# M13
# *Schoenus nigricans-Juncus subnodulosus* mire
# *Schoenetum nigricantis* Koch 1926

**Synonymy**
*Juncus-Schoenus* community Clapham 1940; Valley fen communities Bellamy & Rose 1961 *p.p.*; *Cladium-Schoenus-Juncus* community Haslam 1965; *Schoenus* edge Haslam 1965; *Schoeno-Juncetum subnodulosi* (Allorge 1922) Wheeler 1975, 1980*b p.p.*; *Schoenus nigricans-Juncus subnodulosus* nodum Ratcliffe & Hattey 1982; *Schoenetum nigricantis* Dierssen 1982.

**Constant species**
*Carex panicea*, *Juncus subnodulosus*, *Molinia caerulea*, *Potentilla erecta*, *Schoenus nigricans*, *Succisa pratensis*, *Calliergon cuspidatum*, *Campylium stellatum*.

**Rare species**
*Carex diandra*, *Dactylorhiza traunsteineri*, *Potamogeton coloratus*.

**Physiognomy**
Some of the calcicolous mire vegetation in which *Schoenus nigricans* figures prominently is best included within the *Pinguiculo-Caricetum* and *Carici-Saxifragetum*, where *Schoenus* is overall only occasional and attains local dominance without a marked disruption of the floristic integrity of the communities. In the *Schoenetum nigricantis*, by contrast, *Schoenus* is a very frequent species and consistently associated with other distinctive floristic features. Although its cover is somewhat variable (it can even be absent from fragmentary stands), it is generally the dominant in this community, giving the vegetation a distinctive grey-green coloration through the year, with its semi-evergreen foliage. Very commonly, however, it occurs intermixed with at least some *Juncus subnodulosus*, a rush that is very rare in our submontane calcicolous mires, and sometimes this predominates, when stands have an olive-green hue in spring, turning reddish-brown with the death of the shoots in winter. *Molinia caerulea* is also constant and though usually not of very great abundance, it can be locally prominent, particularly in the more run-down kinds of *Schoenetum*. By and large, it is these plants, accompanied in some sub-communities by other rushes and sedges of medium stature (e.g. *Juncus articulatus*, *J. acutiflorus*, *Carex elata*, *C. diandra*, *C. rostrata*), that form the major structural element of the community, creating the general impression of a rough sward, half a metre or so in height (Wheeler 1975).

On closer inspection, however, it can be seen that it is the size and spacing of the *Schoenus* plants (and, to a lesser extent of the *Molinia*) that exert the strongest influence on the richness and organisation of the associated flora. *Schoenus* is a strongly gregarious, caespitose hemicryptophyte, forming loose to dense tufts of shoots on a partially-buried or emergent rootstock (Sparling 1962*a*, 1968). The tussocks commonly attain a height of 40 cm or more, often having prominent fibrous stools: in some stands much larger individuals can be found; in others, the plants are of considerably smaller stature throughout. Some of this variation may be attributable to the effect of certain environmental factors (see below), but part probably reflects inherent differences in growth form (Wheeler 1975). Usual tussock densities are of the order of 4–5 plants $m^{-2}$, but values of 8–10 $m^{-2}$ are quite frequent, when the canopy of leaves can be virtually continuous (Wheeler 1975). The development of the larger tussocks creates a variety of micro habitats: the depressions or runnels between, which are variously shaded and which can have standing or running water or can be no more than moist for much of the year, and the tussocks themselves, their sides and their tops, the latter far removed from the influence of the calcareous ground water. Such differentiation increases the floristic richness of the community, with $10 \times 10$ m samples commonly having more than 40 species, and is the basis of the frequent juxtaposition here of calcicoles and calcifuges and of aquatics and plants of drier habitats.

Among the associated vascular flora, smaller herbs are important throughout the community and, where the *Schoenus* tussocks are not too closely-spaced, they

can comprise much of the runnel vegetation, forming a lower stratum 10–30 cm tall. Sedges are often a major element with *Carex panicea*, *C. lepidocarpa* and *C. flacca* occurring frequently, *C. nigra* more occasionally. *C. hostiana* and *C. pulicaris* can also be found, though they are strongly preferential for one particular kind of *Schoenetum*, and the community also provides a locus for some of the south-eastern occurrences of *C. dioica*. In stands where the summer water-table is close to or at the surface, mixtures of these sedges tend to form a rather open cover within which there is considerable enrichment by species such as *Equisetum palustre*, *Pedicularis palustris*, *Mentha aquatica*, *Valeriana dioica* and *Cardamine pratensis* and, in some cases, *Parnassia palustris*, *Pinguicula vulgaris* and *Eriophorum latifolium*. More calcicolous assemblages provide a clear floristic link with the *Pinguiculo-Caricetum*, although plants like *Eleocharis quinqueflora*, *Selaginella selaginoides* and *Triglochin palustris*, which are predominantly northern in their distribution, are at most occasional here.

More distinctively, there are frequent records in this component for *Hydrocotyle vulgaris*, *Ranunculus flammula* and the Oceanic Southern *Anagallis tenella*, and for a variety of orchids. *Epipactis palustris* is the commonest of these throughout the community as a whole and it is very characteristic of this kind of vegetation (its other major community being the floristically quite similar *Salix-Campylium* dune-slack) but *Dactylorhiza majalis* also occurs frequently, ssp. *praetermissa* to the south and east, ssp. *purpurella* to the north and west, and *D. fuchsii*, *D. incarnata* and *Gymnadenia conopsea* are also quite common. More locally, there can also be some *Dactylorhiza maculata* ssp. *ericetorum*, *Ophrys insectifera*, *Coeloglossum viride*, *Platanthera bifolia* and the nationally rare *D. traunsteineri*. Where numbers of these are present together and flowering between May and August, this vegetation can present a splendid sight, though variation within and hybridisation between the dactylorchids can make recording a vexatious task.

Taller herbs are generally not of high individual cover in the community, although they can be locally abundant and the emergent flowering shoots of the dicotyledons often make them conspicuous. Among these plants, *Succisa pratensis* is the most common, but also frequent are *Angelica sylvestris*, *Cirsium palustre*, *Filipendula ulmaria*, *Eupatorium cannabinum*, *Oenanthe lachenalli* with *Centaurea nigra*, *Serratula tinctoria*, *Lythrum salicaria*, *Cirsium dissectum* and *Valeriana officinalis* more occasional. Trailing among the vegetation, there can be some *Galium uliginosum* and, less commonly, *G. palustre*.

*Phragmites australis* is also a frequent member of the *Schoenetum*, particularly in ungrazed stands, but it is usually not very vigorous, occurring as sparse shoots or scattered clumps. *Cladium mariscus* occurs occasionally, too, but it is likewise only locally abundant. Where these species are present, then, they typically form a very open upper tier to the vegetation, a metre or so high, but they can give the community a rather different superficial appearance and, particularly where tall-fen dicotyledons are also numerous, bring it close in floristics and structure to certain kinds of Phragmitetalia vegetation, notably the *Peucedano-Phragmitetum*.

