M5
Carex rostrata-Sphagnum squarrosum mire

Synonymy

Oxyphilous fen vegetation Pallis 1911, Godwin & Turner 1933, Tansley 1939 *p.p.*; *Carex rostrata-Acrocladium cordifolium/cuspidatum* sociation Spence 1964 *p.p.*; *Carex lasiocarpa-Myrica* & *Myrica-Carex lasiocarpa* sociations Spence 1964 *p.p.*; *Carex nigra-Acrocladium* sociation Spence 1964 *p.p.*; *Carex rostrata-Aulacomnium palustre* Association Birks 1973; Poor fen communities Proctor 1974 *p.p.*; General fen Adam *et al.* 1975 *p.p.*; *Carex curta-Carex rostrata* community Wheeler 1978; *Caricetum lasiocarpae* Koch 1926 *sensu* Birse 1980 *p.p.*

Constant species

Carex nigra, *C. rostrata*, *Eriophorum angustifolium*, *Potentilla palustris*, *Succisa pratensis*, *Aulacomnium palustre*, *Sphagnum squarrosum*.

Physiognomy

The *Carex rostrata-Sphagnum squarrosum* mire is a fairly heterogenous vegetation type characterised overall by the dominance of sedges with scattered poor-fen herbs over a patchy carpet of moderately base-tolerant Sphagna. The sedge cover is usually a few decimetres tall but quite variable in its abundance. The commonest species throughout are *Carex rostrata* and *C. nigra*, the former generally the more extensive and sometimes with a dense cover, the latter typically less abundant, though locally dominant, as in some stands of the *Carex nigra-Acrocladium* sociation described from Scottish lochs by Spence (1964) and in some of the Malham Tarn fens in North Yorkshire (Proctor 1974). *C. lasiocarpa* extends its occurrence among British mires into this kind of vegetation and it too can attain local prominence, so much so that stands which, on general grounds, clearly belong here have sometimes been included in distinct communities characterised by this sedge: e.g. the *Carex lasiocarpa* sociations of Spence (1964) and the *Caricetum lasiocarpae* (Koch 1926) of Birse (1980). *C. curta*, though generally more characteristic of oligotrophic and base-poor Rhynchosporion pools, is occasionally found (Spence 1964, Birks 1973, Wheeler 1978 who diagnosed a *Carex curta-Carex rostrata* community from the Ant valley in Norfolk) but *C. limosa* is typically absent. Likewise, towards the other extreme, *C. diandra* does not penetrate into this community: it is a good diagnostic species for the closely-related *Carex rostrata-Calliergon* mire. Finally, there may be a little *C. echinata*, especially where the *Carex-Sphagnum squarrosum* mire extends on to firmer flushed peats.

Other vascular plants vary in their prominence and are often limited to scattered individuals but the most frequent species overall are *Potentilla palustris*, *Eriophorum angustifolium*, *Menyanthes trifoliata*, *Galium palustre* and such typical poor-fen herbs as *Succisa pratensis*, *Viola palustris*, *Ranunculus flammula*, *Epilobium palustre* and *Lychnis flos-cuculi* with, rather less commonly, *Equisetum palustre*, *Agrostis canina* ssp. *canina*, *Mentha aquatica*, *Myosotis scorpioides*, *Caltha palustris*, *Filipendula ulmaria* and *Cardamine pratensis*. Very much the same suite of species occurs in a variety of other mire types, notably the *Potentillo-Caricetum rostratae* and the *Carex-Calliergon* mire, in close spatial association with which the *Carex-Sphagnum squarrosum* community is often found. Transitional stands, where there is a strong continuity in this layer of the vegetation, can thus often be found.

The community also encompasses a number of particular lines of floristic variation in this vascular component which, with further sampling, might form the basis of distinct sub-communities but which, in the available data, present the appearance of a continuum within the overall definition. In some stands, for example, the representation of all the herbaceous associates is very poor, such that, with a cover of sedges, there may be just a few plants of *Potentilla palustris* and *Menyanthes*, when the vegetation takes on much of the character of the *Carex rostrata-Sphagnum recurvum* mire or even a *Caricetum rostratae* swamp: *Carex curta* seems to be particularly associated with this kind of transitional

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vegetation (e.g. Birse 1980). In other cases, *Juncus effusus* which is quite frequent here, though usually of low cover, can become prominent, suggestive of some kinds of rush-dominated *Carex echinata-Sphagnum* mire. Then, there are stands in which *Molinia caerulea* and/or *Myrica gale* have local abundance and it is in such situations that *Carex lasiocarpa* seems to be best represented (e.g. Spence 1964, Birse 1980). Finally, on rare occasions, *Phragmites australis* can be patchily abundant with a prominent contingent of poor-fen herbs in vegetation that resembles reed-dominated *Potentillo-Caricetum*.

