W9
Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis woodland

Synonymy
Upland ashwood Tansley 1939; *Corylo-Fraxinetum* Br.-Bl. & Tx 1952 *p.p.*; Herb-rich birchwood Pigott 1956*a* *p.p.*; *Fraxinus-Brachypodium sylvaticum* nodum McVean & Ratcliffe 1962; *Corylus* scrub McVean & Ratcliffe 1962; Mixed deciduous woodland McVean & Ratcliffe 1962; *Betula*-herb nodum, basiphilous facies McVean & Ratcliffe 1962; Ashwood McVean 1964; *Dryopterido-Fraxinetum blechnetosum* Klötzli 1970; *Sorbo-Brachypodietum* Graham 1971; *Fraxinus excelsior-Brachypodium sylvaticum* Association Birks 1973; *Corylus avellana-Oxalis acetosella* Association Birks 1973 *p.p.*; *Betula pubescens-Cirsium heterophyllum* Association Birks 1973; Mixed Deciduous Woodland Ferreira 1978 *p.p.*; Ash-wych elm stand types 1Ab & 1D Peterken 1981 *p.p.*; Hazel-ash stand type 3C Peterken 1981 *p.p.*; Alder stand type 7D Peterken 1981 *p.p.*; Birch stand type 12B Peterken 1981 *p.p.*; *Primulo-Quercetum* J. Tüxen *apud* Birse 1982 *p.p.*; *Querco-Ulmetum glabrae* Birse & Robertson 1976 *emend.* Birse 1984 *p.p.*

Constant species
Fraxinus excelsior, *Corylus avellana*, *Dryopteris filix-mas*, *Mercurialis perennis*, *Oxalis acetosella*, *Viola riviniana*, *Eurhynchium praelongum*, *E. striatum*, *Plagiomnium undulatum*, *Thuidium tamariscinum*.

Rare species
Actaea spicata, *Bromus benekenii*, *Crepis mollis*, *Gagea lutea*, *Polygonatum verticillatum*.

Physiognomy
In the *Fraxinus-Sorbus-Mercurialis* woodland, as in its southern lowland counterpart, the *Fraxinus-Acer-Mercurialis* woodland, *Fraxinus excelsior* and *Corylus avellana* play a major role in the definition of the canopy. Both species are constant here and frequently abundant, often dominating the woody cover in various proportions. Typically, though, trees and shrubs with more continental affinities are very scarce. *Tilia cordata* survives on some Lake District crags in association with the community (Pigott & Huntley 1978), some Cumbrian, Pennine and southern Scottish stands provide northerly localities for *Acer campestre*, *Rhamnus catharticus* or *Euonymus europaeus* (Ratcliffe 1977) and *Viburnum opulus* extends further north in the more oceanic parts of north-west Scotland (Birks 1973, Ratcliffe 1977) but, for the most part, this kind of woodland lies beyond the north-western limit of these species.

By contrast, birch, almost always *Betula pubescens* on the moist soils characteristic of this woodland and increasingly to the north ssp. *carpatica*, and *Sorbus aucuparia* are much more frequent than in most *Fraxinus-Acer-Mercurialis* woodlands. *B. pubescens* is the more common and generally the more abundant but *S. aucuparia* can be locally prominent, especially in ungrazed stands (McVean 1964*a*) and quite commonly the two co-dominate with *Fraxinus* and *Corylus*. *Alnus glutinosa* occurs very occasionally where there is local flushing but it is rarely more than as scattered individuals, a good distinction between this community and the *Alnus-Fraxinus-Lysimachia* woodland, a common kind of flush alderwood in the sub-montane parts of northern and western Britain.

There is a trend within the community from well-developed high-forest canopies to scrubby woodland with only occasional trees. In the former, *Fraxinus* can be accompanied by some *Ulmus glabra*, *Acer pseudoplatanus* and oak, usually here *Quercus petraea* or hybrids, in canopies which, apart from the frequent presence of scattered *B. pubescens* and *S. aucuparia*, can closely resemble those of north-western *Fraxinus-Acer-Mercurialis* woodlands. In such stands, *Corylus* usually dominates in a distinct understorey, often with some other small trees and shrubs, notably hawthorn, here *Crataegus monogyna* with the single striking exception of a far-flung Pennine location for *C. laevigata* (Ratcliffe 1977). At the other extreme, scattered trees, often just *Fraxinus*, emerge from scrubby mixtures of *Corylus*, *B. pubescens*

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and *S. aucuparia*. On the typically irregular topography occupied by this kind of woodland, even the high-forest canopies tend to be uneven-topped and of somewhat patchy cover, but there is a distinct association between the more scrubby stands and more exposed situations like ravine tops and sides in the windy far north-west of Scotland. In the latter area, though, there may have been a long history of timber removal from these woods (McVean & Ratcliffe 1962, McVean 1964*a*, Birks 1973, Birse 1982, 1984). In other stands, a dense shrub layer, and especially an abundance of *Corylus*, reflects past coppicing but this treatment is nothing like as systematic or widespread as in the *Fraxinus-Acer-Mercurialis* woodland. Surviving stands are often remote from existing settlements and ground is frequently intractable and the usual pattern here is of occasional, ill-defined parcels in those woods which are nearer to villages or upland farmsteads.

The irregular topography also has a strong influence on the appearance of the field layer. In marked contrast to many *Fraxinus-Acer-Mercurialis* woodlands, where the vegetation is disposed over undulating plateaus and graded slopes, there is here no consistent pattern of dominance among the herbs. Very commonly, the plants form complex mosaics over the highly uneven, often steep and sometimes unstable deposits of drift or head which can choke upland ravines, or over the intricately-weathered surfaces of rock exposures in pavements or tumbles of boulders. Often, too, local flushing adds further variety. There are also considerable differences in total herb cover. Slumping can create temporarily bare areas and where denser canopy shade is combined with grazing, as in the Typical sub-community, rather open field layers are commonplace, a feature which accentuates the appearance of a diverse patchwork of plants. Even under the lighter canopies of the *Crepis* sub-community, however, where there is no grazing, there is no consistent dominant, but varied mixtures of clumps and tussocks of many different species.

In floristic terms, though, there are some important similarities between the field layers of the *Fraxinus-Sorbus-Mercurialis* and *Fraxinus-Acer-Mercurialis* woodlands. *Mercurialis perennis* itself and *Hyacinthoides non-scripta* are both very frequent and, in many stands, they are patchily dominant in spring and early summer. But they are not so consistently abundant as further south: *Mercurialis* especially tends to do badly on the moist soils here and it thins out markedly towards the north of the range of the community. Both species also tend to suffer from competition from taller herbs in the ungrazed *Crepis* sub-community. The *Fraxinus-Sorbus-Mercurialis* woodland also provides the major northern locus for *Circaea lutetiana* and *Geum urbanum*, and *Geranium robertianum* and *Brachypodium sylvaticum* are very common, too. The last is especially prominent on steeper, somewhat drier banks and overall is as abundant in the community as *Mercurialis*: it has been used in some earlier accounts to define this kind of woodland (e.g. McVean & Ratcliffe 1962, Birks 1973) or sub-divisions of it (e.g. Birse 1984).

But it is often among plants characteristic of heavier, moister soils that the most obvious similarities between the two kinds of woodland are to be seen. Thus *Primula vulgaris, Poa trivialis* and *Deschampsia cespitosa*, all of them species which become very local where the *Fraxinus-Acer-Mercurialis* woodland extends on to the permeable limestones of north-west England, reappear here with renewed frequency. *Viola riviniana* is very common, too, though its frequent companion in the south, *V. reichenbachiana*, only just reaches into the range of the *Fraxinus-Sorbus-Mercurialis* woodland. Low-growing ground-cover plants are also often prominent especially in the more open field layer of the Typical sub-community, though *Lamiastrum galeobdolon* is recorded only in the more southerly stands (probably because low summer temperatures further north inhibit sexual reproduction: Packham 1983) and *Glechoma hederacea* is likewise scarce. But here this niche is well filled by *Potentilla sterilis*, *Veronica chamaedrys* and *V. montana*. *Anemone nemorosa* and *Ranunculus ficaria* can be found occasionally too, though they do not occur as vernal dominants in distinctive zones but with patchy local prominence or scattered throughout. Finally, by contrast with *Fraxinus-Acer-Mercurialis* woodlands on the better-aerated soils of the limestones of north-western England, *Urtica dioica* and *Galium aparine* are of only occasional and local occurrence. In all these respects, the *Fraxinus-Sorbus-Mercurialis* woodland resembles not so much the geographically close north-western *Fraxinus-Acer-Mercurialis* woodlands but the edaphically similar south-eastern types, especially those of wetter areas like the western Weald.

