
M22

Juncus subnodulosus-*Cirsium palustre* fen-meadow

Synonymy

Grass fen Pallis 1911 *p.p.*; Late *Juncetum* Clapham 1940 *p.p.*; *Juncetum subnodulosi* Lambert 1946, 1948; Fen meadow Rose 1950, Willis & Jefferies 1959 *p.p.*, Crompton 1972; Rich-fen meadows Wheeler 1980c *p.p.*

Constant species

Cirsium palustre, *Equisetum palustre*, *Filipendula ulmaria*, *Holcus lanatus*, *Juncus subnodulosus*, *Lotus uliginosus*, *Mentha aquatica*, *Calliergon cuspidatum*.

Rare species

Peucedanum palustre, *Homalothecium nitens*.

Physiognomy

The *Juncus subnodulosus*-*Cirsium palustre* fen-meadow comprises vegetation which has a readily-recognisable general stamp but which shows considerable variation in its floristic composition. The community has a fairly substantial group of constants and numerous occasional to frequent species can make the vegetation very rich, but this associated flora shows considerable variation from stand to stand, with some plants that are of only low to moderate frequency throughout showing local prominence, and widely-represented species sometimes being locally absent. Often here, such differences reflect unique and complex histories of mowing and grazing, treatments of major importance in maintaining this kind of vegetation.

The most prominent structural element in the community typically comprises rushes and sedges of moderate stature, the abundance of which gives the vegetation the appearance of a rank sward, at least when viewed from a distance. In ungrazed stands, the herbage commonly attains 50–80 cm in height, exceptionally up to 1 m, and it can be dense and rather uniform; where stock have access, the dominants may be sparser or distinctly patchy, clumps of the more resistant plants scattered through the stretches of closer-cropped sward.

Prime among the bulkier species is *Juncus subnodulosus*, a plant of broad occurrence in a wide variety of fen types and some swamps, and sometimes only sparsely-represented here, but able to attain its peak of abundance in this community and the most usual dominant. It is a far-creeping rhizomatous perennial, producing an annual crop of sterile shoots in the autumn, borne singly and bearing but a single leaf, but arising so closely on the rhizomes, at 1–3 cm apart, as to be able to produce a very thick and even cover. These shoots elongate to their full height in the spring, when the fertile shoots are also produced, flowering in July and August (a little later to the north), but then often lodging in autumn winds and rain to form a thick and heavy mattress. This can depress the associated flora, though the next crop of sterile autumn shoots readily penetrates it, their fresh-green colour making a sharp contrast against the brown of the decaying mat (Richards & Clapham 1941d).

Although *J. subnodulosus* can be locally complemented or replaced by other dominants and, towards the limits of its rather restricted range, become generally scarce in or be absent from vegetation of this same general character, no other rush or sedge attains such a high overall frequency in the community. Of the additional rushes, the commonest are *J. inflexus*, which is distinctly tussocky, has grey-green foliage and flowers earlier than *J. subnodulosus*, and *J. articulatus*, which often has a decumbent habit here and flowers later; but though these can be locally abundant, they tend to be preferential for particular kinds of *Juncus*-*Cirsium* fen-meadow. *J. effusus* occurs only occasionally, *J. acutiflorus* rarely, and both are typically of low cover, although all four of these rushes can become more consistently common in closely-related types of Molinia vegetation.

More striking in this community is the frequent occurrence and occasional dominance of *Carex acutiformis* or *C. disticha*. Like *J. subnodulosus*, both of these sedges have extensive rhizome systems and neither is densely tussocky, though in *C. acutiformis* the shoots are

tufted and robust, with long leaves that are at first distinctly glaucous, so this species can be conspicuous when present in abundance. *C. disticha* is more readily overlooked, having smaller shoots, borne singly or in pairs, but close inspection often reveals some of its bright green foliage and it, too, can locally replace *J. subnodulosus* as the dominant. Much more occasionally, *C. elata* or *C. paniculata* occur here and their bulky tussocks can exert a stronger structural effect on the vegetation. *C. nigra*, though of rather restricted occurrence and usually part of the lower herbage, is sometimes found as the tussocky var. *subcaespitosa*.

Transitions between this kind of fen-meadow and tall-herb Phragmitetea fen are quite common: the two types of vegetation are fairly often found juxtaposed and it is clear that certain treatments can mediate conversion of the latter into the former. One striking difference between them, however, is that the tall helophyte dominants so characteristic of Phragmitetea communities are here reduced to very patchy occurrence. *Phragmites australis* is the commonest and even this is confined to ungrazed stands which are rarely mown or not at all, and then it usually occurs as sparse shoots forming an open upper tier to the vegetation, a metre or more high. *Calamagrostis canescens* and *Phalaris arundinacea* can also be found occasionally at low covers and in some stands a little *Cladium mariscus* may persist.

Generally, however, the strongest link between the vegetation types is provided by the associated herbaceous flora. In summer, for example, the rush and sedge layer can be overtopped by the tall flowering shoots of a variety of dicotyledons. The most frequent of these throughout the community are *Cirsium palustre*, *Filipendula ulmaria*, *Angelica sylvestris*, *Succisa pratensis*, *Eupatorium cannabinum* and *Scrophularia aquatica*, with more local enrichment by *Lythrum salicaria*, *Lysimachia vulgaris*, *Valeriana officinalis*, *Thalictrum flavum*, *Symphytum officinale* and, in Broadland, the nationally rare *Peucedanum palustre*. Quite commonly, though, grazing keeps this component of the vegetation severely in check, too, eliminating some species and reducing the more resistant to closely-nibbled rosettes.

Much more numerous through the community as a whole, and of greater structural significance, are smaller herbs which form an understorey, up to 50 cm or so high, amongst the dominants, reduced in cover and diversity where the rushes and sedges are dense, correspondingly luxuriant and varied in more open herbage, and again showing physiognomic differences according to the intensity of grazing. Among these plants, grasses are of considerable importance, with species such as *Holcus lanatus*, *Festuca rubra* and, less commonly, *Arrhenatherum elatius*, which on drier, ungrazed ground can grow rank and tussocky, and others like *Poa trivialis*, *Agrostis stolonifera*, *Anthoxanthum odoratum* and *Briza media*,

which form mats or smaller tussocks among them or, in grazed swards, make up a good deal of the short turf. *Molinia caerulea* can also be found here but it is rather patchy in its occurrence and very often of low cover, something which helps set the boundary between this community and related vegetation in the *Cirsio-Molinietum*. Other low-frequency grasses which occasionally grow robust and prominent are *Deschampsia cespitosa* and *Festuca arundinacea*. *Lolium perenne*, *Cynosurus cristatus* and *Phleum pratense* also sometimes figure in transitions to improved swards, as for example where stretches of fen-meadow have been subject to draining and improvement, a widespread event.

Among these grasses, the associates comprise species with a wide representation in wetter vegetation, together with plants more especially characteristic of moist grasslands. The commonest are *Mentha aquatica*, a late-flowerer able to grow through even quite thick mats of lodged rush shoots, *Caltha palustris*, *Equisetum palustre*, *Carex panicea*, *Valeriana dioica*, *Hypericum tetrapterum*, *Hydrocotyle vulgaris*, *Lotus uliginosus*, *Lychnis flos-cuculi*, *Cardamine pratensis*, *Ranunculus acris*, *Potentilla erecta*, *Cerastium fontanum* and *Rumex acetosa*, together with scrambling or sprawling *Galium uliginosum*, *G. palustre*, *Vicia cracca* and *Lathyrus pratensis*. In some stands, additional richness is provided by assemblages characteristic of wet fen or swamps, which can occupy hollows, or by herbs of dry pastures or meadows, and quite specialised floras can sometimes be found in damp ruts or on cattle-poached ground.

In what is typically rather dense herbage, bryophytes play a reduced role with only *Calliergon cuspidatum* and *Brachythecium rutabulum* occurring at all commonly throughout. *Plagiomnium undulatum*, *P. rostratum*, *Rhizomnium punctatum*, *Pseudoscleropodium purum* and *Campylium stellatum* can also be found occasionally, but the cover in the ground layer is rarely extensive, with usually just scattered wefts over the stools and litter.