Throughout the community, even in these transitional stands, the bryophyte carpet helps define the *Carex-Sphagnum squarrosum* mire against the closely-related vegetation types. Sphagna are usually at least patchily prominent but, though the more strictly aquatic and oligotrophic Rhynchosporion species, *S. cuspidatum* and *S. auriculatum*, can occasionally be found here, they are eclipsed by the more broadly-tolerant *S. recurvum*, the more mesotrophic *S. palustre* and, especially distinctive, the mildly base-tolerant *S. squarrosum* and *S. teres*. There can also be a little *S. subnitens* or *S. fimbriatum*. The species-balance in this assemblage, which forms discrete small domes over the ground or sometimes an extensive carpet, is thus quite different from that in the *Carex rostrata-Sphagnum recurvum* mire. Towards the other extreme, *S. contortum*, the most base-tolerant of the Sphagna, is typically rare here: this species has its major locus in the more calcicolous *Carex-Calliergon* mire. And, though *S. warnstorfii* is sometimes recorded where it descends to lower altitudes in north-west Scotland (as in Skye samples: Birks 1973), this species is much more diagnostic of the montane counterpart of the *Carex-Sphagnum squarrosum* mire, the *Carex-Sphagnum warnstorfii* mire.

Some other bryophytes occur commonly and together help confirm the distinctive character of this element of the vegetation. *Aulacomnium palustre*, though it has a fairly wide distribution through the Caricion nigrae mires, is a good diagnostic species of the particular range of variation encompassed by this community and the *Carex-Sphagnum warnstorfii* mire. *Calliergon stramineum* has a rather similar amplitude and here it is as common as, and much more characteristic than, the broadly-tolerant *C. cuspidatum*. Conditions may be sufficiently base-rich here for *C. trifarium* and *C. sarmentosum* though these are essentially species of montane flushes in Britain. More noticeable is the absence of *C. giganteum* and *C. cordifolium* which are such a distinctive feature of some kinds of *Carex-Calliergon* mire and the *Potentillo-Caricetum*. Other obvious absentees along this boundary of the *Carex-Sphagnum squarrosum* mire are larger Mniaceae, like *Plagiomnium rostratum* and *Rhizomnium pseudopunctatum*, and the 'brown mosses', *Campylium stellatum*, *Cratoneuron commutatum*, *Scorpidium scorpioides* and *Drepanocladus revolvens*, so characteristic of more calcicolous sedge-rich mires. Towards the transition to more oligotrophic and base-poor mires, it is noticeable that *Polytrichum commune* is of reduced frequency here.

Habitat

The *Carex-Sphagnum squarrosum* mire is typically found as a floating raft or on soft, spongy peats in topogenous mires and soligenous sites with midly acid, only moderately calcareous and rather nutrient-poor waters. In normal circumstances, the ground surface is kept very moist, though it can become periodically dry and this may permit access to grazing animals and damage by burning.

Among the range of vegetation types in which *Carex rostrata* plays a prominent role, differences in base-status, cation and nutrient content of the substrates and waters are probably of major importance in influencing which particular community develops once the limit of very swampy conditions has been passed. As yet, we do not know very much about how these variables work but what little information there is suggests that the controlling balances might be quite delicate, that the different factors operate in complex interactions and perhaps affect the various structural elements of the vegetation, the bryophyte carpet, the sedge canopy and the herbaceous associates, in only a crudely congruent fashion. It is thus very difficult to provide precise and absolute limits to the kind of mire environment in which the *Carex-Sphagnum squarrosum* community might be found: all that can be done is to indicate its relative position along continuous scales of variation in these factors with some crude thresholds. In general terms, its environmental preferences lie between those of the poor-fen *Carex rostrata-Sphagnum recurvum* mire on the one hand and the rich fen *Carex-Calliergon* mire and *Potentillo-Caricetum* on the other. In the former, where *C. rostrata* is dominant over a ground that has much in common with Rhynchosporion vegetation, the base-status is around pH4; in the latter two communities, where more calcicolous assemblages are characteristic, it is often above pH6, with the *Carex-Sphagnum squarrosum* mire spanning the range between. In this community, dissolved calcium levels are usually of the order 5–15 mg l^{-1} (Proctor 1974) whereas, in the *C. rostrata* rich fens, they are generally higher, sometimes much higher, attaining 50 mg l^{-1} or more (Spence 1964, Proctor 1974, Wheeler 1983). In terms of trophic levels, the substrates and waters of the *Carex-Sphagnum squarrosum* mire are probably richer than those of the *Carex rostrata-Sphagnum recurvum* mire, though perhaps not substantially poorer than those of the *Carex-Calliergon*