Other floristic features, though, are very distinctive and help separate the two communities. First, in the much more humid climate of this sub-montane woodland, ferns are very prominent. *Dryopteris filix-mas* becomes constant here and *D. borreri* also occurs occasionally but it is the high frequency of *Athyrium filix-femina* that is an especially good indicator of soils that are kept moist throughout the year and which show a marked tendency towards superficial eluviation. Where the soils are somewhat drier, as in the Typical sub-community, *Dryopteris dilatata* provides a further enrichment of the fern flora; and locally pronounced surface depression of pH, as occurs very obviously over nidus-capped boulders in the extremely wet climate of north-west Scotland, can allow *Blechnum spicant* to flourish. It may be this tendency towards surface acidity that is responsible for the markedly low frequency of

Phyllitis scolopendrium here, because climatic conditions could scarcely be better for this strongly oceanic fern. Many stands lack the exposures of fissured limestone that it favours, though where the community does extend over scree or pavement (as on the Pennine Carboniferous, the Cleveland Oolite or the Durness Limestone of Skye) it can appear in some local abundance together with smaller calcicolous ferns such as *Asplenium trichomanes*, *A. ruta-muraria*, *A. adiantum-nigrum*, the rarer *A. viride* and *Cystopteris fragilis*. Other ferns recorded in the community at low frequency are *Polystichum aculeatum* and *P. setiferum*. *Pteridium aquilinum* is characteristically uncommon here and hardly ever abundant; with *Thelypteris limbosperma* and increased frequencies of *Blechnum spicant*, it is very much more typical of the analogue of this community on more base-poor sub-montane soils, the *Quercus-Betula-Oxalis* woodland.

The wetness of the soils throughout the year may also play a part in the second distinctive features of the field layer here, the high frequency and abundance of *Oxalis acetosella*. This is not a common species in the *Fraxinus-Acer-Mercurialis* woodland, though it can become locally abundant there, as for example when stands are coppiced, and it seems to be limited by dryness of the soils towards the southern limit of its range (Packham 1978). Here, though, it thrives, whether under the denser tree and shrub canopies of the Typical sub-community or among the luxuriant cover of tall herbs in the *Crepis* sub-community. Interestingly, both *Oxalis* and *Viola riviniana* show the same pattern of a rise to constancy in the sub-montane communities of both mercury and bluebell woods in Britain. And, in geographically intermediate regions, like Derbyshire, they both tend to be more abundant on north-facing slopes (e.g. Grime & Lloyd 1973).

A third characteristic is that the field layer is often quite grassy in appearance. Quite apart from species such as *Brachypodium sylvaticum*, *Deschampsia cespitosa* and *Poa trivialis* and more occasional records for *Bromus ramosus*, *Festuca gigantea*, *Milium effusum* and *Melica uniflora*, there can be prominent *Arrhenatherum elatius* and an abundance of species whose establishment is probably related to grazing by stock and deer, but which flourish best in the more open and less heavily grazed vegetation of the *Crepis* sub-community, e.g. *Dactylis glomerata*, *Holcus lanatus*, *H. mollis*, *Agrostis capillaris*, *Anthoxanthum odoratum*.

Finally, among the herbs, there are some plants which give a distinctly northern feel to this vegetation. The Northern Montane *Rubus saxatilis* and *Actaea spicata* occur very occasionally and, among the preferentials of the *Crepis* sub-community, *Crepis paludosa* itself, *Cirsium helenioides* (both Continental Northern) and *Trollius europaeus* (Northern Montane).

The bryophytes of the community are also distinctive in their abundance and variety, commonly forming a patchy mat, sometimes a virtually continuous carpet, over the surface of the soil and exposed rock. *Eurhynchium praelongum*, *E. striatum*, *Plagiomnium undulatum* and *Thuidium tamariscinum* are all constant, *Mnium hornum* and *Atrichum undulatum* frequent and *Cirriphyllum piliferum*, *Rhytidiadelphus triquetrus*, *Hypnum cupressiforme*, *Plagiochila asplenoides* and *Lophocolea bidentata s.l.* occasional. Various kinds of enrichment of this basic flora are visible in the community. Where the soil is more calcareous, stony or firm or where outcrops of limestone occur, species such as *Fissidens cristatus*, *F. bryoides*, *Thamnobryum alopecurum*, *Tortella tortuosa*, *Homalothecium sericeum* and *Neckera crispa* can appear. Then, with the increasingly wet climate of the extreme north-west, *Hylocomium splendens*, *H. brevirostre*, *Isothecium myosuroides*, *I. myurum* and *Thuidium delicatulum* become more common, and more strictly Atlantic species such as *Metzegeria leptoneura*, *Saccogyna viticulosa*, *Plagiochila spinulosa* and *Scapania gracilis* can be recorded. Many of these are of quite wide edaphic tolerance (Ratcliffe 1968) and some help accumulate distinctly acid mats of humus over the limestone boulders such that quite calcifugous bryophytes make a prominent contribution. Also in this region, the very humid climate encourages a lush growth of species characteristic of rotting wood, on which *Riccardia palmata* and *Scapania umbrosa* are sometimes found, and a very striking epiphytic flora of *Corylus* and *Fraxinus* twigs with festoons of *Ulota calvescens*, *U. phyllantha*, *U. crispa*, *Frullania teneriffae* and *F. dilatata*. Tree boles can support a distinctive clothing of *Hypnum mammillatum* and *Isothecium mysuroides* with *Metzgeria furcata* and *Radula complanata* and ground-growing species can extend up the tree bases (Ratcliffe 1968, 1977, Birks 1973). Fragments of all these components can be found in the community with decreasing frequency and richness in moving away from the far north-west as the climate becomes less humid and locally polluted (e.g. Graham 1971).

Sub-communities

Typical sub-community: *Fraxinus-Brachypodium sylvaticum* nodum McVean & Ratcliffe 1962 *p.p.*; *Betula*-herb nodum, basiphilous facies McVean & Ratcliffe 1962; Ashwood McVean 1964*a p.p.*; *Dryopterido-Fraxinetum blechnetosum*, *Ulmus* variant Klötzli 1970; *Sorbo-Brachypodietum* Graham 1971 *p.p.*; *Fraxinus excelsior-Brachypodium sylvaticum* Association Birks 1973; *Corylus avellana-Oxalis acetosella* Association Birks 1973 *p.p.*; Mixed Deciduous Woodland Ferreira 1978 *p.p.*; *Primulo-Quercetum*, *Deschampsia cespitosa* subassociation J. Tüxen *apud* Birse 1982 *p.p.*;

Querco-Ulmetum glabrae, Typical subassociation Birse & Robertson 1976 *emend.* Birse 1984 *p.p. Fraxinus* and *Corylus* are the most frequent and often the most abundant woody species here with *Betula pubescens* and *Sorbus aucuparia* less common and generally in smaller amounts. There is also a considerable diversity among the associated trees and shrubs. Where the vegetation occurs as high forest, a frequent occurrence here, *Fraxinus* generally dominates in a distinct, though often quite low (usually 12–20 m) and uneven-topped canopy, but there is commonly some *Ulmus glabra* and *Acer pseudoplatanus* and occasionally a little oak, usually *Quercus petraea* or the hybrids, much more rarely *Q. robur*. *Alnus glutinosa* occurs very occasionally and there is sometimes an occasional pine or larch. *Fagus sylvatica* is found very rarely, though some of the planted 'herbaceous beechwoods' described from the Aberdeen area by Watt (1931*a*) are perhaps best considered in relation to this community.