In drier stands, where the summer water-table is well below the surface, much of this floristic richness is lost. Then, the smaller sedges, together with much *Molinia*, other grasses like *Holcus lanatus* and *Festuca rubra*, and often *Lotus uliginosus*, bulk large in the runnels and, especially where *Schoenus* itself is reduced, the vegetation approaches the communities of the Junco-Molinion: such a trend is best seen in the *Festuca-Juncus* subcommunity. To the other extreme, on very wet and flat sites, there can be pools of standing water between the tussocks with enrichment with a more obviously aquatic element, including *Menyanthes trifoliata*, *Equisetum fluviatile*, *Utricularia* ssp. and *Chara* ssp.: this is most noticeable in the *Caltha-Galium* sub-community which is floristically transitional to the *Carex-Calliergon* mire.

Even within the runnels of the *Schoenetum*, drier areas can have a scatter of less calcicolous plants, but more usually it is the tops of the *Schoenus* tussocks (and, sometimes, of the *Molinia*) which provide a niche for such species. *Potentilla erecta* and *Erica tetralix* are the most frequent members of this component but there can also be other ericoids like *Calluna vulgaris* and, to the west, *Erica cinerea*, and some *Drosera rotundifolia* or *Narthecium ossifragum*. *Molinia* can also be found growing epiphytically on the *Schoenus*.

Bryophytes vary considerably in their cover and variety in the community but they can be very extensive (with a total cover up to 70% or so) and, like the vascular plants, show a striking patterning over the various microhabitats, a feature first described by Clapham (1940) from stands of the community in Berkshire. The commonest mosses throughout are *Campylium stellatum* and, particularly where the shade is deeper, *Calliergon cuspidatum*. *Drepanocladus revolvens* (including var. *intermedius*), *Aneura pinguis*, *Cratoneuron commutatum* and *C. filicinum* are also quite frequent and extensive mats of all these species can colonise wetter ground and form a base, kept moist but rarely submerged, for the establishment of the vascular plants. These bryophytes can also grow over very young *Schoenus* tussocks but where larger stools have developed, they are very much confined to the area around their bases. Also common in some stands are *Bryum pseudotriquetrum*, *Plagiomnium elatum*, *P. rostratum* and *Rhizomnium punctatum* which Clapham (1940) noted as characteristic of compacted and rarely submerged peat and the sides of the *Schoenus* stools; this

latter habitat also affords a niche for *Fissidens adianthoides*. More typical of the tussock tops are *Pseudoscleropodium purum*, *Brachythecium rutabulum*, *Aulacomnium palustre* and *Sphagnum subnitens* and, often spreading in considerable abundance over tops, sides and down into drier runnels, *Ctenidium molluscum*. *Lophocolea bidentata s.l.* and *Pellia endiviifolia* also occur occasionally in this community and more unusual species recorded in some stands are *Campylium elodes*, *Riccardia multifida*, *R. chamedryfolia* and *Drepanocladus lycopodioides*.

**Sub-communities**

***Festuca rubra-Juncus acutiflorus* sub-community:** *Schoeno-Juncetum typicum* (Allorge 1922) Wheeler 1980*b* *p.p.*; *Schoenus nigricans-Juncus subnodulosus* nodum Ratcliffe & Hattey 1982 *p.p.* This sub-community comprises the more impoverished stands of the *Schoenetum* where *Schoenus* itself is sometimes much reduced in vigour and cover or even totally absent from vegetation which preserves the general floristics of the community. *Juncus subnodulosus* and *Molinia* are often proportionately more important and mixtures of grasses can make a major contribution to the cover, with *Festuca rubra*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Agrostis canina* ssp. *canina* and *A. stolonifera* well represented. Where tussocks are strongly developed, it is these species, with mixtures of *Carex panicea*, *C. lepidocarpa* and *C. flacca*, which usually clothe much of the runnels. In some stands, *Juncus acutiflorus* is present in small amounts, emphasising similarities with Junco-Molinion vegetation.

Various vascular plants generally characteristic of the *Schoenetum* are reduced here: *Anagallis tenella*, for example, is totally absent and *Pedicularis palustris*, *Epipactis palustris* and other orchids very scarce. The commonest herbs are *Succisa* and *Hydrocotyle* with occasional *Mentha aquatica*, *Equisetum palustre*, *Lotus uliginosus*, *Cardamine pratensis* and *Ranunculus acris* and scattered individuals of *Eupatorium*, *Angelica*, *Cirsium palustre*, *Filipendula ulmaria* and *Valeriana dioica*. *Potentilla erecta* and occasional *Erica tetralix* occur on the tussock tops. *Phragmites* and *Cladium* are infrequent and of low cover but some stands have a patchy canopy of *Myrica gale*.

Bryophytes, too, are relatively few in number here and generally sparse among the rank herbage. *Calliergon cuspidatum* is the commonest species with *Campylium stellatum* somewhat reduced in frequency and other mosses distinctly scarce.

***Briza media-Pinguicula vulgaris* sub-community:** *Schoeno-Juncetum leontodetosum* (Allorge 1922) Wheeler 1975; *Schoeno-Juncetum serratuletosum* (Allorge 1922) Wheeler 1980*b*; *Schoenus nigricans-Juncus subnodulosus* nodum Ratcliffe & Hattey 1982 *p.p.* Compared with the *Festuca-Juncus* sub-community, this kind of *Schoenetum* is often strikingly rich, sharing, with the next, frequent records for such characteristic herbs as *Anagallis tenella*, *Pedicularis palustris* and *Epipactis palustris* and a greater variety of bryophytes. Mixtures of *Schoenus*, *J. subnodulosus* and *Molinia* usually share dominance but the small-herb component of the runnel flora is especially distinctive. Here, *Carex hostiana* and *C. pulicaris* join the other sedges as strong preferentials and there is often some *Briza media*, *Pinguicula vulgaris*, *Parnassia palustris*, *Juncus articulatus* and *Linum catharticum* and occasionally *Selaginella selaginoides*, *Triglochin palustris* and *Plantago maritima* can be found. Such assemblages emphasise the floristic links with the Northern sub-montane fen vegetation of the *Pinguiculo-Caricetum*. Among the sometimes rich mixtures of orchids with frequent *Gymnadenia conopsea* var. *densiflora* and *Dactylorhiza fuchsii*, there is commonly some *D. majalis* ssp. *purpurella*, a further northern element. *Epipactis palustris*, on the other hand, and *Ophrys insectifera*, which occurs occasionally, are species of Continental distribution, as is *Serratula tinctoria*, another good preferential herb. This kind of floristic mix, with both northern and southern plants occurring together, is a striking feature of this sub-community. Other smaller herbs to be found in the runnels include *Polygala vulgaris* and *Trifolium pratense* and, in some stands, *Isolepis setacea*, *Sagina procumbens* and *S. nodosa* have been recorded together (the *Isolepis* variant of Wheeler 1980*b*).

