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## S4

# *Phragmites australis* swamp and reed-beds *Phragmitetum australis* (Gams 1927) Schmale 1939

### Synonymy

*Scirpo-Phragmitetum* Koch 1926 p.p.; *Scirpeto-Phragmitetum medioeuropaeum* (Koch 1926) R.Tx. 1941 p.p.

### Constant species

*Phragmites australis*.

### Rare species

*Cicuta virosa*, *Utricularia intermedia*.

### Physiognomy

All the vegetation types included here are characterised by the generally overwhelming dominance of *Phragmites australis*. However, this is a very polymorphic species and the gross appearance of the vegetation, even with pure stands, can be very variable. Much of this variation is known to be phenotypic adaptation perpetuated in clonal populations and variously described as 'kinds', ecotypes, biotypes or biotopes of reed (e.g. Rudescu *et al.* 1965; Björk 1967; Haslam 1971a, 1972a, Dykyjová 1978a); some is related to genotypic differences (e.g. Björk 1963, 1967; van der Toorn 1972; Riacu *et al.* 1972; Pazourková 1973; Dykyjová 1978a). Although variation in Britain is said to be less than elsewhere (Haslam 1972a) and presumed to be phenotypic, there has been no systematic study of its extent in this country or of its relationships to the kind of environmental differences that are reflected in the floristics of the various kinds of *Phragmitetum*. Here, it is possible only to give a very general indication of the reed morphology in each of the sub-communities.

*Phragmites* is normally a highly gregarious species and individual stands of the community can be very extensive. The vegetation is generally very species-poor and no other species attains even occasional frequency throughout. The *Phragmitetum* is, however, very variable and individual stands may show marked peculiarities of composition.

### Sub-communities

***Phragmites australis* sub-community:** *Phragmites communis* reedswamp Tansley 1911; *Phragmites-Scirpus* associates Pearsall 1918 p.p.; *Phragmites communis-Sparganium minimum* and *Phragmites communis-Littorella* open sociations and *Phragmites communis* society Spence 1964; *Phragmites* monodominant stands Haslam 1971a; *Phragmites nodum* Daniels 1978; Association of *Phragmites australis* and *Schoenoplectus lacustris* Pigott & Wilson 1978 p.p.; *Phragmites communis* swamp sociation Wheeler 1978; *Phragmites australis* reedswamp, species-poor variant Meres Survey 1980; *Scirpo-Phragmitetum typicum* Wheeler 1980; *Phragmites communis* nodum Adam 1981 p.p.; this sub-community includes pure and very species-poor swamps and reed-beds in which *Phragmites* is the sole constant. The reed cover can be open or closed but *Phragmites* is always the most abundant helophyte forming a canopy from about 1–3 m high. Other species can, however, be locally prominent including other swamp dominants such as *Typha latifolia*, *T. angustifolia*, *Carex riparia*, *C. acuta*, *Glyceria maxima*, *Cladium mariscus*, *Scirpus lacustris* ssp. *lacustris* and *S. maritimus*, tall herbs like *Iris pseudacorus* and *Berula erecta*, sprawlers such as *Solanum dulcamara* and *Calystegia sepium* and aquatic species like *Lemna minor*, *Callitriche stagnalis*, *Sparganium minimum* or *Littorella uniflora*. Bryophytes are generally absent.

***Galium palustre* sub-community:** Reed-swamp West 1905 p.p.; *Phragmites communis-Galium palustre* sociation Spence 1964 p.p.; includes *Cicuto-Phragmitetum* Wheeler 1978. Here, the reed cover tends to be a little more open, although it can still be very tall, from 1.5 to 3 m. The vegetation is also somewhat richer with *Galium palustre* constant, *Mentha aquatica* frequent and tall herbs such as *Lythrum salicaria*, *Iris pseudacorus* and *Epilobium hirsutum* occasional, though none of these species is consistently abundant. There is sometimes a

little *Calliergon cuspidatum*, although other bryophytes are rare. Again, a variety of other species can be locally prominent including *Sparganium erectum*, *Carex pseudocyperus* and *Solanum dulcamara*. Some highly distinctive but very locally distributed *P. australis* swamp in which the tall emergent herbs *Cicuta virosa*, *Ranunculus lingua*, *Rumex hydrolapathum* and *Sium latifolium* occur together, with some *Carex pseudocyperus*, *Scirpus lacustris* ssp. *lacustris* and *Typha angustifolia* (the *Scirpo-Phragmitetum* of Wheeler 1978, 1980a; see also the *Ranunculus-Cicuta* variant of Spence 1964) is probably best included in this sub-community.

***Menyanthes trifoliata* sub-community:** Reed-swamp Rankin 1911; *Phragmitetum* Matthews 1914; Reed-swamp Holdgate 1955b p.p.; *Phragmites communis-Galium palustre* sociation Spence 1964 p.p.; *Schoenoplectus lacustris-Phragmites communis* Association, *Phragmites communis-Equisetum fluviatile* subassociation Birks 1973. In these swamps, there is an open reed cover and an understorey of generally small amounts of two of the following: *Menyanthes trifoliata*, *Equisetum fluviatile*, *Carex rostrata* and *Potentilla palustris*. The water surface may have *Nymphaea alba*, *Potamogeton polygonifolius* and *P. natans* and there is sometimes some submerged *Juncus bulbosus* and a variety of aquatics including *Utricularia* spp.

***Atriplex prostrata* sub-community:** *Phragmites* marsh Ranwell 1961; Saline/non-saline transition swamp Gimingham 1964; *Phragmitetum* Chapman 1964; *Phragmites communis* reedbeds Proctor 1980; *Phragmites communis* nodum Adam 1981 p.p.. The stands included here are dominated by a sometimes open cover of often short *Phragmites*. The most frequent associate throughout is *Atriplex prostrata* but it is not invariably present and, though sometimes abundant, it can be very unevenly distributed in individual stands over local accumulations of organic detritus. *Agrostis stolonifera* may also be present with *A. prostrata* or replace it as the most frequent subsidiary species. Many stands also have halophytes. This somewhat flexible combination of features marks off these kinds of reed-beds from those similarly species-poor types in the *Phragmites* sub-community. Three variants can be recognised.

***Atriplex prostrata* variant.** *A. prostrata* is a constant, but often the sole, associate beneath a usually closed canopy of *Phragmites* generally about 1.5 m tall.