In such stands as these, *B. pubescens* (very occasionally with *B. pendula*) and *S. aucuparia* usually form a slightly lower tier, though well-grown specimens can break the main canopy. Beneath them, there is generally a well-defined understorey in which *Corylus* (sometimes increased in cover by coppicing) almost always predominates but *Crataegus monogyna* is very common in this sub-community and it can occasionally rival *Corylus*. *Ilex aquifolium*, *Sambucus nigra* and *Prunus padus* occur sparsely and usually at low cover though *Ilex* is sometimes found in local abundance and with individuals of grand stature. Sapling trees are quite common with young *Fraxinus*, *U. glabra*, *A. pseudoplatanus*, *B. pubescens* and *S. aucuparia*. On more unstable slopes, on the exposed margins of stands and on moving towards the north-west seaboard of Scotland, much scrubbier woodlands of this kind are found with a dominant layer of *Corylus*, *B. pubescens* (often obviously ssp. *carpatica*) and *S. aucuparia*, at around 10–12 m, and with scattered emergent trees, usually *Fraxinus*, much less frequently *U. glabra*, *Q. petraea* or *A. pseudoplatanus*.

The floristics of the field layer are well defined in qualitative terms but the quantitative composition is very variable and quite often the total cover is rather open, especially in denser shade or where the substrate is unstable: extensive stretches of bare soil are common here. Structurally, the most prominent plants are often ferns with large spreading crowns of *Athyrium filix-femina* and dryopteroids, including here *Dryopteris dilatata*. Between these, *Mercurialis perennis*, *Hyacinthoides non-scripta*, *Brachypodium sylvaticum*, *Oxalis acetosella* and *Primula vulgaris* all occur frequently and with patchy local abundance. *Viola riviniana*, *Geranium robertianum*, *Veronica chamaedrys*, *Lysimachia nemorum*, *Poa trivialis*, *Epilobium montanum* and *Sanicula europaea* are quite common too and, again, these can be prominent in small patchy mosaics. More preferential for this sub-community are *Geum urbanum*, *Circaea lutetiana*, *Potentilla sterilis* and, less frequently *Urtica dioica*, *Galium aparine*, *Rubus fruticosus* agg., *Hedera helix*, *Silene dioica* and *Veronica montana*. Seedlings of *Fraxinus* are also very much commoner here than in the *Crepis* sub-community. *Lamiastrum galeobdolon* and, somewhat more extensively, *Arum maculatum* occur in more southerly stands and *Circaea × intermedia*, though rather infrequent, is a good marker of this kind of woodland. *Galium odoratum* likewise occurs rather sparsely but it characteristically picks out little cascades of talus down which water periodically runs. Where larger boulders or outcrops of limestone provide crevices, *Phyllitis scolopendrium* and other calcicolous ferns appear.

Although these woodlands seem to be quite commonly grazed, grasses, apart from *B. sylvaticum*, *P. trivialis* and occasional *Deschampsia cespitosa*, are generally of low abundance here. *Dactylis glomerata* occurs quite frequently and there is sometimes a little *Arrhenatherum elatius* and *Agrostis capillaris*, but they do not attain the lush growth that helps characterise the *Crepis* sub-community. Grazing also restricts the occurrence of plants such as *Cirsium helenioides*, *Crepis paludosa*, *Geranium sylvaticum*, *Filipendula ulmaria* and *Luzula sylvatica* to very occasional specimens in more inaccessible places.

On the more stable areas of bare soil, bryophytes are often very abundant, frequently accounting for up to 50% cover of the ground surface between and among the herbs. All the community constants are well represented and, on patches of compact soil, these together with *Mnium hornum*, *Atrichum undulatum*, *Fissidens cristatus*, *F. bryoides* and *Pellia epiphylla* form a very distinctive suite. Rockier stands and those in more oceanic regions exhibit the characteristic kinds of enrichment described earlier.

***Crepis paludosa* sub-community:** Herb-rich birchwood Pigott 1956*a p.p.*; Hazel scrub McVean & Ratcliffe 1962; Mixed deciduous woodland McVean & Ratcliffe 1962; *Dryopterido-Fraxinetum blechnetosum* Klötzli 1970 *p.p.*; *Sorbo-Brachypodietum* Graham 1971 *p.p.*; *Betula pubescens-Cirsium heterophyllum* Association Birks 1973; Mixed Deciduous Woodland Ferreira 1978 *p.p.*; *Primulo-Quercetum*, *Deschampsia cespitosa* subassociation J. Tüxen *apud* Birse 1982 *p.p.* The woody cover here is less diverse than in the Typical sub-community with *U. glabra*, *A. pseudoplatanus*, oaks and *C. monogyna* occurring only rarely. Quite commonly, too, the canopy is rather open with scattered *Fraxinus*, larger specimens of *B. pubescens* and *S. aucuparia* and very occasional *Alnus*, emerging from a patchy shrub layer with *Corylus* and smaller *B. pubescens* and *S.*

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aucuparia. *Prunus padus* and *Salix cinerea* occur occasionally and *Populus tremula* rarely. Apart from young *B. pubescens* and *S. aucuparia*, saplings are uncommon.

Most of the characteristic community herbs maintain high frequency, though some show a depressed abundance in this vegetation and *Mercurialis* especially is less common and prominent on the sometimes moister soils here. *Dryopteris dilatata* is also very scarce and there is some reduction in ground cover plants like *Potentilla sterilis*; *Fraxinus* seedlings are extremely rare. By contrast, there is a marked increase in a variety of different plants, most colourfully among taller herbs which, where the woody cover is more open, grow luxuriant and flower profusely. *Filipendula ulmaria*, *Conopodium majus*, *Geum rivale* (largely replacing *G. urbanum* in this sub-community), *Rumex acetosa*, *Succisa pratensis*, *Senecio jacobaea*, *Stachys sylvatica*, *Cruciata laevipes*, *Alchemilla glabra* and trailing *Vicia sepium* are all preferential here as well as some distinctly northern species such as *Crepis paludosa*, *Cirsium helenioides* and *Trollius europaeus*. The nationally rare *Crepis mollis* is also found in some stands, providing a rather different phytogeographic link with more continental mountain vegetation of this kind (Pigott 1956*a*, Ratcliffe 1977).

Then, grasses are numerous and patchily abundant with frequent records for *Deschampsia cespitosa*, *Arrhenatherum elatius*, *Agrostis capillaris*, *Anthoxanthum odoratum*, *Holcus lanatus* and *H. mollis*, as well as the community species *Dactylis glomerata* and *Poa trivialis*. *Luzula sylvatica* is also sometimes prominent. *Carex pallescens* is a rather infrequent but very characteristic plant in this vegetation and *Rubus idaeus* can produce a patchy underscrub. Where the substrate is more unstable, as, for example, where local flushing causes a slumping of soil, a more open and lower cover of herbs can develop with mats of *Agrostis stolonifera* and *Ranunculus repens* and scattered *Tussilago farfara*. *Ranunculus ficaria* and *Allium ursinum* may also occur in moister places and *Paris quadrifolia* is scarce but distinctive. Where this sub-community has developed in bouldery woods in the extreme north-west, such grassy tall-herb cover may form a mosaic with fragments of more calcifugous vegetation with *Blechnum spicant* and *Potentilla erecta* on boulder tops but species such as *Vaccinium myrtillus* and *Deschampsia flexuosa* are typically absent.

As in the Typical sub-community, there is generally a diverse and extensive bryophyte flora here, though some bare soil acrocarps such as *Mnium hornum*, *Atrichum undulatum* and *Fissidens* spp. are rather less common. Larger pleurocarps, however, thrive among the damp bases of the herbs and over the extensive litter and some species, like *Cirriphyllum piliferum*, *Rhytidiadelphus triquetrus* and the liverwort *Plagiochila asplenoides* (including var. *major*) increase in frequency. There are some stronger preferentials here, too, with *Rhytidiadelphus squarrosus*, *R. loreus*, *Plagiothecium denticulatum*, *Rhizomnium punctatum* and *Plagiomnium rostratum* enriching the flora. In more oceanic regions, there is the further variety of species able to take advantage of enhanced superficial eluviation on the tops of boulders or the increasingly humid atmosphere.