Sub-communities

Typical sub-community: Rich-fen meadows, *Juncus-Centaurea nigra* nodum, *Juncus-Carex hirta-Deschampsia cespitosa* nodum, *Juncus subnodulosus* nodum (Wheeler 1980c, all *p.p.* In this most common and widespread kind of *Juncus-Cirsium* fen-meadow there are no preferential floristic features over and above those characteristic of the community as a whole and the general impression when this vegetation is compared with that of other sub-communities is one of rank structure and impoverishment. *J. subnodulosus* is frequent throughout and is the commonest dominant, its general abundance being reflected particularly in the sparse representation of smaller herbs. The commonest associates are thus bulkier grasses, such as *Holcus*

lanatus, *Festuca rubra* or, in some localities, *Molinia*, mat-formers like *Agrostis stolonifera* and *Poa trivialis*, taller dicotyledons like *Cirsium palustre*, *Filipendula ulmaria*, *Angelica*, *Succisa* and *Eupatorium*, sprawling plants, and those few shorter species able to tolerate the rank herbage and thick litter, notably *Mentha aquatica* and *Equisetum palustre*. Within this general framework, however, there can be considerable local variation. In some stands, for example, *J. subnodulosus* is supplemented or replaced by other dominants like *J. inflexus*, *J. articulatus*, *Carex acutiformis* or *C. disticha*, sometimes with little effect on the associated flora, in other cases with accompanying differences in composition: in certain localities, dry fen-meadow of this general type can have mixtures of these species, together with *C. hirta* and *Deschampsia cespitosa*, a distinctive assemblage which recurs in the *Briza-Trifolium* sub-community (and which Wheeler (1980c) placed together in a *Juncus-Carex-Deschampsia* nodum). Much more locally, where there are very wet areas within Typical *Juncus-Cirsium* fen-meadow, *C. paniculata* can be locally prominent, dominating the structure of the vegetation with its large tussocks. Ungrazed stands can have patchy *Phragmites*, never very dense but catching the eye with its taller shoots, and some areas show invasion by *Epilobium hirsutum* and *Arrhenatherum elatius*. Yet other tracts show floristic transitions to the richer herbage of the next sub-community (vegetation which Wheeler (1980c) united in a *Juncus-Centaurea* nodum) or to related forms of the *Cirsio-Molinietum*.

***Briza media*-*Trifolium* spp. sub-community:** Rich-fen meadows, *Juncus-Centaurea nigra* nodum p.p., *Juncus-Carex hirta-Deschampsia cespitosa* nodum p.p., *Juncus subnodulosus* nodum p.p., *Juncus-Carex disticha* nodum Wheeler 1980c. *J. subnodulosus* remains the most frequent of the bulkier plants in this sub-community, although *J. articulatus* and *J. inflexus* are both common, and the latter sometimes quite abundant, and *C. disticha* can be locally co-dominant. In general, however, compared with Typical *Juncus-Cirsium* fen-meadow, the rush/sedge tier as a whole here is not so overwhelming in its cover or density.

Correspondingly, the associated flora is that much richer. In the first place, most of the taller dicotyledons of the community, like *Cirsium palustre*, *Filipendula*, *Angelica*, *Eupatorium* and *Succisa*, show an increase in frequency here and are often accompanied by *Centaurea nigra* and *Rumex acetosa*, though, with grazing, which is common in this vegetation, these species are often reduced to rosettes or stumpy stocks and rarely able to put up their flowering shoots. Much more characteristic is a rich suite of plants of small to moderate stature which comprise a dense and varied layer amongst the rush and sedge clumps, up to several dm tall where

grazing is light, forming a much shorter turf where stock are numerous. Grasses are often important in this tier, not only species such as *Holcus lanatus*, *Festuca rubra* and *Molinia*, which can be nibbled down here to small tufts, and *Agrostis stolonifera* and *Poa trivialis*, well adapted to ramifying close swards, but also less bulky species such as *Briza media* and *Anthoxanthum odoratum*, which are able to survive in the shorter herbage. *Juncus articulatus*, too, though able to grow in ascending clumps, is often found in a semi-prostrate form in this vegetation and, quite commonly, there is some *Carex panicea* in the sward, occasionally also some *C. nigra* and *C. flacca* or, usually with *Deschampsia cespitosa*, *C. hirta*. *Cynosurus cristatus* is sometimes found where stands occur among tracts of drier pasture, and *Lolium perenne* and *Phleum pratense* can figure in such situations too.

Intermixed with the grasses is a variety of other herbs. Most frequent among these are *Lotus uliginosus*, *Lychnis flos-cuculi*, *Caltha palustris*, *Ranunculus acris*, *Valeriana dioica*, *Potentilla erecta*, *P. anserina* and *Hypericum tetrapterum*, characteristic of the community as a whole but especially well represented here, and also *Cardamine pratensis*, *Cerastium fontanum*, *Trifolium repens*, *T. pratense*, *Epilobium parviflorum*, *Plantago lanceolata*, *Prunella vulgaris*, *Ranunculus repens*, *Triglochin palustre*, *Rhinanthus minor* and *Dactylorhiza fuchsii*, occurring occasionally elsewhere in the community but strongly preferential to this particular kind of *Juncus-Cirsium* fen-meadow. Other orchids sometimes found here include *D. majalis* ssp. *praetermissa*, *D. incarnata* and *Epipactis palustris*. Then, sprawling among the herbage, there are frequent plants of *Galium uliginosum*, *G. palustre*, *Vicia cracca* and *Lathyrus pratensis*. With the high incidence of grazing, *Phragmites* is scarce here, but wetter patches may show some floristic similarities to the *Iris* sub-community with occasional *Iris pseudacorus*, *Ranunculus flammula*, *Hydrocotyle vulgaris* and *Thalictrum flavum*.

***Carex elata* sub-community:** *Juncus subnodulosus*-*Carex elata* nodum Wheeler 1980c. *Carex elata* is by and large an uncommon plant in fen-meadow vegetation but locally it can occur in some abundance in this kind of *Juncus-Cirsium* community, very occasionally becoming co-dominant with *J. subnodulosus*. *Phragmites* is also often present, forming an open upper tier and there is usually some *Hydrocotyle vulgaris*, but more specifically preferential are *Potentilla palustris*, *Equisetum fluviatile*, *Epilobium palustre*, *Lythrum salicaria*, *Dactylorhiza incarnata* and *Thelypteris palustris*. Some stands have *Pedicularis palustris*, *Menyanthes trifoliata*, *Ranunculus flammula*, *R. lingua* and *Berula erecta* (Wheeler 1975). Grasses and the smaller herbs of the *Briza-Trifolium* sub-community are particularly sparsely represented.

Saplings of *Salix cinerea* sometimes gain a hold on the sedge tussocks.

***Iris pseudacorus* sub-community:** *Juncus subnodulosus*-*Iris pseudacorus* nodum Wheeler 1980c. This sub-community shares with the last frequent records for *Phragmites*, again sparsely represented as an open upper tier, and for *Hydrocotyle*, with occasional *Menyanthes*, *Potentilla palustris* and *Equisetum fluviatile*, and once more the smaller herbs of the *Briza-Trifolium* type of fen-meadow are noticeably sparse. *Carex elata* is occasionally found and tussocks of *C. paniculata* are sometimes prominent, and both *C. disticha* and, particularly, *C. acutiformis* can be locally abundant. Generally, though, it is *J. subnodulosus* which remains dominant.

By mid-summer in this vegetation, however, the continuing prominence of the rush/sedge layer is often masked by the flowering shoots of tall dicotyledons which, together with the scattered reed, give a superficial impression of *Phragmitetalia* fen. Of the general community species, *Cirsium palustre*, *Filipendula*, *Angelica* and *Succisa* all occur commonly and the most frequent of the preferentials is *Iris pseudacorus*. Also distinctive, but rather patchily-represented, are *Lythrum salicaria*, *Lysimachia vulgaris*, *Thalictrum flavum*, *Valeriana officinalis* and, in Broadland, *Peucedanum palustre*, species which, when present in numbers, bring the vegetation particularly close to tall-herb fen. *Calamagrostis canescens*, *Phalaris arundinacea* and *Epilobium hirsutum* can also occur in small amounts and some stands have *Symphytum officinale* and *Calystegia sepium*.