***Puccinellia maritima* variant.** *A. prostrata* is less frequent here but *Puccinellia maritima* forms a sometimes extensive sward beneath the rather open and generally very short (about 75 cm) reed. A variety of other species characteristic of Puccinellion communities may occur and are sometimes locally abundant: *Aster tripolium*, *Plantago maritima*, *Halimione portulacoides* and *Salicornia dolichostachya*.

There is frequently a surface mat of algae.

***Agrostis stolonifera* variant:** Brackish water communities Birks 1973 p.p.; *Phragmites-Agrostis stolonifera* community Wheeler 1980a. *A. prostrata* remains frequent but the distinctive feature is an open or closed mat of sprawling *A. stolonifera* often with some *Festuca rubra* and *Juncus gerardi* and other upper-marsh halophytes.

### Habitat

*Phragmites* is a natural dominant in these vegetation types in a wide range of permanently wet or periodically waterlogged habitats of differing trophic state and with a variety of substrates. Stands are common in open-water transitions around lakes and ponds, in flood-plain mires and in estuaries, where their extent can be considerable, along dykes (including those with brackish water), canals and sluggish lowland rivers, in small pools, peat cuttings and on salt-marshes. The artificial dominance maintained by cropping for reed extends the occurrence of the community into some naturally drier situations.

The success of *Phragmites* as a dominant in such a diversity of habitats is dependent, to a great extent, on its growth habit (see, for example, Rudescu *et al.* 1965; Haslam 1969a, b, c, 1970a, b, 1971c, 1972a; Rodewald-Rudescu 1974; Fiala 1976, 1978). It is a rhizomatous perennial with annual aerial parts and the normal pattern of growth is as follows. Towards late summer, when underground food reserves are attaining a maximum after downward transfer of material from the shoots, a bud grows out from the base of the previous year's vertical rhizome and extends horizontally for some distance. Its apex turns up and the tip then remains dormant, close to the substrate surface where the developmental transition to a shoot will take place, from November to the following spring. In Britain, the emergence of the young shoots (colts) generally begins between late March and late April, continuing, normally in a single sustained burst, for some 1–3 months so that, by June or July, shoot density is at a maximum. Larger buds tend to sprout first and these grow faster to produce taller shoots. Some late emergent buds may go on to produce shoots through the summer but these may suffer in the competition for light within the stand or be killed by frost before or after their growth is arrested by the cooler temperatures after September. Any shoots which are killed after the main emergence period are not replaced. As the shoots extend, the leaves unfurl and, around the vertical rhizomes and shoot bases, there is an extension of the thick felted mass of roots.

Inflorescences begin to emerge from the aerial shoots between late July and early August and they flower about a month later, the fruit ripening by November and

being shed through the winter and spring. As summer progresses, however, nutrients begin to be cycled into the rhizomes, the stems start to harden and the lower leaf blades to drop. Abscission continues into the winter and, by January, most blades have been shed and the stems are dead and brittle. These may remain standing for two or three seasons, as the new annual growth comes and goes, after which they break off close to the ground leaving a stubble which can persist for several more years.

Also in late summer, several new buds begin to form on the upper region of the vertical rhizome. Most of these develop before winter, when they become dormant, and they will produce the aerial growth of the following season, a cluster of shoots, shorter and thinner than the single first generation shoot and less likely to flower. At this time too, as nutrients begin to accumulate again below ground, there is a renewed round of growth in the horizontal rhizome system, new buds growing out from the bases of the vertical rhizomes, extending, branching and developing long, sparse, roots, then turning up ready to initiate new aerial growth in the following spring. After about three seasons, the rhizome system begins to die from behind.

The general appearance of any stand of the *Phragmitetum* is a function of the density and diameter of the buds which exert a primary control on the density and height, respectively, of the aerial shoots (Haslam 1971*b*). These bud characteristics show an inverse relationship with one another and this is perhaps indicative of a potentially equal performance within particular biotopes (Haslam 1971*a*, van der Toorn & Mook 1982). In Britain, the modal density of monodominant stands of *Phragmites* is more than 100 shoots  $\text{m}^{-2}$  and the modal height is usually over 1 m but apparently stable stands can be found with over 200 shorter shoots  $\text{m}^{-2}$  or as few as 30 shoots  $\text{m}^{-2}$  with a modal height of 2.5 m (Haslam 1971*a*). The density and diameter of the developing buds are strongly influenced by the environment of the upper layers of the substrate, especially in late summer and spring, and the extent to which their growth potential is realised is further affected by the environment, both below and above ground, between spring and autumn. The most important variables influencing performance in these ways seem to be the water regime, the trophic state of the medium and the temperature of the environment and their effects are complex and interactive. The water and nutrient regimes also appear to be the major influences on the subsidiary floristic variation visible in the sub-communities.

In general, *Phragmites* performs best and stands of the community are most luxuriant and productive in wet, eutrophic habitats where there is a warm summer. *Phragmites* can survive in a wide variety of water regimes, with water-tables which range between 2 m

above the substrate to more than 1 m below and with various patterns of fluctuation or none (Haslam 1970*c*). The *Phragmitetum* as defined here includes stands from permanently deep and permanently shallow waters, from summer-dry but winter-flooded sites, from places which are permanently moist but never flooded and from situations where there is periodic flooding by fresh, brackish or tidal waters. The maintenance of healthy growth does, however, seem to be favoured by a regularity in the water regime, whether this involves fluctuation or not: sudden changes in water level can severely disrupt the natural rhythm of vegetative growth and may allow vigorous competitors to gain a hold (Haslam 1970*c*, 1971*a*, *b*). The community is noticeably uncommon in habitats which are subject to erratic variation in water level, such as the draw-down zones of reservoirs and spatey rivers.

*Phragmites* can grow well in the reducing conditions which result from waterlogging provided rhizome aeration is maintained (Haslam 1970*c*). This happens through the dead aerial stems, the natural persistence of which roughly matches the life of the rhizomes. If stems become broken and submerged, as may happen with wave action or where cut stubble is flooded too deeply, aeration is impeded and the bud inception in late summer, and perhaps also that in the spring, is reduced (Rudescu *et al.* 1965, Haslam 1970*c*, 1972*b*). Under normal circumstances, standing high water actually favours the development of those thicker and lower autumn buds which have a maximum height potential (Haslam 1971*a*).

