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## W2

# *Salix cinerea*-*Betula pubescens*-*Phragmites australis* woodland

### Synonymy

Fen carr Pallis 1911, Godwin & Turner 1933, Godwin 1936, Tansley 1939, Lambert 1951; Closed carr Pearsall 1918 *p.p.*; *Rhamnetum*, *Franguletum*, *Rhamno-franguletum* Godwin & Tansley 1929, Godwin 1936, 1943a, b; *Betuletum* Godwin & Turner 1933; Semi-swamp and pseudo-swamp carrs Lambert 1951 *p.p.*; *Calamagrostis sere* Poore 1956b *p.p.*; Alder woodland type 2c McVean 1956b *p.p.*; *Betulo-Dryopteridetum cristatae* Wheeler 1978; *Osmundo-Alnetum* (Klötzli 1970) Wheeler 1980c *p.p.*; *Frangula alnus* and *Rhamnus catharticus* sociations Wheeler 1980c *p.p.*; *Betulo-Myricetum gale* Wheeler 1980c *p.p.*; *Alnus-Salix-Betula* woodland Meres Report 1980 *p.p.*; Fen Woodland Fitter *et al.* 1980 *p.p.*

### Constant species

*Betula pubescens*, *Salix cinerea*, *Phragmites australis*.

### Rare species

*Carex elongata*, *Dryopteris cristata*, *D. × uliginosa*, *Peucedanum palustre*, *Pyrola rotundifolia*, *Thelypteris palustris*.

### Physiognomy

The *Salix cinerea*-*Betula pubescens*-*Phragmites australis* woodland is rather variable in the floristics and physiognomy of its woody component. *Salix cinerea* and *Betula pubescens* are the most frequent species throughout and, together with some *Alnus glutinosa*, they usually form the bulk of the canopy. These major colonists show some differences in their preference for the various habitat conditions characteristic of the community (see below) but the chance availability of seed-parents and vagaries of propagule dispersal clearly play a large part in determining the composition and structure of the canopy, especially in the early stage of development (e.g. Godwin 1936). Moreover, these species show some ability to 'leapfrog' over one another in the colonisation process, so that, though *S. cinerea* is a common early invader (e.g. Pearsall 1918, Lambert 1946), it may be

overtaken by waves of *Alnus* (e.g. Pigott & Wilson 1978) or *B. pubescens*. Without extensive detailed studies on a large number of sites, it is difficult to say whether there are consistent sequences of invasion which are reflected in the subsequent woodland structure. Young canopies of this community are certainly very heterogeneous internally and very different, one from another, comprising mixtures of these three species in various proportions, with individuals of different ages, forming a cover that varies from low, open scrub or very dense thickets to taller woodland with some stratification (e.g. Pallis 1911, Godwin & Turner 1933, Lambert 1951). Furthermore, in some stands, other woody species, which are generally no more than occasional through the community as a whole, can attain a striking prominence in the early stages of colonisation and exert a long-lasting, though by no means simple and unchanging, influence on the vegetation. The most renowned example of this is at Wicken Fen in Cambridgeshire where *Frangula alnus* and *Rhamnus catharticus* were, and over much of the fen remain, major components of the canopy (Godwin 1936, Godwin *et al.* 1974) but such local dominance, especially of *Frangula*, can be encountered elsewhere.

The composition and structure of the field layer is strongly influenced by the character of the preceding fen vegetation and the extent to which its various elements can survive in the changing environment. Since both the floristics and physiognomy of the invaded fen and the cover and density of the colonising canopy which increasingly affects it are very variable, the field layer of the community as a whole has few species that provide a strong, consistent core throughout. Of those bulky monocotyledons which commonly dominate the kinds of fen over which this woodland usually develops, only *Phragmites australis* is sufficiently persistent to remain a frequent species overall and, even then, its cover is very variable. In some stands it is very abundant, forming dense patches, a metre or more tall, which dominate the field layer; elsewhere it is much more sparse and, rarely,

it is absent altogether. Other fen dominants, like *Carex acutiformis*, are more sporadic or are generally confined to younger and more open canopies, e.g. *Cladium mariscus* (Godwin 1936, Godwin *et al.* 1974), *Calamagrostis canescens* (Lambert 1951) or, at Woodwalton Fen in Cambridgeshire, *C. epigejos* (Poore 1956b). *Carex paniculata* is another species which can be very persistent but it is scarce in the community and much more typical of the *Alnus*-*Carex* woodland. However, despite their patchy representation, the gross physiognomy of these species means that, when they do occur, they can give stands a striking individuality.

No member of the associated flora of tall-herb fens remains frequent throughout the community but *Thelypteris palustris*, particularly towards the heart of its range in East Anglia, is a distinctive occasional. Indeed, its occurrence in the fen systems there has been associated (Wheeler 1978) with the development of young carr but it remains decidedly local in both the sub-communities, being very abundant in some stands and quite absent from others. The tall dicotyledons characteristic of fens are likewise somewhat patchily distributed. The commonest species throughout are *Filipendula ulmaria* and *Eupatorium cannabinum* with, less frequently, *Lysimachia vulgaris*, *Lythrum salicaria* and the rare *Peucedanum palustre*. Again, these seem to be more frequently found where stands of this woodland have developed among richer fens, such as those of Broadland, but certain of them are also more consistently associated with the *Alnus*-*Filipendula* sub-community. It is possible that variation in this component, like that in the amount of *Myrica gale* and *Molinia caerulea*, which are preferential to the *Sphagnum* sub-community, represents in part differences inherited from the preceding fen vegetation.

Other general floristic features of the field layer are weakly developed but three elements deserve comment, especially in the light of the possible seral developments of the community (see below). First, there is quite commonly an undershrub layer. *Rubus fruticosus* agg. and *Rosa canina* agg. are its most frequent components but, less often, there can be some *Rubus idaeus* (or *R. caesius* at Wicken: Godwin 1936, Godwin *et al.* 1974), *Ribes rubrum* or *R. nigrum*. Second, *Dryopteris dilatata*, generally speaking an uncommon fern of fens, except where it gains a hold on drier sedge tussocks, makes an appearance. And, third, over the sometimes very extensive areas of bare ground, there can be loose mats of *Poa trivialis* and wefts of *Eurhynchium praelongum*.