Bryophytes are again rather poorly represented but the usual *Calliergon cuspidatum* and *Brachythecium rutabulum* are sometimes accompanied by *Campylium stellatum* or *Plagiomnium rostratum*.

Habitat

The *Juncus-Cirsium* fen-meadow brings together secondary herbaceous vegetation developed over a variety of moist, base-rich and moderately mesotrophic peats and mineral soils in southern lowland Britain. It can be found in both soligenous and topogenous habitats, either in and around well-developed springs, flushes and mires, or marking out more ill-defined areas of influence of surface or ground waters. Ultimately, however, the community is always dependent on the maintenance of particular kinds of treatment, being derived from a diversity of other sorts of wetland vegetation by mowing and/or grazing, and it owes much in its floristics and physiognomy to the influence of these factors. Its overall distribution and the extent of stands have been much reduced by the abandonment of more traditional agricultural practices and widespread and intensive land improvement.

In the sequence of wet meadows and pastures in which rushes play a prominent part, the *Juncus-Cirsium* fen-meadow occupies one climatic and edaphic extreme. Its geographical range coincides closely with that of its most usual dominant, *J. subnodulosus* (Richards & Clapham 1941b, Perring & Walters 1962): although some stands, particularly towards the limit of the range of this species, lack the rush while remaining otherwise quite typical, environmental conditions here seem optimal for *J. subnodulosus* and many records for it in local floras probably refer to occurrences in this kind of vegetation (Wheeler 1975: see, for example, Dony 1967, Newton 1971, Messenger 1971). It is a species of wide distribution through western Europe, though it is essentially a plant of lower altitudes, probably confined in Britain to sites below 150 m (Richards & Clapham 1941d), and the prominence of some other members of the community, like *J. inflexus*, *Carex acutiformis*, *C. disticha* and *C. hirta*, reinforces this broad phytogeographic association with the lowland south of Britain. Within these fairly loose limits, however, the range of the rush and of the community are strongly restricted by edaphic factors: thus, it is the distribution of suitably moist, base-rich and not excessively oligotrophic soils that accounts for the general concentration of this kind of vegetation in central and eastern England, rather than any direct influence of a more continental climate. Coincidentally, most stands occur within the 29 °C mean annual maximum isotherm (Conolly & Dahl 1970), but the floristic response in the community to this particular climatic regime is negligible. The only obvious Continental plants occurring here are *Epipactis palustris* and *Oenanthe lachenalii*, and even these are quite scarce; and *Fritillaria meleagris* and *Bromus racemosus*, which are regarded as characteristic of this kind of vegetation on the European mainland, are rare in Britain and usually found in other communities. On the negative side, one might perhaps expect to see *Anagallis tenella* represented more frequently here if suitable soils were common in parts of the country with a more equable climate. But they are not and, in the cool, damper conditions in the western lowlands, where moist acidic soils predominate, the community is largely replaced by the *Juncus-Galium* rush-pasture, a vegetation type that is likewise strongly influenced by treatment, but which has distinctly calcifuge and oceanic features.

In the southern lowlands of Britain, then, the *Juncus-Cirsium* fen-meadow serves as an effective marker of soils which are kept reasonably moist for most of the year and which have moderate to high base-status, with a superficial pH that is almost always between 6 and 8, and usually in the range 6.5–7.5. But the particular situations in which these conditions are met are quite varied and the community can be found over a wide range of profile types, both organic and of predomi-

nantly mineral origin, occurring on fen peats, base-rich alluvial soils and gleys, with or without a humic top, and calcareous pelosols (Avery 1980). In lowland Britain, such soils are concentrated in areas where the soil mantle has been directly derived from lime-rich argillaceous bedrocks or heavy-textured superficials, or where there is local impedance of waters draining from calcareous substrates. There is thus a dense clustering of stands in Norfolk and north-west Suffolk, where the Chalk and the overlying Great Chalky Boulder Clay have a strong influence on pedogenesis and hydrology in and around small mire basins and within the flood-plain mires of Broadland (Pallis 1911, Lambert 1946, 1948). Then, in central England, the ill-drained undulating landscape of north Buckinghamshire, derived from mixtures of boulder clay and glacio-fluvial deposits, is particularly rich in this kind of fen-meadow vegetation (Wheeler 1975, 1983*b*), while, to the north-west, in the Cheshire-Shropshire Plain, peat-filled hollows in a similar drift-derived scenery provide a further centre. Strings of sites can also be found along the foot of the limestone scarps of central England, notably along the Chalk of the Chilterns, where waters emerge at the junction with the Gault Clay, and, less obviously, along the Oolite up through Bedfordshire and Northamptonshire and into the North York Moors, and, at far flung sites in north Wales, notably in Anglesey, below exposures of Carboniferous Limestone (Wheeler 1975). Between these more important remaining localities are numerous scattered sites which probably represent but a small remnant of a once much denser distribution: further sampling through Northamptonshire, Lincolnshire and South Humberside, where there is the most obvious discrepancy between the occurrence of *J. subnodulosus* and the known range of the community, would be of great assistance in assessing the full extent of this survival.

Despite the close correspondence between the range of the community and the distribution of more base-rich moist soils, the calcicolous aspect of the vegetation is actually rather poorly developed. *J. subnodulosus* itself is the best marker of these conditions (Richards & Clapham 1941*d*) and, among our rushy meadows and pastures, this plant is strongly preferential here. *J. inflexus* (Richards & Clapham 1941*a*) and *Carex disticha* (Jermy *et al.* 1982) are somewhat less confined, and, apart from *C. panicea* and *Briza media*, more diminutive calcicoles are rarely prominent. As a group, these plants are usually sufficient to help separate the *Juncus*-*Cirsium* fen-meadow from the *Holco-Juncetum*, the closely-related vegetation type that is characteristic of generally less base-rich gleys through the lowlands of Britain, although the communities do intergrade in transitional habitats under the dominance of *J. inflexus*. However, there is, in the *Juncus*-*Cirsium* fen-meadow, nothing like

the richness and diversity of smaller calcicoles so typical of the base-rich, small-sedge and *Schoenus* fens, despite the fact that the pH of the irrigating waters under such vegetation types is very much the same as here. The difference between the habitats probably lies partly in the nutrient-status of the soils and waters (Wheeler 1975, 1980*c*). In the Caricion davallianae mires, the concentrations of major nutrients are strikingly low and competition in the consequently rather open swards not intense. Here, by contrast, the growth of smaller herbs is often overwhelmed, not simply by the dominants, but also by the potentially vigorous performance of plants which are mostly mesophytes characteristic of a wide range of ranker swards, such as *Holcus lanatus*, *Festuca rubra*, *Poa trivialis*, *Ranunculus acris*, *Vicia cracca* and *Lathyrus pratensis* (which are all good Molinio-Arrhenatheretea species), or of a variety of moister vegetation types, like *Cirsium palustre*, *Equisetum palustre*, *Filipendula ulmaria*, *Lotus uliginosus*, *Lychnis flos-cuculi*, *Valeriana dioica* and *Angelica sylvestris* (typical of the Molinietalia as a whole). Most of the very frequent, and often the more prominent, plants of the community are thus species tolerant of, rather than demanding of, the high base-status of the soils here. As with the other rush-pastures and meadows, then, the general character of the vegetation is often more obvious than the particular.

Compared with the habitats of the *Holco-Juncetum* and *Juncus-Galium* rush-pasture, however, those in which the *Juncus*-*Cirsium* fen-meadow are found include a greater proportion of wetter situations. These other communities are essentially vegetation types of gleyed mineral soils, sometimes with a humic top, but not typically waterlogged to the surface, at least not in summer. The *Juncus*-*Cirsium* fen-meadow does extend on to base-rich soils which are just seasonally waterlogged, as around the margins of spring-fens which are back-gleyed by the flushing-waters, below intermittently active seepage lines, in ill-draining hollows where precipitation induces winter surface-water gleying and in some topogenous fens with a fluctuating ground water-table. But many stands are kept much wetter than this, by constant soligenous through-put, by gross impedance in hollows or by more consistent flooding.

