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Phragmites australis-*Peucedanum palustre* tall-herb fen

Peucedano-Phragmitetum australis Wheeler 1978 emend.

Synonymy

Fen Association Pallis 1911; *Junco subnodulosi-Calamagrostietum canescentis* Korneck 1963 p.p.; *Cladium marisci sensu* Krausch 1964 p.p. and *sensu* Westhoff & den Held 1969 p.p.; *Scirpo-Phragmitetum sensu* Krausch 1964 p.p. and *sensu* Westhoff & den Held 1969 p.p.; *Thelypterido-Phragmitetum* Westhoff & den Held 1969 p.p.; *Thelypterido-Phragmitetum* Kuiper 1957 emend. Segal & Westhoff 1969 p.p.; *Peucedano-Phragmitetum australis* Wheeler 1978 p.p. and *Caricetum paniculatae peucedanetosum* Wheeler 1978.

Constant species

Calamagrostis canescens, *Cladium mariscus*, *Eupatorium cannabinum*, *Filipendula ulmaria*, *Galium palustre*, *Junco subnodulosus*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Mentha aquatica*, *Peucedanum palustre*, *Phragmites australis*, *Calliergon cuspidatum*.

Rare species

Carex diandra, *C. appropinquata*, *Cicuta virosa*, *Lathyrus palustris*, *Peucedanum palustre*, *Sium latifolium*, *Thelypteris palustris*.

Physiognomy

The *Peucedano-Phragmitetum* is a community of herbaceous fen vegetation, somewhat varied in composition but often species-rich and of complex physiognomy (Wheeler 1975, 1978, 1980a). Tall monocotyledons generally make up the major structural component and, of these, *Phragmites australis*, *Cladium mariscus* and *Calamagrostis canescens* are constant and the most usual dominants. Much less frequent throughout but occasionally dominant are *Carex paniculata*, *Glyceria maxima*, *Typha angustifolia*, *Phalaris arundinacea* and *Calamagrostis epigejos*. The gross appearance of the vegetation at any particular time of year depends very much on the phenology of these species and on the fen treatment, if any, but in summer, unmown stands have a

characteristically tall canopy, 1–2 m high, of varying density but often sufficiently thick to give stands a superficially uniform appearance.

Intermixed with these helophytes is a variety of tall herbaceous dicotyledons which, though rarely individually abundant, together give the vegetation a typically colourful appearance in the flowering season. *Lysimachia vulgaris*, *Lythrum salicaria*, *Eupatorium cannabinum*, *Filipendula ulmaria* and *Peucedanum palustre* are constant, the rare milk parsley having its major locus in this community. Also frequent are *Valeriana officinalis*, *Iris pseudacorus* and *Lycopus europaeus* and, rather more unevenly between the various sub-communities, *Angelica sylvestris*, *Cirsium palustre*, *Rumex hydrolapathum*, *Epilobium hirsutum* and *Symphytum officinale*.

Beneath these components, there is a rather variable layer, some 60–80 cm tall, generally dominated by sedges or rushes. *Junco subnodulosus* and *Carex elata* are the most frequent and abundant species here but *C. riparia*, *C. acutiformis*, *C. appropinquata*, *C. lasiocarpa* or *C. diandra* can all attain local prominence. In other cases, *Molinia caerulea*, *Schoenus nigricans* or *Thelypteris palustris* are abundant in this layer.

Smaller herbaceous species show a somewhat patchy occurrence throughout the community, their variety and abundance being greater where the layers of taller and bulkier species are more open. *Mentha aquatica* is the only frequent species throughout but some of the following often occur: *Scutellaria galericulata*, *Hydrocotyle vulgaris*, *Potentilla palustris*, *Oenanthe fistulosa*, *Epilobium palustre*, *Cardamine pratensis*, *Lychnis flos-cuculi* and *Myosotis laxa* ssp. *caespitosa*. In some of the wetter expressions of the community, floating-leaved aquatics may be present.

A variety of sprawlers and climbers may be found, sometimes binding the vegetation into an almost impenetrable tangle. The most frequent of these is *Galium palustre* but *Solanum dulcamara*, *Calystegia sepium*, *Vicia cracca*, *Galium uliginosum* and the rarer *Stellaria palustris* and *Lathyrus palustris* also occur.

Although *Calliergon cuspidatum*, *Campylium stellatum* and *Brachythecium rutabulum* occur in the community, sometimes in abundance over litter or patches of bare substrate, bryophytes are typically not well represented.

Seedlings and saplings of *Salix cinerea* and *Alnus glutinosa* are occasional to frequent throughout the community and, in some sub-communities, are characteristically abundant giving a scrubby appearance to the vegetation. Other generally low-frequency woody species include *Frangula alnus* and *Betula pubescens* and, in one type of *Peucedano-Phragmitetum*, *Myrica gale* forms a distinctive open canopy.

Sub-communities

Seven sub-communities are characterised here. The first two, though they preserve many of the general floristic features of the community, are superficially more distinctive, being diagnosed partly on the dominance of *Carex paniculata* and *Glyceria maxima*, two species which make a negligible contribution elsewhere in the *Peucedano-Phragmitetum*. The five remaining sub-communities are characterised mainly on differences in the tall-herb and sedge/rush layers and, even within individual sub-communities, can be dominated by a variety of helophytes.

***Carex paniculata* sub-community:** Tussock swamp Palis 1911 *p.p.*; *Caricetum acutiformo-paniculatae* V1. & Van Zinderen Bakker 1942 *p.p.*; Primary tussock fen Lambert 1951; *Caricetum paniculatae thelypteridetosum* and *caricetosum acutiformis* Segal & Westhoff 1969; *Caricetum paniculatae peucedanetosum* Wheeler 1978. Here, the physiognomy is overwhelmingly dominated by the sometimes enormous tussocks of *C. paniculata*; indeed, the vegetation looks like a sedge-swamp with a *Peucedano-Phragmitetum* element perched on the tussock tops. The tussocks themselves are frequently up to 1 m or more in height and diameter and from among the spreading crown of shoots grow many of the characteristic tall dicotyledons of the community, *Lysimachia vulgaris*, *Lythrum salicaria*, *Eupatorium cannabinum*, *Peucedanum palustre* and the sprawling *Galium palustre*. There may also be some *Solanum dulcamara*, *Epilobium hirsutum*, *Scutellaria galericulata*, *Calystegia sepium* and *Lycopus europaeus* and, particularly distinctive of this sub-community, *Scrophularia auriculata* and the naturalised alien *Impatiens capensis*. *Thelypteris palustris* is also frequent, sometimes forming a dense cover of fronds. Smaller herbaceous species frequent in other sub-communities here tend to be rare but there may be a patchy mat of *Calliergon cuspidatum*, *Brachythecium rutabulum* and *Lophocolea bidentata sensu lato* over the shoot bases. This is also one of the types of the *Peucedano-Phragmitetum* that is especially prone to invasion

by trees and seedlings and saplings of *Salix cinerea* and *Alnus glutinosa* are often abundant among the herbs.

This sub-community seems to develop by *C. paniculata* gaining a hold on the felted root mat of old *Phragmitetum australis* (Lambert 1951: see below) and reed may remain quite abundant between the expanding tussocks. However, *Calamagrostis canescens* and *Cladium mariscus* and the two most important components of the *Peucedano-Phragmitetum* sedge/rush layer, *Juncus subnodulosus* and *Carex elata*, are generally uncommon. Here, these are sometimes replaced by a variety of tall swamp helophytes and sedges of medium stature which occur patchily in the wet hollows that develop as the bulky tussocks begin to depress the underlying substrate, e.g. *Typha angustifolia*, *Sparganium erectum*, *Carex pseudocyperus*, *C. acutiformis* and *C. riparia*. *Rumex hydrolapathum* and *Ranunculus lingua* may also be locally prominent as emergents. In other cases, open water has just a floating mat of *Lemna minor* or is completely devoid of vegetation.

***Glyceria maxima* sub-community:** Yare Valley fen Palis 1911; *Glycerietum maximae* Hueck 1931 *p.p.*; Primary *Glycerietum* hover fen *p.p.* and Secondary *Glycerietum* fen Lambert 1946; Mowing marsh vegetation Lambert 1948 *p.p.*; *Peucedano-Phragmitetum glycerietosum* Wheeler 1980a. The somewhat varied vegetation included in this sub-community is characterised in general by the prominence of *G. maxima* among the taller fen species. In some stands, it is dominant and its lush growth and the lodging of the shoots tend to depress the richness of the associated flora. *Phragmites* persists, together with most of the tall dicotyledons of the community, and there may be patches of *Epilobium hirsutum* and *Urtica dioica*, some *Caltha palustris* and *Scutellaria galericulata* below and sprawling *Calystegia sepium*. Other stands have a reduced cover of *G. maxima* and here *Phragmites* is normally the dominant in vegetation that is substantially richer, especially in the sedge/rush layer. *Carex elata* and, especially, *Juncus subnodulosus* are more plentiful and some of the typical sedges of the *C. paniculata* sub-community occur here too, sometimes in abundance, with *C. paniculata* itself, *C. riparia* and *C. acutiformis* attaining locally dominant roles. Sprawlers are also more conspicuous with *Galium palustre*, *Solanum dulcamara*, *Vicia cracca* and the rare *Lathyrus palustris*. The last, together with *Thalictrum flavum*, are particularly distinctive of this and the next sub-community within the *Peucedano-Phragmitetum*. Smaller herbs, too, are better represented in this more open vegetation with *Mentha aquatica*, *Myosotis scorpioides* and sometimes *Impatiens capensis*. *Calliergon cuspidatum* and *Brachythecium rutabulum* occur patchily over litter and bare substrate.