### Sub-communities

***Alnus glutinosa*-*Filipendula ulmaria* sub-community:** Fen carr Pallis 1911, Godwin 1936, Lambert 1951; *Rhamnetum*, *Franguletum*, *Rhamno-franguletum* Godwin &

Tansley 1929, Godwin 1936, 1943 *a, b*; Semi-swamp and pseudo-swamp carrs Lambert 1951 *p.p.*; *Calamagrostis sere* Poore 1956b; Alder woodland type 2c McVean 1956b *p.p.*; *Osmundo-Alnetum* (Klötzli 1970) Wheeler 1980c *p.p.*; *Frangula alnus* and *Rhamnus catharticus* sociations Wheeler 1980c *p.p.*; Fen Woodland Fitter *et al.* 1980 *p.p.* In its typical and more mature forms, the canopy in this sub-community is more species-rich, varied and structurally complex than that of the *Sphagnum* sub-community. *Alnus glutinosa* is preferentially frequent here and it can exceed *S. cinerea* and *B. pubescens* in abundance. Well-grown trees, together with occasional *Fraxinus excelsior* and scarcer *Quercus robur*, sometimes form an upper tier to the canopy, reaching 15 m, with somewhat shorter *S. cinerea* and *B. pubescens* beneath. Commonly, however, such stratification is indistinct, even in longer-established stands, and there is often a complete gradation from taller trees and well-grown shrubs to shorter individuals. Among the smaller woody associates, the most frequent are *Crataegus monogyna*, *Frangula alnus* and, especially distinctive of this sub-community, *Viburnum opulus* and *Rhamnus catharticus*. Under more mature canopies, the commonest saplings are of *Alnus* and *Fraxinus*.

Two features can increase the physiognomic complexity of this woody component. First, competition between the developing canopy elements can leave many overtopped shrubs (notably smaller individuals of *S. cinerea* and *Frangula*) dying or dead and their remains can choke the understorey in places and leave an abundance of brushwood litter over the ground. Second, on substrates which are less firm, as for example where there is unconsolidated silt below peat, the weight of the developing canopy may cause some subsidence or surface breakdown of the substrate so that the trees and shrubs sink somewhat or lean over. As a rule, such leaning is not so pronounced as in the *Alnus*-*Carex* woodland where trees are often rooted in *Carex paniculata* tussocks which can eventually roll under the strain, but something approaching swampy conditions can develop locally (as in the situations described as semi-swamp and pseudo-swamp carr by Lambert 1951). Where *S. cinerea* and *V. opulus* topple over, their branches may take root and show a renewed flush of growth in their displaced positions, further increasing the tangle of woody material. Sometimes, this process is repeated producing a 'banyan' physiognomy (e.g. Godwin 1936, Godwin *et al.* 1974). As well as complicating the appearance of the canopy, such developments may have direct consequences for the patterning in the field layer by creating new patchworks of wetter or less-shaded ground.

In general, the field layer under more mature canopies is dominated by mixtures of *Phragmites australis*, occa-

sionally accompanied or sometimes replaced by *Carex acutiformis*, and a variety of tall herbs. Among these latter, the most frequent species are *Filipendula ulmaria*, *Eupatorium cannabinum* and *Urtica dioica* which can each occur as scattered individuals or in locally prominent patches. More occasional and usually less abundant are *Cirsium palustre*, *Angelica sylvestris*, *Epilobium hirsutum*, *Phalaris arundinacea*, *Berula erecta*, *Lycopus europaeus*, *Epilobium palustre*, *Iris pseudacorus*, *Lythrum salicaria*, *Lysimachia vulgaris* and *Peucedanum palustre*. The vegetative vigour and flowering of these species, and of the persistent fen dominants, often show some depression in areas of deeper shade and a resurgence where the canopy opens up with the ageing or death of trees and shrubs (e.g. Godwin 1936, Haslam 1971b, 1972).

Although ferns are not so numerous or varied as in the *Sphagnum* sub-community, the two community species, *Thelypteris palustris* and, on drier knolls, *Dryopteris dilatata*, occur occasionally. Quite often, too, the vegetation is tangled with underscrub, especially of *Rubus fruticosus* agg., and with sprawlers and climbers: *Galium palustre*, *G. aparine* and *Solanum dulcamara* can all be prominent and, among the woody branches, there may be some *Calystegia sepium*, *Tamus communis*, *Humulus lupulus* or *Lonicera periclymenum*. *Carex elongata* survives in vegetation of this sub-community at Askham Bog in North Yorkshire (Fitter *et al.* 1980).

Smaller herbaceous species are, generally speaking, not numerous and, apart from *Poa trivialis* which can grow in large patches, their cover is low, with just scattered plants of, for example, *Mentha aquatica* or *Caltha palustris*. Indeed, in areas of denser shade, there can be large stretches of peat and litter which are totally bare of vegetation apart from bryophytes. These can form an extensive cover, though the species involved are generally few. *Eurhynchium praelongum* and, preferential here, *Brachythecium rutabulum* and *Plagiothecium undulatum* are by far the commonest species, though *Plagiothecium sylvaticum*, *Amblystegium riparium*, *A. serpens*, *Calliergon cuspidatum* and *Lophocolea heterophylla* can also be found. Sphagna are characteristically very scarce in this sub-community.

The woodlands described from Wicken Fen (Godwin & Tansley 1929, Godwin 1936, Godwin *et al.* 1974) are best considered, for the most part, as a distinctive variant of this sub-community. At this site, secondary fen was quickly colonised, on the cessation of mowing, by *Frangula alnus* and smaller amounts of *Rhamnus catharticus*, *Salix cinerea*, *Crataegus monogyna*, *Viburnum opulus* and *Prunus spinosa* to produce a mosaic of young canopies of varying composition and density. Over the first 20 years or so of the invasion, there was a gradual demise, under the thicker scrub, of the once-dominant *Cladium mariscus* (and, to a lesser extent, of

*Phragmites australis*) and its mown-fen associates *Salix repens* and *Molinia caerulea*. These were replaced by an open patchwork of the tall herbs and underscrub characteristic of this sub-community, some species, such as *Eupatorium cannabinum*, *Filipendula ulmaria* and *Angelica sylvestris*, surviving from the preceding fen vegetation and showing an expansion, others, like *Thelypteris palustris*, *Urtica dioica* and *Rubus caesius* invading afresh. Where the scrub remained more open, the fen dominants persisted longer to produce a more mixed field layer. Changes in the developing canopy, due to internal competition between its expanding components and markedly affected by early die-back of *Frangula* after infection by a *Fusarium* sp. and *Nectria cinnabarina*, superimposed on this general trend a fine scale of variation in canopy shade. This was reflected in the field layer by waves of waxing and waning of the tall herbs or, under the initially thinner canopies, of the surviving fen dominants. After some 50 years (Godwin *et al.* 1974), there were signs at Wicken of a reversion to the kind of canopy more typical of this sub-community with the appearance in various parts of the site of *Alnus*, *Betula* spp., *Fraxinus* and *Quercus robur*. However, the field layer of the most closely monitored of the original plots (Reserve A), though it retained a cover of *Rhamnus* and *Frangula*, seemed to have progressed somewhat beyond the limits of this vegetation type. With a reduction in *Phragmites* and tall fen herbs, an increase in *Urtica dioica* and *Poa trivialis* and the appearance of *Glechoma hederacea*, it resembled more the field layer of the *Alnus-Urtica* woodland (see below).

