W5

Alnus glutinosa-Carex paniculata woodland

Synonymy

Swamp carr Pallis 1911; Alder thicket Rankin 1911b p.p.; Valley fen woods Farrow 1915; Alder wood Clapham 1940; Swamp carr and semi-swamp carr Lambert 1951; Alder woodland types 2c p.p. & 3c McVean 1956b; Alder carr Sinker 1962; Valley fen alderwoods Haslam 1965; Osmundo-Alnetum glutinosae (Klötzli 1970) Wheeler 1980c p.p.; Alnus-Salix woodland XXiii Meres Report 1980; Alder stand types 7Ba and 7Bb Peterken 1981; Scutellaria galericulata-Alnus glutinosa Association Birse 1982 p.p.; Woodland plot type 14 Bunce 1982 p.p.

Constant species

Alnus glutinosa, Carex paniculata, Galium palustre, Rubus fruticosus agg., Brachythecium rutabulum, Eurhynchium praelongum.

Rare species

Carex appropinquata, C. elongata, Cicuta virosa, Dryopteris cristata, Peucedanum palustre, Thelypteris palustris.

Physiognomy

The canopy of the Alnus glutinosa-Carex paniculata woodland is characterised by the high frequency and often the great abundance of Alnus but its detailed floristics and physiognomy vary considerably according to the age of the stand and the nature of the substrate. Alnus and Salix cinerea are the most frequent invaders of the kinds of swamp and fen from which this woodland is derived and, in the early stages of colonisation, their proportions are very much a reflection of the chance availability of propagules and the frequency and disposition of sites where seedlings can gain a hold, very often here the tops and sides of Carex paniculata tussocks. In general, though, young stands are characterised by the co-dominance of these two species in low, uneven and open canopies and the general trend with ageing is for S. cinerea to be relegated to an understorey or, where the Alnus grows up to cast a deep shade, to be completely extinguished. Betula pubescens can also appear early in invasion but it is decidedly patchy and its overall frequency is no more than occasional. Once the canopy has thickened up, light quickly becomes insufficient for its establishment. In drier situations, on initially firmer substrates or in sites where the fen mat consolidates with the passage of time, Fraxinus excelsior can become frequent but it generally makes no more than a local contribution to the canopy. Quercus robur can also occur in such situations though it remains rare through the community as a whole.

In young stands, Salix cinerea is frequently the only shrub present and, in general, it remains the commonest species in whatever understorey remains as the trees grow up to form a distinct, tall canopy. On drier substrates, Crataegus monogyna occurs occasionally (rarely C. laevigata) and there are sparse records, too, for Ilex aquifolium, Sorbus aucuparia, Rhamnus catharticus and Salix aurita. Viburnum opulus and Frangula alnus also occur throughout, though both these species, and especially the latter, are preferential for one particular sub-community. Frangula particularly can invade quite early and dense patches of saplings may be gradually grown over by the expanding woodland cover. In general, tree saplings are markedly rare in older stands, with only Alnus regenerating with any frequency under intact canopies.

In richer, well-established stands, the usual appearance of this woodland is of a clearly-defined canopy of well-grown *Alnus*, often multi-stemmed and up to 15 m tall, with scattered associated trees, over a distinct understorey of varying density, though sometimes very tangled and thick. Very often, however, the general pattern of development and structure is complicated by the local effects of substrate instability, exacerbated by the substantial weight of the trees which slowly depress the frequently thin fen mat into the amorphous sediments beneath. As the water-level rises above the tree bases, the *Alnus* can become moribund and die and the

emergent tops of dead trees are a common feature of stands in such situations (Lambert 1951, 1965, McVean 1956b). Where, as is often the case, the alders are rooted in Carex paniculata tussocks, these may eventually roll over so that the trees, though they may survive, tilt at crazy angles (Lambert 1951, 1965). In both these cases, gaps may be opened up in the tree canopy, allowing other woody species, notably the quick-growing Salix cinerea, Betula pubescens and Frangula, to attain a local prominence, provided, of course, that the substrate beneath is not too wet. Where there is a more extensive breakdown of the fen mat with substantial surface waterlogging, a seral regression may occur (see below).

Although the constants of the field layer are few, the general character of the herbaceous vegetation in this woodland is very distinctive. In essence, it represents a modified flora of the preceding fen with but a small, strictly woodland component and structurally the plants are disposed according to the pattern of light and shade and the amount of surface moisture. Of the fen element, the most conspicuous species are usually large sedges, particularly the tussock-forming Carex paniculata, whose individuals can go on growing beneath the canopy to attain enormous size, and which often form a structural framework to the field layer. C. acutiformis is somewhat less frequent but it, too, can be very abundant and, being shade-tolerant, can extend its cover in the developing woodland by the spread of its far-creeping rhizomes. Either of these species may dominate and often both occur together. Other bulky fen sedges recorded less frequently, and then most often in one of the sub-communities, are C. elata, C. appropinquata, C. riparia and C. pseudocyperus. Phragmites australis, which is a prominent feature in many of the invaded fens, persists very patchily: it is quite common in one sub-community though, even there, it is only really abundant under more open areas of the canopy.