Much of the floristic variation in the community can be attributed to differences in the kind and degree of irrigation, and Wheeler (1975) identified two extreme situations with frequent transitions between. The typical spring fen-meadow occurs on sloping ground, sometimes but gently-inclined, in other cases quite steep, where ground waters percolate down to impervious substrates and emerge in clearly-defined, often vigorous, springs or much more diffuse seepage lines. They then run down-slope, sometimes in definite channels or soakways which can feed a stream or basin, sometimes in more indeterminate flushes, the waters soaking away

again where they cross on to pervious materials. Such fens are found at the foot of scarps and on valley sides, sometimes where there is a sharp break in slope, as around the Gordano valley in Avon (Willis & Jefferies 1959), or in more gentle scenery, as in north Buckinghamshire (Wheeler 1975, 1983b) and in some of the Breckland valleys in East Anglia (Bellamy & Rose 1961, Haslam 1965); and on the slopes around hollows and basins, as in the Anglesey fens and in mires in the Cheshire–Shropshire Plain and Norfolk (Wheeler 1975). They are generally of small extent and can show a quite marked difference between the permanently-waterlogged central area, where there is often an ill-structured, sloppy mineral soil, rich in organic matter above, and the surrounds, where better-defined profiles become less strongly gleyed as one moves away.

Usually, however, such fens are occupied by the Typical or *Briza-Trifolium* sub-communities in which *Molinio-Arrhenatheretea* or *Molinietalia* species account for the bulk of the vegetation cover, sometimes with a *Cynosurion* element reflecting the influence of grazing stock within the fen itself or in the pastured surrounds: with their large circumference to area ratio, spring fen-meadows are often characterised by a strong floristic overlap with the vegetation around (Wheeler 1975). The difference between these two kinds of *Juncus-Cirsium* fen-meadow probably lies in their treatment history (see below), but both exhibit a similar variation in their composition according to the degree of water-logging. For example, such local dominants as *Carex disticha* (especially prominent in the *Briza-Trifolium* type), *C. acutiformis* and *C. paniculata* (particularly associated with the Typical sub-community), tend to become most abundant in the very wettest springs, on soft muds and peats where there is a more or less continuous through-put. At the opposite extreme is the kind of vegetation represented in Wheeler's (1980c) *Juncus-Carex hirta-Deschampsia* nodum, especially characteristic of fen edges with transitions to surrounding swards; and his *Juncus-Centaurea* nodum of summer-dry soils.

These latter forms of the Typical and *Briza-Trifolium* sub-communities can also be found where the *Juncus-Cirsium* fen-meadow runs down on to flat ground in badly-drained hollows or valley bottoms with stagnogley or ground-water gley soils. In such situations, described from the Ham area in Kent (Rose 1950), Gordano (Willis & Jefferies 1959) and sites scattered through the Midlands (Wheeler 1975), the stands can be more extensive, forming patches within agricultural fields or occurring as undrained enclaves. Hydrologically, such situations represent a transition to the other distinctive kind of habitat in which this community occurs, where the ground water regime is under topogenous influence. In extreme form, this is well seen around

mire basins, where the humic top to the surrounding gley thickens into a layer of peat, developed under the control of a ground water-table indirectly fed by the springs and seepage lines of the slopes and often showing some seasonal fluctuation, with winter flooding and superficial summer drying. Such conditions are particularly characteristic of small basins in Norfolk, where the *Carex elata* sub-community forms a fringing zone of wet fen-meadow.

Rather similar are those situations where the *Juncus-Cirsium* fen-meadow occurs on sometimes deep peats in extensive flood-plain mires with fluctuating waters of a base-rich character, the movement of which may deposit allochthonous mineral matter. Once much more extensive (e.g. Pallis 1911, Lambert 1946, 1948), such stands can still be seen in parts of Broadland, and more fragmentarily over peaty alluvium on terraces in some lime-rich river valleys elsewhere, and typically they are of the *Iris* sub-community. Both this kind of *Juncus-Cirsium* fen-meadow and, to a lesser extent, the *Carex elata* sub-community, are characterised by a shift away from a prominent *Molinio-Arrhenatheretea* element of grasses and climbers and a supplementing of the *Molinietalia* tall herbs by a variety of plants usually found in *Phragmitetalia* fens, *Phragmites* itself, *Carex elata*, *Calamagrostis canescens*, *Iris pseudacorus*, *Valeriana officinalis*, *Lythrum salicaria* and *Lysimachia vulgaris*.

The striking differences in composition and structure that can be seen among these vegetation types, between, for example, the *Iris* sub-community on the one hand and the *Briza-Trifolium* sub-community on the other, are also a function of variations in treatment. The *Juncus-Cirsium* fen-meadow is a secondary community derived and maintained by mowing and/or grazing, and strictly therefore not always a meadow but often, particularly now, with the demise of large-scale mowing of this kind of vegetation, a pasture. The detailed effects of these treatments here are little understood, and comments in such studies as those of Lambert (1946, 1948) and Willis & Jefferies (1959) and experiments described in Wheeler (1983b) and Wheeler *et al.* (1985) suggest that they can be subtle and diverse. Certainly, the degree of fine variation in the floristics and physiognomy of the vegetation included here suggests a complex pattern of interactions between treatments and soil factors, among which it is difficult to discern more than very general trends. It is highly likely, too, that many sites have a unique history of management, the details of which are now, of course, often irrecoverable.

However, the general influence of such treatments seems to be as follows. First, they have, both of them, produced a strong measure of floristic convergence in a variety of precursors, such that the resulting vegetation types are now characterised, to a greater or lesser degree, by species tolerant of cropping under low-intensity

agricultural regimes, but otherwise of fairly broad ecological amplitude. The substantial group of meadow and pasture mesophytes figures prominently among the most frequent plants of the community and often veils the peculiarities of the vegetation. And the fact that much the same assemblage rises to prominence, under the influence of similar treatments, over less base-rich soils in other parts of the British lowlands, is the main reason why it is difficult to draw hard and fast boundaries between this community and the other *Molinietalia* pastures and meadows. Sometimes, over soils of a transitional character, a little drier and less base-rich than here, it is the identity of the dominant rush that is the deciding factor and, throughout this community, *J. subnodulosus* provides the strongest differential feature. It is well adapted to survive annual summer mowing, the usual cutting regime that was followed here, by virtue of its phenology (Richards & Clapham 1941*d*), and, though reputedly eaten by cattle (Willis & Jefferies 1959), it is generally resistant to grazing (Richards & Clapham 1941*d*, Lambert 1946, 1948).

These features also mean that *J. subnodulosus* is often one of the strongest threads of continuity between this community and the vegetation from which it has been derived: the second treatment-related characteristic of this fen-meadow is the extent to which its floristics are inherited and the ways in which mowing and grazing have mediated the survival or extinction of the species in its various precursors. Usually, there is no firm evidence of what vegetation preceded the development of this kind of fen-meadow, but it is in the *Iris* sub-community (and to a lesser extent, the *Carex elata* sub-community), that the presumed lines of inheritance are clearest. Essentially, this vegetation represents the middle and lower tiers of drier *Phragmitetalia* fen, like the *Peucedano-Phragmitetum* or the *Phragmites-Eupatorium* fen, communities which, like the *Iris* fen-meadow, occur on topogenous peats and mineral soils, but which are either primary fen or secondary mowing-marsh, winter-cut for reed or occasionally summer-cut for sedge. Such mowing regimes leave one or other of the potential dominants able to renew in abundance and exert some control over the associated flora by altering the light penetration. Any switch to more regular summer mowing, which was widely practised in areas like Broadland for the harvesting of 'litter' (e.g. Lambert 1946, 1965), is likely to break the cycle of regeneration of secondary *Phragmitetalia* fen by weakening the dominance of important helophytes like *Phragmites* and allowing resistant plants like *J. subnodulosus* to survive in abundance, particularly on drier ground where it might have some natural edaphic advantage. *J. subnodulosus* is not a formidable shade-caster so taller dicotyledons can persist in some quantity under such conditions, provided they can accumulate sufficient capital via

abundant stem leaves before cutting or through the persistence of rosettes afterwards. And with the regular removal of herbage and the prevention of litter accumulation, smaller fen herbs too are able to thrive. This kind of treatment was undoubtedly responsible for the creation and maintenance of some extensive stands of the community in our larger topogenous fen systems (Lambert 1946), though it must be remembered that annual summer mowing can deflect *Phragmitetalia* fen into other kinds of vegetation than the *Juncus-Cirsium* fen-meadow, notably the *Cirsio-Molinietum* (Godwin 1929): what controls the particular direction of development is not really known, although the nutrient status of the soil probably plays an important part. Except within managed reserves, like Wicken Fen in Cambridgeshire (Wheeler 1975), such marsh mowing is now very rarely practised, though patches of the *Juncus-Cirsium* fen-meadow in wetter hollows within agricultural enclosures may be included in an annual hay-crop.