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mire or some kinds of *Potentillo-Caricetum* (Proctor 1974).

As might be expected, the *Carex-Sphagnum squarrosum* mire is most commonly found in mire systems where the waters are of generally intermediate quality throughout or in situations where one or other of the extremes in environmental variation is locally ameliorated. Two particular habitat types are especially characteristic. Of the former kind are open water transitions or flood-plain mires around lakes or pools fed by only moderately oligotrophic or mesotrophic waters and where the base-status and cation content are fairly low. Such sites are particularly associated with catchments where slates, shales and some kinds of schist predominate and include many of the Scottish localities of the community described by Spence (1964), Birks (1973) and Birse (1980), where the *Carex-Sphagnum squarrosum* mire forms a fairly widespread component of swamp and fen sequences, often developed as floating mats. In some situations of this kind, fluctuations in the water-table may mediate supplies of bases and nutrients to the fen raft and it is possible that the community marks out areas which have become a little elevated above the limit of frequent inundation: this seems to be the case at Crag Lough in Northumberland where Lock & Rodwell (1981) described distinct discs of the *Carex-Sphagnum squarrosum* mire within a tract of the *Potentillo-Caricetum*. Similar oligotrophic nuclei have been reported from the rich-fen systems of lowland Britain (e.g. Pallis 1911, Godwin & Turner 1933, Tansley 1939) though this particular community is rather rare within *Phragmites*-dominated fens.

The other characteristic situation where the *Carex-Sphagnum squarrosum* mire is found is where soligenous influx ameliorates a more extreme mire environment, usually around raised or basin mires but sometimes along the margins of flood-plain mires. By and large, it is seepage of base-rich and calcareous waters which modifies a predominantly oligotrophic and base-poor mire system, a pattern very well seen at Malham Tarn, where a series of springs emerges from surrounding Carboniferous Limestone to feed a soligenous fen complex in the lagg of the raised Tarn Moss (Sinker 1960, Proctor 1974, Adam *et al.* 1975). In this and other analogous sites, the community forms part of the complex transition zone between ombrogenous bog and calcicolous rich-fen, the proportions of the different vegetation types depending on distance from water source and the pattern of drainage and flooding. Much less common is the situation where base-poor waters seep into more calcareous mires, but Wheeler (1978) reported the community from the Ant valley in Norfolk where there was some soligenous influence from nutrient-poor, decalcified brick earth along the margin of the flood-plain.

In both these kinds of habitat, the water-table is typically very close to the surface for much of the year, with perhaps some modest flooding of the bryophyte mat when heavy rain works its way through into basins (e.g Lock & Rodwell 1981) or, more frequently, in winter. Quite commonly, the vegetation occurs as a floating mat bound together below by the robust rhizomes of *Carex rostrata*, *Potentilla palustris* and *Menyanthes*, which can grow very vigorously in the aquatic environment, and then the raft may rise and fall with the fluctuations in water-level, a feature which may be of some significance where the *Carex-Sphagnum squarrosum* mire develops in more mesotrophic situations. Even where the substrates are continuous, the peat is often very soft, sometimes sloppy, which gives the vegetation a measure of protection against the trampling and grazing effects of larger herbivores where stands occur in pastoral landscapes. Where the community runs on to firmer peats around the margins of lakes and basins, it tends to pass to the *Carex echinata-Sphagnum* mire and, where herbivores have access to such transitions, their grazing may favour the spread of *Juncus effusus* throughout the transition.