The other fen element which remains generally prominent comprises tall herbs. Of these, the most frequent throughout are Urtica dioica, Filipendula ulmaria, Eupatorium cannabinum, Cirsium palustre, Valeriana officinalis and Iris pseudacorus with, less commonly, Angelica sylvestris and Valeriana dioica. Where the community has developed from richer fens, Lysimachia vulgaris and Lythrum salicaria often occur and, in Broadland, Peucedanum palustre. Typically, as in the preceding fen, many of these species are rooted on the sides of or atop the Carex paniculata tussocks though Iris is habitually found between them and the others often spread on to the surface of the peat mat as the cover of prominent fen species such as Phragmites and Calamagrostis canescens declines. Here, they may attain patchy local prominence, giving a very variegated effect to the field layer, though where light is further reduced they, too, may show a decline or, as in Iris, stop flowering. Among these

taller species, woodland plants like Geranium robertianum and Circaea lutetiana make a very occasional appearance.

Generally speaking, smaller herbaceous species are rather few in number and rarely prominent. Mentha aquatica and Poa trivialis are by far the most frequent throughout but others recorded (sometimes with preferential frequency in the different sub-communities) include Ranunculus repens, R. flammula, Viola palustris, Hydrocotyle vulgaris, Caltha palustris and Myosotis laxa ssp. cespitosa. In contrast to the tall herbs, these plants are often more common between the sedge tussocks where, even on quite wet substrates, they can form a patchy ground cover. Where the substrate sinks to any marked degree, however, these plants, too, may disappear, leaving a network of sloppy peat surfaces between the tussocks, virtually bare apart from a little Lemna minor and treacherous to the unwary.

Three other elements of the field layer are distinctive and each can be conspicuous. The first comprises ferns, among which *Dryopteris dilatata* is the commonest species throughout, often growing epiphytically on the sedge tussocks or around the tree bases. *Athyrium filixfemina* occurs occasionally, tolerating somewhat wetter conditions and both *Dryopteris carthusiana* and the rare *D. cristata* have also been recorded. Much more strictly confined to the richer woodlands of one of the subcommunities are *Thelypteris palustris* and *Osmunda regalis*.

The second element consists of sprawlers. Galium palustre is a constant of the community and Solanum dulcamara is frequent and the latter, especially in one of the sub-communities, can be extremely abundant. The relative scarcity of Galium aparine and Calystegia sepium here is in contrast to the more eutrophic Alnus-Urtica woodland. Third, adding to the tangled field layer, there are usually some undershrubs. Rubus fruticosus agg. is very frequent, especially on drier ground where, with the more occasional Lonicera periclymenum, it can cover large areas. Ribes nigrum, R. rubrum and Rosa canina agg. can also occur.

Bryophytes are rather variable in their total cover but a number of species occur frequently and these can show a distinct patterning over the various available surfaces (e.g. Clapham 1940). The commonest mosses are Eurhynchium praelongum, Brachythecium rutabulum, Plagiomnium undulatum and Rhizomnium punctatum and each of these, together with the occasional Lophocolea bidentata s.l., can be found on damp ground around the Carex paniculata tussocks or, where the sedge is growing healthily, on the sides or tops of the tussocks. Calliergon cuspidatum is rather more patchily distributed and, usually, it is more common over the bare, wet peat or on the stumpy wet remains of dead sedge. Mnium hornum is common here, too, but it is very much a plant of drier

and somewhat more acid situations, among the decaying leaves of ageing tussocks and on tree bark, around bole bases or on fallen trunks and branches. In general, Sphagna are rare in this community, but small tufts of S. palustre or S. squarrosum may be found where there is seepage of more base-poor waters. A more frequent marker of such conditions here, however, and characteristic of one particular sub-community, is Pellia epiphylla.

Sub-communities

Phragmites australis sub-community: Osmundo-Alnetum glutinosae hydrocotyletosum Klötzli 1970 p.p.; Osmundo-Alnetum glutinosae typicum (Klötzli 1970) Wheeler 1980c p.p.; Alder stand type 7Ba Peterken 1981 p.p.; Scutellaria galericulata-Alnus glutinosa Association Birse 1982 p.p. Alnus is always the dominant in mature tracts of this sub-community though young stands may have much Salix cinerea in the canopy and, in older woodlands, there is frequently some Fraxinus and Betula pubescens. Sorbus torminalis and Populus tremula occur rarely in less swampy situations.

The shrub layer is variable in total cover but there are usually some bushes of S. cinerea and sometimes these are sufficiently tall as to make stratification indistinct. Crataegus monogyna occurs occasionally but Viburnum opulus and Frangula alnus are rare.

The field layer is more species-poor here than in the two other sub-communities but, among the dominants of the preceding fen vegetation, *Phragmites* remains somewhat more frequent than elsewhere, though it is only abundant where the canopy has not yet closed or where developing gaps allow it to expand its cover (Haslam 1971b, 1972). The more usual dominants are *Carex paniculata* or *C. acutiformis* (rarely *C. elata*). Locally, *Scirpus sylvaticus* may totally replace these and its unusual abundance can give the field layer a very distinctive look.