***Symphytum officinale* sub-community:** Wicken Fen species groups 7–13 Yapp 1908; Wicken Fen Mixed Sedge Godwin & Tansley 1929 *p.p.*; Woodwalton Fen *Calamagrostis sere* Poore 1956b; Catcott Heath fen Willis 1967 *p.p.*; *Peucedano-Phragmitetum symphytetosum* Wheeler 1980a. In general floristics, this is much more of a central type of *Peucedano-Phragmitetum* than either the *Carex paniculata* or the *Glyceria* sub-community, although it shows some particular similarities to the latter. Often, however, local variation, especially among the dominants, masks the general features of the vegetation. At Wicken Fen, for example, *Phragmites* and, especially, *Cladium* are prominent (Yapp 1908, Godwin & Tansley 1929, Wheeler 1975); at Woodwalton Fen, *C. canescens* and, more locally, *C. epigejos* are often dominant (Poore 1956b, Wheeler 1975). Among this canopy, though, all the tall dicotyledonous constands of the community are well represented with, in addition, frequent *Iris pseudacorus*, *Lycopus europaeus*, *Angelica sylvestris*, *Cirsium palustre*, *Thalictrum flavum*, *Stachys palustris* (at Woodwalton) and, especially distinctive here, *Symphytum officinale*.

The sedge/rush layer is sometimes extensive, though generally species-poor and, like the helophyte element, variable in its composition. There is usually some *Carex acutiformis* but *Juncus subnodulosus* can vary from being abundant (as in some Wicken stands) to very local or absent (as at Woodwalton). A distinctive feature in some cases, especially where there is little *Cladium*, is the prominence of tussocks of *Molinia caerulea*, often with some *Carex panicea* and *Salix repens* (Wicken); *M. caerulea* was also prominent, with *J. subnodulosus*, in the tall-herb fen vegetation very similar to this sub-community described from Catcott Heath on the Somerset Levels (Willis 1967). There, too, *Thelypteris palustris* was abundant, though it is generally rare in this sub-community.

Smaller herbaceous species are not well represented here, though there are usually some sprawlers with *Galium palustre*, *Lathyrus palustris* and *Calystegia sepium* frequent; at Wicken, *Galium uliginosum*, generally rare in the *Peucedano-Phragmitetum*, is common. Bryophytes are somewhat variable: *Calliergon cuspidatum* and *Campylium stellatum* occur throughout and, in wetter sites, may be prominent; drier stands often have only a few strands of *Brachythecium rutabulum*.

In general, this vegetation is drier underfoot than many types of the community and invasion by woody species is frequent. *Salix cinerea* seedlings and saplings occur commonly, sometimes with *Crataegus monogyna*, *Betula* spp. and *Frangula alnus*. These, together with the varying pattern of dominance and the patchy occurrence of bulky tall herbs, combine to give the vegetation a somewhat scruffy appearance.

Typical sub-community: Bure Valley fen Pallis 1911; Primary *Phragmitetum p.p.* and Secondary *Phragmitetum* Lambert 1946; Mowing marsh vegetation Lambert 1948 *p.p.*; Anthropogenic *Phragmitetum*, *Calamagrostis* and *Juncus* fens Lambert 1951; *Peucedano-Phragmitetum typicum*, typical variant Wheeler 1978. *Phragmites* is the most frequent helophyte here and is usually dominant. *C. canescens* is less common and variable in abundance, being particularly prominent in drier situations such as the well-drained edges of marsh compartments but completely absent from wetter stands. *Cladium* is much less frequent than either of these species, although it may attain local abundance. Tall dicotyledons are well represented with, in addition to the community constants, *Valeriana officinalis*, *Iris pseudacorus*, *Lycopus europaeus*, *Rumex hydrolapathum*, *Angelica sylvestris* and *Cirsium palustre*. *Epilobium hirsutum*, *Phalaris arundinacea* and *Urtica dioica* are uncommon and rarely abundant.

There is usually a prominent understorey of *J. subnodulosus* with varying amounts of *Thelypteris palustris*; in some stands, especially where there is a shrubby element, the latter species forms a thick cover. Sedges are, however, rather infrequent: there is sometimes a little *C. elata* or *C. pseudocyperus* and, more rarely, *C. appropinquata* or *C. acutiformis*. Beneath is a generally species-poor small-herb element: *Mentha aquatica*, *Scutellaria galericulata*, *Potentilla palustris* and *Hydrocotyle vulgaris* occur here, sometimes with *Oenanthe fistulosa*. *Galium palustre* is the only common sprawler. *Calliergon cuspidatum* and *Campylium stellatum* are frequent but rarely abundant. In drier stands, seedlings and saplings of *Salix repens* and *Alnus glutinosa* may be prominent.

***Cicuta virosa* sub-community:** *Peucedano-Phragmitetum cicutetosum* Wheeler 1978. Again, *Phragmites* is usually the most prominent helophyte although *C. mariscus* is also frequent and it may dominate. *C. canescens* is less common here than in the Typical sub-community and rarely abundant; in some stands, it tends to be replaced by *Typha angustifolia* which is preferential for this sub-community. Among the tall dicotyledons, umbellifers are especially prominent: as well as *Peucedanum palustre*, *Sium latifolium*, *Berula erecta* and *Cicuta virosa* are also constant here and, from July to September, give a characteristic white bloom to uncut stands. Many of the other *Peucedano-Phragmitetum* tall herbs remain frequent including *Lysimachia vulgaris*, *Lythrum salicaria*, *Eupatorium cannabinum*, *Iris pseudacorus* and *Lycopus europaeus*. *Ranunculus lingua* is also preferentially constant here. Some species more characteristic of drier fens, such as *Filipendula ulmaria*, *Valeriana officinalis* and *Angelica sylvestris*, are markedly reduced in frequency.

The sedge/rush and small herb layers are typically well developed and species-rich. *J. subnodulosus* and *C. elata* are both constant and each may be abundant and, in addition, *C. pseudocyperus* is preferential here and often noticeable by virtue of its yellow-green shoots. A variety of other sedges of medium size may make a locally important contribution (see variants below). Among smaller dicotyledons, *Mentha aquatica*, *Potentilla palustris*, *Hydrocotyle vulgaris* and *Oenanthe fistulosa* are constant and *Cardamine pratensis* and *Stellaria palustris* occasional. *Galium palustre* occurs throughout. Bryophytes are somewhat variable although *Calliergon cuspidatum* and *Campyllum stellatum* are constant. Bushes of *Saxex cinerea* and *Myrica gale* occur occasionally.

Typical variant: *Peucedano-Phragmitetum cicutetosum*, typical variant Wheeler 1978. In this more species-poor vegetation, *Phragmites* is usually obviously dominant, often with some *Cladium* and *C. canescens*. In wetter stands, *Carex paniculata* or *C. riparia* may attain local prominence. The sedge/rush layer is here less bulky and rich although there is generally some *J. subnodulosus*, *C. elata* and *C. pseudocyperus*. Where *Filipendula ulmaria* and *Valeriana officinalis* occur in this sub-community, it is in this drier variant and here, too, sprawlers may be more conspicuous with *Solanum dulcamara* and *Calystegia sepium*.

***Carex lasiocarpa* variant:** *Cicuto-Caricetum pseudocyperici comaretosum* Van Donselaar 1961 p.p.; *Peucedano-Phragmitetum cicutetosum*, *Carex lasiocarpa* variant Wheeler 1978. Here, *Cladium* and *Calamagrostis canescens* are less frequent and abundant and, although *Phragmites* may remain prominent and be accompanied by *Typha angustifolia*, it is the sedge/rush layer that often comprises the bulk of the vegetation. *J. subnodulosus*, *C. elata* and *C. pseudocyperus* are here accompanied by *C. lasiocarpa*, which may form a thick understorey, and more occasionally by *C. appropinquata* and *C. diandra*. *C. rostrata* has its rare Broadland station in vegetation of this kind and *C. limosa*, although not re-found by Wheeler (1978), also appears to have occurred in Norfolk in this variant. Beneath, smaller herbs are often numerous and abundant: in addition to those characteristic of the sub-community in general, there are frequent clumps of *Menyanthes trifoliata* and *Caltha palustris* and scattered shoots of *Equisetum fluviatile* and *Pedicularis palustris*. The orchids *Epipactis palustris*, *Dactylorhiza incarnata* and *D. majalis* ssp. *praetermissa* occur occasionally and *Alisma plantago-aquatica*, *Baldellia ranunculoides* and *Nymphaea alba* are sometimes found on the oozing peat. Much of the ground surface may, however, be clothed with a carpet of bryophytes studded with the shoots of *Hydrocotyle vulgaris*. As well as *Calliergon cuspidatum* and *Campyllum stellatum*,

there are records for *Calliergon giganteum*, *Riccardia pinguis* and, less frequently, *Bryum pseudotriquetrum*, *Scorpidium scorpioides*, *Plagiomnium elatum* and *Campyllum elodes*.

***Schoenus nigricans* sub-community:** *Peucedano-Phragmitetum schoenetosum* Wheeler 1978. Although *Cladium* and, less frequently, *Phragmites*, normally dominate in this sub-community, the helophyte and tall-herb components are somewhat poorer than in other types of *Peucedano-Phragmitetum*: *Calamagrostis canescens*, *Filipendula ulmaria*, *Angelica sylvestris*, *Cirsium palustre* and *Rumex hydrolapthum* are all, at most, occasional. Beneath, however, the sedge/rush layer is distinctive in the high frequency, and sometimes the abundance, of *Schoenus nigricans*, intermixed with *C. elata* and *J. subnodulosus*. The small herb element, too, has a characteristic quality, although it is somewhat variable: as well as the more usual *Mentha aquatica* and *Hydrocotyle vulgaris* (which are constant here) and *Scutellaria galericulata* and *Oenanthe fistulosa* (which occur occasionally), there is often some *Ranunculus flammula* and *Carex panicea*, sometimes with *Molinia caerulea* and *Salix repens*. Occasional richer areas, usually of small extent and with a lower growth, may have scattered plants of *Pedicularis palustris*, *Carex lepidocarpa* and *Epipactis palustris*. *Osmunda regalis* has been recorded in this sub-community at one site. Along the Thurne valley in Norfolk, this kind of vegetation is additionally distinctive in the presence of numerous plants of *Oenanthe lachenalii* and occasional *Samolus valerandi*. Here, too, there are often abundant lianes of *Calystegia sepium* and sometimes a low carpet of *Agrostis stolonifera*. Bryophytes are typically not well developed.

