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Ombrogenous mires in Islay and Mull

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Synopsis

The vegetation and surface structure of two ombrogenous mires from the Inner Hebrides are described. Two-way indicator species analysis and hand sorting of these data are used to identify vegetation communities. The surface patterning of both sites is examined using levelling data which are related to the water table. From this, four significant surface features are recognised: *hummock*, *ridge*, *hollow* and *pool*. The relationship between the vegetation communities and these features is examined, and the two study sites subsequently compared in terms of these small-scale features. The ombrogenous mires of the Inner Hebrides are then related in the same way to other mire systems described by previous authors.

Introduction

Most of the larger islands of the Inner Hebrides have extensive areas covered by blanket mire which has developed as a result of the strongly oceanic, cool, wet climate. Extensive deep peat deposits occur even at sea level on islands where the geology is conducive to peat development, and shallow blanket peat is widespread on the montane areas of Jura, Skye and Rhum.

In this account, two areas have been chosen to illustrate the range of ecological variation (Fig. 1): (a) Coladoir Bog, Mull, a natural patterned bog and an example of a widespread habitat type mostly severely modified by land use; (b) Glac na Criche, Islay, oceanic blanket mire vegetation having affinities with Western Ireland but not previously described from Scotland.

Plant species of ombrogenous mires are sensitive to the local patterns of waterlogging in the surface peat. Individual species occur at specific heights above or below the water table (Ratcliffe and Walker 1958). The hummock-hollow mosaic of the mire surface provides a wide range of conditions within the small-scale pattern and such patterns become increasingly complex towards the north and west of Britain. Species able to tolerate the oceanic climate along the Atlantic coast of Scotland find there a greater variety of surface features in which they may obtain a suitable niche. These ecological differences between north and south, east and west, must affect the overall distribution of species associations across the country, yet the

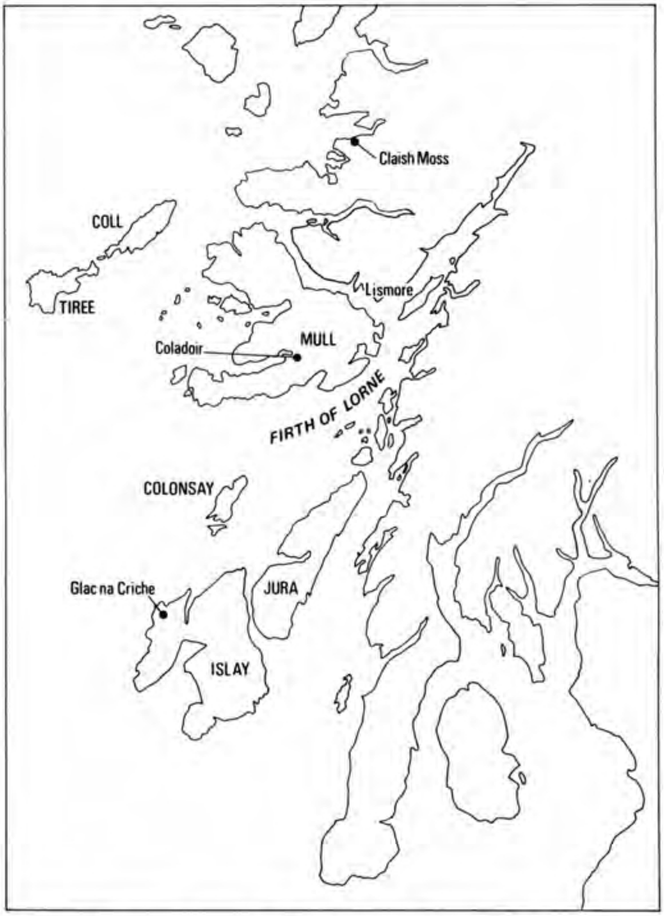


Figure 1. Southern Inner Hebrides showing places mentioned in this paper.

relationship between surface microtopography and vegetation has yet to be explored in detail. This paper examines the relationships which exist on Coladoir Bog and Glac na Criche, and attempts to use these in describing the wider relationships shown by these two mires to similar systems elsewhere in Britain.

All the areas described in this account are regarded by the Nature Conservancy Council as nationally important sites, as defined in *A Nature Conservation Review* (Ratcliffe 1977).

Methods

Survey of Coladoir Bog

Although on a mire individual pools and ridges may be many metres long, they are usually no more than 1 m wide and often much narrower than this. A sample area of 1 m^2, commonly used in peatland work, would tend to overlap a wide range of features within the microtopography. Combining data from different parts of the microtopography in this way can only therefore produce a generalised account of the vegetation. A smaller sample size allows each element to be sampled separately, making it much simpler to determine any relationship between physical patterning and the species mosaic. An extensive literature exists about the problem of plot size and minimal area, and the problem is reviewed by Kershaw (1973, pp. 136–144), who notes, in the same volume, that the use of transect lines can be of 'considerable importance in the description of vegetation change along an environmental gradient, or in relation to some marked feature of topography', citing the isonome method of contiguous quadrats along a transect, described by Ashby and Pidgeon (1942). Kershaw also offers, as an example, a study of the microtopography of an area of hummocks in limestone grassland at Malham Tarn, Yorkshire, while Godwin and Conway (1939) use a version of the isonome method in describing the vegetation of Tregaron Bog.

In order to provide both a general description of the mire vegetation, and a more detailed analysis with which to reveal small-scale vegetation patterns, two types of data were employed. The first, for the general account, is based on a small number of 1 m^2 quadrats collected at random across the site in January 1978; the second employs a version of the isonome method, modified to suit the needs of the present work. Ten transects were located across the mire surface to cover the range of variability within the major physical components of the mire system. Four were placed on the upper bog, three on the lower bog, and three on the marginal and unpatterned surfaces. Each transect was 5 m long, 0·5 m wide, and divided into 250 squares of 10 cm^2. Within each of these squares, species were recorded on a three point scale; 1 = present, 2 = semi-dominant, 3 = dominant. The majority of leafy liverworts were not recorded, but open water was, being recorded on the three point scale in the normal way, as if it were a species. It should be noted that more than one species could be considered dominant within a square, particularly in the case of *Sphagnum* species, which sometimes form dense carpets below a dominant shrub layer or below the water level.

Recording the microtopography

The height of the peat surface above or below the water table was recorded at 10 cm intervals along each transect, and at each interval a reading was taken from the near edge, the middle, and the far edge of the transect line. Where the surface was a wet *Sphagnum* carpet, the rule was gently pressed downwards until some resistance was encountered. Care was taken to ensure that these readings could not be affected by compression of the peat due to the weight of the observer.

Analysis of Coladoir Bog

The 1 m^2 quadrat data were combined with a total species list for the site, and the frequency of occurrence for each species calculated. The transect data were analysed using a two-way indicator species analysis, TWINSPAN, developed by Hill (1979). This method of divisive, polythetic classification assigns each quadrat to a particular vegetation nodum. On completion of the analysis it was thus possible to map the distribution of the various noda recognised by TWINSPAN directly onto the transect lines, and then subsequently relate the distribution of these noda to surface contours plotted from the height data. Each 10 cm^2 could thus be assigned a nodum type and a mean contour height.

It was recognised that even with a 10 cm^2 sample size some overlap of elements was bound to occur. Consequently the range of mean heights for each nodum was plotted as a frequency histogram, and from this it emerged quite clearly that a square with a sudden, large-scale change in height (for instance on a steep pool edge) tended to have a height value lying considerably outside the normal distribution for any given nodum. The mean and standard deviation were therefore calculated for each frequency plot, and those records falling beyond one standard deviation from the mean were discarded.

Survey of Glac na Criche

Two sample sizes were used, one of 20 cm^2 and one of 1 m^2, the latter to provide a broad assessment of the major associations, while the former was more suited to a detailed analysis of the relationship between vegetation and microtopography (see Table 4). Unfortunately measured height data are not available for Glac na Criche, and it is consequently impossible to provide an accurate correlation between the species data for Coladoir and that the Glac na Criche in terms of which noda occupy which *levels*, but the sample quadrats were restricted as carefully as was practical to individual, visually-identified elements of the microtopography.

Coladoir Bog, Mull

General features

Glen More in Mull is exposed to the full force of the Atlantic climate. Along its undulating valley floor, several loops of the Coladoir River enclose large peat deposits, many of which have been changed by intensive drainage and burning, but a few still retain an intact bog surface. The best of these is Coladoir Bog (40 ha) lying between the Coladoir River to the south, and the A849 to the north. The site has previously been described by Jermy and Crabbe (1978).

Mire structure

The site is divided by one of the scattered ridges of igneous bedrock which protrude through the underlying morainic material of the valley floor. The western section of the site is the larger of the two, and lies at an altitude of 15 m OD. It rises sharply to a crown near the northern margin then slopes gently southwards to the lagg stream which forms the southern boundary of the site. At about 20 m OD, the slightly higher eastern area lies on a plateau, above the rocky outcrop which forms the watershed between the two peat nuclei. This mire slopes away to the south-east, gently at first, but with an increasingly steep gradient as it approaches the Gearr Abhainn stream.

Structurally the eastern (or upper) bog in particular has much in common with Claish Moss, Sunart (Ratcliffe 1964). A continuous pool and hummock system covers about 4 ha, and throughout this area the pools occur as long ribbons of water, up to 100 m long but rarely more than 1 m wide, each separated by a similarly shaped ridge of solid peat. This whole pattern is oriented at right angeles to the slope, so the pools lie parallel with the contours, thus offering only the shortest of axes across which any hydrological gradient must operate. Over the flatter central area many pools coalesce to form large anastomosing systems, while on the steeper margins each pool is a discrete linear feature, with often a considerable fall from one pool, across the narrow intervening ridge, to the next pool downslope.

The western (or lower) bog has a more level surface, with the majority of peat ridges rising no more than 10–15 cm above the water table. The ridges are much less solid than those on the upper bog, consisting of soft, unhumified *Sphagnum*, and because this area also appears to have a greater proportion of hollows, the transition from ridge to pool is not as clearly defined. Unlike the upper bog, the area of surface patterning here is discontinuous, only occurring where the overall gradient of the mire is interrupted by several small plateaux. Detailed diagrams (Figs 2a, 2b) indicate the major features and surface contours of Coladoir Bog.

Mire type

Consisting of two nuclei which have coalesced across an intervening ridge, the site could be classed as *intermediate* mire (Ratcliffe 1977) or *ridge-raised* mire (Moore and Bellamy 1974). However, this type usually occurs as a single, isolated mire unit, whereas Coladoir Bog lies within an extensive area of blanket peat. The most striking feature of the mire is the orderly pattern taken up by the hummocks and hollows of the surface; this pattern can be seen quite plainly in Plates 1 and 2. Such patterns resemble the eccentric domed mire complexes described by Ruuhijarvi (1960), while Jermy and Crabbe (1978) describe it as 'raised'. Investigation of the peat depth however, reveals an average of only 3 m, a depth more usually associated with blanket mire. Goode (1972) describes two distinct morphological types of blanket mire, watershed mire and valleyside mire, the former occurring on the gentle slopes of watersheds and low rounded hills, the latter forming almost level expanses of peat alongside the main streams and rivers which dissect a blanket mire landscape. Although within such a landscape these two forms are rarely found as discrete sites but tend to grade from one to the other, watershed mire can usually be recognised by the presence of at least a few broad, even circular, pools whereas in valleyside mire the patterns are always strictly linear. Coladoir Bog is therefore more closely related to valleyside mire than watershed mire and can be regarded as consisting of two associated *valleyside mires* within a landscape of lowland oceanic blanket mire.

Surface vegetation and microtopography of Coladoir Bog

General vegetation structure (see Table 1). (Plant nomenclature follows Clapham *et al.* (1962), Warburg (1963), and Paton (1965). *Sphagnum subsecundum* agg. follows Eddy (1977).