Tall herbs are often prominent but there are no preferentially frequent species among this component, the commonest plants being those characteristic of the community as a whole: Urtica dioica, Filipendula ulmaria, Eupatorium cannabinum, Iris pseudacorus, Cirsium palustre and, less frequently, Lycopus europaeus, Valeriana officinalis, V. dioica and Angelica sylvestris. Lysimachia vulgaris and Lythrum salicaria are both scarce. Ferns, too, though they may be abundant, are not distinctive with only Dryopteris dilatata and Athyrium filix-femina occurring with any frequency. Smaller dicotyledons are also few in number, although Mentha aquatica occurs frequently. Poa trivialis is occasional and Equisetum palustre is weakly preferential here, showing a slight tendency to be more consistently associated with sites where Scirpus sylvaticus is dominant.

Scramblers and underscrub species are often very prominent. Solanum dulcamara is more frequent here than in the other sub-communities and it sometimes forms a virtually impenetrable mass of thin woody shoots. Galium aparine is a little commoner, too, than elsewhere in the community. In drier stands, Rubus fruticosus agg. can be very abundant.

The bryophytes are those characteristic of the community as a whole.

Lysimachia vulgaris sub-community: Osmundo-Alnetum glutinosae lycopetosum Klötzli 1970 p.p.; Alder stand type 7Ba Peterken 1981 p.p. The tree canopy here retains the general floristic features of the previous sub-community and shows the same physiognomic variation with age as is characteristic of the whole community. The shrub layer, however, is somewhat more varied than usual: in addition to frequent bushes of Salix cinerea and the occasional Crataegus monogyna, Frangula alnus and Viburnum opulus occur with preferentially high frequency here and the former can be locally abundant.

However, the most distinctive feature of this vegetation is the field layer, where virtually all the components show greater richness and variety than elsewhere in the community. Among the sedges, both C. paniculata and C. acutiformis remain frequent here and either or both may dominate. Occasionally, they are supplemented or replaced by C. elata (as at Esthwaite North Fen and in ditches at Askham Bog). Other swamp and fen sedges persisting less commonly, and generally in smaller amounts, are C. appropinguata, C. pseudocyperus and C. riparia. Then, C. remota is frequent here, though it is rarely so abundant as to be worthy of calling a dominant. Some stands outside Broadland also provide the open and wet, but not continuously waterlogged, conditions under which C. elongata survives in Britain (David 1978, Wheeler 1980c, 1983). This is the characteristic sedge of this kind of woodland on the Continental mainland, though in this country it also occurs in the Salix-Betula-Phragmites woodland (as at Askham which has probably the largest British colony: David 1978, Fitter et al. 1980) and on open fen.

The tall herbs, too, are striking in their number with the community species all being common and frequently joined by Lysimachia vulgaris, Lythrum salicaria and Lycopus europaeus and, in Broadland, Peucedanum palustre and, less commonly, Impatiens capensis and Thalictrum flavum. The fern component is frequently enriched by Thelypteris palustris, the fronds of which can be very abundant, and, more occasionally, by Osmunda regalis, with stools of sometimes massive size. This latter species was used by Klötzli (1970) to name this whole community but it is rather strictly confined to this particular type of Alnus-Carex woodland and it also occurs in Britain in other kinds of wet woodlands,

though more rarely. Among the smaller dicotyledons, Myosotis laxa ssp. cespitosa is strongly preferential and Cardamine pratensis becomes frequent. Scutellaria galericulata, Viola palustris, Ranunculus repens and R. flammula are slightly more frequent here than elsewhere.

Solanum dulcamara remains common in this subcommunity and there is occasionally some climbing Humulus lupulus. Underscrub can be dense with much Rubus fruticosus agg. especially in drier stands, and occasionally prominent Ribes nigrum and R. rubrum.

Again, the bryophytes are not distinctive.

Chrysosplenium oppositifolium sub-community: Osmundo-Alnetum glutinosae chrysosplenietosum (Klötzli 1970) Wheeler 1980c; Alder stand type 7Bb Peterken 1981. The tree canopy here is simpler and less rich than in the other sub-communities and Alnus is often the only species: large Salix cinerea bushes can occasionally break the canopy but both Fraxinus and Betula pubescens are rare. As this vegetation is not usually developed on mats of fen peat in topogenous mires, there is not the typical pattern of flooding and subsidence of the substrate here, though older Alnus may still tumble over from the tops of sedge tussocks. The shrub layer is poorer in species and often less extensive than in the other sub-communities: Salix cinerea is occasional but Crataegus monogyna is absent and other species are rare.

In the field layer, *C. paniculata* is almost always the dominant with *C. acutiformis* reduced in frequency and rarely abundant. Other sedges are rare or absent and *Phragmites* is very uncommon. As in the first subcommunity, the tall herbs here are usually just those of the community and even some of these (notably *Iris pseudacorus* and *Eupatorium cannabinum*) are reduced in frequency. The one distinctive species in this element, however, is *Oenanthe crocata* which is strongly preferential here and a good marker of these more oceanic alderwoods from their European mainland counterparts. *Epilobium hirsutum* and *Rumex sanguineus* occur occasionally. The ferns are not distinctive.