The best performance seems to be attained in Britain where the water level ranges from +50 cm to -20 cm and where there is flooding for at least several months of the year (Haslam 1970*c*). The dense stands of tall and vigorous *Phragmites* that can develop under such conditions here fall mainly in the *Phragmites* sub-community which is especially characteristic of open-water transitions and flood-plain mires with permanent standing water or a long winter and spring flood and of deeper and wider dykes which never dry.

In the more nutrient-rich of these deeper waters, *Phragmites* has few competitors. *Scirpus lacustris* ssp. *lacustris* is perhaps more tolerant of exposure to wave action and better able to get a hold on coarser substrates but, of other helophytes, only *Glyceria maxima* and *Typha* spp. seem to be able to challenge *Phragmites* and then only under particular conditions (see below). In general, stands of the *Phragmites* sub-community are extensive and species-poor and other species attain only local and very patchy prominence.

In shallower waters, however, or where flooding is rare and/or brief, the growth of *Phragmites* may be less dense and tall and subsidiary species may gain a hold in the more open shallow water, on the litter which begins

to accumulate without prolonged or frequent flooding or on the periodically exposed or accreting substrate, provided they can tolerate a certain amount of shade (Haslam 1971a). The *Galium* sub-community comprises such vegetation on floating rafts of peat over loose silts or on firm organic or mineral material in open-water transitions and flood-plain mires and along water courses where there is a water-table that is below the surface for usually eight months of the year and perhaps often below the upper reaches of the vertical rhizomes in late summer when the following year's buds are forming. In Scottish lakes, Spence (1964) noted depth means and ranges of  $-10$  ( $-40$  to  $+2$ ) cm for the *Galium* sub-community as against  $+13$  ( $-13$  to  $+50$ ) cm for the *Phragmites* sub-community.

The depth penetration of *Phragmites* in any given waters seems to be limited more by the unavailability of nutrients than by any intolerance of prolonged water-logging (Haslam 1970c). Unlike many hydrophytes, the leaves of *Phragmites* die and rot underwater (Hürlimann 1951) and the plants must be capable of sufficiently tall and dense growth to be able to put an effective photosynthesising canopy above the surface. Roughly speaking, about one third or more of the shoot must be out of water (Haslam 1973) and this may not be attainable where short supply of nutrient limits growth. Although *Phragmites* seems to have a small absorption plasticity (Dykyjová 1978b), it certainly grows better in more eutrophic conditions. Both nitrogen and phosphorous have been found to be limiting in a variety of situations (Misra 1938, Hürlimann 1951, Björk 1967, Haslam 1965, 1971c, van der Toorn 1972) and nutrient deficiency can limit bud density (Björk 1967, Haslam 1971a), the development of buds even in initially dense clusters (Haslam 1970b) and bud diameter and subsequent aerial growth (Haslam 1971a). Nutrients can originate from the waters or from existing or accreting substrates and; provided there is an adequate supply, *Phragmites* seems to show few substrate preferences, growing equally well on wholly organic and wholly mineral material (Haslam 1972a). However, since it is a good peat former, it is particularly associated with organic deposits.

In more oligotrophic waters over acid peats or nutrient-poor silts, a thinner cover of *Phragmites* may be found in association with swamp species more tolerant of nutrient-poor situations. The *Menyanthes* sub-community is especially distinctive of such conditions around the margins of lakes to the north and west.

*Phragmites* is moderately tolerant of saline waters and soils: in the Exe estuary in Devon, it occurs over a range of salinities from 2 to  $12 \text{ g l}^{-1}$  (Proctor 1980) and in Poole Harbour, Dorset, it survives in salinities up to about  $22 \text{ g l}^{-1}$ , close to its experimentally determined limit (Ranwell *et al.* 1964, Ranwell 1972). In less saline

waters, quite dense growth is possible and the *Phragmites* sub-community includes some monodominant emergent stands from brackish dykes and estuaries.

Salt, however, is known to decrease or even prevent bud formation at higher concentrations (Ranwell *et al.* 1964, Haslam 1969a, 1972b) and to decrease bud diameter (Haslam 1971a) and stands of the *Phragmitetum* on salt-marshes, though sometimes extensive, often have a rather sparse cover of short shoots. Under such conditions, where there is greater light penetration, there may be a dense subsidiary flora and many stands of the *Atriplex* sub-community are from these situations. The composition of the understorey is somewhat variable, being partly dependent on the regime of tidal inundation and partly on the accumulation of litter which is readily trapped among the reed shoots. At some sites, a very open cover of diminutive *Phragmites* occurs over what is essentially a *Puccinellietum* sward (the *Puccinellia* variant) or even with *Zostera noltii* at low levels on salt-marshes. Such stands may have some sub-surface seepage of fresh water which ameliorates the high salinities resulting from frequent inundation. In other cases, there is a *Juncetum gerardi* kind of understorey at higher levels (some stands in the *Agrostis* variant). Where litter becomes trapped, its decay may release a flush of nitrogen which is often reflected in a patchy cover of *Atriplex prostrata* (*Atriplex* variant). Upper-marsh sites with water seepage may have a thick mat of *Agrostis stolonifera* (some stands in the *Agrostis* variant). Very species-poor salt-marsh stands lacking halophytes are indistinguishable floristically from some *Phragmitetum* in litter-choked or frequently inundated silty sites around inland fresh waters (like those in the *Phragmites-Agrostis stolonifera* community of Wheeler 1980a).

Although *Phragmites* has been reported in Britain from up to about 500 m, it is essentially a lowland plant and the *Phragmitetum* is commonest below 150 m. This is partly a reflection of the distribution of more eutrophic waters but it is probably related to climatic variation and particularly to summer temperatures. *Phragmites* becomes more sterile towards its northern European limit (Dahl 1934, Haslam 1972a) and in Britain must complete most of its cycle of annual growth between April and September. Warmer temperatures influence the attainment of the height potential in aerial shoots by stimulating intercalary and apical growth (Haslam 1969c) but this relationship is confused by the influence of other variables. In Scotland, for example, Spence (1964) calculated a regression of the height of flowering shoots on the mean temperature of the warmest month, but his equation is unlikely to be of national application because waters in the cooler climates of Scotland tend to be more oligotrophic and acid than elsewhere. *Phragmites* from colder parts of Europe



but in richer waters can be taller than Scottish plants (Björk 1967).

