S27

Carex rostrata-Potentilla palustris tall-herb fen *Potentillo-Caricetum rostratae* Wheeler 1980*a*

Synonymy

Caricetum rostratae Rübel 1912 *p.p.*; *Caricetum acuto-vesicariae comaretosum* Passarge 1955; *Carex rostrata* nodum Daniels 1978 *p.p.*

Constant species

Carex rostrata, *Galium palustre*, *Menyanthes trifoliata*, *Potentilla palustris*, *Calliergon cordifolium/cuspidatum/giganteum*.

Rare species

Carex appropinquata, *C. aquatilis*, *C. diandra*, *Lysimachia thyrsiflora*, *Peucedanum palustre*, *Sium latifolium*.

Physiognomy

The *Potentillo-Caricetum rostratae* comprises generally rather species-poor but somewhat varied mixtures of monocotyledons and herbaceous dicotyledons, sometimes developed as a floating mat. Among the monocotyledons, *Carex rostrata* is the most frequent species throughout but other sedges, such as *C. vesicaria*, *C. nigra*, *C. elata* and, more rarely, *C. aquatilis* and *C. appropinquata*, or *Eriophorum angustifolium* may each on occasion replace it as the dominant. In other cases, *Phragmites australis* or, less frequently, *Juncus effusus* or *J. acutiflorus* may dominate (see Sub-communities below).

A consistent feature of the community, however, is the presence of *Potentilla palustris* and *Menyanthes trifoliata* as an open or closed carpet beneath these usually taller species. They can occur in intimate mixtures or as patchy mosaics in which clumps of either attain local dominance and, scattered amongst them, is a variety of herbs, most commonly *Galium palustre* (which can sprawl extensively), *Cardamine pratensis*, *Epilobium palustre*, *Mentha aquatica*, *Myosotis laxa* ssp. *caespitosa*, *Caltha palustris*, *Hydrocotyle vulgaris* and *Veronica scutellata*. Taller species, such as *Angelica sylvestris*, *Cirsium palustre* and *Valeriana officinalis*, are sometimes conspicuous and there is a much greater variety of these in one of the sub-communities. In wetter places, *Equisetum fluviatile* may be abundant and, here too, there may be scattered clumps of *Sparganium erectum* or *Typha latifolia*. *Agrostis stolonifera* with, less frequently, some *A. canina* ssp. *canina* and *Poa trivialis*, can form extensive and thick carpets, sometimes semi-submerged.

Almost always, one or more of the larger *Calliergon* spp., *C. cuspidatum*, *C. cordifolium* and *C. giganteum*, occur and these may form conspicuous patches over the mass of interweaving rhizomes and litter. No other bryophytes are frequent throughout but individual stands may have some *Sphagnum squarrosum* or *S. fimbriatum* or other locally abundant species.

Sub-communities

***Carex rostrata-Equisetum fluviatile* sub-community:** Herbaceous Marsh Matthews 1914 *p.p.*; Mixed Fen Holdgate 1955*b* *p.p.*; Rich fen Sinker 1960 *p.p.*; *Carex rostrata-Acrocladium cordifolium/cuspidatum*, *Potentilla-Acrocladium cordifolium* and *Equisetum fluviatile-Acrocladium cordifolium* sociations Spence 1964; *Potentilla-Acrocladium* nodum Proctor 1974 *p.p.*; 'General Fen' Adam *et al.* 1975 *p.p.*; *Potentillo-Caricetum rostratae typicum* Wheeler 1980*a*; *Potentillo-Caricetum rostratae*, *Lemna minor* variant and Typical variant *p.p.* Ratcliffe & Hattey 1982; includes *Caricetum vesicariae* Br.-Bl. & Denis 1926 and *Lysimachio-Caricetum aquatilis* Neumann 1957 *sensu* Birse 1980. Here are included more species-poor stands in which *C. rostrata* is generally the most abundant monocotyledon forming a thin to dense cover of shoots 30–70 cm tall. In some stands, however, *C. vesicaria* or *C. aquatilis* can dominate and, on occasion, *P. palustris*, *M. trifoliata* or *E. fluviatile* (which is preferential for this sub-community) can be locally abundant. Such vegetation can have a semi-swampy appearance or develop as a floating mat and in areas of open water there may be some *Lemna minor* and various small herbs of water margins, such as