However, very striking here are the small-herb and bryophyte components which form a patchy carpet between the sedge tussocks. Chrysosplenium oppositifolium is strongly preferential and it can be very abundant with frequent Cardamine pratensis, Ajuga reptans and Caltha palustris. Among the bryophytes, Pellia epiphylla becomes very common and Rhizomnium punctatum is somewhat more frequent than in the other subcommunities.

Habitat

The Alnus-Carex woodland is most characteristic of wet to waterlogged organic soils, base-rich and moderately eutrophic, in topogenous and soligenous mires. It is especially associated with fen peats in open water transitions and flood-plain mires where there is a strong influence of calcareous ground water and periodic deposition of allochthonous mineral material in winterflooding but it can occur, too, in basin mires where there is a local influence of more base-rich water from marginal springs and in soligenous mires below seepage lines where very wet mineral soils develop a humose topsoil or thin surface peat. It is essentially a primary woodland, developing naturally from certain kinds of fen in hydrarch successions but drier, older stands have been subject to treatments such as coppicing and grazing.

As with the other main British carr community, the Salix-Betula-Phragmites woodland, the floristics and structure of the developing canopy and understorey are very much dependent on the availability of seed-parents and on propagule dispersion and the composition of the field layer is strongly influenced by the nature of the invaded fen vegetation. Here, though, the frequent presence of upstanding tussocks of Carex paniculata provide sites for early colonisation well before the accumulation of peat has raised the general fen surface above the limit of the winter flood. Very commonly, therefore, this community has the character of a swamp woodland and, in its early stages at least, is free from the complicating effects of human activity that are such a marked feature of many stands of the Salix-Betula-Phragmites woodland. Where C. acutiformis has been the more prominent sedge in the preceding vegetation. invasion of woody species is delayed until the substrate surface begins to rise above the limit of the inundating waters so that the woodland is initially less swampy. Though the fen mat may be depressed somewhat as the woodland ages, most of the trees and shrubs are rooted in the substrate itself and they do not show the same tendency to topple over. Such differences formed the basis of Lambert's separation between 'swamp' and 'semi-swamp' carrs (Lambert 1951, 1965) but it is important to realise that this is an essentially physiognomic distinction that may be of value in understanding the seral development of the woodland and its ultimate structure but which is not reflected in general floristic differences, as indeed Lambert herself acknowledged.

The floristic richness of this kind of woodland is partly related to the richness of the preceding swamp and fen. This is usually primary vegetation without the overwhelming dominance of densely-packed monocotyledonous herbage favoured by mowing. Even where bulky sedges are abundant, the cover is somewhat more open and, especially where *C. paniculata* tussocks predominate, amply provided with a variety of niches where the different associates can gain a hold. The high shade-tolerance of both *C. paniculata* and *C. acutiformis* also means that they persist beneath the developing canopy so there is often a strong floristic and structural

continuity between the woodland and the herbaceous vegetation that is being invaded.

The Lysimachia sub-community includes the most species-rich Alnus-Carex woodlands that were the subject of the early classic accounts from Broadland (e.g. Pallis 1911, Lambert 1951). It is still a prominent feature there in those topogenous mires which remain under the close influence of the calcareous and eutrophic river waters, forming sometimes large stands on waterlogged fen peats around the Broad margins and over larger turf ponds and occurring as narrower strips alongside dykes and sluggish stretches of the rivers. Many stands remain swampy throughout the year, especially where colonisation is recent or where the substrate has begun to sink under the weight of larger trees. In those river systems which experience tidally-related water fluctuations, there is a more frequent pattern of inundation on the ground between the trees. This sub-community is also found occasionally outside Broadland where there is a similar combination of base-richness and moderate eutrophy in the waters and soils, on terraces in some river valleys (as in the Breck: Haslam 1965) and in a few of the Shropshire and Cheshire basin mires (Clapham in Tansley 1939, Sinker 1962). It is also found as a central strip of less acidophilous vegetation in a few soligenous mires, as in certain New Forest valleys (e.g. Rankin 1911b, Rose 1950, McVean 1956b).

The habitat of the more common and more widespread *Phragmites* sub-community is very similar and part of the floristic difference between this vegetation and that of the Lysimachia sub-community is phytogeographical in that more Continental and Continental Northern wetland species, such as *Thelypteris palustris*, Peucedanum palustre and Carex appropinguata, become rarer outside the eastern lowlands. But there may also have been some impoverishment due to human disturbance because many stands of this sub-community survive on fragments of mire which have been much interfered with and which now remain isolated within agriculturally-improved landscapes. There is also the possibility that the *Phragmites* sub-community is associated with less peaty soils or, at least, ones which have a more pronounced influence of minerotrophic waters. This is certainly the case with the distinctive Scirpus sylvaticus-dominated vegetation included here: it is typically found on substrates which below have the consistency and colour of thick tomato soup, indicating iron enrichment.