Habitat

The *Fraxinus-Sorbus-Mercurialis* woodland is characteristic of permanently moist brown soils derived from calcareous bedrocks and superficials in the sub-montane climate of north-west Britain. Over much of its range, it is typically a community of valley heads in the upland fringes but, in the cool oceanic parts of north-west Scotland, it descends almost to sea-level. Timber and underwood removal have affected the floristics and physiognomy and grazing is important in mediating the differences between the two sub-communities.

The climate over the range of the community is cool, wet, windy and cloudy (e.g. Manley 1936, *Climatological Atlas* 1952, Chandler & Gregory 1976) and it affects the vegetation directly, through temperature, humidity and perhaps also through exposure to wind, and indirectly, through the influence of rainfall on soil development. Mean annual maximum temperatures throughout the range are always less than 26 °C, mostly less than 25 °C and substantially lower over much of north-west Scotland (Conolly & Dahl 1970). It is this summer coolness, combined with the high frequency of daytime cloudiness, that seems to affect pollination, fertilisation and seed-ripening in the more continental species characteristic of our mixed deciduous woodlands. Thus, the northern and western limits of woody plants like *Tilia cordata*, *Acer campestre*, *Cornus sanguinea*, *Euonymus europaeus* and *Rhamnus catharticus* (e.g. Pigott & Huntley 1978, 1981) and herbs such as *Lamiastrum galeobdolon* (Packham 1983) and *Arum maculatum*, correspond crudely with the southern and eastern limit of this community and help mark it off from the *Fraxinus-Acer-Mercurialis* woodland. On the positive side, there is an appearance here, especially well seen in less heavily grazed stands, of plants with Northern Montane affinities (e.g. *Prunus padus*, *Rubus saxatilis*, *Actaea spicata*, *Trollius europaeus*) or with Continental Northern distributions (*Crepis paludosa*, *Cirsium helenioides*) which serve to emphasise the links between this vegetation and woodlands in the cooler parts of Northern Europe (e.g. Pigott 1956*a*, 1958, Bradshaw 1962, McVean & Ratcliffe 1962, Birks 1973).

Winter climate, however, is not always severe. Towards the western fringes of the range of the community, February minima are usually above freezing (Chandler & Gregory 1976) and annual accumulated temperatures are, for the most part, above 800 °C (Page 1982). In

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many areas, morning snow-lie is nil or negligible (Ratcliffe 1968, Page 1982). Even where the community extends into the upland fringes, where the winter climate becomes much more bitter (e.g. Manley 1936, 1945), deeply-incised valleys can afford some protection from extreme cold. This moderate to pronounced mildness, combined with the extreme humidity of many sites (with 160 to more than 220 wet days yr^{-1}: Ratcliffe 1968), helps give the woodland, especially its field and ground layers which have the additional protection of the woody cover, its markedly oceanic and winter-green character, with an abundance of ferns and bryophytes. Although this feature becomes much more obvious on the north-west seaboard of Scotland (e.g. McVean & Ratcliffe 1962, Ratcliffe 1968, Birks 1973, Birse 1982, 1984), such that the community takes on much of the character of Irish woodlands of this kind (e.g. Braun-Blanquet & Tüxen 1952), the presence of these elements throughout helps distinguish the community from the *Fraxinus-Acer-Mercurialis* woodland. Ferns and bryophytes do increase somewhat in that vegetation towards the north and west of England and Wales but sharpness of drainage over the permeable limestones there often offsets the effect of increased rainfall. Although the more Atlantic bryophytes disappear fairly rapidly in moving away from the extreme north-west, it is possible that atmospheric pollution plays some part in restricting their occurrence in Pennine stands of the community (e.g. Graham 1971).

In the less continental and more sub-montane and cool oceanic parts of Britain, the *Fraxinus-Sorbus-Mercurialis* woodland is probably the climax community of more base-rich soils. However, certain extremes of climate may play a part in maintaining the vegetation as permanent scrub, even though its essential floristic character is preserved. In the upland fringes, for example, as in valley heads in the Yorkshire Dales and along the Tees and Wear in Durham, stands sometimes extend up over the top of the dale sides and here tree cover thins out with increased exposure to wind and cold. In such situations, the influence of near-freezing ground water in spring may further inhibit the development of an extensive woody cover. Even in the much more equable climate of the far north-west, the very frequent gales may be sufficient to maintain the woody cover as low, wind-pruned shrubs and trees, though here it needs to be remembered that there has probably been extensive removal of any larger timber trees, perhaps over long periods of time (e.g. McVean & Ratcliffe 1962, McVean 1964*a*, Birks 1973, Birse 1982, 1984).

Within the north-western parts of Britain, exposures of calcareous bedrocks are generally small and scattered, with the notable exception of the Carboniferous Limestone which underlies the quite numerous stands of the community clustered in the Pennines. The *Fraxinus-Sorbus-Mercurialis* woodland also occurs over this rock at a few localities in south Wales. Other more extensive calcareous sedimentary deposits on which the community is found are the Jurassic limestones of the northern part of the North York Moors and Skye and the Cambrian/Ordovician Durness Limestone, also on Skye (Birks 1973) and along the Moine thrust on the Scottish mainland (McVean & Ratcliffe 1962). Elsewhere on sedimentary rocks, this woodland can be found picking out more calcareous strata occurring within a mass of more acidic rocks, as over Ordovician and Silurian shales exposed in deeply-cut valleys in parts of Wales and south-east Scotland (Ratcliffe 1977, Ferreira 1978) and, more rarely, on parts of the Devonian Old Red Sandstone in south Wales and Cumbria. Some more basic igneous and metamorphic deposits also provide a suitable substrate, for example calcite beds within the Borrowdale Volcanics in the Lake District, Tertiary basalts on Skye and Mull, and Moine and Dalradian schists in the Scottish Highlands (McVean & Ratcliffe 1962, Birks 1973).

The pronounced wetness of the climate in this region, with annual rainfall always in excess of 1200 mm and, in many areas, more than 1600 mm (*Climatological Atlas* 1952, Chandler & Gregory 1976), means that, even where the soils are derived entirely from native parent materials, there is a strong tendency for them to be continually moist and superficially eluviated of free calcium carbonate. Thus, even where such soils are shallow, they are rarely of the typical dry and calcareous rendzina form so characteristic of *Fraxinus-Acer-Mercurialis* woodlands over the permeable limestones of north-western England. Indeed, where the rainfall is very heavy, quite acid rankers can develop directly over the surface of exposed limestones within stands of this woodland and encourage a sporadic representation of calcifuges, as on Skye (Birks 1973).

Very commonly, however, the direct influence of the calcareous bedrocks on pedogenesis is further reduced by the presence of superficial deposits, especially till or head or more recently redistributed material that has slumped down the often steep slopes here. Even where the rainfall is somewhat less heavy, soils therefore tend strongly towards the brown earth type. Where the superficials have a substantial fine fraction, a frequent occurrence, this further increases the tendency to permanent wetness, often making drainage poor or strongly impeded with marked gleying below (Pigott 1956*a*, 1978*b*). Local flushing with ground water can accentuate this character. It is this heavy and moist nature of many of the soils here that accounts for the general similarity between the field layer of the *Fraxinus-Sorbus-Mercurialis* woodland and that of the south-eastern types of *Fraxinus-Acer-Mercurialis* woodland, with the resurgence of species such as *Primula vulgaris*, *Poa*

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trivialis, *Deschampsia cespitosa*, *Filipendula ulmaria*, *Anemone nemorosa*, the ground-cover replacements for *Lamiastrum galeobdolon* and *Glechoma hederacea* and a relative scarcity of *Urtica dioica* and *Galium aparine*, typical of better-aerated and more eutrophic mull-rendzinas. And, since the soils do not experience summer droughting, *Oxalis acetosella* is able to establish itself as a constant element (Packham 1978).

Where the superficials are more free-draining, plants typical of drier and more calcareous conditions may be able to attain local prominence on soils which tend towards the brown calcareous earth type, but the susceptibility to leaching inhibits this. Moreover, the coarser and more permeable elements in the till are often not of a calcareous nature, but derived rather from siliceous rocks, so that pedogenesis often moves towards the development of surface-acid brown earths.