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Veronica beccabunga or *Apium nodiflorum*. In other cases, *Juncus acutiflorus* or *J. effusus* may dominate. As well as the large *Calliergon* spp., there is sometimes an abundance of *Brachythecium rutabulum*, *B. rivulare*, *Rhizomnium punctatum* or *R. pseudopunctatum*. Among rare species recorded here are *Carex diandra*, *C. appropinquata* and *Lysimachia thyrsiflora*.

***Lysimachia vulgaris* sub-community:** *Carex elata* consocies and Mixed fen associes Pearsall 1918 *p.p.*; *Potentillo-Caricetum rostratae lysimachietosum* Wheeler 1980*a*. *C. rostrata* remains constant here and is sometimes abundant but, more usually, the dominant is *Phragmites*, forming a tall open canopy, *Carex elata* or *C. nigra*, the latter usually in a robust tussocky form (Wheeler 1980*a*, 1982; Jermy *et al.* 1982), *Juncus effusus* or *Eriophorum angustifolium*. Beneath and around these, *P. palustris* and *M. trifoliata* remain prominent with their scatter of small herbs but this sub-community is marked by the high frequency and sometimes the abundance of tall dicotyledons more usually associated with rich-fen vegetation: *Lysimachia vulgaris*, *Lythrum salicaria*, *Peucedanum palustre*, *Lycopus europaeus*, *Lychnis flos-cuculi*, *Ranunculus lingua*, *Rumex hydrolapathum*, *Sium latifolium* and *Iris pseudacorus*. There is also often some *Juncus subnodulosus* and *Campylium stellatum* is a frequent component of the bryophyte layer.

Habitat

The *Potentillo-Caricetum* is most characteristic of peaty soils kept moist by mesotrophic to oligotrophic, neutral to moderately base-rich and calcareous waters. Conditions seem rarely to be stagnant. Although the community is most frequent in topogenous mires, occurring in open-water transitions and basin mires, stands commonly experience some unseasonal flooding and the community seems best developed around areas of diffuse lateral water flow near gentle inflow and outflow streams. It is also found in more obviously soligenous situations: where, for example, throughput ameliorates ombrotrophic conditions around and within some raised mires. It is a primary fen community, although it is sometimes maintained by grazing.

The soil is usually a raw peat or humic gley with a surface or water pH between 5 and 7 and dissolved calcium levels of 10–90 mg l^{-1} (Holdgate 1955*b*, Sinker 1960, Spence 1964, Proctor 1974, Wheeler 1983). The water-table, even in dry weather, is probably at or just below the surface for much of the time (Matthews 1914, Pearsall 1918, Holdgate 1955*b*, Spence 1964). In the growing season, the vegetation is thus kept sufficiently moist but free of lengthy inundation for the characteristic carpet of larger *Calliergon* spp. to develop (Clapham 1940, Segal 1966). The growth of the robust, creeping rhizomes of the understorey of *Potentilla palustris* and *Menyanthes trifoliata* and the accumulation of litter probably play an important role in raising the substrate surface to this level (Matthews 1914, Hewett 1964) and the moss carpet itself may contribute to peat formation and provide a place where smaller herbaceous species can gain a hold (Matthews 1914, Clapham 1940).

Conditions remain, however, sufficiently base-rich and calcareous to inhibit the development of ombrotrophic nuclei and the formation of a *Sphagnum* carpet such as is typical of the rather similar vegetation of the *Carex rostrata-Sphagnum squarrosum* mire. The brief periods of unseasonal flooding characteristic of many basin mires and even moderately large lakes around which the community occurs may be important here. To the north and west, where the *Potentillo-Caricetum* is most widespread, heavy summer rains can produce sudden, sometimes marked, but usually short-lived changes in water-level in such sites (e.g. Holdgate 1955*b*, Proctor 1974, Wheeler 1980*d*, Lock & Rodwell 1981). Even in summer, stands can be encountered with water-tables at any level from almost 40 cm below the surface to more than 10 cm above (Matthews 1914, Pearsall 1918, Holdgate 1955*b*, Spence 1964). In some cases, the vegetation can develop as a floating raft of interweaving rhizomes up to 50 cm thick over peaty or silty ooze and this may rise and fall somewhat with any changes in water-level (Lock & Rodwell 1981) but, even where the vegetation is rooted in a solid substrate, it seems tolerant of this kind of inundation. The atypical tussock form of *Carex nigra*, characteristic of some stands of the community, may indeed be a response to strong fluctuations in water-level (Wheeler 1980*a*, *d*).