The habitat of the *Chrysosplenium* sub-community is much more obviously distinctive. This is typically a woodland of springs and seepage lines where the emergence of somewhat less base-rich waters than is usual for the community keeps the soils very wet but not surface-flooded. The soils often have a mineral base but, over the impervious drift or bedrock substrate, peat can accumu-

late in the waterlogged conditions. Calcicolous species are not so prominent here and, in the carpet of ground vegetation that typically forms on the wet soil between the sedge tussocks, plants like *Chrysosplenium oppositifolium* and *Pellia epiphylla* (regarded by Klötzli (1970) as more typical of his *Pellio-Alnetum*) become very frequent. This is a local woodland type found in often small incised valleys cut into less calcareous bedrocks, as in the Weald.

Zonation and succession

Around standing and slow-moving open waters, the Lysimachia and Phragmites sub-communities are often found in zonations running from woodland, through swamp, to aquatic vegetation, as around some of the Norfolk Broads (e.g. Pallis 1911, Lambert & Jennings 1951, Lambert 1951) and at Sweat Mere (Clapham in Tansley 1939, Sinker 1962). Most frequently, it is *Carex* paniculata swamp that forms an immediate front to the Alnus-Carex woodland but sometimes invasion of the developing sedge tussocks is so rapid that there is no distinct sedge swamp but simply a belt of helophyte swamp dominated by Phragmites australis or Typha angustifolia between the young woodland fringe and the open water. Where invasion has been substantially delayed, a belt of sedge-dominated fen (the Peucedano-Phragmitetum or Phragmites-Eupatorium fen) may supervene between the woodland and the swamp. On drier ground, the Lysimachia and Phragmites sub-communities can pass to drier carr of the Salix-Betula-Phragmites woodland, still over peat, or directly to some kind of mixed deciduous woodland, usually in these southern lowlands, the Quercus-Pteridium-Rubus woodland. However, in the latter case, quite gradual transitions in both woody species and field layer may, in fact, mask discontinuities in substrate and soils, as where mire deposits give way to solid valley sides around.

On more extensive flood-plain mires with a long history of exploitation, various kinds of human disturbance can complicate this basic pattern. Peat-digging, for example, can create new hollows which, when abandoned and flooded and colonised with swamp and swamp-woodland, produce local reversals in the general trend (well seen in some of the profiles of Lambert & Jennings 1951). Then, mowing for fen-crops can create extensive stretches of secondary herbaceous vegetation behind the Alnus-Carex woodland, though in most places such mowing-marshes have been abandoned now and colonised by the Salix-Betula-Phragmites woodland or, where there has been much disturbance and enrichment of the dry peat surface, the Alnus-Urtica woodland. Along the water's edge, too, zonations have been modified, as where boat-traffic and the depredations of coypu have fretted away the fringe of swamp and left rather moribund stands of Alnus-Carex woodland abutting directly on to open water. Eutrophication of open waters has also encouraged the development of *Phragmites-Urtica* fen along the front of some tracts.

There is a continuous series of zonations between the more extensive sequences of vegetation types described above and the much narrower belts of communities found on the peaty terraces of small slow-moving rivers. Here, the Alnus-Carex woodland (usually, in these sites, the *Phragmites* sub-community) can be found occupying the flat and winter-flooded ground of the terrace with fragmentary swamp along the water's edge and a very sharp transition at the valley side to mixed deciduous woodland. Quite commonly, the swamp-woodland is separated from the moving river waters by a narrow belt of the Alnus-Urtica woodland on levees of rich alluvium, behind which conditions may be virtually stagnant. These kinds of patterns now often survive isolated in intensive agricultural or afforested landscapes where the valley sides have been cleared for pasture or a tree crop.

In valley mires where there is some persisting influence of more base-rich and eutrophic waters along the central axis, the Lysimachia or Phragmites subcommunities can occur as a central strip of woodland sandwiched between parallel belts of very wet poor-fen with Sphagna (especially S. recurvum) and dominants such as Carex rostrata, Equisetum fluviatile and Juncus acutiflorus or Junco-Molinion vegetation, which in turn passes to Sphagnum pools and then to wet and dry heath. This is the classic kind of zonation described from some valley mires in the New Forest (Rankin 1911b, Rose 1950, McVean 1956b, Wheeler 1983). Similar, though often compressed and fragmented, patterns can be seen around the margins of some basin mires where there is a local influence of more base-rich soligenous waters in the lagg (as at Rhos-goch Common: Bartley 1960).

The characteristic association of the Chrysosplenium sub-community with seepage zones means that it is often found as small stands isolated within stretches of drier, usually mixed deciduous woodland. In such situations, it can be seen as the less base-rich analogue of the Alnus-Fraxinus-Lysimachia woodland: like that vegetation it usually interrupts stretches of bluebell or mercury woodland or straddles transitions between the two over junctions of less and more base-rich soils. Where seepage is sufficient to create the semblance of a small valley mire, it may form more extensive sinuous stands following the line of water movement.