Describing this mire in a broad context, Jermy and Crabbe (1978) assign the vegetation to the Scirpo-Eriophoretum after Birks (1973), this being the characteristic association of north-west Scottish blanket mire, distinguished by the presence of well

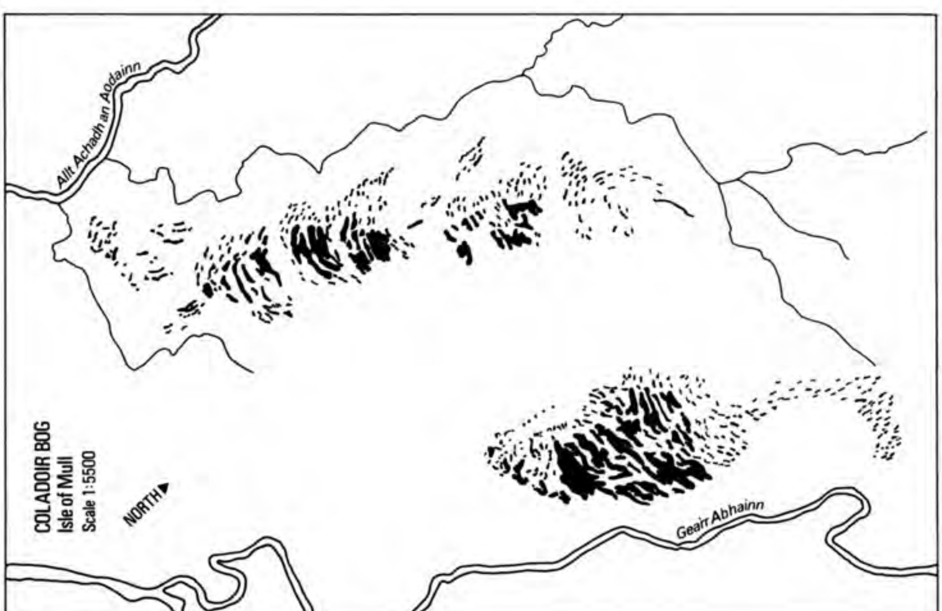


Figure 2a. Pool systems and main physical features of Coladoir Bog.

Figure 2b. Contour map.

Table 1. Coladoir Bog species list, based on $1m^2$ quadrats

Total species recorded	1	2	3	4	5	6	7	8	9	10
Calluna vulgaris	+	+	+	+	+	+	+	+	+	+
Drosera anglica										
D. intermedia										
D. rotundifolia							+	+		
Eleocharis multicaulis										
Erica cinerea										
E. tetralix	+	+	+	+	+	+	+	+		
Eriophorum angustifolium	+	+	+	+	+	+	+		+	+
E. vaginatum			+	+	+	+		+	+	+
Molinia caerulea	+	+	+	+	+	+	+	+	+	+
Myrica gale	+									+
Narthecium ossifragum	+	+	+	+	+	+	+	+		+
Potentilla erecta										
Rhynchospora alba	+	+	+	+	+	+	+	+	+	+
R. fusca										
Trichophorum cespitosum	+	+	+	+	+	+	+	+	+	+
Lycopodium selago										
Sphagnum auriculatum										
S. compactum										
S. cuspidatum	+	+	+				+			
S. magellanicum	+	+	+	+		+	+			
S. papillosum	+	+	+	+		+	+			+
S. plumulosum							+			
S. rubellum	+	+	+	+	+	+	+	+		
S. tenellum	+	+	+	+	+	+	+			
Aulacomnium paulstre										
Campylopus atrovirens			+							
C. flexuosus	+		+							
Hypnum cupressiforme	+		+	+	+	+	+			
Rhacomitrium lanuginosum	+		+	+	+	+		+		
Cephalozia connivens										
Odontoschisma sphagni	+		+	+	+	+	+	+		
Pleurozia purpurea			+	+	+					
Cladonia impexa	+		+	+			+	+		
C. floerkeana										
C. pyxidata										
C. uncialis	+		+		+	+	+			
Parmelia sulcata										

N.B. Quadrats taken in January, therefore certain species (e.g. Drosera) were not recorded from the $1\ m^2$ quadrats, but are included to provide a complete species listing.

developed *Sphagnum* lawns and hummocks, and a wide variety of dwarf shrubs and herbs, it favours deep humified peats on level or gently sloping ground. However, a most distinctive feature of unreclaimed thin peat on Mull, particularly along the lower slopes of uncultivated valleys such as the Coladoir, is the abundance of *Molinia caerulea*. In many places it occurs as almost monotypic stands, and a marked transition is visible between the green slopes of the *Molinia*-dominated valley sides and the browner *Sphagnum*-rich Coladoir Bog occupying the valley floor. Even so, *Molinia* is still relatively abundant on this site when compared with other examples of oceanic mire (cf. Ratcliffe and Walker 1958; Goode and Lindsay 1979). The vegetation of Coladoir is therefore regarded as a *Molinia*-rich facies of the Scirpo-Eriophoretum association.

Other constant species are *Calluna vulgaris, Rhynchospora alba* and *Trichophorum cespitosum*, with *Eriophorum angustifolium* and *Narthecium ossifragum* also abundant. The ground layer is rich in *Sphagna*, the commonest being *S. rubellum* and *S. papillosum*, while *S. magellanicum* forms occasional lawns and *S. cuspidatum* dominates many of the pools. Around the bog margin, *S. tenellum* becomes rather more frequent, replacing many of the other *Sphagna*. Other species found occasionally are *S. plumulosum, S. compactum* (particularly on the drier margin) and, in the pools, *S. auriculatum*. The deeper pools have only *Menyanthes trifoliata*, whereas the shallower hollows support species such as *Drosera anglica, D. intermedia* and *Rhynchospora alba*, as well as the hyper-oceanic *Rhynchospora fusca* in small, dense stands. The drier levels, though often with a *Sphagnum* ground layer, are visually dominated by an open dwarf shrub layer of *Calluna vulgaris, Erica tetralix* and, occasionally, *Myrica gale*, or else a sedge-dominated mixture of *Eriophorum angustifolium, Molinia caerulea* and *Trichophorum cespitosum. Narthecium ossifragum* is particularly abundant within areas of continuous *Sphagnum* lawn. Other bryophytes are relatively uncommon, though *Campylopus atrovirens* forms small dark cushions on areas of wet bare peat, *Rhacomitrium lanuginosum* occurs in just a few locations as a hummock-former, and the small oceanic liverwort *Pleurozia purpurea* is found throughout the ridge vegetation.

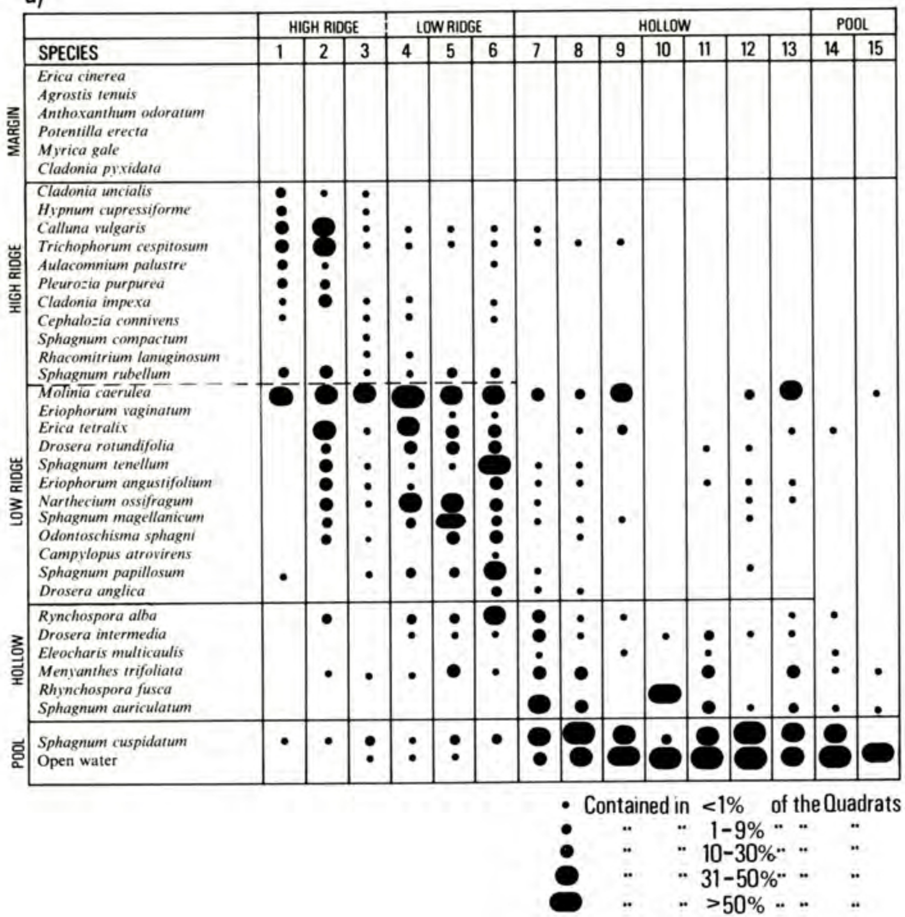
The basic species structure described here differs from sites described for the Outer Hebrides (Goode and Lindsay 1979) and Wigtownshire (Ratcliffe and Walker 1958) largely in relative terms, but certain individual species clearly show a marked climatic influence. *Carex limosa* is a common species of pools in the blanket mire patterns of Sutherland, Ross and Cromarty and the Outer Hebrides, whereas it is found only in the small rich flushes beyond the northern margin of Coladoir. Conversely, *Rhynchospora fusca* is not found (in ombrotrophic mires) in either the Outer Hebrides, or south of Mull, in Wigtownshire. It appears to be restricted to the extreme western coastline of north-west Scotland, and occurs in scattered localities north from Mull almost as far as Cape Wrath. Differences do exist between these broadly similar areas of mire, but not unlike the features by which the various members of a single genus are identified, some of the differences are too subtle to be recognised during a broad, cursory glance; for this a more detailed examination is required.

TWINSPAN analysis (Hill 1979). Although as implemented TWINSPAN uses eight levels of division and may therefore produce anything up to 256 'end groups', many of these must be recombined to a higher level in order to describe a nodum with some recognisable characteristics. For the present study, it was felt that a total of 15 end groups provided a reasonably complete account of the various noda to be found within the overall *Trichophoreto-Eriophoretum* association of the mire surface. Such decisions are inevitably somewhat subjective, but are nevertheless based on a number of different factors which are individually useful, and in combination provide a dependable means of determining the most informative levels of division.

Noda and microtopography. As the 15 end groups (noda) were derived from a mixture of non-patterned and pool system transects, the transects from unpatterned areas were separated from the central transects to produce two species frequency tables; one for the central pool complexes and one for the unpatterned and marginal areas (Table 2a + 2b) in order to highlight any differences which may exist between these areas.