Differences in the balance between nutrient levels, base-richness and calcium content may play some part in influencing the floristic variation between the sub-communities. The *Carex-Equisetum* sub-community is found over the full extent of the pH and calcium content ranges, sometimes in quite mesotrophic mires. It is especially characteristic of open-water transitions around more nutrient-rich lakes to the north and west where base-status and calcium content can be low (Spence 1964) but it also occurs in more base-rich and calcareous basin mires which can be quite oligotrophic (Proctor 1974). The *Lysimachia* sub-community is more strictly confined to this latter site type, occurring, for example, in mires developed in hollows in glacial drift, but it is sometimes found in open-water transitions (e.g. Pearsall 1918) and in artificial hollows (such as peat cuttings or duck decoy pools) in flood-plain mires (Wheeler 1980*a*, 1983). It is also more eastern in its distribution and climate may play some part in its floristic composition.

More accessible stands of the *Potentillo-Caricetum* are often grazed by stock which can eat shrub and tree

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seedlings and which perhaps favour the dominance of *Juncus* spp. that is a marked feature in some places.

Zonation and succession

In more extensive and undisturbed open-water transitions, the *Carex-Equisetum* sub-community (and, rarely the *Lysimachia* sub-community) occurs as part of complete zonations between submerged aquatic vegetation and woodland. Around lakes and some larger basin mires, it is generally fronted by a zone of the *Caricetum rostratae*, the *Equisetetum fluviatile* or, at scattered localities, especially in Scotland, by the *Caricetum vesicariae*. Boundaries between these swamps and the *Potentillo-Caricetum* are often very hazy with a gradual increase in shallower water in *Potentilla palustris* and *Menyanthes trifoliata* and a continuing prominence of the swamp dominants within the fen. In other cases, virtually pure stands of *P. palustris* or *M. trifoliata* themselves may extend out into open water in front of the community (Matthews 1914, Spence 1964, Birse 1980, Lock & Rodwell 1981). At some sites, a belt of the *Phragmitetum* forms a more abrupt outer edge to the *Potentillo-Caricetum* (e.g. Pearsall 1918, Lock & Rodwell 1981).

On drier ground, the community may grade, through an open scatter of *Salix cinerea* bushes, to the *Salix-Carex rostrata* woodland in which some important *Potentillo-Caricetum* species remain as part of the understorey. There is little doubt that such sequences represent a natural succession around more mesotrophic, sometimes base-rich and calcareous lakes and basins to the north and west. At Esthwaite Fen in Cumbria, it has been shown how the *Potentillo-Caricetum* has extended out behind a front of the *Phragmitetum* and been colonised from behind by *S. cinerea* over the past seventy years (Pearsall 1918, Tansley 1939, Pigott & Wilson 1978) and Lock & Rodwell (1981) adduced photographic evidence to support a similar succession at Crag Lough in Northumberland. Spence (1964) described a replacement of *Caricetum rostratae* by the *Potentillo-Caricetum* over fifty years on the shores of Loch Ness in Inverness, although at other sites there has been no perceptible change in the extent of these two communities. The levels of nutrients may play some part in influencing the rate of forward advance of the fen mat in such situations.