The young scrub described by Poore (1956b) from Woodwalton Fen in Cambridgeshire illustrates a different variation on the same theme. Here the major coloniser was *Salix cinerea* with smaller amounts of *Betula* spp. (unusually, mostly *B. pendula*), *Crataegus monogyna*, *Quercus robur*, *Viburnum opulus* and local *Alnus*. *Rhamnus* was rare, *Frangula* limited to a single (perhaps planted) individual and *Fraxinus* absent. The field layer had many of the typical features of this sub-community with frequent, though sparse, *Phragmites*, a strong contingent of tall herbs and well-developed underscrub but intermixed with these were prominent remnants of the rather peculiar secondary fen vegetation typical of this much-modified site: *Calamagrostis canescens*, *C. epigejos*, *Symphytum officinale*, *Lotus uliginosus*, *Thalictrum flavum* and *Vicia cracca*. As at Wicken, these various components came and went somewhat with the closure and thinning of the developing canopy.

***Sphagnum* ssp. sub-community: *Betuletum*** Godwin & Turner 1933; Fen carr Godwin *et al.* 1974 p.p.; *Betulo-Dryopteridetum cristatae* Wheeler 1978; *Betulo-Myricetum peucedanetosum* Wheeler 1980c p.p.; *Alnus-Salix-Betula* woodland XXIii Meres Report 1980.

*Betula pubescens* is almost always the most abundant woody species here, though its stature is very variable. Sometimes it forms the basis of small islands of open birch scrub with saplings only a metre or so high; elsewhere, the cover is more extensive, denser and taller. There is commonly a little *Salix cinerea* but both *Alnus* and *Fraxinus* are markedly less prominent than in the previous sub-community, often occurring just as occasional saplings. *Frangula* can be locally abundant and there is sometimes a little *Salix aurita* and some young *Quercus robur* but *Rhamnus* and *Viburnum opulus* are characteristically absent. Occasionally, bushes of *Myrica gale* and *Salix repens* form a patchy lower tier to the canopy and there can be tangles of *Rubus fruticosus* agg., *Rosa canina* agg. and *Lonicera periclymenum*.

*Phragmites* remains frequent in the field layer and it can be abundant but other fen dominants are generally sparse, even in younger stands: there is occasionally some *Calamagrostis canescens* and, less commonly, *Cladium mariscus*, *Carex elata* or *C. appropinquata* can persist. *C. paniculata*, however, is rare and *C. acutiformis* absent. Tall fen herbs are also rather patchy here compared with the previous sub-community. *Filipendula ulmaria* remains occasional and it can be accompanied, especially among richer fen systems, by *Eupatorium cannabinum*, *Lysimachia vulgaris*, *Lythrum salicaria* and *Peucedanum palustre* but *Urtica dioica* is noticeably very uncommon. Quite often, the field layer is marked by the patchy abundance of various grasses, including *Holcus lanatus*, *Molinia caerulea*, *Agrostis canina* spp. *canina*, *A. stolonifera* and *Poa trivialis*, and there can be scattered tussocks of *Juncus effusus*. *Potentilla erecta* and *Hydrocotyle vulgaris* are occasional associates and, in Broadland, there are rare records for *Pyrola rotundifolia* and *Drosera rotundifolia*.

Two further features are especially characteristic of this vegetation. The first is the abundance and variety of ferns. As well as *Thelypteris palustris*, *Dryopteris dilatata* and *Athyrium filix-femina*, *Dryopteris carthusiana* is more frequent here than in the previous sub-community and of particular note in Broadland is *D. cristata*. This last species seems to thrive best in a more open shrubby cover and its distinctive clusters of bright green, upright fronds often form a striking fringe around the margins of stands or in glades (Wheeler 1978, Page 1982). In denser shade, sparse sterile fronds can sometimes be found. It hybridises with *D. carthusiana* and the large and vigorous *D. × uliginosa* occurs in some stands. Other ferns encountered rarely are *Thelypteris phegopteris*, *T. limbosperma*, *Osmunda regalis* and *Ophioglossum vulgatum*.

The second distinctive characteristic is the abundance of *Sphagna* which can occur as scattered patches around the bases of the *Phragmites* or bush stools or sometimes as a virtually continuous cover. *Sphagnum fimbriatum*,

*S. squarrosum*, *S. palustre* and *S. recurvum* are all very frequent, *S. subnitens* somewhat less so. Other preferential bryophytes here are *Mnium hornum*, *Plagiothecium denticulatum*, *Aulacomnium palustre*, *Rhizomnium pseudopunctatum* and *Calypogeia fissa*.

### Habitat

The *Salix*-*Betula*-*Phragmites* woodland is typically a community of topogenous fen peats. It is especially characteristic of flood-plain mires but can also be found on the terraces of some valley mires and, rarely, in basin mires. It can develop as a primary woodland cover by the direct invasion of herbaceous fen but very many stands represent a secondary succession on abandoned mowing-marsh and these often show floristic and structural peculiarities related to the complex treatment histories of individual sites. Drier stands can show signs of past coppicing.

In primary hydrarch successions, this community is able to develop when the accumulation of consolidated litter eventually raises the surface of the peat mat above the limit of the winter flood (Godwin & Bharucha 1932, Lambert 1951, Poore 1956b). However, quite delicate balances between the timing of the spring fall in the water-table, the amount of residual surface moisture and the germination requirements of the different pioneer species may exert some control over which of these shrubs and trees are able to establish themselves initially. A late fall in the water-table may, for example, inhibit some invaders and not others and it has been suggested (White 1932) that very marked differences between winter and summer water-levels might hinder any kind of colonisation. We know that certain of the important early invaders, such as *Frangula* (Godwin 1943b) and *Alnus* (McVean 1953) have generally high moisture requirements during and after germination but there are no systematic data available on the comparative ability of the shrubs and trees of this community to establish themselves under different conditions.

Other physical features may be important for establishment too. Some species, *Frangula* for example (Kinzel 1926), will not germinate without light. *Rhamnus*, on the other hand, can germinate in darkness (Kinzel 1926) and so can *Alnus*, though it is unable to put up its cotyledons through even a thin covering of soil or litter and needs high light intensities during early seedling growth (McVean 1953), as does *Salix cinerea*. The physiognomy of the existing herbaceous fen vegetation is therefore likely to exert a strong influence on colonisation because, even where abundant seeds drop on to suitably moist surfaces, thick standing dead material (as in *Phragmites*: Haslam 1971a, b), dense winter-green foliage (as in *Cladium*: Lambert 1951), lush early spring growth (as in *Glyceria maxima*: Lambert 1946) or matted litter (Godwin & Tansley 1929) may hinder or



prevent establishment. Certainly, in general, bush and tree growth tends to be more marked where structural variation in the fen vegetation has provided a patchwork of more open areas where seeds could lodge and germinate. The tops of *Carex paniculata* tussocks fulfil such requirements very well but fens in which this species is prominent are invaded early and the derived woodlands preserve a richer and rather different balance of herbaceous species than is usual here. Although *C. paniculata* is an occasional in this community, woodlands in which it remains an important component are included in this scheme in the *Alnus-Carex* woodland.