Light grazing of *Phragmitetalia* fen can have a similar effect to mowing for litter and cattle-pasturing of topogenous mires has produced vegetation akin to the *Iris* sub-community on the kind of grazing-levels, embanked and pumped, which Lambert (1948) described at Rockland and Claxton on the Yare in Norfolk. Grazed topogenous fens of such extensive size are now rare, although some stands of the *Carex elata* sub-community show a rich low-growing herbage around mire basins where cattle have access. In general, however, heavy grazing and the attendant trampling favour the elimination of not only *Phragmites*, but also many of the fen associates tolerant of even quite frequent mowing. In grazed *Juncus-Cirsium* fen-meadow the floristic emphasis is thus of a third kind, with but a small inherited element, but a strong appearance of pasture preferentials. This is best seen in the *Briza-Trifolium* sub-community, most frequently developed around spring-fens and in wet field hollows that are grazed throughout the year or at least in summer. The particular character of the preferential element in the vegetation is rather varied but generally it has affinities with *Cynosurion* swards of varying degrees of base-enrichment, taking in, towards its extremes, more mesophytic calcicoles and some moderate calcifuges. Fairly rich and diverse stretches of such herbage, cropped to a fairly short, rough turf, and kept open, too, by trampling (always likely to produce poaching on these soils), thus form the matrix between the patches of resistant rushes and sedges in this vegetation, the prominence of the elements varying with the initial composition of the sward and the pattern of grazing.

Grazing is nowadays of greater importance in maintaining the *Juncus-Cirsium* fen-meadow than mowing, but many stands bear signs of a fourth kind of treatment, and that is simply neglect, where previous man-

agement has fallen into disuse, as on many mowing-marshes and some grazing-levels, or where it has long been of a rather casual nature, as in wet field bottoms and corners which escape cutting for hay and where stock gain only occasional access. The Typical sub-community seems especially characteristic of such situations and is now the most widely distributed and common kind of *Juncus-Cirsium* fen-meadow, its impoverished floristic composition bearing testimony to the elimination of both *Phragmitetalia* and *Cynosurion* associates with the unchecked growth of the rush and sedge dominants.

Zonation and succession

The *Juncus-Cirsium* fen-meadow is found with a wide variety of swamps, tall-herb fens, other mires and grasslands and woodlands in zonations and mosaics which reflect interactions between edaphic variation and treatments. Many such sequences now bear signs of neglect or disturbance and are often truncated above by improvement of the soils, occurring as isolated fragments within intensive agricultural landscapes. The abandonment of traditional treatments has also allowed many tracts to progress to scrub or woodland in renewed successions.

The most extensive sequences in which the *Juncus-Cirsium* fen-meadow is found occur in large topogenous mires, like the flood-plain fens of Broadland, where the *Iris* sub-community once formed an important part of the patchwork of mowing-marsh. Concentrated on the drier fen margins and maintained by annual summer-cutting for litter, such vegetation typically gave way over the more extensively-flooded peats to the *Peucedano-Phragmitetum* or the more species-poor *Phragmites-Eupatorium* fen, different compartments variously treated for crops of *Phragmites*, *Cladium* or *Glyceria maxima*, according to the timing of mowing and the trophic state of the substrates. And, beyond such communities, around the open waters, and penetrating between the compartments along the actively-maintained dykes, were stands of swamps, such as the *Phragmitetum*, the *Glycerietum maximae* or the *Cladietum* (Pallis 1911, Lambert 1946, 1951, 1965). Such vegetation patterns are now in a state of almost universal neglect, with the various dominants reasserting themselves strongly among the secondary fen and *Phragmites* re-invading the fen-meadows (Wheeler 1975). The boundaries between the fen compartments have been further obscured by the choking of dykes and by the invasion throughout of shrubs and trees. Most of the developing woodland approximates to *Salix-Betula-Phragmites* fen carr, the kind of wet forest which develops in most primary hydrarch successions over more base-rich peats in lowland Britain, and towards which secondary successions tend to converge when restraining treatments are withdrawn (Figure 18).

In some stretches of Broadland, around Hickling, Sutton and Wheatfen broads, for example (Wheeler 1975), such mosaics as these can still be seen in less obscured form and at Wicken Fen some of the mown droves have thin strips of this kind of *Juncus-Cirsium* fen-meadow running between the compartments. Elsewhere, smaller fen basins, like those in Norfolk and Anglesey, and alluvial terraces along chalkland streams, have narrow sequences of fen-meadow, fen and swamp of this basic type. Spring-fed hollows in East Anglia, too, can show compressed zonations from the *Caricetum elatae* swamp to the *Carex elata* sub-community. In such cases, grazing often maintains a short sward, although larger sedge tussocks may provide a niche for the scattered invasion of woody plants.

Although grazed *Juncus-Cirsium* fen-meadow was once an extensive component of the vegetation cover on some flood-plain mires, forming a striking contrast to the mowing-marsh around (Lambert 1948), it is now generally found as small stands marking out waterlogged hollows, seepage lines and springs within enclosed pastures. Where stock penetrate far and regularly on to the wetter ground, the vegetation is usually of the *Briza-Trifolium* type, although there can be considerable floristic and structural differences both within and between stands according to the pattern of flushing and the intensity of grazing. The sharpness of the boundary between the fen-meadow and surrounding sward is also variable, depending on the gradient of soil moisture and whether there have been attempts to improve the pasture around. Often, the context is a *Cynosurion* grassland, like the ubiquitous *Lolium-Cynosuretum* or, on less-improved ground, the *Ceniaureo-Cynosuretum*, both of them agricultural swards of brown soils with free to moderately impeded drainage such as frequently surround flushes and waterlogged hollows with fen-meadow developed over shale and clay landscapes. With such grasslands, the *Briza-Trifolium* sub-community shows a strong floristic continuity through mesophytic herbs such as *Holcus lanatus*, *Festuca rubra*, *Ranunculus acris*, *Trifolium repens*, *Cerastium fontanum*, *Prunella vulgaris*, *Centaurea nigra* and *Cynosurus cristatus*, so the general effect in moving out of the flush is of a loss of rush and sedge dominants and *Molinietalia* herbs and a supplementing of the general *Molinio-Arrhenatheretea* element with a prominent *Cynosurion* component. In other cases, where springs or waterlogged hollows punctuate a landscape dominated by pervious limestones with rendzina soils, the floristic switch around the fen-meadow is to a *Mesobromion* sward, usually of the *Festuca-Avenula* type, with species such as *Briza media*, *Carex flacca*, *Centaurea nigra* and *Trifolium pratense* providing a link. Sometimes, where base-richness of the soils is pronounced, such grassland may provide a context for a wider range of wetter

calicolous communities around areas of soligenous influence, not only fen-meadow of the *Briza-Trifolium* type, but also the *Schoenetum* or, towards northern Britain, the *Pinguicula-Caricetum*. In some sites of this type, too, the *Cirsio-Molinietum* fen-meadow can figure in such mosaics, characteristic of somewhat drier soils than these springs and extending on to less base-rich ones. Its floristic similarity to the *Juncus-Cirsium* fen-meadow is considerable and in some cases it may have been derived from it by selective nutrient depletion with long-continued treatment.