Zonation and succession

The *Carex-Sphagnum squarrosum* mire is characteristically found in zonations and mosaics related to variation in water-level, base-status, cation and nutrient content of the waters and substrates. Such patterns can reflect a process of succession but many seem to be static at the present time.

The simplest sequences are seen in open-water transitions like those described from Scottish lakes by Spence (1964) where the community typically occurs behind a front of the *Caricetum rostratae* (sometimes with *C. lasiocarpa* locally prominent) or the *Equisetetum fluviatile*, with the *Phragmitetum* sometimes represented as a bank of reed beyond the other swamps or on the transition to the mineral soils around the basin. At scattered localities, the *Caricetum vesicariae* is part of such zonations and the whole sequence may be terminated to the landward side by the *Phalaridetum*. Sometimes, the *Carex-Sphagnum squarrosum* mire is an extensive component of the middle portion of these patterns, in other cases it is but a local patchy development within tracts of the *Potentillo-Caricetum*, perhaps representing more oligotrophic nuclei.

Much more complex mosaics are characteristic of those sites where the *Carex-Sphagnum squarrosum* mire occurs as part of soligenous sequences. Here, below springs and around tortuous seepage lines and streams, it can form part of a perplexing mixture of poor and rich fens, notably with the *Potentillo-Caricetum* and the *Carex-Calliergon* mires, with the *Pinguiculo-Caricetum* on more solid base-rich peats and peaty gleys around, and Filipendulion vegetation on mesotrophic alluvium, the whole closely hemmed in by Ericion tetralicis and Erico-Sphagnion vegetation on the ombrogenous deposits above the lagg. As Proctor (1974) showed at Malham Tarn, such patterns have a clear underlying structure in relation to the environmental variables discussed earlier, even though its expression at particular sites can present a superficial picture of great confusion.

Further studies of this kind are needed to give a precise indication of what conditions control the development of this or that kind of poor or rich fen and how the general process of terrestrialisation interacts with the differentiation of flushed and leached areas within mire complexes. We may then be able to see where the *Carex-Sphagnum squarrosum* community fits in successional sequences. In the kinds of mires in which it occurs, two lines of seral development seem possible. In more base-rich complexes, the community is often found in close juxtaposition with the *Salix pentandra-Carex rostrata* woodland, the field layer of which has much in common with this kind of mire (Proctor 1974, Adam *et al.* 1975, Lock & Rodwell 1981) and which, at Crag Lough, seems certainly to have developed from a mosaic of the *Carex-Sphagnum squarrosum* mire and the *Potentillo-Caricetum* with release from grazing (Lock & Rodwell 1981). Where the balance is tipped towards the more base-poor and oligotrophic side, it is possible that some kinds of *Betula-Molinia* woodland (the *Sphagnum* or *Juncus effusus* sub-communities, for example) are a natural successor. The *Carex-Sphagnum squarrosum* mire may itself play an important part in the differentiation of more oligotrophic nuclei that are preferentially invaded by *Betula pubescens*, though this line of development is probably greatly speeded where mires are drained but not subject to too much surface disturbance and eutrophication of the peats. Such successions can be seen locally in lowland flood-plain mires, where different mire and woodland types are involved (Wheeler 1978, 1980*c*) and seem to have been extensive in the past (e.g. Walker 1970), though, at the present time, many zonations in which the *Carex-Sphagnum squarrosum* mire is found look to be more or less stable.

Distribution

The community has a widespread but fairly local distribution mainly in the north-western parts of Britain, probably a reflection more of the survival of suitable sites than of any strict association with the sub-montane environment. It was probably once much more widespread in the lowland south and east where relic stands are likely to occur more widely than the map suggests.

Affinities

The varied and transitional floristic character of the *Carex-Sphagnum squarrosum* mire means that it has sometimes been considered part of more broadly-defined communities (as in some of Spence's (1964) sociations and the 'general fen' of Adam *et al.* (1975)) or placed in fairly heterogeneous vegetation types based on the dominance of particular species, e.g. *Carex lasiocarpa* (Spence 1964, Birse 1980). It clearly belongs among the poor fens of the Caricion nigrae, though its affinities are diverse and multi-directional. First and foremost, it occupies a median position in the sequence of communities ranging from the oligotrophic and calcifuge vegetation of the *Carex-Sphagnum recurvum* mire to the calcicolous rich fens of the Caricion davallianae, like the *Carex-Calliergon* mire. Second, within this middle range, it is closely related to the *Carex-Sphagnum warnstorfii* mire, which can be seen essentially as its montane replacement. Third, it grades to the *Carex echinata-Sphagnum* mire, the typical Caricion nigrae community of shallower, firmer peats with pronounced lateral water movement, and also to the fens and swamps of the Phragmitetea where the *Potentillo-Caricetum* and the *Caricetum rostratae* continue the floristic line into open-water transitions. It seems to have no close equivalent among the mire types of Dierssen (1982).