Along with *Succisa pratensis* and *Serratula*, taller herbs are represented by frequent *Angelica sylvestris*, *Cirsium palustre*, *Eupatorium cannabinum*, *Oenanthe lachenalii* and occasional *Filipendula ulmaria*, and bulkier grasses such as *Festuca rubra* and *Holcus lanatus* can be locally prominent too. *Phragmites* and *Cladium* are sometimes present, though typically they are not abundant. More calcifuge plants can be an important component on the tussock tops, with *Potentilla erecta* and *Erica tetralix* being sometimes joined by *Calluna vulgaris*, *E. cinerea*, *Danthonia decumbens* and *Luzula multiflora*. Where these are prominent over much *Molinia* and with scattered bushes of *Myrica*, they can give this vegetation a rather different look (as in the *Myrica* variant of Wheeler 1980*b*).

Bryophytes are quite numerous and sometimes of high cover with, in addition to *Campylium stellatum* and *Calliergon cuspidatum*, frequent *Drepanocladus revolvens*, *Fissidens adianthoides*, *Cratoneuron commutatum* and occasional *C. filicinum*, *Ctenidium molluscum*, *Bryum pseudotriquetrum*, *Aneura pinguis* and *Pellia endiviifolia*.

***Caltha palustris-Galium uliginosum* sub-community:** Valley fen communities Bellamy & Rose 1961 *p.p.*; *Schoenus* and *Cladium-Schoenus-Juncus* communities

Haslam 1965; *Schoeno-Juncetum caricetosum & cladietosum* (Allorge 1922) Wheeler 1975. *Schoenus*, *J. subnodulosus* and *Molinia* remain of structural importance here but this bulkier component of the vegetation is variously augmented by *Carex rostrata*, *C. diandra*, *C. elata* and, somewhat better represented in this subcommunity than in other kinds of *Schoenetum*, *Cladium* and, to a lesser extent, *Phragmites*. The individual cover of these plants is generally low (although *Cladium* can be locally so abundant as to give the superficial impression of a sedge-bed) and usually they occur in a mosaic with the three constant monocotyledons of the community.

Runnels are often well developed but many of the smaller preferentials of the *Briza-Pinguicula* subcommunity are reduced to occasional occurrences. The commonest species of this element here are *Carex panicea*, *C. lepidocarpa*, *Mentha aquatica*, *Hydrocotyle vulgaris* and, preferentially frequent, *Caltha palustris* and *Valeriana dioica*. In addition to *Epipactis palustris*, there is quite often some *Dactylorhiza incarnata*, *D. majalis* ssp. *praetermissa* and, in some sites, *D. traunsteineri*. Taller dicotyledons are rather more common than elsewhere in the community with, as well as the community species *Succisa*, *Angelica* and *Cirsium palustre*, preferentially frequent *Eupatorium*, *Filipendula ulmaria* and *Lynchnis flos-cuculi*. *Galium uliginosum* and, less commonly, *G. palustre* can be found sprawling among the vegetation and there is often some *Vicia cracca*.

Further distinctive enrichment occurs where, as is quite commonly the case here, there are pools of standing water in the runnels. The presence of *Carex rostrata* and *C. diandra* is especially associated with this kind of situation and these may be accompanied by *Menyanthes trifoliata*, *Equisetum fluviatile*, *Eriophorum angustifolium*, *Utricularia* spp. (including *U. vulgaris*, *U. neglecta* and the rare *U. intermedia*), the rare *Potamogeton coloratus* and *Chara* spp. (including *C. hispida* var. *hispida*, *C. globularis* var. *aspera* and *C. contraria*).

Bryophytes tend to be fewer and less abundant under dense vegetation of this kind but, where the cover is rather more open, and especially where there is a strong differentiation of *Schoenus* tussocks, diversity and cover can be high. All the species of the *Briza-Pinguicula* subcommunity occur frequently here, sometimes with additional rarer plants in the wetter runnels, e.g. *Riccardia chamedryfolia*, *R. multifida*, *Drepanocladus lycopodioides*. But preferentially frequent are those species which seem to be most typical of the sides of the tussocks (*Plagiomnium rostratum*, *P. elatum* and *Rhizomnium punctatum*) or their tops (*Pseudoscleropodium purum*).

**Habitat**

The *Schoenetum* is confined to peat or mineral soils in and around lowland mires irrigated by base-rich, highly calcareous and oligotrophic waters. It is commonest in sites with a strongly soligenous character, being often found below springs and seepage lines and on the flushed margins of more fully-developed valley mires, but it also extends into topogenous basins provided there is close contact with waters draining from lime-rich substrates. Climate, particularly summer warmth, plays an important part in restricting the community to the southern parts of Britain, though this kind of vegetation provides an important locus for outlying occurrences of some northern mire plants and, towards the north and west, begins to grade to sub-montane Tofieldietalia communities. Grazing sometimes influences the structure and floristics of the *Schoenetum* and some stands have been affected by mowing and burning. Shallow peat-digging has been locally important in providing a suitable habitat for the community, but more drastic treatments of mires, particularly draining and eutrophication, have reduced its extent and eliminated it from some areas.

The representation of *Schoenus nigricans* in British vegetation types is a function of a complicated interaction between climatic and edaphic factors. It is generally restricted to lowland areas with a February minimum temperature at or above freezing (*Climatogical Atlas* 1952), a climatic relationship which reflects its general distribution through Europe and which may be related to frost-sensitivity (Sparling 1968). Within this zone, it occurs on wetter, oligotrophic soils, but these show a wide variation in base-status and are represented in a diversity of mire types. In moving across Britain into western Ireland, *Schoenus* becomes less exclusively a plant of base-rich soligenous habitats, extending in north-west Scotland into flushed areas within base-poor ombrogenous mires and then, in Ireland, on to the acidic peats of the bog-plane proper (e.g. Tansley 1911, 1939, Pearsall & Lind 1941, Osvald 1949, Boatman 1957). Sparling (1962*b*, 1967*a*, *b*) has related this trend to a complex of factors connected with increasing oceanicity to the west, and perhaps working through an amelioration in aluminium levels in the substrate, to which *Schoenus* is very sensitive.

Within this spectrum, *Schoenus* occurs as an occasional local dominant in base-rich soligenous mires around the upland fringes of north-west Britain, where the general character of the vegetation is very much determined by the cool sub-montane climate: this is the role it has in the low-altitude stands of the *Carici-Saxifragetum* and, more especially, in the *Pinguiculo-Caricetum*. The bulk of our more calcicolous *Schoenus* vegetation, however, belongs to the *Schoenetum* which is, by contrast, a community of southern Britain, occurring largely in an area bounded by the 25 °C mean annual maximum isotherm (Conolly & Dahl 1970). More Continental species, such as *Juncus subnodulosus*, *Epipactis palustris*, *Serratula tinctoria*, *Dactylorhiza majalis* ssp. *praetermissa* and, more occasionally, *D. traunsteineri* and *Ophrys insectifera*, which are very scarce in northern

mires, are thus characteristic here. However, the ranges of such plants as these and more northerly mire species are by no means mutually exclusive. Arctic-Alpine plants with which *Schoenus* is sometimes associated in the *Carici-Saxifragetum* and the *Pinguiculo-Caricetum* are, of course, quite absent, but some Continental Northern species maintain quite a good representation in the *Schoenetum*. This is especially true towards the north-western limit of its range where summer temperatures are considerably cooler than they are in East Anglia. There, notably in the Anglesey fens, the floristic richness of the *Briza-Pinguicula* sub-community, which is mainly represented in this region, owes much to the mixing of the different phytogeographic elements, frequent *Carex pulicaris*, *Pinguicula vulgaris*, *Parnassia palustris* and *Dactylorhiza majalis* ssp. *purpurella* and occasional *Selaginella selaginoides* occurring with Continental species. Such plants thin out moving further to the south-east but, in East Anglia, the community still provides them (and others like *Carex dioica*, *C. diandra*, *Menyanthes* and *Utricularia* spp.) with important outposts.