Reduction of grazing in the *Juncus-Cirsium* fen-meadow results in an expansion of the bulky dominants and ranker grasses and an overwhelming of the smaller herbs, producing vegetation like that of the Typical sub-community. Patches of this can often be found within stands of the *Briza-Trifolium* sub-community, marking out less-frequented areas of ground, which then acquire some resistance to the reduction of the rough herbage which develops. In other cases, whole springs and hollows, more or less totally free of grazing, in field corners or alongside streams, can be occupied by this kind of fen meadow, sharply delineated from the heavily-cropped pasture around or, where neglect has extended on to drier ground also, grading to some kind of *Arrhenatheretum*, with plants such as *Festuca rubra*, *Holcus lanatus*, *Lotus uliginosus*, *Vicia cracca* and *Lathy-*

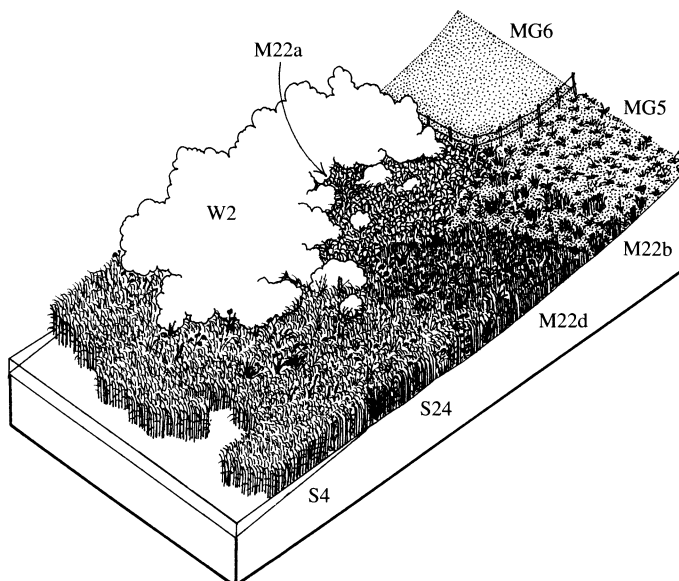
rus pratensis providing some floristic continuity, but dominance passing to *Arrhenatherum elatius* and *Molinietalia* tall herbs being replaced by *Arrhenatherion* umbellifers such as *Heracleum sphondylium* and *Anthriscus sylvestris*. Quite often, too, in such situations as this, the soils are sufficiently eutrophic to allow plants such as *Epilobium hirsutum* and *Urtica dioica* to gain a hold once grazing is relaxed and dense patches of these may be found among mosaics of these two communities. Indeed, a neat experiment described by Wheeler (1983b; see also Wheeler *et al.* 1985) has shown how an enclosed *Juncus-Cirsium* fen-meadow was fairly rapidly replaced by dense *E. hirsutum*, except where pronounced water-logging of the ground maintained ferrous ions at a level toxic to this tall herb, but still harmless to *J. subnodulosus* and its associates. Enrichment of ground waters by the washing out of fertilisers, now a very common feature of the lowland agricultural landscape in Britain, is likely to increase this kind of development in ungrazed stands.

The Typical sub-community of the *Juncus-Cirsium* fen-meadow, with its rank herbage, is perhaps rather resistant to rapid invasion by woody plants and successional developments subsequent to withdrawal of grazing have not been followed. Wetter spring-fens are likely to be invaded by much the same mixture of shrubs and trees as are characteristic colonists in topogenous fen-

Figure 18. Changes in fen and meadow zonation with improvement and neglect.

In the foreground is a traditional sequence in an open-water transition mire from *Phragmitetum* swamp (S4), through mown *Peucedano-Phragmitetum* (S24) and *Juncus-Cirsium* fen-meadow, *Iris* sub-community (M22d) to grazed *Juncus-Cirsium* fen-meadow, *Briza-*

Trifolium sub-community (M22b) and *Centaureo-Cynosuretum* (MG5). With enclosure and improvement of the drier ground, the last is converted to *Lolio-Cynosuretum* (MG6), while neglect of the mowing marsh leads to spread of rank Typical *Juncus-Cirsium* fen-meadow (M22a) and secondary *Salix-Betula-Phragmites* woodland (W2).



meadow, producing *Salix-Betula-Phragmites* woodland, but even in such cases, many stands are so small as to be probably marked out in subsequent woodland cover by just small patches of willow and birch within predominantly drier vegetation. Stands on ground which is not quite so thoroughly waterlogged would perhaps progress eventually to *Fraxinus-Acer-Mercurialis* woodland, whose *Deschampsia cespitosa* sub-community, when coppiced, produces a field layer which has some floristic similarity to the *Juncus-Cirsium* fen meadow. Extensive abandonment of ground, where such seral processes might be studied, has in fact been very unusual in the recent decades of vigorous land improvement and very often now, neglected *Juncus-Cirsium* fen-meadows remain isolated fragments closely hemmed in by much-altered pastures or arable land. Themselves originally of agricultural origin and rarely of spectacular richness, even when less overgrown, they nonetheless frequently provide an important remnant habitat for wetland species which were formerly much more common.

Distribution

The community is of wide distribution on suitably wet and base-rich soils through the southern British lowlands with particular concentrations of stands in East Anglia, north Buckinghamshire and Anglesey. The *Iris* and *Carex* sub-communities are especially well represented on topogenous mires in the first area but are much scarcer elsewhere. The *Briza-Trifolium* sub-community occurs throughout the range but, very frequently, spring-fen stands are of the Typical sub-community and, with neglect and land improvement, distribution of the community is becoming increasingly sparse.

Affinities

It was Wheeler (1975, 1980c) who, in his study of British rich fens, first gave some coherent shape to the diversity of vegetation types included in this community. Previously, assemblages of this kind, usually described under the general heading of 'fen-meadow', had been noted as components of wetland sequences (Pallis 1911, Clapham 1940, Rose 1950, Willis & Jefferies 1959), but rarely described in any detail; or, where subject to closer scrutiny, had been of a rather particular kind, as in the mowing-marsh and grazing-level stands of Lambert (1946, 1948). The treatment here is based heavily on the data and proposals of Wheeler, although many more impoverished stands (the commonest type) have been added and we follow his earlier scheme (Wheeler 1975) in recognising, as well as the *Carex* and *Iris* types, a major split among the remainder based on the presence or absence of the *Briza-Trifolium* preferentials. Many of the divisions outlined in his later proposals (Wheeler

1980c) are thus relegated to a minor level of variation, though one that is often quite striking to the eye and which, as Wheeler himself remarks, is perhaps just a fraction of the possible complex of responses to edaphic and treatment differences in this kind of vegetation.

Such differences, which reflect the diversity of vegetation types that have been converted into this fen-meadow and the peculiarities of site histories, inevitably make the community very cumbersome, with the individual character of particular stands often being more noticeable than their floristic similarities. And what they do have in common is often of a very general nature, with all the constants of the community and many of the most frequent associates being plants of fairly wide ecological tolerance and occurring commonly in other communities, combined frequently here because of a floristic convergence produced by the imposition of mowing and grazing. This characteristic places the *Juncus-Cirsium* fen-meadow unequivocally within the Molinietales of the Molinio-Arrhenatheretea, but it makes the boundaries of the communities against other vegetation types in this order very ill-defined.