Stratigraphical studies in Broadland (Jennings & Lambert 1951, Lambert & Jennings 1951, Lambert 1951, 1965) have shown that the more intact zonations from open water to *Alnus-Carex* woodland represent a primary hydrosere in which aquatic vegetation, then *Typha*, *Phragmites* and *Carex* swamps are naturally succeeded by invasion of woody species. More fragmen-

tary studies at Sweat Mere in Shropshire (e.g. Sinker 1962) suggest that a similar process has occurred there. Although both sedge-swamp and swamp-carr were poorly represented in the numerous profiles examined in Walker's (1970) survey, it seems likely that this succession is the normal one around more base-rich and eutrophic open waters in the British lowlands (Wheeler 1978, 1980c, 1983). Despite the primeval appearance of many stands of this woodland, it is clear that it can develop from open water within little more than a century (Lambert 1951, 1965, Sinker 1962). Some stands, though, may be considerably older because this appears to be a fairly stable kind of vegetation and there is no firm evidence that it habitually progresses to drier carr, say of the Salix-Betula-Phragmites type. This may happen in some more isolated parts of flood-plain mires or in those valley mires where there is substantial deposition of alluvium but often the woodland becomes moribund before the general peat surface has become markedly dry, trees collapsing and sedge tussocks decaying to initiate the cycle of development over again (e.g. McVean 1956b). In some situations, marked enrichment of the waters and substrates (say, through sewage or fertiliser contamination or massive deposition of mineral material), may precipitate a succession to wetter kinds of the Alnus-Urtica woodland.

Although some drier stands of the community may have been cleared in the past for the extension of mowing-marshes (e.g. Lambert 1965), the frequently intractable topography of the *Alnus-Carex* woodland has given it some protection against conversion to secondary fen. However, where clearance has occurred, the community is not able to re-develop on the abandonment of mowing unless there is substantial inundation by base-rich and moderately eutrophic waters, in marked contrast to the *Salix-Betula-Phragmites* woodland which is very often found as a secondary woodland over old mowing-marsh.

Where cattle have access to drier stands, they can graze down the tall herbs and physically damage the sedge tussocks which can lead to a gradual run-down of this woodland type. Light burning of stands among heathland in the New Forest does not totally destroy *Alnus* which can produce abundant basal sprouts (McVean 1956b).

Where the local influence of base-rich waters is ultimately insufficient to offset the development of more acid peat, as in some valley mires and basin mires, the *Alnus-Carex* woodland may give way eventually to *Sphagnum*-dominated mire. Such a development was suggested by Rose (1950) for some New Forest valley mires and it may be happening, too, around the ombrogenous nuclei found in some Broadland fens (as in the Ant valley: Wheeler 1978, 1983). Walker (1970) considered that *Sphagnum*-mire might be a natural climax

of swamp-carr in small inland basins in the British lowlands.

Distribution

The Alnus-Carex woodland is now a fairly local, though quite widespread, community throughout the English lowlands, with a very few localities in Wales and Scotland. The Phragmites sub-community is the commonest and most widely distributed type, being especially well represented in the Shropshire and Cheshire meres. The Lysimachia sub-community is mostly confined to Broadland. The Chrysosplenium sub-community is much rarer but very good stands survive in the Wealden woods with outliers further north.

Affinities

This community has long been recognised, especially in its richer forms with striking swamp physiognomy, as a distinct kind of wet woodland in Britain, comprising, with the Salix-Betula-Phragmites fen carr, most of our remaining woodland cover over lowland fen peats and more base-rich peaty alluvial soils. The two communities are very close floristically and, in some stands, it is only the relative prominence of either bulky sedges or Phragmites that provides a distinction. Klötzli (1970), in fact, does not have an equivalent to the Salix-Betula-Phragmites woodland and neither does Wheeler (1978, 1980c, 1983) who expanded Klötzli's geographical coverage and defined a larger number of sub-communi-

ties. In so far as they have sampled Salix-Betula-Phragmites woodland, their stands have been placed within a single association, the Osmundo-Alnetum. This, however, produced a very variable and bulky vegetation type and it seems better to maintain two distinct communities, especially as such a division is supported by seral and environmental differences. Apart from the separation of samples lacking larger sedges, the treatment of Alnus-Carex woodland here largely follows the expanded account of the Osmundo-Alnetum given by Wheeler (1980c), though his sphagnetosum is much better considered as part of the Betula-Molinia woodland.

Klötzli (1970) conceived the Osmundo-Alnetum as an oceanic replacement along the the western European seaboard of the Carici elongatae-Alnetum and the two communities are generally very similar. Osmunda regalis was considered a good character species but it has not been used for naming here because of its quite severe restriction to the richer stands of the Lysimachia subcommunity. Oenanthe crocata is another good distinct species of the British examples of this kind of woodland but it, too, is largely confined to a single sub-community. Both these species (and indeed the much rarer C. elongata) also occur in other wet woodlands in Britain.

In the more oceanic parts of Britain, the Alnus-Carex woodland is replaced by the Alnus-Fraxinus-Lysimachia woodland and the Chrysosplenium sub-communities of each grade floristically one into the other.