Table 2. Species comparison of noda, numbered 1 to 15 from a) Pool Systems b) Margins of Coladoir Bog

a)



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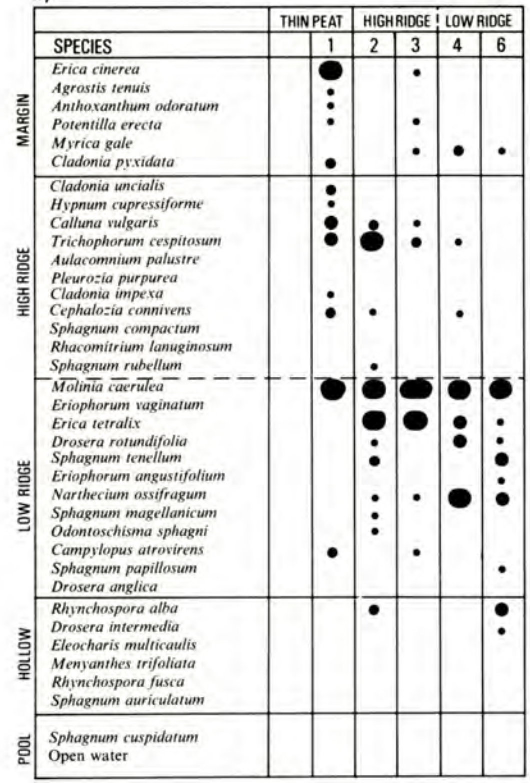


Table 2a represents the range and composition of noda obtained for the central patterned areas, while Table 2b is the species composition found on the margins and unpatterned areas. The ordering of noda in the tables is derived from the relationship between nodum and height above (or below) the water table. This is discussed below, but in effect represents (from left to right) a hydrological gradient from the highest and driest level of the microtopography to the deepest pool level. The species were hand sorted to reflect this gradient more clearly, with dry-indicating species at the top of the table and aquatic species at the bottom.

Table 2 demonstrates that many of the noda indicating drier conditions are common to both the non-patterned surfaces and the central pool systems, whereas the aquatic phase is entirely absent in non-patterned areas. In addition, the general species pattern reveals at least four major species groups which correspond closely to four topographic features recognised in the field. One of these is thin peat found on the rocky margins, while the others occur within areas of surface patterning and are referred to as *ridge, hollow* and *pool*.

The correlation between vegetation and physical features is further demonstrated in Figure 3, which shows the distribution of surface contours and the vegetation noda for Transects 8 and 9. It can be seen from this diagram that simply by indicating the distribution of *ridge, hollow* and *pool* noda the physical surface patterns can be discerned without difficulty.

As the two aspects are so closely linked, it would seem useful to investigate the nature of the microtopography in some detail before proceeding with an account of the individual noda displayed in Table 2. This account can therefore be found below, in "Description of the mire elements".

Nature of the microtopography. Using only those transects located within the pool systems, the contour height frequency plots for each nodum not only confirm the existence of three major elements, but also provide a reasonably detailed account of their physical form. Figure 4 is a graph of mean height above (or below) the water table for each nodum, with 95% confidence limits indicated. (The ordering of noda in Table 2 is derived from this diagram.) A subsequent analysis of variance indicated a significant difference between these means at the 0·1% level. Figure 5 represents a plot of the three major elements—*ridge, hollow* and *pool*—based on the combined height frequencies of all noda.

Figure 5 shows more clearly than any other single piece of evidence the presence of three distinct levels within the microtopography. Although a combined plot of all noda as a single histogram tends to absorb the separate peak which represents *hollow* into a broader *ridge* category, and results in an apparently bimodal distribution with peaks at 'ridge' and 'pool' level, it can be seen from Figure 5 that all those noda defined as *hollow* are confined rigidly to those parts of the microtopography which lie below the water table, and as such form a clearly defined association quite distinct from *low ridge*.

Description of the mire elements

By combining the species data in Table 2 with these three elements of the microtopography, it is possible to produce an account of the mire vegetation which is both descriptive and functional.

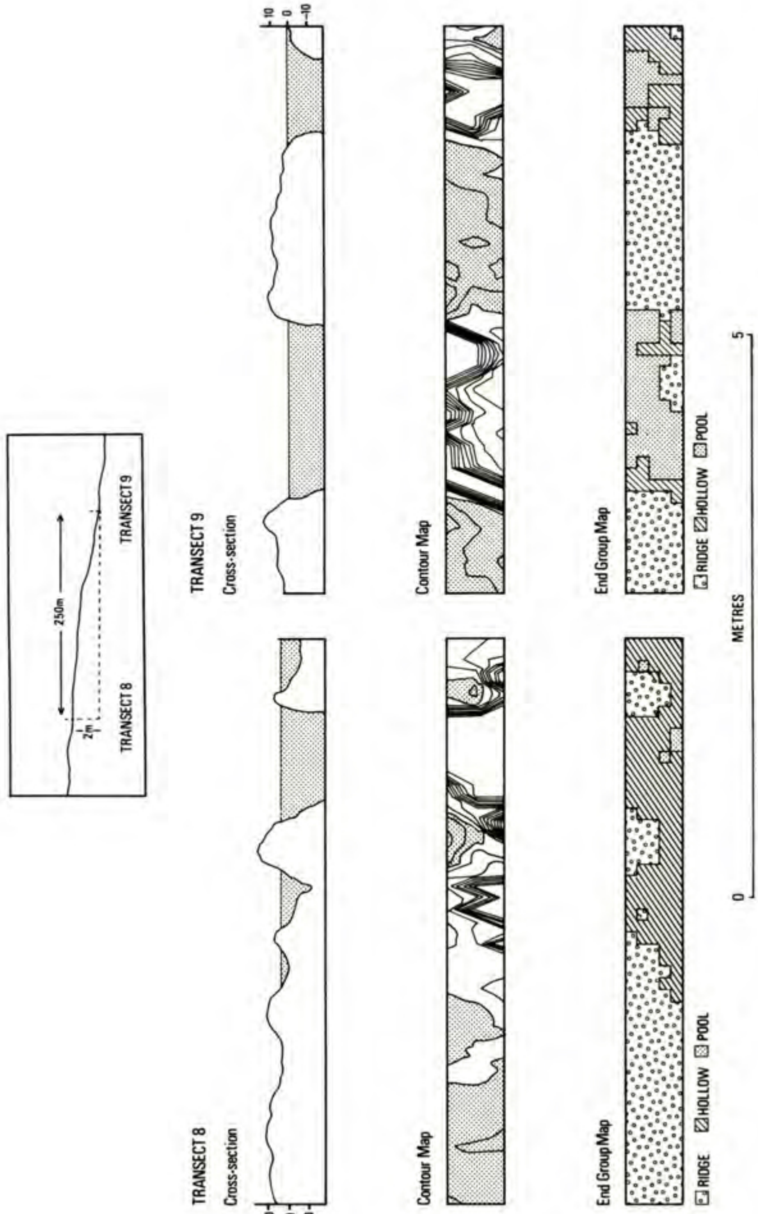


Figure 3. Details of two transect lines at Coladoir Bog.

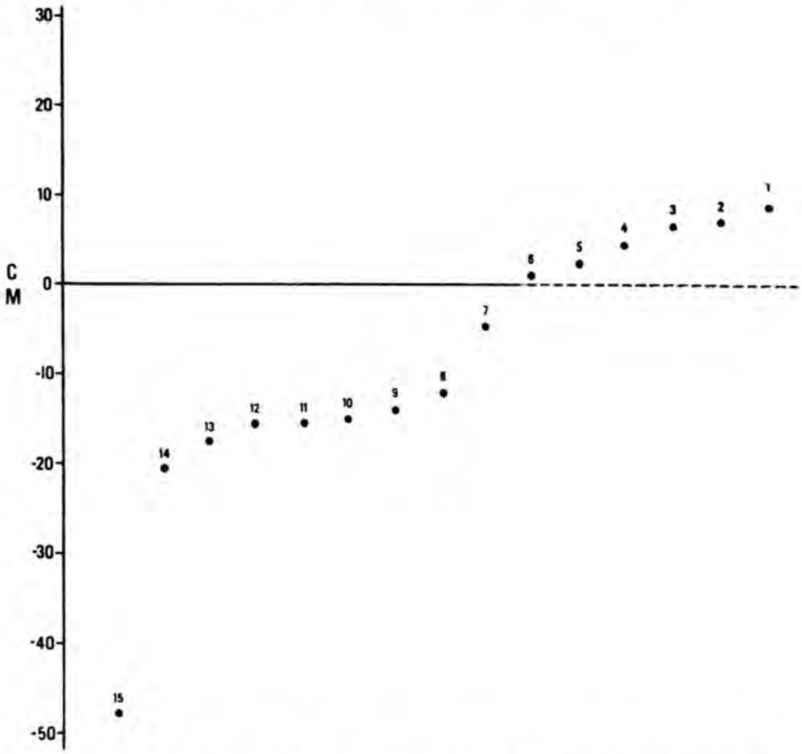


Figure 4. Mean height of noda numbered 1 to 15, above or below water table on Coladoir Bog.

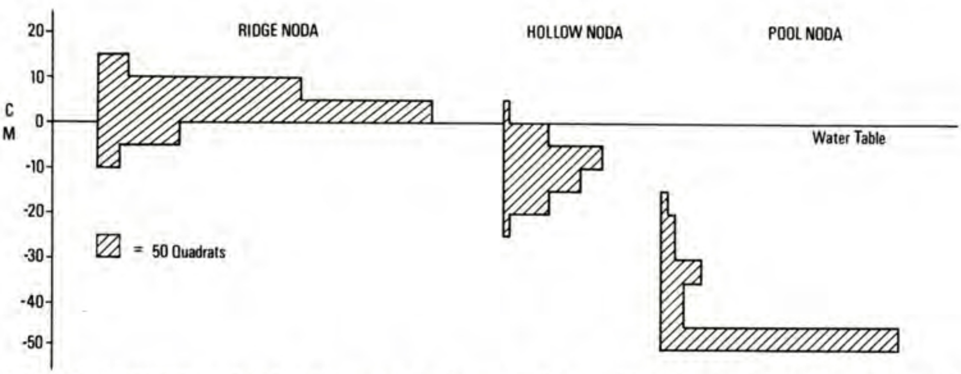


Figure 5. Distribution of noda with respect to the water table, combined for the three major elements of the microtopography from Coladoir Bog.

Ridge level. This refers to anything above the water table, although the vegetation may also occasionally extend a little way below the water table. The majority of heights associated with *ridge* level at Coladoir lie within 10 cm of the water table, although a few rise as high as 15 cm, and occasional hummocks rise much higher. Within areas of surface patterning the ridges are ribbon-like, as described above, and form a complex interconnecting network which at all times lies at right angles to the direction of slope. The process which brings about these patterns has been, and continues to be, the subject of considerable debate (Pearsall 1956; Ratcliffe 1964; Boatman and Armstrong 1968; Goode 1970) although they are undoubtedly an oceanic feature related to excess surface water resulting from the high rainfall common to the Atlantic coastline of Europe. Towards the edges of the patterned areas the ridges tend to broaden out into flat, unbroken examples of drier vegetation which eventually merge with the sloping marginal areas of the site.

The most characteristic feature of the vegetation at *ridge* level is the consistently high cover of *Molinia caerulea*, as previously mentioned. Other species common or abundant at this level are *Calluna vulgaris, Drosera rotundifolia, Erica tetralix, Narthecium ossifragum, Rhynchospora alba, Trichophorum cespitosum*, and the *Sphagnum* species *S. magellanicum, S. papillosum, S. rubellum*, and *S. tenellum*. These combine in various proportions to produce the six noda displayed in Table 2a which, on closer examination, can be seen to fall into two groups: those dominated by ericaceous and "hummock" species, and those with a low cover of ericaceous species but a relative abundance of *Sphagna* or bog 'typics' such as *Drosera rotundifolia* or *Narthecium ossifragum*. Noda 1, 2, and 3 are most abundant between +5 cm and +15 cm, and were thus taken to represent a *high ridge* facies, while noda 4, 5, and 6 are largely confined to the 5 cm just above the water level, and were taken to represent a *low ridge* facies.

High ridge. Nodum 1 (*Calluna—Trichophorum*): By far the most dry-indicating species grouping found within areas of patterning, the most obvious feature of this nodum is the short carpet of *Calluna vulgaris*, although in fact *Molinia* is the most abundant species. Mixed with this patchy dwarf shrub layer are small tussocks of *Trichophorum cespitosum*, while the hummock-forming *Spagnum rubellum* and other species more tolerant of dry conditions such as *Hypnum cupressiforme* and *Aulacomnium palustre* occur occasionally. More will be said about this nodum under the description of the mire margin.