Such superficial deposits have often been laid down or redistributed in very irregular fashion over the rugged topography of valley sides and ravines or in intricate patterns in weathered crevices on pavements and between talus fragments. Flushed areas, too, can have a very complex disposition as ground water meets impervious interbedded deposits in the bedrock sequence or encounters patches of heavier-textured till. Although the *Fraxinus-Sorbus-Mercurialis* woodland is thus generally associated with brown earths, individual stands characteristically have a fine, often complex and sometimes chaotic mosiac of soils which helps account for the diversity of the field layer and the absence of consistent dominants. Commonly, fairly moist and somewhat surface-leached brown earths form the matrix, but steeper, drier banks can have brown calcareous earths and with fragmentary rendzinas over outcrops of harder limestone; here and there, more acid brown earths or rankers can pick out coarse sandy drift or elevated bluffs or boulder tops; and scattered throughout, in hollows, along the foot of slopes or around flushes or below small seepage lines, the soils tend towards surface-water gleys.

It is probable that flushing plays some part in the distinctive character of the *Crepis* sub-community. Increased soil moisture and substrate instability could help retard the development of a dense tree cover and so maintain the patchy shade in which the tall herbs and grasses thrive (e.g. Pigott 1956*a*). Several of the preferentials (e.g. *Filipendula ulmaria*, *Deschampsia cespitosa*, *Geum rivale*, *Crepis paludosa*) are also species which show a clear predilection for moister soils. But grazing is undoubtedly a major factor in limiting the growth of many of its characteristic plants in the Typical sub-community. Stock, usually sheep but sometimes cattle, and both roe (*Capreolus capreolus*) and red deer (*Cervus elaphus*) commonly graze and browse in these woodlands and it is only where they are excluded, either by difficult terrain or by fencing (as in the Rassal Ashwood enclosure: Ratcliffe 1977) that the *Crepis* sub-community develops its full richness and luxuriance.

In contrast to many *Fraxinus-Acer-Mercurialis* woodlands, we know very little of the treatment history of stands of this community. Timber removal has probably contributed to the scrubby physiognomy of many Scottish woods of this kind (e.g. McVean & Ratcliffe 1962, McVean 1964*a*, Birks 1973, Birse 1982, 1984) and confused the limiting effect of climatic exposure. Such coppices as there are seem to be universally neglected (Peterken 1981). It is possible that renewed cutting in wetter sites could favour a temporary development of the *Crepis* sub-community.

Zonation and succession

Transitions between the two sub-communities of the *Fraxinus-Sorbus-Mercurialis* woodland are primarily related to grazing pressure. The *Crepis* sub-community tends to replace the Typical sub-community in areas inaccessible to large herbivores, like ledges and steeper ravine slopes or pavements with numerous deep grikes (e.g. McVean & Ratcliffe 1962, Birks 1973, Ratcliffe 1977) and, because of the topographic irregularity of many sites, such zonations are usually complex mosaics with small fragments of the former scattered through the latter. However, there is no doubt that the *Crepis* sub-community attains its most luxuriant development where lack of grazing is combined with abundant soil moisture, so stands also often pick out dripping rock faces or flushed areas.

Zonations to other kinds of woodland are usually related more directly and exclusively to changes in parent materials and soil conditions. Where the soils are derived entirely from native bedrocks, a common pattern is for the *Fraxinus-Sorbus-Mercurialis* woodland to give way to the *Quercus-Betula-Oxalis* woodland as calcareous rocks with more base-rich mull brown earths pass to more acid deposits with leached brown earths with moder or mor humus. *Betula pubescens*, *Sorbus aucuparia* and *Corylus* may run through both communities, together with *Hyacinthoides*, *Oxalis*, *Viola riviniana* and many of the grasses, but *Fraxinus* (and *Ulmus glabra* if it is present) fade, and herbs such as *Mercurialis*, *Geum urbanum* and *Circaea lutetiana* are replaced by *Potentilla erecta*, *Galium saxatile* and *Pteridium*.

In regular sequences of limestones or calcareous shales and arenaceous strata, a frequent feature of Carboniferous deposits, this kind of zonation can be well ordered and obvious: in parts of the Yorkshire Dales, for example, where deep valleys have been cut through more or less level-bedded rocks, a typical pattern is for the *Fraxinus-Sorbus-Mercurialis* woodland to occupy the valley-side slopes over the Great Scar limestone with the *Quercus-Betula-Oxalis* woodland on the brow tops, over Yoredale deposits (Figure 20). Where sequences are less ordered, deposits thinner or

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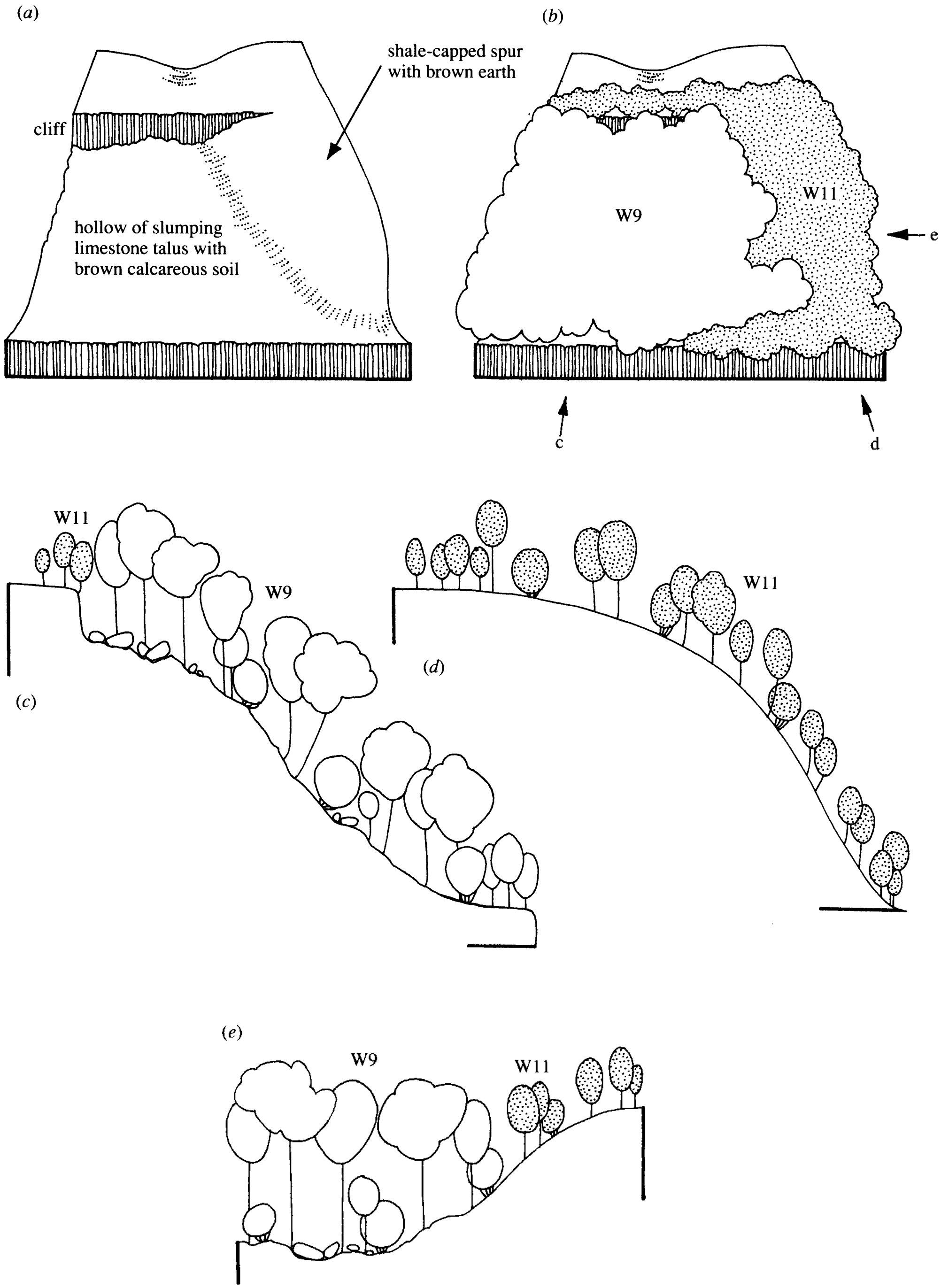
Figure 20. Mixed deciduous and oak-birch woodlands at Kisdon Force, North Yorkshire.
Topography (*a*) with (*b*) the disposition of
W9 *Fraxinus-Sorbus-Mercurialis* and
W11 *Quercus-Betula-Oxalis* woodlands and (*c–e*) sections through and across the hollow and spur.

steeply inclined and incised by actively-eroding streams into younger irregular ravines, the vegetation patterns can be more complex with small fragments of both kinds of woodland succeeding one another up and across the valley sides. This is a feature of sites on Ordovician and Silurian deposits in Wales and south-east Scotland (Ratcliffe 1977, Ferreira 1978). On many igneous and



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metamorphic rocks, more calcareous stretches are exceptional and here very small stands of the *Fraxinus-Sorbus-Mercurialis* woodland can be found embedded within extensive tracts of *Quercus-Betula-Oxalis* woodland or, where there is a more marked shift in rock and soil acidity, the *Quercus-Betula-Dicranum* woodland, as in north Wales, the Lake district and north-west Scotland (Ratcliffe 1977).