Within these limitations imposed by the habitat, chance plays a considerable part in determining which woody species invade and in what order. Clearly, seed-parents must be available. With species such as *Salix cinerea* and *Betula pubescens*, which produce vast quantities of very light fruits that can be carried far by wind, the immediate proximity of existing individuals is less important. With *Alnus* the situation is not so simple because, though its fruits can be wind-dispersed, they seldom seem to be borne far by this means (McVean 1953). Water-dispersal, on the other hand, may be very effective here, as with other species whose fruits float readily, and the winter flood can leave a tide-mark of such disseminules towards its upper limit. For *Frangula* and *Rhamnus*, bird-dispersal is important, though the birds may not roam far and the distribution of excreted seeds may be closely linked to the occurrence of perching and roosting sites (Godwin 1936, 1943a, b). The fruits of *Frangula* are eaten also by fieldmice (*Apodemus* spp.) and seed may germinate from the fruit stores to produce dense tufts of seedlings (Godwin 1936, 1943b). For both these shrubs, simple falling to the ground of the heavy fruits may be a major means of dispersal (Godwin 1943a, b). However, no matter how effective these various mechanisms are, initial discrepancies in the numbers of the different woody species can have a long-lasting influence on the composition of the new canopies produced by colonisation. At Wicken, for example, the striking disparity between the amounts of *Frangula* and *Rhamnus* in the young scrub and the absence of *Alnus* in the early years seemed to be attributable mainly to differences in the numbers of seed-parents when invasion began (Godwin 1936). Even after 50 years, the influence of such differences was still very apparent (Godwin *et al.* 1974).

Human activities can have a marked effect on each of these variables and so influence the rate of colonisation and the composition and structure of the developing canopies. This is true even in primary successions in natural herbaceous fen where interference with surrounding land can affect the progress of invasion but it is seen especially clearly in those mires which themselves have a long history of human interference. Here, the

community has developed over surfaces and from vegetation which have been disturbed or modified to varying degrees and preserves within its canopies the effects of such treatments.

In the first place, the very widespread draining of flood-plain mires has resulted in an artificial lowering of the water-table over many of those remnants of fen that have escaped conversion to intensive agricultural use. Often, such a fall has been so marked that development of this community has been rapidly overtaken by seral progressions to other woodland types, where, that is, woodland has been allowed to grow up at all. In other cases, the substrate has remained sufficiently moist for this community to appear, though the balance of the invading shrubs and trees has been affected. This seems to have happened at Woodwalton (Poore 1956b) where *Crataegus monogyna* and *Quercus robur* were unusually frequent and *Betula pubescens* partly replaced by *B. pendula*. Such anomalous canopies may take many years to equilibrate: indeed, they may never do so before further successional changes ensue.

Sometimes, peat extraction has complicated the influence of the water-table and modified the pattern of invasion by woody species. On a grand scale, of course, digging has created new areas, like the Norfolk Broads, in which the whole process of primary succession has proceeded afresh to leave us with some of our most extensive and natural stands of this community (Lambert 1951, 1965). Elsewhere, it has exposed previously hidden deposits of fen peat on which the later stages of invasion have taken place, as seems to have happened at Woodwalton (Poore 1956b), or left complex surface mosaics of wetter and drier areas over which colonisation has been uneven. At Wicken, for example, scrub development over peat-cut surfaces was confined in the early years to remnant baulks of peat between the excavated furrows which remained too wet for invasion to occur (Godwin 1936). There is evidence, too, that the rather special water regimes within shallow peat-diggings may play some part in determining the floristic differences between the two sub-communities.

The disposition of seed-parents from which invasion can begin has also been affected by human activity. Systematic drainage helped destroy and fragment any existing woodland on some flood-plain mires, such that remnant fens could be left isolated in largely treeless pastoral and arable landscapes. In such cases, any subsequent colonisation has depended on the survival of occasional shrubs and trees in hedges, along ditches and streams and, where the fens were mown, in neglected compartments. Which species remained in surviving mires such as Woodwalton and Wicken may have been entirely a matter of chance. In Broadland, things may have been rather different. Here, the upper reaches of the flood-plain mires remained more closely under the

influence of the natural river drainage and human activity actually increased the movement of water between and over the fens. It is possible, too, that a mixed marsh economy with exploitation of both herbaceous and woodland vegetation persisted longer than elsewhere so that more balanced mixtures of potential invaders remained closer at hand. Certainly, stands of the community in this area have a more uniform canopy composition than those in more isolated stretches of fen. Finally, on the positive side here, it is possible that shrubs and trees were deliberately brought within colonising distance of herbaceous vegetation. Rods of *S. cinerea*, for example, were often used to mark out the limits of peat-holdings and could quickly take root. Woody species were also sometimes planted to stabilize the banks of dikes. Once established, such individuals could provide a local source of seed or a centre of vegetative expansion.

Where suitable soils lie within the range of colonising shrubs and trees, the most important variable influencing the establishment of the community is the harvesting of herbaceous marsh crops which has deflected the natural succession to this woodland type, maintaining herbaceous fen in a wide variety of secondary forms. With the almost total demise of such treatments, extensive stands of the community have developed by secondary succession. As already indicated, the physiognomy of the preceding fen vegetation can exert an influence on the actual process of colonisation by shrubs and trees. Its floristics also make an important contribution to the field layer of the developing woodland, especially in the early stages. Since both the structure and the composition of the herbaceous fen are strongly affected by the mowing regime, the kind of treatment it received can have a long-lasting influence on the appearance of the subsequent woodland vegetation.

In essence, the general characteristics of the field layer of younger stands of the community, whether these arise by primary or secondary succession, are a product of the effects of decreasing light on the invaded fen flora. The rate at which light declines under the woody cover will depend largely on the speed with which the canopy closes, though this is itself much influenced by the initial density of the invading shrubs and trees (e.g. Godwin 1936) and subject to local and temporary reversal in the general trend as canopy components die or open up with ageing. The effects of increasing shade are usually first seen among the one-time fen dominants which, almost without exception, decline. The most persistent of these is *Phragmites* but its continuing high frequency throughout the community is, in part, a reflection of its almost universal prominence in the kinds of fen invaded. It is certainly sensitive to shading, showing a reduction in shoot density, shoot height and flowering (Haslam 1971b, 1972), though its rhizome displays some adap-

tation to lower light levels and the continued growth of its terminal branches may make it very persistent at low abundance (Haslam 1965). Under lighter canopies, it often remains proportionately important and it may even extend its cover to fill gaps left by less tolerant species. Where high light levels are restored beneath canopy gaps, it may show some recovery of a more vigorous growth form (Haslam 1971b). *Calamagrostis canescens* can also be quite persistent, though it is much less uniformly distributed in the invaded fens, so its presence in this community is patchy. When mowing ceases (and this species is very much a plant of drier secondary fens), it often adopts a markedly tussocky habit and, though these tussocks become less vigorous in shade, they can remain prominent for some time (Lambert 1951). At Wicken, *C. canescens* actually increased in some older *Frangula* woodland, perhaps spreading in some areas in response to burning (Godwin *et al.* 1974; see also Luck 1964). *Cladium mariscus* is somewhat different again. It is more shade-sensitive than either *Phragmites* or *C. canescens* (Conway 1942), but, like the former, it can be initially very abundant and last for many years as drawn-up individuals before finally disappearing (Godwin 1936). Finally, among this group, there are *Carex paniculata* and *C. acutiformis*. In contrast to the rest of the dominants, both these are shade-tolerant: indeed, the latter may show a marked spread under developing woodland. They are, however, not widely distributed among the fens from which this woodland develops and remain, at most, occasional in the field layer.