Nodum 2 (*Calluna—Narthecium*) (see Plate 3): Very much dominated by a relatively tall herb/dwarf shrub layer, this nodum is nevertheless rich in mire species typically found where there is a rather more open ground layer. The shrub layer is a dense tangle of *C. vulgaris, Eriophorum angustifolium, Erica tetralix*, and *Trichophorum cespitosum*, beneath which *Cladonia impexa, Narthecium ossifragum, Sphagnum rubellum* and *S. tenellum* are relatively common, though the *Sphagna* tend to occur as the greener shaded forms. Also found here occasionally are *Sphagnum magellanicum, Odontoschisma sphagni* (within the *Sphagnum* carpets), and the oceanic liverwort *Pleurozia purpurea*, together with scattered individuals of *Rhynchospora alba* and odd leaves of *Menyanthes trifoliata* (which does occur along the ridges, despite being generally regarded as an aquatic species).

This is perhaps more similar than most *ridge* noda to anything described by Daniels (1978) for this level, particularly his Nodum 3 (*Calluna–Narthecium*), although the presence of *Rhacomitrium lanuginosum* suggests that he may also have included *hummock* level.

Nodum 3 (*Molinia—dwarf shrub*) (see Plate 4): Recognised by the relatively tall growth of *Molinia*, this tends to occur within areas having a tussocky dwarf shrub layer which is approaching the degenerate phase, and is generally intermixed with

Trichophorum cespitosum or *Eriophorum angustifolium*, although a fairly wide range of species may be found as odd records beneath the *Molinia*. A nodum indicating dry conditions, this too will be discussed further in relation to the noda from the margin.

Low ridge. Nodum 4 (*Molinia—Narthecium*): The transition from *high ridge* to *low ridge* is perhaps even more obvious visually than is indicated by the species frequency, with the latter having a peat surface which is either actually wet and glistening, or which is completely covered with non-hummock-forming *Sphagna*. In this instance it is the wet surface which separates it from the previous noda, and with a much higher abundance of *Molinia* than Nodum 3, it also differs considerably in appearance from this due to an alteration of the growth form of *Molinia*. Whereas in the previous nodum this species occurred as tall stands, here it occurs as individual shots with an open distribution. Associated with *Molinia* is a scattered shrub layer of *Erica tetralix*, with *Narthecium ossifragum* and *Drosera rotundifolia* common throughout. Other species include *Sphagnum magellanicum* and *S. papillosum*, with scattered records for *S. tenellum, Menyanthes trifoliata, Calluna vulgaris, Trichophorum cespitosum* and even *Drosera intermedia* (typical of wet bare peat). Apart from the small patches of *Sphagna*, all these species are rooted in either wet bare peat or a thick mulch of semi-decomposed *Molinia* litter.

Nodum 5 (*Sphagnum magellanicum*) (see Plate 3): One of the most distinctive noda to emerge from the analysis, this represents low hummocks or lawns of *Sphagnum magellanicum*, within which *Narthecium ossifragum* and *Menyanthes trifoliata* form an open field layer. *Molinia* is common, but occurs as scattered individuals. *Drosera rotundifolia* is also fairly common, along with stunted *Erica tetralix* and (within the *Sphagnum* carpet) *Odontoschisma sphagni*. Other occasional species include *Rhynchospora alba, Sphagnum cuspidatum, S. papillosum, S. rubellum,* and scattered examples of *Calluna vulgaris, Drosera intermedia, Eriophorum vaginatum* and *Trichophorum cespitosum*. This community often extends to the water's edge, where it is then replaced abruptly by one of the *pool* noda.

Nodum 6 (*Sphagnum—Rhynchospora alba*) (see Plate 4): Although at first, this nodum may appear similar to Nodum 2, it can be seen from Table 2 that the dense tangle of the herb/dwarf shrub layer by which it can be separated from other *low ridge* noda consists almost entirely of *Eriophorum angustifolium* and *Molinia caerulea*. The mixture of tall *Calluna vulgaris* and tussocks of *Trichophorum cespitosum* found in Nodum 2 is almost entirely absent. However a more fundamental difference can be found in the partially obscured ground layer which, unlike Nodum 2, is composed of a rich mixture of *Sphagnum* species. Consisting mainly of *S. papillosum* and *S. tenellum*, this carpet also contains a scattering of *S. cuspidatum, S. magellanicum* and *S. rubellum*. Another feature is the relative abundance of *Rhynchospora alba* which appears to be at its optimal level just at, or slightly above, the water table. This nodum dominates low islands of ridge whcih lie surrounded by the more aquatic noda, or areas of low ridge which slope gently down to the water table to form shallow hollows. It is rich in species typical of undisturbed mire, and appears to be closely allied to Daniels' Nodum 1 (*Molinia–Erica tetralix*) although *Sphagnum pulchrum* is absent from this site, and *Rhynchospora alba* was not recorded by Daniels.

Hollow level. This is almost entirely restricted to the first 20 cm below the water level. The hollow bottoms may consist of dense *Sphagnum* lawns, compacted *Molinia* litter, tightly interwoven root systems, or solid peat surfaces; consequently the firmness of the substratum varies enormously. Hollows are perhaps the most contentious features of surface pattering, as their origin is considered by many to hold the key to understanding the mechanism by which surface patterns develop. Are hollows drowning ridges, or are they in-filling pools? Indeed precisely *because* they are so often regarded as transitory features within a larger dynamic process, they appear generally to have been overlooked as features in their own right.

Unlike the noda of the *ridge* level, it appears from Figure 4 that individual *hollow* noda are less influenced by their height in relation to the water table. Other factors such as water chemistry may be important. The majority of noda occupy a fairly broad niche within the limits defined above for the level as a whole. Figures for pH, conductivity and major cation concentrations for these noda would be interesting.

Although *Molinia* is still found in many *hollow* noda, the species which particularly characterizes this level is *Sphagnum cuspidatum*. Open water is also a constant feature, while other species which rarely occur at other levels include *Drosera intermedia, Eleocharis multicaulis, Menyanthes trifoliata* and *Rhynchospora fusca. Sphagnum auriculatum* agg. in places forms an intimate mixture with *S. cuspidatum*, particularly where the *Sphagnum* lawn is only just submerged. Due to the relatively species-poor nature of this level many of the noda are characterized, in part, by the proportion of open water to *Sphagnum*. Such variations can make an enormous difference to the structure of the microhabitat, and it is this structure which is important, not just to the mire ecologist investigating pattern dynamics, but also to the invertebrate inhabitants of this niche, and the wader populations to whom these invertebrates are an important food source.

Nodum 7 (*Rhynchospora alba—Drosera intermedia*): This is recognised by its relatively firm, green carpet of *Sphagnum cuspidatum* and *S. auriculatum*, within which *Rhynchospora alba, Drosera intermedia* and *Menyanthes trifoliata* are common. It tends to occur where the *hollow* level is a narrow band separating *ridge* from deep *pool*. Sometimes the transition between Nodum 7 and the deeper level can be abrupt physically, but masked by a more gradual change in the vegetation.

Nodum 8 (*Sphagnum cuspidatum*): This is the nodum which fools the unwary, its apparently firm green *Sphagnum* carpet entirely covering many of the small linear hollows which cluster round the edges of surface patterning, as well as forming wide mats around the margins of deeper pools. A number of species occur as scattered individuals, and *S. auriculatum* forms small, dark patterns within the *Sphagnum cuspidatum* lawn, but the only higher plant commonly found here is *Menyanthes trifoliata*.

Nodum 9 (Molinia—open water): This represents *Molinia*-dominated areas which appear once to have been ridge, but are now flooded and breaking down. Goode (1970) proposes a mechanism by which such a process might occur, though it is not entirely clear how it could operate in this example, as the mechanism involves the formation of discrete runnels between pools. In this case the pool has swamped the entire downslope margin, leaving only the taller tussocks of vegetation to grow. Whatever the process, it appears to be much more common on the upper bog at Coladoir, particularly where the surface patterns persist on the relatively steep slope which eventually becomes the rand of the eastern margin.

Nodum 10 (*Rhynchospora fusca*): At the height of the growing season this is easily recognised by its almost pure stands of *Rhynchospora fusca*. The species forms a floating mat of tightly interwoven roots which then trap leaf litter and particles of peat, binding everything into a surprisingly firm surface. Its distribution in Britain is extremely restricted, though oddly discontinuous, with records as widely scattered as Mid-Wales, Surrey, and Sutherland. However, in all localities, it takes up this same position within the microtopography, or, in the absence of a true microtopography, it uses something of the equivalent *level*, such as old peat cuttings or flooded tracks in the mire.

Nodum 11 (*Sphagnum cuspidatum—S. auriculatum*) (see Plates 3 and 5): Similar to Nodum 21, the major difference is in the much higher water content of the present nodum, and the fairly dense accumulations of *Molinia* litter mixed with the two *Sphagna, S. cuspidatum* and *S. auriculatum*. Rather than forming a tight lawn with an apparently dry surface, it consists of a much looser matrix, and *Drosera intermedia* is a frequent associate.

Nodum 12 (*Open water—Sphagnum cuspidatum*): Though from the species frequencies of Table 2, Noda 8 and 12 appear similar, visually they are different. Nodum 12 represents areas of open water within which a loose matrix of *Sphagnum cuspidatum* hangs suspended, often 5–10 cm below the water level. Occasional pockets of more densely packed *Sphagnum* float at the surface around species such as *Eriophorum angustifolium* or *Molinia caerulea* which grow as emergent vegetation. Such an area provides a complex aquatic habitat which a wide range of invertebrate species are able to use at various stages in their life cycles.

Nodum 13 (*Open water—Molinia*): This would seem to be a later stage in the process described for Nodum 9. The solid surface is covered by a greater depth of water, and *Menyanthes trifoliata* is intermixed with stands of *Molinia*, which grow as emergent vegetation.

Pool level. The distinction between *hollow* and *pool* is usually simple in the field. If a walking stick meets some resistance in the first 10–20 cm, the feature is a *hollow*; if there is no resistance whatsoever even at depths of a metre or more, it is a *pool*. The latter are more common on the upper bog at Coladoir, and are often without any significant areas of marginal *hollow* noda. In such cases the transition from *ridge* level to deep water can be abrupt. Such features may be a direct result of the large excess of precipitation over evapotranspiration, a condition common to all such northern oceanic areas; ombrogenous mires less than 250 km south or 50 km east of Coladoir Bog have no such areas of open water. Deep pools provide habitats for the larvae of dragonfly and water beetles.

Noda 14 and 15 (*Open water*) (see Plates 3 and 5): Nodum 15 represents areas of very deep open water. Nodum 14 is classed as a *pool* nodum for two reasons; firstly it was found that the bottom substrate of this nodum was a rather nebulous colloid of detritus which provided some form of depth reading, but was much less definable than anything encountered at the *hollow* level; secondly it appeared on a number of occasions to represent a form of Nodum 15 subjected to chance colonisation of *Sphagnum cuspidatum*. Despite the somewhat dubious differences in height between these two, it was not felt that they differed sufficiently to assign Nodum 14 to the *hollow* level.

Unpatterned areas. This section is concerned with all those parts of the site which have no accepted surface patterning. As patterning is generally associated with the deeper parts of a peat deposit (Goode 1970), the noda described here are assumed to fall within a general category of *thin peat*, though they represent a wide variety of peat depths, from a few centimetres to one or two metres. They can be further divided into three morphological units, easily identified in the field as: (a) the true margin, or 'rand' surface; (b) central unpatterned parts of the mire; (c) thin peat associated with occasional rocky outcrops.

The most striking feature of the marginal vegetation, clearly demonstrated in Table 2, is the relatively small number of species found here. Despite the addition of nine species recorded only from these noda, even the most species-rich of *marginal* noda has 25% fewer species than the poorest of *ridge* noda from patterned areas. With hindsight, the difference between margin and patterned mire could have been further emphasised if *bare peat* had been recorded as a category in the same manner as described for *open water*; without doubt the former would have characterised the *margin* in much the same way as the latter characterises *hollow* and *pool* levels.

