1–3)	I (1)
Hypericum pulchrum	I (1–3)	I (1)
Triglochin palustris	I (1–2)	I (1)
Trientalis europaea	I (1–4)	
Lophozia ventricosa		
Pohlia nutans		
Cladonia coccifera		

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c	d	15
II (1–3)	II (1–6)	II (1–6)
I (1–3)	I (1–4)	I (1–4)
I (1)	I (1–4)	I (1–4)
I (1–4)	I (1–3)	I (1–4)
I (1)	I (1)	I (1–4)
I (1)	I (1–3)	I (1–4)
I (4)	I (1–3)	I (1–4)
I (1–3)	I (1–4)	I (1–4)
I (1)	I (1–3)	I (1–3)
I (1–3)	I (1)	I (1–3)
I (1)		I (1–4)
	I (1–4)	I (1–4)
	I (1–4)	I (1–4)
	I (1–4)	I (1–6)
	I (1)	I (1–4)
	I (1–4)	I (1–4)
	I (1–4)	I (1–4)
	I (1–3)	I (1–3)
I (1)	I (1–3)	I (1–4)
I (1–3)	I (1–4)	I (1–4)
I (1)	I (1–4)	I (1–4)
I (1)	I (1–4)	I (1–4)
I (1)	I (1–3)	I (1–3)
I (1–3)	I (4)	I (1–4)
I (1–4)	I (1)	I (1–4)
		I (1–3)
		I (1–3)
		I (1–2)
	I (1)	I (1–4)
I (1)	I (1–3)	I (1–3)
I (1)	I (1–3)	I (1–3)
I (1–3)	I (1–3)	I (1–3)

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Number of samples	69	133
Number of species/sample	27 (10–45)	18 (8–41)
Herb height (cm)	27 (9–50)	21 (9–40)
Herb cover (%)	94 (60–100)	92 (85–100)
Bryophyte height (mm)	38 (10–100)	35 (10–80)
Bryophyte cover (%)	32 (10–70)	38 (2–60)
Altitude (m)	177 (45–533)	226 (43–472)
Slope (°)	4 (0–14)	7 (0–42)
Soil pH	5.6 (4.2–7.4)	4.6 (3.6–5.9)

a *Carex panicea* sub-community
b Typical sub-community
c *Cladonia* sub-community
d *Vaccinium myrtillus* sub-community
15 *Scirpus cespitosus-Erica tetralix* wet heath (total)

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23	57	282
15 (7–27)	18 (6–57)	18 (6–57)
23 (10–38)	26 (6–50)	24 (6–50)
94 (70–100)	98 (85–100)	95 (60–100)
20 (10–40)	34 (10–100)	33 (10–100)
41 (2–80)	28 (2–90)	34 (2–90)
283 (57–470)	290 (35–550)	248 (35–550)
16 (0–35)	8 (0–35)	8 (0–42)
4.7 (4.0–6.0)	4.2 (3.5–5.3)	4.6 (3.5–7.4)

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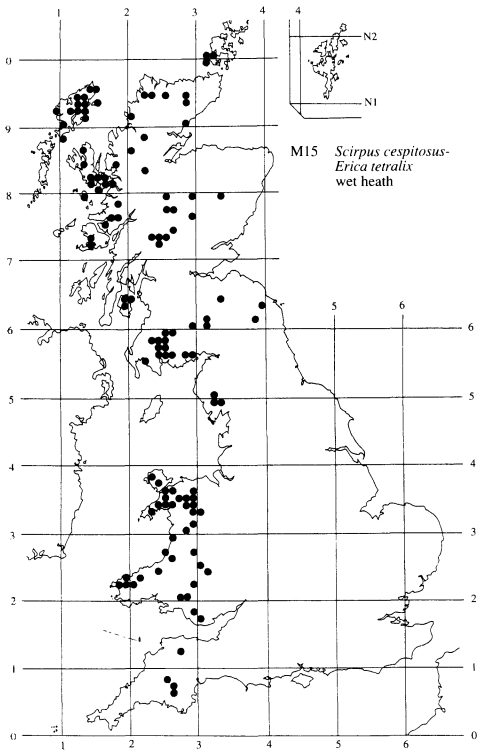