Floristic table W5

	a	b	c	5
Alnus glutinosa	V (1–10)	V (1-8)	V (4-6)	V (1-10)
Salix cinerea	III (3–9)	III (1–6)	II (1–8)	III (1–9)
Fraxinus excelsior	III (1-4)	III (1–4)	I (1)	III (1–4)
Betula pubescens	II (1–7)	III (1–6)	I(1)	II (1-7)
Quercus robur	I (4)	I (1–4)	I (1)	I (1–4)
Salix cinerea	III (2–10)	III (1–6)	II (1-5)	III (1–10)
Crataegus monogyna	II (1-4)	II (1-3)		II (1–4)
Alnus glutinosa sapling	I (1-3)	I (1-3)	I (1-3)	I (1-3)
Ilex aquifolium	I (3)	I (4)	I (1-3)	I (1-4)
Salix aurita	I (4)		I (4)	I (4)
Rhamnus catharticus	I (1-3)	I (1-3)		I (1-3)
Sorbus aucuparia		I (1–3)	I (1–3)	I (1-3)
Frangula alnus	I (1-3)	III (1–4)	I (1)	II (1-4)
Viburnum opulus	I (1-3)	II (1–3)	I (1-3)	I (1-3)
Eurhynchium praelongum	IV (1-3)	V (1-4)	V (1-4)	IV (1-4)
Carex paniculata	IV (1-8)	IV (1-5)	V (1-5)	IV (1-8)
Brachythecium rutabulum	IV (1-4)	III (1–4)	V (1-4)	IV (1-4)

Rubus fruticosus agg.	III (1–6)	V (1–4)	V (1-3)	IV (1–6)
Galium palustre	III (1–3)	V (1–4)	IV (1-3)	IV (1-4)
Solanum dulcamara	IV (1-4)	III (1-4)	II (1-3)	III (1-4)
Phragmites australis	III (1-5)	II (1-4)	I (1-5)	III (1-5)
Galium aparine	II (1-3)	I (1-3)	I (1-3)	I (1-3)
Equisetum palustre	II (1-3)	I (1-3)		I (1-3)
Scirpus sylvaticus	II (1–6)			I (1-6)
Lophocolea heterophylla	II (1-3)			I (1-3)
Plagiothecium denticulatum	II (1-2)			I (1-2)
Callitriche stagnalis	I (2-4)			I (2-4)
Symphytum officinale	I (1-3)			I (1-3)
Dryopteris cristata	I (3-4)			I (3-4)
Holcus lanatus	I (3-4)			I (3-4)
Hedera helix	I (2–4)			I (2-4)
Mnium hornum	III (1-3)	IV (1-3)	II (1-3)	III (1-3)
Lysimachia vulgaris	I (1-3)	IV (1-3)	I (1-3)	II (1-3)
Poa trivialis	II (1-4)	III (1 -4)	II (1-3)	II (1-4)
Lycopus europaeus	II (1-3)	III (1-3)	I (1-3)	II (1-3)
Thelypteris palustris	I (1–4)	III (1–6)	I (1)	II (1–6)
Lythrum salicaria	I (1-3)	III (1-3)	I (1-3)	II (1-3)
Myosotis laxa caespitosa	I (1-6)	III (1–4)	I (1-3)	II (1-6)
Carex remota	I (2-7)	III (1 -4)	I (1-4)	II (1-7)
Ribes nigrum	I (1-2)	II (1–4)	I (1)	I (1-4)
Carex elata	I (6–7)	II (1-8)		I (1-8)
Humulus lupulus	I (1)	II (1–4)		I (1-4)
Osmunda regalis		II (1–8)	I (1)	I (1-8)
Peucedanum palustre		II (1-3)		I (1-3)
Carex pseudocyperus		II (1-4)		I (1-4)
Carex appropinquata		I (1-3)		I (1-3)
Campylium stellatum		I (1–3)		I (1-3)
Impatiens capensis		I (1–3)		I (1-3)
Carex riparia		I (1-4)		I (1-4)
Thalictrum flavum		I (1-3)		I (1-3)
Pellia endiviifolia		I (1–3)		I (1–3)
Rumex hydrolapathum		I (1-3)		I (1-3)
Carex elongata		I (1–2)		I (1–2)
Bryum pseudotriquetrum		I (1)		I (1)
Cardamine pratensis	I (1-3)	III (1-3)	IV (1-3)	III (1-3)
Chrysosplenium oppositifolium	I (1)		V (1-6)	II (1–6)
Pellia epiphylla		II (1)	V (1-3)	II (1-3)
Ajuga reptans	II (1-3)		IV (1-4)	II (1-4)
Caltha palustris	I (1-4)	II (1-3)	III (1–3)	II (1-4)
Rhizomnium punctatum	I (2-3)	II (1-3)	III (1 -4)	II (1 -4)
Lonicera periclymenum	I (1-3)	II (1-3)	III (1–3)	II (1–3)
Oenanthe crocata	I (2-7)	I (1)	III (1–6)	II (1-7)
Ranunculus acris	I (1)	I (1-3)	II (1-3)	I (1–3)
Epilobium hirsutum	I (1-3)		II (1-3)	I (1–3)
Rumex sanguineus	I (2-3)		II (1–3)	I (1-3)
Atrichum undulatum			II (1-3)	I (1-3)