Nodum 1* (*Erica cinerea—Calluna—Trichophorum*): Although previously described as a nodum characterised by *high ridge* species such as *Calluna vulgaris* and *Trichophorum cespitosum*, it can be seen from Figure 2b that its better expression is as an association of *thin peat*, dominated by *Erica cinerea* and *Molinia*. Otherwise the species composition remains relatively unchanged, apart from the loss of *Sphagnum rubellum*, which is replaced by *Campylopus atrovirens*, and the addition of *Potentilla erecta* and *Cladonia pyxidata* (both species of dry peat, often following burning). It is quite likely that, should the water table in the patterned areas be lowered by burning or drainage, this nodum would become more frequent even within the areas of surface patterning.

Nodum 2*: Generally found on those flatter areas of mire between pool systems ('general mire surface' of Goode and Lindsay (1979)), rather than on the *rand* surface, a rather unexpected feature of this nodum in its marginal form is the loss of *Calluna vulgaris*. Being a species more typical of drier conditions, the margins would seem a more suitable habitat for it than the wetter patterned areas. However, appearances may be deceptive; without any microtopography to speak of, the margins may not have a sufficiently dry niche for this species, whereas within a pool and ridge system there may be pockets of relatively well-drained *high ridge* in which it can become established.

Nodum 3*: This is the dominant nodum of the *rand* as it falls the last metre or so to the lagg stream, or where the slope becomes extreme, as along the eastern boundary of the upper bog. Tall *Molinia caerulea* and short *Erica tetralix*, with occasional pockets of *E. cinerea*, cover a dry, bare peat surface.

Nodum 4*: Another of those found on the *general mire surface* and the *rand*, the most notable feature of this nodum in its marginal form is the presence of *Myrica gale*. To some extent the fact that this species was recorded only from the margins, implying its absence from the main patterned areas, is simply a sampling inadequacy because *Myrica* does occur within such areas. It is also, however, an indication that *Myrica gale* is more common on the marginal areas than in the central patterned systems—an indication which confirms a visual impression.

Nodum 6*: Although Nodum 5, the *Sphagnum magellanicum* lawn, is not found outside areas of patterning, a somewhat modified version of the other *Sphagnum*-dominated nodum can be found in many unpatterned areas. The total species list for the marginal form of Nodum 6 is less than half that of the complete nodum, but it can still be recognised by its *Sphagnum* carpet (though now composed almost entirely of *S. tenellum*) and small stands of *Rhynchospora alba*. It is the wettest of the marginal noda, and represents the nearest thing to a *hollow* to be found away from the main areas of patterning. It is a common feature of many damaged mires in western Britain, where burning has left a wet, bare peat surface pock-marked with small, shallow depressions.

Differences between the two mire complexes of Coladoir Bog

The two mire complexes appear to differ in their distribution and abundance of the various elements of the microtopography. Using the four *levels* defined above, this apparent difference was examined using a similar method to that of Ratcliffe and Walker (1958) for the Silver Flowe in describing the differences between the surface patterns of the several mire units at this site. The number of quadrats falling within each level of the microtopography is expressed as a frequency plot, the height of each column being based upon the actual height range for each of these levels (see Fig. 6). The quadrat frequency is indicated by column area, rather than the simple measure of length used by Ratcliffe and Walker.

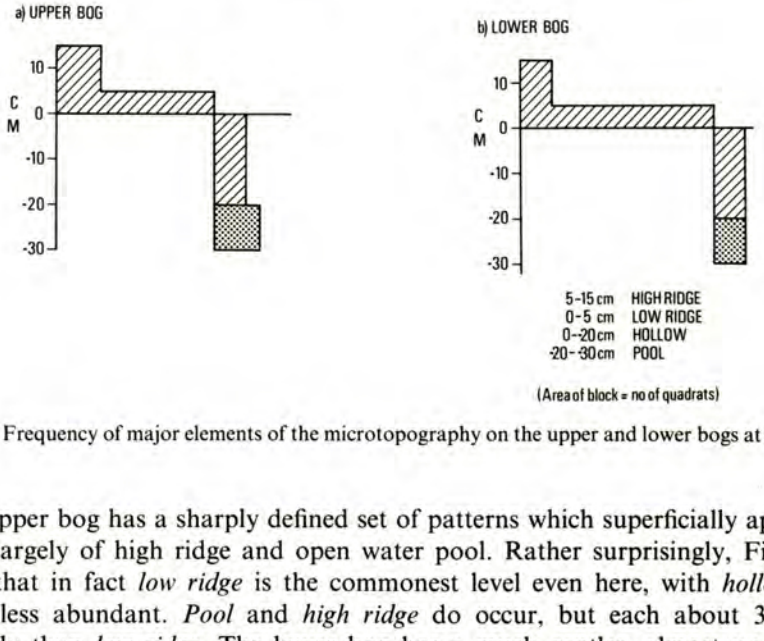


Figure 6. Frequency of major elements of the microtopography on the upper and lower bogs at Coladoir.

The upper bog has a sharply defined set of patterns which superficially appear to consist largely of high ridge and open water pool. Rather surprisingly, Figure 6a reveals that in fact *low ridge* is the commonest level even here, with *hollow* only slightly less abundant. *Pool* and *high ridge* do occur, but each about 35% less frequently than *low ridge*. The lower bog has a much gentler, almost undulating surface, with relatively few areas of high ridge or hummock. Figure 6b demonstrates that here too *low ridge* is the commonest element, but to a much greater degree. *Hollow* is equally common on both bogs, but *high ridge* and *pool* are significantly less common on the lower bog, where even their combined frequencies are 25% less than the total for *low ridge*.

Despite the dominance (in absolute terms) of *low ridge* at Coladoir, the relative distribution of the four major elements agrees fairly well with the general impression gained from a superficial reconnaissance. There are rather more areas of open water and solid ridge on the upper bog, while extensive areas of soft, *Sphagnum* ridge are separated by *hollow* rather than *pool* on the lower bog. The overall dominance of *low ridge* is an interesting feature which will be mentioned again later.

Glac na Criche, Islay

General features

Glac na Criche is a small (30 ha) remnant of oceanic blanket mire on the Atlantic coast of Islay. The original area of bog was formerly more extensive (perhaps 100 ha) but peat cutting and drainage have radically affected the surface topography, vegetation and hydrology of all but the relatively intact central area. This area is located on the watershed between the Gleann Truath Valley and the small valley between Ton Mhor and Am Miador. It is flanked on the north-west by the lee slope of an extensive area of seacliff and to the south-east by old (abandonded) peat cuttings. The peat has developed mainly over metamorphic slates and Phyllites.

The surface of the bog is gently domed towards the centre but has the overall impression of being flat. There is a surface microtopography of hummocks and hollows of low amplitude and towards the centre of the dome there is a series of small vegetated pools, bog hummocks and floating *Sphagnum* lawns (see Plate 6). It is clear from aerial photographs that there have been attempts to drain the area in the past, but the remains of these ditches are surprisingly difficult to detect on the ground, except for the very obvious central ditch cut between the two valleys. This ditch is for the most part ineffectual today and is almost totally vegetated. When the ditch was opened it may have caused the collapse of a more pronounced pool and ridge system, which is today represented by the central pools and rills. The surface of the bog is extremely soft and wet, and has actively growing *Sphagnum* surfaces throughout. In places, especially near the centre, the surface quakes. The cut over area to the east has active bog surfaces in the 'cutaways' but the vegetation of these regeneration surfaces is fundamentally different from the intact bog surface communities.

Surface vegetation and microtopography of Glac na Criche

The two sets of quadrat data were produced as separate tables. Table 3 represents the individual 1 m^2 quadrats, while for Table 4 it was possible to combine the 20 cm^2 quadrats into groups representing the four levels of *high ridge, low ridge, hollow* and *pool*, then calculate the species frequency at each level. The species were then hand sorted to reflect as clearly as possible the hydrological gradient.

General structure of the vegetation (Table 3). The mire surface possesses an average of 20 species in 1 m^2 quadrats with *Cladonia impexa, Calluna vulgaris, Drosera rotundifolia, Erica tetralix, Molinia caerulea, Sphagnum rubellum* and *S. tenellum* constant; *Eriophorum angustifolium, Schoenus nigricans, Succisa pratensis, Potentilla erecta* and *Sphagnum papillosum* common; and *Cladonia unicialis, Drosera anglica, Eleocharis palustris, Narthecium ossifragum, Sphagnum cuspidatum* frequent. A number of other plants, more commonly associated with wet heath rather than blanket mire, were occasionally recorded, namely *Melampyrum pratense, Pedicularis*

Table 3. Glac na Criche species list, based on $1m^2$ quadrats

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
	Quadrats																					
Calluna vulgaris			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Drosera anglica	+	+	+		+	+	+		+	+	+		+									
Drosera rotundifolia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Eriophorum angustifolium					+	+	+	+	+	+	+	+	+	+	+				+	+	+	+
Erica tetralix	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Eriophorum vaginatum					+		+										+	+	+	+	+	
Melampyrum pratense	+				+	+		+						+					+	+		+
Menyanthes trifoliata	+				+																	
Molinia caerulea	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+
Narthecium ossifragum	+		+		+	+			+	+			+		+	+	+					
Myrica gale	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
Pedicularis sylvatica	+				+	+	+	+		+												
Pinguicula lusitanica									+													
Polygala serpyllifolia																			+			
Pinguicula vulgaris							+															
Potentilla erecta						+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+
Rhynchospora alba		+	+			+		+			+		+									
Schoenus nigricans			+	+		+	+	+	+	+	+		+		+	+	+	+				
Succisa pratensis						+		+	+	+	+	+	+	+			+		+	+	+	+
Tichophorum˙ cespitosum				+		+	+		+	+	+	+	+		+	+	+					+
Equisetum palustre	+	+		+	+	+	+			+	+				+	+	+					
Sphagnum cuspidatum	+	+	+		+	+			+	+		+					+	+	+			
Sphagnum imbricatum																				+		+
Sphagnum magellanicum			+	+			+	+		+					+	+	+					
Sphagnum papillosum	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
Sphagnum rubellum	+		+	+	+	+	+	+	+	+	+	+	+	+		+	+	+			+	
Sphagnum auriculatum	+																					
Sphagnum tenellum	+		+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	
Aulacomnium palustre					+									+					+		+	
Campylopus atrovirens			+				+								+		+					
Hypnum cupressiforme										+		+		+		+		+			+	
Cephalozia loitlesbergeri					+				+		+					+	+					
Cephalozia connivens							+				+		+			+	+	+		+	+	+
Lepidozia setecea	+		+				+	+	+	+	+			+	+	+	+	+		+	+	+
Odontoschisma sphagni	+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pleurozia purpurea													+									
Riccardia latifrons								+	+	+	+			+	+	+	+	+		+		+
Cladonia arbuscula			+			+			+	+		+	+	+							+	
Cladonia impexa			+	+	+		+	+	+	+	+		+	+	+	+	+	+	+	+	+	
Cladonia uncialis			+				+		+		+		+	+	+				+			+

sylvaticus, and *Polygala vulgaris*. The *Sphagnum* surfaces support good growths of leafy liverworts, by far the most abundant being *Odontoschisma sphagni* and *Lepidozia setacea*. Other species include *Cephalozia connivens, C. loitlesbergeri, C. media, Gymnocolea inflata, Mylia anomola* and *Mylia taylori*. Although the bryophyte (surface) layer is dominated by *Sphagnum* species, other bryophytes occurring are *Aulacomnium palustre, Campylopus atrovirens, Dicranum bonjeani, D. scoparium, Hypnum cupressiforme, Pleurozia purpurea* and *Pleurozium schreberi*. The *Sphagnum*

Table 4. Species composition of the major elements within the microtopography at Glac na Criche

Species	Hummock	High ridge	Low ridge	Hollow
Eriophorum vaginatum	100			
Sphagnum plumulosum	20			
Hypnum cupressiforme	40	20		
Cladonia uncialis	20	20		
Pleurozium schreberi	20	20		
Sucissa pratense	20	20		
Schoenus nigricans	60		12	
Melampyrum pratense	40	40		
Empetrum nigrum	40	60		
Cladonia impexa	40	80		
Polygala serpyllifola		100		
Pedicularis sylvatica		20		
Plagiothecium undulatum		20		
Dicranum scoparium		20		
Erica tetralix	100	80	80	
Potentilla erecta	80	80	25	
Calluna vulgaris	80	80	37	
Sphagnum rubellum	40	60	37	
Drosera rotundifolia	60	60	87	
Sphagnum papillosum	20	20	100	
S. magellanicum		20	62	
Aulacomnium palustre			12	
Molinia caerulea	100	80	87	16
Myrica gale	80	80	50	16
Narthecium ossifragum	20	20	75	33
Eriophorium angustifolium	80	80	75	83
Eleocharis palustris	20		12	16
Sphagnum tenellum		40	25	16
Odontoschisma sphagni		20	37	16
Menyanthes trifoliata		20	25	33
Drosera intermedia			12	50
Rhynchospora alba			37	66
Drosera anglica			62	66
Sphagnum cuspidatum			37	100
Utricularia minor				33
Sphagnum auriculatum				66

surfaces are dominated by *S. cuspidatum*, *S. papillosum*, *S. rubellum* and *S. tenellum* but *S. imbricatum*, *S. magellanicum*, *S. plumulosum* and *S. auriculatum* also occur.