Among the associates of the invaded fen vegetation, very few retain a high frequency with substantial increase in shade. The most persistent element comprises certain of the taller dicotyledons, notably *Filipendula ulmaria* and *Eupatorium cannabinum*, and these may increase their cover at first as the dominants fade or even reappear where particular mowing regimes had eradicated them. Again, however, their vigour and flowering show a decline as the canopy thickens up and very commonly the most prominent feature of really dense stands of this community is the extent of bare ground. Then, only very shade-tolerant species such as *Poa trivialis* and bryophytes with scattered *Iris pseudacorus* may be able to survive.

The floristic differences between the two sub-communities appear to reflect variation in the base-richness and calcium levels in the peat which, in the topogenous mires of which this woodland is characteristic, are largely dependent on the height and movement of the ground water. The *Alnus-Filipendula* sub-community is, in general, typical of fen peats which remain under the comparatively close influence of the fluctuating water-table. In Broadland, such waters have dissolved calcium levels of 60–120 mg l<sup>-1</sup> (Wheeler 1983) and the surface

pH under this vegetation remains generally high, between 6.5 and 7.5, very much like that beneath the preceding fen vegetation. The *Sphagnum* sub-community, by contrast, is characteristically developed where, for some reason or other, the influence of the base-rich and calcareous ground water is not so great. Sometimes, it is found on areas which are at a slightly higher level than the surrounding peats and/or somewhat further removed from freely-circulating waters in open lakes or dike systems. This was the case at Calthorpe Broad in Norfolk where Godwin & Turner (1933) noted that the *Alnus-Filipendula* sub-community gave way to the *Sphagnum* sub-community with increasing height above and distance from the broad. In other places, the *Sphagnum* sub-community occurs on floating rafts of peat, as in the Ant valley in Broadland (Wheeler 1978, 1980c) and here the rising of the substrate with the waters prevents frequent inundation of the surface layers of the peat. Some of the finest stands in this area occur within fens in shallow nineteenth-century peat-cuttings, like those on the Catfield Fens (Lambert 1965, Wheeler 1978), and here conditions may be virtually stagnant. Whatever its particular situation, the pH beneath the *Sphagnum* sub-community is typically lower than that beneath the *Alnus-Filipendula* sub-community, though not always markedly so, being generally between 5.5 and 6.5.

Differences in trophic levels may be involved here too. When the surface of the more base-rich and calcareous peat under the *Alnus-Filipendula* sub-community dries somewhat in summer, there may be some oxidation and the release of a flush of nutrients (e.g. Haslam 1965). Then, litter turnover may be enhanced and the gradual development of peaty mull soil initiated (e.g. Poore 1956b). In this respect, the markedly preferential abundance of the nutrient-demanding *Urtica dioica* in this sub-community is especially interesting. Under the *Sphagnum* sub-community, by contrast, the greater acidity of the surface layers of the peat may prevent such developments, even when they dry out. The greater isolation from any nutrients in the circulating waters further hinders any tendency towards eutrophication.

### Zonation and succession

In the more extensive flood-plain mires of the Broadland river valleys, it is still possible to see complete and fairly straightforward zonations from open-water vegetation, through swamp and primary fen, to the *Salix-Betula-Phragmites* woodland, over fen peats which are increasingly free from inundation by the seasonally-fluctuating waters (e.g. Pallis 1911, Lambert & Jennings 1951, Wheeler 1980c, 1983). Where the base-status and calcareous nature of the peat are maintained, such sequences involve the *Alnus-Filipendula* sub-community which replaces, beyond the upper limit of the winter flood, the *Peucedano-Phragmitetum*. Local variations in the pat-

tern of water fluctuation and uneven invasion of shrubs and trees frequently blur this boundary so that a hazy zone of scrubby vegetation lies between the fen and the woodland proper. There is variation, too, in the particular kind of *Peucedano-Phragmitetum* to be found in these zonations: along the Bure valley, for example, it is generally the Typical sub-community, dominated by *Phragmites* or less often and perhaps where conditions are more oligotrophic, *Cladium*; in the more eutrophic Yare fens, drier forms of the *Glyceria* sub-community, usually dominated by *Phragmites*, are often involved.

Outside Broadland, where flood-plain mires have been much fragmented and extensively drained, intact zonations of this kind are rare and such sequences as do survive generally have the less species-rich vegetation of the *Phragmites-Eupatorium* fen (most often its *Phragmites* or *Cladium* sub-communities) replacing the *Peucedano-Phragmitetum*. Less commonly, the *Alnus-Filipendula* sub-community may pass directly to the rather dry swamp vegetation of the *Galium* sub-community of the *Phragmitetum*. Transitions of this kind can be seen around some open waters in the Shropshire and Cheshire meres (Sinker 1962, Meres Report 1980) and in more base-rich valley mires, such as those in Breckland (e.g. Haslam 1965).

Stratigraphical studies around the Norfolk Broads (Lambert & Jennings 1951, 1965, Jennings & Lambert 1951, Lambert 1951, Lambert *et al.* 1960, 1965) have shown that zonations of this kind can represent the progress of primary hydrarch successions in which the *Alnus-Filipendula* sub-community is the natural product of invasion of a variety of herbaceous fen types. This sub-community corresponds most closely with Lambert's 'fen carr' but it also includes some of what she would have called 'semi-swamp carr' and 'pseudo-swamp carr', woodlands which differ largely in their physiognomy and whose floristics can be comfortably subsumed within this single vegetation type. Although it has not been confirmed by stratigraphical analysis or long observation elsewhere, it seems likely that this line of development represents the major succession on our more base-rich topogenous mires, except where *Carex paniculata* figures prominently in the primary fens. Its rate of progress is difficult to assess but comparisons of maps led Lambert & Jennings (1951) to suggest that some of the swamp around the Norfolk Broads could have progressed to woodland over 150 years and Haslam (1965) adduced a similar process to have taken some 50 years in a Breckland valley fen.

In many areas, including Broadland where exploitation of the fens was formerly very intensive, such primary succession was deflected by regular mowing for herbaceous crops and many of the present stands of the *Alnus-Filipendula* sub-community are found as the product of secondary invasion among complex patchworks of vegetation types, variation among which is more

closely related to the previous mowing regime and the date of abandonment than to natural differences in the water-level. Often, such patterns have been further complicated by other activities. Where there has been peat-digging, for example, secondary fen and woodland on the drier baulks may be intermingled with primary herbaceous vegetation and woodland developing afresh in flooded workings (e.g. Lambert & Jennings 1951, Wheeler 1978). On more isolated mire fragments, where drainage and even cultivation have occurred over the peat surface, stands of the *Alnus-Filipendula* sub-community can be found developing from fen remnants alongside suites of other rather different vegetation types on even drier and more disturbed ground or isolated within intensive agricultural landscapes.