A second and more local effect of temperature concerns frosts, especially those in spring. Spring frosting can have a marked effect on the performance of *Phragmites* by resulting in an increase in bud density and a lengthening of the period of emergence. These more numerous buds are smaller than would otherwise have been the case and the aerial shoots consequently shorter (Haslam 1971a, 1972a). Emerging later, they may also suffer from competition for light (van der Toorn & Mook 1982). Moderate frosts seem to be the most effective in producing such changes; very heavy or repeated frosts can kill all emergent shoots and effectively prevent their replacement in that season. Such damage can result in marked short-term variation in the appearance of stands of the *Phragmitetum* and this may take some seasons to correct itself (Mook & van der Toorn 1982).

The impact of frosting or of other forms of damage to the buds, such as the scorching that can result from intense burning of the vegetation, is mediated through standing water or a litter cover which insulate against marked temperature variations (Haslam 1971a). With prolonged or frequent inundation, fallen leaves and stems slowly disintegrate to fine particulate material which can be readily washed away (Mason & Bryant 1975). Where flooding is rare or brief, however, and where the standing crop of dead stems is not harvested, decaying material accumulates to form a thick mat of litter which may contribute up to 40% of the total crop in September (Wheeler & Giller 1982a). If this is disturbed by animals or burned off, the buds may be exposed to damage. Haslam (1969b, 1970b, 1971a) proposed a variety of hypotheses to account for different kinds of damage including the killing of existing buds and stimulation of new initials by frosting, and the breaking of dormancy by scorch. Van der Toorn & Mook proposed a simpler model to account for the same effects: that *Phragmites* produces a surplus of autumn buds of which, under normal circumstances, only the dominant apical one undergoes development but in which, if this dominance is removed for whatever reason, all begin to sprout.

When growing well, the *Phragmitetum* is amongst the most productive of all swamp communities, commonly producing a standing crop in Britain of up to  $1 \text{ kg m}^{-2}$  and sometimes approaching  $2 \text{ kg m}^{-2}$  (Buttery & Lambert 1965, Haslam 1972b, Mason & Bryant 1975, Wheeler & Giller 1982a). The distinctive growth habit which leaves an annual crop of dead, foliage-free stems erect, accessible and often with virtually no remains of other plants, makes the vegetation ideal for winter harvesting. Moreover, the removal of this material helps keep down litter and exposes the buds to frost which, if

not too severe or frequent, can thicken up the vegetation and increase the crop. Dense and almost pure stands of the *Phragmitetum* can be maintained under such a regime and natural succession to fen and scrub prevented provided certain conditions are fulfilled. Other species which can readily germinate on the open and almost litter-free cut bed in spring must be destroyed: traditionally this has often been done by natural or artificial flooding. This, however, must not be so deep as to inundate the stubble and impede rhizome aeration, so retarding autumn bud development. And, if heavy or repeated cropping threatens to drain the nutrient reserves of the habitat, flooding with eutrophic waters or artificial fertilising must be undertaken (McDougall 1972, Haslam 1972b). The *Phragmites* and *Galium* sub-communities both contain stands of *Phragmites* treated as commercial reed-beds but floristically indistinguishable from natural swamps.

Cutting of green *Phragmites* after the main emergence period, on the other hand, results in a loss of irreplaceable shoots and a depressed yield in subsequent years (Haslam 1972b). Indeed, summer mowing of mixed stands of *Phragmites* and *Cladium mariscus* has been a standard way of purifying sedge-beds and, when combined with either deep-flooding or drainage such cutting can help eradicate *Phragmites*.

There is also some loss of reed from stands of the *Phragmitetum* because of grazing and browsing by both stock and wild animals including coypu, deer, water vole (Haslam 1972a) and certain wildfowl. Light grazing need not be deleterious because thicker crops of shorter shoots can be produced if leading emergents are bitten off or if disturbance of the litter mat exposes buds to frost (Haslam 1969a, 1971a). However, heavy grazing after emergence may prevent shoot replacement and trampling can damage the upper rhizomes and hinder bud development in the autumn (Rudescu *et al.* 1965, Haslam 1969c, 1971a, 1972b). Grazing combined with drainage is especially effective in speeding reed decline (Lambert 1948, Bittman 1953, Spence 1964).

Where grazing is by terrestrial mammals at the landward margins of swamps, the limit is often set by flooding which prevents access (Haslam 1971a). Coypu and wildfowl, on the other hand, often have their major impact toward the water's edge. Inland populations of larger geese probably have their greatest effect in late spring when succulent shoots are easily accessible and this, of course, is the time when damage can be most severe because such shoots may not be replaced (Haslam 1969b). Geese ingest relatively large quantities of food in relation to their body weight (Ogilvie 1978) and in Czechoslovakian swamps *Phragmites* has been shown to provide up to 90% of the late-spring diet of greylag (Hudec 1973). In Broadland, Boorman & Fuller (1981) concluded that feral greylag and Canada geese had

probably contributed to the recent general decline of swamp vegetation, much of which was *Phragmitetum*. It is also possible that certain wildfowl have altered the balance between different swamp helophytes: in Czechoslovakia, preferential grazing by greylag can give *Typha angustifolia* a temporary advantage against *Phragmites* (Fiala & Kvet 1971, Boorman & Fuller 1981).

Probably much more important in Broadland, though, has been the impact of feral coypu. Although these animals have a preference for *T. angustifolia* (Gosling 1974), they will readily eat reed, nibbling off emergent shoots in spring, pulling down leaves in summer and digging for roots and rhizomes in winter (Ellis 1963, Gosling 1974). Although much damage remains unobserved (coypu are largely nocturnal (Gosling 1979) and their activity is often masked by turbid water or shifting silt), various studies have suggested that much, if not all, the substantial swamp loss around the Broadlands in recent years can be attributed to their sometimes large population and substantial appetites (e.g. Anon. 1978, Gosling 1974, 1975a, b, Boorman & Fuller 1981).

Boorman & Fuller (1981) suggested that such damage might have been exacerbated by the general eutrophication of Broadland waters that has occurred recently, perhaps itself due in part to the faeces of coypu and wildfowl, as well as to the more obvious input of nutrients from fertiliser run-off and sewage. The decline of aquatic macrophytes which has followed this change could have deprived coypu and wildfowl of one food source and concentrated their attention on swamp vegetation; increased deposition of silt could also have made some stands more accessible. There is some evidence, too, that eutrophication can lead to decline in *Phragmites* for other reasons: when emergent shoots, for example, are deprived of light and oxygen by a smothering mat of blooming algae (Klötzli 1971, Schröder 1979) or when low sclerenchyma levels in fleshy reed tissues make stems more susceptible to damage by wave action (Klötzli & Grünig 1976).