Two particular problems should be noted. First, this community forms a national series with the *Holco-Juncetum* and the *Juncus-Galium* rush-pasture, which can be understood in relation to both climatic and edaphic variation in moving from east to west across the lowland south of Britain. Floristic shifts through this series can be seen both among the dominants, where there is a move from *J. subnodulosus* through *J. inflexus* to *J. effusus* and *J. acutiflorus*, and among the associates, where there is a move from more calcicolous to more calcifuge species and an appearance of some oceanic herbs, though the rank growth of the dominants and more bulky companions often masks these peculiarities. In Britain, too, although the two poles of this sequence of communities are very different, certain plants which, on the European mainland would be regarded as diagnostic of the extremes, are much less strictly confined in their occurrence. Thus, though the *Juncus-Cirsium* fen-meadow has frequent records for species like *Caltha palustris*, *Carex disticha*, *Lotus uliginosus* and *Lychnis flos-cuculi*, which would locate it among the Continental Calthion communities (Westhoff & den Held 1969), these all occur elsewhere in the Molinietales in this country and some of them even more widely. And other diagnostic plants of this alliance, such as *Bromus racemosus* and *Fritillaria meleagris*, are rare in Britain and usually found in other communities. At best, then, the *Juncus-Cirsium* fen-meadow can be accommodated into the European framework with some difficulty, and its increasing rarity means that, in many places, it is the *Holco-Juncetum* that is the more familiar British approximation to the Calthion. The relationship of the community to the *Caltha-Cynosurus* flood-pasture, a

third vegetation type which could be referred to this alliance must await further sampling: it has sufficient in common with the *Juncus*-*Cirsium* fen-meadow to be, perhaps, subsumed within it.

The second diagnostic difficulty is in separating this community from the *Cirsio-Molinietum*, a vegetation type likewise derived by mowing and grazing, with strong floristic links through Molinio-Arrhenatheretea herbs like *Holcus lanatus*, *Festuca rubra*, *Vicia cracca*, and Molinietales plants such as *Cirsium palustre*, *Filipendula ulmaria*, *Lotus uliginosus* and *Angelica sylvestris*, and with some parallel suites of preferentials in its sub-communities. *J. subnodulosus* can occur quite frequently in the *Cirsio-Molinietum* and *Molinia* is sometimes found in the *Juncus-Cirsium* fen-meadow but, generally speaking, there is a switch in dominance from the one to the other species in these two communities and a preferential occurrence in the *Cirsio-Molinietum*

of plants like *Cirsium dissectum*, *Carex panicea*, *C. hostiana*, *C. pulicaris* and *Succisa pratensis*, in assemblages similar to Continental Junco-Molinion vegetation (Westhoff & den Held 1969).

Among these suites of vegetation types, *J. subnodulosus* shows a definite peak of occurrence in the *Juncus-Cirsium* fen-meadow but this community contains only a fraction of the assemblages that have sometimes been united, in Continental classifications, in a compendious *Juncetum subnodulosi* (after Koch 1926), characterised by dominance of the rush. Among the vegetation types included there, the *Juncus-Cirsium* fen-meadow compares with the lowland stands separated off from this association into a *Crepido-Juncetum subnodulosi* (Libbert 1932, Tüxen 1937, Oberdorfer 1957) and with a variety of Calthion *Feuchtwiesen* described from Germany (Korneck 1963, Krausch 1964, Passarge 1964, Kloss 1965).

Floristic table M22

	a	b	c	d	22
<i>Juncus subnodulosus</i>	V (1–8)	IV (1–8)	V (1–6)	V (1–8)	V (1–8)
<i>Calliargon cuspidatum</i>	IV (1–5)	V (1–3)	V (1–5)	V (1–3)	V (1–5)
<i>Mentha aquatica</i>	IV (1–7)	V (1–3)	III (1–3)	V (1–3)	IV (1–7)
<i>Holcus lanatus</i>	IV (1–6)	V (1–3)	III (1–3)	IV (1–3)	IV (1–6)
<i>Cirsium palustre</i>	IV (1–4)	V (1–3)	IV (1–3)	III (1–3)	IV (1–4)
<i>Equisetum palustre</i>	IV (2–6)	IV (1–3)	IV (1–3)	II (1–3)	IV (1–6)
<i>Filipendula ulmaria</i>	III (1–7)	IV (1–3)	III (1–3)	V (1–3)	IV (1–3)
<i>Lotus uliginosus</i>	III (1–4)	IV (1–3)	III (1–3)	III (1–3)	IV (1–4)
<i>Cardamine pratensis</i>	II (2–3)	IV (1–3)	II (1–3)	II (1–3)	III (1–3)
<i>Juncus articulatus</i>	II (1–8)	IV (1–6)	II (1–3)	II (1–3)	II (1–8)
<i>Cerastium fontanum</i>	II (1–3)	IV (1–3)		II (1–3)	II (1–3)
<i>Briza media</i>	I (1–6)	IV (1–3)		I (1)	II (1–6)
<i>Trifolium repens</i>	I (1–5)	IV (1–3)		I (1–3)	II (1–3)
<i>Trifolium pratense</i>	I (2–4)	IV (1–3)			II (1–3)
<i>Anthoxanthum odoratum</i>	I (1–5)	IV (1–4)	II (1–3)	I (1–3)	II (1–3)
<i>Molinia caerulea</i>	II (1–7)	III (1–4)	II (1–3)	I (1)	II (1–7)
<i>Rumex acetosa</i>	II (1–4)	III (1–3)	II (1–3)	I (1–2)	II (1–4)
<i>Juncus inflexus</i>	II (1–5)	III (1–6)	II (1–3)	I (1)	II (1–6)
<i>Epilobium parviflorum</i>	II (1–3)	III (1–3)	I (1)	I (1–3)	II (1–3)
<i>Dactylorhiza fuchsii</i>	I (1–4)	III (1–3)	I (1–2)	I (1–2)	II (1–4)
<i>Plantago lanceolata</i>	I (1–4)	III (1–3)	I (1–3)	I (1–3)	I (1–4)
<i>Prunella vulgaris</i>	I (1–4)	III (1–3)		I (1–3)	I (1–4)
<i>Centaurea nigra</i>	I (2–4)	III (1–2)		I (1–3)	I (1–4)
<i>Ranunculus repens</i>	I (1–4)	III (1–3)			I (1–4)
<i>Triglochin palustre</i>	I (1–2)	III (1–2)			I (1–2)
<i>Rhinanthus minor</i>	I (1–4)	II (1–3)	I (3)	I (1–3)	I (1–4)
<i>Carex flacca</i>	I (1–3)	II (1–3)			I (1–3)
<i>Carex hirta</i>	I (1–3)	II (1–3)			I (1–3)
<i>Juncus effusus</i>	I (1–4)	II (1–3)			I (1–4)
<i>Cynosurus cristatus</i>		II (1–3)			I (1–3)
<i>Phragmites australis</i>	II (1–4)	I (1–5)	IV (1–3)	IV (1–4)	II (1–5)
<i>Hydrocotyle vulgaris</i>	II (1–6)	II (1–3)	V (1–3)	IV (1–3)	III (1–6)

<i>Lythrum salicaria</i>	I (2–3)	I (1–2)
<i>Menyanthes trifoliata</i>	I (1–2)	I (1)
<i>Myosotis scorpioides</i>	I (1–3)	I (1)
<i>Campyllum stellatum</i>	I (1–3)	I (1–2)
<i>Plagiomnium rostratum</i>	I (1)	I (1)
<i>Carex elata</i>		
<i>Potentilla palustris</i>		
<i>Galium palustre</i>	II (3–5)	III (1–3)
<i>Epilobium palustre</i>	II (1–3)	I (1)
<i>Equisetum fluviatile</i>	I (1–3)	I (1–3)
<i>Dactylorhiza incarnata</i>		II (1–3)
<i>Berula erecta</i>	I (1–3)	
<i>Pedicularis palustris</i>	I (1–4)	
<i>Salix cinerea</i> sapling	I (1–3)	I (1–3)
<i>Dactylorhiza majalis praetermissa</i>		I (1–3)
<i>Thelypteris palustris</i>		
<i>Ophioglossum vulgatum</i>		
<i>Carex acutiformis</i>	II (1–4)	II (1–4)
<i>Iris pseudacorus</i>	I (1–2)	I (1–3)
<i>Ranunculus flammula</i>		II (1–2)
<i>Valeriana officinalis</i>	I (1–4)	I (1)
<i>Lysimachia vulgaris</i>		
<i>Thalictrum flavum</i>		
<i>Epilobium hirsutum</i>	I (1–3)	
<i>Calystegia sepium</i>	I (1–3)	
<i>Phalaris arundinacea</i>	I (1–4)	
<i>Carex lepidocarpa</i>		I (1–2)
<i>Peucedanum palustre</i>		
<i>Calamagrostis canescens</i>		
<i>Symphytum officinale</i>		
<i>Cladium mariscus</i>		
<i>Galium uliginosum</i>	IV (1–5)	IV (1–3)
<i>Lychnis flos-cuculi</i>	III (1–3)	IV (1–3)
<i>Poa trivialis</i>	II (1–4)	IV (1–3)
<i>Caltha palustris</i>	II (1–4)	III (1–3)