***Myrica gale* sub-community:** *Cladium* anthropogenic fen Lambert 1951; *Peucedano-Phragmitetum myricetosum* Wheeler 1978. In the rather species-poor vegetation of this sub-community, *Phragmites*, *Cladium* or *Calamagrostis canescens* normally dominate. The constant dicotyledons of the community are all well represented but, among other tall herbs, only *Valeriana officinalis* is at all frequent. The sedge/rush layer, too, is not rich: *J. subnodulosus* is generally present, though often in small amounts, and *C. elata* and other sedges are rare or absent. *Thelypteris palustris*, however, is often prominent and there is sometimes a little *Molinia caerulea*. The most distinctive feature of the vegetation, though, is the presence of scattered leggy bushes of *Myrica gale*, often with saplings of *Betula pubescens*, *Salix cinerea* and *Alnus glutinosa*. Beneath this uneven shrubby canopy, smaller herbs and bryophytes are typically sparse: even *Mentha aquatica* is no more than

occasional, although small amounts of *Salix repens* are characteristic.

Habitat

The *Peucedano-Phragmitetum* is generally restricted to fen peats with a moderate to high summer water-table and some winter flooding with base-rich, calcareous and often oligotrophic waters (Wheeler 1978, 1980a, 1983). It is a community of topogenous mires, occurring as primary fen in open-water transitions but being especially characteristic of flood-plain mires where long and complex histories of exploitation for peat and marsh crops have often led to the maintenance of the community as anthropogenic secondary vegetation.

The community is now almost entirely confined to Broadland with a few outlying stations on fragments on flood-plain mires that have escaped drainage and embankment or where a high level of unenriched waters is artificially maintained. Although it was certainly more extensive in the past (e.g. Pallis 1911), it is probably essentially a vegetation type of those areas to the south and east where once extensive flood-plains with calcareous catchments occur in a more continental climate. Some of the most important species in the community, such as *Cladium* and *Juncus subnodulosus*, have a well-established preference for base-rich, waterlogged conditions and others have a Continental or Continental Northern distribution, being generally limited in Britain to wet (though not necessarily base-rich and calcareous) habitats away from the west of the country: e.g. *Ranunculus lingua*, *Rumex hydrolapathum*, *Carex appropinquata*, *C. diandra*, *C. lasiocarpa*, *Cicuta virosa*, *Lathyrus palustris*, *Peucedanum palustre*, *Stellaria palustris*, *Thelypteris palustris* (Matthews 1955, Ratcliffe 1977, Jermy *et al.* 1978).

Within the *Peucedano-Phragmitetum*, many of the floristic differences between the sub-communities seem to be related most clearly to edaphic conditions, particularly the water regime and the trophic state of the substrate. Where the community occurs as primary fen, mostly in the flooded medieval peat diggings of the Broadlands, these variables are largely dependent upon the progress of the natural hydrarch succession around the open waters but, elsewhere, shallow peat extraction and other forms of soil disturbance have much altered the state of the surface, often producing very distinct local conditions for recolonisation. On the more solid peats, too, the community has been and, on a much reduced scale, still is affected by a variety of mowing treatments. The most obvious impact of these seems to be on the quantitative balance between species within the sub-communities affected, thus producing an overlay of variation in dominance upon the more complex, edaphically influenced differences (Wheeler 1978, 1980a) but consistent treatments may well contribute to qualitative

variation between sub-communities (e.g. Godwin 1941; see below).

There are other reasons, too, why it is very difficult to disentangle the influences of soil and treatment variables on differences in composition and structure between and within the various sub-communities. If there is some measure of primary edaphic control on the floristics of the community, then treatment options may well be limited and particular mowing regimes adopted initially to suit the species growing best naturally (Wheeler 1978). Local traditions of treatment may thus have tended to confirm local natural effects and it may be such combinations of influences that are responsible for the rather striking pattern of distribution of some of the sub-communities in particular stretches of fen. Mowing, at least winter mowing for reed, has also traditionally had to be confined to drier areas of fen which means that, in some cases, such interactions between soil and treatment variables have occurred over only part of the range of water and nutrient regimes experienced by the community. Where mowing has occurred, it is likely, too, that the treatment itself has produced some modification of soil conditions with harvesting of the crop, burning of litter, controlled unseasonal flooding and the application of fertilisers or marl. Making sense of all this is not helped by the sometimes fragmentary survival of the community, even in Broadland, and the difficulty of documenting treatment histories, especially now that most of the mowing traditions are defunct. The following therefore provides little more than an indication of the possible habitat relations of the community.

Typically, the *Peucedano-Phragmitetum* occurs on raw peat soils with, in Broadland, a water pH generally between 6.5 and 7.5 and dissolved calcium levels in the range 60–120 mg l⁻¹ (Wheeler 1983). Where the community develops as primary fen around the Broadlands margins, the peat is the often still fairly thin layer of organic material that has been accumulating over the rhizome and root mat of the preceding swamp vegetation and the fen is subject to edaphic conditions which continue to be determined largely by the nearby open waters. The peat is often continuously waterlogged throughout the year and closely exposed to any fluctuations in water-level and to irrigation with any dissolved salts. In such situations, too, the vegetation is inaccessible to grazing stock (though not necessarily to coypu and wildfowl: see below) and often impossible to mow, especially in winter. In general, therefore, the floristics and structure of such primary *Peucedano-Phragmitetum* tend to be strongly influenced by the continuing natural persistence of the one-time swamp dominant. Which particular helophyte it seems to depend partly on the nutrient status of the waters.

Along the Bure and the Ant valleys, it is the Typical

sub-community which comprises the bulk of primary fen with *Phragmites* as the usual dominant over a firm, though sometimes floating, peat raft with a summer water-table around the substrate surface and with often prolonged winter flooding. Much less commonly, *C. mariscus* dominates in essentially similar vegetation: this species is more prominent around isolated, land-locked broads like Upton where it perhaps has the edge on *Phragmites* in more oligotrophic conditions (Lambert 1951, Phillips 1977, Wheeler 1980a). The tall dicotyledons so typical of the *Peucedano-Phragmitetum* may also find it more difficult to gain a hold in *Cladietum* swamp with its very dense shoot cover and often thick litter layer, though the effects of these may be offset somewhat if *Cladietum* is mown: cutting for sedge, being a summer operation carried out when the surface is drier, has perhaps pushed further towards open water than mowing for other crops.

In more eutrophic conditions, *Glyceria maxima* can retain its pre-eminence over *P. australis* in primary fen as well as in swamp (Lambert 1946) and, along the Yare, with its pronounced pattern of tidally influenced irrigation, it is the usual dominant in the fens around the broads and dykes in the *Glyceria* sub-community. This kind of *Peucedano-Phragmitetum* is floristically distinct in the presence of other more nutrient-demanding species, such as *Epilobium hirsutum* and *Typha latifolia*, and it also has frequent *Carex riparia* which is perhaps able to tolerate the often loose substrate: typically, primary fen of the *Glyceria* sub-community develops on a quaking raft of *G. maxima* rhizomes, peat and deposited silt which rises and falls with the fluctuating waters (the 'hover fen' of Lambert 1946). *G. maxima*, however, retains its overwhelming dominance here only so long as there is an adequate supply of nutrients from the freely circulating waters or from more mineral-rich substrates. Lambert (1946, 1948; see also Buttery & Lambert 1965) showed how, around the broads and dykes of the middle Yare, the abundance of the species declined in moving to the centres of fen compartments on peat. With the increased dereliction of dykes and consequent restriction of free water movement since the time of Lambert's surveys, this *G. maxima*-dominated primary fen has become even more restricted in its distribution (Wheeler 1975). Such areas of the *Glyceria* sub-community have not been invaded by shrubs and trees are now much more frequently dominated by *P. australis* and have a richer and often confused associated flora which reflects both the drying and impoverishment of the peat and the complex history of treatment and neglect in this area (see further below).

The *Carex paniculata* sub-community shares certain floristic features with the *Glyceria* sub-community and it, too, may be characteristic of more eutrophic substrates (Lambert 1951). The edaphic conditions are,

however, rather distinctive because, as the *C. paniculata* tussocks enlarge upon the usually firm but often swinging mat of *P. australis* peat where they have gained a hold, they depress it, recreating swampy hollows between them (Lambert 1951, Wheeler 1978, 1980a). It is on the drier sides and tops of the tussocks themselves that much of the *Peucedano-Phragmitetum* flora establishes itself and here the vegetation is very prone to the invasion of woody species which may quickly form a canopy and curtail a primary fen phase.

The *Cicuta* sub-community also occurs as primary fen around some broad margins in the Ant valley, although in this kind of situation it is usually fragmentary and built around scattered *C. paniculata* tussocks (Wheeler 1980a). Elsewhere, however, the *Carex lasiocarpa* variant of this sub-community can be found as a striking kind of unmown fen vegetation in generally small stands in very wet hollows. Sometimes this vegetation occurs as a swinging raft of 50–100 cm of interlacing rhizomes over a suspension of semi-fluid peat and silt, suggesting that it has developed by the closing over of shallow depressions such as those left by nineteenth-century peat digging as on Catfield Fen (Wheeler 1975, 1978). The prominence in this variant of sedges which are also characteristic of the *Carex rostrata-calliergon* fen suggests that a combination of extreme wetness with lack of throughput may play some part in determining the distinctive nature of the associates but the significance of these conditions is unknown (Wheeler 1980c).