As well as providing a food source for some herbivores, larger stands of the *Phragmitetum* can offer a valuable breeding or roosting site for a variety of birds (Fuller 1982). Some species, such as reed warbler (the commonest reed-bed breeder), cuckoo (for which reed warblers provide the commonest host in British wetlands), reed bunting, mallard and moorhen, are by no means restricted to the *Phragmitetum* but most of the British populations of bittern, marsh harrier and bearded tit nest exclusively in the community. Stands vary, however, in their quality for birds, perhaps because of differences in the invertebrate populations which form the prey of smaller passerines or of variation in contiguous wet or dry habitats which are needed as feeding ground: even the best swamps are relatively poor

in breeding species. The community also provides important late summer roosts for large numbers of swallow, sand martin and starling.

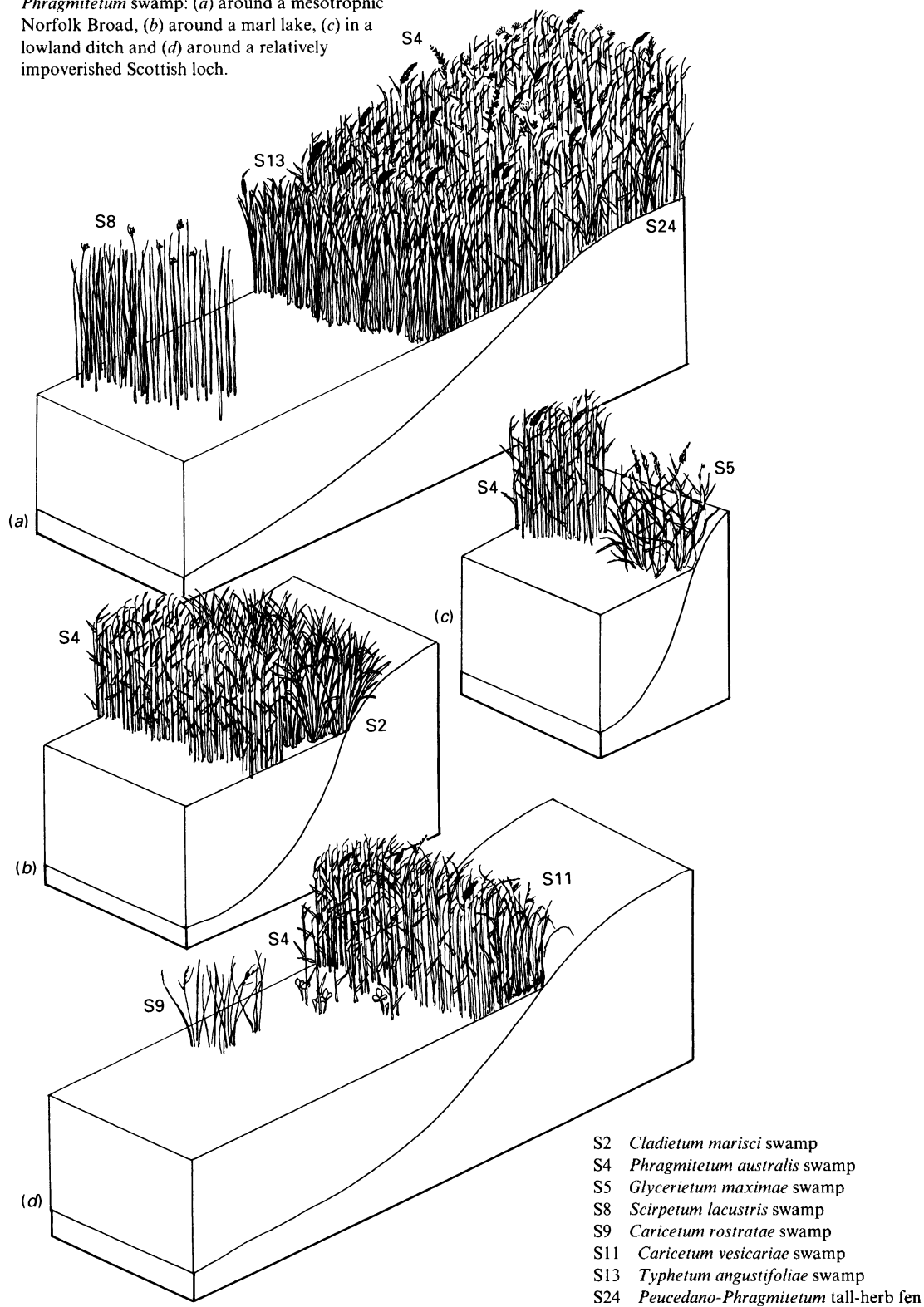
### Zonation and succession

The wide ecological amplitude of *Phragmites* makes the *Phragmitetum* one of the commonest components of zonations in open-water transitions and flood-plain mires and means that a wide variety of other swamp and fen communities, with more exacting species, can be found in association with it. The *Phragmitetum* is also widespread in the more compressed or fragmentary sequences associated with dyke and canal margins and it has a scattered distribution within salt-marsh zonations. It also persists, sometimes because of deliberate treatment as a crop, in the often very complex patterns of vegetation associated with disturbed fens in flood-plain and valley mires.

In more natural situations, the community occurs as part of zonations which can, in any particular site, be related most frequently to a gradient of water-level. In extensive open-water transitions it is often the most distal swamp type giving way directly, in deeper unpolluted waters, to floating-leaved or submerged aquatic vegetation. In some cases, stands are fronted by other swamp types: in lakes to the north and west, there is sometimes a belt of the *Scirpetum lacustris* (Pearsall 1918, Spence 1964) and this pattern was probably, at one time, more widespread (as in Broadland: see Pallis 1911, Lambert & Jennings 1951); in more eutrophic waters, the *Typhetum angustifoliae* occurs in this position (Lambert 1951) (Figure 12) or, in more sheltered sites in the rather peculiar conditions along the Yare valley in Norfolk, the *Glycerietum maximae* (Lambert 1946). Much conflated versions of these sequences occur commonly in mesotrophic and eutrophic dykes and canals (e.g. Haslam 1978).