The *Sphagnum* sub-community is more local than the *Alnus-Filipendula* sub-community and its development has not been studied but it seems to be the product of a divergent succession from the kind described above. Quite small differences in the water regime, in surface pH and nutrient status may be responsible for determining which of the two sub-communities ultimately develops and such variation may be initiated early in the succession, even before the appearance of any woodland cover. Indeed, the *Sphagnum* sub-community is occasionally to be found in some basin and valley mires where the whole character of the habitat is shifted somewhat towards being less base-rich and calcareous. Usually, however, it is the occurrence of such conditions on a more local scale that seems to be the prelude to its appearance. In some cases, it seems possible that the remnants of a former, more extensive cover of acid peat may provide a congenial surface (Wheeler 1978). Ombrogenous peats are known or strongly presumed to have formed within some of the East Anglian floodplain mires in the past (Godwin & Clifford 1938, Poore 1956b, Walker 1970) and, though these have been largely stripped away, fragments may remain. Often, however, the typically small stands of the *Sphagnum* sub-community give every indication of representing new ombrogenous nuclei in which surface layers of more acid peat are accumulating afresh beneath a *Sphagnum* cover (Wheeler 1978, 1980c, 1983). Small domes of *Sphagnum* can sometimes be found within herbaceous fens (e.g. Pallis 1911, Tansley 1939, Wheeler 1983) and these may form the basis of subsequent stands of the *Sphagnum* sub-community, being preferentially invaded from the start by *Betula pubescens*. Such a development seems to be particularly associated with floating mats of fen vegetation like those found in various parts of the Ant valley, most distinctively in shallow peat-cuttings as on the Catfield fens (Wheeler 1978). Here, rich *Phragmites* appears to progress to a striking kind of *Peucedano-Phragmites* dominated by *Carex lasiocarpa*. Within this, small islands of *Sphagnum* form and these then act as centres for *B. pubescens* invasion (Giller

1982, Wheeler 1983). In these fens, and among other kinds developed on solid peat, certain kinds of mowing regime may help accentuate surface impoverishment and acidification so that, once treatment ceases, conditions are inimical to the development of the *Alnus-Filipendula* sub-community.

In other cases, it is possible that the *Sphagnum* sub-community makes a late appearance in the succession, developing from the *Alnus-Filipendula* sub-community as conditions change. Such a process may be natural, as where the accumulation of litter raises the peat surface above the level of close influence by the ground water (e.g. Godwin & Turner 1933) or, as seems to have been the case at Wicken in recent years, it may be precipitated by the artificial prevention of flooding (Godwin *et al.* 1974). Only close monitoring of a variety of particular stretches of fen over long periods could provide some indication of the importance of these various possibilities.

In neither of the two divergent lines of succession is it clear what the final vegetation types might be. It has been suggested on a number of occasions (e.g. Godwin & Turner 1933, Tansley 1939, Lambert 1951) that some kind of oakwood is the natural development from the *Alnus-Filipendula* sub-community. In some sites, transitions between these two woodland types can be found but extrapolating from such sequences to seral developments is dubious because the oak woodland frequently lies on the drier land surrounding the mire where the influence of its ground water had probably never been great. A more likely immediate successor to the *Alnus-Filipendula* sub-community is some kind of drier *Alnus-Urtica* woodland. The virtually complete eclipse of fen herbs in this latter community, the prominence of *Urtica dioica* and Rubi, the appearance of *Sambucus nigra* and the occurrence of a canopy in which *Alnus* generally predominates over *Salix cinerea* and *Betula pubescens* could be seen as natural developments over a peat surface which was being slowly converted to a humose mull with a high nutrient turnover. This kind of process seems to be in train, at least within the field layer, in Reserve A at Wicken (Godwin *et al.* 1974) and within the Askham woods (Fitter *et al.* 1980) and perhaps accounts for some of the later stages of the succession in the Breckland valley mires (Haslam 1965).

The *Sphagnum* sub-community, on the other hand, seems more likely to progress to the *Betula-Molinia* woodland, in certain kinds of which *Sphagnum* remain very prominent, along with an increased cover of *Molinia caerulea*, under an often moribund canopy of *B. pubescens*. Some of the islands of the *Sphagnum* sub-community described from the Ant valley have a core of this kind of woodland in their drier centres (Wheeler 1978, 1980c) and such a development may also have occurred towards the back of Esthwaite North Fen in Cumbria (Pearsall 1918, Tansley 1939, Pigott & Wilson



1978). It is possible that such vegetation might eventually give way to ombrogenous mire with the disappearance of all tree cover, recapitulating the process that seems to have occurred in the past, even on those of our lowland mires which experience a drier climate (Pearsall 1918, Godwin & Turner 1933, Walker 1970, Wheeler 1978, 1983).

The various vegetation patterns which result from the operation of these successions can be further complicated by the close proximity of the products of other seral developments within mires. In some cases, it is variation within the herbaceous vegetation that is being invaded that deflects the succession away from the formation of the *Salix-Betula-Phragmites* woodland. Where *Carex paniculata* is a prominent feature of swamp or primary fen, for example, the invasion of shrubs and trees is often early and results instead in the development of swampy *Alnus-Carex* woodland. Stands of this woodland can be found developing in both flood-plain and valley mires, sometimes between the *Salix-Betula-Phragmites* woodland and open water, sometimes, marking the position of old channels and pools, behind it (e.g. Pallis 1911, Lambert & Jennings 1951). Usually, it is the *Alnus-Filipendula* sub-community that is found in this kind of zonation but, in the Ant valley, some of the larger stands of the *Sphagnum* sub-community have a core of *Alnus-Carex* woodland (Wheeler 1978).

In other cases, variation in the pattern of sediment accumulation may lead to the development of other woodland types alongside the *Salix-Betula-Phragmites* woodland. Where there is deposition of alluvium, for example, more eutrophic fens and woody vegetation can occur among the sequences of communities on the peat. Such patterns are especially characteristic of some valley mires, where levees build up along the water's edge as suspended sediments are dropped in the flood. Then the *Salix-Betula-Phragmites* woodland behind gives way to a fringe of such herbaceous vegetation as the *Phragmites-Urtica* fen or the *Phalaridetum* progressing to wetter kinds of *Alnus-Urtica* woodland, dominated by *Salix purpurea*, *S. triandra*, *S. viminalis* or *S. fragilis*. This kind of transition is a marked feature of the enriched zone alongside the Black Beck in Esthwaite North Fen (Pearsall 1918, Tansley 1939, Pigott & Wilson 1978).

Finally, significant differences in the water regime and in the pH, calcium concentration and nutrient status may create conditions which locally prevent the development of tall-herb fen and subsequent *Salix-Betula-Phragmites* woodland. This seems to happen along the margins of certain of the Broadland flood-plains, where the fens are isolated from the moving waters and in some places influenced by soligenous seepage, and also in some shallow, stagnant peat-cuttings (Wheeler 1978, 1980a, 1983). Here, stretches of the *Salix-Betula-Phrag-*

*mites* woodland give way to small-sedge mires. Similar habitat variation may also play some part in the complex pattern of vegetation types seen in Esthwaite North Fen (Pearsall 1918, Tansley 1939, Pigott & Wilson 1978) where the *Salix-Betula-Phragmites* woodland lies behind a zone of the *Potentillo-Caricetum* fen which is developing into the *Salix-Carex* woodland.