The very local occurrence of the *Schoenetum* within the generally warmer parts of Britain is a strong reflection of its dependence upon continuous irrigation with base-rich and calcareous waters by seepage from lime-rich bedrocks or superficials. The community is best developed on the Chalk and chalky drift of East Anglia, where it occurs around the head-waters of tributaries to the Ouse and the Waveney (Bellamy & Rose 1961, Haslam 1965) and the Ant (Wheeler 1978, 1980*b*; see also Ratcliffe 1977), and in Anglesey, where it is found on the fringes of basin mires that have developed within shallow hollows in Carboniferous Limestone (Wheeler 1975, 1980*b*; Ratcliffe & Hattey 1982). Scattered sites occur elsewhere, notably over Corallian Limestone in the Cothill basin in Berkshire (Clapham 1940), on Oolite in Northamptonshire, on Magnesian Limestone in Nottinghamshire and Durham, and more distantly, on Carboniferous Limestone again in north Lancashire and Northumberland (Wheeler 1975, 1980*b*; Ratcliffe 1977).

Typically, in such situations as these, the flushing waters have a pH between 6.5 and 8.0, with dissolved calcium levels of 60–200 mg $l^{-1}$ (Wheeler 1975, 1983), conditions which are reflected in the prominent calcicolous element among the smaller herbs and bryophytes of the runnels, where the effects of irrigation are felt most directly. The soil types, however, are quite variable. The community can occur on wetter mineral soils, including very ill-structured profiles which are little more than sloppy muds or marls, and on more well-developed surface water gleys, with or without a humic top, and also on peats proper which, on the margins of mires, can be moderately deep. Often, the sites are gently-sloping with a more or less continuous through-put of water but the community can extend on to wet topogenous sites, so long as the base-richness of the substrate is maintained.

One further important characteristic of the soils is that they are very poor in major nutrients, probably especially in phosphorus (Haslam 1965, Wheeler 1983) and this is likely to be important in excluding the community from those parts of valley and flood-plain mires where there is enrichment by the regular deposition of allochthonous mineral material. In such situations, *Phragmites* and tall mesophytic herbs become progressively more important in vegetation like that of the *Peucedano-Phragmitetum* and the *Phragmites-Eupatorium* fen. The *Schoenetum* grades floristically into these communities, particularly through the *Caltha-Galium* sub-community, and, in some sites, it can form a fringe around them, but these elements are generally of low cover in the community itself, so that the vegetation is maintained in a moderately open condition with ample opportunity for the development of smaller, shade-sensitive species. *Schoenus* itself will not tolerate deep shade (Sparling 1968) and is also damaged by the deposition of silt over its shoots (Haslam 1965).

There is no doubt that for the optimal development of the *Schoenetum*, the soil must be maintained in a reasonably moist state throughout the year. *Schoenus* itself will stand some fluctuation in ground-water level (particularly towards the wetter west: Sparling 1962*a*, 1968; Haslam 1965) but it grows best where there is a fairly high and stable water-table and its seed germinates best when the soil surface is kept moist outside the winter months (Sparling 1968). Nonetheless, there is considerable variation in the height of the water-table here and this factor, often interacting with past or present treatments, plays some part in differentiating the sub-communities. The highest summer water-tables are found in the *Caltha-Galium* sub-community,where the *Schoenetum* extends on to flat sites which can have a few centimetres of standing water between the tussocks. This permits the development of an obvious aquatic element in the flora and can encourage an increase in the cover of *Phragmites* and *Cladium*, especially where stands have not been grazed or regularly summer-mown. Then, this vegetation takes on something of the character of a Phragmitetalia fen or of swampy Caricion davallianae vegetation like that in the *Carex-Calliergon* mire. In some situations, this sub-community may represent an early stage in primary hydrarch succession (e.g. Clapham 1940), though there is often the suspicion that it has developed secondarily in wet abandoned peat-cuttings, a common feature on lowland valley and basin mires. And it has probably sometimes been included with neighbouring Phragmitetalia vegetation in marsh crops harvested by mowing.

The *Briza-Pinguicula* sub-community, by contrast, is more typical of situations where the summer water-table is at, or not far below, the surface. In such places, this vegetation has often been open to grazing and trampling by stock and this probably plays some part in the differentiation of more pronounced tussock/runnel systems and in the maintenance of a low, open sward between the tussocks where smaller herbs and bryophytes sensitive to competition can flourish. Other stands of this kind have probably been mown for a mixed litter crop, traditionally cut annually between July and October (e.g. Lambert 1946). Such treatment would be expected to prevent the development of large tussocks but, in transitions to topogenous mires, could maintain the *Schoenetum* against the spread of *Phragmites* and, especially in the typically oligotrophic habitat here, of *Cladium* which, unlike *Schoenus*, cannot recover from annual summer mowing and cannot regenerate well from seed (Godwin 1941, Haslam 1965).

On drier soils still, the *Festuca-Juncus* sub-community is characteristic. In some cases, this kind of *Schoenetum* may represent a natural transition to Junco-Molinion vegetation on the surrounding mineral soils, or a secondary development where mowing and grazing have been relaxed on drier soils, but in many places it seems to have developed because of an artifical lowering of the water-table by drainage operations. Fragmentary stands of this sub-community can still provide relic localities for rarer mire species but they have little of the striking richness of the other kinds of *Schoenetum* (Wheeler 1975, Ratcliffe & Hattey 1982).

**Zonation and succession**

The *Schoenetum* occurs in zonations around springs and seepage lines where natural variation in the vegetation is related primarily to the height of the water-table in sequences of mineral and organic soils, the character and disposition of which are determined by geology and the pattern of flushing. But such zonations have been widely affected by a variety of treatments such as grazing, mowing and peat-cutting, so that some of their components are plagioclimax vegetation, now often further altered by successional changes attendant upon neglect. Other changes have been induced by drainage and eutrophication and widespread improvement of surrounding land has also left many stands isolated and much modified within intensive agricultural landscapes.

In more intact zonations developed over entirely calcareous substrates, the *Schoenetum* typically grades, on the gleyed mineral soils above seepage lines or around more localised springs, to richer kinds of Junco-Molinion vegetation like the *Cirsio-Molinietum*, in which both *Schoenus* and *J. subnodulosus* can persist but where dominance generally passes to *Molinia*. This, in turn, may grade to some kind of Mesobromion grassland on the dry, lithomorphic calcareous soils beyond: usually, within the range of the *Schoenetum*, this is the *Festuca-Avenula* grassland. Where flushing occurs more abruptly over limestone slopes, the *Schoenetum* can give way directly to such a calcicolous sward (Figure 15).