Floristic table M5

Carex rostrata	V (4–8)	*Sphagnum palustre*	III (1–7)
Potentilla palustris	V (1–9)	*Menyanthes trifoliata*	III (1–6)
Aulacomnium palustre	IV (1–6)	*Calliergon cuspidatum*	III (2–4)
Carex nigra	IV (1–5)	*Ranunculus flammula*	III (1–4)
Eriophorum angustifolium	IV (1–4)	*Epilobium palustre*	III (2–4)
Succisa pratensis	IV (1–5)	*Calliergon stramineum*	III (2–5)
Sphagnum squarrosum	IV (7–9)	*Juncus effusus*	III (1–6)
Galium palustre	III (2–4)	*Phragmites australis*	II (2–5)
Sphagnum recurvum	III (1–6)	*Lychnis flos-cuculi*	II (1–3)
Viola palustris	III (1–4)	*Polytrichum commune*	II (1–5)

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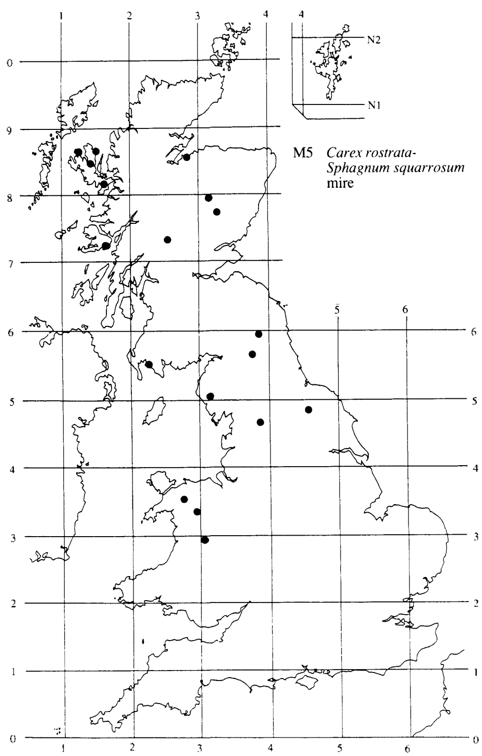
Sphagnum teres	II (2–9)
Carex echinata	II (2–4)
Equisetum palustre	II (1–5)
Molinia caerulea	II (1–4)
Agrostis canina canina	II (2–6)
Mentha aquatica	II (1–4)
Myosotis scorpioides	II (1–2)
Rumex acetosa	II (1–3)
Deschampsia flexuosa	II (1)
Caltha palustris	II (3–6)
Filipendula ulmaria	II (2–5)
Sphagnum subnitens	II (4–5)
Cardamine pratensis	II (1–3)
Sphagnum fimbriatum	I (5)
Equisetum fluviatile	I (1–2)
Rhizomnium pseudopunctatum	I (2–3)
Juncus bulbosus/kochii	I (2)
Cirsium palustre	I (1–3)
Bryum pseudotriquetrum	I (1–2)
Sphagnum contortum	I (2–3)
Carex curta	I (2)
Hydrocotyle vulgaris	I (4–8)
Juncus acutiflorus	I (1–3)
Holcus lanatus	I (3–4)
Chiloscyphus polyanthos	I (1–2)
Stellaria alsine	I (1–2)
Plagiomnium rostratum	I (1–2)
Luzula multiflora	I (1–3)
Juncus articulatus	I (1–3)
Rhytidiadelphus squarrosus	I (2–3)
Number of samples	22
Number of species/sample	17 (10–26)
Herb height (cm)	47 (20–80)
Herb cover (%)	63 (40–80)
Bryophyte height (mm)	55 (5–200)
Bryophyte cover (%)	77 (40–100)
Altitude (m)	327 (61–823)
Soil pH	4.8 (4.4–5.2)



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