Interesting as these seral developments are, the formation of the *Salix-Betula-Phragmites* woodland from a range of primary and secondary fens inevitably results in a loss of diversity among the vegetation. With the demise of mowing, extensive stretches of often species-rich herbaceous vegetation, together with its particular associations of other biota, notably invertebrates (e.g. Ellis 1965), have been lost and the agricultural record, which the pattern of fen compartments, dikes and droves preserved, has been obscured. Only in a very few sites does mowing of fens continue (e.g. Godwin 1978) and attempts to preserve heterogeneity by woodland clearance are laborious and costly. However, where such clearance has been undertaken, at Woodwalton for example (Duffey 1971), the effects have been judged worthwhile. At this particular site, there has been the additional interest of the reappearance, after many years, of *Viola persicifolia* and the spread of *Luzula pallescens* in the open vegetation.

### Distribution

More extensive and undisturbed tracts of the *Salix-Betula-Phragmites* woodland are now largely confined to East Anglia (in Broadland and the valley mires of the Chalk) and some of the Cheshire and Shropshire meres with fragmentary stands scattered elsewhere on remnant fens throughout the lowlands. The *Sphagnum* sub-community is the more local of the two but particularly good stands occur in the Ant valley in Broadland (Wheeler 1978: see Figure 2) and here the spread of this vegetation is of especial significance for the distribution of *Dryopteris cristata* which seems to have increased in recent years (c.f. Petch & Swann 1968, Jermy *et al.* 1978 and Page 1982).

### Affinities

This community takes in most of the woodland recognised as 'fen carr' in British descriptive accounts including more unusual canopies dominated by species such as *Frangula alnus* and *Rhamnus catharticus*. It also includes those *Sphagnum*-rich types which were noted early but not fully described until Wheeler (1978) characterised his *Betulo-Dryopteridetum cristatae*. Although this kind of woodland is very distinctive, especially in its Broadland form on which Wheeler concentrated, it seems best to unite it with the *Alnus-Filipendula* type to form a single woodland community with a more or less common origin. Both sub-communities have counterparts in Continental schemes and fall fairly clearly into

the Salicion cinereae. This alliance has been placed by some authors (e.g. Westhoff & den Held 1969, Wheeler 1980a) in the Franguletea, the class of successional woodlands of minerotrophic fens, by others (e.g. Ellenberg 1978) among the possibly climax communities of the Alnetea glutinosae.

Two problems attend the definition of the community. The first is to separate it from the fen vegetation from which it is derived and to which it frequently grades through a scrubby fringe. Sometimes, vegetation equivalent to that included here has been grouped within primarily herbaceous fen, as in the *Pallavicinio-Sphagnetum* Meltzer 1945, in which Westhoff & den Held (1969) placed woodlands like those of the *Sphagnum* sub-community. Clearly, when invasion of woody species is gradual and sparse, it will be difficult to separate stands of the *Salix*-*Betula*-*Phragmites* woodland from fens like the *Peucedano-Phragmitetum*. Here, the rule of thumb is that, where the developing canopy begins to

modify the invaded fen, the vegetation is best considered as young woodland.

The second difficulty concerns the distinction between this community and other woodlands developing on mires. The *Alnus*-*Carex* woodland is generally considerably more species-rich than the *Salix*-*Betula*-*Phragmites* woodland and usually of different physiognomy with much of its canopy rooted in ultimately unstable *Carex paniculata* tussocks. Although stands with composition and structure intermediate between the two communities can sometimes be found, the traditional separation between 'swamp carr' and 'fen carr' made by Pallis (1911) and confirmed by Lambert (1951) seems basically a sound one.

In their later stages of development, both sub-communities show floristic transitions to other woodland types, the *Alnus*-*Filipendula* type to the drier woodlands of the Alno-Ulmion alliance, the *Sphagnum* type to the mire forests of the Betulion pubescentis.

## Floristic table W2

	a	b	2
<i>Betula pubescens</i>	III (3–8)	V (6–9)	IV (3–9)
<i>Salix cinerea</i>	III (3–9)	IV (2–6)	IV (2–9)
<i>Frangula alnus</i>	I (1–9)	II (4–6)	I (1–9)
<i>Quercus robur</i>	I (6)	I (1)	I (1–6)
<i>Salix aurita</i>	I (4)	I (3)	I (3–4)
<i>Alnus glutinosa</i>	III (4–10)	I (1–4)	II (1–10)
<i>Fraxinus excelsior</i>	II (3–6)	I (1)	I (1–6)
<i>Crataegus monogyna</i>	II (2–5)	I (1–2)	I (1–5)
<i>Viburnum opulus</i>	II (1–6)		I (1–6)
<i>Salix fragilis</i>	I (5–8)		I (5–8)
<i>Rhamnus catharticus</i>	I (3–5)		I (3–5)
<i>Alnus glutinosa</i> sapling	I (3–4)	I (5)	I (3–5)
<i>Fraxinus excelsior</i> sapling	I (1–5)	I (1–7)	I (1–7)
<i>Betula pendula</i> sapling		II (4–6)	I (4–6)
<i>Phragmites australis</i>	V (2–9)	IV (2–8)	IV (2–9)
<i>Filipendula ulmaria</i>	IV (1–7)	II (3–4)	III (1–7)
<i>Brachythecium rutabulum</i>	IV (2–7)	II (2)	III (2–7)
<i>Urtica dioica</i>	III (2–7)	I (1)	II (1–7)
<i>Eupatorium cannabinum</i>	III (3–6)	I (1–3)	II (1–6)
<i>Plagiomnium undulatum</i>	II (2–5)	I (2)	I (2–5)
<i>Galium palustre</i>	II (1–4)	I (1–3)	I (1–4)
<i>Cirsium palustre</i>	II (1–4)	I (2)	I (1–4)
<i>Carex acutiformis</i>	II (2–9)		I (2–9)
<i>Epilobium hirsutum</i>	II (1–4)		I (1–4)
<i>Galium aparine</i>	II (2–5)		I (2–5)
<i>Angelica sylvestris</i>	II (1–4)		I (1–4)