Away from the vicinity of open water, the peat is generally drier with a lower summer water-table and less prolonged winter flooding, if any, and is further removed from any natural enrichment by eutrophic river waters (Giller 1982, Wheeler 1983). In such situations, the vigour of some of the helophytes prominent in certain types of primary *Peucedano-Phragmitetum*, e.g. *Glyceria maxima*, *Typha* spp., may decline and other species more tolerant of drier conditions, e.g. *Juncus subnodulosus*, *Calamagrostis canescens*, become more abundant. Here too, however, in contrast to its often treacherous condition nearer the open water, the community has been accessible for the harvesting of various fen crops and there is little doubt that much *Peucedano-Phragmitetum* has been maintained as secondary fen by a range of cutting regimes which have repeatedly set back the invasion of woody species possible with a lower water-table. Of those forms of the community which at present extend into open-water transitions as primary fen, the Typical and *Glyceria* sub-communities seem able to survive such treatment on drier peats with some modification to their floristics and physiognomy but with their basic integrity intact, except in the most extreme conditions. The *Carex paniculata* sub-community seems to have been rarely mown in its fully-developed natural form because of the obstruction

caused by the bulky sedge-tussocks but it is known that these were sometimes dug out to facilitate cutting and, in Broadland, they found a quaint local use, when trimmed down, as fireside seats and church kneelers (Lambert 1965).

Two further types of *Peucedano-Phragmitetum*, the Typical variant of the *Cicuta* sub-community and the *Schoenus* sub-community, are generally found only on these drier peats and then only where there has been a tradition of mowing. It is consequently particularly difficult here to say what balance of edaphic and treatment variables has influenced their composition. The former occurs on fairly firm peats around Barton Broad and on Woodbastwick Fen where the summer water-table is at least 20 cm below the surface (Wheeler 1975). It has perhaps developed in these sites over shallow nineteenth-century peat diggings which have now acquired a solid infill of new organic matter consolidated by repeated cropping of *Phragmites* (Lambert 1951). The *Schoenus* sub-community is extensive in the Ant and Thurne valleys in similarly drier situations but, where there has been peat digging, it occurs only on the uncut surfaces (Wheeler 1980a). The distinctive stands of this sub-community around the Thurne broads also show some maritime influence with *Oenanthe lachenalii* and *Samolus valerandi* occurring, perhaps in response to percolation of saline water under the fairly narrow bank of dunes that separates these fens from the sea (Wheeler 1980a).

Mowing has also played some part in influencing the vegetation of the *Symphytum* sub-community but also of importance here is the marked association with the driest and sometimes most disturbed peat surfaces on which the *Peucedano-Phragmitetum* occurs (Wheeler 1975, 1980a). This sub-community is found on flood-plains outside Broadland where, now set in drained and improved agricultural landscapes, small fragments of mire remain, their drying peat surfaces often marked by complex patterns of disturbance including peat digging, ditching, the grubbing up of scrub and carr, marling, eutrophication by fertilisers or from farmland run-off and ploughing. Here the *Symphytum* sub-community survives as secondary vegetation, now maintained by renewed mowing, but exhibiting some, often strikingly site-specific, loss of rich-fen species and some gain in plants of disturbed and enriched situations which bear testimony to the long history of interference. This is most noticeable at Woodwalton Fen where the sub-community occurs over the ridge-and-furrow of old cuts in fen peat which seems to have been exposed by stripping of overlying acid peat, then inundated by nutrient-laden water from surrounding farmland and then to have dried (Poore 1956b). The rich-fen element in its flora is markedly impoverished (although *Peucedanum palustre*, together with *Sonchus palustris*, was intro-

duced in the 1920s: Poore 1956b, Duffey 1971) and aggressive species, such as *Calamagrostis epigejos* which is not a fen plant at all (Poore 1956b), have appeared as chance colonists and gained a vigorous hold. At Wicken Fen, where there has been less drastic disturbance and a possibly more consistent tradition of mowing, the *Symphytum* sub-community appears more like other forms of secondary *Peucedano-Phragmitetum*. It here includes some of the vegetation which develops during the mowing cycle on peats with a summer water-table at least 30 cm below the surface (Godwin 1931) and where there has probably been some sporadic peat digging and removal of carr (Godwin 1941, 1978; National Trust 1947; Wheeler 1975). Fragments of fen vegetation akin to the *Symphytum* sub-community have also been recorded from Catcott Heath on the Somerset Levels (Willis 1967) and from Kent (Rose 1950), again isolated within much-altered landscapes and perhaps with similarly peculiar site histories.

It is easy to make general suppositions about the effects of mowing on these sub-communities of the *Peucedano-Phragmitetum* but much more difficult to be precise. Even when mowing was a normal part of the Broadland rural economy (and at one time or another most of the area at present occupied by the community was probably regularly cut: Lambert 1946, 1951, 1965), stretches of fen seem to have been subjected to a complex pattern of treatments which might vary from year to year, from one compartment to the next and even within compartments according to need, available labour, weather conditions and changes of ownership or commonland use. Even at the time of Lambert's (1946) survey of the Yare fens, when there was still some memory of active fen exploitation, it was generally difficult to trace treatment history back for more than 10–20 years. Now, with the almost universal neglect of fens as a source of marsh crops, such local knowledge is largely forgotten and many areas once mown have passed to scrub and carr. In other sites which have long attracted particular interest, such as Woodwalton Fen, treatment records are imperfect (Poore 1956b) and the pioneering work of Godwin (1941), in the rather atypical conditions at Wicken Fen, remains the only published experimental consideration of the effects of mowing on this kind of fen vegetation.

The *Peucedano-Phragmitetum* has traditionally provided four types of crop: *Phragmites* for reed thatch, *Cladium* for sedge thatch, *G. maxima* for green fodder, winter hay or litter and more mixed vegetation, often with abundant *Juncus subnodulosus* and/or *Molinia caerulea*, also for litter. The most obvious general effect of regularly mowing for any of these crops was to set back repeatedly the natural invasion of woody species and so maintain the community, albeit in modified forms as secondary fen. This would probably have been

aided by the keeping of dykes in good repair for water circulation and easy access and in some cases also by controlled flooding, both of which could maintain the substrate in a moister condition than might otherwise have been the case.

Beyond this, mowing seems to have introduced into the community some measure of interchangeability of dominance, still dependent to some extent on edaphic conditions, but controlled to a considerable degree by the timing of the cut. Different mowing regimes are appropriate for each of the crops and, although choosing to mow for one or the other may have capitalised on a natural abundance developed in response to edaphic conditions, cutting at a particular time could select for the continuing abundance of the desired crop and the demise of possible competitors. This is best seen in the case of *Phragmites* and *Cladium*, the two most important traditional crops and the most widespread dominants of the community. Although both these species, and especially the former, have been available for cutting in their often almost pure swamp communities, there is no doubt that they have been selected for in the *Peucedano-Phragmitetum*, particular stands having been treated as either reed-beds or sedge-beds. Mowing for reed has traditionally been carried out in winter when the annual crop of stems so ideal for thatching is dead and it has normally been repeated annually or biennially with no deleterious effect (Haslam 1972a, b; McDougall 1972). *Cladium*, a slow-growing evergreen, is especially susceptible to such treatment and will quickly decline if it is persisted with (Godwin 1929; Conway 1936a, 1937a, 1942). The best period for harvesting sedge is early summer (T. Rowell, personal communication) and, although crops have traditionally been taken only every three to five years to allow adequate recovery (Godwin & Tansley 1929, Godwin 1941, McDougall 1972), this is the time of year when *Phragmites* is most vulnerable to the removal of its flush of green shoots (Haslam 1972a). Within some of the sub-communities of the *Peucedano-Phragmitetum* (notably the Typical and *Symphytum* sub-communities), it is common to find stands which differ only in the proportions of *Phragmites* and *Cladium* which suggests that, although both can naturally occur, treatment has played some part in shifting the balance towards one or the other. Even in those sub-communities where there is a more consistent pattern of dominance (e.g. *Phragmites* in the Typical variant of the *Cicuta* sub-community and *Cladium* in the *Schoenus* sub-community), it is not possible to rule out treatment effects entirely.

Along the Yare, treatment has probably also played some part in determining the composition of the *Glyceria* sub-community. Here, *G. maxima* is much more obviously a natural dominant in both swamp and primary fen provided eutrophic conditions are main-

tained, although it has generally been inaccessible for mowing in the former where it occurs as swinging and often semi-submerged rafts. From primary fen, *G. maxima* was traditionally summer-cut, usually before panicle emergence in June for green feed or winter hay and sometimes again, as part of a litter crop, between July and October (Lambert 1946). Indeed, there is some evidence that as many as three mowings could be made in a single season where growth of the continuously produced summer shoots was especially prolific (Lambert 1946, 1947b). Again, such treatment was inimical to the vigour of any *Phragmites* that gained a natural hold in the less eutrophic areas where it might have an edge on *G. maxima* and could perhaps eliminate it altogether (Lambert 1946). Certainly, with the virtually universal relaxation of cutting in the fens along the Yare, the spread of *Phragmites* as a dominant in the *Glyceria* sub-community is very pronounced, although this is probably also partly due to the neglect of dykes and the consequent restriction of water circulation.

In the days when mowing was in full swing, such treatment differences as these contributed to the often bewildering variety of dominance in particular stretches of fen. Now, much of this variegation is masked by a more uniform advance of scrub and carr over former mowing marsh but evidence from former days and such stands as have a more recent cutting history suggest that these mowing regimes have not been ultimately responsible for the overall floristic differences which characterise the sub-communities. This is not to say that these kinds of regimes have had no effects other than to deflect succession or to alter simple patterns of dominance but it seems that, in general, these impacts have not disrupted the edaphically influenced variation within the community (Wheeler, 1978, 1980a). One effect that does seem to be discernible is an increase in species-richness associated with the regular but infrequent summer mowing for sedge. Indeed, this may contribute to the general species-richness of the community as a whole since sedge mowing has been quite widespread but it is also visible in a more particular way within the community. Winter mowing for reed, although perhaps reducing the cover of other evergreen species apart from *Cladium*, e.g. *Carex paniculata*, *C. riparia*, *C. acutiformis*, might be expected to have little impact on the majority of associates which die down completely in winter and which could perhaps be capable of vigorous growth on the open litter-stripped surface of the mown bed in the following spring (Lambert 1951). Such mowing can, however, produce a marked increase in the density of *Phragmites* by exposing it to the effects of frost (Haslam 1972a, b) and light attenuation in reed-dominated fen vegetation like the *Peucedano-Phragmitetum* can be severe (van der Toorn 1972, Wheeler & Giller 1982a). Both mown and unmown stands of the community

dominated by *Phragmites* can thus be similarly rather species-poor.