Two things confuse this basic pattern of zonation and succession. The first is grazing, which can set back shrub and tree invasion where stock have access to the community. The effect of this is starkly visible at Crag Lough where a fence marks a sharp boundary between open *Potentillo-Caricetum* and closed *Salix-Carex* woodland. Grazing may also blur the boundary between the fen vegetation on the mire surface itself and that on the mineral or peaty soils surrounding it. Even where there is no woodland fringe to the community, this junction may be marked by a zone of Filipendulion vegetation, the *Holco-Juncetum* or the *Phalaridetum arundinaceae* at the limit of inundation or ground-water gleying. Where such margins are grazed, there tends to be a much more gradual transition from rush-pasture or fen-meadow communities to the *Potentillo-Caricetum* (e.g. Ratcliffe & Hattey 1982).

The second feature, which has more complex results, is the variation in base-status, calcium content and nutrient levels that is very characteristic of soligenous areas in basins and around some raised mires. Such differences, which can be very marked over even short distances, are partly a function of distance from springs, seepage lines or streams but they can also be affected by ground-water fluctuations. The *Potentillo-Caricetum* is often found in places where it is difficult to separate the influence of soligenous, topogenous and ombrogenous effects and it frequently forms part of intricate mosaics with other mire communities. Particularly striking examples have been described from Sunbiggin Tarn in Cumbria (Holdgate 1955*b*) and Malham Tarn, North Yorkshire (Sinker 1960, Proctor 1974, Adam *et al.* 1975). Here, around the weaving inflow streams, the community occurs intimately mixed with the *Carex rostrata-Calliergon* fen in a baffling jumble of local differences in bryophyte distribution and dominance by a variety of Carices. The vagaries of dispersal and establishment may play some part in determining such patterns but they are probably also influenced by differences in water chemistry, although these have not been isolated (Proctor 1974, Wheeler 1980*a*, *b*, 1983). In such sites as these, there may also be more obvious zonations between either or both these fens and the *Pinguiculo-Caricetum dioicae* around highly calcareous springs and to Filipendulion vegetation along junctions with unflushed mineral soils or where banks of alluvium have been deposited by moving waters. A patchy development of the *Salix-Carex* woodland may add to the complexity.

In less base-rich and calcareous mires, the *Potentillo-Caricetum* may occur in mosaics with poor-fen vegetation. Small patches of *Sphagnum squarrosum* and *S. fimbriatum* are sometimes found within stands of the community, where, for example, the surfaces of floating rafts are maintained at a high enough level to be free of frequent inundation (Wheeler 1980*a*, *d*; Lock & Rodwell 1981). Where such patches coalesce, other Sphagna, such as *S. palustre*, *S. recurvum* and *S. teres*, and *Aulacomnium palustre* may appear and *Calliergon stramineum* replace *C. giganteum* and *C. cordifolium*. Such changes mark a transition to the *Carex rostrata-Sphagnum squarrosum* community. In other places, the fading of any nutrient enrichment in the water flowing into basin or around raised mires is accompanied by a

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gradation from the *Potentillo-Caricetum* to the much less species-rich *Carex rostrata-Sphagnum recurvum* mire, which has but scattered plants of *M. trifoliata* and *P. palustris* and a very poor representation of other herbs (e.g. Wheeler 1980*d*). Where fragments of ombrotrophic peat remain in such soligenous mires (as in the Malham fens) or where water tracks run in a well-defined lagg around raised mires, the community may pass very sharply to some form of ombrogenous bog or its derivative.

Distribution

The *Carex-Equisetum* sub-community is very much a vegetation type of the north and west with a wide distribution in open-water transitions and basin mires in Wales, northern England and Scotland. The *Lysimachia* sub-community extends the range of the community into eastern England where it occurs uncommonly in small basin mires and rarely in the flood-plain mires of Broadland (Wheeler 1980*a*, *d*, 1983).

Affinities

The *Potentillo-Caricetum* has affinities with a wide variety of other mire types and it is difficult to define its floristic limits exactly. First, it grades through its bryophyte layer to a variety of poor fens of the Caricion canescentis-fuscae and Rhynchosporion alliances in which *C. rostrata* and Junci remain prominent. In some of these, there is also an understorey of *P. palustris* and *M. trifoliata* but they can generally be distinguished by the prominence of a range of Sphagna. Second, it shows clear affinities with some richer Caricion davallianae communities. Here again, *C. rostrata*, *P. palustris* and *M. trifoliata* may remain prominent but other sedges, notably *C. diandra*, *C. lasiocarpa*, *C. nigra* and *C. panicea*, become more important and there is a shift in the bryophyte layer to more calcicolous species. Each of the various communities involved has a fairly well defined core of distinguishing species but there is a virtually continuous spectrum of variation between them all.

