S2
Cladium mariscus swamp and sedge-beds *Cladietum marisci* Zöbrist 1933 *emend.* Pfeiffer 1961

Synonymy
Pure Sedge Godwin & Tansley 1929; *Cladietum* Tansley 1939; *Cladium mariscus* reed-swamp Conway 1942; *Cladium mariscus* primary fen Lambert 1951; *Cladium mariscus* stands Holdgate 1955*b*; *Cladium mariscus* society Poore & Walker 1959; Tall *Cladium mariscus* Haslam 1965; *Cladium mariscus* swamp Ratcliffe & Hattey 1982.

Constant species
Cladium mariscus.

Rare species
Utricularia intermedia.

Physiognomy
The *Cladietum marisci* comprises vegetation overwhelmingly dominated by *Cladium mariscus*. The gregarious stout shoots up to 2 metres tall form a sometimes open patchwork of clumps or a dense cover, often made virtually impenetrable by the tough leaves which are up to 3 m long and characteristically bent over, 1 m or more from the ground. This growth habit, the evergreen nature of the aerial parts and the thick accumulation of slow-rotting litter, sometimes more than 50 cm deep (Godwin & Tansley 1929, Conway 1942), can exclude all possible competitors. No other species is frequent throughout and pure stands are common.

Sub-communities

***Cladium mariscus* sub-community:** *Scirpo-Phragmitetum cladietosum* Messikommer 1928; *Caricetum elatae cladietosum* Libbert 1932; *Cladietum marisci typicum* Krausch 1964 *p.p.*; *Cladietum marisci phragmitetosum* Westhoff & Segal 1969; *Cladietum marisci typicum*, *Cladium-Carex elata* community, *Cladium-Thelypteris* community, *Cladium* sociation Wheeler 1980*a*. Here are included the most dense and/or species-poor stands, ranging from pure *Cladium*, through more open vegetation with occasional shoots of *Phragmites australis* or *Juncus subnodulosus* and sprawls of *Solanum dulcamara* to mosaics of *C. mariscus* with sometimes abundant *P. australis* or scattered tussocks of *Carex elata*.

***Menyanthes trifoliata* sub-community:** *Cladium mariscus-Myrica gale* sociation Spence 1964; *Cladium mariscus-Utricularia intermedia* nodum Ivimey-Cook & Proctor 1966; *Cladietum marisci scorpidietosum* Segal & Westhoff 1969; *Cladietum marisci utricularietosum* and *caricetosum lasiocarpae* Wheeler 1980*a*; *Cladium mariscus-Rubus fruticosus-Myrica gale* community Ratcliffe & Hattey 1982. In this sub-community, the cover of *Cladium* is more open and the plants often shorter, up to about 1 m tall. *P. australis*, *J. subnodulus* and *C. elata* are more frequent here and there are sometimes scattered clumps of *Myrica gale* but the really distinctive feature is the vegetation of the pools of standing water between the *Cladium* shoots. *Menyanthes trifoliata* is the most frequent and abundant species but *Potentilla palustris* and, especially in shallower water, *Carex lasiocarpa*, may be locally prominent. Submerged, there are sometimes festoons of *Scorpidium scorpioides* and *Utricularia vulgaris* with, less frequently, *U. minor*, *U. intermedia* and *Campylium stellatum*. Wheeler (1980*a*) also recorded *Chara vulgaris*, *C. glubularis* var. *aspera* and *C. hispida* var. *hispida* as distinctive aquatics of this vegetation.

Habitat
The *Cladietum* is most characteristic of shallow, standing water in lowland topogenous mires fed by calcareous, base-rich ground water. It occurs, often as small stands, in basin mires and around open-water transitions in larger hollows and flood-plain mires. It may also be found in flooded peat cuttings and around 'pulk-holes'.

The community reaches its optimal development as a swamp. *Cladium* is an evergreen geophyte which, in

many respects, can be regarded as an aquatic species (Conway 1936*a*). It grows best when the water-table remains between about 15 cm below ground and 40 cm above (Conway 1942). Although it can tolerate short periods of drier conditions in summer (e.g. Godwin & Bharucha 1932), vigour is maintained only if the dense mat of fleshy roots is submerged (Conway 1937*b*, 1938). On the other hand, a persistent very high water-table can prevent aeration of the rhizome which occurs by gaseous diffusion down the bases of the dead leaves and through those which, though still green, have ceased growth (Conway 1937*a*). These requirements probably play an important part in limiting the species to situations which are 'too dry for reed and too wet for bushes' (Godwin & Tansley 1929). Swamp dominated by *Phragmites australis*, in which the rhizomes are aerated through the very tall, persistent dead stems (Buttery 1959, Haslam 1972), commonly replaces the *Cladietum* in deeper water in uninterrupted open-water transitions (e.g. Godwin & Bharucha 1932).