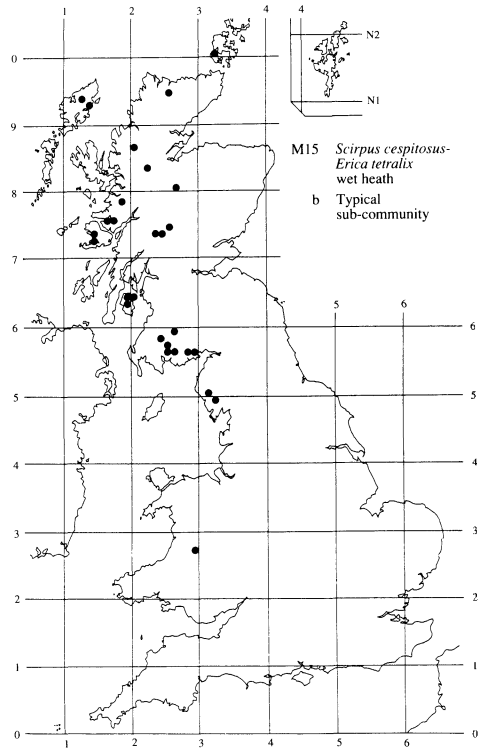

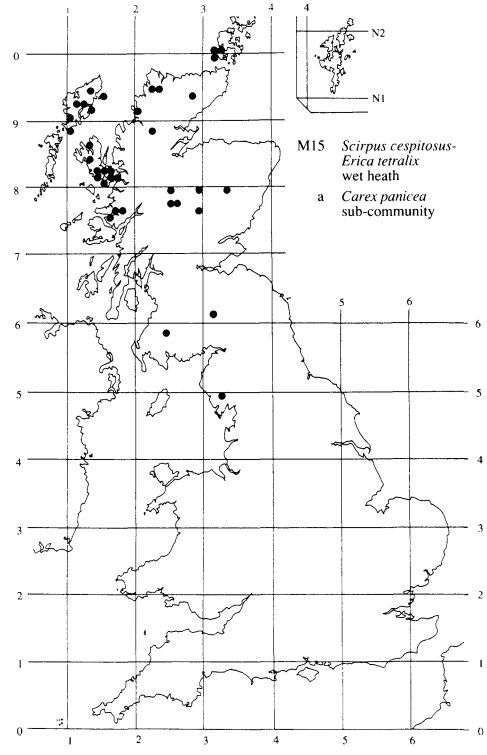

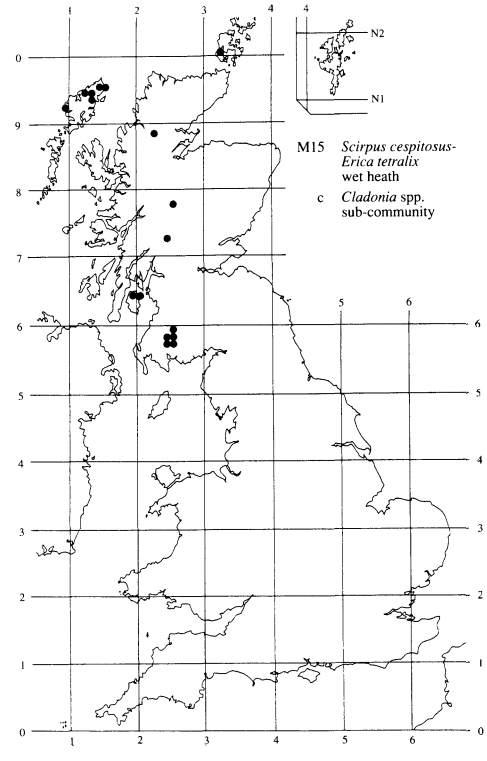

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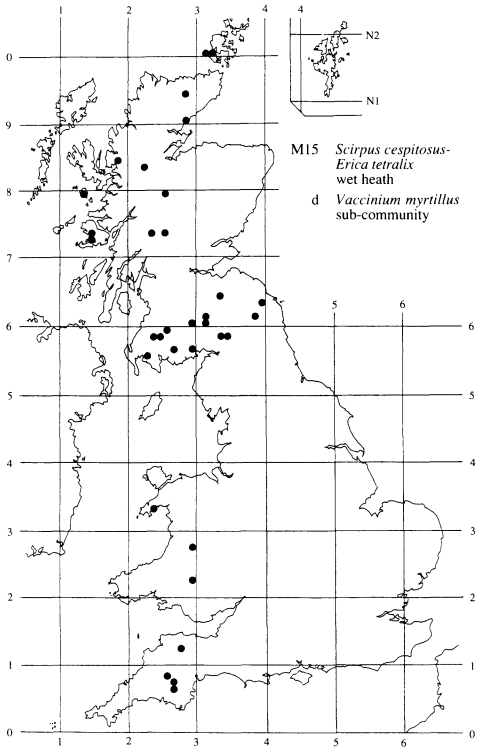

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