Where there is a substantial depth of water available for colonisation, it is usually the *Phragmites* sub-community that leads such sequences or, in poorer waters especially over peat, the *Menyanthes* sub-community (e.g. Birks 1973). In waters which are more shallow throughout, the *Galium* sub-community is more usual. Very commonly, a gradual reduction in water-level is matched by the *Phragmites* sub-community being replaced inshore by the *Galium* sub-community: this is the common pattern in larger lakes in Scotland and north-western England (e.g. Spence 1964). In these regions too, lake stands of the *Phragmitetum* tend to be less extensive, being often restricted to more nutrient-rich areas of deposition, as around the deltas of input streams. This means that the community often forms a complex patchwork around the shores with other swamps like the *Caricetum rostratae* and the *Caricetum vesicariae*.

Figure 12. Some typical zonations with the *Phragmitetum* swamp: (a) around a mesotrophic Norfolk Broad, (b) around a marl lake, (c) in a lowland ditch and (d) around a relatively impoverished Scottish loch.



At some sites, the *Phragmitetum* may give way inshore, but still in standing water, to other swamp types. In oligotrophic calcareous waters, the *Cladietum marisci* may occur here, or in more mesotrophic situations, the *Caricetum paniculatae* (Lambert & Jennings 1951, Lambert 1951). Along the Yare, a narrow front of the *Phragmitetum*, resistant to scour, can protect a bank of the *Glycerietum maximae* (Lambert 1946).

Frequently, however, the community gives way directly to some form of fen. The more landward parts of these zonation are strongly influenced by the trophic state of the substrate and also by human interference which, pushing out to the limit of standing water, has made intact sequences increasingly rare. In the more complete transitions, the *Phragmitetum* may pass gradually, through the *Galium* sub-community and with a progressive increase in the number and variety of associates, to fen vegetation in which *Phragmites* remains a prominent component. On mesotrophic silts and organic soils, there can be a zonation to the *Phragmites-Eupatorium* fen; this is a common, though often rather fragmentary, pattern in some valley mires (e.g. Haslam 1965). On the fen peats of Broadland, the *Phragmitetum* can give way to the very rich and varied *Peucedano-Phragmitetum* (e.g. Pallis 1911, Lambert & Jennings 1951, Wheeler 1978). In more acid and oligotrophic waters, the community may pass to a swinging mat of the *Potentillo-Caricetum rostratae* (e.g. Pearsall 1918, Holdgate 1955b, Pigott & Wilson 1978) which sometimes seems to be able to grow through and beyond the *Phragmitetum*.

In the agricultural lowlands, many transitions of this kind have been truncated by systematic drainage and, even in those few places, like Broadland, where extensive tracts of swamp and fen remain, zonation are very complex and sometimes abrupt because of differences in treatment applied piecemeal to marsh parcels (e.g. Lambert 1948). A very common feature of disturbed and eutrophicated sites throughout the lowlands is the juxtaposition of the *Phragmites* or *Galium* sub-communities with various kinds of *Phragmites-Urtica* fen, the *Phalaridetum* or tall-herb vegetation like the *Epilobietum hirsutae*. Narrow strips of these vegetation types also occur widely in sequences along the banks of dykes.

Although stands of the *Phragmites* sub-community are also found in brackish dykes behind reclamation banks, the majority of salt-marsh and estuarine occurrences of the community are in sites without permanent standing water. Sometimes stands of the *Atriplex* sub-community seem to be simply superimposed upon the existing salt-marsh zonation, occurring within *Puccinellietum* or *Juncetum gerardi* swards. In other cases, this sub-community forms part of the complex of vegetation types that occurs around the upper-marsh transition where there is litter accumulation and/or freshwater

seepage. In estuaries, stands of the *Phragmitetum* sometimes occur in the inverted zonation associated with reversals of salinity gradient.

When undisturbed, the *Phragmitetum* can be a very persistent community. *Phragmites* can retain its dominance under a wide variety of conditions and in optimal habitats stands can be very extensive and long-lived: Rudescu *et al.* (1965) estimated the age of some clones as in excess of 1000 years. Although seed-set, fertility and viability can be good (e.g. Hürlimann 1951, Bittman 1953, Spence 1964, Haslam 1972a), conditions are rarely favourable for the growth of seedlings within existing stands, but this may be of little consequence with such an efficient system of vegetative renewal. *Phragmites* can attain a very high shoot density on healthy advancing fronts (Haslam 1971a, 1972a) and retain it within older stands, producing a canopy that, by mid-summer, has reduced light penetration below very substantially (Buttery & Lambert 1965, Haslam 1971a, 1972a). In deeper water, it has few natural competitors and, on drier ground, an undisturbed litter mat can help prevent the establishment of other species (Haslam 1971a). Stands which suffer moderate damage from frosting, burning or insect infestation seem to possess an ability to restore a balanced shoot production within a few seasons (Mook & van der Toorn 1982).

The essential feature of successful competitors to *Phragmites* seems to be that they can capitalise on light levels under a given water and nutrient regime. Some achieve this by virtue of a different phenology to reed. Both those swamp helophytes which seem able to compete with *Phragmites* in deeper waters, *Glyceria maxima* and *Typha angustifolia*, attain maximum shoot densities and a critical light interception by May, when the emergence of reed shoots is only one third or so complete (Buttery & Lambert 1965, Mason & Bryant 1975). Moreover, *G. maxima* goes on producing shoots until late in the season and not until the shoots lodge is light penetration increased.

Some other species require a drier substrate to invade. *Cladium mariscus* and *Carex paniculata* both seem able to take advantage of the period between the emergence of an accumulating *Phragmites* root felt above the water level and the build-up of litter on the now drier surface (e.g. Lambert 1951). Moreover, both are evergreen and somewhat shade-tolerant and well adapted to survive the gradual depression of the mat of *Phragmites* under the water with the slowly increasing weight of their bulky stocks. *C. mariscus* may have the additional advantage of a greater tolerance of oligotrophic conditions than *Phragmites* (Lambert 1951).