The presence of superficial deposits frequently confuses such zonations. Over more calcareous till or head, the *Fraxinus-Sorbus-Mercurialis* woodland can still be extensive but more arenaceous drift may restrict its occurrence over suitable bedrocks and tends to shift the whole sequence of woodlands towards the more calcifugous extreme. Very heavy rainfall may have the same effect so that, in the far north-west of Scotland, the *Fraxinus-Sorbus-Mercurialis* woodland occupies only the most lithomorphic soils and, even then, can have fragments of much more calcifugous herbaceous vegetation within it on nidus-capped boulders (e.g. McVean & Ratcliffe 1962, Birks 1973).

Zonations to woodland on strongly-flushed soils are also quite common and they almost always involve the *Alnus-Fraxinus-Lysimachia* woodland, the typical alderwood of more base-rich stagnogleys. Species such as *Filipendula ulmaria*, *Deschampsia cespitosa*, *Athyrium filix-femina* and *Lysimachia nemorum* remain prominent in this community and *Viola riviniana*, *Oxalis acetosella* and *Dryopteris dilatata* can run some way into the surrounds but increasing *Alnus* dominance and the appearance of plants like *Chrysosplenium oppositifolium*, *Carex remota*, *C. pendula* and *Juncus effusus* usually serve as a good distinction. Where flushing is regular, as along an impervious parting, the pattern of repeated slumped triangles of this woodland within stretches of *Fraxinus-Sorbus-Mercurialis* woodland can be very striking. Elsewhere the emergence of ground water is much more disordered and the mosaics consequently more complex. However, the frequent association of the *Fraxinus-Sorbus-Mercurialis*, *Quercus-Betula-Oxalis* and *Alnus-Fraxinus-Lysimachia* woodlands on sequences of base-rich, base-poor and gleyed brown earths in the north-west is exactly analogous to zonations of the *Fraxinus-Acer-Mercurialis*, *Quercus-Pteridium-Rubus* and *Alnus-Fraxinus-Lysimachia* woodlands on comparable soils in the south-east, as for example in the Weald.

The landscape context of the *Fraxinus-Sorbus-Mercurialis* woodland is usually that of pastoral agriculture along the upland fringes, where stands of the community represent some of the last vestiges of a woodland cover now confined to the more intractable slopes, crags and pavements. Grazing by stock as well as by deer is frequent in the Typical sub-community and this vegetation sometimes gives way, with varying degrees of sharpness, to semi-natural calcicolous pasture. Usually, this is *Festuca-Agrostis-Thymus* grassland or, in the Pennines, the more surface-leached kinds of *Sesleria-Galium* grassland or, in northern Scotland, the *Dryas-Carex* heath (e.g. Birks 1973). Where limestone crops out as pavement, as on the Yorkshire Dales Carboniferous or the Skye Durness Limestone, fragmentary stands of the community can be virtually confined to drift-filled grikes, forming complex mosaics with the grasslands on the clint surfaces (e.g. Birks 1973). Where grazed stretches are flushed, base-rich small-sedge mires, like the *Carex-Pinguicula* flush, may occur in close juxtaposition with *Fraxinus-Sorbus-Mercurialis* woodland.

Although successions to this community have never been studied, such grasslands as those mentioned above would probably revert back to *Fraxinus-Sorbus-Mercurialis* woodland if neglected: this kind of woodland probably represents the climax vegetation over more calcareous soils in sub-montane and cool oceanic regions. However, on a very local scale, one other kind of agricultural treatment has been important in deflecting progressions to the community. Where tree and shrub cover thins out very substantially in the less-grazed *Crepis* sub-community, the field layer becomes very similar to the *Anthoxanthum-Geranium* grassland. This is the vegetation of the unimproved hay-meadows of sub-montane parts of the Pennines and it seems highly likely that such swards have been derived from this woodland by repeatedly setting back invasion of woody plants by an annual mowing for hay (Pigott 1956*a*, Bradshaw 1962). Zonations between the two communities are rare, but sometimes contiguous stands occur on identical soils, separated only by a wall. Open woodlands very similar to the *Crepis* sub-community have traditionally been mown in other parts of northern Europe (e.g. Nordhagen 1928, 1943, Sjörs 1954, Böcher 1954).

Distribution

The *Fraxinus-Sorbus-Mercurialis* woodland replaces the *Fraxinus-Acer-Mercurialis* woodland in the cooler and wetter north-western parts of Britain. In the Pennines, where Carboniferous Limestone provides more extensive potential sites, the switch between the two communities is especially well seen. Here the *Fraxinus-Acer-Mercurialis* woodland is the more common community over talus slopes in the drier and warmer lower reaches of the dales; the *Fraxinus-Sorbus-Mercurialis* woodland replaces it in damp ravines (like Ling Ghyll), on higher-altitude pavements (like Colt Park) and, more consistently, in the drift-choked tributaries of wetter and cooler Swaledale, Teesdale and Weardale. Further west and north, in Wales, southern and central Scotland, suitable substrates tend to be scarce and stands small and scattered, though the community shows a resurgence in the far north-west where limestones and calcareous igneous and metamorphic rocks are again more abundant. Increasingly here, too, the community shows an enrichment of its bryophyte flora which brings it close to equivalent Irish vegetation (e.g. Braun-Blanquet & Tüxen 1952). The Typical sub-community occurs throughout the range with the *Crepis* sub-community more restricted, though good stands of both types can be found in the Pennines and north-west Scotland.

Affinities

This community brings together a variety of more calcicolous sub-montane woodlands that have often been recognised as distinctive but usually split on the basis of canopy or field layer differences. More orthodox mixed deciduous stands have sometimes been fused with lowland woodlands, as in Klötzli's (1970) *Dryopterido-Fraxinetum*, Peterken's (1981) ash-wych elm stand type 1D or the *Querco-Ulmetum* of Birse (1982, 1984) while types dominated by *Betula pubescens* and *Corylus* have been put alongside more calcifugous woodlands, as in the *Betula*-herb nodum of McVean & Ratcliffe (1962), the *Corylus-Oxalis* Association of Birks (1973) and the 12B hazel-birchwood of Peterken (1981).

As defined here, the community holds together quite well, though its phytosociological affinities are fairly diverse because it characterises sites that, while generally cool and wet, range from mild and oceanic through to harshly sub-montane. The soils too, though comparatively base-rich, often show a combination of wetness with surface eluviation. In one direction, then, there are similarities with the extreme oceanic scrub of western Ireland which Braun-Blanquet & Tüxen (1952) described as *Corylo-Fraxinetum* and, on the other, with the 'Park Meadow' communities described from Norway (e.g. the *Geranium sylvaticum*-reicher Birchenwald of Nordhagen (1928) or the *Betuletum geraniosum subalpinum* of Nordhagen (1943)), Sweden (Sjörs 1954) and Greenland (Böcher 1954). These latter have usually been placed in the Cicerbition alpini where Birks (1973) located the ungrazed stands of his *Betula-Cirsium* Assocation.