Stands which have been mown every four years or so for sedge, on the other hand, are noticeably more species-rich than either unmown sedge-beds (which tend towards the *Cladietum marisci*: see below) or reed-dominated stands of the *Peucedano-Phragmitetum*, not only in vascular associates but also in the variety of bryophytes (Wheeler & Giller 1982a). This may be because, with the removal of the bulky sedge growth and the accumulated litter (both have traditionally been harvested) and the subsequent slow regrowth of the *Cladium*, there is much more opportunity for the establishment of a varied understorey (Godwin 1941, Wheeler & Giller 1982). Moreover, some of the species which are often prominent in mown sedge-beds, e.g. *Juncus subnodulosus*, *Schoenus nigricans*, *Molinia caerulea*, are tolerant of summer mowing and readily respond to it by producing new shoots (Godwin 1941, Lambert 1951, 1965).

Summer mowing of *G. maxima*, by contrast, does not seem to have favoured an increase in the diversity of the *Glyceria* sub-community in wetter, more eutrophic situations along the Yare (Lambert 1946). Even though this was often undertaken annually, the ready production of new shoots and their lodging seems to have militated against much richness in the associated flora. Away from the influence of enriched waters, however, where the vigour of *G. maxima* declined, summer mowing was often accompanied by an increase in other species, notably *J. subnodulosus* (Lambert 1946).

The ability of this species and *Molinia caerulea* to flourish under a regime of annual summer mowing, where other possible competitors were excluded either by the timing and frequency of the cut or by less eutrophic conditions, often enabled a yearly crop of litter vegetation to be taken from stands of the *Peucedano-Phragmitetum* in drier situations (Lambert 1946, 1951, 1965). This kind of treatment can certainly produce gross changes in the community over a fairly short period, converting it to a wholly different vegetation type (Godwin 1941).

The most obvious anthropogenic effect in the community now is due to neglect with the discontinuance of mowing and the natural silting and overgrowth of unmaintained dykes. It is difficult to separate the influences of these (Lambert 1946) but the reversion of fen to woodland is clearly visible throughout Broadland and is reflected in the floristics of the community in two ways. First, there is the general abundance of saplings, especially of *Salix cinerea* and *Alnus glutinosa*, throughout most of the sub-communities. It is possible, too, that the prominence of other species is related to neglect. *Thelypteris palustris*, for example, seems to be more characteristic of stands with frequent bushes, and

Calamagrostis canescens, which responds to the cessation of mowing by producing a pronounced tussock habit (Lambert 1951) is nowadays often very abundant. Second, there is the particular association of the *Myrica* sub-community with derelict mowing marsh, especially in the Ant valley and around Upton and Woodbastwick Fen, where *M. gale* can form a vigorous growth of bushy canopy, often accompanied by low *Salix repens* and frequently saplings of *Betula pubescens*, on peats with a summer water-table 10–40 cm below ground (Wheeler 1975, 1978, 1980a).

Two other fairly recent developments are also having some influence on the floristics of the *Peucedano-Phragmitetum*. There is no evidence to suggest that the well-attested eutrophication of some of the waters of Broadland (e.g. Mason & Bryant 1975) has had any profound effect on wide areas of the community (Wheeler 1978) but, in some sites, for example around the Ant broads, there has certainly been a spread of species-poor tall-herb vegetation among the fens and *Epilobium hirsutum* in particular is now a prominent feature of some stands of the *Carex paniculata* sub-community, so luxuriant in places that some tussocks appear to be dying (B.D. Wheeler, personal communication).

The impact of coypu in Broadland has been most obvious in the swamps, in the recent marked decline of which they have probably played a major role (Boorman & Fuller 1981). The virtually complete removal of the swamp front in some areas might be expected to have a long-term effect on any natural advance of fen vegetation which develops on the swamp raft and it has also exposed the fen more directly to erosion along its existing outer edge. There have also been some direct effects on the community itself. Certain species, such as *Cicuta virosa* and *Rumex hydrolapathum*, have shown a marked decline in some areas since the 1950s; *Lythrum salicaria*, on the other hand, is very coypu-resistant and has spread dramatically over the exposed substrate of some lows cleared of vegetation. In drier places, sustained grazing has produced an increase in *Agrostis stolonifera*, *Festuca rubra* and *Poa trivialis* or set back the invasion of *Salix cinerea*, the bushes of which are browsed and barked or loosened by having their roots gnawed (Ellis 1965).

The complex of open-water transition and flood-plain mires in Broadland, where the *Peucedano-Phragmitetum* forms the major fen element, has a rich invertebrate fauna which has long attracted attention. Although there is no absolute coincidence between the community and organised animal assemblages, it has provided food plants or distinctive physiognomic niches for a wide variety of species, some of which are now virtually restricted to its own range, others of which have become extinct with the advance of fen reclamation. The indigenous race of the swallowtail (*Papilio machaon britanni-*

cus) is a butterfly once fairly common throughout southern England (Ratcliffe 1977) but now confined to Broadland where *Peucedanum palustre* is the major host plant, especially for the first and larger brood of caterpillars. It has been suggested (Ellis 1965) that this species increased as *P. palustre* flourished undisturbed with the demise of mowing and burning but the recent advance of scrub and woodland into the community has made many areas less suitable for breeding and perhaps rendered the swallowtail more susceptible to natural disasters such as unfavourable weather. At Wicken Fen, the extinction of the breeding colony in 1951 has been associated with the decreasing abundance of *P. palustre* (Godwin 1978).

The British race of the large copper butterfly (*Lycaena dispar dispar*) became extinct in 1851 as its home grounds were drained or intensively mown and it became increasingly attractive to collectors. It seems to need a supply of the food plant *Rumex hydrolapathum* out of reach of flood such as is provided by some stands of the *Peucedano-Phragmitetum*. Attempts to introduce other races, *L. d. rutilus* at Wicken where *R. hydrolapathum* grows mainly along the dykes and *L. d. batavus* in the Yare valley where the fens are liable to tidal flood, have failed (Ellis 1965). At Woodwalton Fen, however, the creation of artificial open-water transitions in small saucer-shaped depressions has allowed seeded *R. hydrolapathum* to gain a hold in the optimum conditions for its germination on bare wet peat (Duffey 1968) and to grow up with other vegetation to form secondary flood-free fen which now supports a flourishing colony of *L. d. batavus* (Duffey 1971).

The community also contains some of the food plants of various wainscot moths (Ellis 1965) and stands are often rich in spiders, although the distribution of these is more a reflection of the various physiognomic niches of the vegetation than of its floristics (Duffey 1965). Some species like *Pirata piscatorius* hunt over vegetation at the water surface; others such as *Araneus cornutus* build webs among the tall flowering shoots. *Carex paniculata* tussocks have a particularly diverse and highly organised spider fauna and stacks of cut reed and especially sedge also have their distinctive populations (Duffey 1965).

Zonation and succession

In Broadland, the *Peucedano-Phragmitetum* generally occupies the middle zone of the flood-plain mires between the open water of the rivers and broads and the valley sides. In some places, it forms part of a complete and fairly clear sequence from swamp through fen to scrub and woodland, including vegetation developed over both the colonised margins of the deep peat cuts of the broads and the intact alluvial deposits behind. Such zonations have, however, been much confused,

especially on these drier solid substrates towards their landward limit, by the various traditional mowing treatments and shallow peat digging, and are now further complicated by neglect and the spread of woody vegetation over the abandoned fen compartments and dykes. Towards the open water, the transitions have been truncated somewhat by coypu activity and affected by eutrophication. The whole area occupied by these communities has, moreover, been reduced and fragmented by the progressive reclamation of the flood-plain mires for intensive farming. The *Peucedano-Phragmitetum* therefore survives here as part of sometimes extensive but often isolated tracts of complex vegetation over a largely decayed agricultural landscape now subject to the renewed but modified influence of a flood-plain mire environment.

Those few areas of the community which exist outside Broadland occur in smaller and even more isolated and modified fragments of vegetation, far removed from the natural seasonal fluctuations of large bodies of open water and generally sharply marked off from the surrounding land which has been intensively drained, widely cut over for peat and which now carries improved grassland or arable on its shrunken and wasted surface. Here, extensive zonations are rare, swamp vegetation being largely confined to fragmentary strips in the remaining open dykes and the compartments having complex patterns of fen and woody vegetation much influenced by treatment and neglect.

The natural disposition of the community between swamp on the one hand and scrub and woodland on the other is most clearly related to the water-table and, in some places in Broadland, it is possible to proceed sequentially through the various vegetation types in moving from broad margin to valley side over gently sloping ground that, in summer, is dry to increasingly greater depths and, in winter, is subject to increasingly shorter periods of inundation. Some of the classic profiles provided by Lambert & Jennings (1951) from the Bure valley show this well.