Between these general limits, *Cladium* seems relatively tolerant of the actual level of the water-table except that, in winter, standing water may provide some insulation against frosting of the growing point (which is injured by temperatures below $-2\,^{\circ}C$) and the differentiated leaves (which can withstand temperatures down to $-10\,^{\circ}C$) (von Post 1925, Conway 1938, 1942). It is noteworthy that, to the north of Britain, *Cladium* occurs only in the swamp *Cladietum* and not as a component of drier fens (Wheeler 1975).

It has, however, been suggested (Haslam 1965) that part of the balance between *Cladium* and *Carex elata*, both of which can occur in broadly similar situations, is related to tolerance of short-term variation in water-level. In the west Norfolk basin mires, *C. elata* is limited to sites with a variable water-table, whereas *Cladium* is dominant where the water-table remains more stable. Wheeler (1980*a*) noted that Broadland stands of the *Cladietum* with *C. elata* had a more variable water-table than those from which this sedge was lacking.

The *Cladietum* occurs mostly over fen peat, although it is sometimes found over marly substrates (Ratcliffe & Hattey 1982) and may even colonise bare silts, as around Broadland 'pulk-holes' (Lambert 1951), although severe clogging with mineral material may inhibit rhizome aeration (Haslam 1965). The community is commonly associated with infiltration of calcareous and base-rich water, sometimes by general seepage from surrounding rocks (as in the mires in limestone basins), in other cases by more localised infiltration from springs. Calcium contents of 40–150 mg l^{-1} have been recorded (Poore & Walker 1959, Phillips 1977, Wheeler 1983) with water pH values of 6.0–8.5 (Godwin & Bharncha 1932, Conway 1942, Poore & Walker 1959, Wheeler 1975, 1983). There is, however, some evidence to suggest that *C. mariscus* is not always restricted to such conditions throughout its European range (e.g. Praeger 1934, Skårman 1935).

Cladium may gain some competitive advantage over, for example, *Phragmites*, by a tolerance of the oligotrophic environment that is sometimes associated with such calcareous conditions. In her study of the successions along the Bure valley in Norfolk, Lambert (1951) noted that the importance of the *Cladietum* in the vegetation sequences tended to increase the further the Broads basins were from the river and she suggested that this might be related to a decreased throughput of nutrients. A recent study of Upton Broad (Phillips 1977), where the community is particularly well developed at a site far from the river and also land-locked, has shown not only high levels of calcium but also low amounts of nitrate-nitrogen and phosphate. In the west Norfolk valley mires, *Cladium* is generally absent from those sites where frequent inundation with nutrient-rich mineral sediments allows *Phragmites* to thrive (Haslam 1965).

Stands of the *Cladietum* can provide a good crop of virtually pure 'sedge' for thatch but frequent cutting can modify the floristics of the vegetation. Traditionally, at Wicken and more widely in Broadland, *Cladium* sedge beds were mown in early summer. (T. Rowell, personal communication: cf. Godwin & Tansley 1929), every 3 to 5 years depending on the condition of the ground, and such treatment appears to be optimal for the renewable management of the crop.

With its thick accumulation of dead and decaying leaves beneath, the community is very susceptible to burning when dry. Indeed, dried *Cladium* leaves at one time had a ready use as kindling.

Zonation and succession

The centres of small basin mires and peat cuttings may be completely filled by dense stands of the community. In other cases, the *Cladietum* survives patchily in pools and stagnant dykes within largely terrestrialised mire complexes, giving way to a variety of fen or poor-fen communities. In grossly disturbed and abandoned sites, the community may occur in juxtaposition with the *Phragmites australis-Urtica dioica* fen.