If a *Potentillo-Caricetum* is defined from this range of vegetation types, there is an obvious case for retaining it as a rich Caricion canescentis-fuscae community or a poor Rhynchosporion community but here we follow Wheeler (1980*a*) in placing it within the Magnocaricion. Its links with the diverse tall dicotyledon element of rich fens are seen only in the *Lysimachia* sub-community where it approaches the vegetation of some stands of the *Peucedano-Phragmitetum* but many of its dominants occur as important swamp species in the Phragmitetea and it has strong developmental relationships with some of these. Indeed, some authorities (e.g. Birse 1980) have seen vegetation of this kind as part of association(s) which also include species-poor swamps.

Floristic table S27

	a	b	27
Carex rostrata	V (1–9)	V (1–9)	V (1–9)
Galium palustre	V (1–5)	V (1–4)	V (1–5)
Potentilla palustris	IV (1–8)	V (1–9)	V (1–9)
Menyanthes trifoliata	IV (1–9)	IV (1–9)	IV (1–9)
Equisetum fluviatile	IV (1–8)	II (1–5)	III (1–8)
Juncus acutiflorus	II (1–6)		I (1–6)
Ranunculus flammula	II (1–3)		I (1–3)
Carex vesicaria	I (8–9)		I (8–9)
Carex aquatilis	I (8–9)		I (8–9)
Veronica beccabunga	I (1–5)		I (1–5)
Apium nodiflorum	I (4–5)		I (4–5)
Brachythecium rutabulum	I (1–6)		I (1–6)
Brachythecium rivulare	I (1–4)		I (1–4)
Stellaria alsine	I (1–3)		I (1–3)
Rhizomnium punctatum	I (1–5)		I (1–5)
Rhizomnium pseudopunctatum	I (1–4)		I (1–4)
Potamogeton polygonifolius	I (2)		I (2)
Callitriche stagnalis	I (3)		I (3)
Hypericum elodes	I (7)		I (7)

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Floristic table S27 (*cont.*)

	a	b	27
Ranunculus repens	I (3)		I (3)
Senecio aquaticus	I (1)		I (1)
Carex diandra	I (3)		I (3)
Lysimachia thyrsiflora	I (4)		I (4)
Cardamine amara	I (3)		I (3)
Epipactis palustris	I (1)		I (1)
Angelica sylvestris	II (1–3)	IV (1–4)	III (1–4)
Eriophorum angustifolium	I (1–3)	IV (3–9)	II (1–9)
Phragmites australis	I (5)	IV (4–9)	II (4–9)
Lythrum salicaria	I (1)	IV (1–9)	II (1–9)
Lysimachia vulgaris		IV (1–5)	II (1–5)
Carex nigra	I (3–5)	III (1–9)	II (1–9)
Ranunculus lingua	I (1–3)	III (1–6)	II (1–6)
Lycopus europaeus	I (1–2)	III (1–4)	II (1–4)
Iris pseudacorus	I (1–4)	III (1–3)	II (1–4)
Carex elata	I (5)	III (3–8)	II (3–8)
Lychnis flos-cuculi	I (1)	III (1–3)	II (1–3)
Campylium stellatum	I (1)	III (1–4)	II (1–4)
Juncus subnodulosus		III (1–7)	II (1–7)
Peucedanum palustre		II (1–6)	I (1–6)
Rumex hydrolapathum		II (1–3)	I (1–3)
Sium latifolium		II (1–3)	I (1–3)
Sphagnum fimbriatum		I (1–5)	I (1–5)
Dryopteris cristata		I (1)	I (1)
Cardamine pratensis	III (1–4)	IV (1–3)	III (1–4)
Agrostis stolonifera	III (1–5)	III (1–9)	III (1–9)
Juncus effusus	II (2–8)	III (2–9)	III (2–9)
Epilobium palustre	II (1–6)	III (1–3)	II (1–6)
Mentha aquatica	II (3–8)	III (1–5)	II (1–8)
Calliergon cuspidatum	II (1–5)	III (1–3)	II (1–5)
Calliergon cordifolium	II (2–9)	II (1–2)	II (1–9)
Myosotis laxa caespitosa	II (1–4)	II (1)	II (1–4)
Caltha palustris	II (1–4)	II (1)	II (1–4)
Hydrocotyle vulgaris	II (1–4)	II (2–5)	II (1–5)
Calliergon giganteum	II (1–7)	I (1)	I (1–7)
Agrostis canina canina	II (2–5)	I (1–3)	I (1–5)
Veronica scutellata	II (1–4)	I (2)	I (1–4)
Lemna minor	II (2–3)	I (1)	I (1–3)
Stellaria palustris	I (1–3)	II (1–5)	I (1–5)
Juncus articulatus	I (1–6)	II (2–4)	I (1–6)
Scutellaria galericulata	I (1)	II (1)	I (1)
Cirsium palustre	I (1)	II (1–3)	I (1–3)
Valeriana officinalis	I (1)	II (1–3)	I (1–3)
Myosotis scorpioides	I (2–6)	I (1)	I (1–6)
Solanum dulcamara	I (3–4)	I (1–2)	I (1–4)