The *Peucedano-Phragmitetum* generally occupies the zone where the substrate is sufficiently dry for the overwhelming dominance of swamp helophytes to be challenged by its characteristic suite of fen species but yet sufficiently wet to prevent the permanent establishment of shrubs and trees. The extent of this zone and the sharpness of its boundaries with swamp and woodland vary according to the pattern of interaction between the fluctuating water and the topography of the flood-plain deposits, but they are also influenced by the different tolerances which species have to isolation from the open waters and their irrigating effect. Gradual switches in dominance often blur the junction between swamp and fen and also produce some natural internal heterogeneity with the sub-communities of the *Peucedano-*

Phragmitetum, as can be seen in the relationships between *G. maxima* and *Phragmites* in the *Glyceria* sub-community and *Phragmites* and *Cladium* in the Typical sub-community, and the generally increased prominence of *Juncus subnodulosus* and *Calamagrostis canescens* further away from open water (see Habitat above). The upper boundary between the community and scrub and woodland is also made rather hazy by the varieties of shade tolerance which *Peucedano-Phragmitetum* species have. Some of the important components of the community, e.g. *Carex paniculata*, *C. acutiformis*, *C. vesicaria*, *Calamagrostis canescens* and *Thelypteris palustris*, can persist under a shrub or tree cover producing a diffuse zone of overlap between fen and field layer that does not correspond exactly with the limit of the canopy.

The particular sub-communities of the *Peucedano-Phragmitetum* involved in this basic zonation seem to depend partly on the trophic state of the waters and substrate which may itself be a function of the distance from freely circulating open waters. Along the Yare, with its marked tidally influenced water movement, the usual pattern is for the *Glyceria* sub-community to occur behind a front of the *Glycerietum maximae* swamp, although, with the neglect of the open dyke system along this river, the general prominence of *G. maxima* itself and the gradual nature of the transitions between extensive areas of swamp and primary fen so characteristic of Lambert's (1946) descriptions are much less obvious. In less eutrophic conditions without any pronounced diurnal fluctuation in water-level, the community can be fronted by bands of the *Scirpetum lacustris*, the *Typhetum angustifoliae* and the *Phragmitetum australis* in progressively shallower water, although this sequence has been much fretted by coypu activity (compare the descriptions of Pallis 1911, Lambert 1951 and Boorman & Fuller 1981). In some places, there is then a zone of the *Caricetum paniculatae* which passes to the *Carex paniculata* sub-community of the *Peucedano-Phragmitetum* or, in a few localities, to fragments of the *Cicuta* sub-community. More often, however, the *Phragmitetum* gives way directly to the Typical sub-community. In the most oligotrophic conditions, the *Cladietum marisci* may be the sole swamp community fronting Typical *Peucedano-Phragmitetum* (Lambert & Jennings 1951, Lambert 1951, Wheeler 1980c). In the most natural of these kinds of sequences, the community gives way, with varying degrees of abruptness to woodland with *Alnus glutinosa*, *Salix cinerea* and *Betula pubescens* (Figure 15).

Much of the stratigraphical and observational evidence which has been used to interpret such zonations as the spatial expression of a primary hydrosere has originated from Broadland (e.g. Lambert 1946, 1948, 1951; Lambert & Jennings 1951; Walker 1970; Wheeler

1980c). Here, the *Peucedano-Phragmitetum* includes all the primary fen which develops with the gradual autochthonous accumulation of organic matter over the lake muds around the broad margins, first above the lowest limit of permanent standing water, then up towards the highest bounds ever reached on the flood, with a progressive lowering of the water-table and a reduction in the deposition of any allochthonous sediments. The present distribution of the various kinds of primary *Peucedano-Phragmitetum* in relation to the nutrient conditions of the environment suggests that these may in some way control the particular direction which the succession takes through the community (Lambert 1946, 1951; Wheeler 1980a, c, 1983; Wheeler & Giller 1982a). Lambert (1946, 1951) characterised four major pathways of succession and later observations tend to bear out their early stages except that, at the present time, *Carex acutiformis* seems to have a less distinctive role than she suggested. This species is not a very good diagnostic taxon for any sub-community and, in Lambert's own studies, it was shown to be strongly influenced by mowing (Lambert 1946, 1948) and also to be more characteristic in some places of subsequent woodland than of preceeding fen (Lambert 1951).

In great measure, the direction of the succession seems to be already set by the swamp stage. Although the distinctive fen associates of the *Peucedano-Phragmitetum* show some sorting according to the nutrient status of the waters and substrate, the swamp helophytes continue to exert some influence on the vegetation, especially on its physiognomy, and they contribute to some extent, to the particular floristic character of those sub-communities which occur as primary fen. Their growth form may also influence the speed with which the succession passes, not only from the swamps to the *Peucedano-Phragmitetum*, but also from fen to scrub and woodland. Although the absolute limit of shrub and tree invasion is probably controlled by the water-table, and especially perhaps by its maximum winter level (e.g. Godwin & Bharucha 1932, Godwin 1936), this will itself be influenced by the rate of accumulation of litter and the extent to which seedlings can gain a hold will also be affected by the density of both living and dead material on the ground. Along the Yare, for example, Lambert (1946) noted that scrub development did not generally begin in primary fen of the *Glyceria* sub-community until after the invasion of *Phragmites* when the blanketing effect of the luxuriant and lodged shoots of *G. maxima* was broken up; then abundant *Salix cinerea* appeared, followed by *Alnus glutinosa*. A dense cover of *Cladium* in Typical *Peucedano-Phragmitetum* may be similarly inimical to seedling establishment (Lambert 1951), although at Wicken it has been shown that some woody species can invade virtually pure *Cladietum marisci* directly (Godwin & Tansley 1929, Godwin &

Bharucha 1932, Godwin 1943b). The *Carex paniculata* sub-community, on the other hand, is especially prone to early invasion, with abundant seedlings of both *S. cinerea* and *A. glutinosa* quickly growing up on the tussock tops and forming a canopy (Lambert 1951).

The dominants of primary *Peucedano-Phragmitetum* also exert some influence on the floristics and physiognomy of the eventual woodland cover. The distinctions which Lambert (1951, 1965) made between 'swamp carr' and 'semi-swamp carr' seem to be largely structural and most of the *Alnus*-dominated woodland in which *Carex paniculata* and/or *C. acutiformis* are prominent can be incorporated within the single community of *Alnus glutinosa-Filipendula ulmaria* sub-community of the *Salix cinerea-Betula pubescens-Phragmites australis* is rather similar in its canopy composition but seems to correspond to the 'fen carr' of Lambert (1951, 1965), which she saw as the natural development from the kinds of *Peucedano-Phragmitetum* in which either *Phragmites* or *Cladium* had been dominant.

It is difficult to assess the absolute rate of these kinds of primary succession but Lambert & Jennings (1951) noted that, along the Bure at least, the limits of the open Broadwaters shown on the 1838-41 Tithe Maps coin-

cided roughly with the original limits of lake muds in the deep medieval peat cuttings. This would suggest that, whether the Broadwaters remained open prior to this time for natural reasons or not, most of the visible colonisation from swamp through, in places, to woodland, has occurred within the last 150 years. Stratigraphical analysis of the solid peats and clays nearer the valley sides (Jennings & Lambert 1951, Lambert & Jennings 1951) has revealed a picture of a simpler and more gradual succession following the final marine transgression. Here, vegetation dominated by *Phragmites* seems to have given way directly to 'fen carr', some of which was thought to have a possibly direct continuity with the original woodland cover (Lambert & Jennings 1951).

Over much of the extent of these firmer deposits, however, the long history of interference means that much of the woodland cover is probably of secondary origin. It is very difficult to extract from the diverse relationships between fen treatment and the vegetation, any coherent schemes of secondary succession attendant upon continued treatment or, now, its almost total demise. Nevertheless, a number of tentative observations can be made.

First, on the drier peats at Wicken, Godwin (1941) demonstrated a reversible relationship between sedge-dominated vegetation very similar to the *Symphytum* sub-community and a *Molinia caerulea*-dominated grassy sward based on the frequency of summer cuttings, the latter vegetation being favoured by annual cropping for litter. Comparable vegetation was also

Figure 15. Variations among sequences of swamp, tall-herb fen and woodland vegetation in open-water transition mires around lowland standing and sluggish waters.

					S8 <i>Scirpetum lacustris</i> swamp
					S13 <i>Typhetum angustifoliae</i> swamp
SWAMP	S4 <i>Phragmitetum australis</i> swamp	S3 <i>Caricetum paniculatae</i> swamp	S5 <i>Glycerietum maximae</i> swamp	S4 <i>Phragmitetum australis</i> swamp	S2 <i>Cladietum marisci</i> swamp
TALL- HERB FEN	S26 <i>Phragmites-Urtica</i> fen a <i>Filipendula</i> sub- community	S25 <i>Phragmites-Eupatorium</i> tall-herb fen a <i>Phragmites</i> sub- community	b <i>Carex</i> sub- community	S24 <i>Peucedano-Phragmitetum</i> tall-herb fen a <i>Carex</i> sub- community	
				b <i>Glyceria</i> sub- community	b Typical sub- community
WOOD- LAND	W6 <i>Alnus-Urtica</i> woodland	W2 <i>Salix-Betula-Phragmites</i> Woodland			

shown by Lambert (1946) to be characteristic of areas along the Yare, subject to similar treatment and far from the irrigating effect of the waters. Such sustained summer mowing, especially on drier peats, seems to be one of the most effective ways of breaking the cycle of maintenance of secondary fen by converting the *Peucedano-Phragmitetum* to another vegetation type. Systematic grazing by stock, especially when combined with embankment and drainage, is probably another. On the grazed levels of the Yare, the community appears to develop into the *Holco-Juncetum* under such treatment (Lambert 1948). More drastic disturbance of drier peats may result in oxidation of the organic deposits and a release of nutrients (e.g. Haslam 1965) with an increase in nitrophilous species. Such a development is perhaps already seen within the *Glyceria* and *Symphytum* sub-communities but it may also transform the *Peucedano-Phragmitetum* into the tall-herb fens of the *Phragmites-Urtica* community or the *Epilobietum hirsutae*.

Second, how far such disruptions as these prevent the eventual re-establishment, with neglect, of the kinds of woodland that result from the primary succession is unknown. At Wicken, there seems to have been an opportunistic recolonisation of abandoned sedge-beds with the establishment of a cover largely of *Rhamnus catharticus* and *Frangula alnus* (Godwin 1936, Godwin *et al.* 1974), although *A. glutinosa* is regenerating in places. In the Yare fens, Lambert (1946) suggested that secondary *Alnus* woodland, though readily developing from litter-mown areas, was deficient in *Carex paniculata* as compared with primary carr. It is possible that more disturbed tall-herb fens regress to *Alnus glutinosa-Urtica dioica* woodland.