In larger hollows, the *Cladietum* may give way directly to open standing water or, around 'pulk-holes', it may abut on to bare silt (Lambert 1951). In some sites, there is a swamp mosaic of the community with the *Caricetum elatae*, apparently in relation to the height and short-term variability of the water-table (Haslam 1965). Around more extensive open-water transitions, the *Cladietum* may occur patchily in the shallower waters in association with *Phragmites* swamps and, especially to the north and west, the *Caricetum rostratae* (Holdgate 1955*b*). Exceptionally the community may be found as

part of more intact zonations as at Upton Broad in Norfolk. Here, Lambert & Jennings (1951) described sequences running from the *Typhetum angustifoliae* and/or *Phragmitetum australis* through the *Cladietum* to carr woodland on the thicker, drier peats away from the open broad.

From the more fragmentary pattern of vegetation in the flood-plain mire remnants at Wicken Fen, Godwin & Bharucha (1932) had shown how the distribution of *Phragmites* swamp, the *Cladietum* and carr in such transitions could be related to differences in the height of the water-table, and particularly to the extent of water excess in winter. This they saw as representing a primary succession involving the colonisation of open water by *Phragmites*, still remaining as a swamp along lodes and around pools, the invasion of the *Phragmites* swamp by *Cladium*, best seen in the old peat cuttings, and the gradual colonisation of the 'Pure Sedge' by bushes. Stratigraphical analysis of the Broadland deposits under the zonations described by Lambert & Jennings (1951) revealed a similar picture, except that there, a second phase of *Phragmites* dominance seemed to be interposed between the *Cladietum* and the carr (Lambert 1951).

Despite this, and the rarity with which Lambert (1951) observed direct bush invasion of dense uncut *Cladietum* around the Bure broads, the advance of woody species into the community at Wicken has been plotted in some detail (Godwin & Tansley 1929, Godwin & Bharucha 1932). Here, the most frequent invaders were *Frangula alnus*, then *Rhamnus catharticus*, *Salix cinerea* and *Viburnum opulus*, with very small amounts of *Crataegus monogyna* and *Betula pendula*. These gained a hold in the *Cladietum* towards its uppermost boundary, the seedlings surviving down to a critical limit of bush growth where the peat surface experienced shallow winter flooding of several weeks' duration (Godwin & Bharucha 1932, Godwin 1943*b*). Initial patchy bush colonisation over a period of 20 years or so was followed by gradual infill of the canopy and eventual extinction of the dense *Cladium* cover (Godwin & Tansley 1929, Godwin 1936). The long survival of the sedge was perhaps due to its evergreen nature (Conway 1942).

Studies at Wicken also revealed how repeated summer cutting of the *Cladietum* 'Pure Sedge' might deflect the primary succession to produce 'Mixed Sedge' and 'Litter' (Godwin 1929, 1941; Godwin & Tansley 1929), vegetation represented in this scheme by various kinds of *Cirsio-Molinietum*, described among the mires of Volume 2.

Distribution

The community has a local distribution within the British range of *Cladium* which, as elsewhere in Europe, is benefited by warm summers and the absence of intensive frost (von Post 1925, Conway 1938, 1942). It is best developed in calcareous basin mires which are rather uncommon in this country (Wheeler 1983) but well seen on the Carboniferous Limestone of Anglesey (Wheeler 1975, Ratcliffe & Hattey 1982) and on the west Norfolk commons where drift smears overlie Chalk (Haslam 1965, Wheeler 1975). More isolated occurrences of this kind are on the Carboniferous Limestone of Cumbria, as at Sunbiggin Tarn (Holdgate 1955*b*), where *Cladium* reaches its altitudinal limit of 260 m in Britain, and at Hell Kettles, small subsidence hollows in Magnesian Limestone in south Durham (Wheeler 1980*d*). Other scattered localities sometimes mark localised seepage of calcareous water, as on Wybunbury Moss in Cheshire (Poore & Walker 1959) and on Anabaglish Moss in Wigtownshire (Spence 1964).

The *Cladietum* also occurs around open-water transitions in the apparently more oligotrophic flood-plain mires, as along the Bure (Lambert 1951) and in peat-cuttings, such as the celebrated sites at Wicken Fen (Yapp 1908, Godwin & Tansley 1929).

Affinities

Towards southern Britain, *Cladium* is a component, and sometimes an important dominant, in a variety of fens, most notably the *Peucedano-Phragmitetum australis* and the *Phragmites australis-Eupatorium cannabinum* fens and, less frequently, the *Phragmites australis-Urtica dioica* fen and the *Potentillo-Caricetum rostratae*. As with the *Caricetum elatae*, the *Cladietum marisci* is here retained in a rather strict sense, to contain those species-poor stands in which *Cladium* is dominant in the general absence of large amounts of other important swamp species.