The vegetation of Glac na Criche is unusual in having *Schoenus nigricans* as a dominant species, together with the occurrence of a number of species not commonly encountered on Scottish blanket mires. For the most part, blanket mires in the west of Scotland at this elevation are dominated by the *Trichophorum–Eriophorum* bog of Ratcliffe (1964) or the *Erico–Sphagnetum magellanici* of Moore (1968), and Birse and Robertson (1976). The Scottish blanket mires within the *Trichophorum–Eriophorum* association of Ratcliffe display a clear-cut difference from comparable ombrotrophic mires in Western Ireland (Donegal, Mayo, Galway) in that *Schoenus nigricans* is a constant and often dominant component of the western Irish bogs, replacing *Trichophorum* (or *Eriophorum vaginatum)* in its Scottish equivalents (Ratcliffe 1964). Where *Schoenus nigricans* does occur in western Scottish blanket mires, such as on Rhum and in Sutherland, it is generally associated with water movement through the peat, or local flushing.

The vegetation of Glac na Criche cannot be attributed to any of the existing phytosociological units described for Scotland. Indeed, Ratcliffe points to the almost anomalous absence of *Schoenus*-dominated blanket mire vegetation along the Atlantic seaboard of Scotland, and Birks (1973, pp. 50–51) makes a similar comment when describing the *Trichophoreto–Eriophoretum* bogs of Skye. Glac na Criche forms an important link with the Irish *Schoenus nigricans* bogs of the *Pleurozia purpurea–Erica tetralix* association of Moore (1964). The affinity of Glac na Criche with the Irish blanket mires is reinforced by the presence of 'wet heath' species growing in ombrotrophic conditions (*Melampyrum pratense, Polygala vulgaris*) and this, together with its hyper-oceanic climate, suggests that it is the coastal influence which is at least partly responsible for the development of this community. Factors affecting the distribution of the community type in Ireland have been discussed by Boatman (1957, 1962, 1972), O'Hare (1968), Bellamy (1959) and Sparling (1962, 1967) and are not considered here.

Description of the mire elements

In the initial description of this site, reference was made to a low-amplitude pattern of hummocks and hollows. More general (less precise) usage of these terms might have meant any one of a wide range of surface patterns, but in this case the description is quite specific and thoroughly appropriate. Unlike the patterns described for Coladoir Bog, those found at Glac na Criche are dominated by the *hollow* level, which forms an inter-connecting network of wet *Sphagnum*-dominated lawns, and within which examples of *low ridge, high ridge* or *hummock* occur as slightly elongated, isolated islands (see Plate 7). The extreme linearity of the Coladoir patterns is missing, as is the abundance of open water. The pools occupying the very centre of the mire can be classed as *deep pool*, but their orientation and dimensions are much less well-defined than those at Coladoir.

High ridge/hummock level. A mosaic of hummock (to 30 cm) and ridge is found throughout the entire surface of the intact mire. The higher ridges are clearly defined by the occurrence of large tussocks of *Schoenus nigricans* with *Eriophorum vaginatum* and *Molinia caerulea*. A well-defined dwarf shrub layer is also present at this level, and consists of *Calluna vulgaris, Empetrum nigrum, Erica tetralix* and *Myrica gale*. Species more usually associated with burning or drainage are present in an apparently natural setting; such species include *Melampyrum pratense, Potentilla erecta* and *Succisa pratensis*. Higher hummocks support *Cladonia impexa* and *C. arbuscula*, both of which are locally dominant. Less hydrophilous species confined to higher hummocks are *Empetrum nigrum, Hypnum cupressiforme, Pedicularis sylvatica* and *Pleurozium schreberi*, each of which can become locally dominant. The higher *Sphagnum* hummocks, particularly those of *Sphagnum imbricatum*, are often rich in liverworts.

High ridge level. Rather curiously, this level appears to be characterised by the presence of *Polygala serpyllifolia*, though it is perhaps more easily visually identified by the absence of *Schoenus nigricans, Eriophorum vaginatum* and the extreme hummock-forming *Sphagna*. It has a fairly dense dwarf shrub layer of *Calluna vulgaris, Erica tetralix* and, as a constant, *Myrica gale*, which is overtopped by a tangle of *Eriophorum angustifolium* and *Molinia caerulea*. Beneath this cover, species typical of the *hummock* level such as *Empetrum nigrum, Melampyrum pratense, Pleurozium schreberi, Sphagnum rubellum* and *Cladonia uncialis* can be found, together with others more typical of wetter conditions, such as *Drosera rotundifolia, Sphagnum papillosum* and *S. tenellum*.

Low ridge level. Because of the very wet nature of the site, the low ridges support some species more typical of pool sides, or *Sphagnum*-lawn edges, such as *Drosera anglica* and *Menyanthes trifoliata*. However, this level is typified by *Narthecium ossifragum, Rhynchospora alba*, a high cover of *Sphagnum*, an abundance of *Drosera* spp. (often with all three species growing together), and good growths of leafy liverworts. *Molinia caerulea* remains abundant, as does *Erica tetralix*, but *Myrica gale* and *Calluna vulgaris* are found here much less frequently. *Sphagnum papillosum* and *S. magellanicum* provide an almost continuous ground layer, though of the two the former is the more abundant.

Hollow and pool level. Hollows and pools are vegetated with *Carex limosa, Juncus bulbosus, Sphagnum cuspidatum* and *S. auriculatum*. Only occasionally are there areas with open water, but where this occurs *Utricularia minor* is often found associated with submerged *Sphagna*. There are no distinct edges to the ridges and hollows, with *Sphagnum cuspidatum, Drosera anglica* and *Rhynchospora alba* gradually merging into the more solid ridges. A species-rich *hollow* community is common in which *Carex limosa, Drosera anglica, Drosera intermedia, Eriophorum angustifolium, Menyanthes trifoliata, Rhynchospora alba* and aquatic *Sphagna* occur.

Differences between Coladoir Bog and Glac na Criche

For two areas of blanket mire occupying the same general climatic zone, Coladoir Bog and Glac na Criche are remarkably dissimilar. The striking abundance of *Schoenus nigricans* within the central patterns of Glac na Criche, together with the dominance of the *hollow* level at this site, are in marked contrast to the *Molinia*-dominated ridges and deep, open water pools of Coladoir Bog.

The coastal influence on the species composition of Glac na Criche has already been discussed. However, a more typical 'flush' community, dominated by *Schoenus nigricans*, is found on both Islay and Mull; indeed, such a community lies along the northern boundary of Coladoir Bog. The fact that this latter site shows none of the coastal influence evident at Glac na Criche, with *S. nigricans* and *Polygala serpyllifolia* restricted to marginal areas, suggests that despite its location, it is relatively sheltered from the worst of the Atlantic storm spray by the length of Loch Scridain. It can, therefore, be looked on as an example of a climatic formation, whereas Glac na Criche owes something to both climate and maritime influence.

The differences in surface patterns may also be a result of this coastal influence, but it is difficult to see how such a mechanism might operate. Certainly the two sites appear to possess a different range of elements, Glac na Criche having the higher of the two with *hummock, high ridge, low ridge* and *hollow*, while Coladoir is largely *high ridge, low ridge, hollow* and *pool*. Glac na Criche has been drained in the past, and although most of the drains are now only visible on aerial photographs, it seems likely that the initial impact was profound. If so, the present *Sphagnum*-rich nature of the site is proof of a successful period of regeneration, but the range of mire elements and the lack of any clear orientation in the surface patterns may well bear witness to this chequered history. Certainly one would expect the *pool* level to suffer as a result of drainage more immediately and profoundly than any other level.

Discussion of mire systems

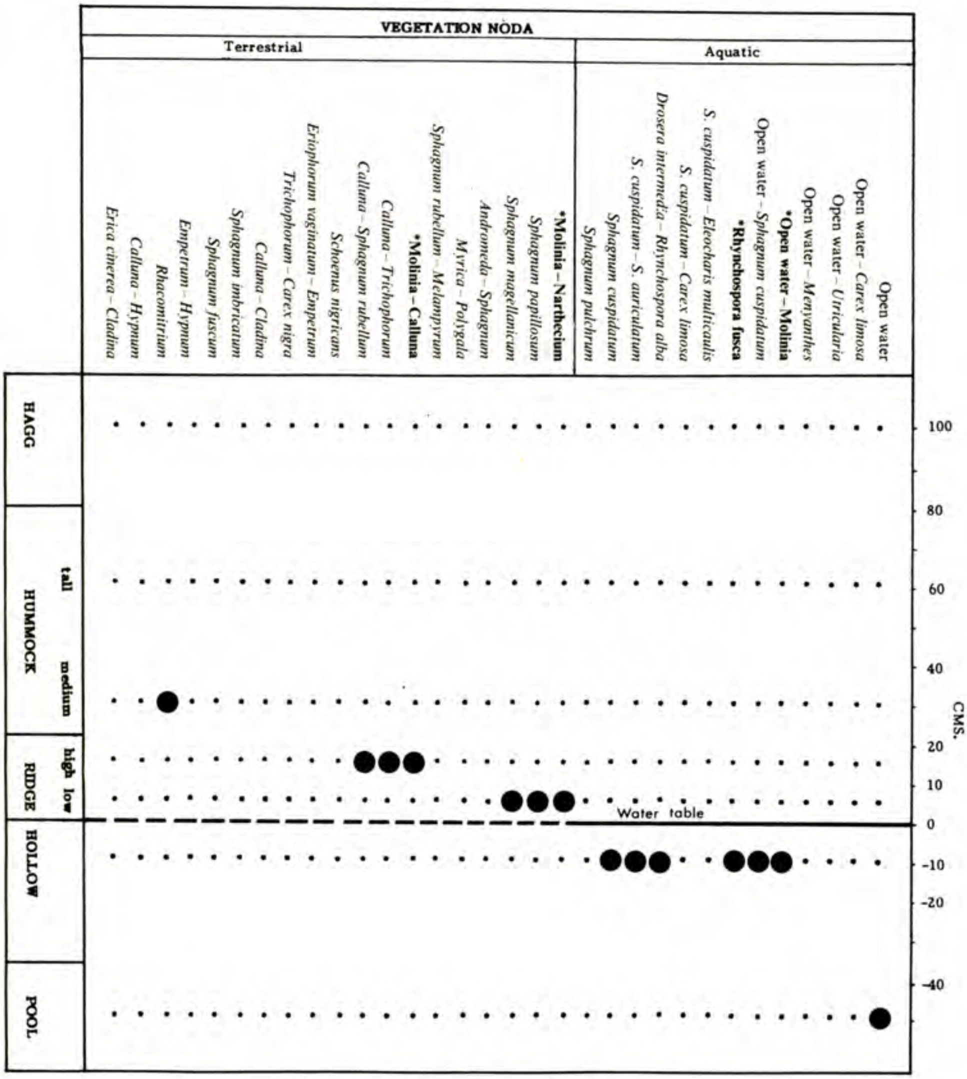
The ombrogenous mires of the Inner Hebrides form part of a series of mires which represent a hyper-oceanic extreme; in Europe, other members of that series are found only along Scotland's Atlantic seaboard and the west coast of Ireland (Goodwillie 1980). Several authors have described examples of this geographically restricted group (Pearsall 1956; Ratcliffe and Walker 1958; Gimingham *et al.* 1961; Boatman and Armstrong 1968; Goode and Lindsay 1979; Boatman *et al.* 1981). From such accounts it is clear that within this limited geographical range there is sufficient variation in climate and landform to produce a number of distinct sub-types, but repeated attempts to define the differences between these have tended to cloud, rather than clarify, the issue.