Floristic table W5 (cont.)

	a	b	С	5
Dryopteris dilatata	III (1–4)	IV (1-4)	III (1 -4)	III (1-4)
Cirsium palustre	III (1-3)	III (1-3)	IV (1-3)	III (1-3)
Mentha aquatica	III (1–4)	III (1–3)	III (1–3)	III (1–4)
Urtica dioica	III (1-3)	III (1–4)	III (1–3)	III (1-4)
Filipendula ulmaria	III (1 -4)	III (1-5)	III (1 -4)	III (1-5)
Carex acutiformis	III (1 - 8)	III (1-5)	II (1–6)	III (1–8)
Eupatorium cannabinum	III (1 -4)	III (1 -4)	II (1–4)	III (1–4)
Iris pseudacorus	III (1-4)	III (1 -4)	I (1-3)	III (1 -4)
Valeriana officinalis	II (1-3)	III (1-3)	III (1-3)	III (1-3)
Calliergon cuspidatum	I (1-3)	III (1–4)	III (1 -4)	II (1-4)
Plagiomnium undulatum	II (1–4)	II (1-3)	III (1 -4)	II (1-4)
Angelica sylvestris	II (1-3)	II (1-3)	III (1–4)	II (1-4)
Athyrium filix-femina	II (1-3)	II (1-4)	II (1-3)	II (1-4)
Valeriana dioica	II (1–4)	II (1-3)	I (1–4)	II (1-4)
Geranium robertianum	I (1-3)	II (1-3)	II (1-3)	I (1-3)
Phalaris arundinacea	I (1–6)	II (1-4)	I (1)	I (1–6)
Scutellaria galericulata	I(1)	II (1-3)	I (1)	I (1-3)
Viola palustris	I (3)	II (1-3)	I (1)	I (1-3)
Ranunculus repens	I (2–6)	II (1-3)	I (1)	I (1-3)
Lophocolea bidentata s.l.	I (3)	II (1-3)	I (1)	I (1-3)
Ranunculus flammula	I (1)	II (1-3)	I (1)	I (1-3)
Juncus effusus	I (1–7)	II (1-3)	I (1)	I (1-3)
Sphagnum palustre	I (1–6)	II (1-3)	I (1-3)	I (1-6)
Dryopteris filix-mas	I (1-3)	I (1-3)	I (1-3)	I (1-3)
Circaea lutetiana	I (1-5)	I (1–3)	I (1–3)	I (1-5)
Rosa canina agg.	I (1-3)	I (1–3)	I (1)	I (1-3)
Berula erecta	I (2–4)	I (1–3)	I (1)	I (1–4)
Glyceria maxima	I (1-3)	I (1-3)	I (1-3)	I (1-3)
Scrophularia aquatica	I (1-3)	I (1)	I (1)	I (1-3)
Equisetum fluviatile	I (1-3)	I (1-3)	I (1-3)	I (1-3)
Calliergon cordifolium	I (1)	I (1-3)	I(1)	I (1-3)
Sphagnum squarrosum	I (1)	I (1-3)	I (1)	I (1-3)
Hydrocotyle vulgaris	I(1)	I (1)	I(1)	I (1)
Dryopteris carthusiana	I (1)	I (1)	I (1)	I (1)
Deschampsia cespitosa	I (1-3)		I (1-3)	I (1-3)
Ligustrum vulgare	I (1-3)		I (1)	I (1-3)
Hypericum tetrapterum	I (1-3)		I(1)	I (1-3)
Equisetum telmateia	I (1)		I (1)	I (1)
Amblystegium serpens	I (1-3)	I (1-3)		I (1-3)
Myosotis scorpioides	I (1-3)	I (1-3)		I (1-3)
Calamagrostis canescens	I (7)	I (1–6)		I (1-7)
Calystegia sepium	I (1-3)	I (1-3)		I (1-3)
Hypnum cupressiforme	I (1-3)	I(1)		I (1-3)
Lychnis flos-cuculi	I(1)	I (1-3)		I (1-3)
Cicuta virosa	I (1–7)	I (1-3)		I (1-7)
Agrostis stolonifera	I (1-3)	I (1)		I (1-3)
Ranunculus lingua	I (1)	I (1)		I (1)

Number of samples Number of species/sample	46 20 (4–44)	46 29 (21–45)	15 26 (16–42)	107 24 (4–45)
Epilobium parviflorum		I (1)	I (1)	I(1)
Sphagnum fimbriatum		I (1–3)	I (1)	I (1-3)
Cardamine amara		I (1–4)	I (1-3)	I (1-4)
Plagiomnium rostratum	I (1)	I (1)		I (1)
Sparganium erectum	I (1–3)	I (1-3)		I (1-3)
Ribes rubrum	I (1)	I (1–3)		I (1-3)

- a Phragmites australis sub-community
- b Lysimachia vulgaris sub-community
- c Chrysosplenium oppositifolium sub-community
- 5 Alnus glutinosa-Carex paniculata woodland (total)