In some places, the re-development of woodland is complicated by the possibility of surface acidification of undisturbed peats which are now above the water-table. In Broadland, the *Schoenus* sub-community is associated with uncut baulks and, with a cessation of mowing, this vegetation is rapidly invaded by *Myrica gale*, first to form the *Myrica* sub-community of the *Peucedano-Phragmitetum* and then a *Myrica* scrub. This, in turn, may progress to the *Betula-Molinia* woodland (Wheeler 1980c). The recent marked expansion of *B. pubescens* on the drier peats at Wicken (Godwin *et al.* 1974) seems to be related to surface acidification. Indeed, it is not impossible that here and in some parts of Broadland there survive, as at Woodwalton (Poore 1956b), fragments of a pre-existing cover of acid peat that has been systematically stripped off (Wheeler 1978).

Third, the flooding of shallow peat cuttings, such as those dug quite extensively in some Broadland valleys in the mid-nineteenth century, seems to have created rather specialised conditions for the development of a somewhat different hydrosere to any of those characteristic of the broads margins themselves. Here, swamp

vegetation may include stands of that distinct form of the *Galium palustre* sub-community of the *Phragmitetum* which Wheeler (1980a) termed *Cicuto-Phragmitetum* developed over a floating raft of *Typha angustifolia* remains (see also Lambert 1951). Other such flooded workings are at present occupied by rafts of the *Carex lasiocarpa* variant of the *Cicuta* sub-community of the *Peucedano-Phragmitetum* and it is possible that the two are serally related (Wheeler 1980c). Within areas containing stands of either or both of these vegetation types there are sometimes small islands of the *Sphagnum* sub-community of the *Salix cinerea-Betula pubescens-Phragmites australis* woodland often picked out by the prominence of the bright green fronds of *Dryopteris cristata* around the margins (Wheeler 1978). At least some of these seem to represent the development of ombrotrophic nuclei on floating rafts of peat which are kept out of reach of flooding with the calcareous and nutrient-rich broads waters (Wheeler 1978, 1980c, 1983; Giller 1982). Although such mires seem to have formed within the nearby Fens (e.g. Godwin & Clifford 1938, Poore 1956b; see also Godwin & Turner 1933, Walker 1970), their formation in Broadland at the present time seems to be strongly associated with artificial habitats. Even the large island at the north end of Barton Broad, which has a particularly extensive stand of this kind of woodland (Wheeler 1978), is known to have been piled around the edge and infilled with slushy dredgings (Lambert & Jennings 1965).

The vegetation of these shallow peat diggings is often further complicated by their isolation from the main paths of water movement through the broads and dykes and by the possible lateral seepage of water at the junctions of the flood-plain mire with the valley sides. It is in such positions that the *Cicuta* sub-community can occur in striking mosaics with a carpet of the *Carex rostrata-Calliergon* fen. These mosaics, which Wheeler (1978, 1980a) included within the *Peucedano-Phragmitetum* as the sub-community *caricetosum* but which are fully described in this scheme under the *Carex-Calliergon* fen, are the locus of a number of Broadland rarities, including *Liparis loeselii*, *Anagallis tenella*, *Drosera anglica*, *Parnassia palustris* and *Hypericum elodes*. The detailed environmental relationships of this kind of vegetation and its possible role in any fen succession are unknown.

Distribution

The most extensive tracts of the community occur in the middle reaches of the Yare, Bure, Ant and Thurne valleys in Broadland, east Norfolk. The *Symphytum* sub-community has been recorded from Wicken and Woodwalton Fens in Cambridgeshire and rather similar vegetation has been described from Catcott Heath in Somerset and the Ham fens in Kent.

Even in those areas which have been designated as nature reserves, the ongoing processes of terrestrialisation and recolonisation by shrubs and trees are reducing the extent of the *Peucedano-Phragmitetum* or modifying its floristics. Although a patchwork of fen and scrub may be valuable in some respects (for breeding or migrant passerines, for example: see Fuller 1982), the generally open character of former areas of mowing marsh has, in many places, been lost and some species characteristic of regularly managed fen have declined or become extinct (e.g. Wheeler 1978).

Affinities

Despite the traditional concentration on the richer fen vegetation of Broadland to the neglect of less striking communities elsewhere, the strong internal cohesion of the *Peucedano-Phragmitetum* argues powerfully for its treatment as a discrete unit with its natural centre of distribution in that region. As defined here, the community is very much as characterised by Wheeler (1975, 1978, 1980a) and, as such, it includes vegetation which, in some Continental schemes (e.g. Krausch 1964, Westhoff & den Held 1969), would be considered as especially rich forms of more broadly based *Phragmitetum* and *Magnocaricion* communities. Other European classifications (e.g. van Donselaar 1961, Korneck 1963, Segal & Westhoff 1969 in Westhoff & den Held 1969), have, however, recognised parallel vegetation types to the *Peucedano-Phragmitetum*, although they have dif-

fered as to whether the affiliations of such communities are with the *Magnocaricion* (the view favoured by Wheeler) or the *Cicution virosae*.

In this scheme, the *Peucedano-Phragmitetum* lacks two of the sub-communities which Wheeler (1980a) distinguished. His *caricetosum* is here considered better placed within the *Carex rostrata-Calliergon* fen and his *arrhenatheretosum* is treated as part of the *Phragmites-Urtica* fen. By contrast, Wheeler's *Caricetum paniculatae peucedanetosum* (Wheeler 1978, 1980a) is taken into the *Peucedano-Phragmitetum* to effect a consistent separation between swamps and fens.

The community shows a complex pattern of affinities with other types of fen and with swamp, woodland and fen meadow vegetation. It is closely related in a general way to the *Phragmites-Eupatorium* fen which, though it lacks some of the rich-fen species, has a similarly varied medley of dominants and it grades through the *Glyceria* and *Symphytum* sub-communities to the *Phragmites-Urtica* fen. The range of possible helophyte dominants in the *Peucedano-Phragmitetum* provides a clear link with a variety of swamp communities and the sedge/rush layer continues to be a prominent part of some fen meadow vegetation. The community grades floristically to some woodlands, notably through the *Myrica* sub-community to the *Betula-Molinia* woodland and, in a more general way, to the woodlands with mixtures of *Alnus glutinosa*, *Salix cinerea* and *Betula pubescens*.

Floristic table S24

	a	b	c
<i>Phragmites australis</i>	V (3–7)	V (1–7)	V (1–7)
<i>Galium palustre</i>	V (2–5)	V (1–3)	IV (1–3)
<i>Lysimachia vulgaris</i>	IV (1–4)	V (1–3)	V (1–3)
<i>Peucedanum palustre</i>	V (1–5)	III (1–3)	III (1–5)
<i>Eupatorium cannabinum</i>	V (2–7)	IV (1–3)	V (1–3)
<i>Lythrum salicaria</i>	IV (1–5)	IV (1–3)	III (1–3)
<i>Juncus subnodulosus</i>	I (2–3)	III (1–5)	IV (1–5)
<i>Calliergon cuspidatum</i>	IV (1–2)	III (1–3)	IV (1–5)
<i>Calamagrostis canescens</i>	II (1–3)	II (1–3)	V (1–7)
<i>Filipendula ulmaria</i>	II (1–4)	V (1–5)	V (1–5)
<i>Mentha aquatica</i>	II (1)	III (1–3)	IV (1–3)
<i>Cladium mariscus</i>	I (1)		III (1–9)
<i>Carex paniculata</i>	V (5–9)	V (1–5)	I (1–3)
<i>Scutellaria galericulata</i>	IV (1–4)	IV (1–3)	
<i>Brachythecium rutabulum</i>	III (1–2)	III (1–3)	III (1–3)
<i>Solanum dulcamara</i>	III (1–3)	III (1–3)	I (1–3)
<i>Impatiens capensis</i>	IV (2–6)	II (1–3)	
<i>Lemna minor</i>	III (1–3)		
<i>Scrophularia aquatica</i>	II (1–4)		
<i>Sparganium erectum</i>	I (1–2)		
<i>Glyceria maxima</i>	I (1–3)	V (1–9)	
<i>Epilobium hirsutum</i>	III (2–8)	V (1–5)	
<i>Myosotis scorpioides</i>	I (1–2)	IV (1–3)	
<i>Carex riparia</i>	I (2–3)	IV (1–3)	
<i>Vicia cracca</i>		IV (1–3)	I (1–3)
<i>Caltha palustris</i>		IV (1–3)	
<i>Equisetum palustre</i>		III (1–3)	
<i>Typha latifolia</i>		III (1–3)	
<i>Carex acutiformis</i>		IV (1–5)	V (1–3)
<i>Thalictrum flavum</i>		IV (1–3)	V (1–5)

d	e	f	g	24
V (1-7)	V (1-7)	V (1-9)	V (1-7)	V (1-9)
V (1-3)	V (1-3)	V (1-3)	V (1-3)	V (1-5)
IV (1-3)	IV (1-3)	IV (1-3)	V (1-3)	V (1-4)
V (1-5)	IV (1-3)	V (1-3)	V (1-3)	V (1-5)
IV (1-3)	IV (1-3)	IV (1-3)	III (1-3)	IV (1-7)
III (1-3)	IV (1-3)	IV (1-3)	IV (1-3)	IV (1-5)
V (1-7)	V (1-5)	V (1-5)	IV (1-3)	IV (1-7)
III (1-5)	V (1-3)	III (1-5)	II (1-3)	IV (1-5)
IV (1-5)	III (1-3)	II (1-3)	IV (1-7)	IV (1-7)
IV (1-5)	I (1-3)	II (1-3)	V (1-3)	IV (1-5)
III (1-3)	V (1-3)	V (1-3)	II (1-3)	IV (1-3)
II (1-7)	IV (1-7)	V (1-7)	V (1-7)	IV (1-9)
I (1-3)	I (1-3)		I (1-3)	II (1-9)
III (1-3)	II (1-3)	II (1-3)	II (1-3)	II (1-4)
I (1-3)	I (1-3)			II (1-3)
I (1-3)	II (1-3)	I (1-3)	I (1-3)	II (1-3)
I (1-3)	I (1-3)			I (1-6)
				I (1-3)
				I (1-4)
				I (1-2)
				I (1-9)
I (1-3)	I (1-3)		I (1-3)	I (1-8)
	I (1-3)	I (7)		I (1-7)
	I (1-3)	I (1-3)		I (1-3)
				I (1-3)
I (1-3)	II (1-3)		I (1-3)	I (1-3)
I (1-3)			I (1-3)	I (1-3)
				I (1-3)
I (1-3)		II (1-3)	I (1-3)	II (1-5)
	I (1-3)			II (1-5)