This treatment approximates most nearly to the revision of the *Cladietum marisci* of Zöbrist (1935) proposed by Pfeiffer (1961) and followed by Wheeler (1975, 1980*a*). In this view, the community is essentially a species-poor swamp, although it contains some vegetation in which other possible swamp dominants, such as *Carex elata*, are locally prominent and thus takes in such communities as the *Caricetum elatae cladietosum* of Libbert (1932). In addition, the *Cladietum* as understood here includes some stands with much *Phragmites* which Wheeler (1975, 1980*a*), following Pfeiffer (1961), retained in a *Cladium*-rich type of *Scirpo-Phragmitetum* (similar to the *Scirpo-Phragmitetum cladietosum*) of Messikommer (1928)).

Such an approach contrasts with that of Krausch (1964) and Oberdorfer (1965) who, alongside a species-poor swamp core, included within the *Cladietum* some rich-fen vegetation that is here grouped in the *Peucedano-Phragmitetum* and *Phragmites-Eupatorium* communities.

Floristic table S2

	a	b	2
Cladium mariscus	V (5–10)	V (7)	V (5–10)
Calliergon cuspidatum	II (1–5)		I (1–5)
Solanum dulcamara	II (1–5)		I (1–5)
Salix cinerea sapling	I (2–3)		I (2–3)
Fissidens adianthoides	I (1)		I (1)
Equisetum palustre	I (1)		I (1)
Phragmites australis	II (1–6)	V (1–8)	III (1–8)
Menyanthes trifoliata	I (1–3)	IV (1–8)	II (1–8)
Potentilla palustris		II (1–5)	I (1–5)
Carex lasiocarpa	I (5)	II (1–5)	I (1–5)
Scorpidium scorpioides	I (1–3)	II (1–3)	I (1–3)
Utricularia vulgaris		II (1–3)	I (1–3)
Mentha aquatica		II (1–5)	I (1–5)
Utricularia minor		I (1–3)	I (1–3)
Utricularia intermedia		I (1–3)	I (1–3)
Riccardia multifida		I (1)	I (1)
Campylium stellatum		I (1–5)	I (1–5)
Hippuris vulgaris		I (1)	I (1)
Sphagnum subnitens		I (1)	I (1)
Carex panicea		I (1)	I (1)
Caltha palustris		I (1)	I (1)
Carex rostrata		I (1)	I (1)
Juncus subnodulosus	II (1–5)	III (1–8)	III (1–8)
Galium palustre	I (2)	II (1–3)	I (1–3)
Carex elata	I (3)	II (3)	I (3)
Myrica gale	I (8)	II (5)	I (5–8)
Lythrum salicaria	I (1)	I (1)	I (1)
Number of samples	30	24	54
Number of species/sample	5 (1–12)	9 (7–10)	7 (1–12)

a *Cladium mariscus* sub-community
b *Menyanthes trifoliata* sub-community
2 *Cladietum marisci* (total)

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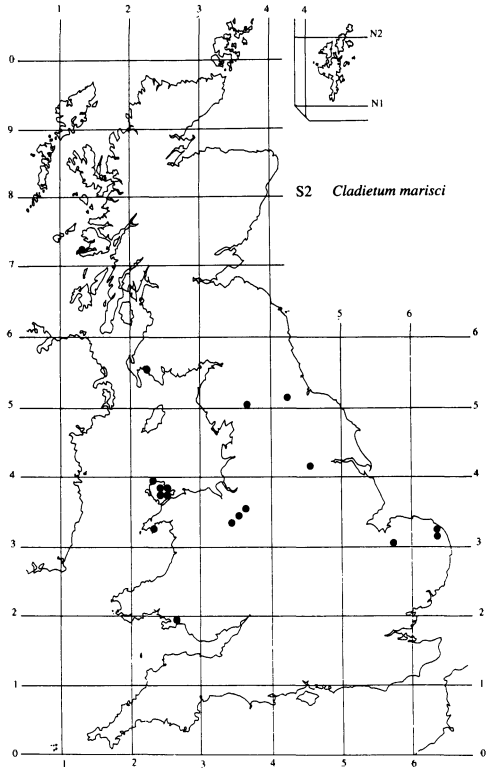

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