**Floristic table W2 (cont.)**

	a	b	2
<i>Mentha aquatica</i>	II (3–5)		I (3–5)
<i>Solanum dulcamara</i>	II (1–5)		I (1–5)
<i>Caltha palustris</i>	I (2–4)		I (2–4)
<i>Phalaris arundinacea</i>	I (3–7)		I (3–7)
<i>Stellaria media</i>	I (3)		I (3)
<i>Lycopus europaeus</i>	I (2–4)		I (2–4)
<i>Calystegia sepium</i>	I (4–5)		I (4–5)
<i>Carex acuta</i>	I (4–8)		I (4–8)
<i>Epilobium palustre</i>	I (2–3)		I (2–3)
<i>Hedera helix</i>	I (1–5)		I (1–5)
<i>Plagiothecium sylvaticum</i>	I (2–3)		I (2–3)
<i>Amblystegium riparium</i>	I (2–3)		I (2–3)
<i>Symphytum officinale</i>	I (2)		I (2)
<i>Fraxinus excelsior</i> seedling	I (2–3)		I (2–3)
<i>Tamus communis</i>	I (3–4)		I (3–4)
<i>Amblystegium serpens</i>	I (2–3)		I (2–3)
<i>Geranium robertianum</i>	I (1–4)		I (1–4)
<i>Deschampsia cespitosa</i>	I (3–4)		I (3–4)
<i>Glechoma hederacea</i>	I (2–4)		I (2–4)
<i>Humulus lupulus</i>	I (3–5)		I (3–5)
<i>Sphagnum squarrosum</i>	I (4)	V (2–7)	III (2–7)
<i>Sphagnum fimbriatum</i>	I (5)	V (4–7)	III (4–7)
<i>Sphagnum recurvum</i>	I (3)	IV (2–6)	III (2–6)
<i>Sphagnum palustre</i>		IV (3–8)	III (3–8)
<i>Lonicera periclymenum</i>	I (3–5)	III (1–6)	II (1–6)
<i>Mnium hornum</i>	I (1–3)	III (1–3)	II (1–3)
<i>Plagiothecium denticulatum</i>	I (1)	III (1–3)	II (1–3)
<i>Holcus lanatus</i>	I (1–5)	III (2–5)	II (1–5)
<i>Juncus effusus</i>	I (2–3)	III (2–5)	II (2–5)
<i>Dryopteris carthusiana</i>	I (3–4)	II (1–3)	I (1–4)
<i>Hydrocotyle vulgaris</i>	I (4)	II (3–4)	I (3–4)
<i>Molinia caerulea</i>	I (5)	II (2–6)	I (2–6)
<i>Potentilla erecta</i>	I (3)	II (2–4)	I (2–4)
<i>Calypogeia fissa</i>	I (2–3)	II (1–2)	I (1–3)
<i>Myrica gale</i>		II (5)	I (5)
<i>Dryopteris cristata</i>		II (1–3)	I (1–3)
<i>Aulacomnium palustre</i>		II (2)	I (2)
<i>Rhizomnium pseudopunctatum</i>		II (2–3)	I (2–3)
<i>Agrostis canina canina</i>		II (3–7)	I (3–7)
<i>Agrostis stolonifera</i>		II (1–4)	I (1–4)
<i>Carex vesicaria</i>		I (4–6)	I (4–6)
<i>Calliergon giganteum</i>		I (3–7)	I (3–7)
<i>Deschampsia flexuosa</i>		I (4)	I (4)
<i>Sphagnum subnitens</i>		I (1–4)	I (1–4)
<i>Thelypteris phegopteris</i>		I (3–8)	I (3–8)
<i>Carex nigra</i>		I (2)	I (2)
<i>Thelypteris limbosperma</i>		I (3–4)	I (3–4)

<i>Orthodontium lineare</i>		I (2–3)	I (2–3)
<i>Quercus petraea</i> seedling		I (1)	I (1)
<i>Menyanthes trifoliata</i>		I (2–3)	I (2–3)
<i>Eurhynchium praelongum</i>	III (2–6)	III (2–5)	III (2–6)
<i>Dryopteris dilatata</i>	II (1–4)	II (2)	II (1–4)
<i>Poa trivialis</i>	II (2–7)	II (3–4)	II (2–7)
<i>Rubus fruticosus</i> agg.	II (2–8)	II (2–4)	II (2–8)
<i>Thelypteris palustris</i>	II (4–5)	II (1–5)	II (1–5)
<i>Ajuga reptans</i>	I (3–4)	II (2–4)	I (2–4)
<i>Lotus uliginosus</i>	I (3–4)	II (3)	I (3–4)
<i>Rosa canina</i> agg.	I (2–4)	II (2–4)	I (2–4)
<i>Athyrium filix-femina</i>	I (1–4)	I (2–4)	I (1–4)
<i>Berula erecta</i>	I (4)	I (3)	I (3–4)
<i>Carex paniculata</i>	I (3–7)	I (1)	I (1–7)
<i>Carex remota</i>	I (1–3)	I (1–3)	I (1–3)
<i>Cladium mariscus</i>	I (2–4)	I (1–3)	I (1–4)
<i>Equisetum palustre</i>	I (1–4)	I (2–3)	I (1–4)
<i>Peucedanum palustre</i>	I (3)	I (1–3)	I (1–3)
<i>Lythrum salicaria</i>	I (3–4)	I (1–3)	I (1–4)
<i>Lysimachia vulgaris</i>	I (2)	I (1–3)	I (1–3)
<i>Juncus subnodulosus</i>	I (4)	I (1–3)	I (1–4)
<i>Glyceria maxima</i>	I (1–2)	I (3)	I (1–3)
<i>Calamagrostis canescens</i>	I (2–3)	I (1–4)	I (1–4)
<i>Rubus idaeus</i>	I (4)	I (2)	I (2–4)
<i>Pellia epiphylla</i>	I (2)	I (2)	I (2)
<i>Lophocolea heterophylla</i>	I (1–3)	I (2)	I (1–3)
<i>Scutellaria galericulata</i>	I (3)	I (2)	I (2–3)
<i>Lophocolea bidentata</i> s.l.	I (4)	I (2–3)	I (2–4)
<i>Valeriana officinalis</i>	I (2–4)	I (1)	I (1–4)
<i>Calliargon cuspidatum</i>	I (4–5)	I (1–3)	I (1–5)
<i>Atrichum undulatum</i>	I (3)	I (1)	I (1–3)
<i>Campylopus paradoxus</i>	I (3)	I (2)	I (2–3)
<i>Hypnum cupressiforme</i>	I (3)	I (2)	I (2–3)
<i>Pohlia nutans</i>	I (4)	I (3)	I (3–4)
Number of samples	33	11	44
Number of species/sample	18 (7–27)	23 (15–30)	19 (7–30)
Tree height (m)	9 (5–11)	8 (6–10)	9 (5–11)
Tree cover (%)	74 (5–100)	67 (50–85)	72 (5–100)
Shrub height (m)	4 (3–5)	5 (3–6)	4 (3–6)
Shrub cover (%)	8 (0–100)	15 (0–60)	10 (0–100)
Herb height (cm)	86 (10–200)	80 (10–200)	85 (10–200)
Herb cover (%)	86 (25–100)	86 (50–100)	86 (25–100)
Ground height (mm)	16 (10–30)	8 (5–10)	14 (5–30)
Ground cover (%)	8 (0–85)	63 (50–80)	42 (0–80)
Altitude (m)	23 (1–45)	59 (30–76)	36 (1–76)

a *Alnus glutinosa*-*Filipendula ulmaria* sub-communityb *Sphagnum* sub-community2 *Salix cinerea*-*Betula pubescens*-*Phragmites australis* woodland (total)