Accounts of mire systems have traditionally described areas of surface patterning as a hummock-hollow complex. This term is generally understood to mean an undulating mosaic within which dry hummocks are separated by shallow hollows lying at, or below, the water table, but when applied to the surface patterns of oceanic mires this model is clearly too simple. The present work has established the existence of five distinct elements in the microtopography of Coladoir Bog and Glac na Criche (*hummock, high ridge, low ridge, hollow, pool*) and has used these to describe significant differences between the two sites. Previous authors (Ratcliffe and Walker 1958; Gimingham *et al.* 1961; Goode and Lindsay 1979), faced with the complex patterns of oceanic mires, have introduced structural elements such as 'flat', 'ridge' and 'pool', but unfortunately the multiplicity of definitions used for the various elements described has left a rather confusing tangle of terminology, although much of this confusion is simply the result of assigning a number of different names to the same element, rather than the identification of new features.

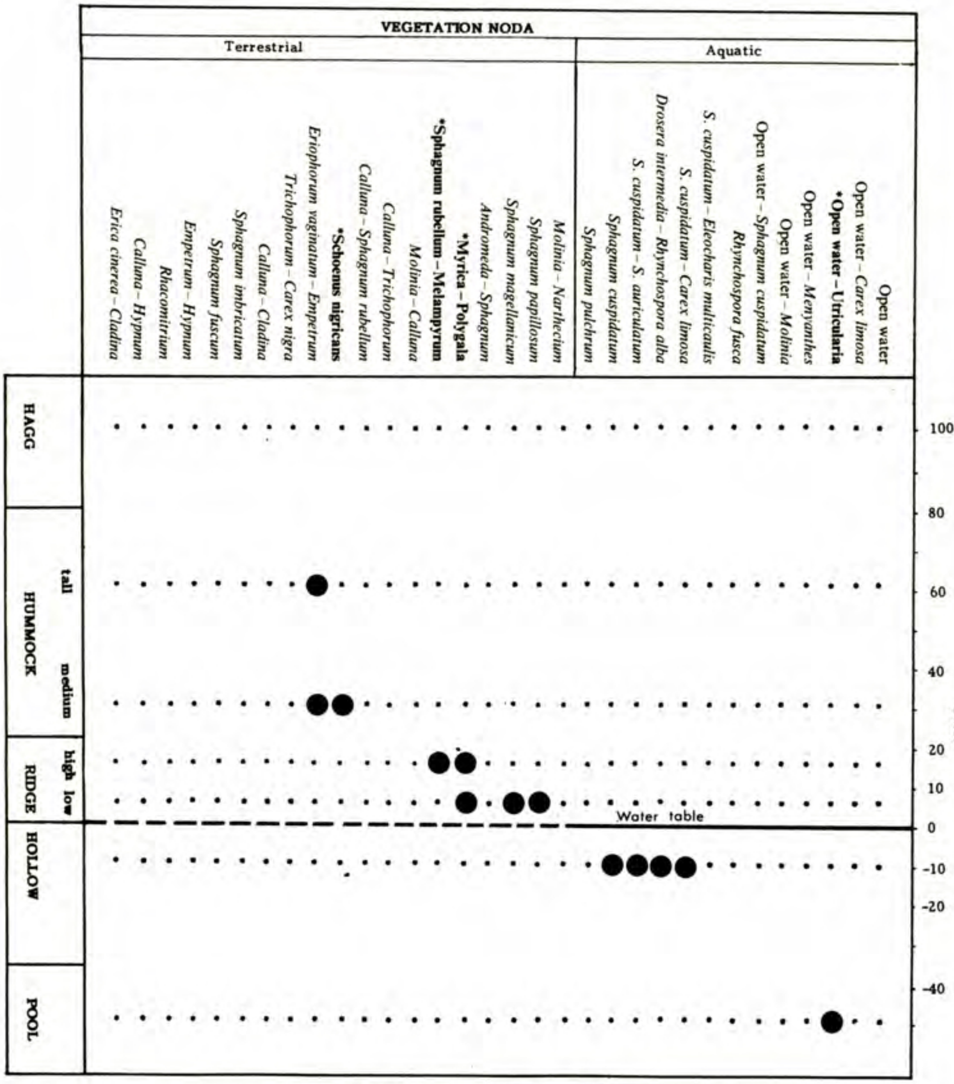
The five elements, or levels, described in the present work can be recognised in the published accounts referred to above, although several are not defined in quite the same way or with the same name, and no single author has used all five. However, there are sufficient similarities to enable useful comparisons to be drawn between the ombrogenous mires of the Inner Hebrides and published accounts of similar mires from other geographical areas. Table 5 is presented here as a summary of the differences between the ombrogenous mires of the Inner Hebrides, the Outer Hebrides, and a site in Dumfries and Galloway, based on the present work and two previous studies (Ratcliffe and Walker 1958; Goode and Lindsay 1979). It uses both microtopography and vegetation pattern to highlight the individual noda which characterise each mire sub-type, offering a clear, easily visualised description of each mire surface, and enabling direct comparisons to be made between sites.

In their account of the Silver Flowe, in Wigtownshire, Ratcliffe and Walker (1958) used the terms 'tall hummock', 'medium hummock', 'drier-type flat', 'flat', 'shallow pool' and 'deep pool'. The fact that this range includes elements which occur as high as 60 cm above the water table suggests that their 'hummock' level is approximately

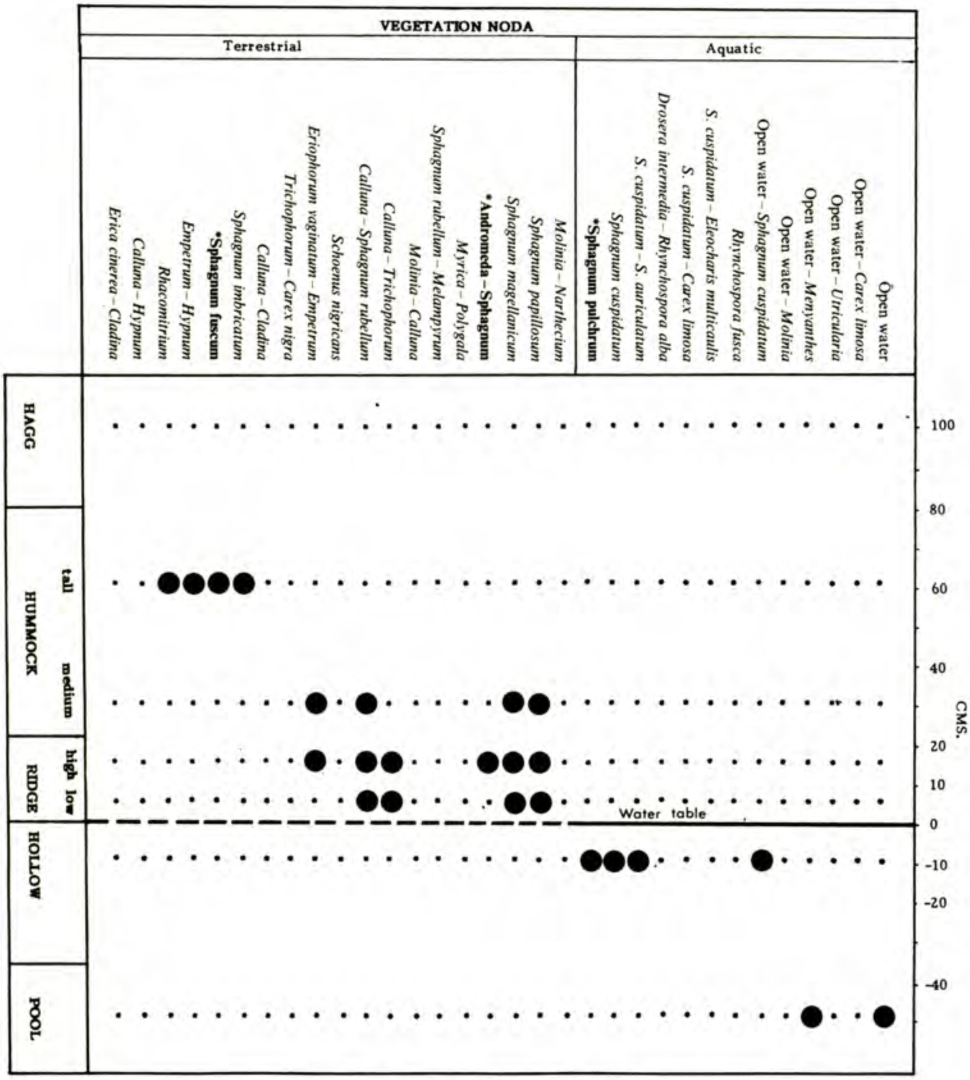
Table 5. Distribution of vegetation noda for four areas of western Scottish blanket mire, indicating the location of these noda in relation to the range of pattern elements found on each site. Noda are ordered with the driest on the left and the wettest on the right, and those unique to one site are preceded by an asterisk: a) Coladoir Bog, Mull, b) Glac na Criche, Islay, c) Silver Flowe, Galloway, d) Outer Hebrides.
Data for Silver Flowe taken from Ratcliffe and Walker (1958), and for the Outer Hebrides from Goode and Lindsay (1979).