In the other direction, where the *Schoenetum* occurs above and sometimes extends on to deeper peats which have accumulated in valleys and basins under the close influence of calcareous and oligotrophic ground waters, the community can pass directly to some kind of Phragmitetalia vegetation, often the *Cladietum marisci*, on the waterlogged organic soils. Sometimes, in such sequences, the *Schoenetum* can itself be zoned, the *Festuca-Juncus* sub-community occupying the drier ground, the *Briza-Pinguicula* the moister soils and the *Caltha-Galium* the wettest, and the last type can also be found in hollows on peat with the *Carex-Calliergon* mire among a matrix of the *Cladietum*. Such patterns as these are especially characteristic of the Anglesey mires such as Cors Bodeilio, Cors y Farl, Cors Goch and, to a lesser extent, Cors Erddreiniog (Wheeler 1975, Ratcliffe & Hattey 1982 Site group IX).

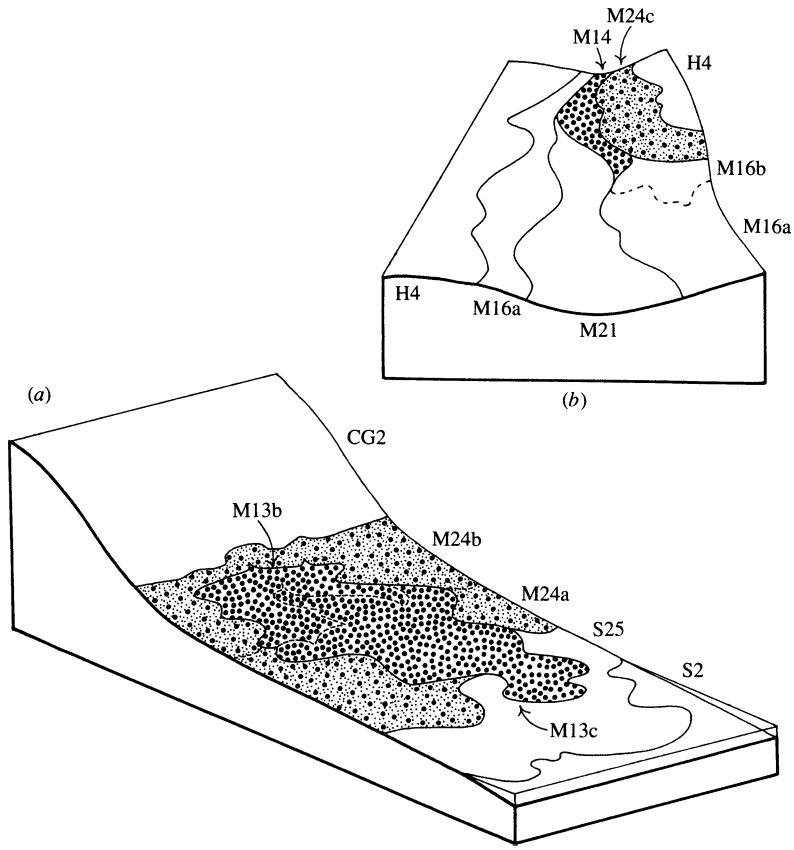
In less consistently oligotrophic situations, the *Schoenetum* occurs in generally similar zonations, but in association with other communities. Where it occurs around valley mires, for example, in which the peats experience some deposition of allochthonous mineral material, it can give way below to the *Phragmitetum australis* swamp or some kind of Phragmitetalia tall-herb fen, generally the *Phragmites-Eupatorium* community. This is well seen in some of the East Anglian fens like Smallburgh, Scarning, Redgrave/South Lopham and Thelnetham/Blo' Norton (Bellamy & Rose 1961, Haslam 1965, Wheeler 1975, 1978, Ratcliffe 1977). And, where the gleyed soils around the flushes are somewhat richer than those typically supporting the *Cirsio-Molinietum*, the *Schoenetum* can grade above to the *Juncus-Cirsium* community or the *Holco-Juncetum* and thence, on the drier mineral profiles, to some kind of Cynosurion sward. Where irrigation with calcareous waters is a very local phenomenon within tracts of acidic substrates and soils, the community can be found among more calcifugous vegetation. On some of the Norfolk heaths, like Buxton Heath for example, where calcareous drift occupies the bottoms of some hollows and valleys the *Schoenetum* passes, above the seepage lines, to the *Ericetum tetralicis* on base-poor gleys. Other *Schoenus* vegetation in these 'mixed mires' is, however, perhaps better placed in the *Schoenus-Narthecium* community.

Traditional treatments have variously influenced zonations such as these. The middle and drier parts of the sequences were often subject to grazing by stock, the middle and wetter parts to mowing for hay, litter or marsh crops like sedge and reed. Such treatments had the general effect of holding back succession to wood-

land throughout, but they have probably also influenced the balance of the different components, increasing the extent of one community against another according to the particular regimes of grazing and mowing adopted, treatments which affect the vegetation directly but also modify the nutrient budget of the system. As far as the *Schoenetum* itself is concerned, the former effects have probably modified transitions to tall-herb fens and swamps by influencing the amounts of *Phragmites* and *Cladium* in the vegetation (e.g. Godwin 1941, Haslam 1965), and altered the balance within the community between the *Schoenus*, *J. subnodulosus* and *Molinia*. And alterations in nutrient budget perhaps play a part in the balance between the *Schoenetum* and the *Cirsio-Molinietum* and *Juncus-Cirsium* community (Wheeler 1983). Treatment regimes have been very variable so actual zonations can be similarly diverse, added to which we now often see their influence blurred by the effects of long neglect, particularly over the surface of peats where mowing for marsh crops has fallen into virtually total disuse. A common pattern now is for the *Schoenetum* to form the wettest component in a fairly open herbaceous sequence, still maintained by grazing, and to give way below to very dense sedge- or reed-beds or to woodland that has colonised tall-herb fen and swamp.