The establishment of most other species within the *Phragmitetum* depends upon some reduction in reed vigour to open the canopy and an amelioration of the blanketing effect of the accumulating litter mat. There



may be an opportunity for some species to invade in those situations where, with slow terrestrialisation, a still thin litter mat is exposed to decreasing periods of winter submergence with ever shallower waters. The development of the *Galium* sub-community from the *Phragmites* sub-community occurs in this way as relatively shade-tolerant herbs are able to establish on the damp litter in spring. As the reed cover becomes less vigorous on the drier substrate, there may be a continuing natural succession to the richer vegetation of the *Phragmites-Eupatorium* or *Peucedano-Phragmitetum* fens and thence to fen carr (e.g. Tansley 1939, Lambert & Jennings 1951, Lambert 1951, Wheeler 1980c). At various stages in such sequences, winter-cropping of reed can help the *Phragmitetum* persist against the tendency towards invasion of competitors or confuse the natural succession.

More drastic disturbance of the water regime or of the litter mat may produce a strong disruption in the natural growth rhythm of *Phragmites*, giving any invaders a season or more's advantage. The rapid drop in water level consequent upon drainage can produce such results (Haslam 1970c, 1971a, b) as can very severe and repeated frost or mismanagement of reed-beds. If there is surface disturbance, eutrophication of oxidising organic matter is often followed by the development of the *Phragmites-Urtica* community with its very characteristic patches of nitrophilous tall herbs (e.g. Haslam 1965). The enrichment of dyke waters by fertiliser runoff and sewage and the disturbance involved in dyke clearance and dredging is often marked by successions to this fen on the banks.

On some ungrazed salt-marshes, the *Phragmitetum* has replaced parts of stands of the *Spartinetum townsendii* but the status of the community in general successions of salt-marshes is difficult to assess (Ranwell 1961, 1964a, 1972).

### Distribution

The *Phragmites* sub-community is widespread throughout the British lowlands. The *Galium* sub-community

has also been encountered in most regions, although it appears especially conspicuous around Scottish lakes where it is the major drier *Phragmites*-dominated community, replacing such fens as the *Phragmites-Eupatorium* community and the *Peucedano-Phragmitetum*. The *Menyanthes* sub-community has been recorded only from isolated localities in the north-west and Scotland.

The variants of the *Atriplex* sub-community have a more patchy distribution on coastal and inland salt-marshes and (without halophytes) around some inland freshwater bodies. Although the *Phragmitetum* is rare on the western Scottish coast (Adam 1978), some of the largest intertidal stands in the country occur in eastern Scotland, notably on the Tay (Ingram *et al.* 1980).

### Affinities

The *Phragmitetum* as diagnosed here is a narrower unit than some of the reed-swamp communities defined from mainland Europe, such as the *Scirpo-Phragmitetum* of Koch (1926) or its amendments like the *Scirpeto-Phragmitetum* Tüxen 1941 which have included vegetation dominated by other swamp helophytes. As with all species-poor swamps, there may be difficulties of definition where *Phragmites* dominance is giving way to species such as *Scirpus lacustris* ssp. *lacustris*, *Typha angustifolia*, *Cladium mariscus* and *Carex paniculata*. Mixed stands where *Phragmites* has a quantitatively subordinate role have been assigned to sub-communities in the vegetation types dominated by these other species.

More species-rich stands of the *Phragmitetum* show affinities to the often *Phragmites*-dominated vegetation of the *Phragmites-Eupatorium* fen but the more consistent presence there of species such as *Lythrum salicaria*, *Eupatorium cannabinum*, *Filipendula ulmaria* and *Iris pseudacorus* is generally a good demarcation. Likewise, although stands of the *Phragmitetum* may have scattered clumps of tall herbs such as *Urtica dioica* and *Epilobium hirsutum*, these are much more frequently conspicuous in the *Phragmites-Urtica* fen.

Floristic table S4a

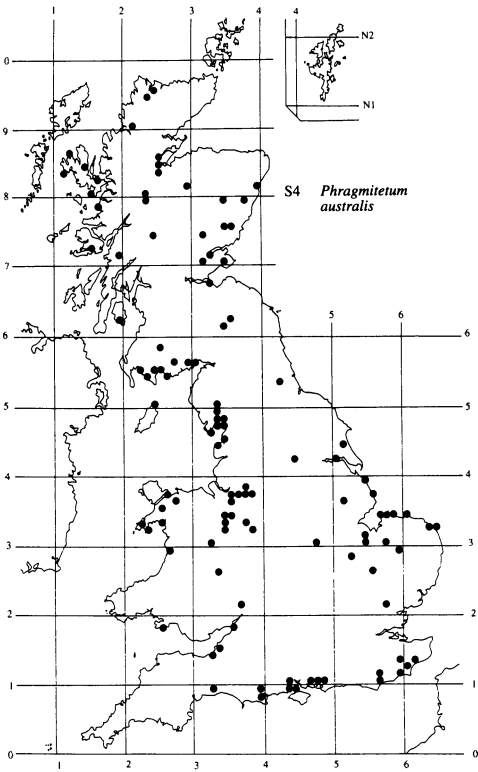
	4a
<i>Phragmites australis</i>	V (5–10)
<i>Solanum dulcamara</i>	I (1–5)
<i>Typha latifolia</i>	I (1–6)
<i>Lemna minor</i>	I (4–8)
<i>Carex riparia</i>	I (1–3)
<i>Iris pseudacorus</i>	I (3–5)
<i>Typha angustifolia</i>	I (2–5)
<i>Carex acuta</i>	I (2–4)
<i>Glyceria maxima</i>	I (1–4)
<i>Oenanthe crocata</i>	I (1–4)
<i>Callitriche stagnalis</i>	I (2–5)
<i>Cladium mariscus</i>	I (1–5)
<i>Calystegia sepium</i>	I (1–8)
<i>Carex lasiocarpa</i>	I (5–7)
<i>Berula erecta</i>	I (1–5)
<i>Scirpus maritimus</i>	I (2–5)
<i>Carex panicea</i>	I (3–7)
<i>Ranunculus flammula</i>	I (2–3)
<i>Cardamine pratensis</i>	I (2–3)
<i>Hydrocotyle vulgaris</i>	I (3–4)
<i>Juncus effusus</i>	I (1–3)
<i>Salix cinerea</i> sapling	I (1–3)
<i>Sphagnum recurvum</i>	I (5–7)
<i>Molinia caerulea</i>	I (1–10)
<i>Eriophorum angustifolium</i>	I (4)
<i>Galium aparine</i>	I (2)
<i>Rubus fruticosus</i> agg.	I (1)
Number of samples	176
Number of species/sample	3 (1–12)
Vegetation height (cm)	182 (70–300)
Vegetation cover (%)	94 (20–100)