<i>Calystegia sepium</i>	II (1–3)	IV (1–5)	IV (1–3)
<i>Lathyrus palustris</i>	I (2)	IV (1–5)	III (1–3)
<i>Symphytum officinale</i>			IV (1–3)
<i>Phalaris arundinacea</i>			III (1–5)
<i>Galium uliginosum</i>		I (1–3)	III (1–3)
<i>Calamagrostis epigejos</i>			II (1–7)
<i>Cicuta virosa</i>			
<i>Ranunculus lingua</i>	II (1–3)	I (1–3)	
<i>Carex pseudocyperus</i>	II (1–4)		
<i>Berula erecta</i>	I (2–4)		
<i>Sium latifolium</i>			
<i>Typha angustifolia</i>	II (2–4)		
<i>Carex lasiocarpa</i>			
<i>Carex appropinquata</i>			
<i>Pedicularis palustris</i>			
<i>Menyanthes trifoliata</i>		I (1–3)	
<i>Equisetum fluviatile</i>		I (1–3)	
<i>Calliargon giganteum</i>			
<i>Riccardia pinguis</i>			
<i>Carex lepidocarpa</i>			
<i>Schoenus nigricans</i>			
<i>Oenanthe lachenalii</i>			
<i>Ranunculus flammula</i>			
<i>Samolus valerandi</i>			
<i>Cirsium dissectum</i>			
<i>Myrica gale</i>			
<i>Salix repens</i>			II (1–3)
<i>Betula pubescens</i> sapling			
<i>Potentilla erecta</i>			
<i>Valeriana officinalis</i>	I (2–2)	V (1–3)	II (1–3)
<i>Iris pseudacorus</i>	II (1–2)	IV (1–3)	V (1–3)
<i>Lycopus europaeus</i>	III (1–3)	III (1–3)	I (1–3)

II (1-3)	II (1-3)	III (1-3)	II (1-3)	II (1-5)
I (1-3)			I (1-3)	II (1-5)
				I (1-3)
I (1-3)			I (1-3)	I (1-5)
			I (1-3)	I (1-3)
				I (1-7)
I (1-3)	V (1-3)			I (1-3)
I (1-3)	IV (1-3)	I (1-3)	I (1-3)	II (1-3)
II (1-3)	IV (1-3)			I (1-4)
II (1-3)	IV (1-3)	II (1-3)		II (1-4)
I (1-3)	IV (1-3)			I (1-3)
I (1-3)	III (1-3)	I (1-3)		I (1-4)
	III (1-7)			I (1-7)
I (1-3)	II (1-3)			I (1-3)
I (1-3)	II (5)	I (1-3)	I (1-3)	I (1-5)
I (1-3)	II (1-5)			I (1-5)
I (1-3)	II (1-3)			I (1-3)
I (1-3)	II (1-3)			I (1-3)
	I (1-3)			I (1-3)
	I (1-3)			I (1-3)
				I (1-3)
	I (1-3)	IV (1-3)	I (1-3)	I (1-3)
		IV (1-3)		I (1-3)
	I (1-3)	III (1-3)		I (1-3)
	I (1-3)	II (1-3)	I (1-3)	I (1-3)
		I (1-3)		I (1-3)
I (1-3)	II (1-3)	I (1-3)	V (1-5)	II (1-5)
I (1-3)	I (1-3)	II (1-3)	IV (1-3)	II (1-3)
I (1-3)	I (1-3)	I (1-3)	III (1-3)	I (1-3)
			I (1-3)	I (1-3)
V (1-3)	I (1-3)	IV (1-3)	III (1-3)	III (1-3)
IV (1-3)	IV (1-3)	III (1-3)	II (1-3)	III (1-3)
IV (1-3)	IV (1-3)	III (1-3)	I (1-3)	III (1-3)

Floristic table S24 (cont.)

	a	b	c
<i>Salix cinerea</i> saplings	IV (2–7)	III (1–5)	III (1–3)
<i>Thelypteris palustris</i>	V (3–8)	II (1–3)	
<i>Alnus glutinosa</i> sapling	V (1–5)	II (1–3)	
<i>Angelica sylvestris</i>		IV (1–3)	III (1–3)
<i>Carex elata</i>	I (2)	IV (1–3)	I (1–3)
<i>Cirsium palustre</i>		II (1–3)	IV (1–3)
<i>Rumex hydrolapathum</i>	II (1–4)	III (1–3)	I (1–3)
<i>Campylium stellatum</i>			IV (1–5)
<i>Epilobium palustre</i>		III (1–3)	
<i>Potentilla palustris</i>	I (2)		
<i>Hydrocotyle vulgaris</i>			I (1–3)
<i>Oenanthe fistulosa</i>			
<i>Cardamine pratensis</i>	I (1)	II (1–3)	
<i>Lotus uliginosus</i>			I (1–3)
<i>Agrostis stolonifera</i>			I (1–3)
<i>Lychnis flos-cuculi</i>			I (1–3)
<i>Stellaria palustris</i>	I (1–2)		
<i>Plagiomnium rostratum</i>			II (1–3)
<i>Carex panicea</i>			III (1–3)
<i>Molinia caerulea</i>			II (1–3)
<i>Myosotis laxa caespitosa</i>			
<i>Urtica dioica</i>	I (1–2)		I (1–3)
<i>Rubus fruticosus</i> agg.			I (1–3)
<i>Epilobium parviflorum</i>			I (1–3)
<i>Rhinanthus minor</i>			I (1–5)
<i>Poa trivialis</i>		I (1–3)	I (1–3)
<i>Holcus lanatus</i>			I (1–3)
<i>Bryum pseudotriquetrum</i>			I (1–3)
<i>Campylium elodes</i>			I (1–3)
<i>Rhizomnium punctatum</i>			
<i>Dactylorhiza incarnata</i>			I (1–3)
<i>Dactylorhiza majalis praetermissa</i>			

d	e	f	g	24
II (1-5)	III (1-3)	II (1-3)	IV (1-3)	III (1-7)
IV (1-5)	II (1-3)	I (1-3)	IV (1-3)	III (1-8)
II (1-3)	I (1-3)	III (1-3)	II (1-3)	II (1-5)
III (1-3)		I (1-3)	II (1-3)	II (1-3)
II (1-3)	IV (1-5)	IV (1-5)		II (1-5)
III (1-3)	I (1-3)	I (1-3)	II (1-3)	II (1-3)
IV (1-3)	II (1-3)	I (1-3)		II (1-4)
II (1-3)	IV (1-3)	III (1-3)	II (1-3)	II (1-5)
II (1-3)	II (1-3)	I (1-3)	II (1-3)	II (1-3)
IV (1-5)	IV (1-3)	II (1-3)	III (1-3)	II (1-5)
III (1-5)	IV (1-3)	V (1-3)	II (1-3)	II (1-5)
II (1-3)	IV (1-3)	II (1-3)	I (1-3)	II (1-3)
II (1-3)	II (1-3)	I (1-3)	I (1-3)	I (1-3)
III (1-3)	I (1-3)	I (1-3)	I (1-3)	I (1-3)
II (1-3)	I (1-3)	III (1-3)		I (1-3)
II (1-3)	II (1-3)	II (1-3)		I (1-3)
II (1-3)	III (1-3)	I (1-3)		I (1-3)
I (1-3)	I (1-3)	I (1-3)		I (1-3)
	I (1-3)	II (1-3)	I (1-3)	I (1-3)
	I (1-3)	I (1-3)	II (1-3)	I (1-3)
II (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 (1-5)
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 (1-3)	I (1-3)	I (1-3)	I (1-3)

<i>Plagiomnium elatum</i>			I (1–3)		I (1–3)			I (1–3)
<i>Fissidens adianthoides</i>			I (1–3)			I (1–3)		I (1–3)
<i>Frangula alnus</i> sapling			I (1–3)				I (1–3)	I (1–3)
<i>Cirsium arvense</i>			I (1–3)		I (1–3)			I (1–3)
<i>Hypericum tetrapterum</i>				I (1–3)	I (1–3)			I (1–3)
<i>Lathyrus pratensis</i>				I (1–3)	I (1–3)			I (1–3)
<i>Valeriana dioica</i>				I (1–3)	I (1–3)	I (1–3)	I (1–3)	I (1–3)
<i>Carex diandra</i>					I (2)	I (1–3)		I (1–3)
<i>Epipactis palustris</i>					I (1–3)	I (1–3)		I (1–3)
<i>Succisa pratensis</i>						I (1–3)	I (1–3)	I (1–3)
Number of samples	12	11	11	22	17	21	12	107
Number of species/sample		21 (14–32)	25 (17–35)	23 (17–34)	28 (19–39)	21 (14–36)	20 (14–29)	

- a *Carex paniculata* sub-community
- b *Glyceria maxima* sub-community
- c *Symphytum officinale* sub-community
- d Typical sub-community
- e *Cicuta virosa* sub-community
- f *Schoenus nigricans* sub-community
- g *Myrica gale* sub-community
- 24 *Peucedano-Phragmitetum* (total)