Such transitions have become more frequent with the

Figure 15. *Schoenus* communities among fen (*a*) and bog (*b*) sequences.
M13b *Schoenetum* mire, *Briza-Pinguicula* sub-community
M13c *Schoenetum* mire, *Caltha-Galium* sub-community
M14 *Schoenus-Narthecium* mire
M16a *Ericetum tetralicis* wet heath, Typical sub-community
M16b *Ericetum tetralicis* wet heath, *Succisa-Carex* sub-community
M21 *Narthecio-Sphagnetum* valley bog
M24a *Cirsio-Molinietum* fen-meadow, *Eupatorium* sub-community
M24b *Cirsio-Molinietum* fen-meadow, Typical sub-community
M24c *Cirsio-Molinietum* fen-meadow, *Juncus-Erica* sub-community
CG2 *Festuca-Avenula* grassland
S2 *Cladietum* swamp
S25 *Phragmites-Eupatorium* fen
H4 *Ulex minor-Agrostis* heath

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extensive drainage of impeded soils in the British lowlands, either locally or as a result of major works which have lowered the water-table in whole catchments (as on the Little Ouse where the Thelnetham and Blo' Norton fens have been affected: Ratcliffe 1977). Such treatment tends to speed colonisation of any unreclaimed mire fragments by woody vegetation and has probably destroyed many stands of *Schoenetum* itself. Even where the community persists, it is often in the form of the impoverished *Festuca-Juncus* sub-community or transitions to rank Junco-Molinion vegetation. On its other boundary, where it grades on to drier soils, the community has suffered by assiduous agricultural improvement right up to spring and flush lines such that natural zonations are often truncated above, any remaining *Schoenetum* closely hemmed in by arable land or modified pasture. Eutrophication by fertiliser run-off or drift is a common danger to the community in such situations and, with enrichment of peats by drainage and surface oxidation, the vegetation is open to conversion to Filipendulion tall-herb communities, with the *Phragmites-Urtica* fen on any fragments of wetter soils.

With such complex modifications of the habitat of the *Schoenetum*, it is difficult to tell what the natural seral development of the community might be. Scattered saplings of *Alnus glutinosa*, *Betula pubescens* and *Salix cinerea* can sometimes be found in ungrazed stands (Wheeler 1975) and it is possible that mixed canopies of such species could come to dominate in some kind of *Salix-Betula-Phragmites* woodland over topogenous peats (Wheeler 1980*c*). Local development of ombrotrophic nuclei in such situations, or the formation of raised areas within soligenous mires, probably favours a spread of *Molinia* and preferential invasion by *B. pubescens* with the eventual formation of some type of *Betula-Molinia* woodland. *Schoenus* itself, of course, may play an important role in providing initial sites for the development of acidophilous elements in the flora but, although it can persist for a considerable time under shading branches, it quickly succumbs to the formation of a closed canopy.

**Distribution**

The *Schoenetum* is widespread but decidedly local throughout lowland England and Wales, being restricted by both the natural scarcity of suitable situations and extensive destruction of habitats. The *Caltha-Galium* sub-community is concentrated in East Anglia, the *Briza-Pinguicula* sub-community in Anglesey, where it represents a geographical transition to the *Pinguiculo-Caricetum* which replaces the *Schoenetum* in the submontane north-west. The *Festuca-Juncus* sub-community occurs throughout the range and in many much-modified sites is the only type of this mire represented.

**Affinities**

The *Schoenetum* as defined here includes most of the calcicolous mire vegetation from lowland Britain in which *Schoenus nigricans* plays a leading role, along with a variety of more Continental associates. It corresponds closely with Wheeler's (1975, 1980*b*) *Schoeno-Juncetum*, uniting his sub-associations into a smaller number of vegetation types and adding new data, particularly from more impoverished stands, like many of those in Ratcliffe & Hattey's (1982) survey of Welsh mires. Although the community has a unique combination of constants, many elements of its flora are species of wide ecological amplitude and the *Schoenetum* has strong affinities in a number of directions. Among other calcicolous mires, it grades through the *Briza-Pinguicula* sub-community to the *Pinguiculo-Caricetum*, and through the *Caltha-Galium* sub-community to the *Carex-Calliergon* mire; there are also clear overlaps, through the tall-herb element, with the Phragmitetalia fens. Even more obviously, the *Schoenetum* has a substantial component of Molinietalia herbs and throughout, but especially in the *Festuca-Juncus* sub-community, grades to Holco-Juncion fen-meadows.

In a broader phytosociological context, the community forms part of a series of *Schoenus*-dominated vegetation types that extends throughout the lowlands of western Europe and can be regarded as part of a compendious central and west European *Schoenetum nigricantis* (*sensu* Koch 1926, but not Tansley 1939). Within this association, regional variations have been recognised as geographical races (Koch 1926, Duvigneaud 1949), often upgraded as vicariants represented in Czechoslovakia (Klika 1929), Poland (Matuszkiewicz 1981), Germany (Tüxen 1937, Kloss 1965), The Netherlands (Westhoff & den Held 1969), Belgium (Duvigneaud & Vanden Berghen 1945, Vanden Berghen 1952), France (Allorge 1922, Lemée 1937) and Ireland (Braun-Blanquet & Tüxen 1952). In such a series, our *Schoenetum* falls between the communities described from France, where Atlantic species like *Anagallis tenella*, *Cirsium dissectum* and *Oenanthe lachenalii* occur along with a strong contingent of Continental plants, and the *Cirsio-Schoenetum* characterised from Ireland which tends towards the *Schoenus*-dominated stands in our *Pinguiculo-Caricetum*. Allorge (1922) and Lemée (1937) also include in their community some vegetation where *Schoenus* itself is more poorly represented, but where *J. subnodulosus* dominates the characteristic flora of the community, a phenomenon seen here in certain stands of our *Festuca-Juncus* sub-community. In a sense, however, the prominence of *J. subnodulosus* through much of the *Schoenus*-dominated vegetation of southern Britain is a fortuitous reflection of the particular situation in which many stands are found, in or close to wetter fen.

We have not therefore followed Wheeler (1975, 1980*b*) in diagnosing this community as synonymous with Allorge's (1922) *Schoeno-Juncetum*. The general balance of species in the associated flora of the *Schoenetum* in Britain places the community firmly among the Caricion davallianae mires.