Floristic table S4b

	4b
<i>Phragmites australis</i>	V (5–10)
<i>Galium palustre</i>	IV (1–5)
<i>Mentha aquatica</i>	III (1–6)
<i>Epilobium hirsutum</i>	II (1–4)
<i>Iris pseudacorus</i>	II (1–5)
<i>Lythrum salicaria</i>	II (1–4)
<i>Calliargon cuspidatum</i>	II (1–4)
<i>Sparganium erectum</i>	I (3–7)
<i>Carex pseudocyperus</i>	I (1–8)
<i>Sium latifolium</i>	I (1–3)
<i>Rumex hydrolapathum</i>	I (1–3)
<i>Carex riparia</i>	I (1–4)
<i>Typha angustifolia</i>	I (1–3)
<i>Lemna minor</i>	I (2–4)
<i>Berula erecta</i>	I (1–3)
<i>Cicuta virosa</i>	I (1–3)
<i>Juncus subnodulosus</i>	I (1–3)
<i>Lotus uliginosus</i>	I (2–3)
<i>Angelica sylvestris</i>	I (1–3)
<i>Solanum dulcamara</i>	I (1–4)
<i>Lychnis flos-cuculi</i>	I (2–3)
<i>Equisetum palustre</i>	I (1–4)
<i>Lycopus europaeus</i>	I (2–3)
<i>Phalaris arundinacea</i>	I (1–3)
<i>Urtica dioica</i>	I (1–2)
<i>Poa trivialis</i>	I (3–4)
<i>Holcus lanatus</i>	I (3–4)
<i>Agrostis stolonifera</i>	I (1–5)
<i>Filipendula ulmaria</i>	I (6)
<i>Ranunculus lingua</i>	I (1)
<i>Brachythecium rutabulum</i>	I (2)
<i>Cardamine pratensis</i>	I (3)
<i>Equisetum fluviatile</i>	I (4)
<i>Myosotis laxa caespitosa</i>	I (3)
<i>Myosotis scorpioides</i>	I (1)
<i>Oenanthe fistulosa</i>	I (1)
<i>Salix cinerea</i> sapling	I (1)
Number of samples	61
Number of species/sample	8 (2–15)
Vegetation height (cm)	205 (150–300)
Vegetation cover (%)	99 (95–100)

Floristic table S4c

	4c
<i>Phragmites australis</i>	V (5–10)
<i>Menyanthes trifoliata</i>	IV (1–4)
<i>Equisetum fluviatile</i>	IV (1–3)
<i>Carex rostrata</i>	IV (2–4)
<i>Nymphaea alba</i>	III (1–6)
<i>Potentilla palustris</i>	III (1–3)
<i>Potamogeton polygonifolius</i>	II (1–3)
<i>Juncus bulbosus</i>	II (2–4)
<i>Potamogeton natans</i>	II (3)
<i>Utricularia minor</i>	I (2)
<i>Eleocharis palustris</i>	I (2)
<i>Juncus articulatus</i>	I (3)
<i>Potamogeton gramineus</i>	I (1)
<i>Carex lasiocarpa</i>	I (2)
<i>Eriophorum angustifolium</i>	I (3)
<i>Sparganium minimum</i>	I (1)
<i>Utricularia intermedia</i>	I (1)
<i>Utricularia vulgaris</i>	I (1)
<i>Hippuris vulgaris</i>	I (1)
Number of samples	8
Number of species/sample	6 (3–10)
Vegetation height (cm)	150
Vegetation cover (%)	78 (20–100)



Floristic table S4d

	4di	4dii	4diii
<i>Phragmites australis</i>	V (9–10)	V (6–10)	V (5–10)
<i>Atriplex prostrata</i>	V (1–6)	III (6–10)	III (1–5)
<i>Puccinellia maritima</i>		V (2–7)	II (2–3)
<i>Aster tripolium</i>	I (1)	III (2–4)	
Algal mat	I (5–6)	III (5–8)	I (6–7)
<i>Plantago maritima</i>		II (3–6)	I (2–4)
<i>Salicornia dolichostachya</i>		II (2–3)	I (2)
<i>Halimione portulacoides</i>		II (1–9)	
<i>Cochlearia anglica</i>		I (2–4)	
<i>Limonium</i> cf. <i>vulgare</i>		I (1–3)	
<i>Agrostis stolonifera</i>	I (1)	I (4)	V (3–7)
<i>Juncus gerardi</i>		I (3–4)	III (2–8)
<i>Festuca rubra</i>	I (3–4)	I (4–8)	II (2–6)
<i>Armeria maritima</i>		I (4)	I (2–4)
<i>Amblystegium riparium</i>			I (2–6)
<i>Oenanthe lachenalii</i>			I (2–3)
<i>Matricaria maritima</i>			I (1–4)
<i>Carex otrubae</i>			I (2–3)
<i>Calystegia sepium</i>			I (2–6)
<i>Ranunculus sceleratus</i>			I (2–5)
<i>Glyceria fluitans</i>			I (3–5)
<i>Apium graveolens</i>			I (3–4)
<i>Juncus maritimus</i>			I (4–6)
<i>Elymus repens</i>			I (4–6)
<i>Oenanthe crocata</i>			I (2–5)
<i>Juncus articulatus</i>			I (2–3)
<i>Holcus lanatus</i>			I (2–4)
<i>Galium uliginosum</i>			I (2–3)
<i>Rumex crispus</i>			I (2–4)
<i>Sonchus arvensis</i>			I (3–4)
<i>Atriplex littoralis</i>			I (2–4)
<i>Galium aparine</i>			I (3)
<i>Eleocharis palustris</i>			I (3)
<i>Glaux maritima</i>	I (2)	II (2–3)	II (2–8)
<i>Triglochin maritima</i>		II (2–5)	II (2–3)
<i>Scirpus maritimus</i>		II (2–7)	II (1–5)
<i>Elymus pycnanthus</i>	I (3)	I (3–4)	I (5)
<i>Aster tripolium</i> (rayed)	I (2)	I (3–4)	I (1–4)
<i>Cochlearia officinalis</i>		I (3)	I (2–3)
<i>Suaeda maritima</i>		I (3–4)	I (3)
Number of samples	11	21	27
Number of species/sample	3 (2–4)	6 (4–8)	7 (4–17)
Vegetation height (cm)	151 (120–200)	73 (20–150)	147 (40–300)
Vegetation cover (%)	100	91 (40–100)	96 (70–100)