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Polygonum amphibium	I (3–6)	I (2–4)	I (2–6)
Sparganium erectum	I (2–5)	I (1–3)	I (1–5)
Filipendula ulmaria	I (1–2)	I (1–2)	I (1–2)
Carex paniculata	I (1–3)	I (1–4)	I (1–4)
Poa trivialis	I (1–2)	I (1)	I (1–2)
Lotus uliginosus	I (2–3)	I (1)	I (1–3)
Holcus lanatus	I (1–6)	I (1–4)	I (1–4)
Eleocharis palustris	I (1–3)	I (1)	I (1–3)
Typha latifolia	I (2–4)	I (1–2)	I (1–4)
Sphagnum squarrosum	I (2)	I (1–5)	I (1–5)
Salix cinerea sapling	I (3)	I (1–4)	I (1–4)
Carex appropinquata	I (8)	I (1)	I (1–8)
Drepanocladus fluitans	I (4)	I (1)	I (1–4)
Equisetum palustre	I (2)	I (1)	I (1–2)
Chiloscyphus polyanthos	I (1)	I (2)	I (1–2)
Bryum pseudotriquetrum	I (1)	I (1)	I (1)
Cratoneuron filicinum	I (1)	I (1)	I (1)
Lophocolea bidentata s.l.	I (1)	I (1)	I (1)
Number of samples	197	23	220
Number of species/sample	10 (6–16)		

a *Carex rostrata-Equisetum fluviatile* sub-community

b *Lysimachia vulgaris* sub-community

27 *Potentillo-Caricetum rostratae* (total)

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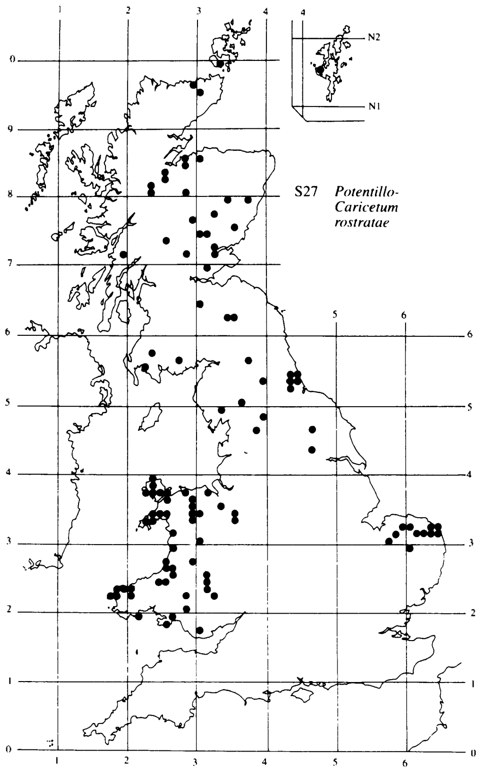

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