## Floristic table M13

| | a | b | c | 13 |
|---|---|---|---|---|
| *Carex panicea* | V (3–4) | V (1–5) | V (1–4) | V (1–5) |
| *Juncus subnodulosus* | IV (1–4) | V (1–7) | V (1–7) | V (1–7) |
| *Schoenus nigricans* | IV (1–4) | V (1–7) | V (1–8) | V (1–8) |
| *Molinia caerulea* | IV (1–4) | V (1–7) | V (1–7) | V (1–7) |
| *Calliergon cuspidatum* | IV (1–4) | V (1–3) | V (1–5) | V (1–5) |
| *Succisa pratensis* | IV (1–3) | V (1–4) | IV (1–3) | IV (1–4) |
| *Potentilla erecta* | IV (1–3) | V (1–3) | IV (1–4) | IV (1–4) |
| *Campylium stellatum* | III (1–3) | V (1–4) | V (1–4) | IV (1–4) |
| *Angelica sylvestris* | II (1–3) | IV (1–3) | IV (1–3) | III (1–3) |
| *Cirsium palustre* | II (3) | IV (1–3) | IV (1–3) | III (1–3) |
| *Mentha aquatica* | II (1–3) | IV (1–3) | IV (1–3) | III (1–3) |
| *Epipactis palustris* | I (1–3) | III (1–3) | IV (1–3) | III (1–3) |
| *Phragmites australis* | II (1–3) | III (1–3) | IV (1–7) | III (1–7) |
| *Anagallis tenella* | | V (1–3) | IV (1–4) | III (1–4) |
| *Equisetum palustre* | II (1–3) | III (1–3) | IV (1–3) | III (1–3) |
| *Pedicularis palustris* | I (1–3) | IV (1–3) | III (1–3) | III (1–3) |
| *Drepanocladus revolvens* | I (1) | III (1–4) | III (1–5) | II (1–5) |
| *Fissidens adianthoides* | | III (1–3) | III (1–4) | II (1–4) |
| *Bryum pseudotriquetrum* | | II (1–3) | III (1–3) | II (1–3) |
| *Aneura pinguis* | | II (1–3) | III (1–3) | II (1–3) |
| *Sphagnum subnitens* | I (1–3) | II (1–4) | II (1–3) | II (1–4) |
| *Pellia endiviifolia* | | II (1–3) | II (1–3) | II (1–3) |
| *Ctenidium molluscum* | | II (1–6) | II (1–4) | II (1–6) |
| *Eriophorum latifolium* | | II (1–4) | II (1–4) | II (1–4) |
| *Anthoxanthum odoratum* | III (1–3) | III (1–3) | I (1–3) | III (1–3) |
| *Holcus lanatus* | III (1–3) | III (1–3) | I (1–3) | III (1–3) |
| *Festuca rubra* | III (3–4) | II (1–3) | I (1–3) | II (1–4) |
| *Juncus acutiflorus* | II (1–4) | | | I (1–4) |
| *Agrostis canina canina* | II (1–3) | | | I (1–3) |
| *Carex flacca* | III (2–4) | IV (1–3) | II (1–4) | III (1–4) |
| *Briza media* | | V (1–4) | II (1–3) | II (1–4) |
| *Dactylorhiza fuchsii* | | V (1–3) | II (1–3) | II (1–3) |
| *Cratoneuron commutatum* | I (1–3) | IV (1–4) | II (1–4) | II (1–4) |
| *Centaurea nigra* | I (1–3) | IV (1–3) | II (1–3) | II (1–3) |
| *Gymnadenia conopsea* | | IV (1–3) | II (1–4) | II (1–4) |
| *Parnassia palustris* | | IV (1–3) | II (1–3) | II (1–3) |
| *Pinguicula vulgaris* | | IV (1–4) | II (1–4) | II (1–4) |
| *Carex hostiana* | | IV (1–4) | I (1–3) | II (1–4) |
| *Serratula tinctoria* | | IV (1–3) | I (1–3) | II (1–3) |
| *Carex pulicaris* | | IV (1–3) | I (1–3) | II (1–3) |
| *Juncus articulatus* | | IV (1–4) | I (1–3) | II (1–4) |

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| | | | | |
|---|---|---|---|---|
| *Polygala vulgaris* | | IV (1–3) | | II (1–3) |
| *Agrostis stolonifera* | II (3–4) | III (1–3) | I (1–3) | II (1–4) |
| *Oenanthe lachenalii* | I (1) | III (1–3) | II (1–3) | II (1–3) |
| *Ranunculus flammula* | I (1–3) | III (1–3) | II (1–3) | II (1–3) |
| *Luzula multiflora* | I (1–2) | III (1–3) | I (1–3) | II (1–3) |
| *Danthonia decumbens* | I (2–3) | III (1–3) | | II (1–3) |
| *Dactylorhiza majalis purpurella* | | III (1–3) | I (1–3) | II (1–3) |
| *Linum catharticum* | | III (1–3) | I (1) | II (1–3) |
| *Trifolium pratense* | | III (1–3) | | I (1–3) |
| *Myrica gale* | II (1–4) | II (1–4) | | I (1–4) |
| *Calluna vulgaris* | | II (1–3) | I (1) | I (1–3) |
| *Triglochin palustris* | | II (1–3) | I (1–3) | I (1–3) |
| *Selaginella selaginoides* | | II (1–3) | I (1–3) | I (1–3) |
| *Hypericum pulchrum* | | II (1–3) | | I (1–3) |
| *Plantago maritima* | | II (1–4) | | I (1–4) |
| *Ophrys insectifera* | | II (1–3) | | I (1–3) |
| *Isolepis setacea* | | I (1–3) | | I (1–3) |
| *Eupatorium cannabinum* | II (1–3) | III (1–3) | V (1–4) | III (1–4) |
| *Valeriana dioica* | II (1–3) | II (1–3) | IV (1–3) | III (1–3) |
| *Filipendula ulmaria* | II (1–3) | II (1–3) | IV (1–3) | III (1–3) |
| *Galium uliginosum* | I (1–3) | II (1–3) | IV (1–3) | II (1–3) |
| *Caltha palustris* | I (1) | I (1–3) | IV (1–3) | II (1–3) |
| *Lychnis flos-cuculi* | I (2) | I (1) | III (1–3) | II (1–3) |
| *Pseudoscleropodium purum* | I (1–3) | I (1–3) | III (1–4) | II (1–4) |
| *Dactylorhiza incarnata* | | II (1–3) | III (1–4) | II (1–4) |
| *Dactylorhiza majalis praetermissa* | | I (1) | III (1–3) | II (1–3) |
| *Plagiomnium elatum* | | I (1) | III (1–3) | II (1–3) |
| *Vicia cracca* | | I (1–3) | III (1–3) | II (1–3) |
| *Menyanthes trifoliata* | I (1–3) | I (1) | II (1–4) | I (1–4) |
| *Eriophorum angustifolium* | | I (1–3) | II (1–3) | I (1–3) |
| *Plagiomnium rostratum* | | I (1) | II (1–3) | I (1–3) |
| *Carex elata* | | I (1) | II (1–4) | I (1–4) |
| *Rhizomnium punctatum* | | | II (1–3) | I (1–3) |
| *Carex diandra* | | | II (1–4) | I (1–4) |
| *Riccardia chamedryfolia* | | | II (1–3) | I (1–3) |
| *Philonotis calcarea* | | | II (1–3) | I (1–3) |
| *Riccardia multifida* | | | II (1–3) | I (1–3) |
| *Carex rostrata* | | | I (1–4) | I (1–4) |
| *Potamogeton coloratus* | | | I (1–3) | I (1–3) |
| *Utricularia* spp. | | | I (1–3) | I (1–3) |
| *Carex lepidocarpa* | III (2–3) | IV (1–4) | III (1–4) | III (1–4) |
| *Hydrocotyle vulgaris* | III (2–3) | II (1–3) | III (1–5) | III (1–5) |
| *Lotus uliginosus* | II (1–3) | III (1–3) | III (1–3) | III (1–3) |
| *Carex nigra* | II (1–3) | II (1–3) | II (1–4) | II (1–4) |
| *Erica tetralix* | II (1–3) | II (1–3) | I (1–3) | II (1–3) |
| *Lophocolea bidentata s.l.* | II (1–3) | I (1–3) | II (1–3) | II (1–3) |
| *Cardamine pratensis* | II (1–2) | I (1) | II (1–3) | II (1–3) |
| *Cladium mariscus* | II (1–4) | I (1–4) | II (1–7) | II (1–7) |
| *Ranunculus acris* | II (1–3) | II (1–3) | I (1–3) | II (1–3) |
| *Lythrum salicaria* | I (1) | II (1–3) | II (1–3) | II (1–3) |