Such diagnoses stress the more peculiar features of the vegetation included here. Its more general affinities place it somewhere in the Fagetalia, though exactly where is more of a problem. It is the north-western counterpart of the calcicolous Carpinion woods of the south-east and Birse (1980, 1982, 1984) favoured locating his communities in this alliance. Both Graham (1971) and Birks (1973), on the other hand, noted the suggestion of Shimwell (1968*b*, 1971*c*) that a new alliance, the Fraxino-Brachypodion, might be needed to contain British woodlands beyond the geographical limit of the Fagion. A more satisfactory position might be within the Alno-Ulmion (*sensu* Ellenberg 1978 and equivalent to the Alno-Padion Knapp 1942): this would recognise the general similarities of the vegetation with more calcicolous mixed deciduous woodland while acknowledging the links with woodland of more strongly-gleyed mineral soils like the *Alnus-Fraxinus-Lysimachia* woodland.

Floristic table W9

	a	b	9
Fraxinus excelsior	IV (1–9)	III (3–5)	IV (1–9)
Sorbus aucuparia	III (1–4)	V (3–5)	III (1–5)
Betula pubescens	III (1–7)	III (1–9)	III (1–9)
Alnus glutinosa	I (1–7)	I (4–9)	I (1–9)
Ulmus glabra	III (1–10)	I (1–6)	II (1–10)
Acer pseudoplatanus	III (1–9)	I (5–9)	II (1–9)
Quercus petraea	II (1–9)		I (1–9)
Quercus robur	I (1–8)		I (1–8)
Betula pendula	I (1–5)		I (1–5)
Fagus sylvatica	I (1–10)		I (1–10)
Pinus sylvestris	I (1–7)		I (1–7)
Quercus hybrids	I (1–7)		I (1–7)
Corylus avellana	IV (1–9)	V (4–9)	IV (1–9)
Crataegus monogyna	III (1–7)	I (5)	II (1–7)
Fraxinus excelsior sapling	II (1–7)	I (3)	I (1–7)
Ulmus glabra sapling	II (1–4)		I (1–4)
Acer pseudoplatanus sapling	I (1–5)		I (1–5)
Sambucus nigra	I (1–4)		I (1–4)

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Floristic table W9 *(cont.)*

	a	b	9
Ilex aquifolium	I (1–4)		I (1–4)
Betula pubescens sapling	I (2–4)	II (1–9)	I (1–9)
Sorbus aucuparia sapling	I (1–4)	II (1–5)	I (1–5)
Prunus padus	I (1–4)	II (3–4)	I (1–4)
Salix cinerea		I (3–4)	I (3–4)
Populus tremula		I (4–6)	I (4–6)
Oxalis acetosella	IV (1–7)	V (3–5)	IV (1–7)
Thuidium tamariscinum	IV (1–6)	IV (2–5)	IV (1–6)
Viola riviniana	IV (1–4)	IV (1–4)	IV (1–4)
Plagiomnium undulatum	IV (1–6)	IV (1–2)	IV (1–6)
Mercurialis perennis	IV (1–10)	III (1–4)	IV (1–10)
Dryopteris filix-mas	IV (1–9)	III (2–5)	IV (1–9)
Eurhynchium striatum	IV (1–8)	III (2–4)	IV (1–8)
Eurhynchium praelongum	V (1–7)	III (2–3)	IV (1–7)
Circaea lutetiana	III (1–7)	II (1–3)	III (1–7)
Geum urbanum	III (1–7)	II (1–3)	III (1–7)
Potentilla sterilis	III (1–4)	II (1–4)	III (1–4)
Dryopteris dilatata	III (1–6)	I (1–3)	II (1–6)
Fraxinus excelsior seedling	III (1–5)	I (1)	II (1–5)
Fissidens taxifolius	II (1–5)	I (1)	I (1–5)
Pellia epiphylla	II (1–4)	I (2–4)	I (1–4)
Galium aparine	II (1–4)		I (1–4)
Urtica dioica	II (1–6)		I (1–6)
Rubus fruticosus agg.	II (1–10)		I (1–10)
Silene dioica	II (1–7)		I (1–7)
Hedera helix	II (1–8)		I (1–8)
Brachythecium rutabulum	II (1–4)		I (1–4)
Veronica montana	II (1–4)		I (1–4)
Milium effusum	I (1–2)		I (1–2)
Eurhynchium swartzii	I (1–6)		I (1–6)
Arum maculatum	I (1–2)		I (1–2)
Adoxa moschatellina	I (1–4)		I (1–4)
Anthriscus sylvestris	I (1–2)		I (1–2)
Lamiastrum galeobdolon	I (1–5)		I (1–5)
Circaea × *intermedia*	I (2–6)		I (2–6)
Festuca gigantea	I (1–2)		I (1–2)
Phyllitis scolopendrium	I (1–6)		I (1–6)
Filipendula ulmaria	II (1–6)	IV (1–6)	III (1–6)
Brachypodium sylvaticum	II (1–7)	IV (4–7)	III (1–7)
Conopodium majus	II (1–5)	IV (1–4)	III (1–5)
Crepis paludosa	I (1)	IV (1–4)	II (1–4)
Cirriphyllum piliferum	II (1–8)	III (1–4)	II (1–8)
Deschampsia cespitosa	II (1–7)	III (3–7)	II (1–7)
Rhytidiadelphus triquetrus	II (1–9)	III (1–6)	II (1–9)
Plagiochila asplenoides	II (1–6)	III (1–4)	II (1–4)

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Arrhenatherum elatius	II (1–4)	III (1–5)	I (1–5)
Agrostis capillaris	II (1–5)	III (1–6)	I (1–6)
Geum rivale	I (1–2)	III (2–5)	I (1–5)
Cirsium helenioides	I (1)	III (4–6)	I (1–6)
Vicia sepium	I (1–2)	III (1–2)	I (1–2)
Geranium sylvaticum	I (1)	III (1–5)	I (1–5)
Anthoxanthum odoratum	I (1)	III (3–6)	I (1–6)
Holcus lanatus	I (1–6)	III (1–4)	I (1–6)
Rhytidiadelphus squarrosus	I (2)	III (1–5)	I (1–5)
Ranunculus ficaria	I (1)	III (1–3)	I (1–3)
Ranunculus repens	I (1–2)	III (1–4)	I (1–4)
Holcus mollis	I (1–7)	III (1–5)	I (1–5)
Rumex acetosa		III (1–3)	I (1–3)
Succisa pratensis	I (1)	II (1–4)	I (1–4)
Senecio jacobaea	I (1)	II (1–2)	I (1–2)
Agrostis stolonifera	I (2–4)	II (2–5)	I (2–5)
Tussilago farfara	I (2–5)	II (3–5)	I (2–5)
Stachys sylvatica	I (1–4)	II (1–3)	I (1–4)
Plagiothecium denticulatum	I (1–2)	II (1–2)	I (1–2)
Stellaria holostea	I (1–5)	II (1–3)	I (1–3)
Blechnum spicant	I (1)	II (1–4)	I (1–4)
Melica uniflora	I (1–4)	II (1–4)	I (1–4)
Rubus idaeus	I (1–6)	II (1–5)	I (1–6)
Ranunculus acris	I (1–2)	II (1–3)	I (1–3)
Potentilla erecta	I (1)	II (1–4)	I (1–4)
Rhytidiadelphus loreus	I (2–4)	II (2–6)	I (2–6)
Allium ursinum	I (1–5)	II (1–2)	I (1–2)
Rhizomnium punctatum	I (1–5)	II (1–4)	I (1–5)
Carex pallescens		II (1–2)	I (1–2)
Cruciata laevipes		II (1–4)	I (1–4)
Alchemilla glabra		II (1–2)	I (1–2)
Plagiomnium rostratum		II (1–3)	I (1–3)
Trollius europaeus		I (3–4)	I (3–4)
Mnium hornum	III (1–8)	III (1–7)	III (1–8)
Hyacinthoides non-scripta	III (1–9)	III (1–4)	III (1–9)
Geranium robertianum	III (1–5)	III (1–5)	III (1–5)
Athyrium filix-femina	III (1–8)	III (2–5)	III (1–8)
Atrichum undulatum	III (1–7)	III (3–5)	III (1–7)
Poa trivialis	III (1–6)	III (1–3)	III (1–6)
Dactylis glomerata	II (1–4)	III (1–5)	II (1–5)
Dryopteris borreri	II (1–6)	II (3–6)	II (1–6)
Primula vulgaris	II (1–5)	II (3–5)	II (1–5)
Veronica chamaedrys	II (1–5)	II (2–4)	II (1–5)
Lophocolea bidentata s.l.	II (1–6)	II (1–3)	II (1–6)
Lysimachia nemorum	II (1–4)	II (1–4)	II (1–4)
Epilobium montanum	II (1–5)	II (1–2)	II (1–5)
Sanicula europaea	II (1–8)	II (1–3)	II (1–3)
Hypnum cupressiforme	II (1–4)	II (1–6)	II (1–6)
Prunella vulgaris	I (1–3)	I (1–3)	I (1–3)
Galium odoratum	I (1–6)	I (1–3)	I (1–6)
Bromus ramosus	I (1–3)	I (1)	I (1–3)