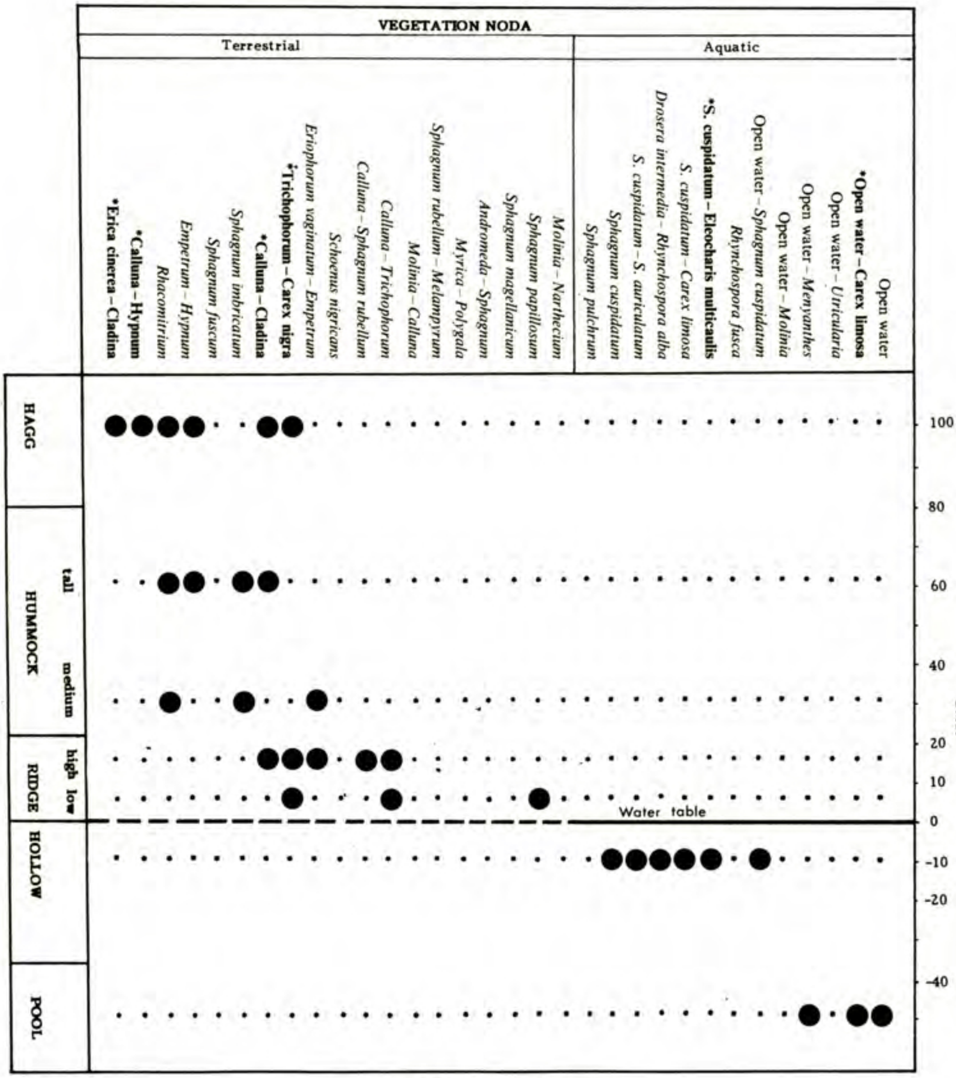
a) Coladoir Bog, Mull



b) Glac na Criche, Islay



c) Silver Flowe, Galloway



d) Outer Hebrides

equivalent to that same level described for Glac na Criche, rather than anything found at Coladoir. However, the species within that level differ quite markedly between the Wigtownshire and Islay locations. The 'drier-type flat' is recorded fairly consistently at 15 cm above the water table, corresponding well with the upper level of *high ridge* from Coladoir, while the wetter 'flat' community (generally *Sphagnum*-dominated) lies in the range 1–12 cm, thus to some degree equivalent to *low ridge* level. Pool depths show a fairly wide variation, but generally those with a *Sphagnum* carpet fall within the defined limits of *hollow*, while those with dominant *Batrachospermum* (open water) tend to be deeper than 20 cm and therefore equivalent to *pool*.

Dominating the 'medium-' and 'tall-hummocks' are species such as *Rhacomitrium lanuginosum, Empetrum nigrum, Sphagnum fuscum, S. imbricatum* and *S. rubellum,* all of which are rare or absent from Coladoir, but which occur on Glac na Criche at the *hummock* level. However, the addition of species such as *Melampyrum pratense, Schoenus nigricans* and *Succisa pratensis* to the *hummock* community on Islay clearly demonstrates its closer affinities with Irish blanket mire systems.

Coladoir Bog and the Silver Flowe are obviously closely related, but important differences confirm that they are distinct examples within a general trend of increasing oceanicity as one moves further north and west in Britain. Within the *ridge* levels, *Sphagnum papillosum* occupies a slightly lower level than *S. magellanicum*, as it does on Coladoir, but the abundance of *Eriophorum vaginatum* on the Silver Flowe is not seen here, being apparently replaced by *Molinia caerulea*. In the *hollows, Sphagnum pulchrum* is missing from Coladoir, but in its place are *Rhynchospora fusca* and *Drosera intermedia*, both hyper-oceanic species not found on the Wigtownshire site, which lies 150 km south-south-east of Mull. The absence of *hummock* level from Coladoir may not be entirely a climatic response, but at least partly an indication of that site's lack of damage, as there is some evidence to suggest that certain hummock formations are encouraged by burning, or other forms of damage which produce a localised fall in the water table. However, a much more detailed investigation is required before the mechanism for such a process could be confirmed and explained.

One of the present authors has described the blanket mires of the Outer Hebrides in much the same terms as used in the present paper (Goode and Lindsay 1979). However, in describing the features of the Outer Hebrides, the term 'ridge' is taken to include all three levels of *low ridge, high ridge* and *hummock*. Within this broad category species particularly characteristic of fire-damaged surfaces—*Carex panicea* (erroneously called *C. nigra*), *Eriophorum vaginatum, Hypnum cupressiforme, Polytrichum alpestre* and *Potentilla erecta* are common or abundant. The species which make up the bulk of the ridge level at Coladoir are also found in the Outer Hebrides, but any differences which may exist between the two areas are masked by the overall level of damage found in the Outer Hebrides. In the 'shallow hollows' and 'deep pools', however, burning has had less direct impact, and here it is possible to see the effect of an extreme oceanic climate. The *hollow* level is almost characterised by dense stands of *Eleocharis multicaulis* growing within *Sphagnum cuspidatum* lawns which, on Mull, tend to remain uncolonised by other species, while in both the *hollow* and *pool* level, *Carex limosa* (a species of poor-fen on Mull) forms prostrate carpets across many of the *Sphagnum*-dominated hollows, and floats in small rafts on the surfaces of the deep pools.

Goode and Lindsay (1979) also describe two features not encountered on Mull or

Islay to any significant degree; these are 'overflow channels' (or runnels) and 'eroded haggs'. The former have been discussed by previous authors, mainly in relation to the Silver Flowe (Goode 1970; Boatman *et al.* 1981), where they are proposed as important and dynamic features in the process of ridge and pool development. Similar areas are found on Coladoir Bog, often associated with *Campylopus atrovirens, Narthecium ossifragum* and *Myrica gale*, but no quadrat data are available for these features. Erosion is not a threat to either Glac na Criche or Coladoir Bog, but it is worth noting that the species associations of eroded hagg-tops in the Outer Hebrides closely resemble an extreme form of *hummock* level, or the marginal noda found associated with thin peat. Erosion appears to truncate the range of levels normally found on a site, reducing everything to areas of *high hummock* separated by bare erosion gullies. Were either Coladoir Bog or Glac na Criche to be damaged, it might be assumed that only modified forms of the present highest levels would survive.

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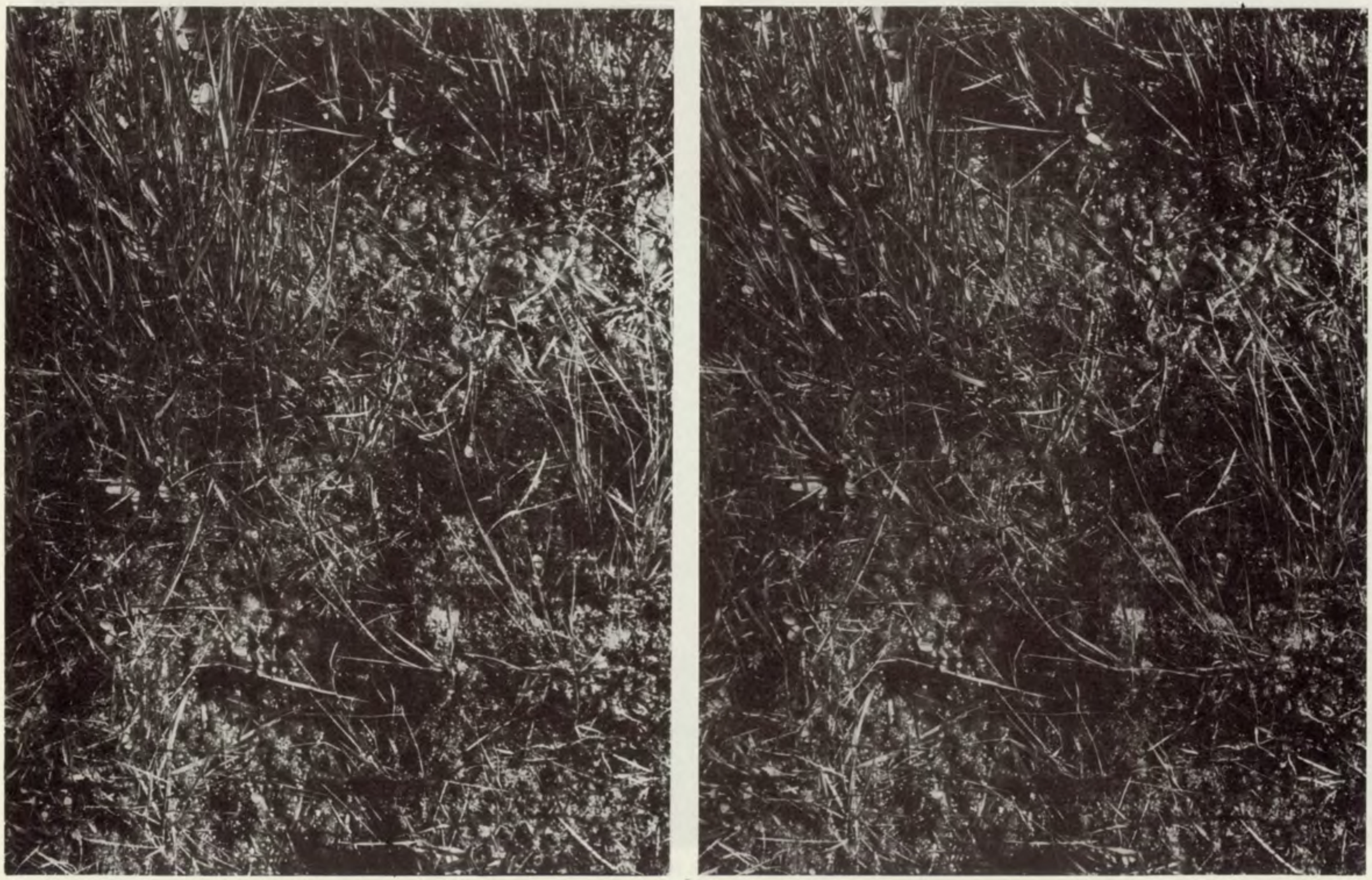
Plate 1. Aerial photograph of Coladoir Bog. 1: upper bog; 2: lower bog.

Plate 2. Pool and ridge surface patterns on Coladoir Bog, Mull. Open water pools are clearly visible, separated by long, narrow ridges. Note the abundance of *Molinia caerulea* on these ridges.

Plates 3a and 3b. Stereo pair with an example of ridge Nodum 2 bottom right grading into ridge Nodum 5 middle right. Pool Nodum 15 is present across the top, with hollow nodum 11 bottom left.



Plates 4a and 4b. Stereo pair showing a thin narrow band of hollow Nodum 8 running from bottom middle to top left. It lies between patches of ridge Nodum 6 bottom right and ridge Nodum 3 top right.

Plates 5a and 5b. Stereo pair, with sharply-defined hollow-pool transition. Pool Nodum 15 can be seen upper left, while hollow Nodum 11 is bottom centre. Centre right is a small area of ridge Nodum 5.

Plate 6. General view of Glac-na-Criche, Islay, showing low-amplitude hummock-hollow patterning. Note the absence of open water pools, which are here replaced by 'hollow' communities.

Plate 7. Detail of surface pattern at Glac-na-Criche, showing scattered hummocks containing *Schoenus nigricans* surrounded by broad 'hollows' dominated by Sphagnum species.