III (1-3)	III (1-3)	I (1-3)
II (1-4)	II (1-4)	I (1-4)
II (1-3)	II (1-2)	I (1-3)
II (1-3)	II (1-3)	I (1-3)
II (1)	II (1-2)	I (1-2)
V (1-4)	I (1-2)	I (1-4)
IV (1-3)	II (1-2)	I (1-3)
IV (1-3)	III (1-3)	II (1-5)
III (1-2)	II (1-3)	II (1-3)
III (1-3)	II (1-2)	I (1-3)
III (1-3)	II (1-2)	II (1-3)
II (1-3)	I (1-3)	I (1-3)
II (1-3)	I (1)	I (1-4)
II (1-2)		I (1-3)
II (1-3)	I (1)	I (1-3)
II (1-3)		I (1-3)
I (1-2)		I (1-2)
I (1)	IV (1-6)	II (1-6)
II (1-3)	V (1-3)	I (1-3)
II (1-3)	III (1-3)	I (1-3)
I (1-3)	III (1-3)	I (1-4)
I (1-3)	III (1-3)	I (1-3)
	III (1-2)	I (1-2)
I (1-3)	II (1-3)	I (1-3)
I (1-2)	II (1-3)	I (1-3)
	II (1-3)	I (1-4)
	II (1-3)	I (1-3)
	II (1-3)	I (1-3)
	II (1-4)	I (1-4)
	II (1-3)	I (1-3)
	I (1-2)	I (1-2)
III (1-3)	III (1-3)	III (1-5)
III (1-3)	IV (1-3)	III (1-3)
II (1-3)	IV (1-3)	III (1-4)
IV (1-3)	IV (1-3)	III (1-4)

Floristic table M22 (cont.)

	a	b	c	d	22
<i>Carex panicea</i>	II (1–7)	V (1–3)	IV (1–3)	III (1–3)	III (1–7)
<i>Festuca rubra</i>	III (1–5)	V (1–4)	II (1–3)	III (1–2)	III (1–5)
<i>Agrostis stolonifera</i>	III (2–5)	V (1–5)	II (1–2)	III (1–3)	III (1–5)
<i>Ranunculus acris</i>	II (1–4)	V (1–3)	III (1–3)	III (1–3)	III (1–4)
<i>Valeriana dioica</i>	III (1–4)	IV (1–5)	III (1–3)	III (1–3)	III (1–4)
<i>Vicia cracca</i>	III (1–5)	IV (1–3)	II (1–3)	III (1–3)	III (1–5)
<i>Lathyrus pratensis</i>	III (1–5)	IV (1–3)	III (1–3)	I (1–2)	III (1–5)
<i>Brachythecium rutabulum</i>	II (1–4)	III (1–2)	II (1–2)	IV (1–3)	III (1–4)
<i>Angelica sylvestris</i>	III (1–6)	III (1–3)	II (1–3)	III (1–2)	III (1–6)
<i>Succisa pratensis</i>	II (1–5)	III (1–3)	II (1–3)	III (1–3)	III (1–5)
<i>Carex disticha</i>	II (1–7)	III (1–6)		III (1–6)	III (1–7)
<i>Potentilla erecta</i>	II (1–4)	III (1–3)	I (1)	IV (1–3)	II (1–4)
<i>Eupatorium cannabinum</i>	II (1–3)	II (1–3)	II (1–3)	II (1–3)	II (1–3)
<i>Hypericum tetrapterum</i>	II (1–2)	II (1–3)	II (1–3)	I (1–3)	II (1–3)
<i>Arrhenatherum elatius</i>	II (1–4)	II (1–3)	II (1–3)	I (1–3)	II (1–4)
<i>Scrophularia auriculata</i>	II (1–4)	II (1–3)		I (1)	II (1–4)
<i>Potentilla anserina</i>	I (1–3)	II (1–3)	I (1)	I (1)	I (1–3)
<i>Deschampsia cespitosa</i>	I (1–3)	II (1–3)	I (1)	I (1)	I (1–3)
<i>Carex nigra</i>	I (1–6)	II (1–4)	I (1)		I (1–6)
<i>Pulicaria dysenterica</i>	I (1–6)	II (1–3)		I (1)	I (1–6)
<i>Rumex conglomeratus</i>	I (1–3)	I (1–3)	I (1–3)	I (1–3)	I (1–3)
<i>Myosotis laxa caespitosa</i>	I (1–2)	I (1–3)	I (1–3)	I (1–3)	I (1–3)
<i>Plagiomnium undulatum</i>	I (1–3)	I (1–3)	I (1–3)		I (1–3)
<i>Rhizomnium punctatum</i>	I (1–3)	I (1–3)	I (1–3)		I (1–3)
<i>Oenanthe lachenalii</i>	I (1–3)	I (1–3)	I (1–3)		I (1–3)
<i>Potentilla reptans</i>	I (1–4)	I (1–3)		I (1–3)	I (1–4)
<i>Epipactis palustris</i>	I (1–5)	I (1–3)		I (1–3)	I (1–5)
<i>Lophocolea bidentata s.l.</i>	I (1–2)		I (1–3)	I (1–3)	I (1–3)
<i>Lycopus europaeus</i>	I (1–3)		I (1–3)	I (1–3)	I (1–3)
<i>Scutellaria galericulata</i>	I (1–2)		I (1–3)	I (1–3)	I (1–3)
<i>Eriophorum angustifolium</i>		I (1–6)	I (1–3)	I (1–3)	I (1–6)
<i>Luzula multiflora</i>		I (1–3)	I (1–3)	I (1–3)	I (1–3)

<i>Phleum pratense</i>	I (1–3)	I (1–3)
<i>Veronica beccabunga</i>	I (1–3)	I (1–3)
<i>Ajuga reptans</i>	I (1–4)	I (1–3)
<i>Rumex sanguineus</i>	I (1–3)	I (1–3)
<i>Cirsium arvense</i>	I (1–3)	I (1–3)
<i>Pseudoscleropodium purum</i>	I (1–3)	I (1–3)
<i>Achillea ptarmica</i>	I (1–4)	I (1–3)
<i>Festuca arundinacea</i>	I (1–3)	I (1–3)
<i>Cratoneuron filicinum</i>	I (1–3)	
<i>Solanum dulcamara</i>	I (1–3)	
<i>Lemna minor</i>	I (1–3)	
<i>Plagiomnium affine</i>		I (1–3)
<i>Cirsium dissectum</i>		I (1)
<i>Eleocharis palustris</i>		I (1–3)
<i>Carex rostrata</i>		
<i>Polygonum amphibium</i>		
<i>Stellaria palustris</i>		
<i>Eleocharis uniglumis</i>		

Number of samples	94	51
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- a Typical sub-community
- b *Briza media*-*Trifolium* spp. sub-community
- c *Carex elata* sub-community
- d *Iris pseudacorus* sub-community
- 22 *Juncus subnodulosus*-*Cirsium palustre* fen-meadow (total)

		I (1-3)
		I (1-3)
		I (1-4)
		I (1-3)
		I (1-3)
		I (1-3)
		I (1-4)
		I (1-3)
	I (1-3)	I (1-3)
	I (1-3)	I (1-3)
I (1-3)		I (1-3)
I (1-3)		I (1-3)
	I (1-3)	I (1-3)
	I (1-3)	I (1-3)
I (1-3)	I (1-3)	I (1-3)
I (1-3)	I (1-3)	I (1-3)
I (1)	I (1)	I (1)
I (1-3)	I (1-3)	I (1-3)
<hr/>		<hr/>
10	21	176
<hr/>		<hr/>