Floristic table W9 *(cont.)*

	a	b	9
Valeriana officinalis	I (1–4)	I (1–4)	I (1–4)
Pteridium aquilinum	I (1–6)	I (1–9)	I (1–9)
Galium saxatile	I (1–2)	I (2–4)	I (1–4)
Isothecium myurum	I (1)	I (1–3)	I (1–3)
Ctenidium molluscum	I (1–6)	I (1–5)	I (1–6)
Digitalis purpurea	I (1–3)	I (1–3)	I (1–3)
Acer pseudoplatanus seedling	I (1–6)	I (1)	I (1–6)
Plagiothecium succulentum	I (1–4)	I (1–3)	I (1–4)
Heracleum sphondylium	I (1–4)	I (1–3)	I (1–4)
Rosa canina agg.	I (1–4)	I (2)	I (1–4)
Fissidens bryoides	I (1–5)	I (1–4)	I (1–5)
Hylocomium brevirostre	I (1–2)	I (3–5)	I (1–5)
Polytrichum formosum	I (1–2)	I (2–3)	I (1–3)
Cardamine flexuosa	I (1–4)	I (1–4)	I (1–4)
Ajuga reptans	I (1–5)	I (1–2)	I (1–5)
Anemone nemorosa	I (1–5)	I (1–3)	I (1–5)
Luzula sylvatica	I (1–8)	I (4–7)	I (1–8)
Thuidium delicatulum	I (1–2)	I (3–6)	I (1–6)
Hylocomium splendens	I (1–2)	I (3–4)	I (1–4)
Isothecium myosuroides	I (1–5)	I (1–4)	I (1–5)
Fragaria vesca	I (1–3)	I (1–2)	I (1–3)
Angelica sylvestris	I (1–3)	I (5)	I (1–5)
Carex sylvatica	I (1–2)	I (1–4)	I (1–4)
Chrysosplenium oppositifolium	I (1–5)	I (3)	I (1–5)
Dicranum scoparium	I (1–3)	I (1–2)	I (1–3)
Cirsium palustre	I (1)	I (2)	I (1–2)
Alchemilla xanthochlora	I (1)	I (1–2)	I (1–2)
Rubus saxatilis	I (1)	I (3)	I (1–3)
Pellia endiviifolia	I (1–4)	I (1)	I (1–4)
Number of samples	93	24	117
Number of species/sample	32 (18–74)	47 (35–73)	36 (18–74)
Tree height (m)	17 (7–25)	12 (10–16)	16 (7–25)
Tree cover (%)	77 (10–100)	41 (0–100)	63 (0–100)
Shrub height (m)	5 (1–8)	5 (4–7)	5 (1–8)
Shrub cover (%)	38 (0–100)	28 (0–90)	32 (0–100)
Herb height (cm)	44 (10–122)	65 (15–80)	48 (10–122)
Herb cover (%)	76 (10–100)	68 (55–90)	68 (10–100)
Ground height (mm)	28 (10–80)		28 (10–80)
Ground cover (%)	45 (0–100)	24 (5–70)	37 (0–100)
Altitude (m)	113 (6–335)	209 (16–305)	139 (6–335)
Slope (°)	21 (0–70)	25 (2–50)	21 (0–70)

a Typical sub-community
b *Crepis paludosa* sub-community
9 *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* woodland (total)

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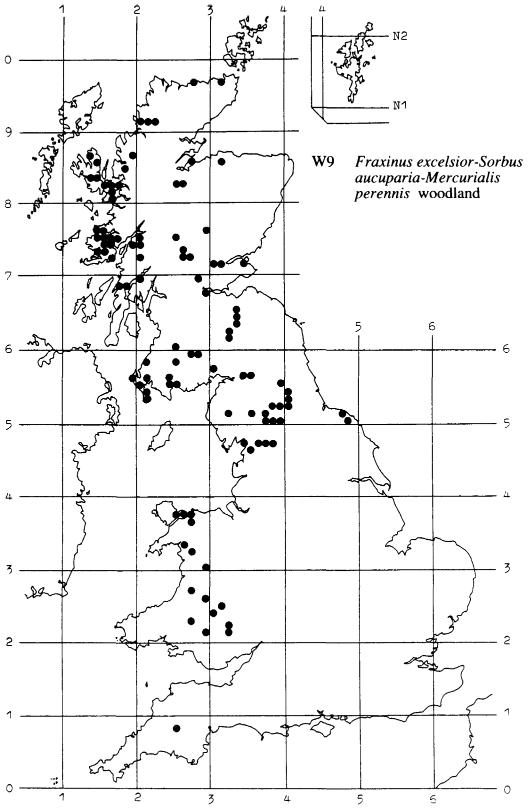

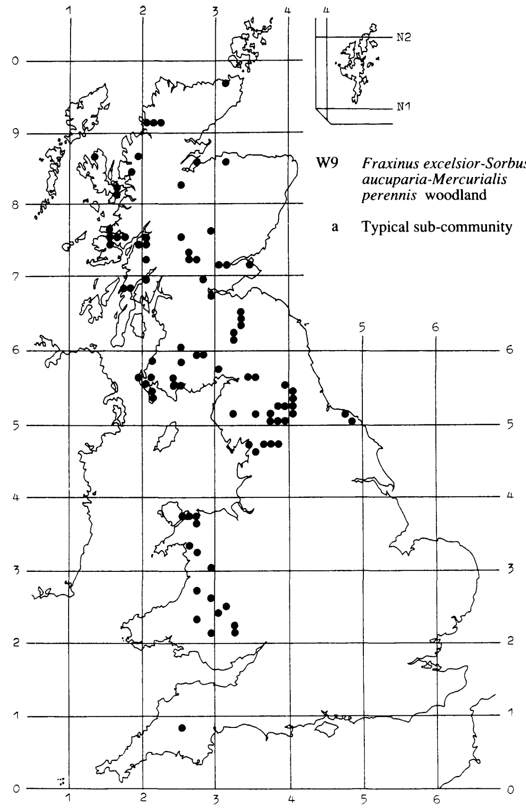

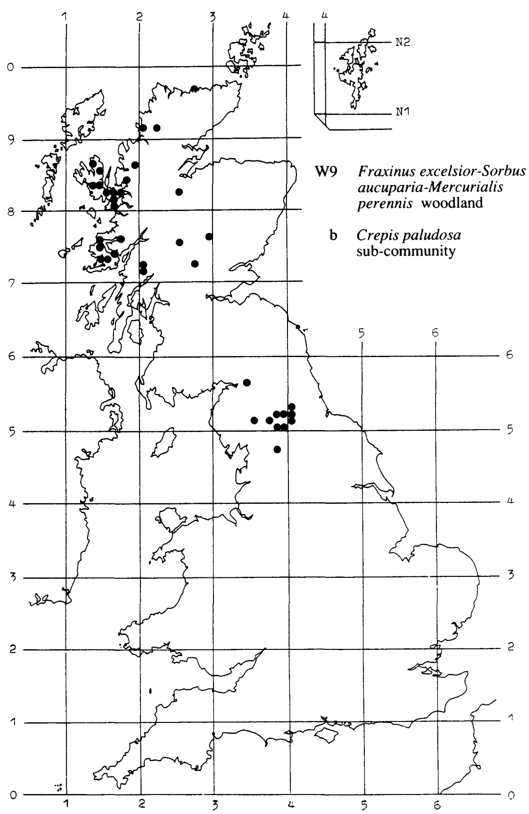

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