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**Floristic table M13** *(cont.)*

| | a | b | c | 13 |
|---|---|---|---|---|
| *Cratoneuron filicinum* | I (1–3) | II (1–3) | II (1–4) | I (1–4) |
| *Cirsium dissectum* | I (1–3) | I (1–3) | II (1–3) | I (1–3) |
| *Epilobium palustre* | I (1–3) | I (1–3) | II (1–3) | I (1–3) |
| *Equisetum fluviatile* | I (1–4) | I (1) | II (1–3) | I (1–4) |
| *Leontodon taraxacoides* | I (1) | I (1–3) | I (1–3) | I (1–3) |
| *Aulacomnium palustre* | I (1–4) | I (1–3) | I (1–3) | I (1–4) |
| *Galium palustre* | I (1–2) | I (1) | I (1–3) | I (1–3) |
| *Valeriana officinalis* | I (2–3) | I (1) | I (1–3) | I (1–3) |
| *Brachythecium rutabulum* | I (1–3) | I (1) | I (1–3) | I (1–3) |
| *Euphrasia officinalis* agg. | | II (1–3) | I (1) | I (1–3) |
| *Lathyrus pratensis* | I (1–2) | | I (1–3) | I (1–3) |
| *Trifolium repens* | I (1–3) | I (1–3) | | I (1–3) |
| *Taraxacum officinale* agg. | | I (1–3) | I (1) | I (1–3) |
| *Eleocharis quinqueflora* | | I (1–3) | I (1–3) | I (1–3) |
| *Carex dioica* | | I (1) | I (1–3) | I (1–3) |
| *Hypericum tetrapterum* | | I (1–3) | I (1–3) | I (1–3) |
| *Dactylorhiza traunsteineri* | | I (1–3) | I (1–3) | I (1–3) |
| *Drosera rotundifolia* | | I (1–3) | I (1–3) | I (1–3) |
| Number of samples | 69 | 25 | 32 | 126 |
| Number of species/sample | 14 (7–27) | 45 (26–57) | 44 (30–65) | 27 (7–65) |

a *Festuca rubra-Juncus acutiflorus* sub-community
b *Briza media-Pinguicula vulgaris* sub-community
c *Caltha palustris-Galium uliginosum* sub-community
13 *Schoenetum nigricantis* (total)

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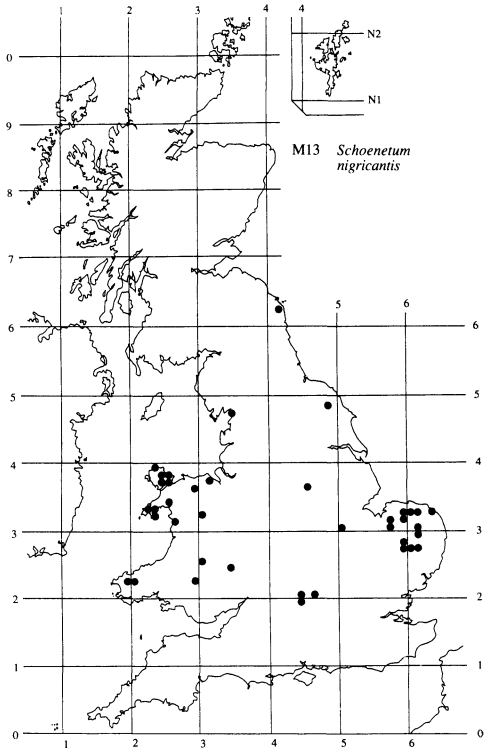


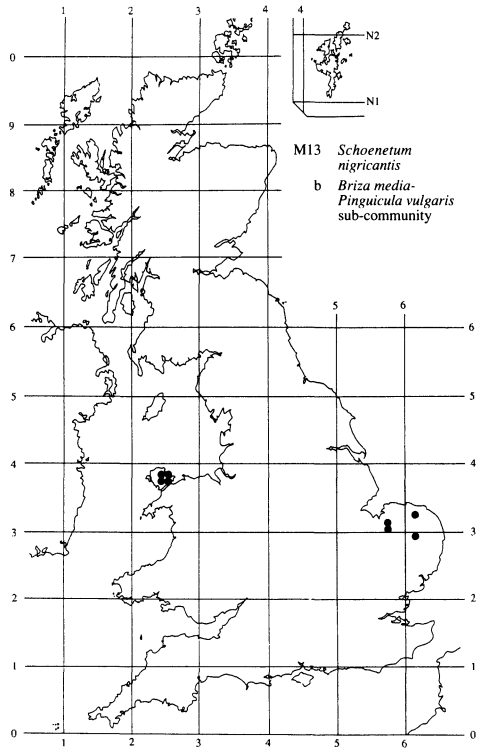


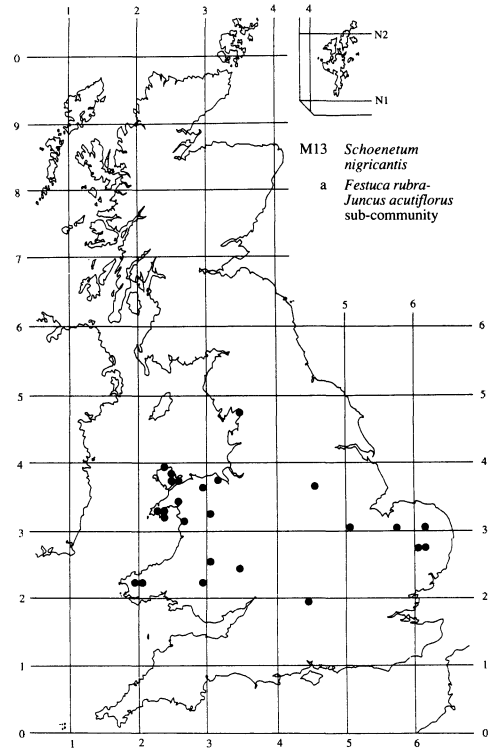


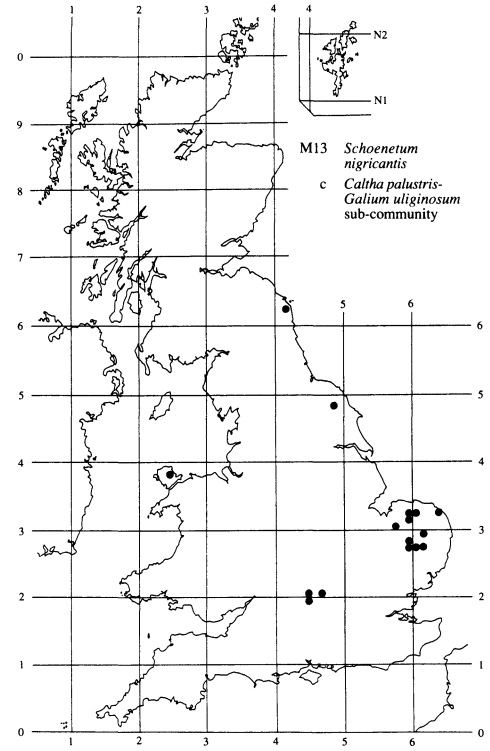


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